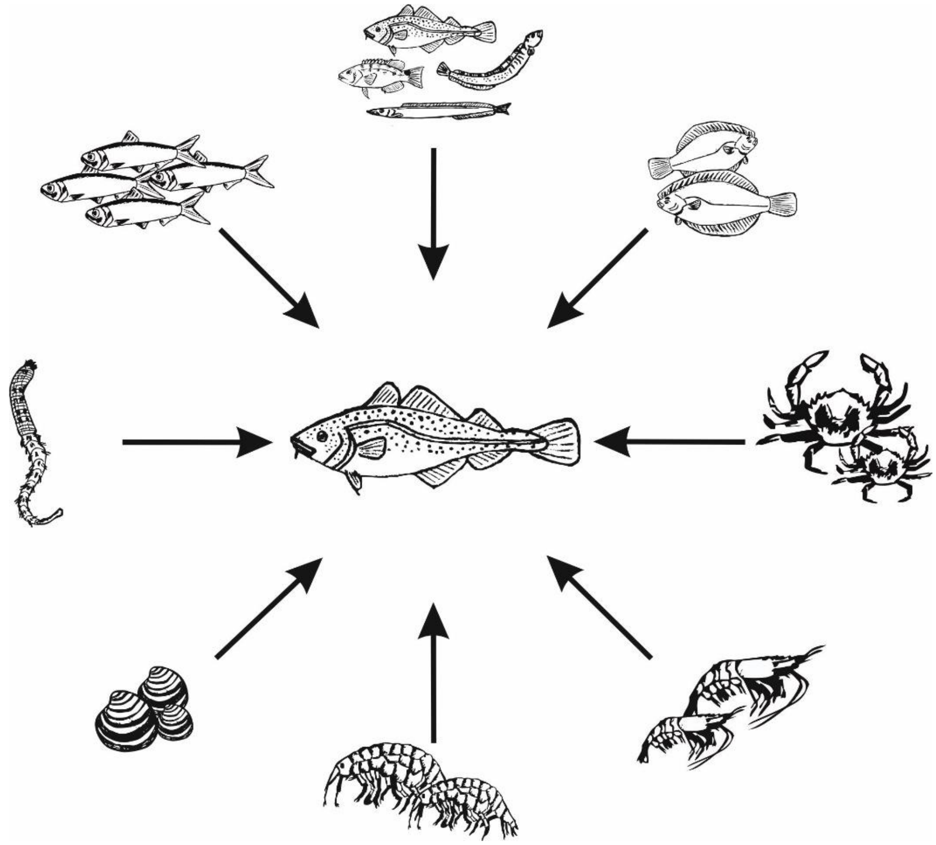
Spatio-temporal distribution, food intake and growth of cod (*Gadus morhua* L.) in the Western Baltic Sea

Steffen Funk



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Summary

The present thesis deals with patterns in depth and habitat use, seasonal and depth-specific food intake and growth of cod (*Gadus morhua* L.) in the Western Baltic Sea (WBS). Cod is the commercially most important demersal species in the WBS and therefore also of pronounced scientific interest. Despite decades of research and stock monitoring important knowledge gaps still remain, limiting our understanding of the ecology of cod in the WBS. The results presented in this thesis reveal the important role of shallow water habitats in the seasonal depth use of cod in the Western Baltic, their essential role for the seasonal food intake and thus, their important impact on the seasonal growth of cod. Furthermore, the effect of extreme summer periods in relation to habitat selection and resulting negative effects on seasonal growth are discussed. Finally, it is shown that the methods presented in the study such as (a) using fishers' knowledge to reveal patterns in depth use, (b) using different fishing methods to enhance depth and habitat coverage in stomach sampling in order to analyze depth-specific patterns in food intake, and (c) using individual-based bioenergetic growth models to detect seasonal patterns in growth, can enhance our ecological knowledge not only for cod in the Baltic Sea, but provide practical approaches to be used also in other ecosystems and for other species.

In chapter I („Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea") the seasonal spatial distribution of cod in the Western Baltic Sea was investigated. Seasonal patterns in the selection of reported and observed fishing grounds of local gillnet fishers were analyzed. Depth-use of cod was revealed to be related with sea surface temperature and stratification. Moreover, applying a multinomial logistic regression model revealed close relations between selected habitat type, sea surface temperature and catch depth. It was found that cod inhabit deep areas > 15 m depths mainly during winter (spawning time) and during peak summer periods (aestivation period), while cod tend to reside in shallower areas for the rest of the year. The results were further used to develop a conceptual model, wherein the distinct up-and down-slope movements, which cod display over the season, were related to ecological, life-history and physiological traits of Atlantic cod known from the literature.

In chapter II („Patterns in seasonal and depth-specific food intake of adult cod (*Gadus morhua*) in the Western Baltic Sea“) seasonal patterns in food intake and diet composition of cod in the Western Baltic Sea were investigated with special attention to shallow habitat sites < 20 m, which have been often neglected in previous stomach content analyses in the area. The results displayed clearly distinct depth-specific and seasonal patterns in the diet composition of cod, with an increasing proportion of fish prey with increasing residence depth and an increasing proportion of benthic invertebrates in the diet composition with decreasing residence depth for all cod length classes. Especially the common shore crab (*Carcinus maenas*) was revealed as one of the major prey items of cod in shallow water habitats, even for large individuals > 60 cm. An application of generalized additive models revealed cod stomach content weight to be dependent on ambient temperature, cod length and residence depth. Shallow water habitats were shown to be important feeding grounds of cod in the Western Baltic Sea, while the observation of empty stomachs and low stomach contents at residence depths > 20 m led to the assumption of a food scarcity at deeper areas.

In chapter III (“An individual-based bioenergetic growth model for adult cod (*Gadus morhua*) in the Western Baltic Sea”) seasonal patterns in growth of cod in the Western Baltic Sea were investigated. The individual-based bioenergetic growth model presented in this study was developed using information on seasonal depth use and depth-specific food intake derived from the previous chapters. Growth predictions from the bioenergetic growth model displayed clear seasonal patterns. Largest growth increments were observed at phases of intensive shallow water use. The smallest growth increments were predicted for winter. Moreover, we observed temporally negative growth increments (weight losses) in relation with extreme summer periods and a related use of deep habitat sites. The seasonal growth prediction was further used to examine whether the recently described formation of translucent otolith ring zones during summer for Western Baltic cod is related to temperature and/or slow growth. The predictions of large growth increments during the summer half-year pointed strongly towards a temperature related formation of hyaline otolith ring structures. Finally, von Bertalanffy growth parameters calculated

from the bioenergetic model were compared with recently published ones based on tag-recapture experiments, which showed a high correspondence and thus, highlighted the potential of our model approach as a practical alternative to traditional growth calculation methods.

Zusammenfassung

Die vorliegende Dissertation befasst sich mit Mustern in der Tiefen- und Habitat-Nutzung, der saisonalen und tiefenspezifischen Ernährung sowie dem Wachstum des Dorsches (*Gadus morhua* L.) in der westlichen Ostsee. In der westlichen Ostsee ist der Dorsch die kommerziell wichtigste, demersale Fischart und daher von einem großen wissenschaftlichen Interesse. Trotz jahrzehntelanger Forschung und jährlichem Bestandsmonitoring bestehen immer noch wesentliche Wissenslücken im Verständnis der Ökologie des Dorsches in der westlichen Ostsee. Die Ergebnisse der vorliegenden Arbeit veranschaulichen die große Bedeutung von Flachwasserhabitaten in der saisonalen Tiefennutzung von Dorschen in der westlichen Ostsee, die Rolle dieser Areale als wichtige Gebiete für die saisonale Nahrungsaufnahme und das damit verbundene Wachstum des Dorsches. Des Weiteren werden die Auswirkungen von Hitzeperioden auf die Habitatwahl des Dorsches, sowie auf sein Wachstum diskutiert. Letztlich wird herausgestellt, dass die hier vorgestellten Methoden, wie (a) die Nutzung des Wissens lokaler Fischer zur Erfassung der räumlich-zeitlichen Verbreitung, (b) die Verwendung verschiedener Fangmethoden zur Verbesserung der räumlichen Habitat-Abdeckung, um tiefenspezifische Muster in der Nahrungsaufnahme zu detektieren, sowie (c) die Nutzung eines Individuen-basierten bioenergetischen Modells zur Erkennung saisonaler Wachstumsmuster, unser ökologisches Verständnis nicht nur vom Dorsch in der westlichen Ostsee, sondern auch für viele andere Arten und Bestände in anderen Ökosystemen verbessern können.

In **Kapitel I** („Gillnet fishers‘ knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea) wurde die saisonale, räumliche Verteilung des Dorsches in der westlichen Ostsee untersucht. Zu diesem Zweck wurden saisonale Muster in der Auswahl berichteter und beobachteter Tiefen und Habitaten zur gezielten Dorschfischerei in der westlichen Ostsee von lokalen Stellnetzfischern ausgewertet. Es konnte gezeigt werden, dass die Tiefennutzung mit der Wasseroberflächentemperatur sowie der Stratifizierung des Wasserkörpers zusammenhängt. Die Anwendung eines multinomialen logistischen

Regressionsmodells deckte zudem Zusammenhänge zwischen Habitattypen, der Wasseroberflächentemperatur und der ausgewählten Aufenthaltstiefe auf. Areale tiefer als 15 m wurden von den Dorschen maßgeblich nur während des Winters (zur Laichzeit) sowie während des Hochsommers (während der Übersommerungsperiode) genutzt. Unsere Ergebnisse dienten ferner zur Entwicklung eines konzeptionellen Modells mit vier Phasen, dass die Hang-auf- und Hang-abwärts-Bewegungen der Dorsche in der westlichen Ostsee in Zusammenhang mit aus der Literatur bekannten Eigenschaften des Atlantischen Dorsches in Bezug auf Lebenszyklus, Physiologie und Ökologie stellt.

In **Kapitel II** („Patterns in seasonal and depth-specific food intake of adult cod (*Gadus morhua*) in the Western Baltic Sea“) untersuchten wir saisonale Muster in der Nahrungsaufnahme und Nahrungszusammensetzung des Dorsches in der westlichen Ostsee unter besonderer Berücksichtigung von Flachwasserhabitaten, die in bisherigen Mageninhaltsuntersuchungen im Untersuchungsgebiet stark vernachlässigt wurden. Die Ergebnisse zeigten klare tiefenspezifische und saisonale Muster in der Nahrungszusammensetzung des Dorsches, wobei generell mit zunehmender Tiefe der Anteil Fischbeute und mit abnehmender Tiefe der Anteil benthischer Invertebraten in der Nahrungszusammensetzung aller Dorschlängenklassen zunahm. Vor allem die Strandkrabbe (*Carcinus maenas*) konnte als einer der Hauptbeuteorganismen im Flachwasser auch für große Dorsche identifiziert werden. Durch die Anwendung generalisierter additiver Modelle konnten zudem Zusammenhänge zwischen Mageninhaltsgewichten der Umgebungstemperatur, der Räuberlänge und der Tiefe festgestellt werden. Eine besondere Bedeutung in der saisonalen Nahrungsaufnahme kam dabei den Flachwasserhabitaten zu, während für die tiefen Habitate eine Nahrungslimitation zu vermuten ist.

In **Kapitel III** (“An individual-based bioenergetic growth model for adult cod (*Gadus morhua*) in the Western Baltic Sea”) wurden saisonale Wachstumsmuster des Dorsches in der westlichen Ostsee untersucht. Das in dieser Studie vorgestellte individuelle Wachstumsmodell wurde dabei unter Verwendung von Informationen zur saisonalen Tiefennutzung und tiefen-spezifischen Nahrungsaufnahme erstellt.

Unsere Modellresultate zeigten klare saisonale Muster im Wachstum des Dorsches, wobei der größte Längenzuwachs mit Phasen intensiver Flachwassernutzung im Herbst zusammenfiel. Das langsamste Wachstum konnte im Winter beobachtet werden. Zudem beobachteten wir zeitweise Gewichtsverluste der Dorsche im Hochsommer im Zusammenhang mit stark ausgeprägten Hitzeperioden und einer resultierenden Nutzung tiefer Areale. Ferner wurden unsere Modellvorhersagen verwendet, um die Frage zu klären, ob die kürzlich gezeigte Anlage hyaliner Otolithen-Ringstrukturen des Dorsches in der westlichen Ostsee während des Sommerhalbjahres eher durch verlangsamtes Wachstum während dieser Zeit oder durch die hohen Umgebungstemperaturen zu erklären ist. Die Anlage großer Längeninkremente während des Sommerhalbjahres deutete dabei stark auf eine temperaturbedingte Anlage der hyalinen Ringstrukturen hin. Letztlich wurden von Bertalanffy Wachstumsparameter verglichen, einmal berechnet aus den Modellvorhersagen sowie einmal aus aktuellen Markierungsexperimenten, wobei sich eine hohe Übereinstimmung zeigte und somit das Potential unseres Modellansatzes als Alternative zur traditionellen Wachstumsberechnung bestätigt wurde.

General introduction

Cod in the Western Baltic Sea

The Atlantic cod (*Gadus morhua* Linneaus, 1758) is a demersal fish species of the family Gadidae of the order Gardiformes (Cohen et al., 1990; Nelson, 2006). It is widespread in the North Atlantic, where several stocks are distinguished, displaying differences in genetics, phenotypes and life history traits. All cod stocks were/or still are of high commercial importance (Kurlansky, 1997; Link, 2008; FAO, 2011), and most of the stocks are still heavily exploited. Several cod stocks collapsed since the 1990s (see Frank et al., 2016) due to high fishing pressure and some stocks are currently still threatened to collapse. Cod is one of the most heavily exploited fish species world-wide and hence it is not surprising that a lot of scientific effort was and still is undertaken to better our ecological understanding of this species. This made cod also into one of the most frequently investigated marine species over the years (Brander, 1997). However, despite decades of research unsuspected behaviour and stock dynamics suggest that our ecological understanding of cod is still insufficient and requires further investigations. For example, the cod stock off newfoundland showed still no sustained sign of recovery even though the fishery was closed since 1992 (Lilly, 2008). Other cod stocks such as the North Sea cod stock showed really high variability in recruitment which could not be explained well by traditional stock recruitment relationships only (Olsen et al., 2011).

In the Baltic Sea two different populations of cod are presently distinguished in management (see ICES, 2019a, 2019b), namely the Western Baltic cod (*Gadus morhua* L., WBC) and the Eastern Baltic cod (*Gadus morhua callarias*, EBC). The two cod subspecies differ in phenotype such as morphometric characteristics (Berner and Vaske, 1985; Müller, 2002), otolith shapes (Paul et al., 2013; Hüssy et al., 2016) and haemoglobin type (Sick, 1965), in genotype and in spawning behaviour such as spawning time and main spawning areas (Bleil and Oeberst, 2005). The development of the two Baltic cod subspecies is explained by two different temporal colonization events of the Baltic proper by cod from adjacent water bodies. The phylogenetic origin of the *Gadus morhua callarias* has not yet been fully deciphered. It displays a strong genetic variation compared to other cod populations which is explained by long temporal isolation of the stock and adaptive evolutionary processes to the specific environmental conditions of the Baltic Sea. It was hypothesized that the colonization of the Baltic Sea by EBC followed the last glacial retreat from this area 8000 years ago and that the stock originated from the Northeast Arctic cod stock in the Barents Sea (Sick, 1965). However, more recent genetic studies showed a higher similarity of the EBC to North Sea cod than to the stock from the Barents Sea (Nielsen et al. 2001; Andersen et al., 2009). It is rather certain, in contrast, that the origin of WBC can be traced back to a second wave of colonization of the Baltic Sea by cod from the North Sea (Sick, 1965). This assumption is mainly supported by its strong genetic similarity with the cod population in the Kattegat, which in turn displays high genetic similarity with the North Sea cod population (Nielsen et al., 2003).

The main distributional areas of the two Baltic cod populations can be also separated. WBC is mainly distributed in the area of the Western Baltic Sea (Fig. 1), which is formed by the Belt Sea, the Sound and the Arkona Sea, while EBC is distributed mainly in the Eastern Baltic Sea, i.e. from the Arkona Sea eastwards in the area of the central and Southern Baltic Sea and up to the Bothnian Sea (Bagge et al., 1994). Especially, the Arkona Sea is known as the transition zone of the two Baltic cod stocks (Eero et al., 2014). However, the borders of the distributional ranges of the two stocks are considered to be fluent. For example, recent studies using genetics and otolith shape analysis gave evidence for the occurrence of *Gadus morhua callarias* in the Belt Sea (Schade et al., 2019). In contrast, the occurrence of *Gadus morhua* L. along the coast of Poland in the Southern Baltic Sea (i.e. eastwards from the Arkona Sea) was also indicated by a recent genetic study (Strognaov et al., 2018). It is hypothesized that the co-existence of the two Baltic cod stocks in the Arkona Sea and in adjacent areas mainly depends on feeding migrations, larval drift and spill-over effects (Aro, 1989; Eero et al., 2012a; Petereit et al., 2014). However, these mixing dynamics are still not understood sufficiently (Schade et al., 2019).

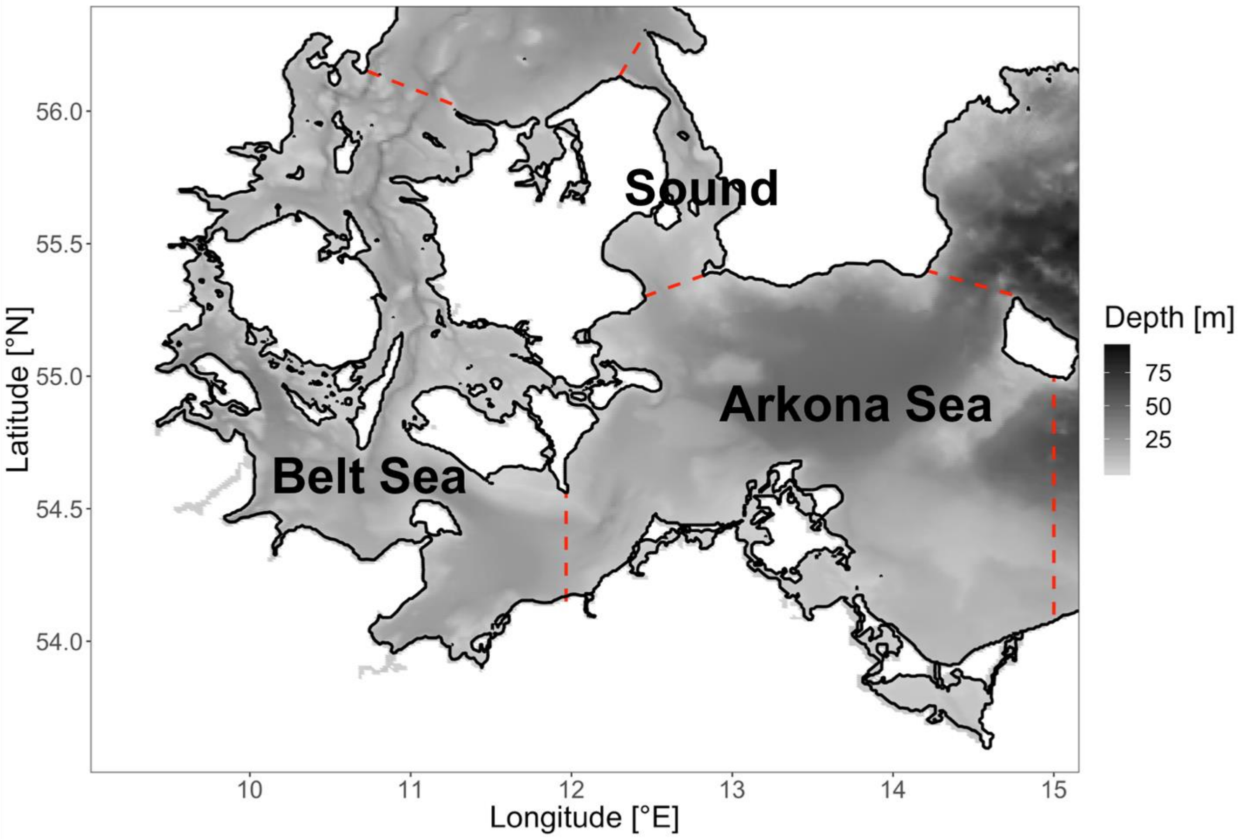

Figure 1. Bathymetry of the Western Baltic Sea. Dashed red lines indicate borders between ICES Subdivisions (SD22 – Belt Sea; SD23 – Sound, and SD24 – Arkona Sea).

The main distributional areas of the cod stock differ greatly in hydrographic conditions. Compared to the Eastern Baltic Sea, which is characterized by large, deep basins with more than 100 m depths, the Western Baltic Sea is relatively shallow. In detail 60 % of the area are shallower than 20 m depths and 21 % are even shallower than 10 m depths (ICES, 2017; Tab. 1). Furthermore, also salinities differ markedly between the Western and the Eastern Baltic Sea. The Western Baltic Sea is characterized by several shallow obstacles such as the Darss Sill, limiting inflows of water with high salinities from the Kattegat region to the Eastern parts of the Baltic Sea. This limited saltwater inflow in combination with river runoffs results in a constant decrease of salinity from the western to eastern parts of the Baltic Sea. Especially in the channels and basins of the Baltic Sea the water column is highly stratified with low salinities in surface layers and higher salinities at bottom water layers. These strong stratifications hamper mixing processes and thus, the introduction of oxygen in the deeper water layers. Thus, the introduction of oxygen is severely limited to saltwater inflow events. However, the frequency of strong saltwater inflow events is observed to decrease and as a result hypoxic zones have formed. These hypoxic zones can be found especially at the deep basins in central Baltic Sea and it was revealed that they are negatively affecting EBC reproduction (Plikshs et al., 1993; MacKenzie et al., 2000) and nutritional condition due to decreased food supply (Casini et al., 2016). While hypoxia is a problem often mainly associated with the eastern Baltic Sea only, it, however, occurs also regularly in the Western Baltic Sea, where it can be observed mainly during mid-or late summer months (Weigelt, 1987; Karlson et al., 2002) in the deeper channels > 20 m depths. Although these formation of hypoxic zones in the Western Baltic Sea are spatially and temporally limited, they are known to affect the species in the Western Baltic Sea (Weigelt, 1987).

Table 1. Area shares absolute (nm^2) and relative (%) per depth layer for the total Western Baltic Sea and per subareas. Numbers were taken from the Baltic international trawl survey manual (ICES, 2017).

Area	Belt Sea	%	Sound	%	Arkona Sea	%	total	%
total	5162.8	100	896.5	100	6509.3	100	12568.6	100
< 20 m	3622.4	70	722.6	81	3246.9	50	7591.9	60
< 10 m	1489.5	29	319.2	36	785.4	12	2594.1	21

WBC and EBC are assessed and managed in two different stocks since the 1970s (ICES, 1971; 1974; Eero et al., 2014). Originally cod was allocated to the two cod stocks by a simple geographical separation based on the main distributional areas (i.e. all cod from Bornholm westwards were allocated to the WBC stock and all cod from Bornholm eastwards to the EBC stock). However, since the Arkona Sea was revealed as an important transition zone of the two stocks, the stock separation in the assessment was also changed. From mid-2010s onward, cod in the Arkona Sea is allocated to both Baltic cod stocks by using allocation keys based on otolith shape readings from scientific survey catches and commercial catches in the area (ICES 2015). Using these allocation keys, it was revealed that large parts of the cod inhabiting the Arkona Sea consisted of EBC, which led to a decreased estimation of the overall spawning stock biomass (SSB) of WBC and in contrast an increased estimation of EBC SSB.

In the Baltic Sea cod is the commercially most important, demersal fish species. Both cod stocks are heavily exploited. Since the 1990s both stocks showed steady decline in their spawning stock biomass and are currently out of biological safe limits (ICES 2019a, 2019b).

For the eastern Baltic cod, a decline in nutritional condition has been observed since 1994 (Eero et al., 2015). Further since the mid-2000s, when EBC biomass started to increase, the proportion of cod with low condition indices increased rapidly due to density effects. Moreover, an absence of larger cod was observed in surveys and commercial fishery in 2013 and 2014 (Eero et al., 2015). Recent studies of Casini et al. (2016) showed that increased hypoxic condition in the central Baltic resulted in the disappearance of mobile benthic epifauna organisms such as the Isopod species *Saduria entomon*, which was considered one of the main prey species of EBC. Additionally, the key forage fish species of EBC, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), showed low abundances in the main distribution area of the EBC (Eero et al., 2012b). This combined lack of benthic and fish prey is considered one of the major causes for the observed decreased condition for EBC and is also likely negatively affecting growth of EBC. A reduced growth however could not be validated by traditional techniques such as length-age calculations, since otolith age readings proved difficult due to the formation of variable and various ring structures. These probably result from the variable feeding and hydrographic conditions cod experiences over its seasonal life cycle (Hüssy, 2016).

For the WBC the drastic decline in SSB which can be observed since the late 1990s (ICES, 2019) was mainly related to overfishing and in the last decades to a combination of high fishing pressure and several years of very low recruitment (ICES, 2019). The reasons leading to the great variability in recruitment are still not fully understood. Hüssy (2011) listed human activities (i.e. anthropogenic pollution or downstream transported dissolved sediments) that influence the cod egg buoyancy and survival (von Westernhagen et al., 1988; Ericson et al., 1996), as well as temperature (von Westernhagen, 1970) as possible drivers affecting the recruitment success of cod in the Western Baltic Sea. In addition, recent publications found negative effects of warming on recruitment of WBC (Stiasny et al., 2018; Voss et al., 2019).

In contrast to the EBC, the growth of WBC is generally considered to be better understood (McQueen et al. 2019b). However, this understanding of growth actually refers only to a calculation of growth rates using tag-recapture experiments or length at age calculation. The actual processes leading to the observed growth patterns have not been sufficiently investigated and understood so far. In addition, there are still knowledge gaps and uncertainties about the spatio-temporal distribution and the food intake of WBC, which most likely limit our current ecological understanding of this species in the area. However, shedding light on these uncertainties will be an indispensable prerequisite in order to decipher the growth processes of WBC and will improve our general knowledge on the ecology of cod in the area of the Western Baltic Sea. Finally, a better understanding of the seasonal lifecycle of WBC (e.g. spatio-temporal distribution, ambient temperatures, consumption) may also help us to find possible new explanations for the interannually varying recruitment strengths.

Uncertainties concerning the spatio-temporal distribution of WBC

The spatio-temporal distribution of cod in the Western Baltic Sea is mainly monitored by an international coordinated research trawl survey, the Baltic International Trawl Survey (BITS). The BITS is conducted twice a year in the first and the fourth quarter, respectively. During the BITS a standardized trawling gear is used. Fishing is only limited to known towable sites in depths > 10 m, wherein most of the trawling effort is conducted in depths > 20 m (ICES, 2017). This is mainly due to the fact that shallow areas are often characterized by hard structured grounds, such as rocky reef structures, cobbles, boulders and gravel, which pose a high risk for damaging the standardized trawl gear. However, 60 % of the whole area of the Western Baltic Sea is shallower than 20 m depths and 21 % are even shallower than 10 m (Tab.1). In the area of the Belt Sea and the Sound, the main distributional area of the Western Baltic cod stock, these shallow areas < 20 m depths are even accounting for higher shares (Tab. 1). Thus, large parts of the area are currently under- or even unrepresented in the monitoring survey design of the BITS. Studies on juvenile cod in the Belt Sea, revealed these shallow areas to be important nursery grounds (Zarkeschwari, 1977; McQueen, 2019a). However, the role of these areas in the seasonal distribution of adult cod in the Western Baltic cod has remained unclear so far. The question whether the sampling design of the BITS surveys covers the essential habitats of cod in the Western Baltic Sea adequately is difficult to assess, since nearly all information on the spatio-temporal distribution is directly derived from them. However, there are differences in the catch composition of the quarter 1 and quarter 4 survey, which can be most likely related to differences in seasonal abundances and thus, at least pointing towards differences in spatio-temporal distribution of cod in the area. This is further supported by looking at the effort distribution between active (i.e. trawl) and passive (i.e. mostly gillnet) commercial cod fishery within the area. For targeted cod trawl fishery, commercial fishers often use otter trawl gear with rubber discs, bobbins or rollers on the footrope. These specialized trawl gears minimize the risk of damaging the net when fishing on hard substrates and thus enabling commercial trawl fishery to fish at some habitat sites which would be considered non towable during scientific trawl surveys. However, commercial trawl fishery is legally banned within 3 nm from the German shoreline and hence the fishery effort is mostly restricted also to deeper habitat sites > 15 m depths. In contrast passive fishery using gillnets, such as single layer set nets and trammel nets, are allowed to fish up to a minimum distance of only 200 m to the shoreline. Moreover, the use of small vessels and their passive gear enables fishing on nearly all kind of habitat types and almost all different depths. When looking at the monthly cod landings by the passive and active fishery in the Belt Sea, we observe clearly distinct seasonal differences in the amount of cod caught by the two fleets (Fig. 2). The trawl fishery land cod mostly in the first and at the end of the fourth quarter and additionally to a lower extent during July and August in the third Quarter (Dorrien et al., 2013). In contrast the commercial gillnet fishery lands highest amounts of cod at the end of the third and the beginning of the fourth quarter). These differences in the amount of cod landed by the two fleets are most likely explained by differences in the seasonal distribution of cod. Therefore, it can be assumed that cod tend to reside at greater depths when high amounts of cod are landed by the trawl fishery. In contrast it can be assumed that cod reside in shallower coastal areas, and are thus less available for trawl fishery, in the second and at the beginning of the fourth quarter, when the landings by the gillnet fishery exceed those from the trawl fishery. Thus, we can assume that cod at least temporally use shallower water layers which are insufficiently covered in the BITS design. Therefore, we have to consider alternative methods to traditional scientific trawl surveys to reveal the spatio-temporal distribution of cod in the area of the Western Baltic Sea and to assess the role of shallow areas < 20 m depths in the seasonal life cycle of WBC.

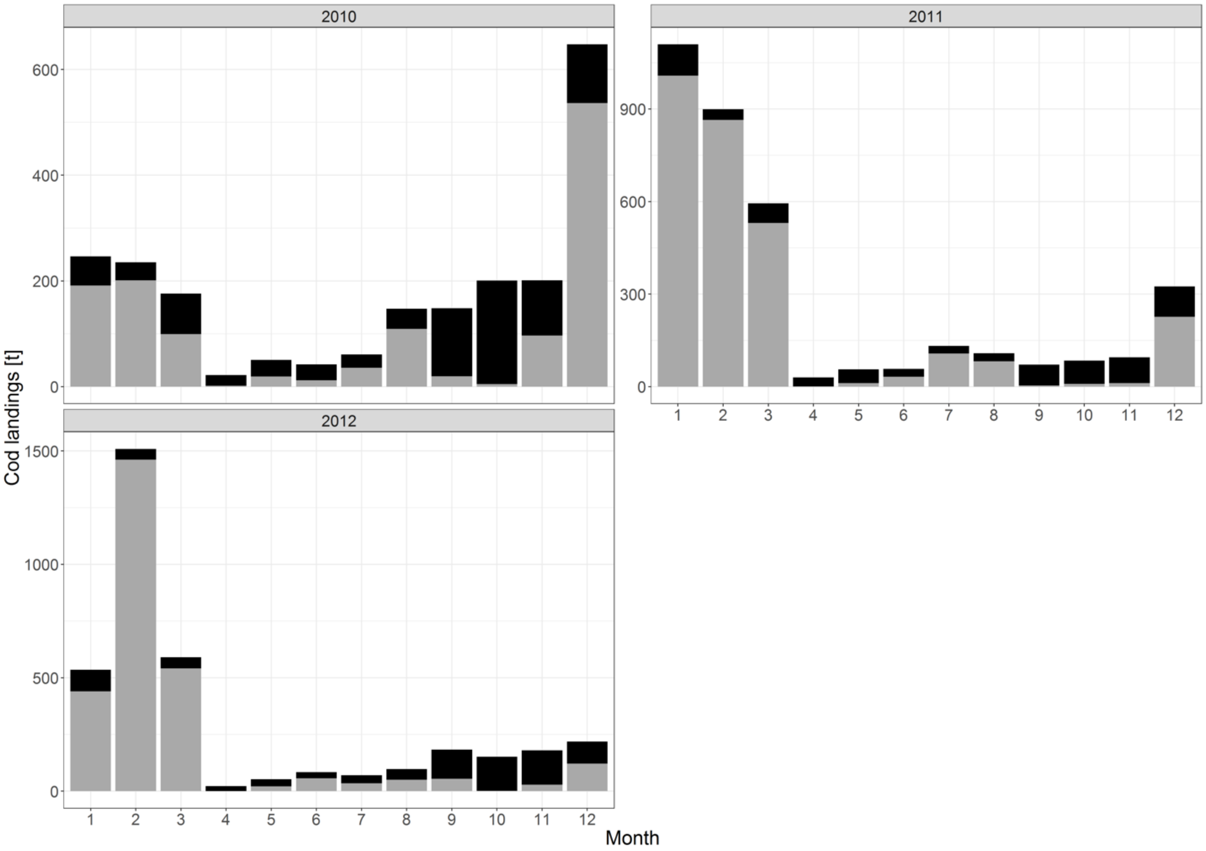

Figure 2. Monthly cod landings between 2010 and 2012 by German commercial trawl (grey) and German gillnet fishery (black) in the ICES statistical rectangles 37F9 to 38G1 in the Belt Sea. Data was taken from Dorrien et al. (2013).

Uncertainties concerning the food intake of WBC

Sound knowledge about the food intake and diet composition of a target species is important to understand trophic interactions and thus, its role in the food webs of an ecosystem as well as to understand patterns or changes in nutritional condition and growth. Moreover, stomach content data form the basis for multispecies models, ecosystem-based models and bioenergetics growth models. While food web modelling approaches got increasingly popular in the last decades, only little effort was undertaken for new and repeated stomach sampling programs. Hence, even new modelling approaches are often based on somewhat outdated stomach data. In contrast to most ecosystems, the Baltic Sea was covered more regularly with stomach samplings in the last decades (see Arntz, 1974, 1977; Zarkeschwari, 1977; Schulz, 1987, 1988, 1989a, 1989b; Weber and Damm, 1991; Hüssy et al., 1997; Dziaduch, 2011; Pachur and Horbowy, 2013; Casini, 2016), especially with regard to cod, which is considered the apex predator in this ecosystem. However, the research effort was unevenly distributed between the two Baltic cod populations and clearly focused on EBC. Thus, there have been several studies focusing on the diet composition and food intake of the EBC since the 1990s, while in contrast the most recent studies dealing with the diet composition of cod in the Western Baltic Sea originated from stomach samplings conducted in the 1980s (Schulz, 1987, 1988, 1989a, 1989b; Weber and Damm, 1991). It seems unlikely that these data from the 1980s represent the current ecological situation in the area of the Western Baltic Sea, especially since the area was subject of substantial changes in hydrographic and ecological conditions since the 1980s (Möllmann et al., 2009; Morholz et al., 2015). For example prey availability for cod may have substantially changed due to decreases in biomass for some forage fish species such as herring (ICES, 2019c) or the introduction of new invasive species in the ecosystem such as the round goby (*Neogobius melanostomus*) (unpublished data cited in Corkum et al., 2004; Hempel et al., 2017).

The somewhat outdated stomach data available for cod in the Western Baltic cod is one reason calling for a new stomach sampling project to ensure quality and reliability of future model results. Furthermore, another reason for a new sampling project is derived directly from the uncertainties on the spatio-temporal distributions of cod in the Western Baltic Sea and the role of shallow water habitats in the seasonal life cycle of WBC. Most stomach samplings conducted in the area were based on research trawl surveys, such as the BITS, which focused mainly on deep habitat sites of > 20 m depths and neglected shallow areas and hard structured grounds. We do not know to what extent these areas are used by cod so far. However, we got a first indication for temporal usage of shallow areas from the seasonal patterns in the commercial fishery. Prey composition and food intake of cod in these areas might be completely different from those in the deeper habitats. Hence, the sampling design used in the previous stomach sampling programs is likely limiting our ecological understanding of cod in the area.

Uncertainties concerning seasonal growth patterns of WBC

As mentioned earlier, the growth of cod in the Western Baltic Sea is well understood compared to the growth of cod in the Eastern Baltic Sea. A recent study of McQueen et al. (2019b) combined data from tag-recapture experiments and length at age data from otolith age readings and provided new, more reliable growth parameter estimates. Furthermore, the tag-recapture data gave insights about seasonal growth patterns. Cod displayed variable growth patterns over the year peaking during autumn. It was hypothesized that these growth patterns may reflect variable environmental conditions such as seasonal changes in ambient temperature or changes in food availability. Furthermore, studies of McQueen et al. (2019a) and Krumme et al. (unpublished) revealed new insights on the formation of hyaline and opaque otolith ring patterns in juvenile and adult cod. The regular formation of otolith ring patterns enables age-determinations for many fish species since often per year one hyaline (i.e. translucent) and one opaque otolith ring zone are formed. Traditionally, the formation of hyaline ring zones is mainly explained by slow growth, while opaque ring patterns are formed during good growth periods. For many species it has been shown that hyaline ring patterns are formed during winter, when energy intake and growth are decreased. Hence translucent rings are often called “winter-rings”. However, the tag recapture studies of McQueen et al. (2019a) and Krumme et al. (unpublished) using a tetracycline-hydrochloride mark on otoliths to validate the timing of the translucent ring formation showed that the hyaline ring structures in WBC were formed during the summer-half year. Referring to recent literature on Atlantic cod, the formation of translucent zones can be related to changes in ambient temperature, by reduced growth or to a combination of both factors (Høie and Folkvord, 2006; Høie et al., 2008; Neat et al., 2008), wherein high ambient temperatures support the formation of translucent ring structures, while low temperatures support the formation of opaque ring structures. Whether the hyaline ring formation in cod in the Western Baltic Sea is mainly related to changes in ambient temperature or to reduced food intake and related decreased growth, has not been investigated so far.

A possible solution to better understand seasonal growth patterns and thus gain new insights on formation of translucent ring patterns, might be achieved by applying a bioenergetic growth model. Bioenergetic models are described by an energy balance equation, wherein the growth rate of a fish is determined as the difference between food consumption rate and the sum of energy losses, i.e. metabolic losses including specific dynamic action and waste losses (Kitchell et al., 1977). Hence, applying a bioenergetic growth model requires a sound knowledge on a number of physiological processes. For Atlantic cod many of those such as gastric evacuation (Ursin et al., 1985; dos Santos and Jobling, 1991; Temming and Andersen, 1994; dos Santos and Jobling, 1995; Andersen, 2001; Temming and Herrmann, 2003, Andersen et al., 2016), consumption (Temming and Herrmann, 2003), net conversion efficiency (Temming and Herrmann, 2009) or metabolic rates (Saunders, 1963; Jobling, 1982) were already investigated in a number of laboratory studies over the last decades. Hence, cod seems to be the ideal case study species for setting up a bioenergetics model to validate seasonal growth patterns. However, setting up a bioenergetics growth model requires moreover information on the spatio-temporal distribution, since the physiological processes in a poikilothermic species such as cod are directly linked to the ambient temperature discovered by the cod. Furthermore, knowledge on the food intake on these residence sites is an indispensable prerequisite to calculate consumption rates and related energy uptake.

General hypotheses – the scope of the thesis

The objectives of this thesis were (i) to reveal the spatio-temporal distribution of cod in the Western Baltic Sea and (ii) to detect seasonal and/or depth specific patterns in the seasonal food intake of cod in this region. Finally, we wanted to use the new information on spatio-temporal and food intake to set up a bioenergetic growth model to (iii) explain patterns in seasonal growth of cod in the Western Baltic Sea.

In **chapter I** the depth and habitat use of cod in the Western Baltic Sea was investigated. The general hypothesis was that cod at least temporally uses habitat sites and depths, which are not sufficiently covered by the current monitoring survey design, such as from the Baltic International Trawl Survey, and hence that the information on spatio-temporal distribution of cod in the western Baltic, Sea which is mainly inferred from these scientific trawl surveys only, hampers our understanding on the real spatio-temporal distribution of cod in the area. This hypothesis was tested by using local fishers' knowledge, wherein catch depths for cod reported by gillnet fishers in interviews conducted in 2016 were used supported by cod catch depths selected by gillnet fishers recorded by at-sea observers in 2011 and 2016 to detect patterns in depth distribution in relation to sea surface temperature and stratification. Moreover, information on the habitat types selected for targeted cod fishing reported during the interviews was used to detect seasonal habitat use of cod.

The aim of **chapter II** was to obtain a new up-to date picture of the diet composition and food intake of cod in the Western Baltic Sea, with a particular focus on seasonal and depth-specific differences. The first hypothesis of the study was that the old stomach data most likely do not reflect the current ecological situation due to substantial changes of the ecosystem and the introduction of new invasive species affecting the prey availability of cod. The second hypothesis was that, essential habitats such as shallow areas < 20 m depths and hard structured grounds are highly relevant and change our understanding of the diet composition and food intake of cod. The hypotheses were tested by conducting a new stomach sampling program of cod in the Western Baltic Sea during 2016 and 2017 using a number of different methods and fishing techniques to maximize depth coverage. The observed diet composition of cod was compared to those from previous studies. Moreover, effects of catch depths, predator length and season on diet composition and stomach content weights were tested applying multinomial regression and general additive models.

In **chapter III** a bioenergetic growth model of cod in the Western Baltic cod was set up. The idea of the study was to use new information on the spatio-temporal distribution of cod derived from chapter I and information on the depth specific food intake of WBC derived from chapter II to set up a seasonally resolved bioenergetic growth model to reflect seasonal growth patterns. To validate the bioenergetic growth model, growth rates of cod were compared with growth rates observed in the field calculated from length at age data obtained from scientific research surveys. Moreover, von Bertalanffy growth equation parameters were compared to recently published ones based on length at age data from tag-recapture experiments. Furthermore, monthly average growth rates per age class calculated from the biogenetic model and predicted temperature at residence depth of the cod were related to the formation of translucent ring patterns during the summer half year.

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Chapter I

Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea

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Abstract

Practical and applied knowledge of local fishers can help to improve our understanding of target species ecology and fisheries management decisions. In the Western Baltic Sea (WBS), the spatio-temporal distribution of cod is still largely unknown despite decades of research. We studied changes in cod distribution by obtaining information on temporal depth and habitat use of cod from commercial gillnet fishers using semi-directive interviews supplemented by at-sea observer data. Linear and non-linear regression analysis revealed significant relationships between depth use of cod and sea surface temperature (SST) as well as thermal stratification. Moreover, habitat use was related to SST and residence depth of cod. Areas deeper than 15 m were favoured from late December until March during low SST and a mixed water column (spawning), and also from July until August during high SST and strong thermal stratification (summer aestivation). Shallower areas were favoured during the rest of the year. Hence, the depth and habitat use displayed distinct seasonal up- and downslope movements of cod. This work highlights the importance of shallow-water and structured habitats for cod in the WBS and the value of local knowledge held by fishers for a better understanding of the distributional dynamics of important marine resource populations.

