



Seasonal changes in vertical distribution patterns of cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea

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ABSTRACT

Hydroacoustic single fish detection and corresponding hydrographic measurements were used to study seasonal changes in vertical distribution of adult cod (*Gadus morhua*) in relation to ambient environmental conditions in the Bornholm Basin, central Baltic Sea. Sampling was conducted in April, June and August covering the years 2006–2009. Vertical distribution of individual fish was resolved from hydroacoustic single-target detection in combination with a fish-tracking algorithm and related to ambient hydrographic conditions. Based on a generalized linear effect model, both salinity and oxygen concentration were identified as key parameters affecting cod vertical distribution. Results also showed a clear seasonal effect with a more shallow distribution as the spawning season progressed and oxygen concentrations in the deep parts of the basin deteriorated. The upper limit of the distributional range was mostly constituted by the halocline and remained rather constant, whereas increasing oxygen depletion in the deep water layers lifted the lower boundary of the vertical distribution, leading to the observed upward shift in the overall distribution pattern. The results presented in this study highlight a significant shortcoming of the assessment survey design established for this species, as the observed shift in vertical distribution is not taken into account, thus introducing a potential bias into a data series used to tune the ICES standard stock assessment of this species.

Key words: environmental thresholds, generalized linear model, oxygen depletion, vertical distribution

INTRODUCTION

In recent years, much attention has been paid to distributional characteristics of adult cod in the central Baltic Sea in relation to ambient hydrographic conditions. The semi-enclosed brackish Baltic Sea is characterized by strong vertical thermohaline stratification with a permanent halocline separating low salinity surface waters from highly saline deep waters. Due to irregular inflow events of saline and oxygen-rich water masses from adjacent North Sea regions and resulting stable stratification inhibiting mixing and thus transport of oxygen from upper to deeper layers, oxygen depletion is a common phenomenon, especially in the deep basins of the southern and eastern Baltic Sea (Matthäus and Franck, 1992; Hinrichsen *et al.*, 2002). Hinrichsen *et al.* (2002) showed a distinct decay of the 'reproductive volume' (RV) for cod in the central Baltic sea, especially between quarters 2, 3 and 4. The RV is the volume of water with physical conditions favoring successful development of cod eggs (salinity >11, oxygen concentration >2 mL L⁻¹, temperature >1.5°C; Wieland *et al.*, 1994). As the depth of the oxygen depletion layer changes over the season due to oxygen consumption, vertical distribution patterns of adult cod in relation to ambient hydrographic conditions are most likely to change as well within the course of the year.

Spatial distribution patterns of cod in the Baltic Sea have previously, been related to bottom depth and spawning behavior (Aro, 1989; Sparholt *et al.*, 1991; Bagge *et al.*, 1994). The environmental influence on vertical distribution of cod in relation to clupeid prey was investigated by Neuenfeldt (2002) and Neuenfeldt and Beyer (2003). Further, oceanographic influences on the temporal and spatial distribution of cod outside their main spawning time were analyzed by Hjelm *et al.* (2004) based on trawl surveys. Tomkiewicz *et al.* (1998) investigated cod horizontal and vertical distribution during spawning time using a combination of trawl- and hydroacoustic data, whereas Hinrichsen *et al.* (2007) used early egg stages of cod as a proxy for

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adult distribution patterns during spawning. More recently, advanced tagging techniques have been applied to study cod distribution patterns. Neuenfeldt *et al.* (2009) identified vertical excursions of cod into hypoxic deep layers with data storage tags, recording *in situ* ambient habitat conditions of individual cod. Schaber *et al.* (2009) applied hydroacoustic single fish tracking to identify environmental influences on habitat preferences and limits during spawning time in 2 years with contrasting hydrographic conditions. All these studies revealed that ambient hydrographic factors not only directly and indirectly affect early life stages, but also have a significant effect on the vertical and, due to the basin geometry, also the horizontal distribution patterns of adult cod. Similar to early life stages, salinity and oxygen concentration have also been identified as key parameters in that they constitute the upper and lower boundaries of suitable habitat in the strongly stratified deep basins of the central Baltic Sea. Tomkiewicz *et al.* (1998) showed that cod in the central Baltic started to accumulate when ambient oxygen concentration exceeded 2.5 mL L^{-1} , whereas cod was mostly absent in water layers with lower oxygen concentrations. Based on hydroacoustic data, providing high resolution information on the horizontal and vertical distribution, Schaber *et al.* (2009) have shown that spawning cod, even though partially distributed in layers outside their preferred habitat, generally avoid salinities <11 and oxygen concentrations below 1.5 mL L^{-1} .

