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Original Article

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

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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-directed interviews supplemented by at-sea observer data. Linear and non-linear regression analyses 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. The depth and habitat use displayed distinct seasonal up- and downslope movements of cod. This study 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.

Keywords: cod, habitat use, local knowledge, spatio-temporal distribution, Western Baltic Sea

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 has 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 avoided 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 cover 21% (Figure 1, ICES, 2017). Neglecting such large parts of the area likely limits the knowledge that 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. In comparisons to the BITS method, local fishers in the WBS often operate year-round,

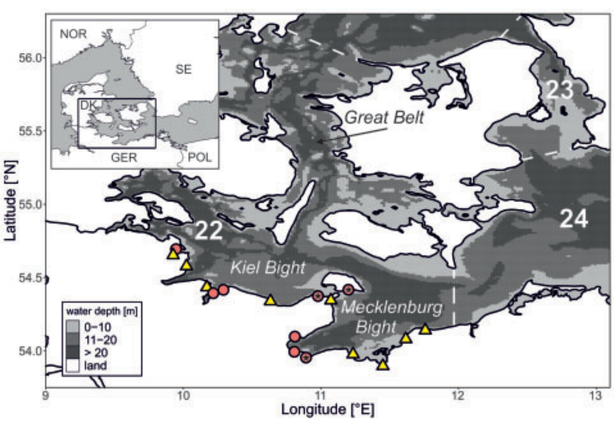

Figure 1. Bathymetry of the study area in the Western Baltic Sea. Red dots: ports with interviewed gillnet fisher (in 2016) and where at-sea observers started sampling trips of gillnet fishers in the period between 2011 and 2016. Yellow triangles: ports from which at-sea observers started sampling trips 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, and 24—Arkona Sea). Mecklenburg Bight, Kiel Bight, and Great Belt indicate subareas within the Belt Sea (SD22).

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 *et al.*, 2004; Zukowski *et al.*, 2011; DeCelles *et al.*, 2017). Hence, using local knowledge of fishers can help to improve the scientific 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 *et al.*, 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). 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. including non-trawlable sites). Thus, the 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 (mostly >20 m depths).

In contrast to trawlers, the commercial gillnet fishery lands cod year-round, with highest landings during October and November, 2 months when landings from trawlers tend to be relatively low (although during these months commercial trawl vessels are not subject to further legal restrictions) (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 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 German gillnet fleet between 2011 and 2016. 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. In addition, we aim to combine our gained knowledge with existing literature documenting life history and physiological and ecological traits of Atlantic cod in the WBS to develop a comprehensive conceptual model on seasonal depth and habitat use.

Material and methods

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, and brackish-water area (common salinity range: 10–25 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 (Figure 1). It is the core area of the western Baltic cod stock (Figure 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 5493 tonnes in 2011 to 2014 tonnes in 2018 (ICES, 2019a). In this period, Germany contributed between 44 and 51% of these landings. Of the German landings, on average, 60% were from active (trawl) vessels and 40% were from passive (mostly gillnet) fishing vessels between 2011 and 2018. A spawning closure from 1 April till 30 for trawl vessels on the commercial cod fishery in SD22 was implemented in 2008 and lasted until 2015 (EU, 2007; Eero *et al.*, 2019). In 2016, the spawning closure was changed to the period 15 February till 31 March. In 2017 and 2018, it was further extended to 1 February. During the spawning closures from 2008 to 2015, gillnet vessels were allowed to have only five fishing days over the whole time period. From 2016 to 2018, gillnet vessels were allowed to fish without day limits during the spawning closures but were restricted to operate in water depths <20 m only.

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 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 ∼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 registered vessels 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 (Figure 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 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; UK, unpublished data). Fishers can use both GNS and GTR on 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 2595 tonnes and 4586 tonnes annually from 2011 through 2016 (ICES 2019a).