1. Introduction

The habitat selection of a species is understood to represent a behaviour aiming to optimize the individual fitness, which consists of numerous trade-offs of needs and constraints (Fretwell and Lucas, 1969; Sih, 1980; Werner et al., 1983; Orians and Wittenberger, 1991). Typical trade-offs in aquatic systems consist of food availability, avoidance of predation and thermoregulation (Mehner, 2012; Freitas et al., 2016). Information about temporal and spatial fish distribution patterns is fundamental to understand population dynamics. Furthermore, it can help to evaluate adaptation processes of fish species to environmental changes such as regional warming. However, the understanding of habitat selection and related trade-offs of many fish species is still limited (Freitas et al., 2016).

In the Western Baltic Sea (WBS), cod (*Gadus morhua* L.) has typically been the most important commercial fish species in the demersal assemblage. Since the late 1990s catches and spawning stock biomass have been in constant decline (ICES, 2019a), likely due to overexploitation and the negative effects of warming on recruitment (Stiasny et al, 2018; Voss et al., 2019). Despite decades of research on the ecology of Western Baltic cod (e.g. Berner, 1967, 1973, 1981; Bagge, 1969; Thurow, 1970; Otterlind, 1985) some fundamental concepts – including seasonal and spatial distribution – remain poorly understood (Hüssy, 2011). Information about distribution of cod in the WBS have mainly been inferred from trawl catches during internationally coordinated, standardized research surveys such as the Baltic International Trawl Survey (BITS). This is reflective of a historical focus of scientists on the major landings originating from the trawl fisheries and a reliance on research vessels (mainly) operating with trawls in deeper soft bottom areas. To avoid gear damage, scientific trawl surveys are often limited by the nature of the sea floors. For example, hard bottom structures (i.e. cobbles, boulders, or rocky reef structures) are usually neglected resulting in both a limited area and habitat coverage of the scientific trawl surveys. In the WBS, hard bottom structures can often be found in depths shallower than 20 m, so that the BITS stations are mainly distributed in depths > 20 m (ICES, 2017). Consequently, shallow-water areas and hard structured benthic habitats are underrepresented or not covered at all by BITS. However, areas shallower than 20 m water depth cover 60% of the WBS, and areas shallower than 10 m water depth still cover 21% (Fig. 1, ICES, 2017). Neglecting such large parts of the area likely limits the knowledge fishery scientists have about the spatial distribution of cod in the WBS. For instance, Zarkeschwari (1977) and McQueen et al. (2019b) have shown that these shallow areas, particularly seagrass meadows, are important feeding habitats for age 0 and age 1 cod.

Standard biological sampling techniques like scientific trawl surveys are typically conducted on a large spatial scale, use only one gear type, cover a limited range of habitats and only provide a temporal snapshot of complex ecosystem dynamics (Macdonald et al., 2014; DeCelles et al., 2017). In contrast, local knowledge held by commercial fishers can integrate comprehensive lived experiences across diverse temporal and spatial scales (Murray et al., 2008b; DeCelles et al., 2017). Such comprehensive experiences are unattainable by standard BITS surveys. In comparisons to the BITS method, local fishers in the WBS often operate year-round, on smaller spatial scales, use different gear types (i.e. both passive and active gear), fish on different habitat types (i.e. also non-trawlable sites) and interact with their target species on a daily basis. Over the course of their multidecadal careers, commercial fishers accumulate a comprehensive knowledge about temporal and spatial patterns in distribution and behaviour of their target species (Bergmann, 2004; Zukowski et al., 2011; DeCelles et al., 2017). Hence, considering local knowledge of fishers can help to improve the understanding of temporal and spatial abundance patterns of target species (Beaudreau and Levin, 2014; MacDonald et al. 2014; Hedeholm et al., 2016; Figus et al., 2017), particularly identifying and localizing essential fish habitats such as important feeding or spawning grounds (Ames, 1997; Maurstad and Sundet, 1998; Neis, 1999; Bergmann et al. 2004; Murray et al., 2008a; DeCelles et al., 2017).

In the WBS, cod is caught by active and passive commercial fishing gear, and by recreational fishers (ICES, 2019a). Vessels in the commercial trawl fishery land cod mostly during the first quarter, at the end of the fourth quarter and partly during the peak summer months (Dorrien et al., 2013; Kraak et al., 2019). Hence, it can be hypothesized that in the months when cod fishing is open but there are no or only low cod landings by trawlers, cod may use non-trawlable habitats or areas close to the shoreline, where trawling is prohibited. In Germany trawling is legally restricted to areas with a minimum distance of 3 nm from the shoreline (§ 13 III KüFVO; § 10 I KüFVO-MV) while gillnet fishing is permitted up to 200 m from the shore (§ 14 I KüFVO; § 20 VIII KüFVO-MV). Moreover, the use of small boats and passive gears enables gillnet fishers to fish on almost all habitat types (i.e. also non-trawlable sites). Thus, commercial gillnet fishery has constant access to nearly all depths in the WBS, while the commercial trawl fishery is mostly limited to deeper, trawlable areas only (mostly > 20 m depths).

In contrast to trawlers, the commercial gillnet fishery land cod year-round, with highest landings during October and November, coinciding with the period of minor landings from trawlers (although commercial trawl vessels are not subject to further legal restrictions during these months) (Dorrien et al., 2013). Therefore, gillnet fishers constitute a resource user group with potentially important and detailed local knowledge on the seasonal depth and habitat use of cod in the WBS.

The local knowledge of gillnet fishers and documentation of accompanied gillnet trips, by at-sea observers, form the basis for the study presented here. This study aims to identify patterns in the seasonal depth and habitat use of cod in the WBS by using information from the local WBS gillnet fleet. We gathered information on catch depths and fishing grounds through interviews with gillnet fishers and through reviewing logs of gillnet trips documented by at-sea observers. Additionally, we aim to combine our gained knowledge with existing literature documenting life history, physiological and ecological traits of Atlantic cod in the WBS to develop a comprehensive conceptual model on seasonal depth and habitat use.

2. Material and methods

2.1. Study area and cod fishery

The WBS is composed by the Belts Sea (ICES subdivisions (SD) 22, the Sound (SD23) and the Arkona Sea (SD24). The Belt Sea (SD22) is a relatively shallow (98% of the area is shallower than 30 m), stratified, microtidal, brackish-water area (common salinity range: 10 to 25 PSU) in the temperate zone. It is characterized by continuous wind-induced fluctuations in hydrography, mainly due to 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 (Fig. 1). It is the core area of the Western Baltic cod stock (Fig. 1). Mixing with Eastern Baltic cod (EBC) is considered negligible (ICES, 2019b), although recent findings suggest that there could also be some EBC resident in the Belt Sea (McQueen et al. 2019a).

The main demersal target species in SD22 are cod and flatfishes, which are mostly caught in a mixed fishery. Cod in SD22 is fished by Denmark and Germany. Commercial cod landings from SD22 decreased from 5,493 t in 2011 to 2,014 t in 2018 (ICES, 2019a). In this period Germany contributed between 44% and 51% of these landings, with on average 60% contribution by active (trawl) fishery and 40% by passive (mostly gillnet) fishery vessels between 2011 and 2018. A spawning closure from April 1st till 30th for trawl vessels on the commercial cod fishery in SD22 was implemented in 2008 and lasted until 2015 (Eero et al., 2019; EU, 2007). In 2016, the spawning closure was extended to the period February 15th till March 31st. In 2017 and 2018, it was further extended to February 1 to March 31st. During the spawning closures from 2008 to 2015, gillnet vessels were allowed to have only five fishing days. From 2016 to 2018 gillnet vessels were allowed to fish without day limits but restricted to operate in water depths < 20 m only.

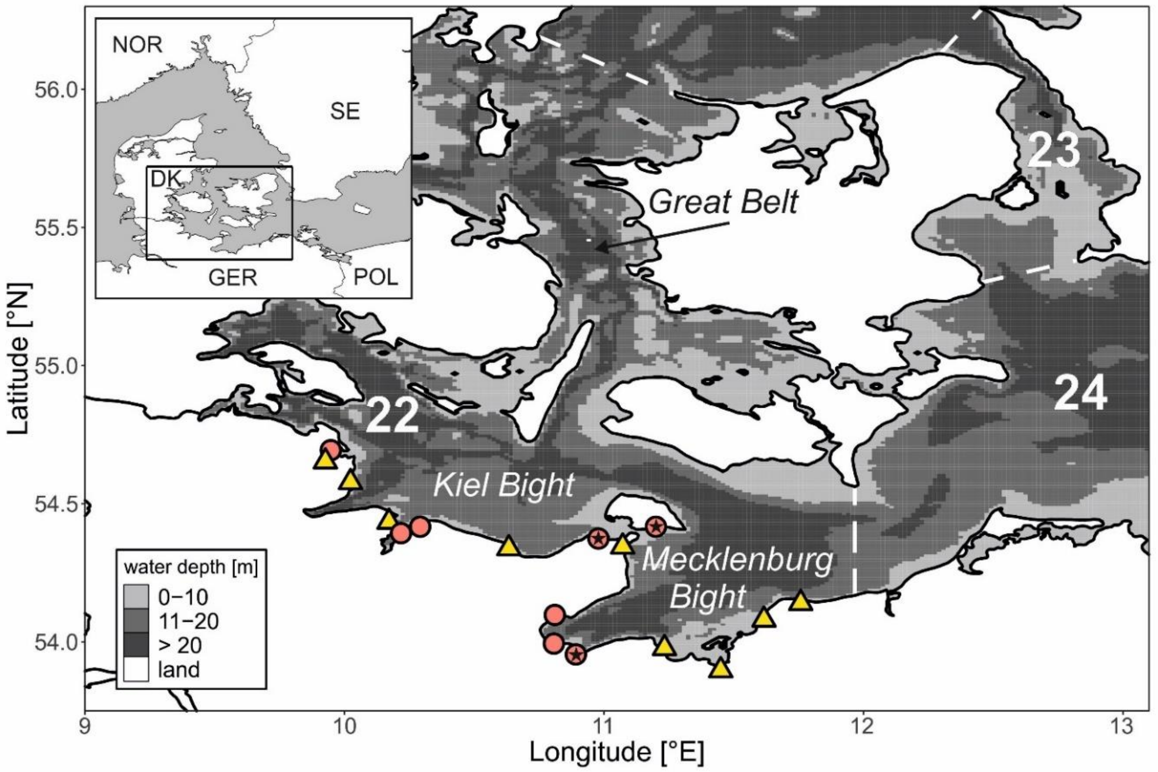

Figure 1. Bathymetry of the study area in the Western Baltic Sea. Red dots: ports with interviewed gillnet fisher (in 2016) and where at-sea observers started sampling trips of gillnet fishers in the period between 2011 and 2016. Yellow triangles: ports from which at-sea observers started sampling trips of gillnet fishers in the period between 2011 and 2016 and no interviews were conducted in 2016. Stars: the three German ports with highest cod landings from passive fishery (from north to south: Burgstaaken, Heiligenhafen and Travemünde). White dashed lines: borders of ICES subdivisions (22 – Belt Sea, 23 – Sound, 24 – Arkona Sea). Mecklenburg Bight, Kiel Bight and Great Belt indicate subareas within the Belt Sea (SD22).

2.2. Characteristics of the German commercial fleet targeting cod in SD22

In the period between 2011 and 2016 the German commercial fleet fishing in SD22 comprised on average 25 trawlers (vessel lengths: 12 m to < 24 m), 55 full-time gillnetters (mostly with vessel lengths of 8-12 m) and 225 with vessels < 8 m (either part-time or full-time fishers) which were engaged in fishing. Vessels ≥ 8 m account for about 98 % of the total official German cod landings in SD22 by weight (in average between 2011 and 2018). The official cod landings of vessels < 8 m are negligible, although they account for the vast “majority” of vessels on the water in the study area. During the study period (2011-2016) cod was landed in 15 German ports in SD22. Burgstaaken, Travemünde and Heiligenhafen are the three ports that received the most cod by weight from the German commercial gillnet fishery fleet during this period (Fig. 1).

Gillnetters targeting cod mostly use single layer gillnets (GNS), and less often trammels nets (GTR) (pers. comm. with gillnet fishers). GNS consist of only one layer of meshes, while GTR used in the Baltic Sea consist of three layers of meshes, with mesh openings partly overlapping. Gillnet fishers targeting cod in SD22 are required to use a minimum gillnet mesh size of 110 mm (the diagonal distance between knots; § 10 KüFVO; § 15 II KüFVO-MV). GNS and GTR display differences in species- and size-selectivity. For this study it is relevant to note that GTR has a higher catch selectivity on flatfish species and hence is often used to increase the flatfish proportion in the catch (pers. comm. with commercial fishers in SD22; Krumme, unpubl. data). Fishers can use both GNS and GTR at the same fishing trips and it is not mandatory to report the proportions and exact mesh sizes in the logbooks. Therefore, we cannot provide detailed proportions of the use of GNS and GTR in the German gillnet fleet in SD22. Commercial cod catches with other passive gear types like pound nets and long lines are minor. There is, however, a large recreational fishery targeting cod in SD22, which removed between 2,595 t and 4,586 t annually in the period of 2011-2016 (ICES 2019a).

2.3. Interviews

Between April and December 2016, we interviewed a total of 16 commercial fishers from 8 ports of Schleswig Holstein, Germany (from north to south: Maasholm, Laboe, Wendtorf, Heiligenhafen, Burgstaaken, Neustadt, Niendorf, Travemünde) (Fig. 1). Experiences from numerous documented at-sea observer trips show that in SD22 gillnet fishers usually conduct day trips and operate within the proximities of their home port (Krumme, unpublished data). All, except one, were full-time fishers with vessel lengths of 8-12 m. Thus, we interviewed 15 out of 55 (27%) active German commercial gillnet fishers classified as “full-time” active in SD22 in 2016. We primarily contacted full-time gillnet fishers because their activities, unlike trawlers or part-time gillnetters, target cod year-round and in all depths of water. The eight ports covered in average around 60% of all cod landed by the passive gear fleet in SD22 (reference period: 2011-2016).

We based our interviews on the assumption that gillnetters usually concentrate their fishing effort on those locations and depths where the abundance of their target species tend to be highest (Erisman et al., 2011). Hence, interviews focused on eliciting mean cod catch depths and habitats selected for fishing over time.

First, we chose to interview the fishers in the ports face-to-face following the snowball-sampling principle (Bernard, 2011). We assumed that a face-to-face conversation would be the best way to gather local and experiential knowledge. Moreover, face-to-face interviews can provide an opportunity to ask follow-up and spontaneous questions about the topic of interest and for clarification (Ritchie, 2003; Bryman, 2012). Furthermore, this method offered the opportunity to be directly forwarded to other fishers in the same port by colleagues who had previously been interviewed by us. At first, we contacted three fishers (known to the authors due to previous cooperation) in the ports of Travemünde, Burgstaaken and Heiligenhafen (one in each harbour). However, unlike our expectations, it was difficult to meet more fishers in the ports or to convince them to take part in the survey. This was mainly due to the very variable working hours of the fishers and the lack of idle time during their stay in port. Given the small number of fishers we could talk to in the ports (N = 6), we decided to contact additional fishers by phone. To talk to fishers on the phone, we started with a list of contacts of German gillnet fishers in SD22, provided by the Thünen Institute of Baltic Sea Fisheries (Thünen-OF). The list contained fishers known from previous cooperations or from at-sea observer trips. Similar to the face-to-face contact, on the phone participants were asked to recommend other fishers. This way, a total 10 of fishers were successfully contacted via phone.

We began each interview informing the fishers about the unknown spatio-temporal distribution of cod in the area and the problems and uncertainties that occur when information is inferred from traditional scientific trawl surveys only. Furthermore, we clarified that sharing their detailed local knowledge with us could possibly contribute to a better scientific understanding of the ecology of Western Baltic cod. Subsequently, fishers were asked to take part in the survey. All participants willing to take part gave their verbal consent to use all information derived from the interviews for this scientific study and possible scientific publications resulting from them. The participants were informed that they had the possibility to withdraw their consent at any time by contacting the authors per phone or via e-mail. A detailed description of the informed consent procedure is given in the supplementary material S1.

Before starting the interviews, fishers were asked if they fish for cod year-round in the area, which was confirmed by all 16 participants. This question was asked to ensure that only fishers that are likely to provide complete information on the seasonal habitat and depth use of Western Baltic cod were considered.

Demographic or other sensitive information concerning the survey participants was not queried or evaluated in the context of this study. However, all 16 participants are, registered commercial fishers, and have cooperated with the Thünen-OF for years. Using information from the fleet registry, we deduced that none had < 10 years commercial fishing experience, at least eight had > 20 years of experience and one had > 60 years of professional experience in targeting cod with gillnets in SD22.

The semi-directed interviews (see Huntington, 2000) were based on a brief interview protocol with only two questions. Both questions had two parts: a categorical part (a directed response request in a pre-determined format) and an open-ended part (where each interviewee was encouraged to elaborate on his experiences and choices regarding catch depth and selection of ground type for cod fishing). The scientists inserted the essence of the answers in a prepared table (recording form); the interviews were not voice-recorded. The questions and recording form (translated from German into English) are given in the supplementary material S2.

For both questions, the fishers were not directed to focus on a specific year or group of years, but rather to describe their general preferences and general experiences over time. We decided to treat all answers as average values over the previous five years before the interviews were conducted (i.e. the period 2011 to 2015). Gillnet fishers in the WBS usually fish relatively localised and the interviewed fishers fished in the area since many years (see above), so that it seems reasonable to assume that the main spatial area experienced by each fisher was located in SD22. We treated all responses equally across the study area.

The first question was an open-ended question about the selected catch depths for a targeted cod fishing, to be given in metres on a half-monthly basis for an entire year. In the case of imprecise answers such as "shallower" or "rather deeper", the fishers were asked again to specify and provide an exact depth information in metres. In cases when fishers gave depth ranges for a half-month, the mean value was recorded.

Next, we asked a categorical question about the ground structures (i.e. habitat types) they select for a targeted cod fishing, again using half-monthly intervals. Given experience on the naming of fishing grounds by the fishers from previous personal contacts and conversations, six habitat type categories were provided:

hard ground (including cobbles, boulders, and rocky reef structures; see definition by Bergmann et al., 2004); mud; mussel beds; sand; seagrass meadows; and, wrecks. However, we pointed out that adding other habitat types was allowed. Each participant could select multiple habitat types per half-month interval.

If the fishers provided additional information, it was also noted on the recording form (supplementary material S2). This information included reasons for selecting a fishing gear (e.g. GNS or GTR), net lengths, soaking times, distance to the shore, mesh sizes, or professional knowledge such as personal explanations and experiences with cod catches at certain periods or under certain weather conditions, or reasons for the selection of fishing grounds at certain periods.

The length of the interviews varied between 10 and 40 minutes, depending on the amount of additional information provided and the willingness and patience of the fishers to respond to queries for additional information by the scientists. The first author of this study conducted all face-to-face interviews, the phone calls were conducted by a student assistant.

2.4. At-sea observer data

A second data source was anonymised at-sea observer data collected within the EU-co-funded Data Collection Framework (DCF) by the Thünen-OF. The aim of using logs of at-sea observers was to provide an additional verified data source on specific catch depth selections of fishers in the area, as well as to derive extra variables for data analysis. In addition, observer data (GPS position, date) allow to directly link the observed catch depths to the specific environmental conditions (e.g. water temperatures). The data set contained 97 trips sampled by an at-sea observer onboard of 34 different commercial gillnetters catching cod between September 2011 and December 2016 in SD22. Recorded parameters included the mean catch depths of GNS and GTR, mesh size diameters and the amount and size distribution of cod catches. All 15 interviewed full-time fishers were part of the 34 gillnetters with trips sampled by at-sea observers.

2.5. Temperature data

We used measurements of sea surface temperature (SST) and sea bottom temperatures (SBT) within the study area between 2011 and 2016 to characterize the thermal habitat of Western Baltic cod. Data from SD22 were downloaded from the ICES oceanographic database (ICES, 2014). We computed half-monthly averages of SST and SBT (calculated as mean temperature for the depth layer 20 to 25 m) for subsequent implementation in the statistical modelling (seasonal temperature curves are given in the supplementary figure S1). As a proxy for stratification, we calculated the difference between half-monthly SST and SBT, termed as $T_{Diff.}$.

We assumed the catch depth reported by the interviewed gillnet fishers to be the result of experience over several years (i.e. treated them as average values over the previous five years). Therefore, we computed average values for SST, SBT and $T_{Diff.}$ over the previous 5 years before the interviews were conducted (2011-2015). For the at-sea observer data, half-monthly mean values of SST, SBT and $T_{Diff.}$ of the sample year were assigned to the sampled fishing trip.

2.6. Statistical analysis

We used the interview and observer data in statistical modelling to relate the reported and the observed selected catch depth with temperature variables (see section *2.6.1. Temperature effect on catch depth*), to develop depth use models. In addition, the observer data were used to assess relationships between selected gillnet mesh sizes and selected catch depth (see section *2.6.2. Mesh size effects on catch depth*). The interview data concerning the habitat types selected by the fishers were used for multinomial regression modelling to develop a habitat use model (see section 2.6.3. *Habitat use*).

2.6.1. Temperature effect on catch depth

We compared linear regression (LM) and generalized additive models (GAM) to investigate the effect of sea water temperature on catch depth of cod. SST, SBT and $T_{Diff.}$ were used as explanatory variables. Due to cross-correlation (Pearson correlation coefficient $r = 0.74$ for SST and SBT between 2011 and 2016), SST and SBT were not used simultaneously. Non-linearity in the effect of explanatory variables was taken into account through applying a number of polynomial terms in LMs.

In GAMs, non-linearity is represented by smoothing terms (Hastie and Tibshirani, 1986), and we selected the optimal effective degrees of freedom (edfs) for the smoothing terms on sea water temperature variables using a set validation approach (James et al., 2013). Here, GAMs are fitted to a randomly chosen half of the observations. Subsequently, the fitted models were used to predict the second set of the observations and assessed using mean squared errors (MSE). The procedure was repeated 100 times keeping edfs for the smoothing terms between 2 and 5. Comparisons of the MSE revealed no significant differences (ANOVA, p > 0.05) between the models. Hence, for easier interpretation, a maximum number of edfs = 2 was applied for all smoothing terms.

Model selection was conducted through a backward selection procedure using Akaike's Information Criterion (AIC; Aikaike, 1974). We selected the more complex model if the AIC + 2 was ≤ the AIC of the less complex model. Our model selection exercise revealed only marginal differences in model performance between GAMs and LMs. Only LMs are presented in the results, due to easier interpretation and better reproducibility of model predictions. Results of the GAMs are presented in the supplementary Table S1.

Selected LMs for *Catch depth [m]$_i$* based on interviews and at-sea observer data were described by:

$$Catch\ depth\ [\mathrm{m}]_i = \beta_0 + \beta_1 SST\ [°\mathrm{C}]_i + \beta_2 (SST\ [°\mathrm{C}]_i^2) + \beta_3 (T_{Diff}[°C]_i) + \varepsilon_i \tag{1}$$

with β_0 – the coefficient of the intercept, β_1 – the coefficient of the linear term on SST at half-month i, β_2 – the coefficient of the polynomial term of order 2 on SST at half-month i, β_2 – the linear term on $T_{Diff.}$ at half-month i, and ε_i – a random error term at half-month i.

We tested for significant differences between the observer and interview models by comparing the coefficients of the different LMs with a Z-test (Clogg et al., 1995):

$$Z = \frac{\beta_1 - \beta_2}{\sqrt{SE\beta_1{}^2 + SE\beta_2{}^2}} \tag{2}$$

with β_i – the coefficient of model i and $SE\beta_i$ – the standard error of coefficient β_i.

2.6.2. Mesh size effects on catch depth

We assumed that fishers choose mesh size diameters according to the expected size of individual cod (e.g. they use larger mesh size diameters if larger cod are targeted). Therefore, we tested for significant relationships between catch depth and mesh sizes used. We assumed that significant relationship may function as a proxy for characterising size-related patterns in depth use by cod. Mesh sizes and gear type information were only available from the at-sea observer data. Therefore, we included mesh size diameter as a factor in the LM for the at-sea observer data. We tested different factor levels for possible mesh size categories (i.e. starting with 10 mm mesh size bins and then, step by step, summarising the non-significant factor levels) and eventually found only two of the mesh size categories to be significant in the model runs: 110-119 mm and 120-240 mm. Gear type (GNS and GTR) was included as a potential categorical predictor in the LMs, but was excluded from the chosen model due to poorer model performance.

The selected model for the *Catch depth [m]$_{ij}$* including mesh size category is described by:

$$Catch\ depth\ [\mathrm{m}]_{ij} = \beta_0 + \beta_1 SST\ [°\mathrm{C}]_{\,i} + \beta_2 (SST\ [°\mathrm{C}]_{\,i}^{\,2}) + \beta_3 (T_{Diff}[°C]_i) + f(mesh\ size_j) + \varepsilon_{ij} \qquad (3)$$

with β_0 – the coefficient of the intercept, β_1 – the coefficient of the linear term on SST at half-month i, β_2 – the coefficient of the polynomial term of order 2 on SST at half-month i, β_2 – the linear term on $T_{Diff.}$ at half-month i, $f(mesh\ size_j)$ – the effect of mesh size category j, and ε_{ij} – a random error term at half-month i and mesh size j.

Additionally, we tested for a difference in central tendencies of cod sizes between the two types of mesh size categories. We used cod length measurements from all 97 at-sea observer trips used in our study. The observed cod lengths were assigned to one of the two mesh size categories, which were subsequently compared statistically. Since the requirements for a parametric test were not met, a Wilcoxon rank-sum test was applied.

2.6.3. Habitat use

The information on sea floor properties reported by the fishers was used to calculate the mean reported habitat use (RHU) per half-month. Each habitat type reported by a single fisher for a given half-month was weighted by the overall number of habitat types reported by this fisher for that time step.

$$RHU_{ik}[\%] = \frac{\sum_{j=1}^{n} \frac{N_{ijk}}{\sum_{i=1}^{m} N_{ijk}}}{n} * 100 \text{ for } N_{ijk} = \{0,1\} \text{ and } \sum_{i=1}^{m} N_{ijk} \neq 0 \qquad (4)$$

with RHU_{ik} – mean reported use of habitat type i in half-month k, N_{ijk} – presence of fisher j in habitat type i in half-month k, m – number of habitat types, and n – number of fishers.

For statistical modelling of the habitat type selection, we applied multinomial log-linear models (McCullagh and Nelder, 1989), which allowed the use of a polytomous response variable. A presence-absence matrix for all habitat types was created, treating the information per fisher and each half-month period as a single observation. A number of models were applied, in which the polytomous response variable was modelled as a function of water temperature (i.e. SST and SBT) and the proxy for thermal stratification $T_{Diff.}$. SST and SBT were not used simultaneously due to cross- correlation (see above). We additionally included catch depths reported by the fishers as an explanatory variable and hence assigned these to the respective habitat types. Non-linearity in the effect of explanatory variables was taken into account by applying polynomial terms in the models. Furthermore, we tested for interactions between explanatory variables. For model selection, we used a backward selection procedure using AIC (AIC selection criteria as mentioned above).

The final model for the habitat selection was described by:

$$\ln\left(\frac{P_i}{P_{ref.}}\right) = \beta_{0i} + \beta_{1i}(SST_j) + \beta_{2i}(catch\ depth_j) \qquad (5)$$

with P_i – probability for the use of habitat type i, $P_{ref.}$ – probability for the use of the reference habitat type (”hard ground”), β_{0i} – Intercept for habitat type i, β_{1i} – coefficient for linear effect of SST and habitat type i, SST_i – half-monthly mean SST at reported time j, β_{2i} – coefficient for linear effect of reported catch depth and habitat type i, $catch\ depth_j$ – reported catch depth at time j.

Goodness of fit of the finally selected multinomial logistic regression model was assessed using McFadden’s Pseudo R^2 (McFadden, 1974).

$$R^2_{McFadden} = 1 - \frac{\log(L_c)}{\log(L_{null})} \tag{6}$$

with L_c – maximized likelihood of the finally chosen multinomial logistic regression and L_{null} – maximized likelihood for the null model.

2.7. Software used

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

3. Results

3.1. Seasonal variability in catch depths

The catch depths of cod in the Belt Sea reported by gillnet fishers ranged between 2.5 m and 24.5 m (Fig. 2) showing a W-shaped depth pattern over the year. Deeper catch depths were reported from the end of December to the first half of March, and during the peak summer period in July, while shallower depths were indicated mostly during spring (between April and June) and autumn (between September and early December) (Fig. 2A). Mean catch depths were deepest in January/February (18.0 m ± 4.9 m) and shallowest from late September to early November (6.0 m ± 3.4 m).

Observer-based catch depths virtually replicated the seasonal W-shaped pattern reported by fishers (Fig. 2B). Catch depths ranged between 2.5 and 22.5 m in May and February, respectively. Mean catch depth was deepest in late February (20.5 m) and shallowest in late September (4.5 m ± 0.5 m).

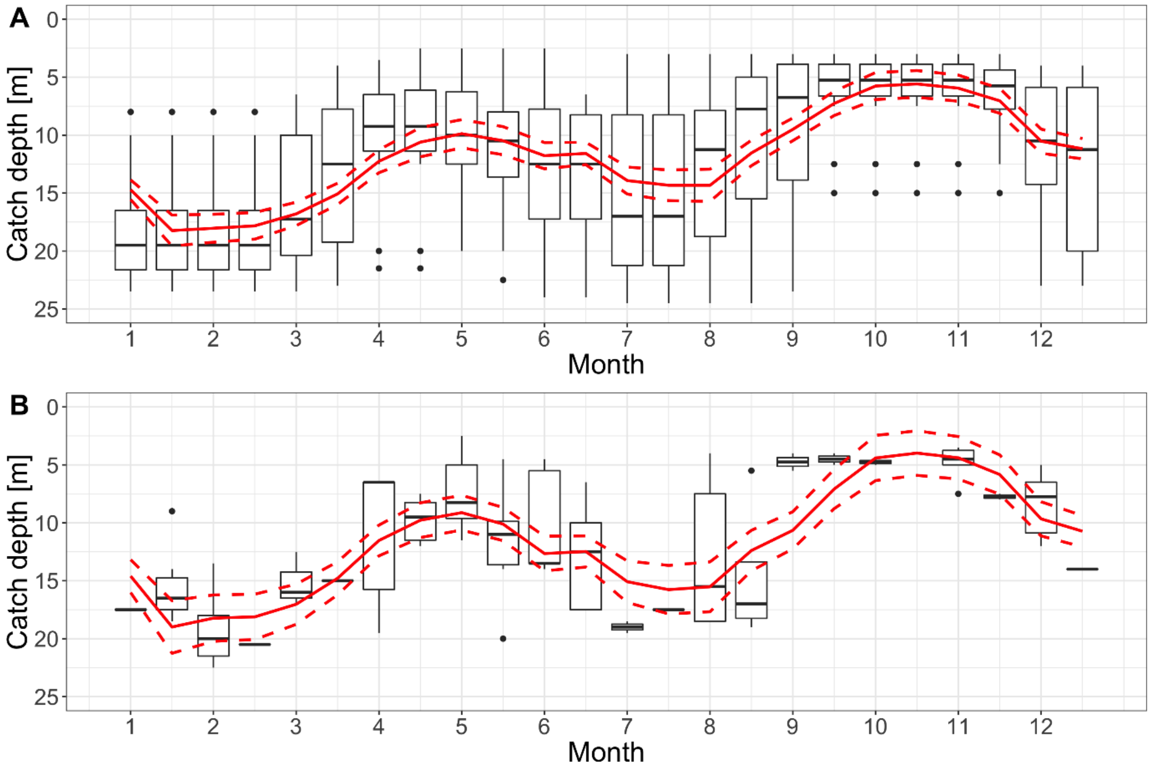

Figure 2. Seasonal variability of catch depths of Western Baltic cod reported by 16 gillnet fishers (A) and at-sea observers that sampled 97 gillnet trips (B). Boxplots show median and first and third quartile (hinges) of the reported depth per half-month. Whiskers extend from the upper/ lower hinge to the largest value no further than 1.5 * IQR from the hinge, respectively (IQR - the distance between the first and the third quartile). Black dots represent outliers which are depth values further than 1.5 * IQR from the upper or lower hinge. Red lines display predicted catch depths calculated from linear regression models LM 1 (A) and LM 2 (B), respectively. Dashed lines indicate upper and lower confidence intervals for catch depth predictions.

3.2. Temperature effects on catch depth

LMs using SST and $T_{Diff.}$ as predictors explained between 32% (based on interviews; LM1) and 44% (based on at-sea observer data, LM2) of the total variance in the data set (Tab. 1). Linear and polynomial terms of SST as well as the linear term for $T_{Diff.}$ were highly significant ($p < 0.001$). The effect of the SST on catch depth followed an optimum curve (Fig. 3A) with the shallowest catch depths of 6.0 m and 4.7 m occurring during medium SSTs of 13.3 °C and 12.7 °C for LM1 and LM2, respectively. In both models $T_{Diff.}$ was positively and linearly related to catch depth, indicating that catch depth increased as long as SST exceeded SBT, and decreased when SBT exceeded SST (Fig. 3B). A z-test revealed no significant differences between parameter coefficients of LM1 and LM2 (Tab. 1).

Table 1. Parameter estimates and significance levels for the final models (LM – Linear model). LM1 – interview model, LM2 – at-sea observer model, LM3 – at-sea observer model including mesh size category. $\beta 1$ – linear SST effect, $\beta 2$ – polynomial SST effect, $\beta 3$ – linear T_{Diff} effect, Mesh 110-119 mm – effect of mesh size category 110-119 mm, SE – standard errors, p-value – significance level; z- and p-values derived for the comparison of LM1 and LM2; adjusted explained variance (R^2) for all LMs.

	LM1			LM2			Comparison of LM1 and LM2		LM3		
Parameter	Estimate	SE	p-value	Estimate	SE	p-value	z-value	p-value	Estimate	SE	p-value
Intercept	22.98	0.91	0.00***	25.14	1.68	0.00***	1.13	0.87	24.11	1.56	0.00***
$\beta 1$	-2.55	0.22	0.00***	-3.21	0.38	0.00***	-1.52	0.06	-2.73	0.36	0.00***
$\beta 2$	0.1	0.01	0.00***	0.13	0.02	0.00***	1.5	0.07	0.11	0.02	0.00***
$\beta 3$	0.67	0.12	0.00***	0.8	0.17	0.00***	0.62	0.27	0.58	0.16	0.00***
Mesh 110-119 mm									-3.9	0.89	0.00***
Adjusted R^2	0.32			0.44					0.53		

significance codes: $p < 0.05$ – *; $p < 0.01$ – **; $p < 0.001$ – ***

3.3. Effect of mesh size on catch depth

Similarly to LM1 and LM2, the effects of SST and $T_{Diff.}$ in LM 3 showed a hump-shaped and positive linear relationship with catch depth, respectively; both were highly significant ($p < 0.001$).

Model performance of the at-sea observer model was improved when accounting for mesh size as an additional predictor and explained 53% of total variance (Tab. 1). The significant effect of the factor mesh size demonstrated that nets with smaller mesh sizes (110-119 mm) were set shallower (on average in 3.9 m) compared to gillnets with larger mesh sizes (120-240 mm) (Fig. 3C and 3D). The median length of individuals caught with smaller mesh sizes was smaller (46.5 cm) and individuals caught with larger mesh sizes were larger (53.5 cm; Wilcoxon rank-sum test, $p < 0.001$; supplementary material figure S2).

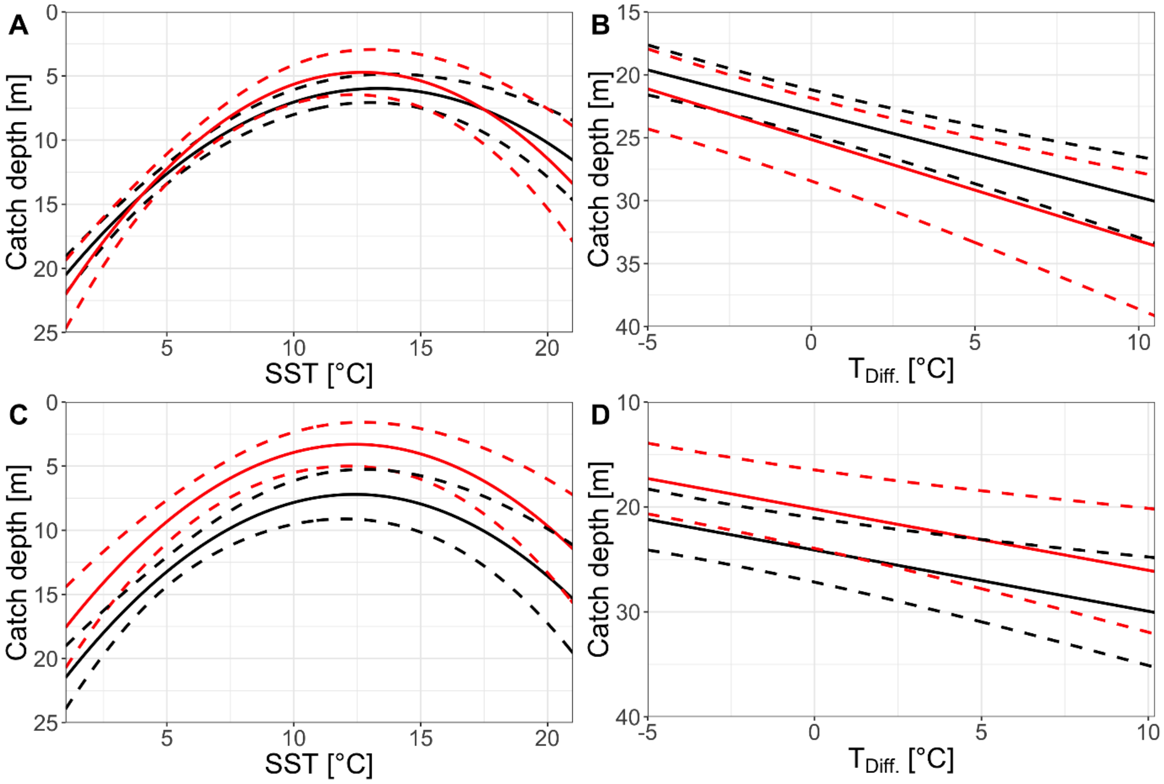

Figure 3. Statistical models of catch depth of cod. Partial dependence plots show the mean effects (solid lines) and 95% confidence intervals (dashed lines) for linear regression models LM1 (A and B; black lines), LM2 (A and B red lines) and LM3 (C and D; red lines – mesh size category 110-119 mm, black lines – mesh size category 120-240 mm); SST – sea surface temperature, $T_{\text{Diff.}}$ – stratification index.

3.4. Seasonal variability in habitat use

The main habitat type which gillnetters used for setting their nets was hard ground (RHU varying between 63% and 93%) (Fig. 4). Mussel beds were also used during the whole year, but only with an RHU ranging between 3% and10%. Seagrass meadows were used in spring and especially towards the end of the year (RHU with a maximum of 30%). Sand, mud and wrecks were only used occasionally and only to low degrees.

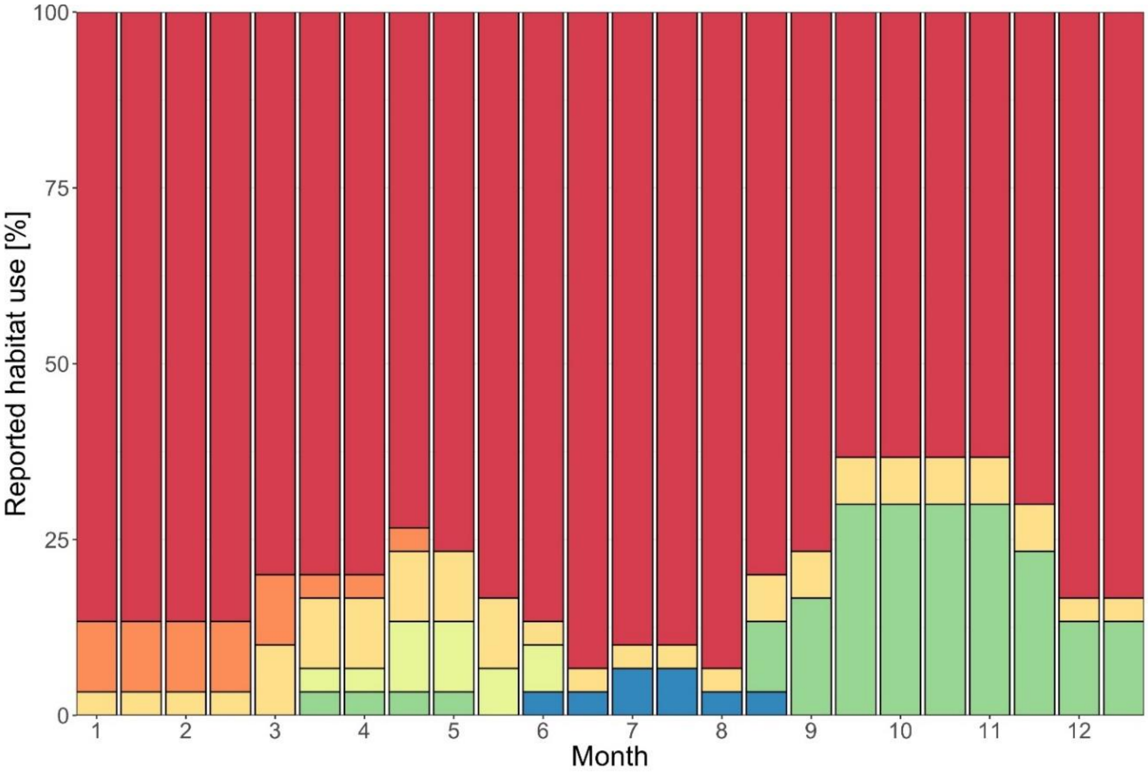

Figure 4. Seasonal variability in habitat use reported by 16 gillnet fishers per half-month period. Colours indicate habitat types (red – hard ground, orange – mud, yellow – mussel beds, light green – sand, green – seagrass, blue – wrecks).

3.5. Effects of SST and catch depth on habitat use

The multinomial log-linear model displayed a significantly better performance compared to the null model (McFadden pseudo $R^2 = 0.26$). Predicted probabilities for the use of hard ground as habitat type for fishing showed an increasing trend with increasing catch depth. In general, predicted probability for selection of hard ground was highest, except for catch depths < 5 m, for which a preference for sand and seagrass was predicted (Fig. 5). Probabilities for sand and seagrass showed a strong decrease with increasing catch depth. Moreover, probabilities for fishing on sand showed a strong decrease with increasing SST (Fig. 5F). Probabilities for a selection of mussel beds were highest at medium catch depths between 5 and 10 m (Fig. 5). The probability for wrecks and mud increased with increasing catch depth. Moreover, the probability of fishing on mud was found to increase with decreasing SST, in contrast the probability of fishing on wrecks increased with increasing SST (Fig. 5A, E).