However, all of the studies mentioned were restricted to observations at a single point in time (e.g., Tomkiewicz *et al.*, 1998; Neuenfeldt and Beyer, 2003), a short time slot during main spawning activity (Schaber *et al.*, 2009) or modeling approaches (Hinrichsen *et al.*, 2007). Even more importantly, in some cases the sampling gear applied was not able to resolve small-scale distribution patterns vertically due to large vertical net-mouth openings of several meters (Tomkiewicz *et al.*, 1998; Neuenfeldt, 2002; Hjelm *et al.*, 2004) or – where data storage tags were used – sampling was limited to very few individuals (Neuenfeldt *et al.*, 2007, 2009).

Previous studies showed that applying hydroacoustic methods and especially single fish detection and tracking algorithms revealed reliable real-time and small-scale *in situ* distribution characteristics of Baltic cod on a population level (Schaber *et al.*, 2009). In the present study, we analyzed small-scale vertical distribution patterns of adult cod along transects within the Bornholm Basin during 2006–2009 over 3 months covering the second and third quarter of each year using the same methods. The main focus was

to identify hydroacoustically the temporal and spatial course in small-scale (vertical) distribution patterns of cod at population level during large parts of their annual spawning cycle. To identify the underlying reasons for different distribution patterns, changes in ambient hydrographic conditions were related to the observed distribution of cod.

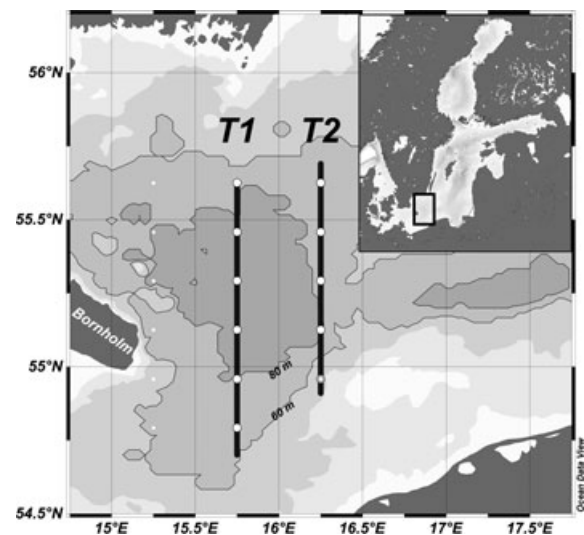
MATERIAL AND METHODS

Hydroacoustic data

Hydroacoustic data were recorded on 10 research cruises of R/V *Alkor* in June and August 2006, April, June and August 2007 and 2008, and April and August 2009. No hydroacoustic data were available for April 2006 due to logistical restraints or for June 2009 due to unfavorable weather conditions. Hydroacoustic measurements were carried out mostly at nighttime on two parallel longitudinal transects covering the deep parts of the Bornholm Basin with a spacing of 30 nautical miles between transects. Longitudinal transect position was $15^{\circ}45'00''\text{E}$ and $16^{\circ}15'00''\text{E}$ (Fig. 1). Data were collected with a Simrad hull-mounted split-beam transducer ES38-B and a Simrad scientific echosounder EK60 operated at 38 kHz by SIMRAD ER60-Software (Kongsberg Maritime AS, Horten, Norway).

To meet requirements for single fish tracking (see ICES, 2007), a short pulse duration (0.256 ms; high vertical resolution) and high ping rate (high horizon-

Figure 1. Sampling area in the Bornholm Basin, central Baltic Sea. Longitudinal hydroacoustic transects T1 and T2 are indicated (black lines). White dots represent station grid for stationary hydrographic CTD measurements. Inlet marks location of sampling area in Baltic Sea.



tal resolution) were set. Prior to the surveys, echosounder and transducer had been calibrated with the standard copper sphere method described by Foote *et al.* (1986) and ICES (2001). Ship speed at which the transects were covered was 10 knots (kn, 1 kn \sim 0.5 m s⁻¹) in 2006 and 5 kn in 2007–2009.

ECHOVIEW software (Sonardata, 2007; <http://www.echoview.com>) was used for post-processing of hydroacoustic data. None of the echoes detected within the upper 10 m of the water column were considered for analysis as they may have originated from turbulence caused by ship operation. Noise signals and scattering layers were manually marked in the echograms and excluded from further processing. In some cases, hydroacoustic data were not exclusively recorded at nighttime but also covered dusk and dawn. Therefore, the detection of echoes scattered from clupeid schools could not be avoided, as clupeids begin to migrate vertically upwards and disperse during dusk, and *vice versa* during dawn (Nilsson *et al.*, 2003). Therefore, a school detection algorithm (component of ECHOVIEW, for settings see Nilsson *et al.*, 2003) was applied to identify possible signals resulting from clupeid schools. Corresponding schools were excluded from further processing.