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) (Figure 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 (UK, unpublished data). All, except one, were full-time fishers with vessel lengths 8–12 m. Thus, we interviewed 15 (27%) of 55 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 □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 tends 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 local and experiential knowledge can be gathered best in face-to-face interviews, which also provide the opportunity to ask follow-up and spontaneous questions about the topic of interest and for clarifications (Ritchie, 2003; Bryman, 2012). Furthermore, we expected that interviewed fishers would forward us directly to other fisher colleagues in the same port for further interviews. 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 port). However, unlike our expectations, it was difficult to meet more fishers in the ports or to convince them to take part in the study. This was mainly due to the extremely 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 cooperation or from at-sea observer trips. Similar to the face-to-face contact, on the phone, participants were asked to recommend other fishers. In this way, a total of 10 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 via 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 (including 15 full-time fishers and 1 part-time fisher). This question was asked to ensure that only fishers who 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 were registered commercial fishers at the time of this study (2016) and had cooperated with the Thünen-OF in previous 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 (where responses to a directed question were requested 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 recorded the answers in a prepared table (recording form); the interviews were not voice recorded. The questions and recording form are given in the Supplementary Material S2 (translated from German into English).

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 5 years before the interviews were conducted (i.e. the period 2011–2015). Gillnet fishers in the WBS usually fish in relatively localized areas, and the interviewed fishers had fished in the same area(s) for many years (see above). 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.

In the first interview question, we asked fishers to describe catch depths for targeted cod fishing (to be given in metres on a half-month 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.

In the second interview question, we asked fishers to share which ground structures (i.e. habitat types) they selected for targeted cod fishing (again using half-month 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.

For both interview questions, fishers were encouraged to elaborate on their experiences. 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 min, depending on the amount of additional information provided or on the willingness and patience of the fishers to respond to queries for additional information on the part of the scientists. The first author of this study conducted all face-to-face interviews; the phone calls were conducted by a student assistant.

At-sea observer data

A second data source was anonymized at-sea observer data collected within the EU-co-funded Data Collection Framework 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 for directly linking 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 on board 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.

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 20–25 m) for subsequent implementation in 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 $T_{\text{Diff.}}$.

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 5 years). Therefore, we computed average values for SST, SBT, and $T_{\text{Diff.}}$ 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 $T_{\text{Diff.}}$ of the sample year were assigned to the sampled fishing trip.

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 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 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 Habitat use).

Temperature effect on catch depth

We compared linear regression [linear model (LM)] and generalized additive models (GAMs) to investigate the effect of sea water temperature on catch depth of cod. SST, SBT, and $T_{\text{Diff.}}$ 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 (MSEs). The procedure was repeated 100 times keeping edfs for the smoothing terms between 2 and 5. Comparisons of the MSE revealed no significant differences (Analysis of variance (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; Akaike, 1974). We selected the more complex model if the AIC +2 was less than or equal to 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:

$$\text{Catch depth } [\text{m}]_i = \beta_0 + \beta_1 \text{SST } [^\circ\text{C}]_i + \beta_2(\text{SST } [^\circ\text{C}]_i^2) + \beta_3(T_{\text{Diff.}}[^\circ C]_i) + \varepsilon_i, \quad (1)$$

where β_0 is the coefficient of the intercept, β_1 is the coefficient of the linear term on SST at half-month *i*, β_2 is the coefficient of the polynomial term of order 2 on SST at half-month *i*, β_2 is the linear term on $T_{\text{Diff.}}$ at half-month *i*, and $\epsilon\varepsilon_i$ is 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):

$$Z = \frac{\beta_1 - \beta_2}{\sqrt{\text{SE}\beta_1{}^2 + \text{SE}\beta_2{}^2}}, \quad (2)$$

where β_i is the coefficient of model *i* and $\text{SE}\beta_i$ is the standard error of coefficient β_i.