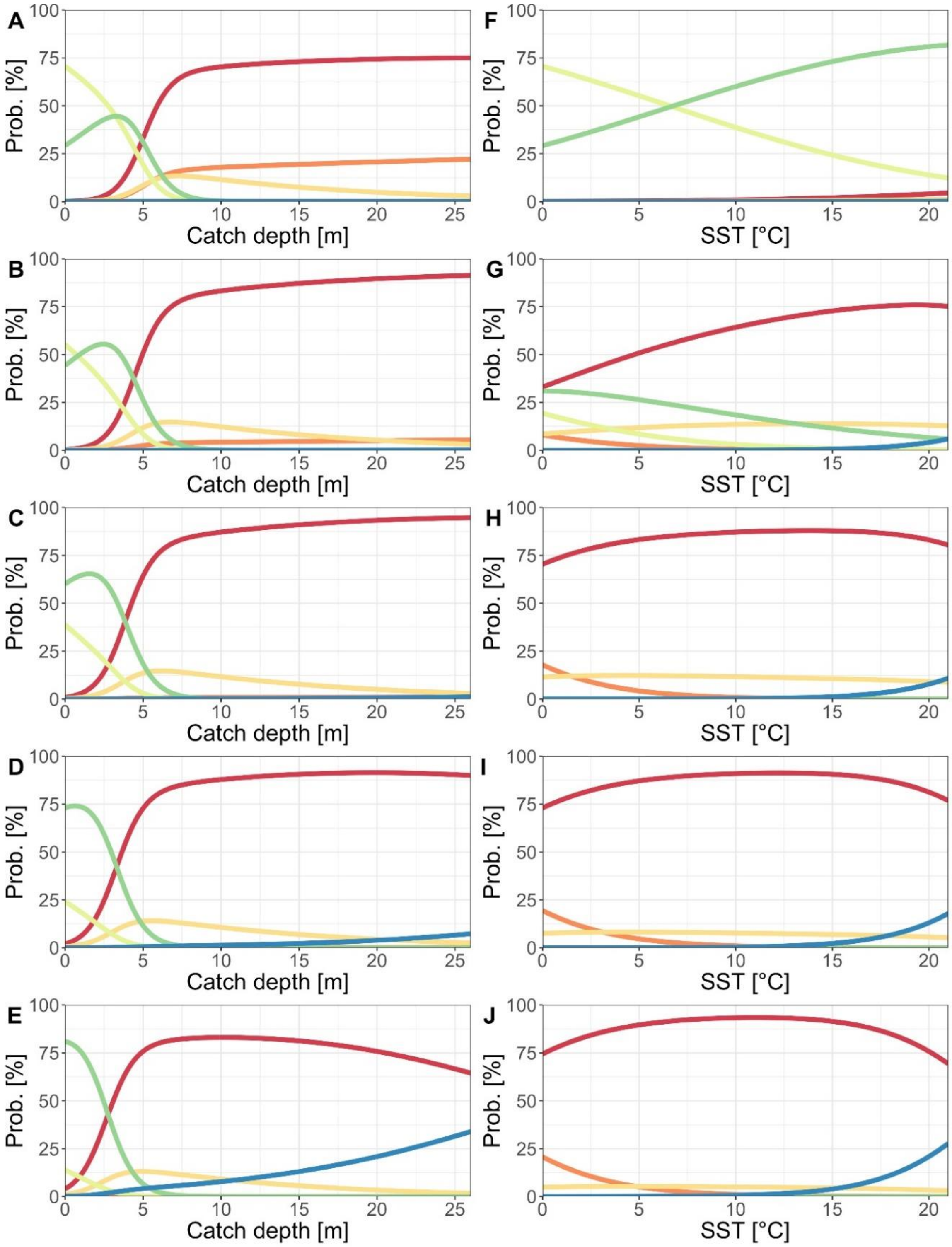

Figure 5. Statistical models of habitat use of Western Baltic cod. Plots show the partial effects of catch depth (left plots) and SST (right plots) on relative probabilities (Prob. [%]) of habitat type selection by gillnet fishers predicted using multinomial log-linear modelling; same colour code of habitat types as in Fig.4; A to E – SST set constant to 0, 5, 10, 15 and 20 °C, respectively; F to J – catch depth set constant to 0, 5, 10, 15 and 20 m, respectively.

Table 2. Parameter estimates and significance levels for the final multinomial logistic regression model. Reference habitat type: hard ground. SE – Standard Error, p-value – significance level.

Habitat type	Parameter	Estimate	SE	p-value
Mud	Intercept	-1.46	1.18	0.22
	Catch depth [m]	0.01	0.06	0.87
	SST [°C]	-0.32	0.12	0.01**
Mussel beds	Intercept	-0.9	0.56	0.11
	Catch depth [m]	-0.09	0.03	0.01*
	SST [°C]	-0.02	0.03	0.54
Sand	Intercept	6.26	2.45	0.01*
	Catch depth [m]	-1.36	0.43	0.00**
	SST [°C]	-0.25	0.11	0.03*
Seagrass	Intercept	5.38	1.26	0.00***
	Catch depth [m]	-1.09	0.2	0.00***
	SST [°C]	-0.12	0.06	0.04*
Wrecks	Intercept	-10.91	3.18	0.00***
	Catch depth [m]	0.11	0.06	0.07.
	SST [°C]	0.37	0.18	0.04*

significance code: p < 0.1 –., p < 0.05 – *, p < 0.01 – **, p < 0.001 – ***

4. Discussion

Applying local knowledge of fishers in environmental management questions has gained increasing research interest in recent years, and several studies have demonstrated how it can help to improve management decisions (Bergmann et al., 2004; Yates, 2014; Stephenson et al., 2016). We have demonstrated that a combination of commercial gillnet fishers' knowledge derived from interviews and gillnet trips sampled by at-sea observers can be used to gain a profound understanding of the small-scale depth and habitat use patterns of cod in the Western Baltic Sea. Our results suggest that both depth and habitat use are closely related to SST and stratification. Our results also highlight the importance of shallow-water and hard ground habitats in the life cycle of adult cod in the region.

4.1. Variables determining depth and habitat use of cod

Temperature is often considered a key factor affecting the large-scale distribution of Atlantic cod (Drinkwater, 2005). However, studies focusing on the effect of temperature on the depth distribution of cod on small spatial and temporal scales are rare. Tagging studies are an exception to this but are costly and strongly depend on recaptures (e.g. Lawson and Rose, 2000; Pálsson and Thorsteinsson, 2003; Neuenfeldt et al., 2007) or stationary behaviour (Freitas et al., 2015; 2016). Using local knowledge of fishers, we found a hump-shaped effect of SST on the depth use of cod in the WBS, showing the shallowest distribution at SSTs between 12-14 °C. The results indicate that cod move upslope to shallow waters when SST approaches the peak (at 12 or 14 °C), and downslope towards deeper habitats when SST moves apart from the peak. Furthermore, in our data it was evident that stratification dynamics play a significant role in explaining the depth distribution of cod in SD22. Our results indicate that cod use deeper areas as summer approaches and when there is increasing temperature stratification in the water column. Under mixed conditions, our results indicate that shallow-water habitats are preferred. Interestingly, recent studies using acoustic telemetry in a South Norwegian fjord revealed a similar temperature-driven behavioural pattern where cod tended to reside at shallow and structured habitats and moved deeper when ambient temperatures exceeded a threshold around 16 °C (Freitas et al., 2015, 2016).

The results of our study also suggest potential size-related differences in depth use of cod. We found that gillnets with smaller mesh sizes were set in shallower waters than gillnets with larger mesh sizes. Since fishers reported that selection of mesh sizes was positively related to the expected fish sizes at the fishing grounds (Interviewee 1, pers. comm.), we hypothesize that larger cod use deeper waters than smaller conspecifics because deeper waters usually have lower water temperatures. Several laboratory studies have demonstrated negative correlations between optimal water temperature and body size in cod (Lafrance et al., 2005; Björnsson et al., 2007; Pauly, 2010). Hence, the size-related differences in depth use we found here may be explained by ontogenetic differences in thermal preferences. This difference might be intensified by the fact that smaller cod have been found to display more pronounced diurnal movements towards shallower waters than larger individuals (Olsen et al., 2012; Freitas et al., 2015).

We also found habitat selection of gillnet fishers to depend on SST and reported catch depth of cod. Interviewed fishers tended to encounter cod above structured habitat types such as hard ground, seagrass and wrecks (in deeper areas during high SSTs in peak summer). From this, we conclude that cod tend to favour those structured habitat types. These structured habitat types simultaneously provide both shelter and resting sites (Gregory and Anderson, 1997; Hemminga and Duarte 2000; Reubens et al., 2013) and high faunal abundances and thus enhanced food supply for cod (Bell and Pollard, 1989; Kristensen et al., 2017).

The relationship between habitat type and depth use can be explained by a depth-specific availability of each habitat type. For example, seagrass is described to occur only in depths between one to six metres in the Baltic Sea (Boström, 2003). In areas deeper than 15 m, hard ground is also less available and hence artificial reefs are of particular interest for cod when using greater depths. We expect that habitat selection of cod outside the spawning season serves three main purposes, namely: maximization of food supply; shelter; and, thermoregulation (Mehner, 2012; Freitas et al., 2016). In contrast, during spawning time in winter cod were also caught on muddy habitats in the deeper basins and channels of the WBS. These deeper areas offer little food and shelter but provide the highest salinities, which are important for egg fertilization and egg buoyancy (Nissling and Westin, 1997; Petereit et al., 2014).

It should be noted that our study has caveats regarding the data and information used in our analysis. A primary caveat is that the catch depth derived from gillnet fishers and at-sea observers does not necessarily include the endpoints of the daily movements. Most of the nets are set over-night in locations where cod are expected to pass at dusk and dawn during their diel feeding movements connecting deeper daytime resting with shallower night-time feeding sites (Zarkeschwari, 1977; Pihl, 1982; Burrows et al., 1994). Hence, cod may have used even shallower waters when caught in shallow water. In contrast, from January to March our catch depths are likely to be underestimated. Gillnet fishers indicated that in winter they would set their gillnets even deeper than reported, but trawling activities in areas > 20 m render this a poor strategy, potentially leading to damage or loss of their gear (Interviewee 1, pers. comm.). Another potential caveat results from our sampling design. We obtained our data from interviews with local fishers and observer logs. Both data sets involved a group of fishers which almost all had a formal or informal long-term relationship with scientists and observers of the Thuenen-OF. The data of this group of fishers is therefore not necessarily representative for the entire gillnet fishery fleet in SD22. However, it was not the aim of the study to provide detailed controlled, or representative data about the fishing behaviour of the entire gillnet fishery fleet in the study area. Rather, the study aimed to derive new insights about the seasonal depth and habitat use of cod in SD22 on the basis of the local fishers' experience with targeting and encountering cod. Intentionally, these new insights should help to identify weaknesses in the current BITS survey design. Further, the combination of the gained knowledge from the fishers and the data derived from traditional scientific surveys and from literature may contribute to a better understanding of the spatio-temporal distribution of cod in the area.

4.2. Seasonal cycle of depth and habitat use

Our results on distribution patterns using the local knowledge of fishers allowed us to derive a conceptual model of the seasonal depth and habitat use of Western Baltic cod (Fig. 6). We found that phases of deeper and shallower habitat use alternated according to season. Deeper habitats were mainly used from winter to spring during pre-spawning and spawning periods (*Phase 1*), and during an aestivation period in summer (*Phase 3*). Shallow-water habitats were used after spawning (*Phase* 2), and in autumn, presumably for building up and refilling energy reserves (*Phase 4*).

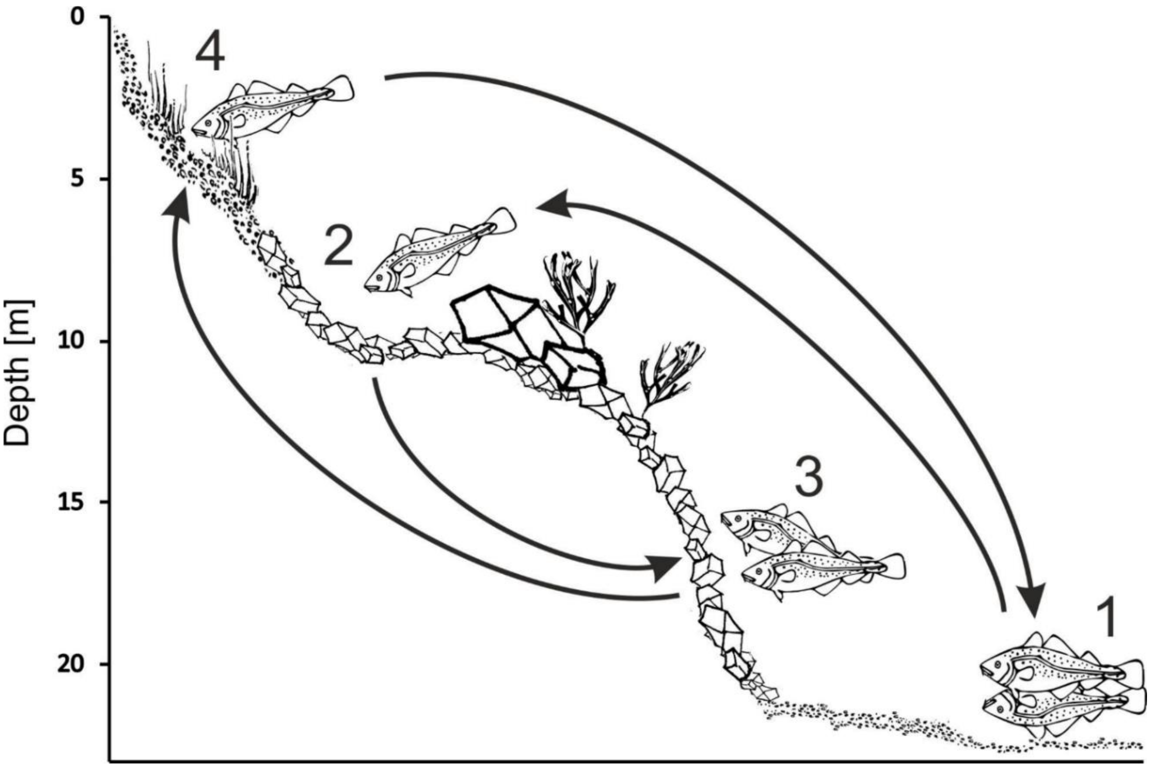

Figure 6. Conceptual model of seasonal changes in depth and habitat use of adult cod in the Western Baltic: phase 1 – pre-spawning and spawning period in deeper waters; phase 2 – post-spawning period in shallower waters; phase 3 – aestivation period during summer in deeper waters; phase 4 – period of shallow water use. Seafloor structures indicate habitat types often used by cod during each phase and depth: in shallow waters down to 6 m depth – seagrass meadows, in medium depth – hard ground, and in the deep channels > 20 m depth – mud.

Phase 1 (January to April) coincides with the pre-spawning and spawning time of cod in the Western Baltic Sea (Bleil and Oeberst, 1997; Bleil et al., 2009). At this time of the year cod use deeper, more saline waters, which often are also slightly warmer waters, likely maximizing food availability, temperature preferences and egg development. The downslope movement of cod towards the spawning grounds presumably depends on the ripening process of the gonads. Cod seem to use hard ground at intermediate depths during the pre-spawning period and enter the deeper basins and channels only for spawning. Visiting deeper, more saline areas to spawn coincides with the seasonal cycles of mobile epifauna such as small demersal fish, caridean shrimps and brachyuran crabs, which are known to be important prey organisms for coastal cod (Zarkeschwari, 1977; Pihl, 1982; Hop et al., 1992). These mobile epifauna leave shallow-water areas with decreasing water temperatures in late autumn and winter (Pihl and Rosenberg, 1982) to use deeper areas. Thus, the movement of cod towards deeper, warmer areas may also follow changes in food availability. Moreover, cod may select deeper, warmer water during pre-spawning time because the warmer water positively affects gonadal maturation (Cote et al., 2004). Most importantly, higher salinities in the deeper area provide appropriate environmental conditions for egg fertilization and buoyancy during and after spawning (Nissling and Westin, 1997; Petereit et al., 2014).

The observed variability in catch depth and depth use of cod during the spawning time is likely related to spawning behaviour. Males tend to spawn during the entire season while females only gradually enter the spawning grounds, leaving soon after releasing their eggs (Morgan and Trippel, 1996). Thus, a large proportion of the mature individuals caught in shallower areas during spawning time most likely are pre-spawning or returning post-spawning females. Furthermore, immature fish tend to stay in shallower waters during the spawning season as described for two- to three-year-old Atlantic cod in coastal areas of Newfoundland (Cote et al., 2004).

In *Phase 2* between April and June, when SST and stratification increase rapidly, Western Baltic cod tend to use waters shallower than 10 m. This shallow distribution may be linked to increasing availability of mobile epifauna during spring warming (Pihl and Rosenberg, 1982) and refilling of energy reserves after spawning. *Phase 2* ends when SST in shallow areas exceeds the 12 to 14 °C optimum, likely forcing cod to move downslope into the deeper waters which more closely match their optimal temperature range.

In *Phase 3* cod further retreat towards deeper areas in response to rising SST and stratification in summer. However, the downslope movement of cod is limited by hypoxic areas forming in the deeper basins and channels during summer. This is similar to the hypoxic zones restricting downslope movements of cod in a Norwegian fjord (Freitas et al., 2015, 2016). In contrast, the mobile epifauna, their main prey, moves in the opposite direction towards warmer shallow-water areas (Pihl and Rosenberg, 1982). Thus, shallow-water use is a trade-off between thermal tolerance limits and high food availability in shallow coastal waters (Freitas et al., 2016). Cod is likely food-limited during the peak summer period. Moreover, this phase is likely an aestivation period for cod with decreased activity or even a period with down-regulated metabolism processes such as observed for the freshwater gadoid *Lota lota* under unfavourable high temperature summer conditions (Hardewig et al., 2004). During peak summer fishers report to fish on low-activity aggregations of cod by setting the gillnets very close to each other to increase the probability of entanglement during this period of reduced activity and movement of cod. In some cases, gillnets are even set criss-crossing each other, a fishery called “point fishery” (Interviewee 1, pers. comm.). These peak summer aggregations are also targeted by anglers (S. Funk, pers. obs.; H.V. Strehlow, pers. comm.) and trawlers with specialized gear (pers. comm. with trawl fishers by U. Krumme). This observation strongly suggests a reduced activity of cod between the second half of June and the beginning of September where the fish use deeper areas. Furthermore, this is in line with the slight decrease in the magnitude of diel vertical movements of cod under thermal stratification observed by Freitas et al. (2015) in a Norwegian fjord.

It is noteworthy that strong wind events during the peak summer period can cause local disturbance of the thermal stratification resulting in temporary temperature drops close to the coast (local upwelling) which result in opportunistic changes in cod distribution. Cod apparently quickly take advantage of windows of opportunity and temporarily enter the shallow habitats to feed (Freitas et al., 2015, 2016). This opportunistic behaviour of cod has been witnessed by fishers, who reported high cod abundance in very shallow water during peak summer after strong wind intervals (Interviewee 2, pers. comm.).

In *Phase 4*, with temperatures decreasing and thermal stratification weakening in September, cod are again able to use the highly productive shallow-water habitats for feeding, particularly in October and November. During this period consumption of cod is likely high, enabling individuals to recover from aestivation and to build up energy reserves for the winter and to prepare for the next spawning season. With a further decrease in SST ambient temperatures fall below the metabolic optimum and cod start to move downslope entering again into *Phase 1*.

4.3. Conclusion

Our study demonstrates how local knowledge of fishers can provide a unique data source to develop a thorough understanding of the distributional dynamics of an important marine resource population. By using local knowledge of gillnet fishers, we were able to document how depth and habitat use of cod in the WBS are closely related to SST and stratification. Our results highlight the importance of shallow-water and hard ground habitats in the seasonal life cycle of adult cod in the region (area SD22). This new knowledge on depth and habitat use calls for an improved consideration of shallow-water areas and habitat types, e.g. in the design of monitoring surveys for Western Baltic cod.

Our results showing water temperature-related distributional changes in habitat use raise serious concerns about an existing bias in the catchability of the standard trawl survey data (BITS) collected each first and fourth quarter and used in the stock assessment of Western Baltic cod. When cod tend to use shallower habitats in the fourth quarter, the trawl survey catchability is probably much lower (underestimation of true abundances) than in the first quarter when cod is aggregated at the spawning grounds (overestimation of true abundances). This may be exacerbated if the shallow-water proportion of the population not covered by the survey is not constant, but differs in a non-systematic way with regards to age groups, sex or fish weights between quarters or years. In the future possible intra- and interannual differences in cod habitat use and related survey catchability as well as resulting problems in usability of survey indices for stock assessment may become even more pronounced given the prospects of global warming. Hence, improvements of the present survey and exploration of alternative or supplementary survey approaches may be advisable.

This study implies, that fisheries scientists may currently miss an important part of the picture needed for a thorough understanding of the ecology of cod in the Belt Sea, by not working closely together with local fishers. One efficient way to advance our knowledge on the ecology of target species, but also to improve the design of scientific fishery surveys, could therefore be to focus more on comprehensive interviews and questionnaires with local fishers on a regular basis. Eventually, this sort of methodological improvement could be completed through more collaborative efforts by commercial fishers, scientists and managers.

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Supplementary material

Supplementary material S1. Description of the informed consent.

The following was verbally communicated to the fishers selected for an interview (face-to-face in the harbour as well as on the phone) prior to the interview. For the sake of this publication, the description of the informed consent (“Erläuterungen zur informierten Einwilligung”) was translated from German into English by the authors.

Participation: Taking part in the interview is voluntary. Interviewees may refuse to take part in the research or exit the research at any time without penalty. Participants are free to decline answers on any particular question they do not wish to answer.

Benefits and Risks: The participants will receive no direct financial benefits from the research study. There are no foreseeable risks involved in participating in the study other than those encountered in day-to-day life. However, their responses may help to improve the ecological understanding of depth and habitat use of Western Baltic cod in the region, which might affect scientific research actions or stock management in the future.

Confidentiality: Participants are kindly asked to respond to the questions, which will be written down on a recording form. The information written down by the researchers during the interviews on the recording form can be inspected by the respective participant at any time upon request. Recording forms are stored at the Institute of Marine Ecosystem and Fisheries Science at the University of Hamburg. For further analysis of the data concerning the depth and habitat use of fish, answers of the fishers will be completely anonymized, keeping only information on the respective home-port of the participant and the responses to habitat and depth use. Hence, no one will be able to identify the participants via their answers. The data from the study will be analysed to infer qualitative information on depth and habitat use of cod in the study area. This information will be used for a student’s thesis (University of Hamburg) and a possible subsequent publication.

Interview consent and anonymity: Participants are asked to give verbal consent in terms of the informed consent prior to the interviews. If the participants take part in the survey, they have to know that they are no longer anonymous to the researcher, however no names or identifying information will be included in the study (or, if the scientists wish to quote statements with the name of a particular fisher, they must first obtain the agreement of the respective participant). Participants may withdraw consent to participate in this study at any point. Should the participants choose to withdraw their consent, the researchers will delete all data collected from them.

Contact and follow-up information: There are no foreseen follow-up meetings or presentations for the participants to keep them informed about the progress of the study, the data analysis or the results. However, participants are invited to ask about the progress of the study at any time actively by contacting responsible researchers at the Thünen Institute of Baltic Sea Fisheries (Uwe Krumme) or at the Institute of Marine Ecosystem and Fisheries Science at the University of Hamburg (Steffen Funk).

If the participants feel that they have not been treated according to the content of this form, or that their rights as a participant in research have not been honoured during the course of the study, or they have additional questions, concerns or complaints that they wish to address to someone other than the investigators, they may contact the coordinator of this study, Uwe Krumme (Thünen-Institute of Baltic Sea Fisheries).

Supplementary material S2. Questionnaire and recording form.

Questionnaire on passive cod fishery in the Western Baltic Sea

1. ***Where** do you fish **when** for cod? Please provide half monthly information on the catch depth (in metres) you select for targeted cod fishery in the Belt Sea.*

2. *Which ground structures (habitat types) do you select for targeting cod over the course of the year. Please name one or more habitat types (choose from the list or add other habitat types) you typically select for targeted cod fishery on a half monthly basis.*

Habitat types
Hard ground (cobbles, boulders, gravel, rocky reef structures, stone fields)
Mud
Mussel beds
Sand
Seagrass meadows
Wrecks

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	January		February		March		April		May		June	
Selected catch depth [m]												
Habitat type												
Gear (GNS/GTR)												
Distance to the shore												
Soaking time												
Net length and number of nets												
Mesh size *(diagonal between knots)*												
Additional information												

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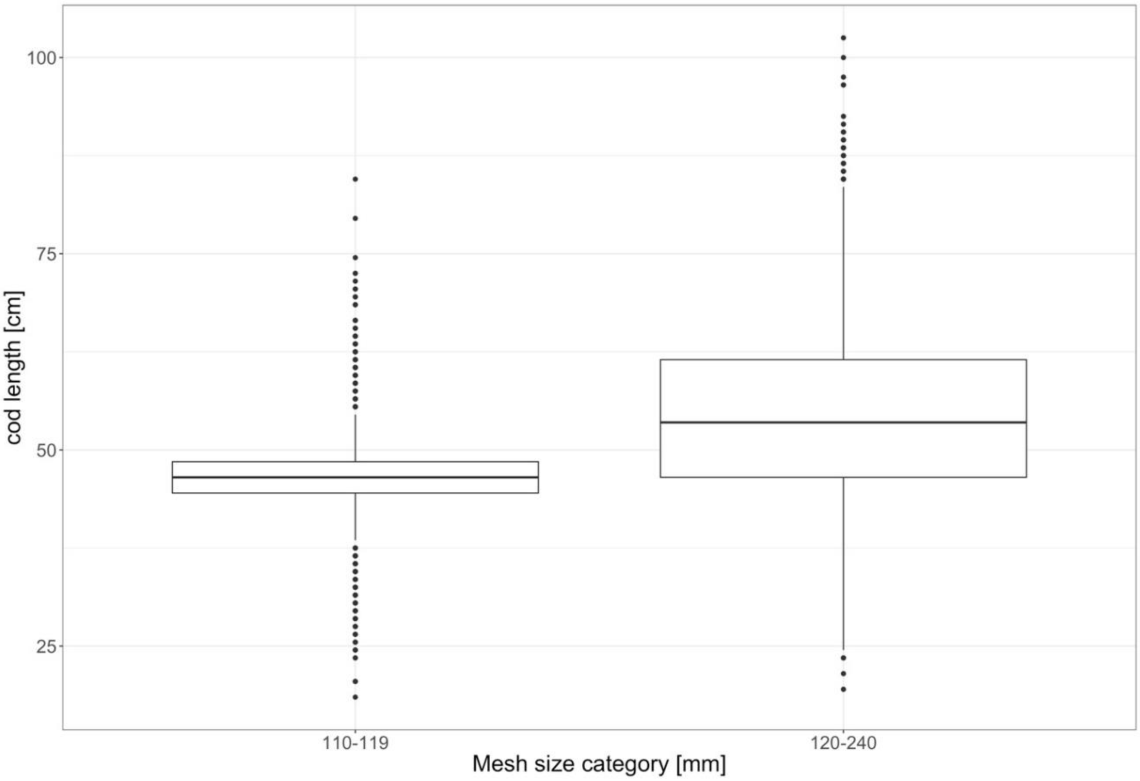
	July		August		September		October		November		December	
Selected catch depth [m]												
Habitat type												
Gear (GNS/GTR)												
Distance to the shore												
Soaking time												
Net length and number of nets												
Mesh size *(diagonal between knots)*												
Additional information												

Supplementary table S1. Parameter estimates and significance levels for established generalized additive models (GAM) with chosen k of 3. GAM1 – interview model, GAM2 – at-sea observer model, GAM3 – at-sea observer model including mesh size as categorical variable. s(SST) – smoothing term on sea surface temperature, s(T_{Diff}) – smoothing term on T_{Diff}, mesh size 110-119 mm - effect of factor mesh size category 110-119 mm, SE – standard errors, p-value – significance level; edf – effective degrees of freedom of the smooth term; adjusted explained variance (R^2) for all GAMs.

	GAM1			GAM2			GAM3		
Parameter	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	11.84	0.28	0.00***	11.24	0.41	0.00***	12.45	0.46	0.00***
mesh size 110-119 mm							-3.94	0.88	0.00***
smoothing terms	edf	p-value		edf	p-value		edf	p-value	
s(SST)	1.97	0.00***		1.98	0.00***		1.99	0.00***	
s($T_{Diff.}$)	1.79	0.00***		1	0.00***		1.27	0.00**	
adjusted R^2	0.33			0.45			0.55		

significance codes: $p < 0.05$ – *; $p < 0.01$ – **; $p < 0.001$ – ***

Supplementary figure S1. Seasonal development of mean half-monthly SST (blue) and SBT (red) between 2011 and 2016 in the western Baltic Sea.



Supplementary figure S2. Boxplots showing the size distribution of cod in two mesh size categories (left: 110-119 mm; n = 4674 measured fish; right: 120-240 mm: n = 6224 measured fish) from 97 at-sea observer trips conducted between 2011 and 2016

Chapter II

Patterns in seasonal and depth-specific food intake of adult cod (*Gadus morhua*) in the Western Baltic Sea

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Abstract

Stomach content collections are a foundation for food-web studies and multi-species models. However, the spatio-temporal sampling coverage is usually restricted to scientific trawl surveys, often not covering the full distributional range of the target species during short survey periods. We present a study on the diet composition of Western Baltic cod (WBC) with 3150 stomachs sampled year-round between 2016 and 2017 using angling, commercial gillnets, commercial trawling and research surveys to enhance spatio-temporal coverage. Statistical modelling revealed significant relationships between diet composition, catch depth, fish length and season. Cod diet composition in shallow areas (< 20 m depth) was dominated by benthic invertebrate species, mainly the common shore crab *Carcinus maenas*. Generalized additive modelling identified a negative relationship between catch depth and stomach content weight, which suggests reduced food intake in winter when cod use deeper areas during spawning time and during peak summer when cod tend to avoid high water temperatures. Our results highlight the importance of shallow areas as major feeding habitats of adult cod in the Western Baltic Sea, which were previously neglected. Compared to cod diet data from the 1960s and 1980s restricted to trawlable areas (mostly > 20 m depth), herring had only a minor contribution and round goby occurred as a new prey species. Our results strongly suggest that previous trawl surveys severely overestimated the role of forage fish and underestimated the role of invertebrate prey. Overall the previous perception, that WBC is mainly a piscivorous predator, seems no longer valid.

1. Introduction

Fisheries management is still mostly based on single species models, though multi-species and ecosystem-based management approaches gain more and more importance in fisheries science and are increasingly implemented. A high variety of different multi-species modelling approaches were developed in the last decades such as: multi-species virtual population analyses (e.g. Horbowy, 1989; Neuenfeldt and Köster, 2000), multivariate autoregressive models (e.g. Lindegren et al., 2010), dynamic models (Heikinheimo, 2011), physiological structured models (e.g. for the Baltic Sea: Van Leeuwen et al., 2008), Ecosim with Ecopath models (e.g. Harvey et al., 2003; Tomczak et al., 2012) or spatially disaggregated models (Lindegren et al., 2014). One major aspect in all these approaches is the linkage between species of different trophic levels in an ecosystem, which is based on predator-prey interactions. Such information is traditionally derived from stomach data bases. However, these and even new modelling approaches (e.g. Stäbler et al., 2019) are often based on information derived from historic stomach sampling projects dating back decades, such as from the “year of the stomach” in 1991 in the North Sea. Despite recent changes in many coastal-marine ecosystems (e.g. Sala et al., 2004; Byrnes et al., 2007; Norkko et al., 2007), efforts for new stomach sampling projects are scarce. Hence, the reliability and quality of many model outputs may be limited because the old stomach data may be outdated and potentially biased due to incomplete sampling designs conducted during those times.

Unlike the North Sea, the Baltic Sea has experienced stomach samplings on a relatively regular basis, at least with regard to the commercially most important demersal fish species cod (*Gadus morhua*) (e.g. Arntz, 1974, 1977; Zarkeschwari, 1978; Schulz, 1987, 1988, 1989a, 1989b; Weber and Damm, 1991; Hüssy et al., 1997; Dziaduch, 2011; Pachur and Horbowy, 2013; Casini et al., 2016). Cod is considered the apex predator in the Baltic Sea and major efforts were invested to improve the understanding of the trophic role of cod in the temperate estuarine food webs of the Baltic Sea.

In the Baltic Sea area, two cod stocks are distinguished in fisheries management, the Western and the Eastern Baltic cod stock, which display differences in genotype, phenotype and life history traits (Sick, 1965; Berner and Vaske, 1985; Nielsen et al., 2003; Bleil and Oeberst, 2005; Paul et al., 2013, Hüssy et al., 2016; Weist et al., 2019). The management assumes that Western Baltic cod (WBC) uses the shallower basins in the west (i.e. in the Belt Sea, in the Sound and in the Arkona Sea) while the Eastern Baltic cod (EBC) mainly uses the deeper basins in the east such as the Bornholm and the Gdansk basin. These basins differ remarkedly in hydrological conditions. However, in the last decades the diet studies mainly focussed on the role of EBC in the eastern Baltic food web (e.g. Hüssy et al., 1997; Dziaduch, 2011; Pachur and Horbowy, 2013; Casini et al., 2016). These studies showed for example that EBC relies currently strongly on clupeid prey species such as central Baltic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), while benthic invertebrates such as the giant isopod (*Saduria entomon*) play only a minor, though likely an important role in the overall food intake of EBC (Røjbek et al., 2014; Casini et al., 2016; Neuenfeldt et al., 2019).

The only available studies focussing on the feeding ecology of cod in the Western Baltic Sea originated from stomach samplings between the 1960s and 1980s (Arntz, 1974, 1977; Zarkeschwari, 1978; Schulz, 1987, 1988, 1989a, 1989b; Weber and Damm, 1991). These data are most likely not representing the current ecological situation due to substantial changes of the hydrographic and ecological conditions of the Baltic Sea in the last decades (Möllmann et al., 2009; Mohrholz et al., 2015). It is likely that concurrent to these ecological changes also prey availability of cod changed since the 1980s. For example, Western Baltic spring spawning herring, which was one of the main prey species of WBC in the historic diet studies, showed a steady decline in spawning stock biomass since the 1990s

(ICES, 2019c) and thus, might be less available as prey for WBC. Moreover, new invasive species, such as the round goby (*Neogobius melanostomus*), established in the Western Baltic Sea (unpublished data cited in Corkum et al., 2004; Hempel, 2017; Oesterwind et al., 2017) and may provide a new potential prey species for WBC similar to recent observations for EBC (Pachur and Horbowy, 2013).

Besides, the spatial coverage of stomach samples from the historical data bases both in the Eastern and in the Western Baltic Sea is limited due to the fact that shallower regions (< 20 m depths) were heavily underrepresented in the stomach sampling designs. Most stomach samplings in the Western Baltic Sea were conducted during scientific trawl surveys using standardized otter trawl gear. In the Western Baltic Sea shallower areas are often characterised by hard bottom structures, such as gravel, cobbles, boulders, and rocky reef structures and thus, pose a high risk of damaging the fishing gear. Therefore, scientific trawling and related stomach sampling was and still is severely limited to known trawlable sites (i.e. mostly soft bottom structures in depths > 20 m), while areas shallower than 20 m are largely neglected, despite the fact that they account for 60% of the total area in the Western Baltic Sea (i.e. of the ICES subdivisions (SD) 22, 23 and 24) (ICES, 2017). Thus, most of the historic investigations were based on the untested assumption that the stomach samples from areas > 20 m depths are representative for the feeding habits of the whole cod stock in the Western Baltic Sea. A rare exception is the study of Zarkeschwari (1977) who sampled stomachs of juvenile cod during scientific trawling in coastal areas of the Kiel Bight at 5 m depths. He found clear differences in diet composition of juvenile cod from shallower areas compared to deeper areas. Moreover, he highlighted the role of shallow-water areas as important feeding habitats for juvenile cod. However, the role of shallow-water areas as feeding habitats for adult cod in the Western Baltic Sea is still unclear and information is restricted to areas > 20 m water depth. This is of even more concern because recently Funk et al. (unpublished), using interviews with gillnet fishers and at-sea observer data along the Baltic coast of Schleswig Holstein (Germany), revealed an intensive use of shallow-water habitats (≤ 10 m depths) by adult cod during spring and autumn. Given that shallower habitats were largely neglected in previous stomach samplings, the available diet data may be biased and provide only an incomplete picture on the actual dietary composition and habitat use of cod in the Western Baltic Sea.

Area and depth coverage in stomach sampling design may be significantly enhanced when also fishing methods other than standardized scientific trawling are considered, e.g. commercial samples and recreational fishing. Especially the use of passive gears, such as gillnets or fishing rods, enable year-round fishing on a variety of habitat types and at almost any water depth (Hamley, 1980), thus providing an efficient way to acquire stomach samples from previously undersampled cod habitats the Western Baltic Sea.

Here, we present a new investigation into the diet composition of adult cod in the Western Baltic Sea based on a national year-round stomach sampling campaign in SD22. Cod stomach samples were collected monthly between February 2016 and December 2017 using different gears (i.e. gillnets, otter trawl gear and fishing rods) and methods (i.e. commercial samples, scientific trawl surveys and angling) to enhance spatial and temporal coverage. We analysed (1) seasonal and depth-specific patterns in diet composition and food intake of cod and (2) compare the food compositions of cod between our current and the historic cod diet investigations in the Western Baltic Sea dating back to the 1960s. Finally, we assessed (3) the potential bias from a sampling neglecting that shallow-water areas are major feeding grounds for adult cod in the Western Baltic Sea.

2. Materials and methods

2.1. Study area

The study area was located in the Belt Sea, ICES SD22 (Fig. 1A). The Belt Sea is a stratified, brackish-water area (common salinity range: 10 to 25) in the temperate zone and forms together with the Sound (SD23) and the Arkona Sea (SD24) the Western Baltic Sea (WBS). SD22 is a relatively shallow area. Areas shallower than 20 m water depth amount to a total of 70% of the Belt Sea and areas shallower than 10 m water depth still cover 29% (Fig. 1B, ICES, 2017). The Belt Sea is microtidal (tidal range: ~ 10 cm) and characterized by continuous wind-induced fluctuations in hydrography (Leppäranta and Myrberg, 2000; Snoeijs-Leijonmalm and Andrén, 2017), mainly due to 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. SD22 is the distributional core area of the Western Baltic cod stock and mixing with Eastern Baltic cod (EBC) is considered negligible (ICES, 2019b), although recent findings of McQueen et al. (2019) suggest that some EBC may be resident in the Belt Sea. Since the late 1990s catches and spawning stock biomass of WBC are in constant decline (ICES, 2019a), which is likely due to overexploitation and the negative effects of regional warming on recruitment (Stiasny et al, 2018; Voss et al., 2019).

2.2. Stomach sampling

A total of 3350 cod stomachs were collected on 86 fishing trips in the Kiel Bight and Mecklenburg Bight, the two major basins within the Belt Sea (Fig. 1A), between February 2016 and December 2017 (Fig. 1B). We used stomach samples from scientific trawl surveys, commercial fishing (both trawls and gillnets) and angling to maximize depth, habitat and seasonal coverage (Supplementary material figure S1.1). A detailed description of the sampling methods and the processing of the samples is given in the Supplementary material (S1).

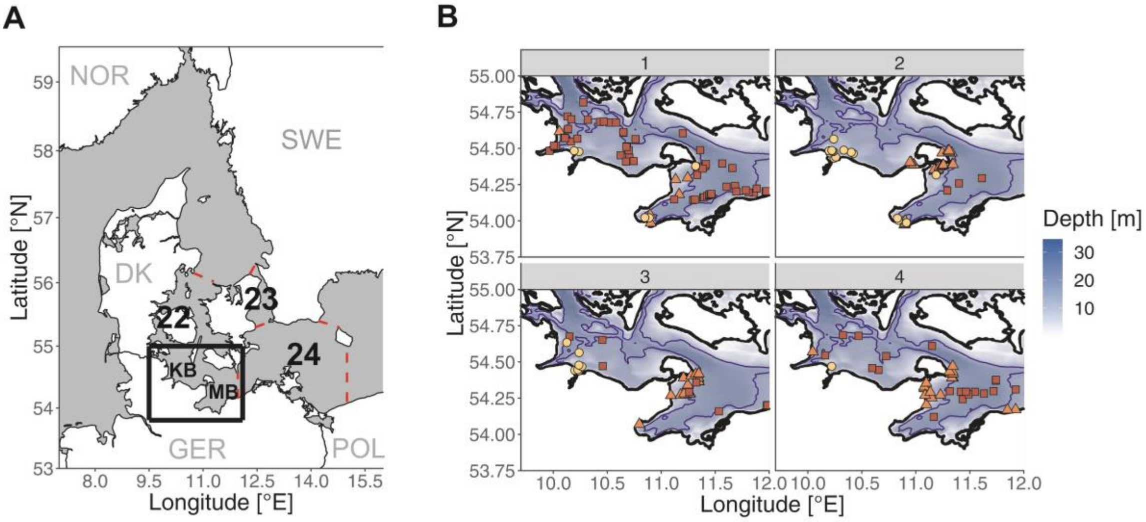

Figure 1. Overview map of the study area (A) and quarterly fishing locations of the different sampling methods used in the stomach sampling in 2016 and 2017 in the Belt Sea (B). Black numbers indicate ICES subdivisions of the Western Baltic Sea: 22 – Belt Sea, 23 – Sound, and 24 – Arkona Sea. Dashed red lines indicate subdivision borders. MB (Mecklenburg Bight) and KB (Kiel Bight) indicate the two major basins within the study area (black rectangle). Blue contour line in B indicates 20 m depth line. The different symbols indicate fishing positions per gear type: yellow dots – angling, orange triangles – gillnet, and red rectangles – trawling.

2.3. Size categories of cod

Length of cod sampled for stomach analysis ranged between 11 cm and 107 cm. The size ranges differed strongly between sampling methods. Since individuals < 31 cm (i.e. smaller than the minimum conservation reference size of 35 cm) were mostly caught only during the research trawl surveys, we decided to retain only individuals ≥ 31 cm (N = 2919) for further data analysis. For the investigation of size-dependent diet trends, we classified individuals into five length classes: 31-40 cm, 41-50 cm, 51-60 cm, 61-70 cm and ≥ 71 cm.

2.4. Stomach content analysis

Cod stomachs were analysed in the laboratory of the University of Hamburg. The samples were defrosted and adherent veins were carefully removed from the outer stomach tissue. Adherent water was removed for ~ 5 seconds with paper tissues and stomachs were weighted (accuracy: 0.001 g). Subsequently, stomachs were opened and the contents and mucus were thoroughly removed from them before the empty stomachs were again weighted.