The single target detection operator of the ECHOVIEW software was applied to identify single target echoes. Target strength (TS) is a function of fish size (e.g., Foote, 1987; McQuinn and Winger, 2003). In our study, a minimum threshold of -37 dB was set for acceptance of an echo as originating from (adult) cod. This restricted detections to fishes with a length of more than 30 cm but prevented inclusion of echoes scattered by clupeid sprat (*Sprattus sprattus*) and, more likely, herring (*Clupea harengus*) (McQuinn and Winger, 2003; Peltonen and Balk, 2005; Fässler and Gorska, 2009). Therefore, the effects of hydrographic parameters on the distribution patterns of juvenile cod could not be observed.

The detection algorithm chosen was based on target strength and angular position data. Parameters used for detection of single targets were (minimum and maximum length of a single target pulse, respectively) 0.49 and 1.51 times normalized pulse length (0.256 ms) and 12.0 dB for maximum beam compensation.

To avoid pseudo-replication of targets by processing several echoes scattered by a single fish, a target-tracking algorithm was implemented on the data, allowing an aggregation of several single echoes to one track and thus allocating multiple consecutive echoes to a single fish. Due to a continuous forward motion of the ship and thus the echorecorder, the acceptance range for combining consecutive echoes to one fish

was set higher on the horizontal than on either lateral or vertical axes. Therefore, the longitudinal axis was allocated 50% weight. Due to different vessel velocity in 2006 and the consecutive years, the minimum targets and pings required for acceptance of a fish track were set to 3 (10 kn) and 5 (5 kn).

Relevant data recorded from resulting tracks of all identified fish included mean geographical position, mean depth, mean target strength and mean distance to sea floor.

Hydrographic data

Ambient hydrographic data were either measured on a regularly spaced 10-nautical mile station grid spatially complying with the transects (2006 to June 2007, Fig. 1) or measured continuously along the transects during acquisition of hydroacoustic data (August 2007–2009). In the former case, a vertically deployed ADM-CTD (conductivity, temperature and depth) probe was operated; in the latter, the probe was mounted on a towed frame and continuously operated in undulating oblique hauls to increase spatial and vertical resolution. Parameters recorded by the probe were temperature, salinity and oxygen concentration. To enhance the resolution of stationary CTD data and thus allocate real-time ambient hydrography to each fish detected by hydroacoustic measurements, a hydrodynamic model was applied. This model, based on the free surface Bryan–Cox–Semtner model (Killworth *et al.*, 1991), has a horizontal resolution of 5 km and 60 specified vertical levels. Descriptions of modifications and adaptations of the model to Baltic Sea requirements can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000). The physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (Lehmann, 1995; Hinrichsen *et al.*, 1997; Lehmann and Hinrichsen, 2000). Hydrographic data recorded by the undulating, towed CTD probe were allocated to individual fish by assigning the horizontally nearest dataset with measurements of referring depth strata to each fish.

Graphical mapping of both hydroacoustic and hydrographic data was performed using OCEAN DATA VIEW software (Schlitzer, 2007; <http://odv.awi.de>).

Statistical analyses and effect modeling

When studying the effect of environmental factors on the vertical depth of cod, explorative investigations were begun using symmetric Pearson-type correlation coefficients. Given the knowledge gained, the next step was to formulate the following ANCOVA-like generalized linear regression model (GLM):

$$Z = b_0 + \sum_i (b_i \times i) + \sum_j (c_j \times j) + \varepsilon \quad (1)$$