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 characterizing 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, summarizing the non-significant factor levels) and eventually found only two of the mesh size categories to be significant in the model runs: 110–119 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:

$$\text{Catch depth } [m]_{ij} = \beta_0 + \beta_1 \text{SST } [^\circ\text{C}]_i + \beta_2(\text{SST } [^\circ\text{C}]_i^2) + \beta_3(T_{\text{Diff.}}[^\circ C]_i) + f(\text{mesh size}_j) + \varepsilon_{ij,} \quad (3)$$

where β_0 is the coefficient of the intercept, β_1 is the coefficient of the linear term on SST at half-month *i*, β_2 is the coefficient of the polynomial term of order 2 on SST at half-month *i*, β_2 is the linear term on $T_{\text{Diff.}}$ at half-month *i*, $f(\text{mesh size}_j)$ is the effect of mesh size category *j*, and $\epsilon\varepsilon_{ij}$ is a random error term at half-month *i* and mesh size *j*.

In addition, 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.

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:

$$\text{RHU}_{ik}(\%) = \frac{\sum_{j=1}^{n} \frac{N_{ijk}}{\sum_{i=1}^{m} N_{ijk}}}{n} \times 100 \text{ for } N_{ijk} = \{0,1\} \text{ and } \sum_{i=1}^{m} N_{ijk} \neq 0, \quad (4)$$

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

For statistical modelling of the habitat type selection, we applied multinomial logistic regression 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 $T_{\text{Diff.}}$. 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:

$$\ln\left(\frac{P_i}{P_{\text{ref.}}}\right) = \beta_{0i} + \beta_{1i}(\text{SST}_j) + \beta_{2i}(\text{catch depth}_j), \quad (5)$$

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

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

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

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).

Results

Seasonal variability in catch depths

The catch depths of cod in the Belt Sea reported by gillnet fishers ranged between 2.5 and 24.5 m (Figure 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) (Figure 2a). Mean catch depths were deepest in January/February (18.0 ± 4.9 m) and shallowest from late September to early November (6.0 ± 3.4 m).

Observer-based catch depths virtually replicated the seasonal W-shaped pattern reported by fishers (Figure 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).

Temperature effects on catch depth

LMs using SST and $T_{\text{Diff.}}$ 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 (Table 1). Linear and polynomial terms of SST and the linear term of $T_{\text{Diff.}}$ were highly significant ($p < 0.001$). The effect of the SST on catch depth followed an optimum curve (Figure 3a) with the shallowest catch depths of 6.0 and 4.7 m occurring during medium SSTs 13.3 and 12.7°C for LM1 and LM2, respectively. In both models, $T_{\text{Diff.}}$ 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 (Figure 3b). A *z*-test revealed no significant differences between parameter coefficients of LM1 and LM2 (Table 1).

Effect of mesh size on catch depth

Similarly to LM1 and LM2, the effects of SST and $T_{\text{Diff.}}$ on LM3 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 (Table 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) (Figure 3c and d). 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 Figure S2).

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%) (Figure 4). Mussel beds were also used during the whole year, but only with an RHU ranging between 3 and 10%. 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.

Effects of SST and catch depth on habitat use

The multinomial logistic regression model displayed a significantly better performance compared to the null model (McFadden pseudo $R^2 = 0.26$). Parameter estimates are given in Table 2. 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 the selection of hard ground was highest, except for catch depths <5 m, for which a preference for sand and seagrass was predicted (Figure 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 (Figure 5f). Probabilities for a selection of mussel beds were highest at medium catch depths between 5 and 10 m (Figure 5). The probability for wrecks and mud