Stomach content weights (W_{SC}) 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 peracarids), class level (e.g. for echinoderms, molluscs), or only to phylum level (e.g. for annelids). If the digestion of the prey was already progressed too far to allow identification to the levels described above, items were allocated to the categories unidentified fish, unidentified crustaceans or unidentified invertebrates. Prey organisms were categorized into three stages of digestion: 0 – intact prey with minimal signs of digestion (skin, fins or legs and flesh are complete); 1 – partly digested, and 2 – heavily digested (only bones, otoliths or shells and small amount of flesh left).

It should be noted that the shares of hard-shelled crustaceans, especially the share of common shore crab, in the diet of cod could be slightly overestimated compared to fish prey and especially compared to Annelid prey due to differences in the gastric evacuation time. In general, compared to fish prey, crustaceans show slower digestion due to the chitinous exoskeleton, while Polychaeta show a faster digestion than fish (Andersen et al., 2016; dos Santos and Jobling, 1995; Temming and Herrmann, 2003).

For each prey item the mass fraction (W_{Prey}) was determined (accuracy: 0.001 g). If entire prey organisms were found in the stomachs, the size of each item was measured. The weight of mucus was determined by calculating the difference of mass of W_{SC} and the sum of W_{Prey}.

2.5. Standardization of prey weights

Larger predators are able to eat larger and heavier prey organisms or simply more in total than smaller individuals. By calculating the mean diet composition of a length class, an unintended weighting of the stomach contents of larger predators may occur. We 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. Prey weights of each predator of a given length in a certain length class were standardized to the size of a medium-sized predator (i.e. geometrical mean length of the fish in a given length class). For this purpose, we used a weight-based standardization approach (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 $R^2 = 0.85$, $a = 8.32 * 10^{-6}$, $b = 3.69$).

$$W_{ES} = a * L_{Pred}{}^{b} \qquad (1)$$

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

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

$$W_{Prey(stand)i,j,k} = \frac{W_{Prey\ i,j,k} * a * GM_k{}^{b}}{a * L_{Pred\ j}{}^{b}} \qquad (2)$$

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

2.6. Comparison of stomach data derived from different fishing methods

To avoid bias in mean calculation and statistical modelling when combining data obtained by different sampling methods, we tested for differences in standardized stomach content weights of predators between different sampling methods (i.e. gillnetting, trawling and angling).

We decided to apply statistical tests for group comparisons of length-standardized stomach content weights per length class, 5 m-depth strata (0-5 m, 6-10 m, 11-15 m, 16-20 m, and ≥ 21 m), and month (pooled over both sampling years), if sample sizes per gear type were ≥ 10 (see supplementary material Table S2.2).

For 94% of cases where samples from two or more different fishing gears were available for the same cod length class, 5 m-depth strata and month, sample size was < 10 and thus these cases were not considered for statistical comparison. However, in four cases a statistical test could be applied (Tab. 1). Group comparisons between gillnet and trawl samples revealed no significant differences in median stomach content weights except for the length class 41-50 cm in July originating from the depth stratum 16-20 m, where significantly higher median stomach content weights were observed for the gillnet samples.

The stomach content weights of angling samples could only be compared once (length class 61-70 cm, July, depth stratum 16-20 m) to samples from the other gears. No significant differences in mean stomach content weight between the groups was detected (see supplementary material S2). Overall, the majority of statistical comparisons of length-standardized cod stomach content weights per length class, month, and 5 m-depth strata revealed no significant differences between gear types, and visual comparisons of groups with sample sizes < 10 also suggested a high level of similarity in stomach content weights among gear types (supplementary figure S2.1). Therefore, we assumed that the effect of the sampling method was minor and we further assumed that a combination of the different data should be permitted in terms of mean calculation and statistical modelling. Hence, no further standardization of stomach data resulting from different gear types was applied (for further details see supplementary material S.2).

Table 1. Summary table for statistical comparisons of standardized stomach content weights between gear types used for cod stomach sampling. Numbers per gear type denote the number of individual stomachs per month, length class and depth stratum that were compared.

Length class	Month	depth strata	Gear type Angling	 Gillnet	 Trawl	Applied statistical test	p-value
41-50 cm	July	16-20 m	NA	12	45	Man-Whitney-U test	<0.001***
51-60 cm	July	16-20 m	4	34	56	Man-Whitney-U test	0.316
61-70 cm	July	16-20 m	12	50	50	ANOVA	0.642
61-70 cm	August	16-20 m	NA	32	38	Man-Whitney-U test	0.162

Significance code: $p < 0.1$ -., $p < 0.05$ - *, $p < 0.01$ - **, $p < 0.001$ - ***

2.7. Relative diet compositions

Prior to statistical analysis we calculated mean weights per prey type, predator length class, and 5 m-depth stratum using the length-standardized stomach content weights. We decided to first calculate monthly means and subsequently use them to calculate quarterly means, to avoid unintended weightings resulting of unbalanced sample numbers between months. We used quarterly intervals (1: January – March, 2: April – June, 3: July – September, 4: October – December) as a proxy for seasonality, reflecting winter, spring, summer and autumn, respectively.

2.8. Prey groups

We allocated all organisms observed in the stomachs into 11 main prey groups: Annelids, the common shore crab *Carcinus maenas*, Clupeiformes, Echinodermata, Mollusca, Peracarida, Pleuronectiformes, other invertebrata, other/or unidentified fish, other/or unidentified crustaceans and other prey. For the statistical analysis we only used stomachs containing at least one of the above listed main prey groups (N = 2275).

2.9. Analysis of diet clusters

We applied Ward’s hierarchical agglomerative clustering (Murtagh and Legendre, 2014) based on Euclidean distances of relative prey group compositions between cod stomach samples over all quarters, length classes, and 5 m-depth strata 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.

2.10. Relationship of diet clusters with depth, cod length and season

We also analysed seasonal, depth-specific and length-specific effects determining the diet composition of cod. The identified diet cluster membership for every stomach was used as categorical polytomous response variable in multinomial logistic regression modelling. We used depth stratum and predator length as continuous explanatory variables accounting for depth- and length-specific effects on the diet composition. We 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 Akaike's Information Criterion (AIC; Akaike, 1974). We selected the more complex model if the AIC + 2 ≤ AIC of the less complex model. In the multinomial logistic regression modelling the first diet cluster (later termed as "other/unidentified fish cluster"; see 3.3.) was used as reference category. The final model included cod length, depth stratum and quarter as explanatory variables and interaction terms between the explanatory variables.

$$\ln\left(\frac{\pi_i}{\pi_{ref.}}\right) = \alpha_i + \beta_{1i}x_1 + \cdots + \beta_{ni}x_n \tag{3}$$

with $\pi_{ref.}$ – probability of membership in reference cluster, π_i – probability of membership in cluster *i*, α_i – intercept for cluster *i*, $\beta_{1i}\ldots\beta_{ni}$ – coefficients for variables 1 to n, and $x_1\ldots\ x_n$ – variables 1 to n.

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

$$R^2{}_{McFadden} = 1 - \frac{\log\,(L_c)}{\log\,(L_{null})} \tag{4}$$

with L_c – maximized likelihood of the finally chosen multinomial logistic regression and L_{null} – maximized likelihood of the null model.

2.11. Relationship of stomach content weight with depth, predator length and season

We applied Generalized Additive Modelling (GAM) to investigate the variables affecting the stomach content weight of adult cod with season. In general, stomach content weights showed a skewed distribution with many low values and few high values. Hence, we choose to use log-transformed stomach content weights as the response variable for our statistical modelling approach. We tested for size-dependent and depth-specific effects by using cod length and depth stratum as explanatory variables. Seasonal effects were accounted for in the models by implementing the factor variables month and quarter, and/or the continuous variable temperature at depth stratum in our models. 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 Kiel Lighthouse, Darss Sill and Fehmarn Belt buoy (BSH; https://www.bsh.de). Daily mean water temperatures for every 5 m-depth stratum were calculated over all three measuring positions and allocated to the cod samples. In the GAM, non-linearity is represented by smoothing terms (Hastie and Tibshirani, 1986), and we selected the optimal effective degrees of freedom (edfs) for the smoothing terms on depth stratum, water temperature at depth stratum and cod length variables using a set validation approach (James et al., 2013). Model selection was conducted through a backward selection procedure using AIC as described for the multinomial logistic regression modelling above.

The finally selected GAM for log-transformed stomach content weight (g) was described by:

$$Log(SCW[g]_i) = \beta_0 + s(T\,[°C]_i, k = 3) + s(D[m]_i, k = 3) + s(L\,[cm]_i, k = 3) + \varepsilon_i \qquad (5)$$

with SCW – stomach content weight, β_0 – intercept, s – smoothing term, k – effective degrees of freedom +1, T – temperature at catch depth, D – catch depth, L – cod length, and ε_i – error term.

2.12. 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 and Ripley, 2002), *mgcv* (Wood, 2011), *plyr* (Wickham, 2011), *reshape2* (Wickham, 2007), *ggplot2* (Wickham, 2009), *cowplot* (Wilke, 2017), *visreg* (Breheny and Burchett, 2017) and *mapdata* (Brownrigg, 2018).

3. Results

3.1. Stomach contents

The proportion of empty stomachs varied among the cod length classes between 14% (cod length class 51-60 cm) and 27% (cod length class 71 cm) (Tab. 1). 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 >71 cm. 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 (Tab. 2).

The length-standardized stomach content weights over both sampling years varied within all length classes (Fig. 2). During the summer period, between June and July, lowest median stomach content weights 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 stomach content weight of all cod 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 ≥ 61 cm also showed higher median stomach content weights in spring and autumn. However, the median stomach content weight in December showed higher values compared to November (Fig. 2).

Table 2. Numbers of cod 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).

Length class	31-40 cm		41-50 cm		51-60 cm		61-70 cm		71 cm +	
Month	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

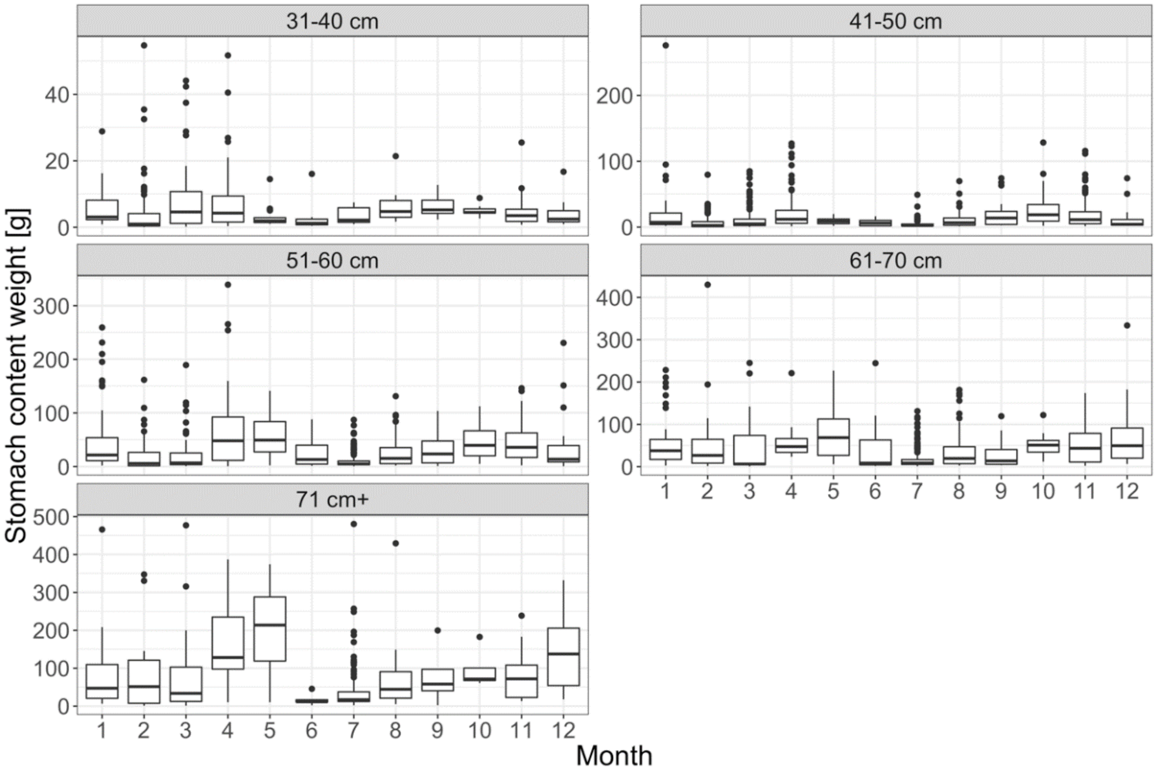

Figure 2. Stomach content weights [g] (including mucus) per predator length class (panels) and month. Boxplots show medians with first and third quartiles (hinges) of the observed stomach content weights from the Belt Sea (SD22). Stomach content weights were length-standardized within each length class. Whiskers range from the upper/lower hinge to the largest value, but no further than 1.5 * IQR (the interquartile range) from the hinge, respectively. Black dots represent outliers which are stomach content weights above 1.5 * IQR from the upper hinge.

3.2. Diet composition

The common shore crab *Carcinus maenas* was the key food item in all cod sizes (Fig. 3). The proportion of common shore crabs generally decreased with increasing depth. An exception from this pattern was the third quarter when *C. maenas* occurred also in stomachs from the deepest depth strata (up to 98% of the total stomach content weight 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 category of cod caught in medium depths (i.e. 11-15 m) in the second quarter (up to 99% of the total stomach content weight). Lowest proportions of *C. maenas* were observed in the first quarter.

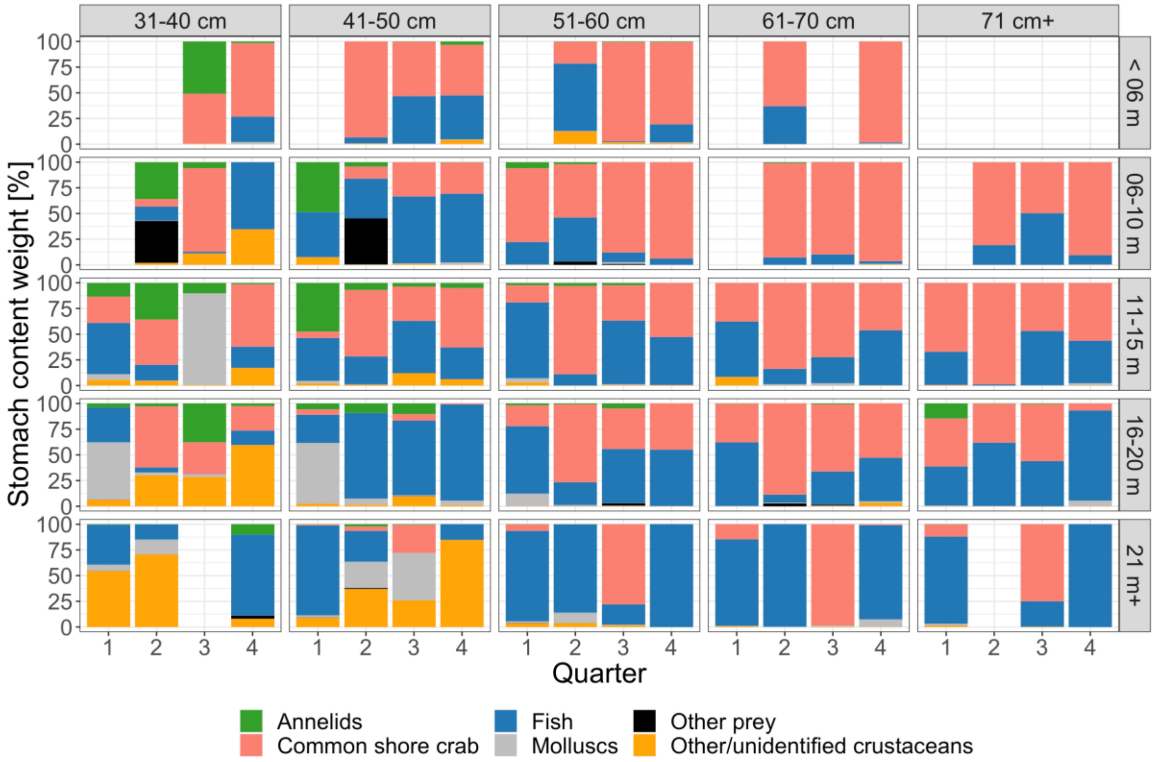

Figure 3. Relative diet composition according to cod stomach weight and length class depth stratum and quarter from the Belt Sea (SD22). Stomach content weights were length-standardized within each length class. Empty bar corresponds to depth and quarter with no sample of a given fish size.

Another major food category was fish (Fig. 3). A total of 36 different prey fish species were found in the stomachs, including six flatfish species, three clupeid species (including herring and sprat) and 27 other fish species. 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). However, a general increase of the share of fish prey with cod length was not observed (Fig. 3).

Fish consumed by cod ≥ 51 cm consisted mainly of demersal roundfish and flatfish species. The diet fraction of flatfish increased with increasing cod size, maximally amounting to 91% of the prey fish composition, and 48% of the total stomach content (i.e. for ≥ 71 cm in the third quarter). In contrast, in cod < 51 cm flatfishes occurred only rarely with maximally 7% of the total stomach content.

Other important fish prey were clupeid species. Higher proportions of sprat were mostly observed in stomachs of cod caught deeper than 10 m, while herring was a major food item of cod caught in shallower areas (i.e. < 16 m depth), especially in the second quarter. Furthermore, herring and sprat occurred mostly in diets of cod < 61 cm.

Cod cannibalism was observed in 5% of all cod stomachs and within all cod 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 (> 71 cm) in the depth stratum 6-10 m in the third quarter and in length class 41-50 cm in the deepest depth stratum (≥ 21 m) in the fourth quarter.

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 ≥ 51 cm (over 50% of the total diet composition) were found in the fourth quarter in the deepest depth stratum (≥ 21 m) of the study area.

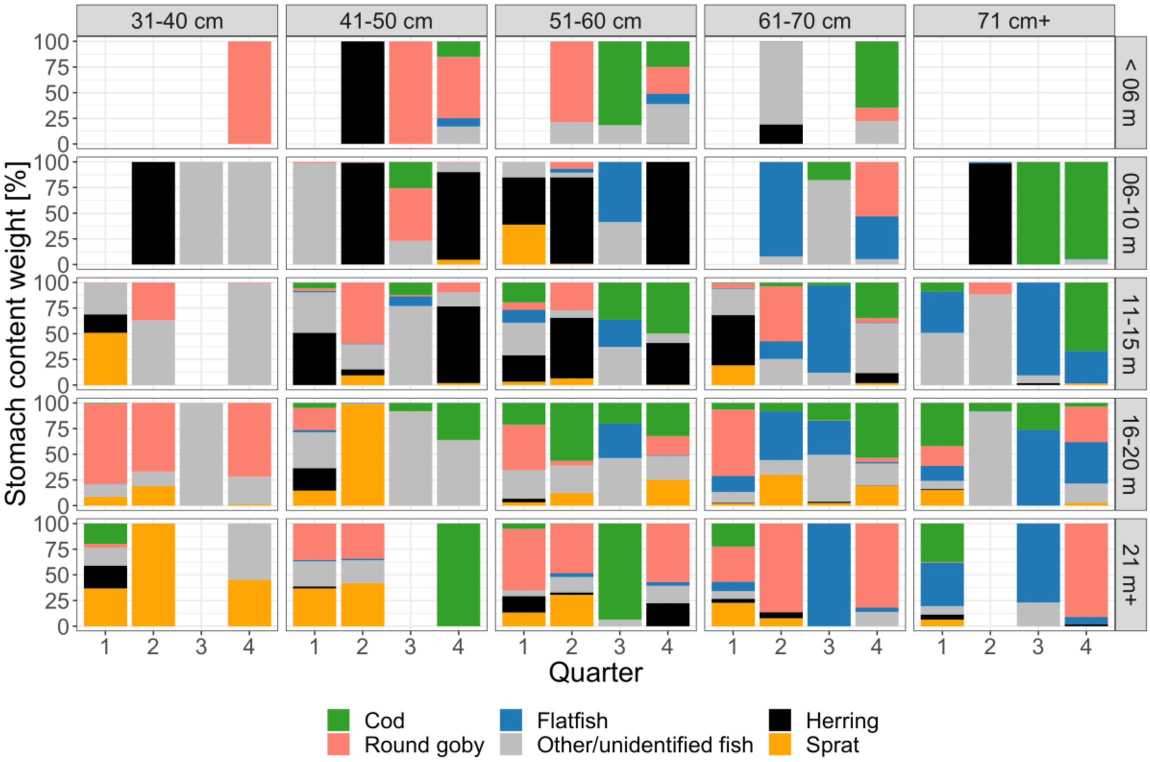

Figure 4. Relative prey fish diet composition according to cod stomach weight and length class as well as depth stratum and quarter from the Belt Sea (SD22). Stomach content weights were length-standardized within each length class. Empty bar corresponds to depth and quarter with no sample of a given fish size.

3.3. Diet clusters

Hierarchical clustering of all individual cod diet compositions identified eight diet composition clusters (Fig. 5). All clusters were dominated by one prey group used to identify the clusters: 1 – Other/unidentified fish, 2 – Common shore crab, 3 – Other/unidentified crustaceans, 4 – Flatfishes, 5 – Peracarids, 6 – Molluscs, 7 –

Clupeiformes, and 8 – Annelids (Fig. 5). The diet cluster dominated by the prey group Common shore crab contained most stomach samples (N = 764 or 32%), followed by the diet cluster dominated by Other/unidentified fish (N = 521 or 22%). The lowest number of stomachs was allocated to the diet cluster dominated by Molluscs (130 or 5%) (Fig. 5).

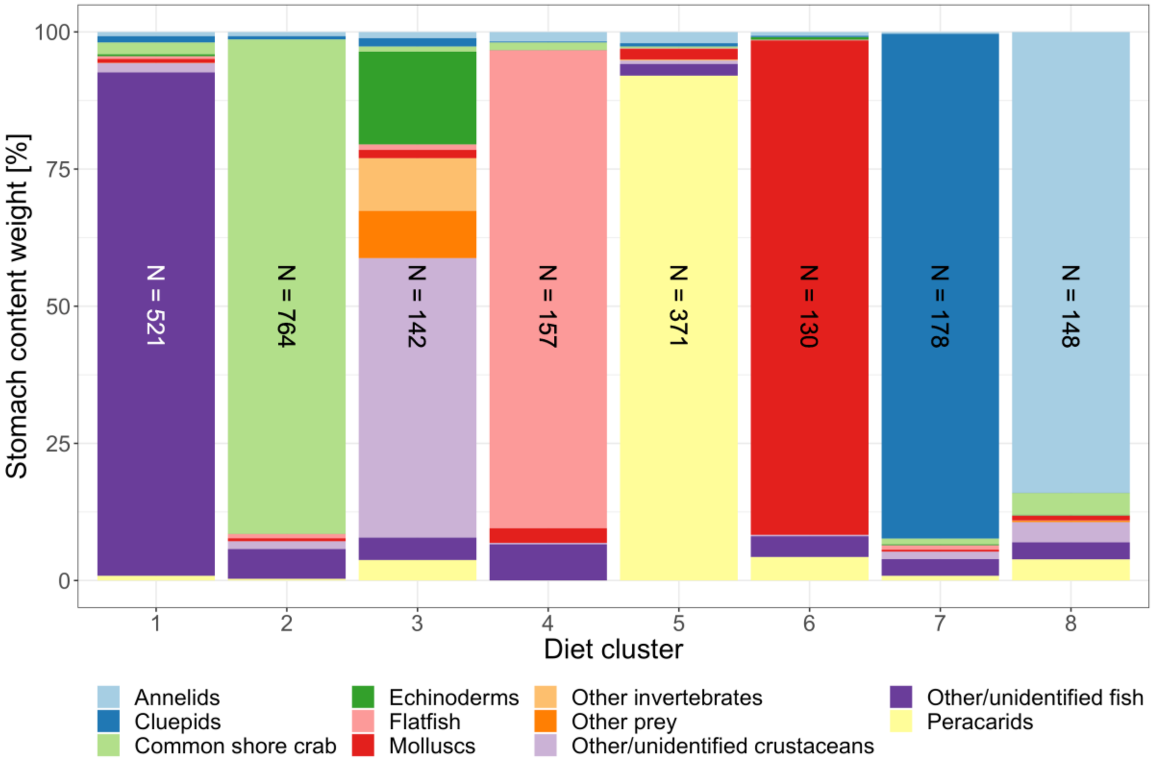

Figure 5. Relative prey group composition of identified diet clusters (1 – Other/unidentified fish, 2 – Common shore crab, 3 – Other/unidentified crustaceans, 4 – Flatfishes, 5 – Peracarids, 6 – Molluscs, 7 – Clupeiformes, 8 – Annelids). N displays numbers of stomachs allocated to the diet cluster.

3.4. 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 pseudo $R^2 = 0.2$), suggesting that fish length, depth stratum and season have a major influence on the diet composition of adult cod (Fig. 6). The supplementary table S3.1 contains a list with all 84 model coefficient estimates. Smaller cod generally showed a great variability in diet cluster membership, while larger cod > 65 cm belonged mostly to the clusters of Other/unidentified fish and Common shore crab (Fig. 6). 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/unidentified fish cluster membership increased with increasing depth stratum. For cod < 50 cm an increased probability for the Peracarids cluster with increasing depth stratum was predicted. Additionally, seasonal effects were detected for example for large cod > 70 cm which showed an increased probability for the Flatfish cluster in shallower waters < 15 m depth in the third quarter (Fig. 6).

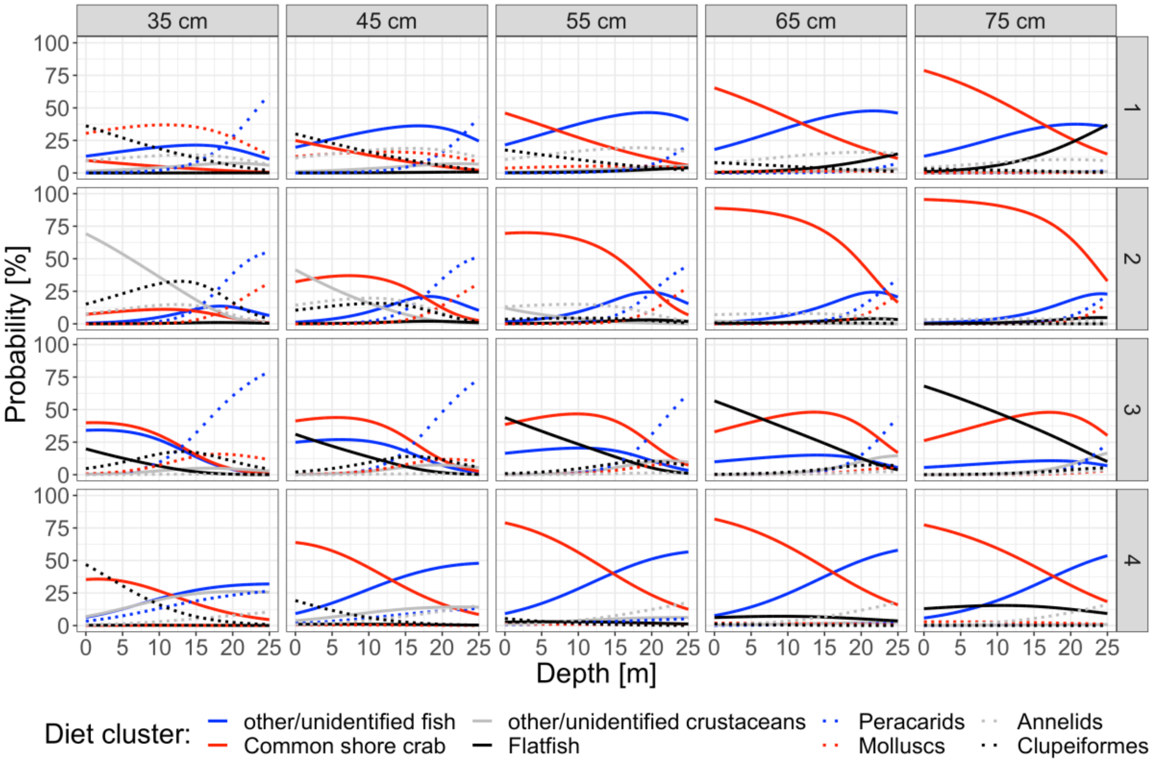

Figure 6. Statistical model of diet cluster membership of adult cod from the Belt Sea (SD22). Plots show the partial effects of catch depth (Depth), quarters (quarters 1 to 4 are shown vertically below each other) and predator length (fixed predator lengths from 35 to 75 cm are shown from left to right) on the probability [%] of diet cluster membership.

3.5. Length, depth and temperature effects on the stomach content weight of adult cod

The GAM using depth stratum, water temperature at depth stratum and cod length as explanatory variables explained 40% of the total variance in the data set. Depth stratum and water temperature showed negative relationships with the log-transformed stomach content weights (Fig. 7A, B). In contrast, cod length showed a positive relationship with the log-transformed stomach content weights (Fig. 7C). While the curve of the effect of water temperature showed a linear course, the shape of the depth stratum and length effect curves resembled an exponential function (Fig. 7 A, C). All smoothing terms were highly significant ($p < 0.001$, Tab. 3).

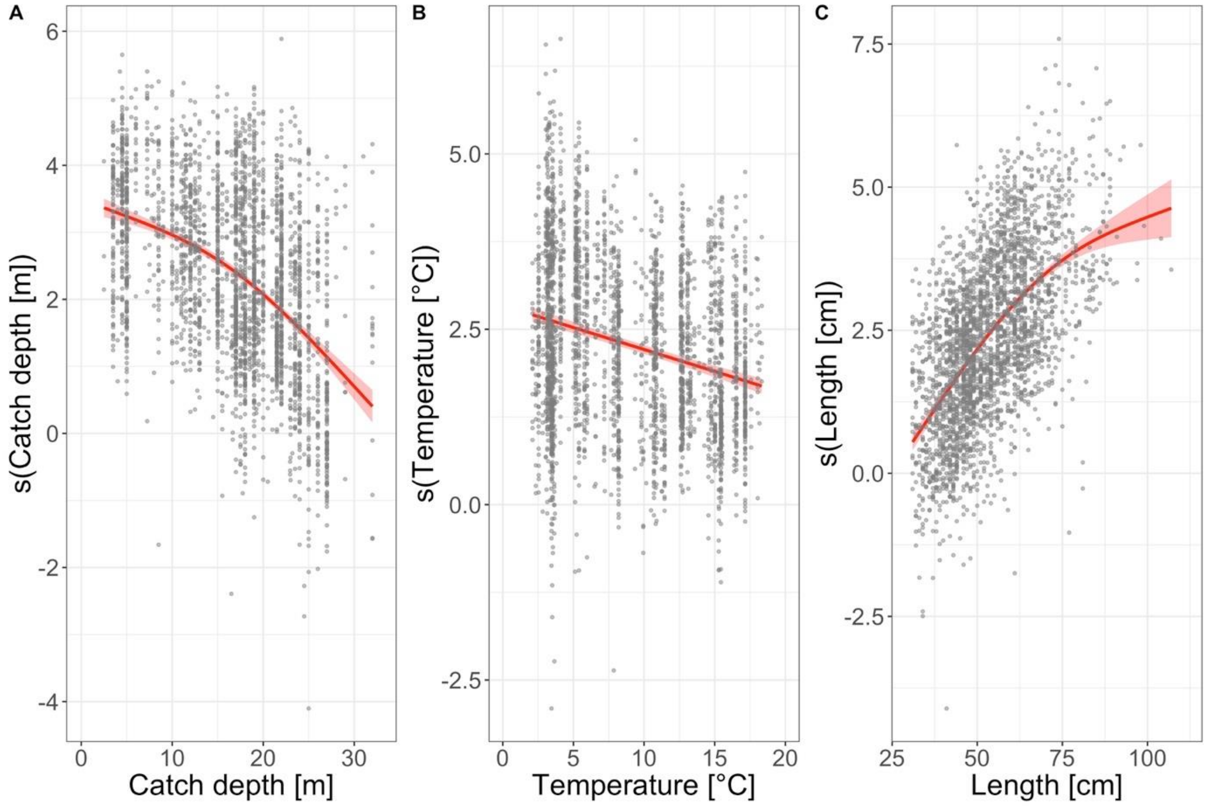

Figure 7. Effect curves (red lines) and confidence intervals (red shading) of the explanatory variables catch depth (A), water temperature at catch depth (B) and length of cod (C) used in the finally chosen GAM. Partial residuals are displayed as grey dots.

Table 3. Parameter estimates and significance levels for established generalized additive model (GAM). s(Catch depth) – smoothing term on catch depth, s(Water temperature) – smoothing term on the water temperature at catch depth, s(Length) – smoothing term on the length of cod, SE – standard errors, edf – effective degrees of freedom of the smooth terms, p-value – significance level, explained deviance and explained variance (R^2) of the finally chosen GAM.

Parametric coefficients			
	Estimate	SE	p-value
Intercept	2.3	0.021	<0.001
Approximate significance of smoothing terms			
		edf	p-value
s(Catch depth)		1	<0.001
s(temperature)		1.966	<0.001
s(Length)		1.958	<0.001
Deviance explained = 40.5%			
R^2 = 0.40			

4. Discussion

Our results comprising year-round samples collected with different gear types from major depths and habitats revealed that the diet composition and stomach content weight of cod in the Belt Sea (SD22) was affected by body length, season and water depth. We observed highest stomach contents in shallower areas, which strongly point towards an important role of shallow-water areas for the seasonal food intake of cod. The common shore crab is a major food item of all size classes of cod in the Belt Sea but the importance decreased with water depth. The importance of fish, mainly flatfish and small demersal fish species, increased with water depth. Hence, given the current environmental settings of the Belt Sea, focusing on habitats > 20 m depths only would largely underestimate the importance of benthic invertebrate prey and overestimate the importance of fish prey in the area.

4.1. Comparison with historic stomach data

Since the historic cod diet investigations in the Belt Sea consistently originated from trawl samplings which were conducted mostly in depths > 20 m, a comparison with our new findings is limited to the depth stratum > 20 m. In 2016 and 2017 we observed decreasing proportions of benthic invertebrates in the cod diet with increasing depth for most length classes of cod. Cod ≤ 50 cm were an exception, they still had high probabilities of a dominance of invertebrates such as peracarids even in areas deeper than 20 m water depth. Benthic invertebrates were also identified as important food organisms of adult cod which were caught during scientific trawl surveys in depths > 20 m in the Kiel Bight in the 1960s (Arntz, 1977). In the 1960s especially high proportions of the mussel species *Arctica islandica* often dominated the stomach contents, even of larger cod (Arntz, 1977). However, polychaeta and crustaceans were also observed in considerable high frequencies in the diet of adult cod in the 1960s (Arntz, 1977). In contrast, stomach samplings in depths > 20 m in the Belt Sea from 1981 to 1989 (Weber and Damm 1991) revealed that the diet of cod consisted only to a lower percentage of benthic invertebrates than in Arntz (1977). Apparently, there was a decrease in the amount of benthic invertebrates from the 1960s to the 1980s in the Kiel Bight which Weber and Damm (1991) related to several events of oxygen depletion in the 1980s, which negatively affected the populations of sessile benthic invertebrates such as

A. islandica (Weigelt and Rumohr, 1986). Since these extreme larger scale events of oxygen depletion in the 1980s a recolonization of the deeper channels in the Belt Sea by benthic invertebrates may have occurred (Zettler et al., 2001) so that in present times this resource is more available again in depths > 20 m. Oxygen depletion events occurred also regularly in the last decades, though rather locally and temporally limited (Karlson et al., 2002). Hypoxia affects mostly the recruitment of *A. islandica*, while adults are described as extremely tolerant against oxygen depletion events (Zettler et al., 2001). Hence, overall negative effects on the stock biomass of *A. islandica* are only expected when sequential events of oxygen depletion occur at the same locations (Zettler et al., 2001). However, we are unable to relate our recent proportions of *A. islandica* in the diet of cod to temporal changes in local bivalve abundance because bivalve distribution is patchy and it is possible that differences in the proportions of *A. islandica* in cod diet are only due to sampling at different locations rather than to temporal changes in overall availability to cod.

We observed highest proportions of *A. islandica* in stomach samples from the second and the third quarter, which coincided with the observations of Arntz (1977) who observed highest frequencies after spawning time and in early summer. Unlike Arntz (1977), we observed higher proportions of *A. islandica* for cod in length classes < 51 cm only, while Molluscs in general played a minor role in the diet of larger cod. Arntz (1974) hypothesised that also trawl activity may affect the intake of *A. islandica* by cod. Since he often observed muscle tissue of *A. islandica* with only small parts of shell in the cod stomachs, he assumed that cod may ingest mussels previously damaged by otter boards. Thus, fluctuations in the amount of *A. islandica* consumed by cod might be also related to differences in trawl activity in the study area.

Clupeids were a major prey item of cod in the Belt Sea in Weber and Damm (1991). This coincided with the investigation from Schulz (1988), which was based on quarterly stomach samplings of cod collected during research trawl surveys between 1978 and 1984 in the Mecklenburg Bight (eastern part of the Belt Sea) and the Arkona Sea. Herring was the main prey organism of cod in the 1980s (Schulz 1988), which accounted for high proportions in the diet of cod in all four quarters. In contrast, herring was observed only to a minor extent in the diet of cod in 2016 and 2017. Herring might be less available as prey for cod now compared to the 1980s due to a decline in the spawning stock biomass of spring spawning Western Baltic herring in the study areas since the 1990s (ICES, 2019c). Hence, 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 lack of herring compared to the 1980s when herring was more abundant. In our studies higher shares of herring were only found in the second quarter in the cod length classes ≤ 50 cm, in the depth strata 6-10 m and 11-15 m. If these depths would have been neglected in our sampling design, as done in previous stomach samplings in the region, herring would have been recorded in minor proportions only, since they were absent in most stomach samples from depths > 15 m.

In addition, round goby was available as a new fish prey item in our samples, not detected the 1960s and 1980s. Round goby was found in stomachs of cod of all length classes and various depth strata. Higher proportions of round gobies were found especially in the first and fourth quarter in depths ≥ 16 m, while they occurred in shallower areas mainly between the second and the beginning of the fourth quarter. This might reflect a seasonal vertical movement pattern of round gobies from shallower to deeper areas with decreasing water temperature (Sapota and Skóra, 2005; Christoffersen et al., 2019), similar to the native sand goby *Pomatoschistus minutus* (Arntz, 1974). Round gobies are poor swimmers and have only poor anti-predatory attributes, rendering them a relatively easy prey for cod 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. The round goby is an invasive species in the Baltic Sea and was first recorded in the southern Baltic Sea in 1990 (Skora and Stolarski, 1993), where it was also observed as a new prey species of cod (Almqvist et al., 2010; Pachur and Horbowy, 2013). From the bay of Gdansk, the round goby spread towards northern and western areas of the Baltic Sea, being firstly recorded at Rugia Island in 1999 by fishers (unpublished data cited in Corkum et al., 2004), and a few years later in adjacent waters of the Belt Sea at the River Trave and in the Kiel Canal (Hempel, 2017).

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). However, the share of *C. maenas* in our samples from depths > 20 m was greater and the overall dietary importance of the common shore crab including all depth strata was outstanding. For example in the investigations of Schulz (1988) *C. maenas* occurred only to a lower extent, with lowest proportion of only 1% in the stomach contents in length class 35-44 cm and highest proportion of 6% of the stomach content of cod ≥ 65 cm, while we observed proportions of more 90% of common shore crabs for some length classes and quarters. Long-term, depth-specific trends of *C. maenas* abundance in the Belt Sea are unknown but two local gillnet fishers with professional experience of > 20 years fishing in the Mecklenburg Bight (i.e. one fishing mainly around Fehmarn and the other fishing mainly in the area north of Travemünde) reported that adult cod in the shallower areas have always fed on common shore crabs in high amounts as far as they can remember (pers. comm. with local gillnet fishers by lead author). This ecological fisher knowledge suggests that if there has been a change in the importance of *C. maenas* as prey species, this change probably occurred more than 20 years ago. Another explanation of the relatively high shares of *C. maenas* in the cod 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 general, benthic invertebrates likely have always played a major role as food items for WBC but the results from the historic trawl samples were unable to appropriately reflect this. Our samples suggest that in areas deeper than 20 m benthic invertebrates (mainly *C. maenas*) are more important in the diet of cod now than in the 1960s and 1980s. In areas shallower than 20 m water depth they dominate the prey composition at least for the past 20 years. Hence, the picture of cod as a major fish predator in the Belt Sea is no longer valid.

4.2. Ontogenetic feeding shift of adult cod

In previous studies on the diet composition of cod in the Western Baltic Sea, which were entirely based on scientific trawl samples from depths > 20 m, a shift from benthic invertebrate prey towards fish prey with increasing predator length was described (Arntz, 1977; Bagge, 1979; Schulz, 1988; Weber and 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 proportions of benthic invertebrates (between 2% in the period January to June, and 21% in the period July to December).

Our data confirm an ontogenetic shift from benthic invertebrate to fish prey only when also focussing on the diet composition of cod sampled at 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%), while for larger length classes the diet was dominated by fish prey (84 to 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 cod length classes. This might be explained by the fact that the feeding areas of cod and the areas, where cod were caught, differed in this time. As mentioned earlier, the shallower areas are likely to offer a higher food supply of mobile epifauna organisms, such as *C. meanas*, during the summer period. Hence, cod might have performed nocturnal feeding excursions to these shallower, more attractive feeding grounds while resting in deeper water during daytime (Freitas, et al. 2015). In addition, a generally decreased food intake in combination with prey-specific gastric evacuation rates of crustacean species may lead to the fact that invertebrates with chitinous exoskeletons such *C. maneas* remain longer in the stomachs than for example fish prey (Andersen et al., 2016; dos Santos and Jobling, 1995; Temming and Herrmann, 2003). Hence, a slight overestimation of the proportion of common shore crabs cannot be excluded. This overestimation might be even more pronounced in the third quarter, when high ambient temperatures lead to in general increased gastric evacuation rates.

However, unlike the historic and recent picture emerging from samples of areas deeper than 20 m water depth, a focus on areas shallower than 20 m water depth did not find evidence for an ontogenetic feeding shift from invertebrates towards fish with increasing cod size. In contrast, overall a dietary shift towards higher proportions of common shore crabs with increasing cod size was observed. For cod > 50 cm, the common shore crab was the main prey organism in shallower areas. However, we also observed seasonal differences in the proportion of *C. maenas* in the diet of cod. Interestingly, we observed lowest shares of common share crabs in the first quarter, similarly 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 temperatures condition (Dries and Adelung, 1982) which presumably makes them more difficult for cod to detect.

4.3. Seasonal and depth-specific feeding patterns

The depth-specific patterns in the diet composition of cod in the Belt Sea suggests that previous investigations based on samples from water deeper than > 20 m could provide only an incomplete picture on the real diet composition of cod in the Belt Sea. We 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, while the role of fish as prey for adult cod is overestimated. The importance of shallow-water areas as feeding habitats of cod in the Belt Sea is emphasized by the observed depth-specific patterns in the stomach content weights. The statistical modelling results suggested that cod length, water temperature and depth stratum affect the stomach content weight of adult cod. Increasing catch depth showed a clear negative effect on the stomach content weight of cod, underlining the great importance of shallower water areas for the quantitative food intake of cod in the Belt Sea. Interviews about the monthly catch depth of commercial gillnet fishers in the Belt Sea revealed that cod display two distinct periods of shallow-water use in spring and autumn as well as two periods of deeper water use in winter and summer (Funk et al., unpublished). The shallow-water phases in spring and autumn coincide with the periods of post- and pre-spawning period 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., unpublished). The intensive use of shallow-water areas may reflect a higher prey availability and accessibility in these areas during spring and autumn. Mobile epifauna organisms, such as the common shore crab, are known to display seasonal up- and downshore movements in relation to changing water temperatures (Pihl and Rosenberg, 1982). Mobile epifauna remains in deeper, warmer areas during winter, and returns to shallower coastal waters with rising water temperatures in spring (Pihl and Rosenberg, 1982), thus leading to a regularly fluctuating food supply for cod in these areas. In turn, this may concurrently lead to a generally decreased food availability at deeper habitat sites (> 20 m) during the summer period.

We especially observed low stomach content weights of cod in the deepest depth stratum > 20 m. The observed lower stomach content weights of adult cod at the deeper habitats might be explained by a lower feeding activity and/or food scarcity. Deeper areas are used by adult cod mostly during winter and summer (Funk et al., unpublished). In winter during spawning time (Bleil et al., 2009) WBC move to the deeper, more saline areas which provide suitable conditions for egg buoyancy (Nissling and Westin, 1997; Petereit et al., 2014). In contrast, the movement towards deeper areas in summer are most likely an avoidance response towards high water temperatures in shallower areas.

In winter food intake might be reduced due to a combination of low temperatures, reduced gastric evacuation and spawning activity. Slow gastric evacuation should, however, lead to a fuller stomach at the same feeding rate, but our stomach content weights were actually lower than 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 and Trippel, 1999). Hence, lower stomach content weights in winter are most likely related to spawning-induced depression in feeding activity in cod.

In summer, when water temperatures are highest, local gillnet fishers report of a period with an in general decreased activity of cod (Funk et al. unpublished; pers. comm. with local gillnet fishers by lead author). These periods of low movement activity during peak summer may also go along with a reduced feeding activity due to temperature stress, which might explain the low stomach content weights in peak summer months (i.e. from late June to the end of August). However, in fish high temperatures lead to lower stomach contents at a constant feeding rate and the two effects can only be separated at a given temperature with a gastric evacuation model that covers also suboptimal temperatures. For example, experiments of Tyler (1979) showed a decreasing gastric evacuation rate beyond 15 °C in juvenile cod. During summer, water temperatures can exceed 15 °C even in depths > 20 m (for example in July 2016; BSH unpublished data), which than lead to a rather suboptimal gastric evacuation rate. These reduced gastric evacuation processes should be even more pronounced during summer in water layers above the thermocline (< 15 m depths), which display even warmer ambient temperatures, which temporally exceed even 20 °C (see Funk et al., unpublished). During the peak summer months, we also observed highest proportions of completely empty stomachs in depths > 20 m, pointing towards an overall depressed feeding activity of cod 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.

Moreover, the effect of a generally decreased food intake during the summer period might get even more pronounced under the occurrence of hypoxia. The formation of hypoxic zones occurs regularly during the summer period in the Western Baltic Sea, as a result of reduced wind forcing and a lack of oxygen-rich saltwater inflows from the Danish Straits (Weigelt, 1987).The occurrence of hypoxic zones is mostly restricted to the deeper channels and basins of the Western Baltic Sea in depth > 15 m (Weigelt, 1987). However, these depths display the most favourable temperature conditions for adult cod during the peak summer time, and thus, hypoxia may restrict the downslope movement of cod to intermediate depth only (i.e. to the slopes and borders of the deeper basins), which are characterized by rather suboptimal ambient temperature conditions. These higher ambient temperatures will result in an increased standard metabolism (Pörtner, 2010) and thus, in a general decreased scope for activity such as for feeding.

An alternative interpretation for low stomach contents in summer in the areas deeper than 20 m might be limited food availability. As mentioned above, literature describes distinct seasonal distribution patterns for mobile epibenthos organisms (Pihl and Rosenberg, 1982), which tend to remain in shallower coastal waters from spring to late autumn, thus likely leading to a limited food supply for cod at deeper habitats during this time. However, when water temperatures rise and a strong thermal stratification forms, cod display a distinct downslope shift in distribution towards the slopes and borders of the deeper basins in the Western Baltic Sea. This movement likely reflects a behavioural response to avoid unfavourable high temperatures in the shallower areas (Funk et al., unpublished). Thus, especially during the peak summer period in July and August, cod have to make a trade-off between prey availability and physiological temperature tolerance limits in the shallow coastal zone (Funk et al., unpublished). The assumption of food limitation at water depths > 20 m in summer is further supported by observations of local gillnet fishers (pers. comm. with local gillnet fishers by lead author), who temporarily reported high abundances of cod in shallow waters after strong-wind pulses during the peak summer period. Strong wind events during the peak summer period can cause local disturbances of the thermal stratification resulting in temporary temperature drops close to the coast (local upwelling), which may result in opportunistic local changes in cod distribution. A similar behaviour was described for summer upwelling events in coastal cod in a south Norwegian fjord and it was hypothesized that cod quickly take advantage of windows of opportunity and temporally enter the shallow habitats to feed (Freitas et al., 2015; 2016). The argument of food scarcity and size-indiscriminate feeding (Ursin and 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 rathkeii* in areas > 20 m water depths in the third quarter.

Overall, the spatio-temporal dynamics of the stomach content weights highlight the importance of shallow-water areas, particularly in spring and autumn when cod intensively feed on *C. maenas* in these areas. In winter during spawning in deeper, more saline areas, the feeding activity is generally reduced. During peak summer, access to the shallow-water feeding grounds is limited due to thermal tolerance limits, so that cod have to reside in deeper areas, though opportunistic use of shallow-water areas can occur with local upwelling pulses (Funk et al., unpublished).

4.4. Estimating the potential bias resulting from limited spatial coverage

Unlike the historic perception of Belt Sea cod as a year-round fish predator, our new, more comprehensive data highlight that cod in this area mainly relies on benthic invertebrates such as *C. maenas* captured in shallow-water areas. Moreover, our monthly sampling revealed strong seasonal, size- and depth-specific patterns in habitat and food use. Based on these new results it is very likely that previous investigations on diet composition and consumption in the area, based on trawl data from habitats > 20 m depths, were largely biased. However, it is difficult to assess the order of magnitude of the potential bias in consumption using our results. The use of different gear types and methods significantly improved our spatio-temporal coverage, but it also makes it difficult to standardize and weight the results, for example by using catch-per-unit-effort values to calculate representative diet compositions for a length class over the whole study area.

Here we attempt to provide a first impression of the potential bias that can occur by presenting the differences in the diet composition and stomach content weights of cod, when samples are either taken from preferred habitat sites or from trawlable sites > 20 m depth only (as usually done in historic diet investigations). We use the quarterly median cod catch depths reported by local gillnet fishers (Funk et al., unpublished) to achieve a first approximation of the quarterly favoured residence depths of cod (Tab. 4). When we subsequently compare relative diet composition and median stomach content weights for the 5 m depth strata which correspond to the assumed favoured residence depth to diet compositions of cod from depths > 20 m, we yield a preliminary impression of the differences.

Comparisons of the depth-centred diet compositions display several striking differences. For cod caught at depths > 20 m higher shares of fish prey occurred across almost all length classes and quarters, except for the third quarter (Fig. 8). The most striking differences emerge for the second quarter, where we observe particularly higher shares of common shore crab in the diet at the assumed favoured residence depth (6-10 m) compared to those from the 21 m+ depth stratum. For example, for the cod length class 61-70 cm in the second quarter we observed common shore crab accounting for more than 90% of the total diet composition at the assumed residence depths, while it was absent from the diets of individuals caught in depths > 20 m.

The comparison of depth-centred median stomach content weight revealed also strong differences (Fig. 8). We consistently observed higher median stomach content weights in the samples at the assumed residence depths, except for two cases (i.e. the fourth quarter for length class 71 cm+ and the first quarter for length class 41-50 cm). These differences were most pronounced in the second and the third quarter, e.g. in the third quarter, cod in length > 70 cm displayed an eight times higher median stomach content weight at the assumed residence depth than individuals sampled at depths > 20 m. Although these comparisons are only rough estimations, they indicate the order of magnitude of bias of both stomach content weights and diet compositions which can occur when essential habitats are not covered. Consequently, planning stomach sampling programs of demersal fish stocks in general should consider the full known spatio-temporal distributional dynamics of the target species to avoid the collection of potentially biased data.

Table 4. Monthly and quarterly median catch depths for cod reported by 16 gillnet fishers located in the study area during interviews in 2016 (Funk et al., unpublished) and corresponding assumed residence 5 m-depth stratum per quarter.

Quarter	Month	Monthly median depth [m]	Quarterly median depth [m]	Allocated 5 m-depth strata
1	January	19.5	19.00	16-20 m
	February	19.5		
	March	15		
2	April	9.25	10.00	6-10 m
	May	10		
	June	12.5		
3	July	17	8.25	6-10 m
	August	10		
	September	5.5		
4	October	5.25	6.00	6-10 m
	November	5.5		
	December	11		

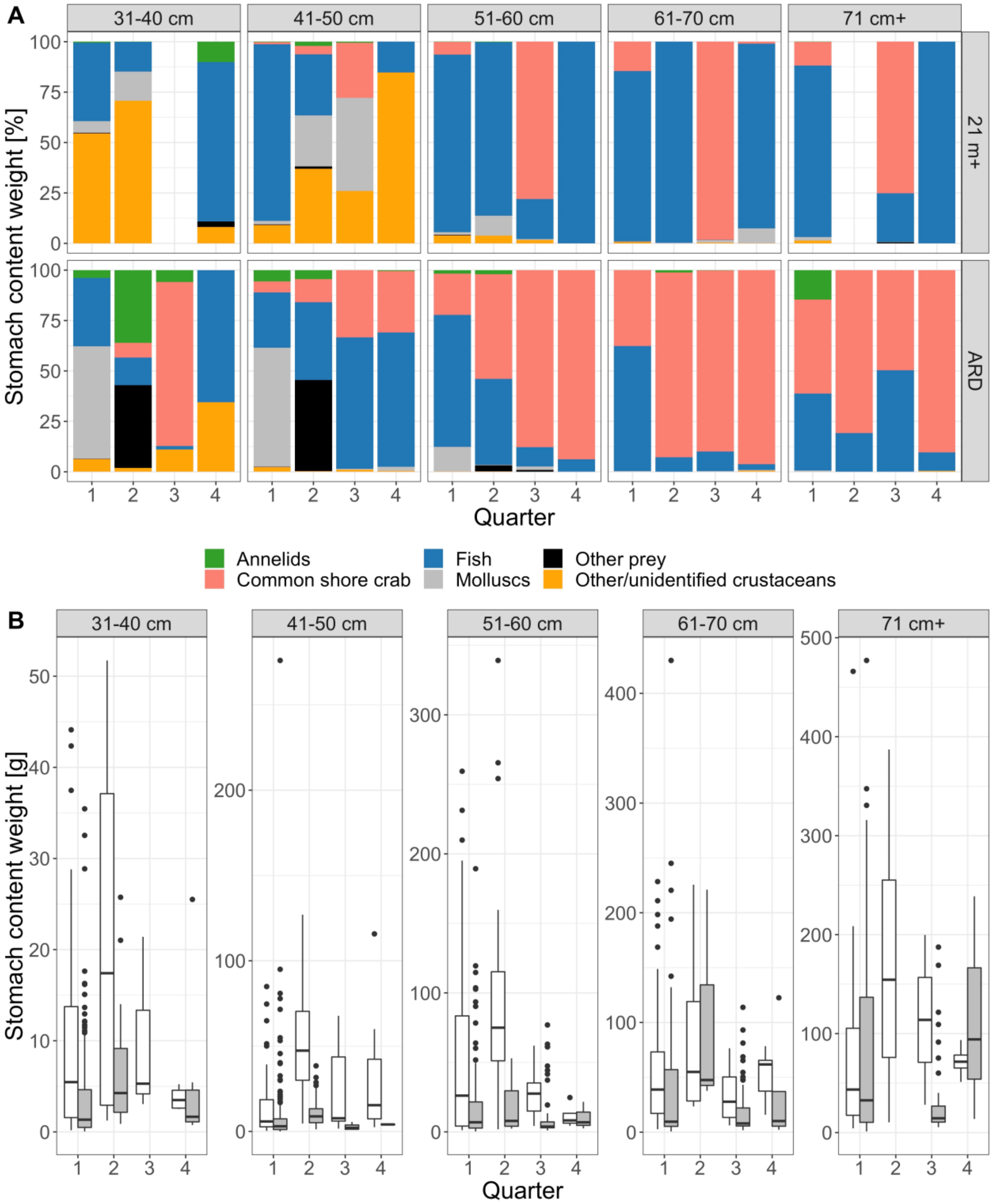

Figure 8. Comparison of relative diet composition (A) and stomach content weights (B) per predator length class and quarter between samples from assumed residence depth stratum – ARD (Quarter 1: 16-20 m; Quarter 2 to 4: 06-10 m) and samples from depth stratum 21 m+ in the Belt Sea. Colours of boxplots indicate depth strata (white – assumed residence depth stratum; grey – stratum 21 m+). Stomach content weights were length-standardized within each length class. Whiskers range from the upper/lower hinge to the largest value, but no further than 1.5 * IQR (the interquartile range) from the hinge, respectively. Black dots represent outliers which are stomach content weights above 1.5 * IQR from the upper hinge.

4.5. Conclusion

Our study revealed seasonal, size- and depth-specific effects on the food intake of WBC affecting both the diet composition and stomach content weights, which could only be detected by applying a thorough sampling design with a high spatial and temporal resolution. Furthermore, we highlight the importance of shallow-water areas for the food intake, with the common shore crab *C. maenas* as the major prey item of cod in the Belt Sea.

The previous perception that Belt Sea cod is mainly a piscivorous predator seems no longer valid. Our results demonstrate that historic studies that neglected shallow waters < 20 m depth led to a sizeable underestimation of the importance of benthic invertebrates and an overestimation of fish prey in the diet composition of cod in the area. Moreover, this study provides support for using several catching methods in stomach sampling programmes of demersal species in waters characterised by strong seasonal dynamics to increase the spatio-temporal coverage and thus provide more accurate data for food web analyses and multi-species models.

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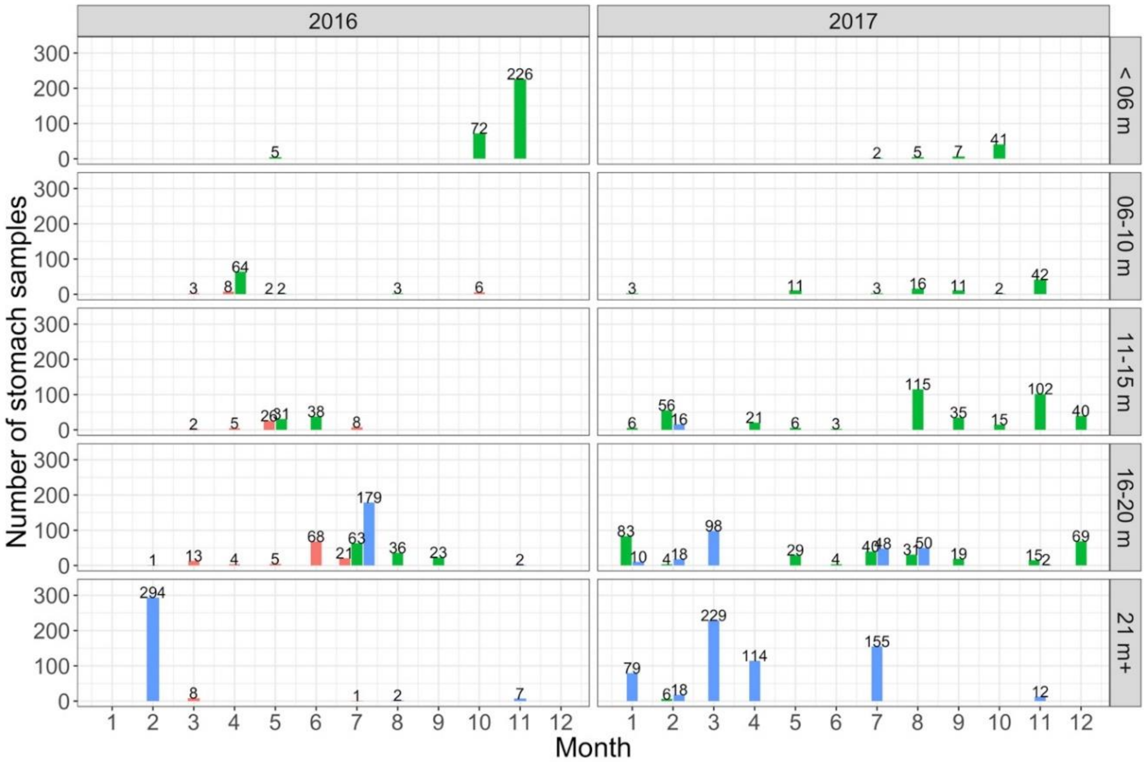
Supplementary material

S1. Stomach sampling



Supplementary figure S1.1. Number of stomachs from cod ≥ 31 cm per month, depth strata, sampling year and sampling method (red – angling, green – gillnetting, blue – trawling).

Angling

Between March and October in 2016 a total of 13 angling samplings were conducted. The fishing trips were carried out with the small research vessel Seabull and a motorboat of the University of Hamburg (UHAM) as well as with the two recreational fishing charter vessels Ostpreußen 1 and Monika, which are based in the harbour of Heiligenhafen. For angling, fishing rods with artificial fishing baits and lugworms (*Arenicola marina*) were used. An on-board observer recorded the GPS positions of the fishing positions as well as the catch depth for each cod caught during the fishing trips.

Commercial fishing

Between April 2016 and December 2017 stomach were sampled from 12 gillnet and 9 trawling vessels during a total of 54 fishing trips. For gillnet fishing the fishers used set gillnets (GNS) and trammel nets (GTR) with mesh size diameters between

110 and 240 mm. The soaking times varied among fishing trips between 4.5 to 48 hours. In case of commercial fishing, otter bottom trawls (OTB) and otter twin trawls with a T90 or BACOMA cod end as selection device were used. Trawling duration varied among fishing trips between 30 and 257 minutes (for the issue of ongoing gastric evacuation on see below S2).

In 25 out of the 54 commercial fishing trips, a scientific observer was on board recording fishing positions and gear information as well as taking the stomach samples directly after the catch.

Additionally, cod for stomach content analysis were available from unsorted catch subsamples purchased by the Thünen Institute of Baltic Sea Fisheries (Thünen-OF) as part of the EU-financed data collection framework (DCF). These cod were stored on ice after capture, transported by car to Rostock and gutted at the laboratory of the Thünen-OF. The fishers provided information on the fishing depths and catch positions for these cod samples.

Research surveys

Stomach samples were taken during four research cruises conducted by the UHAM and five surveys conducted by the Thünen-OF.

The cruises SB 728 in November 2016, SB 731 in March 2017 and SB 742 with the research vessel (RV) Solea were part of the Baltic International Trawl survey (BITS). All samples were taken following the BITS protocol (ICES, 2017).

In case of the other research surveys start positions for trawling were selected at trawlable sites only and mostly at sites where fish was detected on echograms.

As trawling gear, a young-fish net with a cod end mesh size of 6 mm was used on RV Heinke and RV Alkor while on RV Clupea and RV Solea bottom otter trawls of type TV300/60 were used. Standard tow duration was set to 30 minutes. However, in some cases, the tow duration was increased or decreased due to ad-hoc decisions of the cruise leader, e.g. to increase catch or prevent damaging the gear on rocky grounds.

During the cruise CLU 319 with RV Clupea, GNS were used as fishing gear with a mesh size diameter of 100 mm. The soaking time was 24 hours.

Processing of stomach samples

The total length of the caught cod was measured and their stomachs were removed. On board of the commercial fishing vessels and during angling, the stomach samples were stored on ice and deep-frozen (-16°C) afterwards ashore. In case of the purchased samples and the research surveys, the stomachs were deep-frozen immediately after gutting.

Cod showing signs of regurgitation (e.g. everted swim bladders or gill rakers attached with remains of the food as well as cod showing signs of net-feeding, e.g. non-digested food attached to the gill rakers or the oesophagus) were excluded from the stomach analysis.

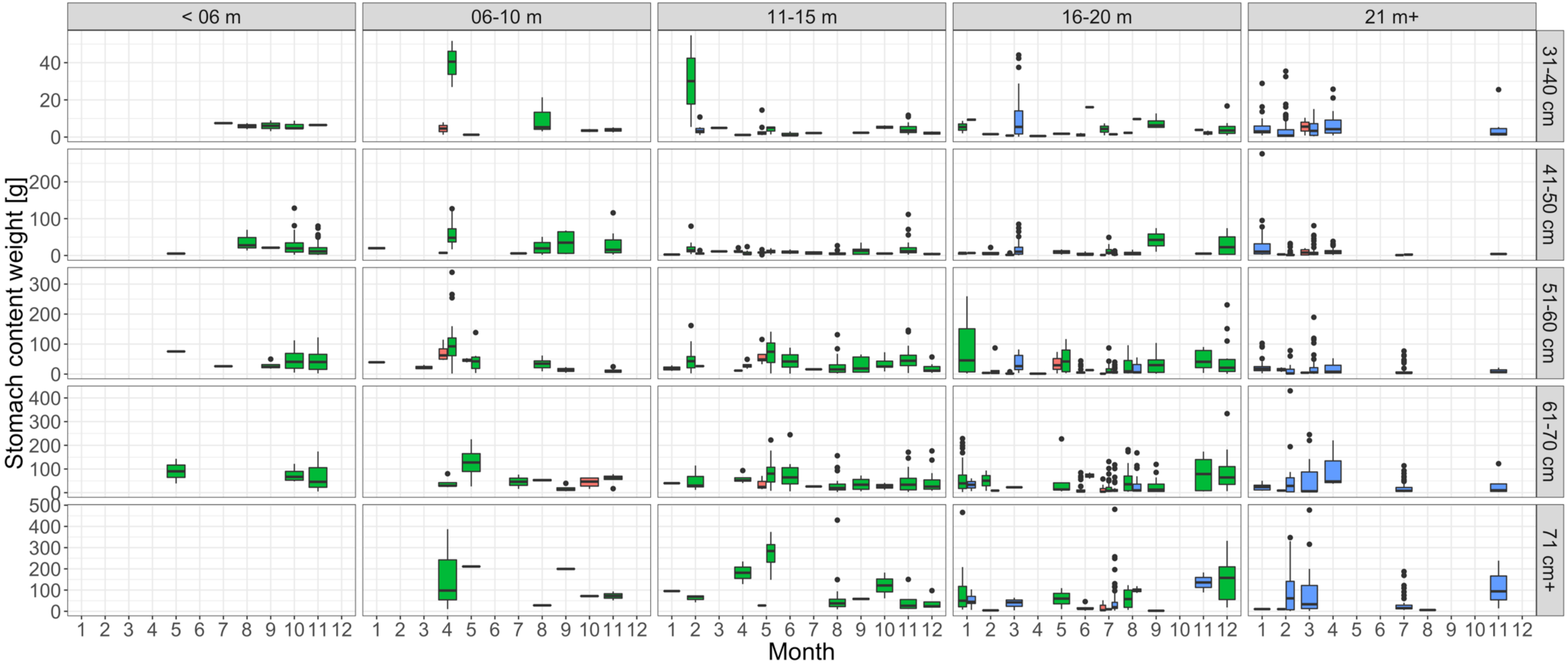
S2. Discussion of sampling methods

The use of capture methods other than trawling in stomach sampling programs is often debated. Stomach samples from gillnets are considered biased by the effect of ongoing gastric evacuation. Individuals which get entangled in the nets may survive several hours before the nets get hauled, and thus, stomach fullness observed in gillnet samples may display a decreased level of stomach fullness compared to trawl samples (Bromley, 1994). However, we observed in on-board samplings that several individuals were already dead, when the nets were hauled (pers. observation by lead author). An increased stress level of the fish when getting entangled may lead to a quick death and thus to a sudden stop of gastric evacuation processes. However, for all animals caught alive, it could not be detected how long they had stayed in the nets and hence the bias resulting from ongoing gastric evacuation processes could not be assessed. However, we suspect that cod caught alive were mostly entangled only shortly before the nets were hauled and therefore, we assume the bias related to ongoing gastric evacuation as negligible.

Other studies hypothesize in contrast that higher stomach contents might be observed in gillnet samples than in trawl samples due to the fact that gillnets catch mainly active (i.e. feeding) fish while trawl gear displays a higher catchability for inactive (i.e. non-feeding) fish (Hayward et al.,1989). We hypothesize that the gillnets, if set over 24 hours (as mostly done for the stomach samplings of 2016 and 2017), will catch approximately the same shares of individuals starting and ending their daily feeding movements and thus they should provide good estimates for daily mean stomach content weights. Cod caught with trawl gear may have been less active. However, we hypothesize that these lower stomach contents observed in cod caught with trawl gear may be more attributed to depth rather than to a gear effect. This assumption is supported by the fact that gillnet catches in deeper areas also showed lower stomach content weights and no statistically significant differences from trawl samples in the same months, strongly pointing towards a general comparability of stomach data derived by the two fishing methods.

The use of angling as a method in stomach sampling has also been critically questioned, since it is hypothesized that baited hooks unintendedly showed a higher catchability for hungry fish (i.e. fish with low stomach contents) (Bromley, 1994; Iyabo, 2014) and thus led to a general underestimation of stomach content weights in the field. Unfortunately, the statistical comparison of our stomach samples collected during angling with those collected with gillnets and trawl was limited to one depth stratum, month and length class combination only. For this case we found no significant differences in stomach content weights between the fishing gears. However, in this case the stomach content weights were relatively low for all cod. The observation of relatively full stomach content weights in shallow water contradicts the hypothesis, that only hungry cod are caught during angling sampling. For example, the angling samples for May in 11-15m depths and for April in 6-10 m depths showed only marginal differences to stomach contents of cod caught with gillnets with slightly lower stomach content weights observed for the angling samples (supplementary figure S2.1.). Hence, it can be hypothesized that higher-order factors other than hunger play a role (e.g. aggression caused by the bait, or food envy towards other individuals) for a decision whether or not a cod attacks a bait.

Generally, our comparisons suggest that cod stomach data obtained from different fishing gears is comparable both in terms of food quantity and quality. However, evaluation of a gear effect on diet composition may require a thorough experimental set up using different fishing methods at the same area and at the same day and location, as well as shorter soaking times and more frequent hauling intervals for gillnets over 24 hours.



Supplementary figure S2.1. Boxplots of stomach content weights within each length-class per 5 m-depth strata, cod length class and sampling method (red – angling, green – gillnetting and blue – trawling) in 2016 and 2017. Stomach contents were length-standardized within each length class.

Supplementary table S2.2. Numbers of stomachs per sampling method, 5 m depth stratum, cod length class and month in 2016 and 2017. Yellow shading indicates samples used for statistical comparison of stomach content weights between sampling methods.

Length class	Depth stratum	Month	Angling	Gillnet	Trawl
31-40 cm	< 06 m	7	NA	1	NA
31-40 cm		8	NA	2	NA
31-40 cm		9	NA	2	NA
31-40 cm		10	NA	3	NA
31-40 cm		11	NA	1	NA
31-40 cm	06-10 m	4	2	3	NA
31-40 cm		5	NA	1	NA
31-40 cm		8	NA	3	NA
31-40 cm		10	NA	2	NA
31-40 cm		11	NA	2	NA
31-40 cm	11-15 m	2	NA	2	8
31-40 cm		3	1	NA	NA
31-40 cm		4	NA	1	NA
31-40 cm		5	12	3	NA
31-40 cm		6	NA	3	NA
31-40 cm		7	1	NA	NA
31-40 cm		9	NA	1	NA
31-40 cm		10	NA	2	NA
31-40 cm		11	NA	25	NA
31-40 cm		12	NA	4	NA
31-40 cm	16-20 m	1	NA	2	2
31-40 cm		2	NA	NA	1
31-40 cm		3	1	NA	31
31-40 cm		4	2	NA	NA
31-40 cm		5	2	NA	NA
31-40 cm		6	4	1	NA
31-40 cm		7	NA	3	2
31-40 cm		8	NA	2	1
31-40 cm		9	NA	4	NA
31-40 cm		11	NA	1	2
31-40 cm		12	NA	9	NA
31-40 cm	21 m+	1	NA	NA	26
31-40 cm		2	NA	NA	147
31-40 cm		3	2	NA	25
31-40 cm		4	NA	NA	28
31-40 cm		11	NA	NA	6

Length class	Depth stratum	Month	Angling	Gillnet	Trawl
41-50 cm	< 06 m	7	NA	1	NA
41-50 cm		8	NA	2	NA
41-50 cm		9	NA	2	NA
41-50 cm		10	NA	3	NA
41-50 cm		11	NA	1	NA
41-50 cm	06-10 m	4	2	3	NA
41-50 cm		5	NA	1	NA
41-50 cm		8	NA	3	NA
41-50 cm		10	NA	2	NA
41-50 cm		11	NA	2	NA
41-50 cm	11-15 m	2	NA	2	8
41-50 cm		3	1	NA	NA
41-50 cm		4	NA	1	NA
41-50 cm		5	12	3	NA
41-50 cm		6	NA	3	NA
41-50 cm		7	1	NA	NA
41-50 cm		9	NA	1	NA
41-50 cm		10	NA	2	NA
41-50 cm		11	NA	25	NA
41-50 cm		12	NA	4	NA
41-50 cm	16-20 m	1	NA	2	2
41-50 cm		2	NA	NA	1
41-50 cm		3	1	NA	31
41-50 cm		4	2	NA	NA
41-50 cm		5	2	NA	NA
41-50 cm		6	4	1	NA
41-50 cm		7	NA	3	2
41-50 cm		8	NA	2	1
41-50 cm		9	NA	4	NA
41-50 cm		11	NA	1	2
41-50 cm		12	NA	9	NA
41-50 cm	21 m+	1	NA	NA	26
41-50 cm		2	NA	NA	147
41-50 cm		3	2	NA	25
41-50 cm		4	NA	NA	28
41-50 cm		11	NA	NA	6

Length class	Depth strata	Month	Angling	Gillnet	Trawl
51-60 cm	< 06 m	5	NA	1	NA
51-60 cm		7	NA	1	NA
51-60 cm		9	NA	4	NA
51-60 cm		10	NA	39	NA
51-60 cm		11	NA	36	NA
51-60 cm	06-10 m	1	NA	1	NA
51-60 cm		3	3	NA	NA
51-60 cm		4	4	29	NA
51-60 cm		5	2	7	NA
51-60 cm		8	NA	7	NA
51-60 cm		9	NA	2	NA
51-60 cm		11	NA	4	NA
51-60 cm	11-15 m	1	NA	3	NA
51-60 cm		2	NA	13	1
51-60 cm		4	1	6	NA
51-60 cm		5	4	13	NA
51-60 cm		6	NA	14	NA
51-60 cm		7	2	NA	NA
51-60 cm		8	NA	48	NA
51-60 cm		9	NA	12	NA
51-60 cm		10	NA	7	NA
51-60 cm		11	NA	24	NA
51-60 cm		12	NA	8	NA
51-60 cm	16-20 m	1	NA	26	NA
51-60 cm		2	NA	1	5
51-60 cm		3	4	NA	8
51-60 cm		4	2	NA	NA
51-60 cm		5	3	20	NA
51-60 cm		6	18	1	NA
51-60 cm		7	4	34	56
51-60 cm		8	NA	31	7
51-60 cm		9	NA	19	NA
51-60 cm		11	NA	8	NA
51-60 cm		12	NA	15	NA
51-60 cm	21 m+	1	NA	NA	27
51-60 cm		2	NA	2	44
51-60 cm		3	2	NA	46
51-60 cm		4	NA	NA	20
51-60 cm		7	NA	NA	50
51-60 cm		11	NA	NA	3

Length class	Depth stratum	Month	Angling	Gillnet	Trawl
61-70 cm	< 06 m	5	NA	3	NA
61-70 cm		10	NA	4	NA
61-70 cm		11	NA	13	NA
61-70 cm	06-10 m	4	NA	4	NA
61-70 cm		5	NA	4	NA
61-70 cm		7	NA	2	NA
61-70 cm		8	NA	2	NA
61-70 cm		9	NA	4	NA
61-70 cm		10	4	NA	NA
61-70 cm		11	NA	6	NA
61-70 cm	11-15 m	1	NA	1	NA
61-70 cm		2	NA	9	NA
61-70 cm		4	NA	4	NA
61-70 cm		5	3	11	NA
61-70 cm		6	NA	14	NA
61-70 cm		7	1	NA	NA
61-70 cm		8	NA	34	NA
61-70 cm		9	NA	4	NA
61-70 cm		10	NA	2	NA
61-70 cm		11	NA	20	NA
61-70 cm		12	NA	17	NA
61-70 cm	16-20 m	1	NA	35	2
61-70 cm		2	NA	2	1
61-70 cm		3	NA	NA	1
61-70 cm		5	NA	5	NA
61-70 cm		6	27	2	NA
61-70 cm		7	12	50	50
61-70 cm		8	NA	22	38
61-70 cm		9	NA	16	NA
61-70 cm		11	NA	5	NA
61-70 cm		12	NA	27	NA
61-70 cm	21 m+	1	NA	NA	6
61-70 cm		2	NA	2	14
61-70 cm		3	NA	NA	18
61-70 cm		4	NA	NA	3
61-70 cm		7	NA	NA	50
61-70 cm		11	NA	NA	5

Length class	Depth stratum	Month	Angling	Gillnet	Trawl
71 cm+	06-10 m	4	NA	3	NA
71 cm+		5	NA	1	NA
71 cm+		8	NA	1	NA
71 cm+		9	NA	1	NA
71 cm+		10	2	NA	NA
71 cm+		11	NA	2	NA
71 cm+	11-15 m	1	NA	1	NA
71 cm+		2	NA	3	NA
71 cm+		4	NA	2	NA
71 cm+		5	1	6	NA
71 cm+		8	NA	19	NA
71 cm+		9	NA	2	NA
71 cm+		10	NA	2	NA
71 cm+		11	NA	5	NA
71 cm+		12	NA	4	NA
71 cm+	16-20 m	1	NA	15	5
71 cm+		2	NA	1	NA
71 cm+		3	NA	NA	3
71 cm+		5	NA	2	NA
71 cm+		6	6	NA	NA
71 cm+		7	3	4	74
71 cm+		8	NA	4	4
71 cm+		9	NA	1	NA
71 cm+		11	NA	NA	2
71 cm+		12	NA	13	NA
71 cm+	21 m+	1	NA	NA	1
71 cm+		2	NA	1	11
71 cm+		3	NA	NA	36
71 cm+		7	NA	NA	39
71 cm+		8	NA	NA	2
71 cm+		11	NA	NA	3

S3. Multinomial regression model

Supplementary table S3.1. Parameter estimates and significance levels for the finally selected multinomial logistic regression model. SE – Standard Error, p-value – significance level (significance code: p < 0.1 – . , p < 0.05 – *, p < 0.01 – **, p < 0.001 – ***). Cluster numbers display the diet clusters revealed by hierarchical clustering with 1 – Other fish (reference cluster), 2 – Common shore crab, 3 – Other invertebrates, 4 – flatfish, 5 – Peracarids, 6 – Molluscs, 7 – Annelids, and 8 – Clupeids.

Cluster	Coefficient	Estimate	Std. Errors	z value	p value	signif.
2	Intercept	-2.1	0.9	-2.34	0.02	*
	length	0.05	0.01	4.22	0.00	***
	depth	-0.11	0.03	-3.59	0.00	***
	quarter 2	2.75	1.54	1.78	0.08	.
	quarter 3	1.05	1.2	0.87	0.38	
	quarter 4	3.05	1.06	2.88	0.00	**
	depth:quarter 2	-0.08	0.05	-1.6	0.11	
	depth:quarter 3	0.11	0.05	2.22	0.03	*
	depth:quarter 4	-0.04	0.04	-0.93	0.35	
	length:quarter 2	0.01	0.02	0.25	0.80	
	length:quarter 3	-0.02	0.02	-0.97	0.33	
	length:quarter 4	-0.03	0.02	-1.81	0.07	.
3	Intercept	0.3	1.38	0.22	0.83	
	length	-0.07	0.02	-3.64	0.00	***
	depth	0.06	0.04	1.41	0.16	
	quarter 2	9.56	2.51	3.81	0.00	***
	quarter 3	-4.44	2.04	-2.17	0.03	*
	quarter 4	3.25	1.82	1.78	0.07	.
	depth:quarter 2	-0.36	0.08	-4.61	0.00	***
	depth:quarter 3	0.17	0.08	1.95	0.05	.
	depth:quarter 4	-0.08	0.06	-1.33	0.18	
	length:quarter 2	-0.07	0.04	-1.61	0.11	
	length:quarter 3	0.06	0.03	2.18	0.03	*
	length:quarter 4	-0.03	0.03	-0.9	0.37	

4	Intercept	-11.5	1.47	-7.84	0.00	***
	length	0.12	0.02	6.78	0.00	***
	depth	0.09	0.04	2.09	0.04	*
	quarter 2	8.11	3.62	2.24	0.03	*
	quarter 3	8.3	1.74	4.77	0.00	***
	quarter 4	4.66	2.07	2.25	0.02	*
	depth:quarter 2	-0.1	0.11	-0.92	0.36	
	depth:quarter 3	-0.17	0.06	-2.8	0.01	**
	depth:quarter 4	-0.19	0.07	-2.7	0.01	**
	length:quarter 2	-0.1	0.05	-1.93	0.05	.
	length:quarter 3	-0.05	0.02	-1.94	0.05	.
	length:quarter 4	-0.02	0.03	-0.62	0.53	
5	Intercept	-0.8	0.98	-0.81	0.42	
	length	-0.12	0.01	-9.06	0.00	***
	depth	0.26	0.04	7.5	0.00	***
	quarter 2	-0.38	2.17	-0.17	0.86	
	quarter 3	-1.06	1.55	-0.68	0.50	
	quarter 4	4.03	1.77	2.28	0.02	*
	depth:quarter 2	-0.06	0.07	-0.84	0.40	
	depth:quarter 3	0.11	0.07	1.55	0.12	
	depth:quarter 4	-0.25	0.05	-4.57	0.00	***
	length:quarter 2	0.06	0.03	2.18	0.03	*
	length:quarter 3	0.03	0.02	1.56	0.12	
	length:quarter 4	0.01	0.03	0.23	0.82	
6	Intercept	5.45	1.17	4.66	0.00	***
	length	-0.13	0.02	-6.8	0.00	***
	depth	-0.03	0.03	-0.8	0.43	
	quarter 2	-9.36	3.23	-2.9	0.00	**
	quarter 3	-6.33	2.04	-3.11	0.00	**
	quarter 4	-11.56	2.78	-4.16	0.00	***
	depth:quarter 2	0.31	0.1	2.99	0.00	**
	depth:quarter 3	0.29	0.09	3.24	0.00	**
	depth:quarter 4	-0.1	0.11	-0.9	0.37	
	length:quarter 2	0.08	0.04	2.08	0.04	*
	length:quarter 3	0.04	0.03	1.33	0.18	
	length:quarter 4	0.2	0.05	3.73	0.00	***

7	Intercept	3.21	1.39	2.31	0.02	*
	length	-0.06	0.02	-2.76	0.01	**
	depth	-0.11	0.04	-2.76	0.01	**
	quarter 2	4.65	2.3	2.02	0.04	*
	quarter 3	-3.48	1.84	-1.89	0.06	.
	quarter 4	3.2	2.19	1.46	0.14	
	depth:quarter 2	-0.05	0.06	-0.75	0.45	
	depth:quarter 3	0.26	0.07	3.62	0.00	***
	depth:quarter 4	-0.11	0.07	-1.65	0.10	.
	length:quarter 2	-0.07	0.04	-1.65	0.10	.
	length:quarter 3	0.01	0.03	0.42	0.67	
	length:quarter 4	-0.06	0.04	-1.57	0.12	
8	Intercept	0.38	0.81	0.47	0.64	
	length	-0.02	0.01	-1.74	0.08	.
	depth	-0.01	0.03	-0.43	0.67	
	quarter 2	3.42	1.72	1.99	0.05	*
	quarter 3	-7.42	3.4	-2.18	0.03	*
	quarter 4	-2.72	1.37	-1.99	0.05	*
	depth:quarter 2	-0.17	0.05	-3.14	0.00	**
	depth:quarter 3	0.21	0.16	1.33	0.18	
	depth:quarter 4	0.06	0.05	1.3	0.19	
	length:quarter 2	-0.01	0.03	-0.29	0.77	
	length:quarter 3	0.04	0.04	0.88	0.38	
	length:quarter 4	0.02	0.02	0.71	0.48	

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Chapter III

An individual-based bioenergetic growth model for adult cod (*Gadus morhua*) in the Western Baltic Sea

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Abstract

Growth is a key component in fish stock dynamics. Since it was revealed that several gadoid stocks showed inconsistencies in growth estimates derived from traditional otolith readings, effort has shifted to alternative growth estimation methods. One alternative is the application of bioenergetic modelling, which uses information on ambient temperature, food intake and physiological processes to estimate growth. In this study, we present an individual-based bioenergetic model for adult cod in the Western Baltic Sea, using information on seasonal depth-distribution and depth-specific food intake. Our results showed that growth of cod varies with season with fastest and slowest length growth taking place in autumn and in winter, respectively. During peak summer periods we observed occasional weight losses. Model results were used to investigate whether the recently validated formation of translucent zones (TZ) on Western Baltic cod otoliths during summer are related with temperature and/or

growth. The realization of large daily length increments of the modelled cod during summer in combination with high ambient temperatures at residing sites of the cod pointed strongly towards temperature related TZ formations rather than be induced by reduced growth. Comparisons of von Bertalanffy growth parameter estimates derived from our bioenergetic model with empiric parameters estimated from tag recapture data revealed a good correspondence and highlights the potential of our method.