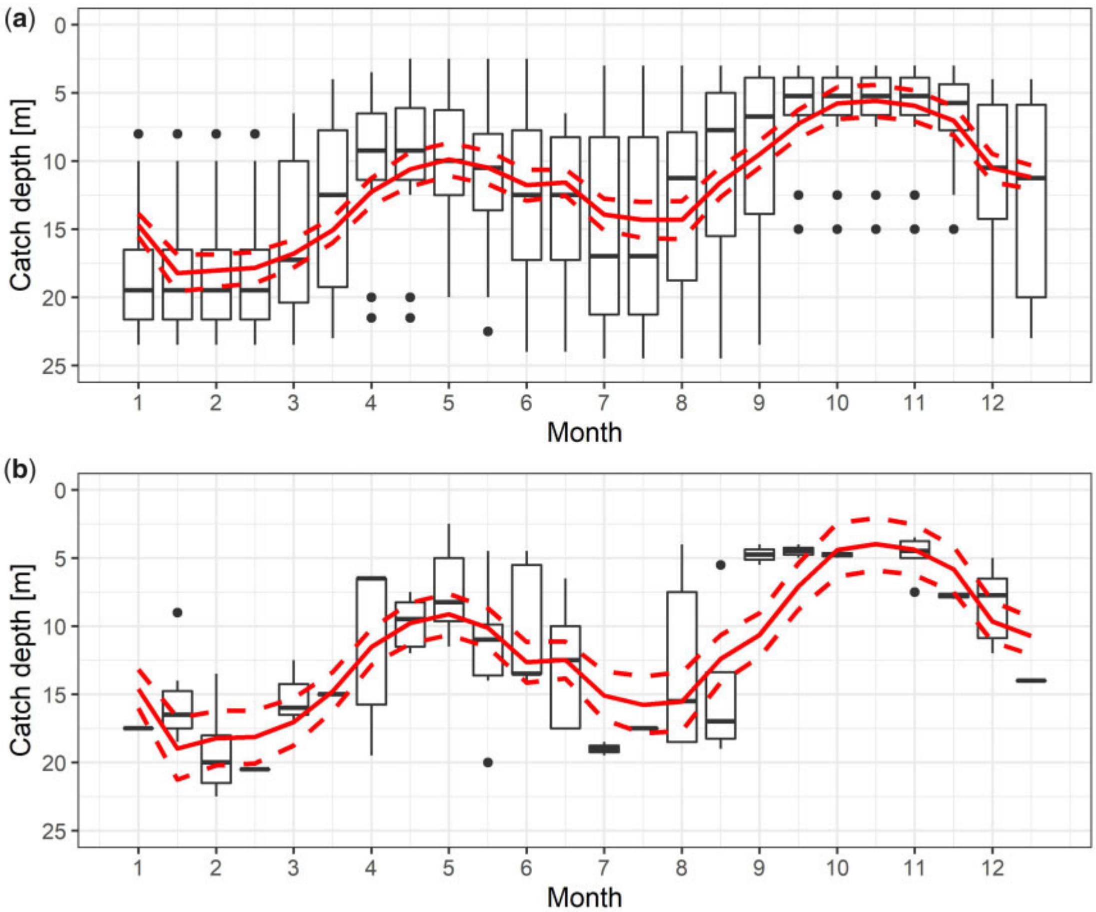

Figure 2. Seasonal variability in catch depths of western Baltic cod reported by 16 gillnet fishers (a) and at-sea observers who sampled 97 gillnet trips (b). Boxplots show median and first and third quartiles (hinges) of the reported depth per half-month. Whiskers extend from the upper/lower hinge to the largest value no further than 1.5 × interquartile range (IQR) from the hinge, respectively (IQR—the distance between the first and third quartiles). Black dots represent outliers that 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 LM1 (a) and LM2 (b). Dashed lines indicate upper and lower confidence intervals for catch depth predictions.

Table 1. Parameter estimates and significance levels for the final models (LM).

	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		

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; *z*- and *p*-values derived for the comparison of LM1 and LM2; adjusted explained variance (R^2) for all LMs.
p-value, significance level (significance codes: $^{***}p < 0.001$).

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 (Figure 5a and e).