1. Introduction

The growth of fish species is one of the key components for understanding their stock dynamics and a prerequisite for stock assessment and management. Traditionally, age-readings and length at age relationships derived from samples from a stock are used to calculate growth rates of a stock. However, there are two important cases of gadoid species in European waters, Eastern Baltic cod (*Gadus morhua*) and European hake (*Merluccius merluccius*), with substantial uncertainties regarding their age-determinations derived from otolith readings (de Pontual et al., 2006; Hüssy et al., 2016). In case of the Eastern Baltic cod the formation of intermediate otolith rings renders age estimation difficult and make reliable estimations of growth impossible. This has drastic negative effects on stock assessment. These problems in age-reading led first to a stop of analytical age-based assessments and finally to a suspension of the scientific advice (ICES, 2015). For the age determination of Western Baltic cod otolith readings are considered less severe than in Eastern Baltic cod. However, in the past, the temporal formation of the first translucent zone (TZ) was highly controversial and therefore, led to uncertainties in the age determination of about one year (McQueen et al. 2019a). Clarity in age determination for the Western Baltic cod was finally reached by using a tetracycline-hydrochloride induced permanent fluorescent mark on otoliths in tag-recapture experiments which revealed the formation of TZs during the summer season in juvenile (McQueen et al., 2019b) as well as in adult individuals (Krumme et al., unpublished). However, it remained unclear whether changes in ambient temperature (Høie and Folkvord, 2006; Neat et al., 2008) and/or seasonal fluctuations in feeding patterns (Høie et al., 2008) lead to the formation of these translucent otolith ring patterns.

Tag-recapture experiments such as conducted in the Western Baltic Sea (McQueen et al., 2019a, McQueen, et al., 2019b, Krumme et al., unpublished) can not only be used for the temporal determination of TZs in otoliths. They are rather a commonly accepted alternative to traditional otolith age-readings in terms of growth determination in long-lived fish species such as gadoids (McQueen et al., 2019a; Piñeiro et al., 2007; Shackell et al., 1997; Tallack, 2009). However, tagging is costly and the reliability and quality of the growth estimates strongly depends on the recapture rates. For example, current tag-recapture experiments on Western Baltic cod resulted in recapture rates of less than 1% and thus, show the difficulties of this approach (Krumme et al., unpublished). Another alternative to the traditional methods of growth estimation is bioenergetic modelling (Hansen, 1993; Ney, 1993). Bioenergetic models are, based on the second law of thermodynamics, described by an energy balance equation. The growth rate of a fish is determined as the difference between food consumption rate and the sum of energy output rates, which include metabolic losses, specific dynamic action and waste losses (Kitchell et al., 1977). In the last decades, bioenergetic models were established to estimate growth of fish under controlled aquaculture conditions (e.g. Cuenco et al., 1985) as well as for fish stocks in more variable natural environments (e.g. Beauchamp, 2009; Constantini et al., 2008; Kitchell et al., 1977). Bioenergetic growth modelling in natural environment requires a sound knowledge on the spatio-temporal distribution of the modelled species and in-situ environmental conditions, especially ambient temperature. Temperature directly affects the physiological processes, including energy uptake through consumption and metabolic losses. Moreover, in order to estimate reliable food energy intake rates, studies on stomach content weight, diet composition and on gastric evacuation rates are prerequisites. However, if this information is available, bioenergetic modelling may provide a good alternative to traditional growth estimation methods, especially for species such as Eastern Baltic cod, where otolith age-readings are unfeasible. For cod, many physiological processes such as gastric evacuation (Andersen, 2001; Andersen et al., 2016; dos Santos and Jobling, 1991,1995; Temming and Andersen, 1994; Temming and Herrmann, 2003; Ursin et al., 1985), consumption (Temming and Herrmann, 2003), net-conversion efficiency

(Temming and Herrmann, 2009) and metabolic rates (Jobling, 1982; Saunders, 1963) have been well studied for decades in laboratory experiments, making it an ideal case study species for bioenergetic modelling. In this study, we use cod from the Belt Sea (southwestern part of the Western Baltic Sea; SD22) to set up a bioenergetic growth model. Growth parameter estimates of Western Baltic cod are also available from a tag-recapture study published in 2019 (McQueen et al., 2019a), which give us an excellent starting position to test the performance of our model. Furthermore, recent findings on spatio-temporal distribution (Funk et al., unpublished) and feeding ecology of cod in the Western Baltic Sea (Funk et al., unpublished) lay down the necessary (updated) data basis for a bioenergtic growth model of Western Baltic cod.

This study aims (i) to set up an individual-based bioenergetic model of cod in the Belt Sea and compare the model results to recent growth estimations from tag-recapture data to evaluate bioenergetic growth modelling performance. Moreover, we want to examine (ii) if the individual-based biogenetic modelling provides insights into TZ formation in otoliths of cod in the Western Baltic Sea and whether these are related to ambient temperature and/or growth.

2. Materials and methods

2.1. Study area

We choose to set up our model for cod in the Belt Sea, ICES subdivision (SD) 22 (Fig. 1). The Belt Sea is a stratified brackish-water and microtidal area (tidal range: ~ 10 cm) in the temperate zone (Leppäranta and Myrberg, 2000; Snoeijs-Leijonmalm and Andrén, 2017). SD22 forms together with the Sound (SD23) and the Arkona Sea (SD24) the Western Baltic Sea. The area is characterized by continuous fluctuations in hydrography, mainly due to wind-induced 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. The Belt Sea is generally relatively shallow. Areas shallower than 20 m water depth amount to 70% of the Belt Sea and areas shallower than 10 m water depth still cover 29% (Fig. 1, ICES, 2017).

SD22 is also (together with SD23) known as the core area of the Western Baltic cod stock, while SD24 is known as the transition zone between the Eastern and the

Western Baltic cod stock (Bleil et al., 2009; Hemmer-Hansen et al., 2019). A mixing between the two stocks is considered negligible in SD22 (ICES, 2019).

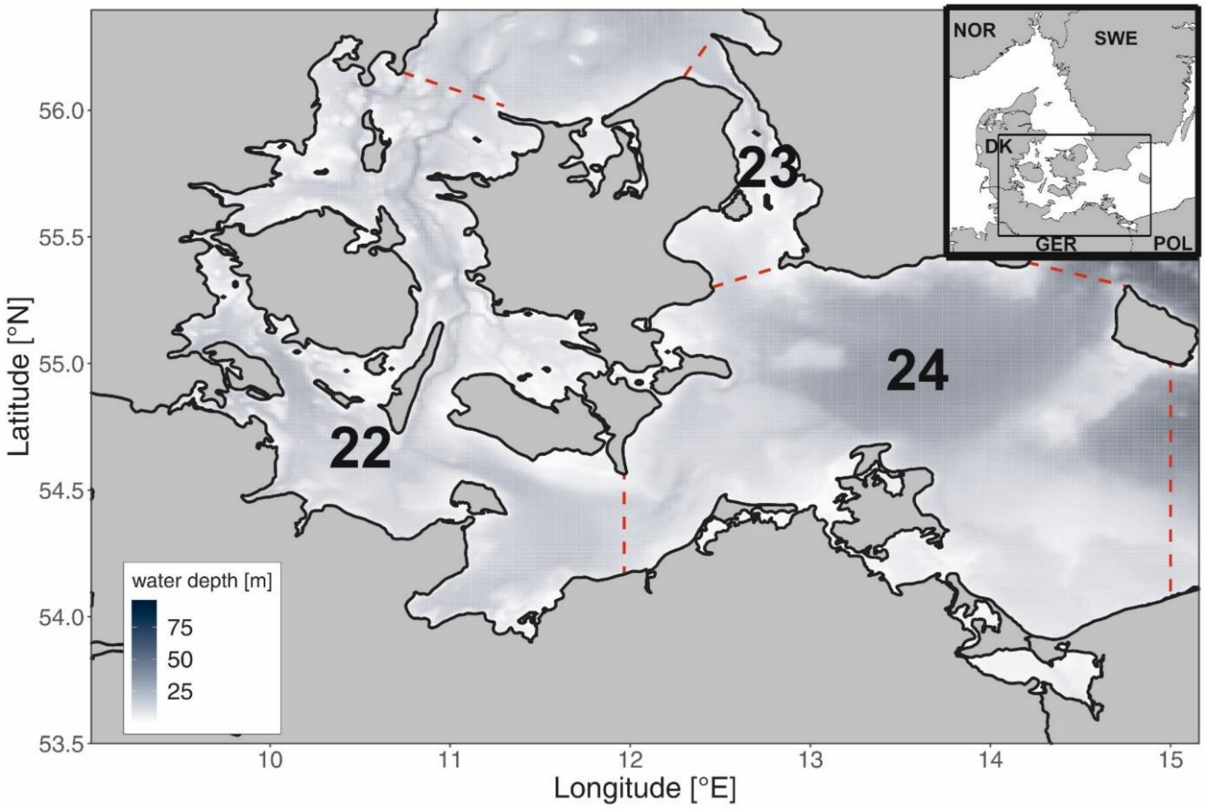

Figure 1. Bathymetric map of the Western Baltic Sea. The dashed red lines indicate the borders of the subdivisions, which form the Western Baltic Sea: The Belt Sea (SD22; the chosen study area), the Sound (SD23), and the Arkona Sea (SD24).

2.2 Bioenergetic model

To perform our bioenergetic model, we used a number-of sub models, including models on depth-use, stomach content weights and diet composition as well as a number of functions describing the physiological processes (Fig. 2). We used an individual-based modelling approach to model the yearly growth of cod in the Belt Sea. The individual behavior of cod was taken into account in the modelling approach by randomly adding observed variation on the predictions of the sub-models. Growth of cod was modelled on a daily basis over a time of 365 modelling days for a given modelling year j. Predictions of sea surface temperature (SST) and of a value for the proxy of stratification were derived from a hydrodynamic model of the study area for each time step i in the specific modelling year j. These temperature values were used in addition to the length of the cod at time step i (at i = 1, length = initial length) to predict the residence depth of the individual using a depth use submodel. Subsequently, ambient temperature (temperature at residence depth) was allocated to the predicted residence depth of the cod at time step i.

Information on the residence depth, temperature at residence depth and cod length at time step i were then used to predict the stomach content weight of the cod. We moreover used the cod length and residence depth at time step i in addition to information on the quarter (resulting from the Julian day at time step i) to determine the diet composition of the cod at time step i.

Subsequently, information on cod length, on diet composition, on the temperature at residence depth and on stomach content weight at time step i were used to calculate the daily consumption of the cod at time step i.

Furthermore, losses through standard metabolism were estimated in our model by calculating a maintenance ration using the weight of the cod, the food composition and the ambient temperature at time step i (at i = 1 the weight was directly calculated from the initial length). From the difference of the daily consumption and the metabolic rate the food for growth at time step i was derived, which was further used to calculate the weight and length gain of the modelled fish at time step i (Fig. 2).

Detailed descriptions for all used submodels, physiological functions, allocations and initial values used in our bioenergetic modelling approach are given below.

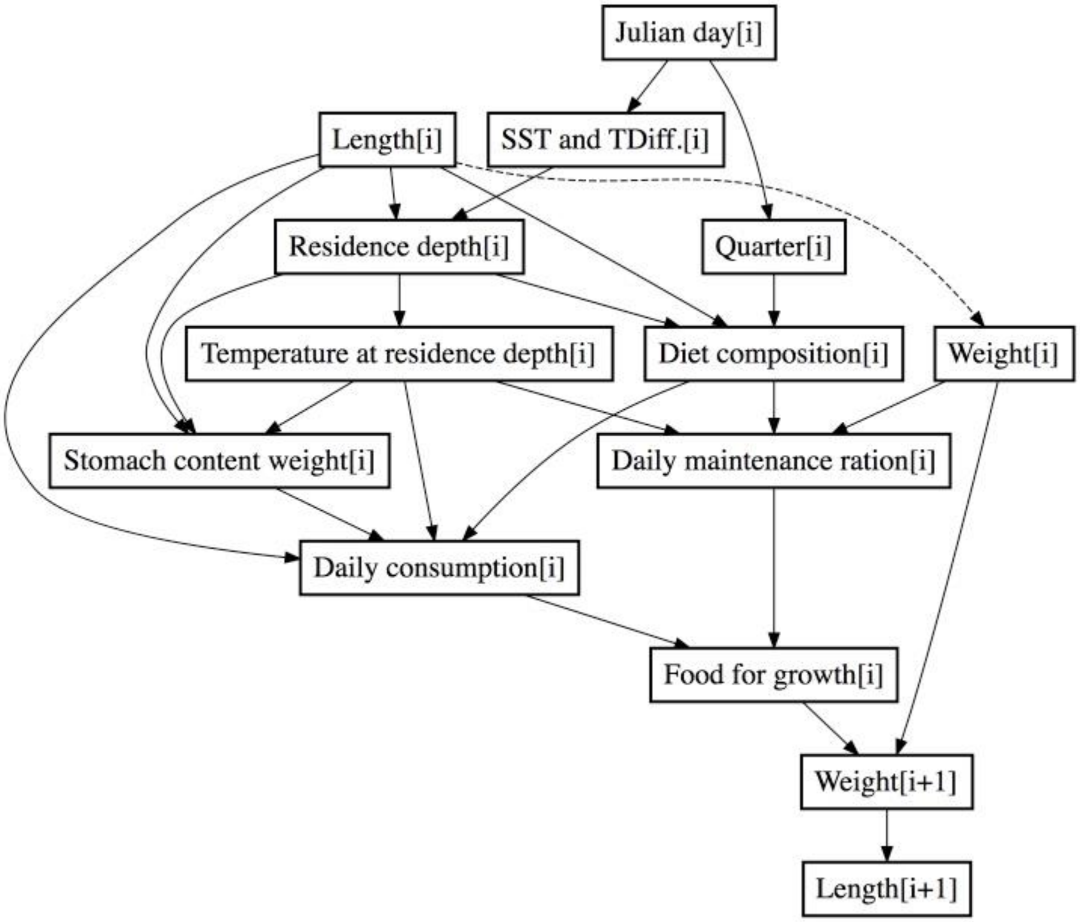

Figure 2. Schematic representation of the individual-based bioenergetic growth model at time step i. Arrows displaying pathways between sub-models and physiological functions. The dashed arrow denotes the pathway to estimate the initial weight which is only used at time step i = 1.

2.2.1. Initial length

For initial length at age we used age-based length measurements from the Baltic International Trawl Surveys (BITS) in the first quarter (of the period 1991-2018) downloaded from the International Council for the Exploration of the Sea (ICES) database DATRAS (Database of Trawl Surveys of BITS, extraction 14th of May 2019, ICES, Copenhagen). We chose to use BITS data from SD22 and SD23 (core areas of the Western Baltic cod stock) to increase the overall number for subsequent calculation of length weight relationships. We assume survey catches do better reflect the real length distributions in the population for males than for females (see supplementary material S1). Hence, we set up our model for males only.

2.2.2. Length-weight relationships

Some of the sub-models used in our modelling approach are based on length, while other functions, for example the function describing standard metabolism, are based on cod weight. Hence, a permanent transfer between length and weight is a prerequisite in our modelling approach. Therefore, we developed two different length-weight relationships (LWR) from the BITS data, one for post-spawning males ($LWR_{post\text{-}spawning}$; N = 3512; $R^2 = 0.95$) (1), and one for spawning individuals ($LWR_{spawning}$; N = 236; $R^2 = 0.98$) (2).

$$Weight\ [g]_{post-spawning} = 0.010 * Length\ [cm]^{2.97} \tag{1}$$

$$Weight\ [g]_{spawning} = 0.008 * Length\ [cm]^{3.05} \tag{2}$$

Since we wanted to model adult, i.e. mature, cod we had to consider energetic losses due to spawning activity, i.e. the levy of reproductive products. The start weight of the individual cod at modelling day 1 was calculated by using $LWR_{post\text{-}spawning}$, to account for weight losses caused by spawning activity. We decided to start our modelling with post-spawning fish and end up modelling before spawning. We simplified spawning activity, to a single day. Thus, we could model the growth of cod over 365 days without considering losses due to batch spawning. We chose the 14th of February (Julian day 45) as the day of spawning and the 15th of February as the starting day of our bioenergetic modelling. It should be noted, that the 14th of February reflects a date in the beginning of the spawning season of cod in the Belt Sea, which is known to extend from January to June (Kändler, 1949; Thurow, 1970; Bleil et al., 2009). Our modelling ended at the 14th of February (Julian day 45) of the following year. All further translations from length to weight and vice versa during the modelling were calculated by using the $LWR_{spawning}$.

2.2.3. Water temperature data

Water temperature data were taken from the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM; Lehmann and Hinrichsen, 2000; Lehmann et al., 2002; Lehmann et al., 2014; for further description see supplementary material S2). We calculated daily mean temperature values over the whole area of ICES SD22 with 3 m depth strata. We used the temperatures of the depth stratum 0-3 m as sea surface temperature (SST) for later use in the depth use modelling. In addition, a proxy for stratification (TDiff.) was estimated by calculating the temperature difference between the depth strata 0-3 m and the mean of the depth strata 21-23 m and 24-27 m (reflecting the sea bottom temperature in the deeper channels of the Belt Sea).

2.2.4. Residence depth and water temperature at residence depth

In order to predict the daily residence depth of cod we used a depth use model based on knowledge of gillnet fishers (Funk et al., unpublished). This model predicts specific depths selected by gillnet fishers for targeting cod in relation to the sea surface temperature and stratification. Following the assumption that the fishers always tend to fish where the cod tend to move across, this model should allow to use gillnet catch depth estimates directly as an estimate for the residence depth of cod. The used model included the explanatory factor variable mesh size with the two categories 110-119 mm and ≥ 120 mm. Funk et al. (unpublished) revealed that larger mesh sizes were typically used in deeper waters, and they related this with a size-related depth use of cod.

Looking at relative selectivity curves of gillnets with mesh sizes of 110 mm (supplementary material S3), the peak in relative retention can be observed at total lengths of less than 50 cm decreasing sharply with increasing cod length. At a body length of 55 cm, gillnets with a mesh size of 110 mm display a relative selectivity of less than 25%. Hence, in our spatial modelling we decided that cod < 55 cm should use shallower habitats, i.e. choosing depth like fishers using mesh sizes of 110 mm (3), while cod ≥ 55 cm should use deeper habitats, i.e. choosing depth like fishers using mesh sizes of ≥ 120 mm (4).

$$Res.d._{Cod<55cm,i}\ [m] = 20.21\ [m] - 2.73\ [m * °C^{-1}] * SST_i\ [°C] + 0.11\ [m * °C^{-2}] * SST_i\ [°C]^2 + 0.58\ [m * °C^{-1}] * TDiff.[°C] + \varepsilon_i\ [m] \quad (3)$$

$$Res.d._{Cod\geq 55cm,i}\ [m] = 24.11\ [m] - 2.73\ [m * °C^{-1}] * SST_i\ [°C] + 0.11\ [m * °C^{-2}] * SST_i\ [°C]^2 + 0.58\ [m * °C^{-1}] * TDiff.[°C] + \varepsilon_i\ [m] \quad (4)$$

With $Res.d._{Cod<55cm,i}\ [m]$ – Residence depth of cod < 55cm at time step i, $Res.d._{Cod\geq 55cm,i}\ [m]$ – Residence depth of cod ≥ 55cm at time step i, $SST_i\ [°C]$, sea surface temperature at time step i, TDiff. – proxy for stratification at time step i, and ε_i – random model residual at time step i.

We added variability to the depth use of cod by adding a random residual of the depth use model on each depth prediction. Since depths > 25 m are rare in the Belt Sea and the Sound we decided to artificially limit the residence depth predictions to a maximum of 25 m. The minimum residence depth was set to zero.

Furthermore, we assigned the ambient temperature to each residence depth estimate by allocating the mean temperature values of the corresponding closest depth stratum taken from the BSIOM.

2.2.5 Stomach content weight and diet composition

We used models from Funk et al. (unpublished) to predict the daily stomach content weights and compositions of cod from the Belt Sea. Funk et al. (unpublished) provide depth-stratified stomach data for cod in SD22 on a monthly basis from 2016 and 2017. The use of different sampling methods (i.e. commercial trawl and gillnet fishery, scientific trawl surveys and angling samples) enabled a thorough spatio-temporal coverage including also shallow and hard structured habitats largely neglected in previous stomach sampling designs (Funk et al., unpublished).

We predicted the stomach content weight by using the Generalized Additive Model (GAM) described by Funk et al. (unpublished), where cod length, residence depth and water temperature at residence depth were used as explanatory variables. See supplementary material S4 for further descriptions of the GAM. We added a randomly chosen residual of the GAM model on the predicted log-transformed stomach content weight to take observed variability in stomach content weights into account. The predicted stomach content weight estimates derived from the GAM contained digestive mucus, which was corrected subsequently by subtracting a length-based estimate of the mucus weight (supplementary material S5).

Moreover, we used the multinomial logistic regression model described by Funk et al. (unpublished) to predict the probabilities for diet cluster membership in relation to cod length, quarter (derived from the Julian day at time step i) and residence depth. The applied model predicts the probability of membership for eight diet clusters as conceived in the study of Funk et al. (unpublished), namely 1 – other/unidentified fish, 2 – common shore crab, 3 – other/unidentified crustaceans, 4 – Flatfishes, 5 – Peracarids, 6 – Molluscs, 7- Clupeiformes, and 8 – Annelids. Each of these diet clusters, was mainly dominated by a specific prey group, according to which a prey specific gastric evacuation coefficient (ρ_k) and a prey specific energy content was assigned at every time step i (supplementary material S6). To take variability in diet composition between individuals into account, we used predicted probabilities for all clusters and created a vector containing each diet cluster x times, where x equals the rounded probability percentage predicted for each cluster by the model at time step i. Subsequently, a diet cluster was randomly chosen from the vector and used as diet cluster for the cod at the time step i.

2.2.6. Daily consumption

Based on the prediction of stomach content weight at time step i as well as the allocated gastric evacuation constant ρ_k and allocated temperature at residence depth we calculated daily consumption estimates by using the formula of Temming and Herrmann (2003) (6). In this approach, the predicted stomach content weight was used to reflect a mean stomach content weight of the modelled cod over 24 hours.

While the function for daily consumption of cod by Temming and Herrmann (2003) uses the weight of the predator, we assume that daily consumption is more dependent on the cod length instead of the weight, and thus, fluctuations in weight at a given length should not affect consumption rates. Hence, we used a full weight ($W_{F\ i}$) based on the current length of the predator at time step i calculated with the LWR$_{\mathrm{spawing}}$ instead of using the current predator weight at time step i (5).

$$W_{F\,i} = 0.008\,L_i^{3.05} \tag{5}$$

with $W_{F\,i}$ – length dependent full weight of the cod at time step i, and L_i – length of the cod at time step i.

$$C_{24\,i} = 24 * \rho_{k\,i} * W_{F\,i}^{0.305} * e^{0.11 * T_i} * S_i^{0.5} \tag{6}$$

with $C_{24\,i}$ – daily consumption at model time step i, $\rho_{k\,i}$ – allocated prey specific gastric evacuation constant for predicted diet cluster k at time step i, $W_{F\,i}$ – length dependent full weight of the cod at time step i, T_i– the allocated temperature the residence depth of the cod at time step i, and S_i – the predicted stomach content weight at time step i.

2.2.7. Daily maintenance ration

For calculating growth in our bioenergetic model, we followed the overall K3 approach presented in Temming and Herrmann (2009). Both, consumption and metabolic losses are expressed in rations of prey. The difference between these gives the food for growth, which is subsequently multiplied by a prey specific net conversion efficiency, termed K3, to estimate the weight gain of the predator. K3 includes all other energetic losses due to excretion, feces and specific dynamic action.

The daily maintenance ration was calculated using the parameter estimates derived from laboratory experiments investigating the routine metabolism of Atlantic cod (Panten, 1995). The formula of the maintenance ration was further corrected by a temperature factor derived from laboratory experiments of Saunders (1963) (7). In contrast to the calculation of the daily consumption, we assume that daily maintenance ration is directly dependent on the current fish weight and, thus, fluctuations in the body weight of cod should directly affect routine metabolism. Hence, we decided to use the current predator weight at time step i (W_i) for the calculation of the daily maintenance ration. Moreover, we added an activity multiplier (Act) for cod activity in the field of 1.25 for the calculation of the daily maintenance ration which was taken from Hansson et al. (1996).

$$R_{maint\ i}[kcal * \ day^{-1}] = 0.012 * \ e^{0.056*T_i} * \ W_i^{0.736} * Act \qquad (7)$$

With $R_{maint\ i}$ – maintenance ration at time step i, T_i – the allocated temperature the residence depth of the cod at time step i, W_i – the weight of the cod at time step i, and Act – the activity multiplier.

We used the allocated prey energy density of the predicted diet composition cluster k at time step i to transform the maintenance ration from kcal in g of ingested food (8).

$$R_{maint\ i}[g * \ day^{-1}] = \frac{R_{maint\ i}[kcal * \ day^{-1}]}{E_{k\ i}[kcal * g^{-1}]} \qquad (8)$$

With $R_{maint\ i}$ – the maintenance ration at time step i, and E_k– the prey specific energy density of allocated diet composition cluster k at time step i.

2.2.8. Growth of cod

Estimates of daily consumption and daily maintenance ration were used to estimate the daily food for growth following the approach of Temming and Herrmann (2009) (9).

$$ffg_i\ [g * \ day^{-1}] = \ C_{24\ i}\ [g * \ day^{-1}] - \ R_{maint\ i}[g * \ day^{-1}] \qquad (9)$$

With ffg_i – the food for growth at model time step i, $C_{24\ i}$ – the daily consumption at model time step i, and $R_{maint\ i}$ – the maintenance ration at model time step i.

We calculated the daily growth increment in weight by multiplying the daily food for growth with the conversion efficiency K3 (Temming and Hermann, 2009). In our model, K3 was set to a constant value of 0.35. Observed K3 values in laboratory feeding experiments of cod conducted by Temming (1995) ranged between 0.303

(cod fed with *Crangon crangon*) and 0.55 (cod fed with *Pomatoschistus* spp.). Since recent investigations on the diet composition of cod in the Belt Sea revealed high contributions of benthic invertebrates and especially crustacean species (Funk et al., unpublished), we chose to use a rather suboptimal K3 with 0.35 in the bioenergetic growth model. Daily growth increment was added to the current weight of the predator giving the starting weight for the next time step (10).

$$W_{i+1} = W_i + ffg_i * K3 \tag{10}$$

With W_{i+1} – the weight of the cod at time step i+1, W_i the weight of the cod at time step i, ffg_i – the food for growth at time step i, and $K3$ – the conversion efficiency.

Furthermore, we calculated L_{i+1} from W_{i+1} by using the LWR$_{\text{spawning}}$ (11). Using this formula, a loss in weight would result in a decrease in length, which is not reasonable under a physiological point of view. Hence, in this case we decided to set L_{i+1} equally to L_i (12).

$$L_{i+1} = \frac{W_{i+1}^{(\frac{1}{3.05})}}{0.008} \tag{11}$$

$$L_{i+1} = L_i \; if \; L_i > \frac{W_{i+1}^{(\frac{1}{3.05})}}{0.008} \tag{12}$$

With L_{i+1} – length of the cod at time step i+1, W_{i+1} – weight of the cod at time step i+1, and L_i – length of the cod at time step i.

2.3. Application of bioenergetic model results

2.3.1. Comparing predicted growth with field observations

Growth modelling was performed for the ages 2 to 4 for the years 2016 and 2017, which were the years used for the stomach sampling. The growth of 1000 individual fish for the age classes 2-4 and both sampling years were modelled over a time of 365 modelling days. The predicted end lengths (predicted end length of cod grown over 365 starting in 2016 and 2017) were then compared with observations in the field derived from the BITS Q1 in 2017 and 2018.

Moreover, we calculated the parameters k and L_∞ of the Von Bertalanffy Growth Function (VBGF) from our model predictions (13, 14). For this we pooled together all growth estimates from our model runs for both modelling years (N = 6000) and calculated a linear regression where the predicted growth increment was explained by the initial start length. The resulting parameter estimates of intercept and slope were used as VGBF parameters E and $-k$, respectively (13). The VBGF parameter estimates derived from the bioenergetic model estimates were compared with those derived from a recent tag-recapture study (McQueen et al., 2019a).

$$\frac{\Delta L}{\Delta t} = E - k * L \tag{13}$$

$$L_\infty = \frac{E}{k} \tag{14}$$

With $\frac{\Delta L}{\Delta t}$ – the change in total length of cod ΔL over the time Δt, E – reflecting the hypothetical maximum growth increment for a total length of 0 cm, k – the VGBF growth rate, L – the start length of the cod, and L_∞ – the hypothetical maximum length of the cod.

2.3.2. Assessing the role of temperature and food on TZ formation

Recently evidence was found that TZ formations in otoliths of juvenile and young adult cod from the Belt Sea occur the during summer season (McQueen et al., 2019b; Krumme et al., unpublished). Plonus et al. (unpublished) related TZ formations to ambient water temperatures exceeding length-related temperature thresholds, here termed $T_{opt.}$ Following the approach of Plonus et al. (unpublished) we used a length-modified version of the equation presented by Björnsson et al. (2001), which is originally used for calculating the optimal growth temperature of Icelandic cod. As in the approach of Plonus et al. (unpublished), we calculated the predator weight directly from the predator length in the equation using a length weight relationship ($LWR_{spawning}$) (15).

$$T_{opt} = 18.28 - 1.43 * \ln\,(0.008 * L^{3.05}) \tag{15}$$

with T_{opt} – length related temperature threshold, and L – length of the cod.

2.4. Software used

The bioenergetic growth model was set up in the statistical software and programming environment R (R Development Core Team, 2017), using the packages *plyr* (Wickham, 2011), *MALDIquant*, (Gibb and Strimmer, 2012), *ggplot2* (Wickham, 2009), *cowplot* (Wilke, 2017), *mgcv* (Wood, 2011) and *nnet* (Venables and Ripley, 2002).

3. Results

3.1. Model output plots

Prediction plots derived from the model runs for age 3 cod in 2016 and 2017 are shown in Figure 3 and 4, respectively. Prediction plots for cod ages 2 and 4 are given in the supplementary material S7.

SSTs differed in 2016 and 2017 among seasons (Fig. 3A & 4A). For example, n 2017 modelling started with negative SSTs and thus, colder than in 2016, when SSTs were above 0 °C. Moreover, 2016 displayed especially high maximum SSTs in summer exceeding > 20 °C, which were not found in summer 2017.

The median depth-use prediction of cod showed an m-shaped pattern over the modelling time in both years in 2016 and in 2017, including two periods of shallow water use (Fig. 3B & 4B) one during spring and one in autumn. Especially during summer period, age 3 cod in 2016 selected depths deeper than 20 m, while in 2017 also use of shallower waters was predicted in summer.

In both years, cod encountered a great span of water temperatures at their residence depths. For example, temperature at residence depth ranged for age 3 cod from below 4 °C in winter to more than 15 °C in summer periods (Fig. 3C & 4C).

Median consumption in percent of body weight of age 3 cod ranged between 0.24 and 1.35%, and 0.28 and 1.37% in 2016 and 2017, respectively (Fig. 3D & 4D). In July 2016, when feeding at depths > 20 m, low daily consumption was predicted by the model. This period of especially low consumption was displayed in the plot by the 25% quantile, which extended to the zero line (Fig. 3D).

Maintenance ration of age 3 cod varied over the modelling time between 0.23 and 0.77% body weight in 2016 and between 0.26 and 0.76% body weight in 2017 (Fig. 3E & 4E). Highest median maintenance rations were predicted for September (at Julian day 266) and for July (at Julian day 205) in 2016 and 2017, respectively.

Median food for growth of cod 3 ranged between -0.08 and 0.63% body weight in 2016 and 0.003 and 0.70% body weight in 2017, respectively (Fig. 3F & 4F). Highest median values of daily food for growth were observed in both modelling years during the periods of shallow water use in spring and autumn. In 2017, the model also predicted high values of daily food for growth with > 0.5% body weight at the end of July, when cod used median depths around 11 m. However, in the same period in 2016 weight losses occurred, linked to negative values of daily food for growth (Julian day 208-2015; Fig. 3F). These weight losses in 2016 were also predicted for age 2 and age 4 cod.

Predicted median end lengths of age 3 cod were 55.08 and 56.04 cm at the 14th February in 2017 and 2018 (Fig. 3H & 4H), which corresponded to a median annual increase in length of 13.08 and 13.05 cm over 365 modelled days, respectively.

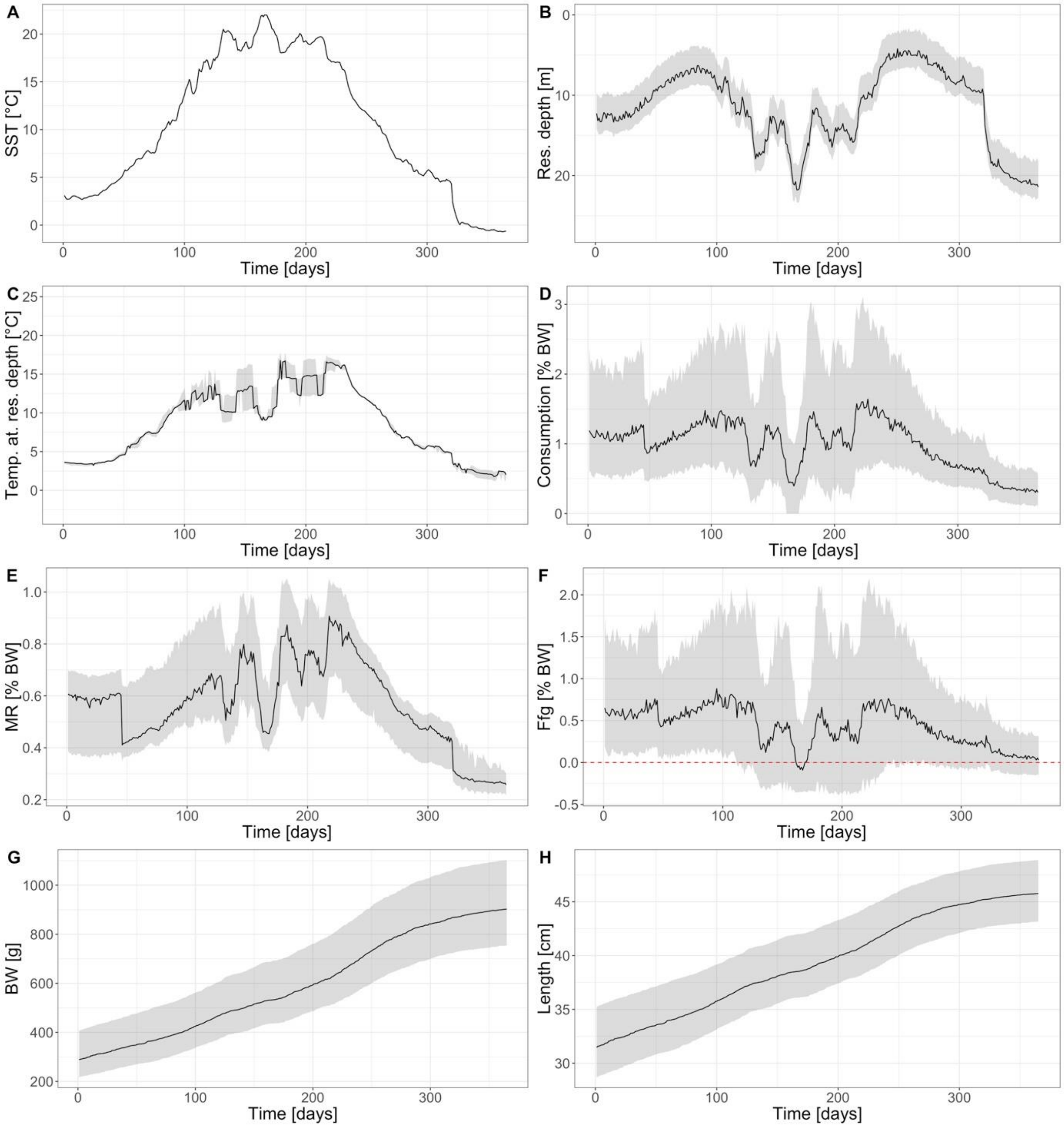

Figure 3. Model output plots for predicted Sea Surface Temperature (A), residence depth (Res. depth) of cod (B), temperature at residence (res.) depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), body weight (BW) in gram (G) and length in cm (H). In panels b to h median values calculated for 1000 cods of age 3 over 365 modelling days starting at the 15th of February 2016 is displayed by a solid black line, the grey shading indicates 25% and 75% quantiles.

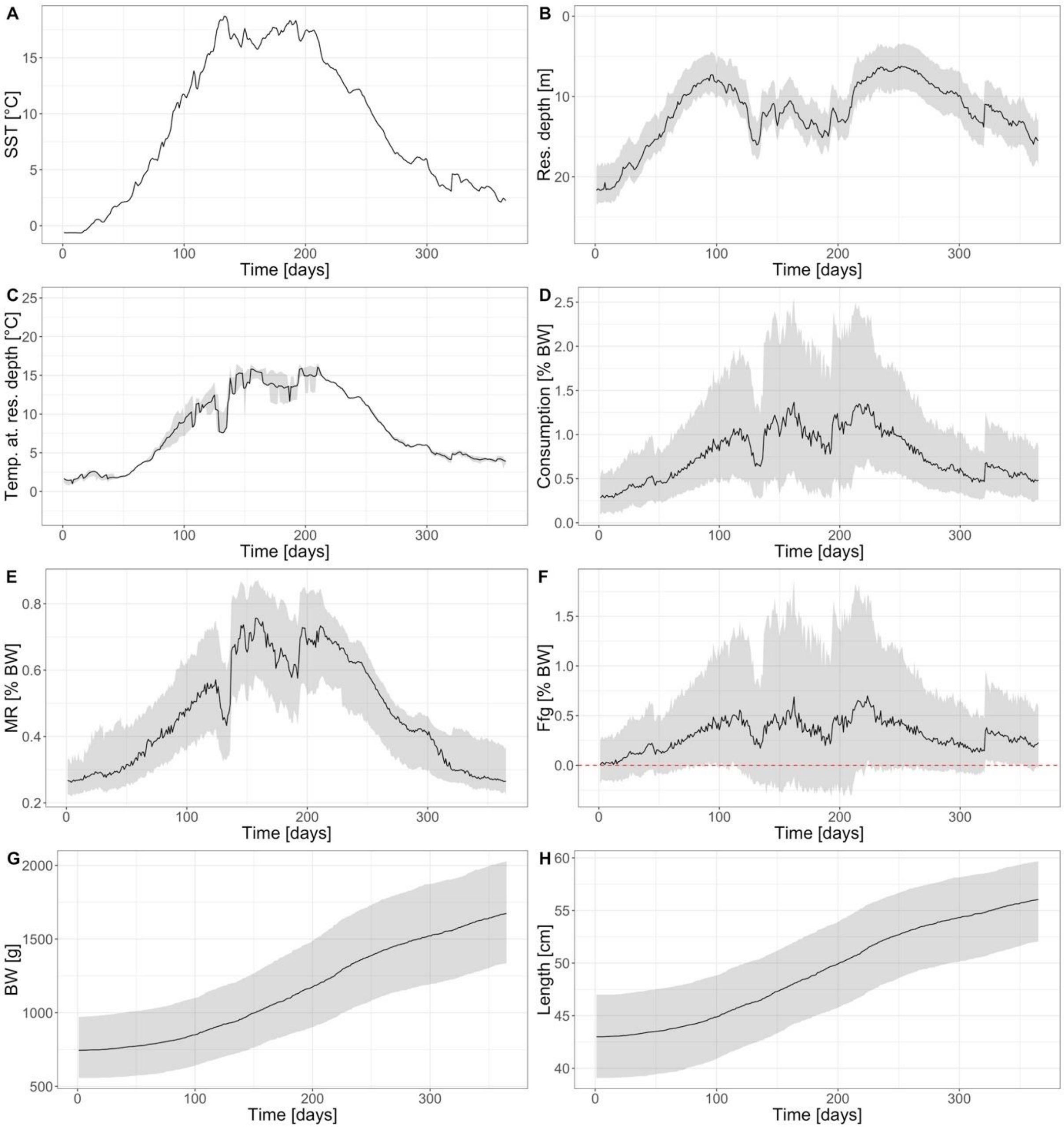

Figure 4. Model output plots for predicted Sea Surface Temperature (A), residence depth (Res. depth) of cod (B), temperature at residence (res.) depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), body weight (BW) in gram (G) and length in cm (H). In panels b to h median values calculated for 1000 cods of age 3 over 365 modelling days starting at the 15th of February 2017 is displayed by a solid black line, the grey shading indicates 25% and 75% quantiles.

3.2. Seasonal patterns in growth

Daily median length increments of the modelled 1000 cod per month varied over the seasons and among age classes. In the model run starting in February 2016, variability over the season was less pronounced compared to the model run starting in February 2017 (Fig. 5).

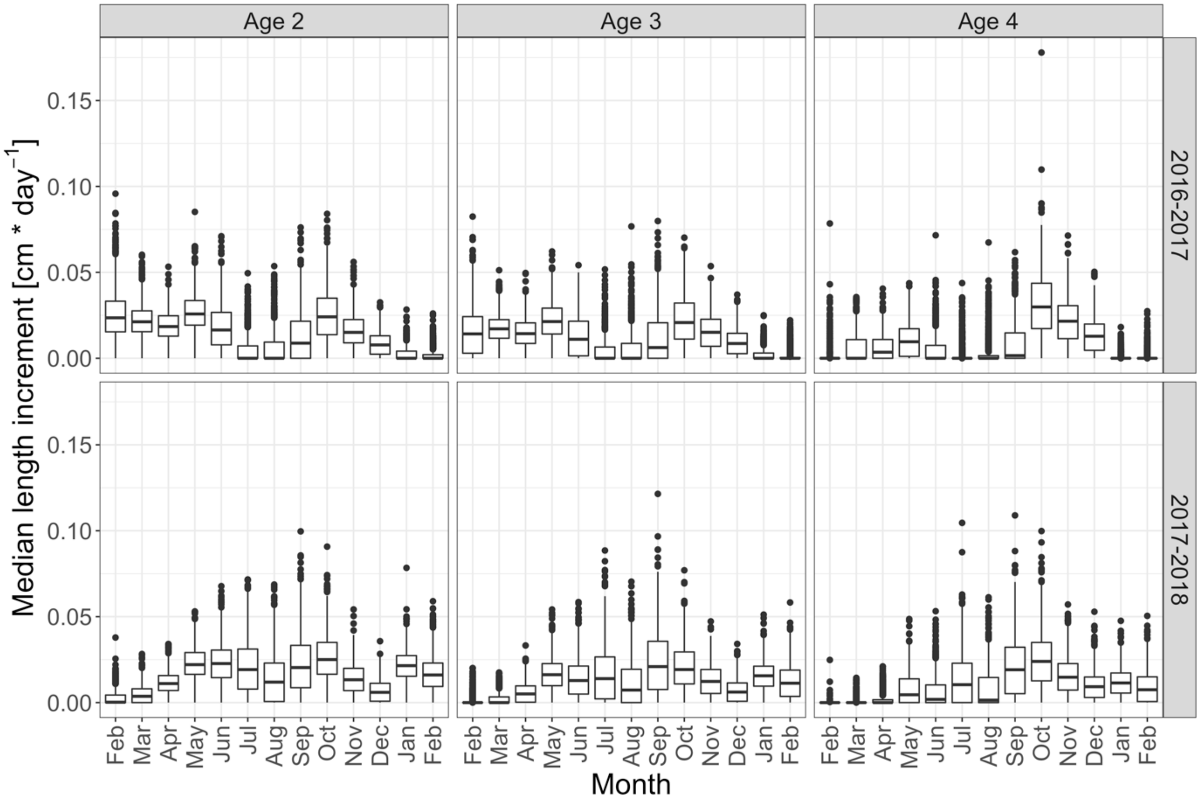

Figure 5. Daily median length increments per month for the modelled age classes 2 to 4 starting in February 2016 and 2017, respectively. Boxplots display median and first and third quartile (hinges) of the median length increments per day over 1000 modelled cod. Whiskers extend from the upper/ lower hinge to the largest value no further than 1.5 * IQR from the hinge, respectively (IQR - the distance between the first and the third quartile). Black dots represent outliers which are length increment values further than 1.5 * IQR from the upper or lower hinge.