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

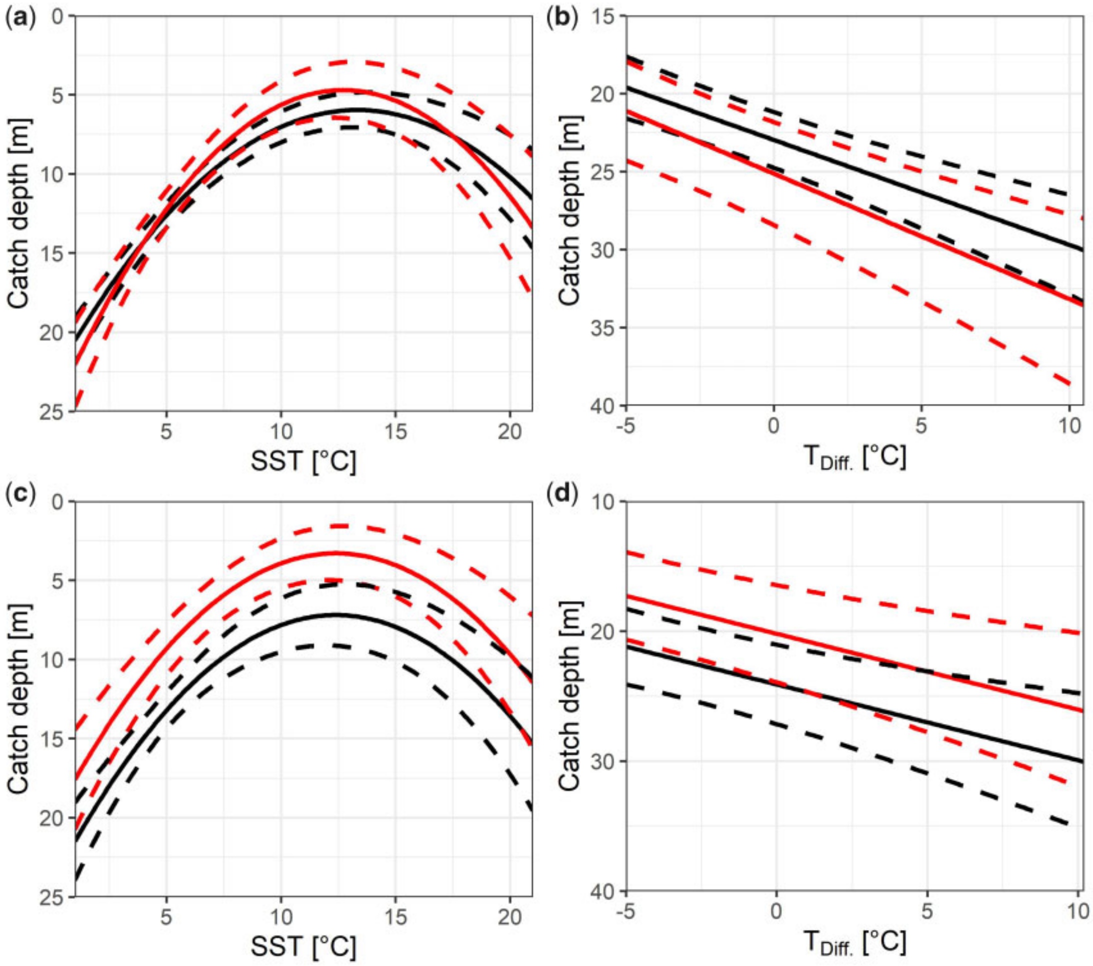

Figure 3. Statistical models of catch depth of cod. Partial dependence plots show the mean effects (solid lines) and 95% confidence intervals (dashed lines) for linear regression models LM1 (a and b; black lines), LM2 (a and b; red lines), and LM3 (c and d; red lines—mesh size category 110–119 mm, black lines—mesh size category 120–240 mm); T_{Diff}, stratification index.

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 WBS. 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.

Variables determining depth and habitat use of cod

Temperature is often considered as 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 and 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 of □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

Table 2. Parameter estimates and significance levels for the final multinomial logistic regression model.

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*

Reference habitat type: hard ground., *p*-value—significance level (significance code: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$).
SE, standard error.