Cod in both years showed highest daily median length increments in October. Cod starting in February 2017 displayed an increase in daily median length increment from February to May, which was not found in 2016. However, for both years a peak in median daily length increments was found in May. In the summer period between June and August the daily median length increments decreased in both years, which was more pronounced in older cod. Moreover, this decrease was more pronounced in the summer 2016 compared to summer 2017. From September onwards we observed for both years a second increase in daily median length increments peaking in October and starting to decrease again from October to February in 2016 and 2017 (Fig. 5).

3.3. Predicted vs. observed changes in cod length

Linear regression through the origin between predicted median end length and observed median length of the corresponding age class taken from the BITS Q1 in surveys 2017 and 2018, displayed a slope of 1.03 ($p < 0.01$, $R^2 = 0.99$) and thus revealed a slight overestimation of median length predicted by our bioenergetic growth model (Fig. 6). Growth of age 3 cod was underestimated for both modelling years, while the growth of age 4 cod was overestimated in both years. For age 2 cod our predictions showed an overestimation in growth for cod starting in 2017 and an underestimation for cod starting in 2017.

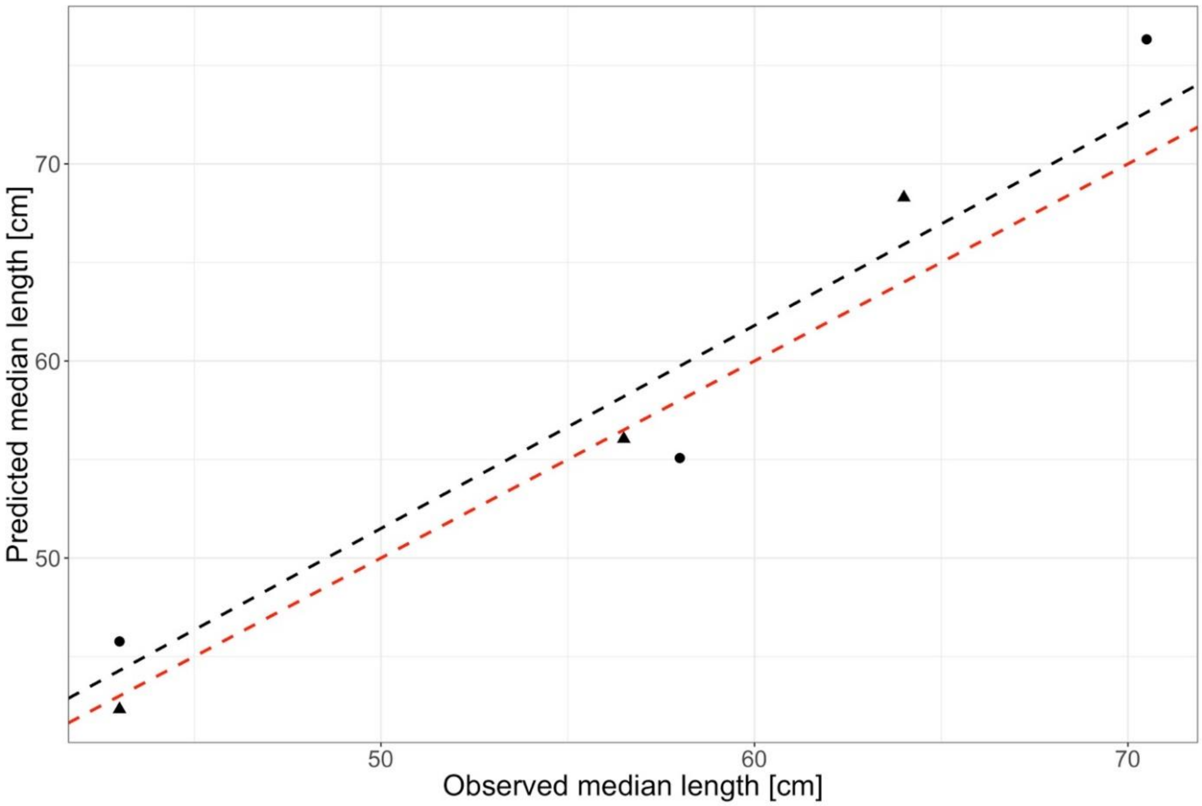

Figure 6. Relation between predicted median end lengths of cod (starting ages 2-4 grown over 365 days) and observed median length of corresponding age classes (ages 3-5) in the field taken from BITS Q1 surveys in 2017 and 2018 (dots – median cod length in February 2017; triangles – median cod length in February 2018). Dashed black line indicates linear regression between predicted and observed median lengths through the origin. Dashed red line goes through the origin and has a slope of one.

3.4. VBGF parameter estimates

There was a significant relationship ($p < 0.001$, $R^2 = 0.57$) between start lengths and yearly length increments (linear regression calculated using the pooled model predictions from both modelling years and all age classes 2 to 4; Fig. 7A). The VBGF parameters estimated using the parameters of the linear regression (slope = -0.11, Intercept = 17.77) were $k = 0.11$ and $L_\infty = 155.44$ cm. There was a slight pattern in the residuals of the linear regression, displaying underestimations at the lower and upper boundaries for the predicted growth increments by the VBGF compared to the growth increments derived from the bioenergetic growth model. Additionally, overestimations of growth increments by the VBGF at intermediate start length between 50 and 57 cm (Fig. 7B) were observed. The estimated VGBF parameters coincided highly with those estimated from tag-recapture data (McQueen et al., 2019a) with $k = 0.11$ and $L_\infty = 154.56$ cm.

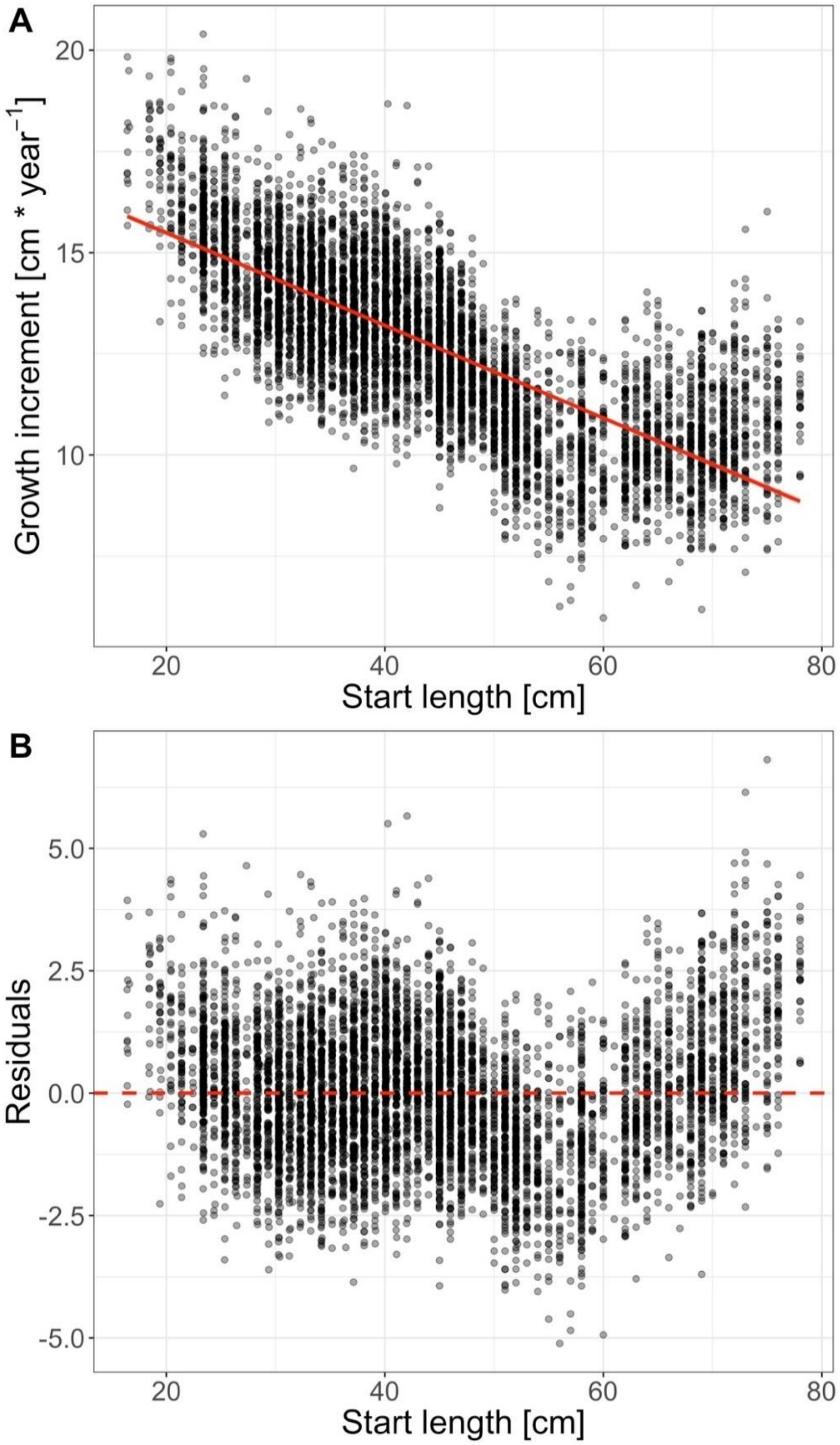

Figure 7. Linear regression between predicted length growth increment and start length (A) and length residuals (observed – predicted length) plotted against the start length (B).

3.5. Temporary exceeding of calculated $T_{opt.}$

For all modelled ages (2 to 4) and modelling years the median encountered temperature at residence depth exceeded the medium optimum temperature. The median temperatures at residence depth in 2016 were predicted to exceed $T_{opt.}$ from April until November. In 2017 the optimum temperatures were not exceeded before May (Fig. 8).

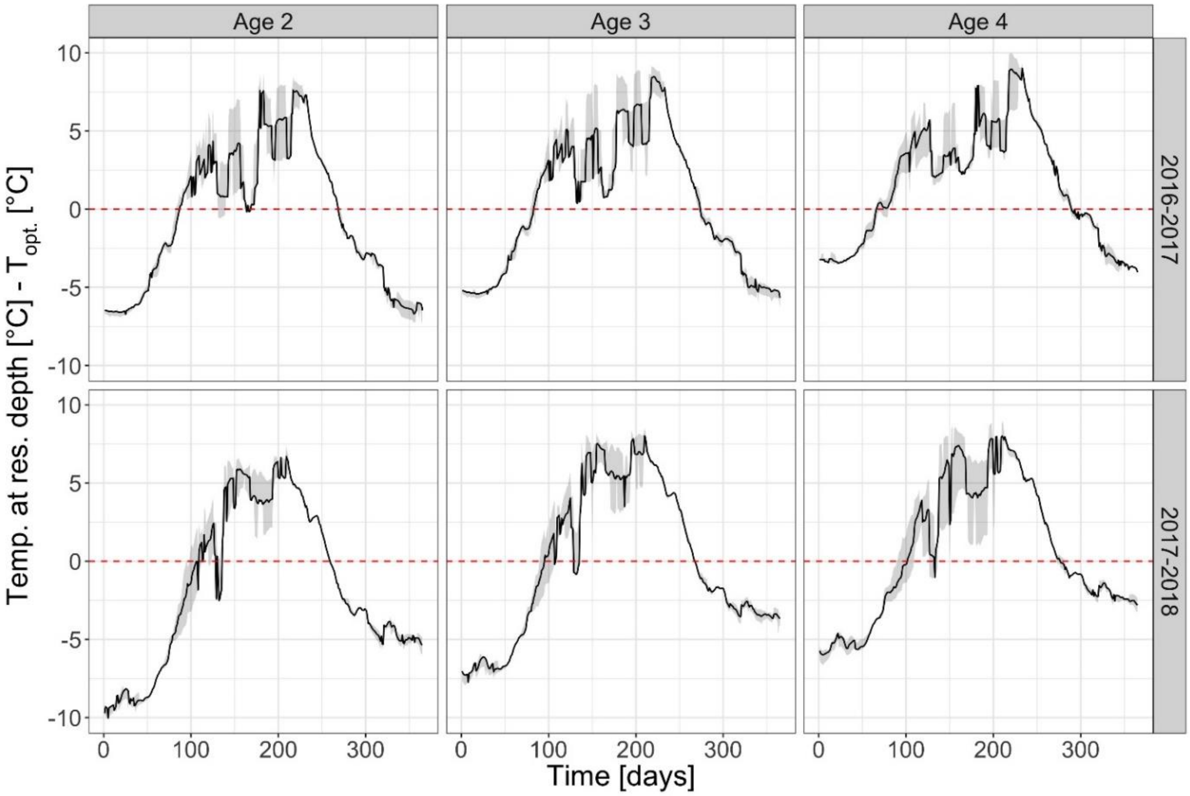

Figure 8. Difference between median Temperature at residence depth (Temp. at res. depth) encountered of 1000 individually modelled cod per age class and modelling year and calculated median length related T_{opt}. displayed over the modelling time. Dashed red line indicates temperature threshold of $T_{opt.}$. Positive values are indicating that predicted temperatures at residence depth exceed the calculated $T_{opt.}$.

4. Discussion

4.1. Method discussion

We presented the calculation of bioenergetic models as an alternative method for conventional cod growth estimations such as otolith age-readings or tag-recapture experiments.

However, the calculation of an individual-based bioenergetic growth model requires a sound knowledge on spatio-temporal distribution, food intake and physiological processes of the target species. Cod is a relatively well studied species and several studies on physiological processes are available (Andersen, 2001; Andersen et al., 2016; dos Santos and Jobling 1991, 1995; Jobling, 1982; Saunders, 1963; Temming and Andersen, 1994; Temming and Herrmann, 2003, 2009). However, it was not possible to find information for all prey-specific gastric evacuation coefficients needed and hence we had to take values from other species considered to be similar. These are of course rough assumptions which certainly led to slight bias in the model calculation. Moreover, our model may suffer from the assumption of a net conversion efficiency, which was set on a constant value and did not change with diet composition. Furthermore, we assumed constant allocation in somatic growth and energy storage over the whole modelling time, and also did not differentiate between different ages or lengths. Studies of Andersen et al. (2003) focusing on laboratory experiments with the gadoid species whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) gave hints for variations in energy allocation in relation to food quality (relation of protein and fat of the prey) and predator size. Hence, more laboratory experiments are needed even for “well-studied” fish such as cod, with regard to prey-specific evacuation, conversion efficiency and energy allocation. Moreover, uncertainties in our model are caused by the implementation of the depth-use model based on fishers’ knowledge (Funk et al., unpublished). The mesh size factor used as explanatory variable in the model gave hints for a length-related difference in the seasonal depth use. However, the implementation of this size-dependent effect was proved to be rather difficult. We decided to make a “sharp cut” from cod length of 55 cm onwards. At this length the smaller net meshes (< 120 mm) showed a much worse selectivity (less than 25%), which led to the assumption that the fishers probably suspect only few cod > 55 cm when using the smaller mesh sizes. This “sharp cut” in the depth use from a certain length on was relatively fair to implement. However, it is more likely that the length effect in depth use shows a rather gradual transition towards favouring deeper residence depths with increasing length. Clarity about this might be given by future acoustic telemetry studies in the area as already conducted for Norwegian coastal cod from a south Norwegian fjord region (Freitas et al., 2015; Freitas et al., 2016).

4.2. Comparisons of modelled cod growth with survey and tag-recapture data

Comparisons with field observations (derived from BITS Q1) revealed that the growth estimates derived from our individual-based modelling approach are in good agreement with field age-length observations from the field as well as with newest findings on growth of Western Baltic cod based on tag-recapture experiments (McQueen et al., 2019a). Linear regression between predicted and observed length (from BITS Q1 data), showed only a slight overestimation in our model (slope = 1.03). Especially, for fish in age class 4 the predicted length in the following year exceeded the observations recorded during BITS Q1 survey for age 5 cod. An explanation for this might be given by size-selective fishing mortality, leading to a shift in the size distribution towards smaller, slower growing fish at older age classes in the field (Lee, 1912; for cod see Kristiansen and Svåsand, 1998). The VBGF parameters derived from our individual-based bioenergetic growth model with $k = 0.11$ and $L_\infty = 155.44$ cm are surprisingly close to VBGF parameters for cod in the Western Baltic Sea recently published by McQueen et al. (2019a) with $k = 0.11$ and $L_\infty = 154.56$ cm applying the Laslett-Eveson-Polacheck (LEP) approach (Laslett et al., 2012; Eveson et al., 2004) to estimate growth from a combination of tag-recapture data, length-frequency and length-at-age of additional field samples. It was shown by McQueen et al. (2019a) that the LEP method led to more reliable estimates of the VBGF parameters for cod in the Western Baltic Sea compared to previous studies (Bagge, 1974; Froese and Sampang, 2013), especially for the L_∞. However, the residuals of our calculated linear regression between growth increment and start length displayed a pattern, especially at the upper (> 60 cm) and lower (< 25 cm) boundaries of the given start length, representing an underestimation of growth by the VBGF. The observed underestimation of length growth increments by the VBGF at cod sizes < 25 cm, which was not observed by McQueen et al. (2019a), may reflect shortcomings in our modelling approach due to the limited size range of cod used for the calculation of sub-models of stomach content weight and diet composition

(Funk et al., unpublished). Since Funk et al. (unpublished) used only cod ≥ 31 cm to parameterize the submodels used here, we had to extrapolate for smaller cod sizes. In contrast, the observed pattern in residuals at larger start length (> 60 cm) can also be observed in the residual plot of the tag-recapture and age-at length data presented by McQueen et al. (2019a). Thus, both approaches showed a trend towards an underestimation of growth by the VBGF at cod lengths > 60 cm. In our bioenergetic model, this increase in length growth for large cod > 60 cm results from a length-related change in diet composition. Large cod > 60 cm displayed a greater probability for feeding on flatfishes (Funk et al., unpublished). Lean flatfishes are evacuated faster than chitinous crustacean organisms (Temming and Herrmann, 2003; Andersen et al., 2016) and are additionally offering higher prey-specific energy densities. Ontogenetic diet shifts, which lead to an increased growth rate of larger individuals have also been reported for other species e.g. *Osmerus eperlanus* (Vinni et al., 2004). Such discontinuities in growth rates are however not accounted for in the classical VBGF.

4.3. Seasonal growth patterns

In addition to the aggregate length growth estimates, the bioenergetic model approach generated seasonal growth patterns showing the periods where cod tend to reside in shallow-water habitats (< 10 m depths) during spring and autumn, which were also revealed as important feeding and growth periods. Especially in October we observed largest daily median length increments. These findings agree closely with the results of McQueen et al. (2019a) based on tag-recapture data, where a peak in growth rate of cod was observed in autumn. The observed larger growth increments can be referred to higher prey availability in shallower areas and consequently higher food intake by cod when re-returning to shallow-water habitats when water temperatures decrease after the summer (Funk et al., unpublished). Moreover, we found relatively small length increments during the use of habitats > 20 m in winter and summer. Smaller growth increments during winter coincide with the spawning period of cod in the Western Baltic in deeper areas (Bleil et al., 2009), when cod display reduced feeding activity due to pre-spawning and spawning behaviour (Fordham and Trippel, 1999). Moreover, prey availability of cod might be limited at deeper habitats leading to the observed lower stomach content weights (Funk et al., unpublished). In summer, a second period of deeper-water use of cod can be observed in the Belt Sea which can be related to an avoidance behaviour (Funk et al., unpublished). With continuously increasing water temperatures in the resource-rich shallow habitats when summer approaches, the thermal tolerance limits of cod become exceeded and they have to move to deeper, colder waters (Funk et al., unpublished).

Our model reveals that high ambient temperatures and related high metabolic costs in combination with reduced food intake at habitats located deeper than 20 m can lead to a loss in weight during the peak summer period. This effect was more pronounced for larger individuals (> 55 cm) residing in greater depths and displaying higher metabolic rates than smaller individuals. However, such weight losses were predicted only temporal (only for July 2016) und extreme temperature conditions (SST > 20 °C, temperatures at residence depths > 15 °C). Since the development of reproductive products is highly dependent on energy intake (Kjesbu et al., 1991; Lambert and Dutil, 2000), negative effects on the overall recruitment success of the Western Baltic cod stock might be suspected due to long-lasting heat-periods. These potential negative effects may become even more pronounced when heat periods increase in frequency or tend to prolong in duration due to climate change (HELCOM, 2013).

4.4 Temperature-related TZ formations

Our bioenergetic model provided new insights for a possible explanation of the temporal formation of translucent zones in the otoliths of adult cod in the Western Baltic Sea. The formation of translucent zones in cod can be induced by changes in ambient temperature, by reduced growth or a combination of both (Høie and Folkvord, 2006; Høie et al., 2008; Neat et al., 2008). The formation of TZs in the otoliths of Belt Sea cod during summer has been validated for both juvenile (McQueen et al., 2019b) and young adult cod (Krumme et al., unpublished). Moreover, it was found that the time-span where TZ structures are formed extends with cod age (Krumme et al., unpublished). For example, age 3 cod TZ formation can be observed from April to November, while for age 1 cod already opaque ring structures were observed from October onwards (Krumme et al., unpublished). In our growth modelling, for all modelled age classes (2-4) and years, growth increments were largest during the second half of the year and thus, during the period when the formation of the TZs was observed in the field. Moreover, during the winter when the formation of opaque ring patterns can be observed in the field, our model revealed smallest growth increments. Hence, it seems unlikely that the TZ formation during the summer season can be related to reduced growth and thus, points rather towards a temperature-induced TZ formation.

This was supported when calculating the period in which the temperature threshold $T_{opt.}$ was exceeded. Following the approach of Plonus et al. (unpublished), the exceeding of length-related temperature thresholds gives a good indication for temperature-related formation of TZs. We calculated that median temperatures at residence depths of cod exceeded the calculated length-related temperature thresholds depending on temperature of the modelling year and age-class from April (in 2016) or May (in 2017) and stayed above the threshold until November. These findings coincide surprisingly well to the field observations of TZ formations (Krumme et al., unpublished) and hence, give a strong indication for a first-order temperature-related TZ formation in otoliths of cod in the Western Baltic Sea.

4.5. Conclusion

Our study demonstrated that bioenergetic growth models can be used as an alternative to classical growth calculation approaches. VBGF parameters derived from our growth models were surprisingly close to recently published studies based on tag-recapture methods and hence, highlight the potential of our model approach as a reliable and cost-efficient alternative to tag-recapture experiments. While in tag-recapture studies growth patterns can be observed only, the bioenergetic model provides direct insight into the mechanistic processes taking place, such as reduced or increased consumption leading to the observed growth patterns. For example, our model revealed that large growth increments observed in spring and autumn were mainly related to shallow water use of cod and related to an increased consumption rate. Furthermore, the results from our bioenergetic model strongly suggest that the TZ formation observed during summer is primarily temperature-induced. Hence, bioenergetic modelling offers a promising approach, especially for Eastern Baltic cod, which recently showed problems in traditionally applied age readings. Applying those kinds of bioenergetic growth models for Eastern Baltic cod may also provide a basis for length-based population models in the future.

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Supplementary material

S1. Assumed Sex-related differences in the catch composition of BITS hauls

Sex-specific differences in growth and maturity are common in gadoid species and are also reported for Atlantic cod. Females grow faster, while males reach often maturity earlier in age and size. Moreover, sampling of international trawl surveys take place mostly in deep trawlable areas, which are used by cod for spawning. Non-mature individuals or skip-spawners tend to use shallower areas with higher food availability (Funk et al., unpublished) and are therefore underrepresented in the survey catches. Hence, especially female individuals in younger age classes might be underrepresented in BITS catch compositions. Due to these sex-specific differences the trawl survey catches are likely to better reflect the real length distributions in the populations for males than for females. Hence, our model was set up for males only.

S2. Used hydrodynamic model

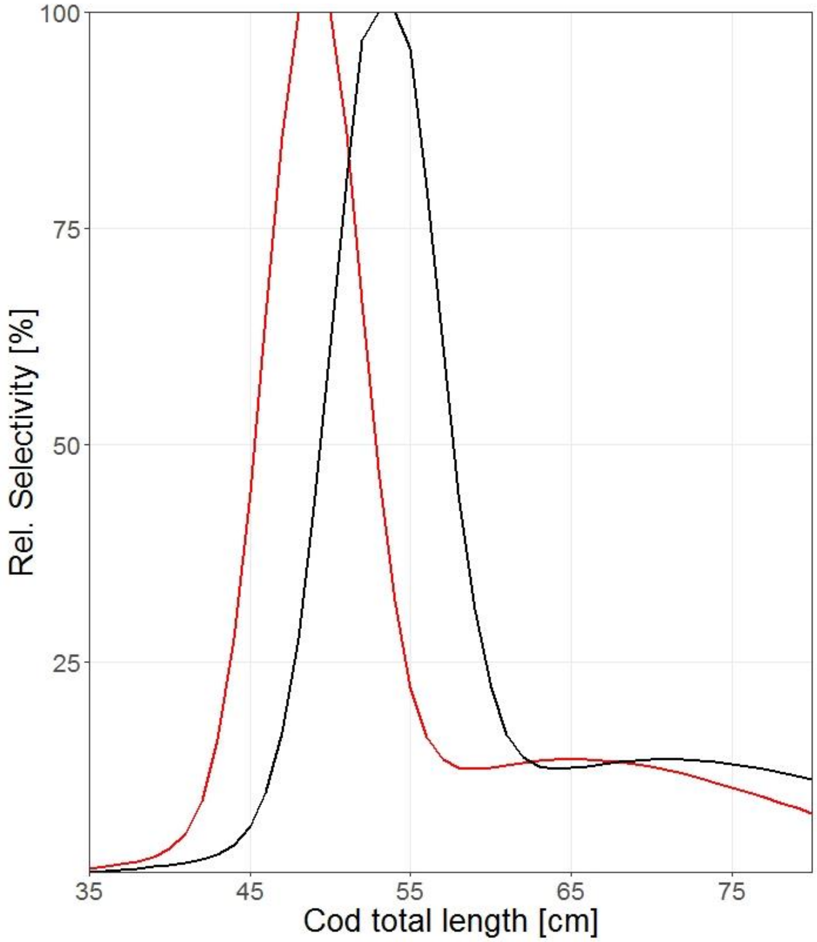
We used the current version of the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM; Lehmann and Hinrichsen, 2000; Lehmann et al., 2002; Lehmann et al., 2014) in order to get spatial and temporal dissolved temperature information. The horizontal resolution of the coupled sea ice–ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. At the western boundary, a simplified North Sea is connected to the model domain to provide characteristic North Sea water masses. Here, sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index; Lehmann et al., 2002; Novotny et al., 2006) were taken as additional boundary condition. The model is forced by a meteorological database which for the period under consideration covers the whole Baltic drainage basin on a regular grid of 1 x 1° with a temporal increment of 3 hours. The database consists of synoptic measurements that were interpolated onto the regular grid with a two-dimensional optimum interpolation scheme. Besides temperature, further prognostic variables of the model are the baroclinic current field, the 3-D salinity and oxygen distributions, and the 2-D surface elevations and the barotropic transport. Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen et al., 1997; Lehmann and Hinrichsen, 2000).

S3. Relative selectivity of gillnet mesh size diameters

The mesh size of gillnets was used as categorical variable in the depth-use model of cod (Funk et al., unpublished). Two mesh size diameters 110-119 mm and ≥ 120 mm were distinguished. We calculated the relative catch selectivity in relation to cod length for two gillnet mesh size diameters, 110 mm and 120 mm, respectively (Fig. S3.1). Parameter estimates used in the calculations were taken from Madsen (2007). The relative selectivity was calculated by using the formula:

$$R(L) = e^{-\frac{(L-a_1*MS)^2}{2(b_1*MS)^2}} + \omega * e^{-\frac{(L-a_2*MS)^2}{2(b_2*MS)^2}}$$

with $R(L)$ – the relative selectivity, a_1 and b_1- parameters determining the location and spread of the primary mode, a_2 and b_2- parameters determining the location and spread of the secondary mode, ω - weighting factor, L – length of the cod, and MS – the mesh size diameter (Wileman et al., 2000) Parameter estimates used for calculations $a_1 =$ 4.45, b_1 = 0.265, $a_2 =$ 5.92, b_2 = 0.265 and $\omega =$ 0.137 were taken from Madsen (2007).



Supplementary figure S3.1. Relative catch selectivity (Rel. Selectivity [%]) of gillnets (red – mesh size diameter of 110 mm, black – mesh size diameter of 120 mm) in relation to cod length.

S4. *Calculation of stomach content weights*

In the GAM taken from Funk et al. (unpublished) log transformed stomach content weight of cod is explained by residence depth, cod total length and temperature at residence depth. Temperature data used for model parametrization were taken from the MARNET temperature measurement system of the Bundesamt für Seeschifffahrt und Hydrographie (BSH) recorded at the measuring positions Kiel Lighthouse, Darss Sill and Fehmarn Belt buoy. Daily mean temperatures for every 5 m depth strata were calculated over all three measuring positions and allocated to the cod samples. In the GAMs, non-linearity is represented by smoothing terms (Hastie & Tibshirani, 1986), and selected the optimal effective degrees of freedom (edfs) for the smoothing terms on residence depth, temperature at residence depth and cod length variables using a set validation approach (James et al., 2013).

$$\log(S_{PM\,i}\ [\mathrm{g}]) = s(T_i[°\mathrm{C}], k = 3\ ) + s(D_i\ [\mathrm{m}], k = 3\ ) + \ s(L_i\ [\mathrm{m}], k = 3) + \varepsilon_i$$

with $S_{PM\,i}$ – stomach content weight including prey weight and digestive mucus at time step i, $s()$ – smoothing term, k – effective degrees of freedom + 1, T_i – the temperature at residence depth at time step i, D_i – residence depth at time step i, L_i – length at time step i, and ε_i – random residual at time step i.

S5. Correction of stomach content weight estimates

We developed a relationship between mucus weight and empty cod stomach weight using measurements from the stomach content data base of cod in the Western Baltic Sea derived from the stomach sampling program in 2016 and 2017 presented in Funk et al. (unpublished).

$$S_{PM}\ [\mathrm{g}] = \ 0.162\ * \ W_{estom}\ [\mathrm{g}]$$

with S_{PM} – stomach content weight including prey weight and digestive mucus, and W_{estom}– the weight of the empty cod stomach.

Furthermore, we set up a relationship between cod length and empty stomach weight by using a power function (N = 3350, R^2 = 0.80).

$$W_{estom}\ [\mathrm{g}] = \ 1.692e^{-5} * \ L\ [\mathrm{cm}]^{3.542}$$

with W_{estom}– the weight of the empty cod stomach, and L – the total length of the cod.

Subsequently, the stomach content weight estimates derived from the GAM were corrected by subtracting the hypothetical weight fraction of digestive mucus. In case that $S_{corr\,i}$ was negative, it was set to zero.

$$S_{corr\ i} = S_{PM\ i} - 1.692e^{-5} * L_i^{3.542} * 0.162 ,$$

$$S_{corr\ i} = 0\ if\ S_{PM\ i} \leq 1.692e^{-5} * L_i^{3.542} * 0.162$$

with $S_{Prey\ i}$ – corrected stomach content weight without digestive mucus at time step i, $S_{PM\ i}$ – stomach content weight including prey weight and digestive mucus at time step i, and L_i – length of the cod at time step i.

S6. Prey-specific gastric evacuation rates and energy densities

We allocated prey specific gastric evacuation rates and energy densities found in the literature to the predicted diet clusters (supplementary table S.5).

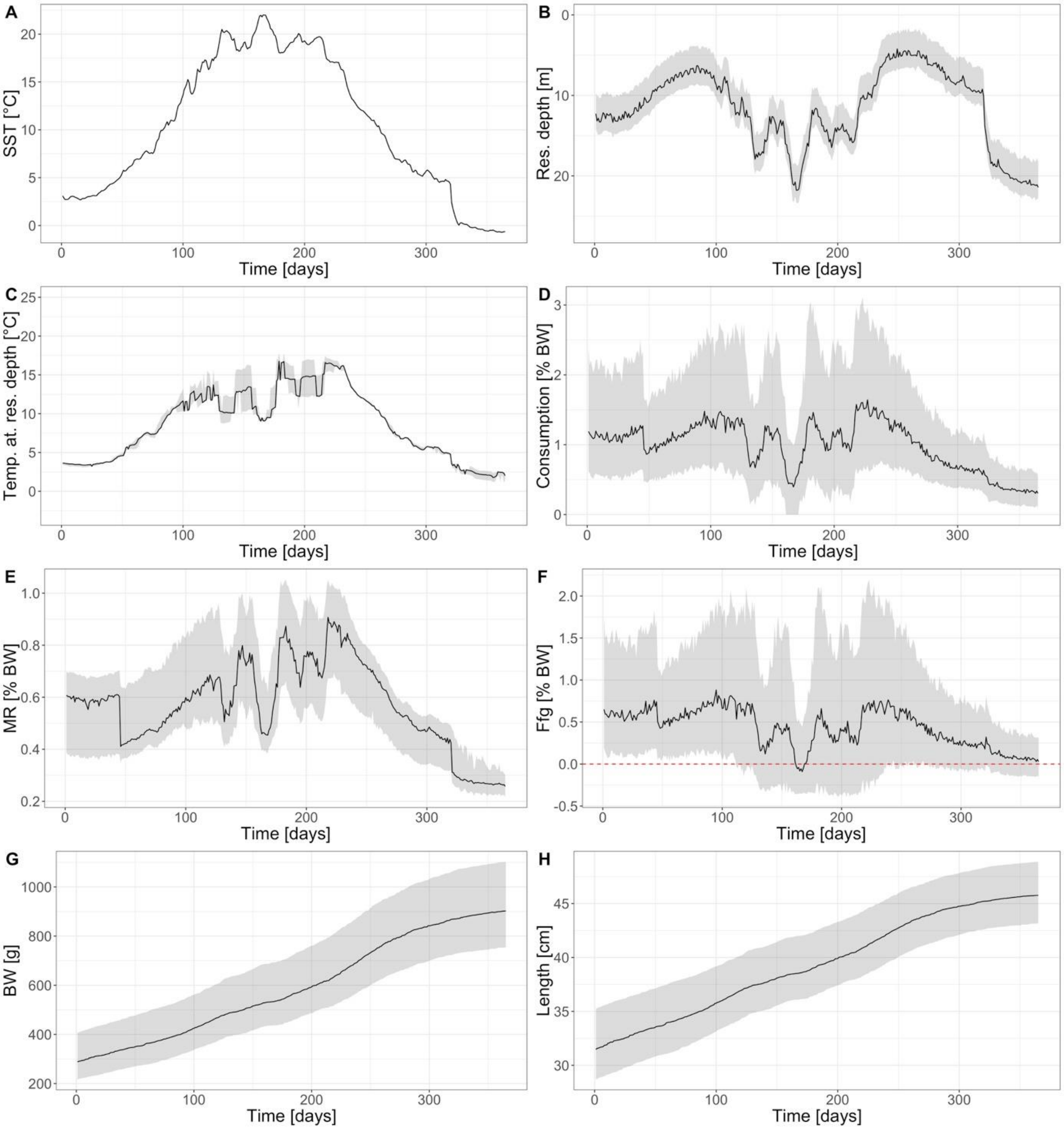
For Annelids and flatfish cluster energy densities and ρ_k were taken from values given for *Arenicola marina* and *Hippoglossoides platessoides*, respectively (Temming and Hermann, 2003).

For molluscs no information on gastric evacuation rates were available. The mollusc cluster was characterized large proportions of bivalves such as *Arctica islandica* (Funk, unpublished). However, often only muscle tissue was observed in the stomachs. Hence, we assumed the molluscs cluster to be faster digested than fish prey due to the lack of hard tissues such as bones. Thus, we allocated the same ρ_k and energy density to the mollusc cluster as chosen for the Annelid cluster. For the Peracarid and other crustaceans cluster energy density values and gastric evacuation coefficients were calculated as a mean value derived from the decapod species *Crangon crangon* and *Pandalus borealis* (Temming and Hermann, 2003). For the other fish, cluster energy density was calculated as a mean of energy density values given for whiting (≥ 3 cm to < 13 cm) and goby species (≥ 3 cm to < 13 cm) (Temming and Hermann, 2003), while for the clupeid cluster a mean of the energy densities given for *Clupea harengus* and *Sprattus sprattus* was calculated (Temming and Hermann, 2003). For *Carcinus maenas* we used an energy density of 2810 $J*g^{-1}$ wet (de Oliveira Duro, 2016). Gastric evacuation formula described by Temming and Herrmann (2003) was fit to experimental data of cod fed with the brachyuran prey species *Liocarcinus depurator* and *Chionoecetes opilio* (Andersen et al., 2016). Derived calculated prey-specific gastric evacuation coefficients ($\rho_{Liocarcinus\ depuprator}$ = 0.0034; $\rho_{Chionoecetes\ opilio}$ = 0.0028) and the prey specific energy densities for both species (taken from Andersen et al. 2016; E. dens.$_{Liocarcinus\ depurator}$ = 3540 J*g^{-1}; E. dens.$_{Chinoecetes\ opilio}$ = 4530 J*g^{-1}) were used to calculate linear regression (ρ_k = - 0.005 * Energy density + 0.055). Subsequently, this relationship was used to calculate a ρ_k estimate for the given prey energy density.

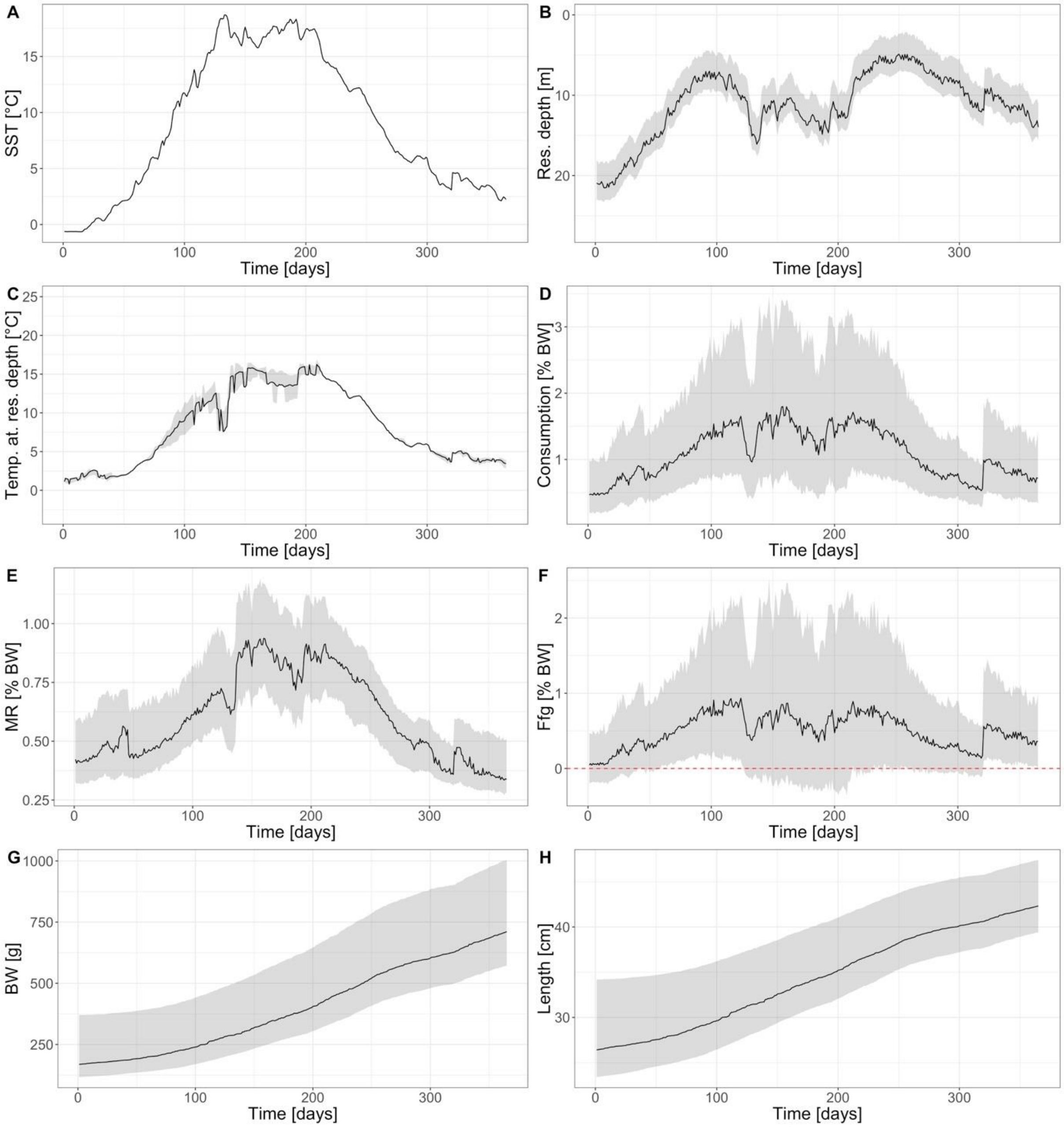
Supplementary table S6.1. Prey specific gastric evacuation constant – ρ_k and prey specific energy density per diet composition cluster.

cluster	ρ_k	energy density (J*g^{-1} wet)
Annelids	0.01414	2500
Clupeids	0.00507	6580
Common shore crab	0.00381	2810
Flatfish	0.00677	3000
Molluscs	0.01414	2500
Other fish	0.00597	4230
Other crustaceans	0.00445	4580
Peracarids	0.00445	4580

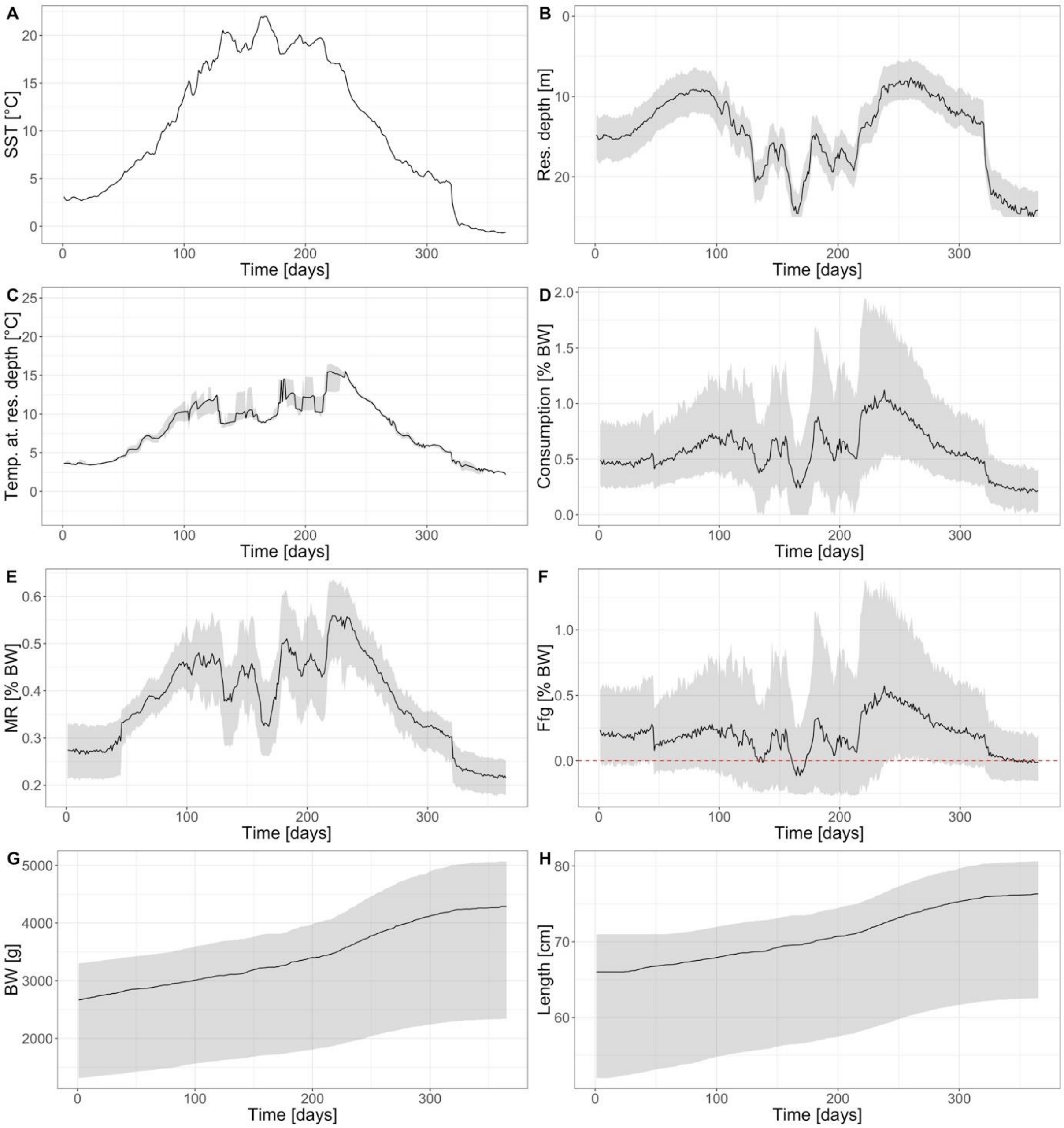
S7. Bioenergetic growth model predictions for cod ages 2 and 4



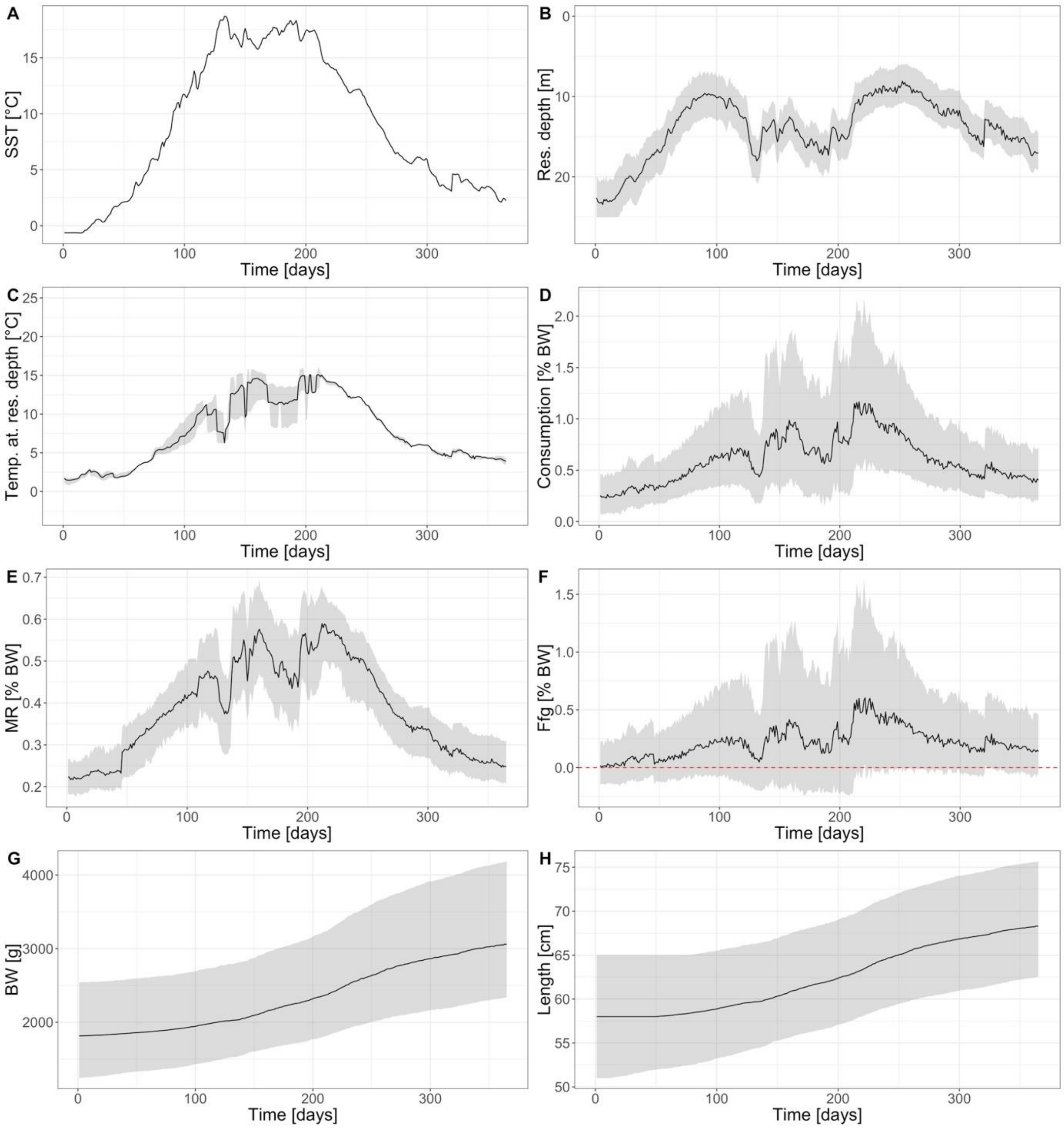
Supplementary figure S7.1. Model output plots for predicted Sea Surface Temperature (A), residence depth of cod (B), temperature at residence depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), bodyweight (BW) (G) and length (H). In panels b to h median values calculated for 1000 cods of age 2 over 365 modelling days starting at the 15th of February 2016 is displayed by a solid black line while the grey shading indicates 25% and 75% quantiles.



Supplementary figure S7.2. Model output plots for predicted Sea Surface Temperature (A), residence depth of cod (B), temperature at residence depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), bodyweight (BW) (G) and length (H). In panels b to h median values calculated for 1000 cods of age 2 over 365 modelling days starting at the 15th of February 2017 is displayed by a solid black line while the grey shading indicates 25% and 75% quantiles.



Supplementary figure S7.3. Model output plots for predicted Sea Surface Temperature (A), residence depth of cod (B), temperature at residence depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), bodyweight (BW) (G) and length (H). In panels b to h median values calculated for 1000 cods of age 4 over 365 modelling days starting at the 15th of February 2016 is displayed by a solid black line while the grey shading indicates 25% and 75% quantiles.



Supplementary figure S7.4. Model output plots for predicted Sea Surface Temperature (A), residence depth of cod (B), temperature at residence depth (C), consumption in % bodyweight (D), maintenance ration (MR) in % bodyweight (E), food for growth (Ffg) in % bodyweight (F), bodyweight (BW) (G) and length (H). In panels b to h median values calculated for 1000 cods of age 4 over 365 modelling days starting at the 15th of February 2017 is displayed by a solid black line while the grey shading indicates 25% and 75% quantiles.

S8. References for supplementary material

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General discussion

The role of shallow water habitats in the seasonal life cycle of adult WBC

One of the main objectives of the thesis was to identify the role of shallow water habitats in the seasonal life cycle of adult cod in the Western Baltic Sea. Since shallow water habitats were previously neglected in the international monitoring surveys and stomach sampling designs, it remained unclear whether and to what extent these areas are used by cod. Using reported and observed catch depths of local gillnet fishers, we were able to reveal patterns in the seasonal depth and habitat use of cod (**chapter I**), wherein cod displayed a clear preference towards residing in depths < 20 m outside the spawning season. In spring and autumn cod largely uses even depths shallower than 10 m depths. Moreover, we revealed a clear preference of cod for using vegetated and hard structured habitat areas, while soft bottom structures, which are however mostly selected for fishing during scientific trawl surveys, are used only to a lower extent and mostly temporally limited to the spawning time. Hard structure habitats such as areas with cobbles, boulders and gravel were so far neglected in the monitoring survey as well as in most of the previous stomach samplings. Since we revealed these neglected habitats, being essential for cod in the area (**chapter I**), the question can be raised how representative the previous surveys and stomach data really are for the stock.

We assumed that the preference for shallow habitat sites < 20 m depths, which cod display outside the spawning season, can be related to a higher prey availability for cod in these areas (**chapter I**). This hypothesis was supported by the results of our stomach content analyses of cod stomachs sampled in 2016 and 2017, where we especially focussed on seasonal and depth-specific effects on the diet composition and food intake of cod (**chapter II**). We observed clearly distinct relationships between stomach content weight and catch depth of cod, with highest stomach content weights related to shallow habitat sites. The observation of low stomach contents during deep-water use in combination with the observation of size-indiscriminate feeding lead moreover to the assumption of food scarcity for cod in depths > 20 m (**chapter II**).

Hence, we concluded that the shallow feeding grounds are of special importance for the seasonal food intake and thus, for the seasonal growth of cod in the area.

The higher food supply in shallow areas, at least during parts of the year, can be explained by the high importance of benthic invertebrates such as the common shore crab (*Carcinus maenas*) and small demersal fish, such as goby species, in the overall diet composition of cod in the western Baltic Sea. These mobile epifauna species also show distinct seasonal patterns in depths use, preferring shallow inshore areas from spring to autumn and moving deeper to warmer water layers when temperatures start to decrease in late autumn to winter (Arntz 1974; Dries and Adelung 1982; Pihl and Rosenberg, 1982). We revealed, furthermore, the common shore crab as one of the main prey species of cod in the Western Baltic Sea, especially for large individuals (> 60 cm) (**chapter II**). However, it remains so far unclear, if the importance of common shore crabs in the overall diet compositions of cod has changed in the last decades. Decreases in the stock of herring, which was named as the main prey of cod in diet composition of cod in diet studies conducted in the 1970s and 1980s may point towards a compensatory feeding behaviour (ICES, 2019c; Schulz, 1989; **chapter II**). Such a temporal shift in the diet composition of cod may also have altered the depth-use behaviour and thus the importance of shallow water areas as feeding habitats for cod in the Western Baltic Sea over the last decades. However, gillnet fishers with more than 30 years of professional experience reported that over their decades of fishing operations they did not observe any change in cod depth-use patterns or cod diet compositions and that, as far as they can remember, cod have always fed largely on common shore crab (pers. comm. with local gillnet fishers). Therefore, it can be assumed that benthic invertebrates such as the common shore crab and shallow areas have always played a major role for the food intake of cod in the Western Baltic Sea or at least that if the role of benthic invertebrates in the diet composition of cod has changed, this change must have taken place more than 30 years ago.

On the other side it must be kept in mind that the spawning stock biomass of cod in the Western Baltic Sea declined sharply since the 1980s and was on a low level in 2016 and 2017 (ICES, 2019a), when the stomach sampling was conducted. With larger stock size and resulting higher densities in preferred habitats sites (i.e. shallow and structured habitats) a density-dependent spill over effect may occur, where individual cod move towards adjacent less-preferred habitat sites (i.e. towards deeper and/or unstructured habitat sites). Such density-dependent changes in habitat use of Atlantic cod have been observed for the stock off Newfoundland, where juvenile individuals usually prefer vegetated habitats such as seagrass meadows (Laurel et al., 2004). However, they start to inhabit unvegetated habitats (i.e. unstructured sandy grounds) more frequently when cod densities increase at the preferred habitat sites (Laurel et al., 2004). Since we revealed that also the diet composition of cod differs in relation to the habitat (i.e. in relation to depth; **chapter II**), a shift of the prey organisms of evaded cod is likely. Thus, with a larger cod population and a resulting habitat shift by part of the population towards deeper waters the role of benthic invertebrates and thus, the role of shallow water habitats, may decrease in importance for the whole cod population. It remains still unclear to what extent density dependent effects towards greater use of deep-water habitats outside of the spawning season occurred at stock size levels of Western Baltic cod stock in the 1980s. On the one hand, the high sample numbers of cod caught by scientific trawl fishery during all four quarters during the stomach sampling in the 1970s and 1980s in the Mecklenburg Bight and Arkona Sea (Schulz, 1989) may point towards a generally greater use of habitats > 20 m depths by cod at that time. However, on the other hand, also in the stomach samplings of the 1970s and 1980s by Schulz (1989) we can observe differences in sample numbers between the quarters, with lower catches in quarter 2 and 3 and highest catches in quarter 1. This may indicate that there were also seasonal differences in depth use of cod in the 1980s, wherein accessibility of the trawl fishery to cod was limited in periods of distinct shallow-water use. However, since neither the number of stations, nor the total fishing efforts in the different quarters is given in the publications of Schulz (1989), we are not even able to identify if these sample numbers are really due to a lower catchability or more due to an unevenly distributed sampling effort between the quarters. Hence, the role of shallow water areas for cod in the past cannot be quantified. In future studies, comparisons of stable isotopes from cod from the 1980s and recent samples may shed more light on possible temporal changes in habitat use and food composition of cod in the Western Baltic Sea.

However, at the current stock status, it can be assumed that no density dependent spill over effects occurred and that the seasonal patterns in the landings of trawl and gillnet fishery (Dorrien et al., 2013) indicate that most of the cod stock display the seasonal depth movement pattern revealed in our study (**chapter I**). Hence, it can be concluded that for the WBC the shallow water habitats < 20 m depth as well as its main prey in these areas, the common shore crab, are currently playing an essential role in the life cycle of WBC.

The extent to which the food intake in the shallow areas is important for the overall annual growth of cod was further highlighted by applying the bioenergetic growth model (**chapter III)**. We observed highest consumption rates as well as greatest growth increments in relation with periods of shallow water use. Interestingly, we calculated highest consumption rates during shallow water use in autumn, while we observed highest stomach content weights in spring (**chapter II**; **chapter III**). This can be explained by higher ambient temperatures at the shallow feeding grounds in autumn compared to spring which lead to an overall increased gastric evacuation (dos Santos and Jobling, 1995) and thus, ultimately to a calculation of higher daily consumption estimates (Temming and Herrmann, 2003). In contrast, we observed lowest growth rates or even weight losses when cod resided at deeper habitat sites (i.e. > 20 m), for example during spawning time in winter and during peak summer period with long-lasting high temperatures (**chapter III**). This highlights the importance of shallow water habitats as major feeding grounds for cod and consequently the importance for its annual growth in the area.

The effect of extreme-summer periods on the growth rates of adult WBC

We revealed two distinct down-slope movements towards deeper habitats > 15 m depths, one in winter during spawning time and one during peak summer period. We found this movement behaviour in summer related to high sea surface temperatures impacting mostly shallow feeding areas < 15 m depths in combination with a strong thermal stratification during summer period (**chapter I**). We hypothesized that cod make a trade-off between food availability and physiological temperature tolerance limits in shallower water layers, as is also assumed for cod in the southern Norwegian fjords (Freitas et al., 2015, 2016).

The Western Baltic Sea is characterised by strong thermal stratification during summer period (for example see Weigelt, 1987). Sea surface temperatures often exceeds 20 °C in midsummer and the shallow areas consequently heat up strongly (BSH, unpublished data). Ambient temperatures affect several physiological processes in poikilotherm species such as cod (see Tyler, 1970). Specifically, the standard metabolic rate of cod increases exponentially with ambient temperatures (Saunders, 1963; Edwards et al., 1972). This effect is in absolute terms more pronounced in large cod, which can be explained by the multiplicative relationship between body weight and temperature in the formula describing the maintenance requirements of cod (1).

$$R_{maint} = a * W^{c} * e^{A*T} \tag{1}$$

with R_{maint} – maintenance, a – weight coefficient, W – fish weight, c – weight exponent, A – temperature coefficient, and T – ambient water temperature.

Moreover, since dissolved oxygen in the water decreases with increasing temperatures, poikilotherm fish, such as cod, will reach oxygen deficit more quickly at high temperatures when routine metabolism and thus oxygen demand of cod is already increased (Pörtner et al., 2010). These oxygen deficit problems under high temperature conditions are, again, more pronounced in large cod. This can be explained by the growth relation between total body volume and body surfaces, such as e.g. the gill surface, as explained in the classical growth theory of Bertlanaffy (1934; 1938). While the oxygen requirements of an ectotherm fish increase proportionally with its body weight, the gill surface increases in relation to the body weight with a power of less than one. This means that the relative gill area (= gill surface / body weight) decreases with increasing fish size (Pauly, 1981), which implies that a small fish can absorb more oxygen relative to its body size than a large fish. Therefore, under high ambient temperature, when metabolism is increased, a large cod will become faster oxygen-limited than a small conspecific. These two size-related processes eventually result in a size related change of the thermal optimum of cod, wherein larger cod prefer colder ambient temperatures than smaller conspecifics (Lafrance et al., 2005; Righton et al., 2010). In addition to body size, the haemoglobin genotype and the reproductive state are also described as factors which influence the thermal optimum of cod (Petersen and Steffensen, 2003; Lafrance et al., 2005; Righton et al., 2010; Behrens et al., 2012). For example, optimum temperature for growth and food conversion of adult islandic cod was determined as 7 °C (Björnsson et al., 2001). However, Righton et al. (2010) highlighted that Atlantic cod stocks in different areas showed adaptations to local temperature conditions. Thus, in a shallow habitat such as the Western Baltic Sea, which is characterised by strong warming in summer, cod may be thermally adapted to the warm ambient temperatures and thus optimum temperatures and thermal tolerance limits of Western Baltic cod are likely higher than those from cod inhabiting colder waters such as the Icelandic stock. Nevertheless, also higher thermal optima of WBC are exceeded when temperature rises in the shallow water layers above the thermocline (i.e. in waters shallower < 15 m) during late spring and summer. Hence, we explained the observed down-slope movements in the seasonal depth distribution of cod in summer as an avoidance behaviour. (**chapter I**). Due to the fact that temperature optima and temperature tolerance limits decrease with cod size (Lafrance et al., 2005; Righton et al., 2010), it seems likely that larger cod leave the shallow feeding grounds earlier than their small conspecifics and also tend to stay in deeper and colder habitats. Such ontogenetic differences in depth-use were already observed in acoustic telemetry studies of cod in the South Norwegian Fjord (Freitas et al., 2015, 2016). Size-related differences in depth use of cod in the Western Baltic Sea are also indicated by the gillnet mesh-size effect in the depth use model (**chapter I**). We found gillnetters using larger mesh sizes ≥ 120 mm at deeper habitats than mesh sizes ≤ 120 mm. Since larger mesh sizes have a greater selectivity for larger cod (Krumme, unpublished data), it confirms that larger cod tend to reside at deeper habitats than smaller individuals.

Gillnet fishers furthermore reported of cod aggregations at habitat sites > 15 m depths during peak-summer which display only low movement activity, and which are targeted by a special fishing behaviour called “point-fishery” (**chapter I**). These reports of low cod activity during peak-summer periods led to the hypothesis that cod may down-regulate their activity and thus, their overall metabolism during critical high temperature conditions, such as observed for the freshwater gadoid species *Lota lota* (Hardewig et al., 2004, **chapter I**). Down-regulated enzyme activity during high ambient temperatures was also observed for western Atlantic cod in studies of Guderley et al. (1996) at the coast off Newfoundland. They explained this regulation with a reduced feeding activity of cod, during periods with lower food supply in summer periods. Down regulated feeding activity during summer in relation to decreased prey availability was also hypothesized for North Sea cod, where cod tagged with data storage showed less movement activity and less pronounced daily vertical movements during summer (Turner et al., 2002). That study assumed that cod change their feeding behaviour from an active hunting to a “sit and wait strategy”, which is less energy expensive and is a more energy efficient strategy during periods with overall decreased prey availability. In contrast, Temming et al. (2004) related the behavioural change of cod to an ontogenetic change in behaviour of a forage fish species. In the period between June and July, 0-year-old sandeel start their nocturnal burying behaviour, whereas they tend to stay in midwater before. Hence, an active termination of the vertical migration resulting in an aggregation on a demersal prey concentration might be an alternative explanation for behavioural change displayed by the North Sea cod during peak summer period (Temming et al., 2004).

We observed highest proportions of empty stomachs and only low stomach content weights and daily consumption rates at habitat sites > 20 m depths during peak summer period (**chapter II**; **chapter III**). Currently, we are not able to distinguish whether these low consumption rates are more related to a general food limitation or more related to an overall down-regulated feeding activity during this period. However, it seems most likely that both factors are contributing.

Furthermore, we hypothesized that long-lasting warm periods during summer may negatively affect cod growth (**chapter III**). Strong warming of the water during the midsummer period can temporarily lead to temperatures above 15°C even in the deeper parts of the Belt Sea (>15 m). Hence, cod are exposed to unfavourable high temperatures even at their aestivation habitats, resulting in an increased standard metabolism. This increased standard metabolism in combination with observed low consumption rates may lead to negative energy budget and may result in energy losses such as predicted by our bioenergetic model (**chapter III**). This weight loss predicted by our models coincides with the observation by local fishers (pers. comm. U. Krumme,) of very small cod livers during summer, followed by a rapid increase after cod re-returned to their shallow feeding habitats.

The occurrence of hypoxic zones aggravates these negative effects occurring during peak-summer periods. In the Western Baltic Sea, hypoxia occurs temporally limited and outside the spawning periods of cod. Hypoxia is often the result of (Karlson et al., 2002), a lack salt water inflow events, from the Kattegat into the deeper channels > 20 m of the Western Baltic Sea, in combination with oxygen-consumption processes in the deeper water layers and reduced wind forcing (Weigelt, 1987). The spatially distribution of hypoxic zones in the channels of the Western Baltic Sea changes from year to year. In areas where hypoxia occurs, the depth distribution of cod is restricted to shallower areas such as the slopes and borders of the channels which match the oxygen-requirements of cod, while deeper areas, providing more favourable temperature conditions, cannot be used by cod. Hence, the formation of hypoxic zones can result in higher metabolic cost and energy deficits during peak summer period. To what extend these temporal restrictions in depth use affect annual growth rates, might be analysed using the individual-based bioenergetic modelling (**chapter III**) with an implementation of a temporally limitation of maximum residence depths.

In addition to growth effects, also reproductive success could be negatively affected by summer starvation, since the development of reproductive products is highly dependent on energy intake (Kjesbu et al., 1991; Lambert and Dutil, 2000). These negative effects will get even more pronounced when several years characterized by long-lasting extreme summer periods occur in a row possibly leading to “skip-spawning” (i.e. the omission of spawning). Skip-spawning was observed in some cod stocks such as from Northeast Arctic (Skjæraasen et al., 2012) and Newfoundland (Rideout et al., 2000). It was assumed that the omission of spawning is caused by a lack of energy to initiate development or re-ripening of gonadal products (Rideout et al., 2000; Skjæraasen et al., 2012). It was hypothesized that skip-spawning represents a trade-off behaviour between current and future reproductive success wherein individuals skip spawning after initial maturation in order to maximize their lifetime fitness and thus, enhance the chance of a successful spawning in the following year (Skjæraasen et al., 2012). However, it has not been investigated so far if skip-spawning occurs in WBC. Skip-spawning individuals are likely residing in shallower waters with higher food availability (i.e. intermediate depths ~15 m with hard structured grounds) than the deeper channels (**chapter I**). Hence, it can be assumed that the proportion of skip-spawning individuals is not represented well in the survey catches. However, the omission of spawning, if occurring on larger scale, may contribute to the great annual variability in recruitment observed for the WBC especially, since the spawning stock biomass and the number of recruits seem to be decoupled since the 2010s (ICES, 2019a). Hence, in order to better understand skip-spawning behaviour or in general the negative effects of summer-starvation on growth and reproduction, further investigations, especially focussing on the energy allocation processes, are required. A general better understanding of these energy allocation processes will enhance the parametrization of bioenergetic models and thus, the quality of the outcome. These models will improve our understanding of interannual differences in growth rates and reproduction of cod in the Western Baltic Sea such as shown for the Northeast Arctic cod (Jørgensen and Fiksen, 2006). Furthermore, additional monitoring of cod on shallow habitat (i.e. on non-spawning habitats) during the spawning time should be considered. Such monitoring programs will provide valuable insights whether and to what extent skip-spawning occurs in the Western Baltic Sea and thus, may help to better our understanding on the large interannual variability in WBC recruitment.

As discussed above the negative effects of high temperatures during peak summer temperatures are more pronounced in large cod, which are especially valuable for the reproduction of the stock, since their eggs displays higher quality (Marteinsdottir and Steinarsson, 1998). In addition, large cod are most likely also more vulnerable to targeted fishing during summer periods. Due to the ontogenetic changes in thermal preferences and resulting depth use large cod are likely the first individuals entering the deeper habitat sites > 15 m during the summer half year and thus the activity range of the commercial trawl fishery. In addition, the inactive and aggregative behaviour displayed by the cod during summer presumably makes them especially vulnerable for trawl fishery. However, these aggregations are also targeted by gillnetters when they are using “point fishery” (**chapter I**).This hypothesis is supported by observed catch compositions of commercial trawlers, which showed an increased catch of especially large cod (i.e. ≥ 60 cm) caught with rock-hopper gear at hard ground habitats at the slopes and borders to the deeper basins (pers. obs. during stomach samplings from commercial trawl catches in summer 2016; pers. comm. U. Krumme). For example, average cod sizes in those trawl catches can even exceed 70 cm, while outside the summer period individuals in sizes of 70 cm and more account only for minor proportion in the most trawl catches (Krumme, unpublished data). It is likely that the summer-fishing pressure on large cod becomes even more pronounced by introduction of spawning-closures. Traditionally, the commercial trawl fishery fleet in the Western Baltic Sea fished most of their cod quota during cod spawning season (Dorrien et al., 2013). With the introduction of a spawning closure such as introduced in 2016 and 2020, trawl fishing is legally banned in February and March. Thus, the commercial trawl fishery fleet likely shift their fishing effort to other times of the year targeting especially large cod. These large cod (“super-spawners”) account for only a small proportion of the total SSB of WBC over the last decades (ICES, 2019a). Hence the targeted summer trawl fishery might eventually result in an additional negative effect on the recruitment of WBC.

To what extent can the new results concerning the WBC be transferred to other cod stocks?

The Western Baltic Sea and especially the Belt Sea, which was selected as study area for this thesis, is considered a very special coastal and shallow habitat and hence, it is unclear to what extent our new results concerning the ecology of cod inhabiting this area are relevant for other cod and fish populations.

Even stocks from adjacent areas, such as the Eastern Baltic cod, are likely displaying different behaviour in depth use, food intake and growth. The Eastern Baltic Sea for example differs largely in hydrographic conditions from the Western Baltic in salinity but also bathometric properties. Moreover, species diversity differs between the areas in relation to salinity, whereat higher species richness can be observed in both fish and benthic invertebrates for the more saline Western Baltic Sea (Bonsdorff, 2006; Pecuchet et al., 2016). The decrease in species richness from west to east likely affects prey availability for the cod stocks inhabiting the two areas. For example, the common shore crab, which was revealed as one of the major prey items of cod in the Belt Sea is decreasing sharply in abundance from the Belt Sea eastwards. The distribution of common shore crab in brackish water depends on active osmotic regulation. Salinities of approximately 11 PSU can be found as a lower threshold for its distribution (Schlieper, 1974; Dries and Adelung, 1982). Hence it is likely that the availability of *Carcinus maenas* as prey for cod decreases sharply from the Mecklenburg Bight eastwards. This assumption is supported by first preliminary results from cod stomach samplings in the Arkona Sea, where the frequency of *Carcinus maenas* in cod stomach contents was much lower compared to the Belt Sea (Funk, unpublished data). In SD24 common shore crabs were observed mostly in cod stomachs sampled close to the shoreline during the third quarter, while they were generally absent in stomachs of cod caught in the central Arkona basin (Funk, unpublished data). The common shore crab individuals observed in the cod stomachs in SD24 are most likely individuals that immigrated to the coastal area of Rugia island during summer period from the more saline area of the Mecklenburg Bight in the west. Successful recruitment of common shore crabs in SD24 can be considered negligible, since salinities of less than 10 PSU, which can be observed in the upper coastal water layers already observed at eastern longitudes of Rugia island, are not matching salinity needed for larval development (Bravo et al., 2007). Thus, the major prey item of WBC the shallow habitats < 20 m is unavailable for cod in the eastern Baltic Sea. The only large benthic invertebrate species in the Eastern Baltic sea is the giant isopod *Saduria entomon*. In contrast to the common shore crab, which can be found in shallow coastal areas < 10 m depth in high abundances in the Belt Sea, the distribution of *Saduria entomon* is restricted to depths > 10 m, which is related to its cold-water preferences (HELCOM, 2013). McCrimmon and Bray (1962) observed that densities of *Saduria entomon* were highest on mud bottoms and lowest on gravel and sand.

Since the only large benthic invertebrate species *Saduria entomon* is absent from shallow water layers < 10 m and shows a preference for soft bottom habitats (Theede, 1974), it can be assumed that shallow hard structured grounds are less attractive in terms of food supply of invertebrates in the Eastern Baltic Sea especially for large cod. Additionally, also the number of forage fish species typically found at the vegetated, structured habitat sites in the Western Baltic Sea such as goldsinny wrasse (*Ctenolabrus ruprestris*) decrease from west to east with decreasing salinity, with Bornholm displaying the most easterly boundary of its distributional area (Ojaveer et al., 1981). However, sometimes, especially in late autumn and winter, even freshwater fish species such as for example perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) can be observed in the shallow coastal zones in SD24 and SD25, which display an additional source of forage fish species for cod in the shallow waters in the Eastern Baltic Sea (Funk, unpublished data; Hornetz, unpublished data).

Not only different prey availabilities between the Western and Eastern Baltic Sea influence the role of the shallow water habitats for the cod in the areas, but also the different life cycles of the two cod stocks themselves. As the western Baltic cod, also the eastern Baltic cod migrate to deeper saline layers during the spawning season. Eastern Baltic cod egg buoyancy requires salinities of 10 PSU, which can be found only in the deep basins of the eastern Baltic Sea, such as the Bornholm Basin, at depths > 60 m. Therefore, EBC is at least temporally restricted to very deep habitats, which are not available to cod in the western Baltic Sea. Furthermore, tagging studies by Neuenfeldt et al. (2007) showed that some individuals stay at depths > 70 m even outside the spawning season. Which might indicate a year-round importance of deep water. In contrast, trawl catches of EBC in shallow water habitats < 20 m depths in SD24 and SD25 conducted by the Thünen Institute of Baltic Sea fisheries and the University of Hamburg (Krumme, unpublished data), revealed that the shallow water habitats are at least partly used by EBC stock.

Peak spawning of WBC takes place in winter and early spring (i.e. from February to April) while peak spawning of EBC takes place in summer during July and August (Bleil et al., 2009). Hence, when WBC display distinct movement patterns into shallow habitats in April and May, EBC is in preparation for spawning, and likely utilizes deeper habitats. In contrast, during winter and early spring when WBC aggregates on its spawning grounds, EBC may use shallow habitats.

Using the WBC as an example, we were able to show how important seasonal changes in depth- and habitat use can be. Furthermore, our comparisons with the EBC that seasonal changes in depth and habitat use are also likely in other cod stocks. Although our finding regarding the role of shallow water habitats for the WBC cannot be transferred directly to other stocks from adjacent areas, the methods presented in this thesis can be applied to other stocks in other ecosystems, and thus, should help to improve our understanding of their spatio-temporal distribution, food intake and growth.

The use of fishers' knowledge

The problem that information on the spatio-temproal distribution of target species are mainly inferred from international coordinated research trawl surveys is not specific for the WBC but is a major problem for many target species in several ecosystems. As already discussed in this thesis (**chapter I**), hard structured, vegetated and shallow (< 10 m depth) habitats, which display essential habitats for cod in many ecosystems (North Sea: Bergmann et al., 2004; Newfoundland: Laurel et al., 2004; Norwegian Fjord: Freitas et al., 2016) but also for a number of other target species (for example whiting and haddock; see Bergmann et al., 2004) are often neglected in the sampling design of research surveys such as the Baltic international trawl survey (ICES, 2017a) or the international bottom trawl survey (IBTS) in the North East Atlantic (ICES, 2017b).

An important addition to research surveys are tagging experiments. Especially the use of data storage tags, which provide information on the residence depth, the ambient temperature and the ambient salinity gained increasing interest in the last decades (e.g. in the North Sea: Turner et al., 2002; and in the Baltic Sea: Neuenfeldt et al., 2007). Based on this information, the seasonal movement of the tagged individuals can be traced back to identify habitat selection or spawning migrations. However, the quality of tagging study data strongly depends on the recapture rates of tagged individuals. While in historic tagging studies of cod in the Baltic Sea recapture rates of over 30 % were reached (Berner, 1974), recapture rates in recent tagging studies were surprisingly low**.** For example, recapture rate of cod in the Baltic Sea in the TABACOD project reached only ca. 1 % in 2018 (T-bar tags: 1% recapture; data storage tags: 4% recapture) (www.tabacod.dtu.dk/deutsch/results; latest accessed 06.01.2020). In tagging studies of juvenile cod caught in pound nets in the Belt Sea recapture rates of even less than 1 % are reported (Stötera, 2017). These much lower recapture rates might be explained by the widespread use of fish gutting machines on commercial trawl vessels. The single cod are not gutted by hand by the fishers, but mechanically, which makes it easier to overlook the tagged individuals. On the other side tagging is relatively costly.

The here presented method of using local fishers' knowledge (**chapter I**) displays a very cost-efficient and practical alternative or addition to tagging programs and scientific research surveys to detect seasonal depth- and habitat use of target fish species. The perception of the marine environment by fishers and scientists often differs markedly (DeCelles et al., 2017). Traditional biological sampling such as scientific trawl surveys are usually conducted on a large spatial scale, but provide only temporal snapshots of complex ecosystem dynamics (Murray et al., 2008; Macdonald et al, 2014; DeCelles et al. 2017). However, fishers gain experience about their target species on a daily basis and, over the years, they often achieve a sound knowledge on seasonal spatial distributions of targeted species and their behavior such as spawning or feeding migrations (Bergmann et al., 2004; Zukowski et al., 2011; DeCelles et al., 2017). Hence, fishers' knowledge can help to better identify and localize essential fish habitats such as important feeding or spawning grounds, as well as to better our understanding of spatio-temporal abundance patterns of fish populations. (Ames, 1997; Maurstad and Sundet, 1998; Neis, 1999; Bergmann et al., 2004; MacDonald et al., 2014; Hedeholm et al., 2016; DeCelles et al., 2017). In our study, we used two sources of fishers' knowledge, one derived directly from the fishers by using semi-structured interviews and one indirectly by inferring information on the spatial depth-use from at-sea observation by scientific observers on-board of the commercial fishing vessels (**chapter I**). The use of two different sources of fishers' knowledge fulfilled two main purposes, which was (i) the validation of the data quality derived through the interviews and (ii) the increase of the sample size. However, the two knowledge sources also differ in the quality of the data. While the observer data enables the allocation of a certain selected catch depth of a fisher to the environmental conditions of the specific day, the interview data displayed an accumulated knowledge and behavior over the years and thus, may provide a more robust data source for the general trends in the seasonal catch depth selection of fishers. Moreover, the use of interviews gave us additional information why certain habitat types are selected during certain periods (**chapter I**). We were able to show high correspondence of the data from the two different knowledge sources which highlighted the value and quality of them.

Hence, we strongly believe that the use of knowledge from local resource users, of commercial fishers but also of recreational fishers, derived directly through interviews but also indirectly by at-sea observations, will provide a practical and cost-efficient alternative or addition to traditional methods to identify temporal and spatial distribution patterns and thus better understanding of the ecology of many target species in several ecoregions.

The use of recreational and commercial fisheries in stomach sampling programs

We also shed light on the problem of insufficient area-coverage in historic diet investigations of cod in the Western Baltic Sea. This problem is, again, not a Western Baltic Sea case-specific issue only, but is common among several species and ecosystems, since most stomach sampling programs were and still are conducted during research trawl surveys. An example is the stomach sampling program in the “Year of the stomachs” 1991 (ICES, 1991), a data set which is still largely used in recent publications (for example see Stäbler et al., 2017). All these stomach sampling programs are based on the untested assumption that they reflect the diet composition of the investigated stock adequately.

The use of stomach data from recreational fishing was also applied in a recent investigation on diet composition of Norwegian coastal cod in northern Norway, presenting the use of citizen science as a cost-efficient alternative to traditional stomach sampling methods and highlighting its potential for coastal ecological monitoring (Enoksen and Reiss, 2018). The use of gillnets was also already presented in several diet studies (for example Hop et al., 1992). Both methods have the great advantage that they enable fishing in nearly all different depths and on nearly all kind of different habitat types and thus, enhance depth coverage and habitat coverage in stomach sampling compared to samplings based on scientific trawling only. However, in literature it is also discussed that the methods differ largely in catch selectivity. For example, trawl fishing displays a higher selectivity for passive fish, while in contrast passive gear have a higher catchability for active fish (Hayward et al.,1989). In our study, we presented a combination of various fishing methods, angling, scientific and commercial trawling and gillnetting, which eventually enabled a high spatial coverage and a high temporal resolution. However, it should also be noted that the use of different methods has one major drawback, namely that a standardisation of fishing effort between the different fishing methods is hardly possible.

The use of bioenergetic models to develop age-independent growth estimates

We presented the use of a bioenergetic growth model in **chapter III**. Our growth estimates derived from the bioenergetic growth model coincided highly with those, derived from latest tag-recapture experiments (McQueen et al., 2019), which gives confidence in the quality of our model results. For many stocks, such as Western Baltic cod, growth is considered to be understood well but this does not include the physiological processes and interactions with the environmental conditions leading to the observed growth patterns. We know the growth rates of the fish, but we do not know what caused them. By applying a bioenergetic model the seasonal variations in growth could be explained from a combination of seasonally and spatially resolved stomach and temperature data. There are at least two important cases of gadoid species, where traditional otolith age-readings proved difficult, namely European hake (*Merluccius merluccius*) and Eastern Baltic cod (de Pontual, et al. 2006; Hüssy et al., 2016). Especially, for these stocks the bioenergetic model could be applied to calculate age-independent growth estimates (**chapter III**). Such length related growth estimates may form the basis for a length-related stock assessment in future.

Conclusion and outlook

In summary, this thesis highlighted the important role of shallow water habitats in the seasonal life cycle of Western Baltic cod, their importance as major feeding grounds and their importance for the seasonal growth of cod. Moreover, we revealed the effect of temperature on the depth- and habitat use and especially the negative effect of long-lasting high temperature conditions during peak summer period on cod growth. We furthermore hypothesized that cod in the Western Baltic Sea might be able to down-regulate their metabolism under peak-summer temperature conditions. This hypothesis needs further investigation. Maybe enzyme activity measurements may shed light on these possible regulatory processes. New evidence of this possible metabolic self-regulation may help us to better understand the impact of extreme temperature conditions on the physiological processes of cod in the Western Baltic and will also enhance the parametrization in future bioenergetic modelling.

We further hypothesized that long-lasting high temperatures and the resulting decrease of food intake and growth may influence the fecundity of cod or may even lead to skip-spawning behaviour. These hypotheses need also more consideration, since they may help us to better understand the great interannual variability observed in Western Baltic cod recruitment.

Finally, while our results concerning the role of shallow water habitats cannot be directly transferred to other cod stocks, the presented methods may, however, improve the ecological understanding of cod and other species in likewise structured ecosystems.

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Individual contributions to chapters with multiple authors

Chapter I – Gillnet fishers‘ knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea
S. Funk, U. Krumme, A. Temming, and C. Möllmann

All analyses, text writing and graphical illustrations were performed by S. Funk under supervision of C. Möllmann and A. Temming who critically reviewed the chapter. C. Möllmann and U. Krumme helped to develop the idea of the study. U. Krumme provided observer data and personal contacts to local gillnet fishers, and critically reviewed the text of the chapter.

Chapter II – Patterns in seasonal and depth-specific food intake of adult cod (*Gadus morhua*) in the Western Baltic Sea
S. Funk, R. Frelat, C. Möllmann, A. Temming, and U. Krumme

All analyses, text writing and graphical illustrations were performed by S. Funk under supervision of C. Möllmann and A. Temming who critically reviewed the paper. R. Frelat helped in the statistical analysis of the data and critically reviewed the chapter. U. Krumme and A. Temming helped to develop the concept of the study. U. Krumme provided personal contacts to local fishers, helped to coordinate the stomach sampling, and critically reviewed the text of the chapter.

Chapter III – An individual-based bioenergetic growth model for adult cod (*Gadus morhua*) in the Western Baltic Sea
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All analyses, text writing and graphical illustrations were performed by S. Funk under supervision of C. Möllmann and A. Temming who critically reviewed the chapter. A. Temming and J.-P. Herrmann helped to develop the idea of the study. U. Krumme and J.-P. Herrmann critically reviewed the chapter. H.-H. Hinrichsen provided the temperature data used in the model and critically reviewed the text of the chapter.

Hereby, I confirm the accuracy of the statements above,

Steffen Funk	Prof. Dr. Axel Temming
(Doctoral candidate)	(on behalf of the supervisors)

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Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift “Spatio-temporal distribution, food intake and growth of cod (*Gadus morhua* L.) in the Western Baltic Sea” selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Ort, Datum	Steffen Funk

Certification of Written English Quality

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To whom it may concern,

I have briefly reviewed the thesis „Spatio-temporal distribution, food intake and growth of cod (*Gadus morhua* L.) in the Western Baltic Sea" written by Steffen Funk. The thesis is written in English. As a native English speaker, I can attest that the writing (grammar and syntax) is acceptable. The English writing within this thesis is of sufficient quality to move forward with the submission and review process.

Sincerely,

Prof. Myron A. Peck