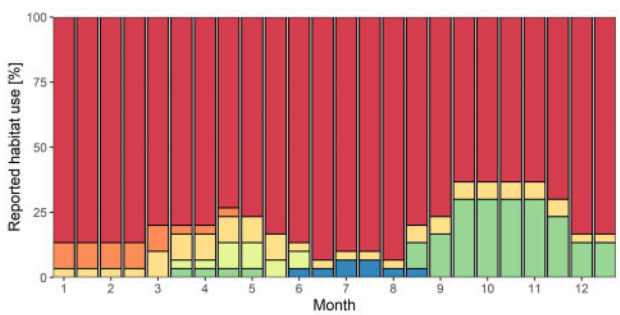

Figure 4. Seasonal variability in habitat use reported by 16 gillnet fishers per half-month period. Colours indicate habitat types (red—hard ground, orange—mud, yellow—mussel beds, light green—sand, green—seagrass, and blue—wrecks).

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 1–6 m in the Baltic Sea (Boström *et al.*, 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 the 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 overnight 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 the damage or loss of their gear (Interviewee 1, pers. comm.). Another potential caveat is the non-random selection of interviewed fishers. Almost all fishers had a formal or informal long-term relationship with scientists and observers of the Thuenen-OF. The data of this group of fishers are therefore not necessarily representative for the entire gillnet fishery fleet in SD22. However, the aim of our study was not to rely on a representative subgroup of fishers to share information. Rather, we aimed to collect in-depth local knowledge about behaviour of cod in SD22, using a subset of knowledgeable and cooperative fishers targeting cod in that same area. We believe we achieved that aim.

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 (Figure 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*).

Phase 1 (January–April) coincides with the pre-spawning and spawning time of cod in the WBS (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

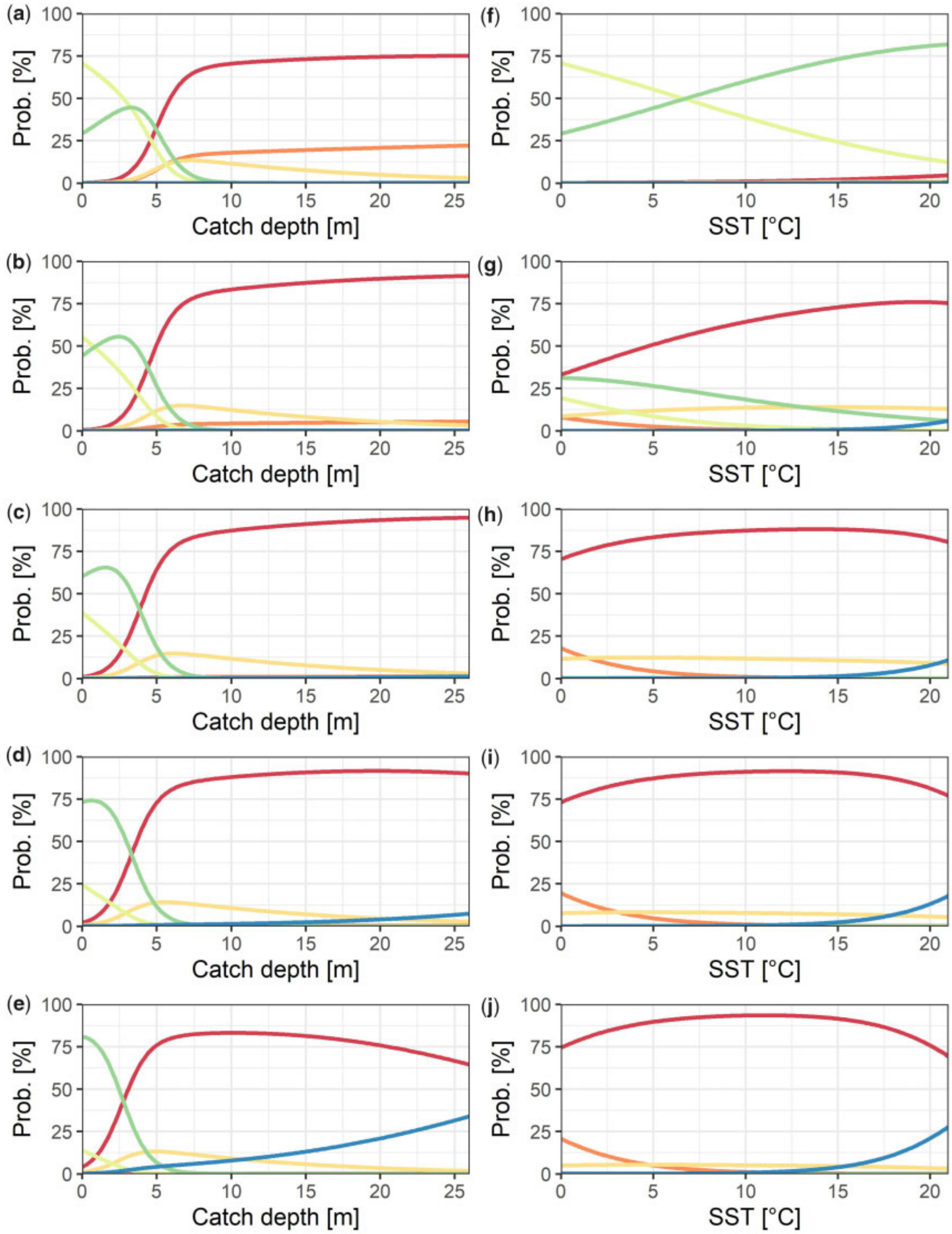

Figure 5. Statistical models of habitat use of western Baltic cod. Plots show the partial effects of catch depth (left plots) and SST (right plots) on relative probabilities [(Prob. (%)] of habitat type selection by gillnet fishers predicted using multinomial log-linear modelling; same colour code of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

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

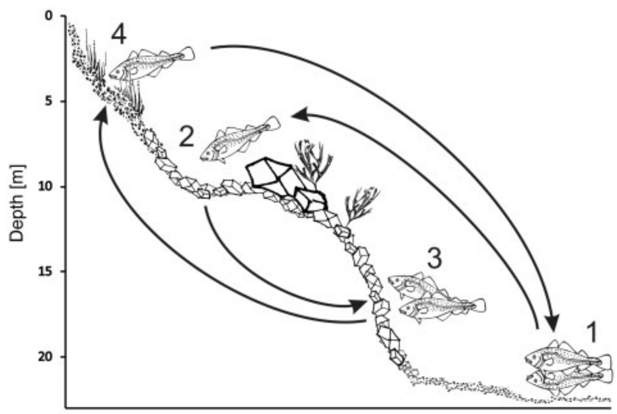

Figure 6. Conceptual model of seasonal changes in depth and habitat use of adult cod in the Western Baltic: Phase 1—pre-spawning and spawning period in deeper waters; Phase 2—post-spawning period in shallower waters; Phase 3—aestivation period during summer in deeper waters; and Phase 4—period of shallow 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.

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 2- to 3-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 12–14°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 (SF, pers. obs.; H. V. Strehlow, pers. comm.) and trawlers with specialized gear (with trawl fishers by UK, pers. comm.). 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, 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*.

Conclusions

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 (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 suggest distributional changes in cod habitat use related to water temperature. These results 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 condition 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 in the present survey and exploration of alternative or supplementary survey approaches may be advisable (see e.g. Caiger *et al.*, 2020).

This study implies that fisheries scientists may currently miss an important part of the picture needed for a thorough scientific understanding of the ecology of cod in the WBS. An efficient way to advance our knowledge about cod ecology while improving the design of scientific fishery surveys could be to promote cooperation between local scientists, managers, and fishers. We recommend that scientists, managers, and fishers in SD22 (and elsewhere) consider working together to develop comprehensive interview protocols and questionnaires, to be administered on a regular basis (e.g. annually).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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