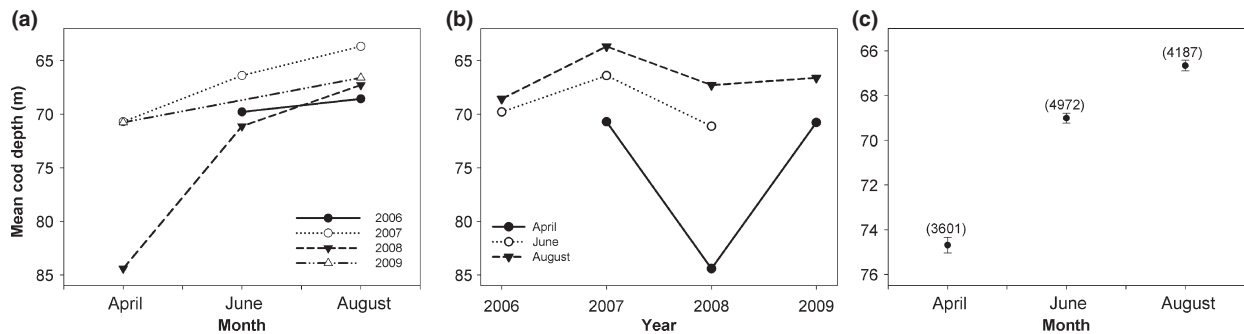
where Z is cod depth and ε is the associated error term, with homogeneous, normally distributed variance and white noise being assumed. Following the backward variable selection approach, we started with the full model and initially included all linear combinations of the abiotic factors i available (such as oxygen, salinity, temperature) to reduce the risk of estimation bias by falsely excluding a non-redundant variable. Pre-analyses revealed a significant interactive year-month effect. Thus, linear combinations of all year-month effect level combinations j available were also included to avoid bias through ignoring these. The subscripts i and j behind the sum signs in Eqn (1) refer to the $i = 1, \dots, k$ linear combinations regarding the abiotic factors and $j = 1, \dots, l$ linear combinations regarding the year-month levels. Conversely, to avoid bias through multi-collinearity (redundant or overlapping information), each pair of abiotic factors included was orthogonalized, and the residual factors which *per se* are uncorrelated were used (otherwise, the so-called variance-inflation factor would increase dramatically, inflating the errors of the parameters estimated). This was accomplished by first fitting a linear calibration model between the variable pairs affected and then removing any linear trend (linear correlation) from them to give uncorrelated residuals which are then taken instead of the original variable itself. This treatment is similar to what is known as pre-whitening in time series analysis. The model diagnostics included testing the null hypotheses of homoscedasticity of the final model residuals, of non-significant parameters, of no factor interactions, and of normal residual distribution. The finally best model was selected using the coefficient of determination and was also based on the strength of the positive correlation between predicted and observed cod depth values.

RESULTS

A total of 12 760 cod were identified with hydroacoustics along the transects sampled in 2006–2009. Pronounced vertical patterns were identified during the sampling period. These patterns are represented by an upward shift of the mean depths of cod from April to August in each year observed. Both between years and between months, the differences in depth distributions were highly significant ($\alpha = 0.05$; Fig. 2a,b). The overall mean (\pm SE) vertical distribution was greatest in April (74.69 ± 0.35 m) and was significantly decreased by June (69.01 ± 0.22 m) and August (66.66 ± 0.24 m; Fig. 2c).

Figures 3 and 4 show examples of seasonal distribution patterns along transect 1 in 2007 and 2008 in relation to the ambient hydrographic parameters salinity and oxygen. In April 2007 (Fig. 3), water layers below 75–80 m were characterized by oxygen depletion, and the ambient oxygen concentration in these layers was <1 mL L⁻¹. Hydroacoustically identified cod were distributed between 89 and 55 m depth. North of 55°N, cod were almost exclusively distributed in the pelagic. More southerly, demersal cod were observed dwelling slightly above the sea floor. By June, oxygen depletion in the deep parts had progressed, with layers below 70 m showing ambient oxygen concentrations of <1 mL L⁻¹. The overall distributional range of cod was between 23 and 92 m depth, the largest fraction being observed in layers >50 m depth with salinities exceeding 11. A substantial part of all cod observed were distributed in depths below 70 m and thus in oxygen levels below 1 mL L⁻¹, but the fraction of cod distributed directly above the sea floor had diminished compared with April. An upward shift in aggregate vertical distribution was most pronounced in August, when cod were observed between 30 and 78 m depth. Again, the largest fraction was distributed in salinities >11 . The lower distribution boundary mostly followed the 1 mL L⁻¹ oxycline and no further cod were observed near the sea floor, with a few exceptions in the very south of the transect in an area where the oxycline met the sea floor at approximately 70 m depth. The upward shift induced by oxygen depletion in the deep parts of the Basin was even more pronounced in 2008 (Fig. 4). In April, the water body was well oxygenized, with oxygen levels exceeding 2 mL L⁻¹ in depths >90 m. Cod were observed from 44 m depth to the deepest parts of the Basin (99 m). The largest fraction was densely aggregated in the deep parts of the basin between 55.4°N and 55.0°N in depths below 80 m directly above the sea floor up to 10 m above. Progressive oxygen depletion led to deterioration of oxygen concentration in the deep parts by June 2008. By then, water layers below 70 m near the northern and southern margins of the deep Basin and below 90 m in the central part were characterized by an ambient oxygen concentration of <1 mL L⁻¹. Although cod was distributed at similar depths as in April (40–95 m), the number of dense aggregations near the sea floor had decreased. North of 55°N, the largest part of cod observed was distributed in layers several meters above the sea floor, with only a minor fraction dwelling close to the sea floor. South of that area, ambient oxygen concentration was well above 1 mL L⁻¹. There, cod densely aggregated at the sea

Figure 2. Mean annual depth distribution of adult cod (*Gadus morhua*) per month (a) and mean monthly depth distribution per year (b) throughout the observation period ($N = 12\,760$). (c) Overall mean (\pm SE) monthly depth distribution of cod. Numbers in brackets indicate number of cod identified. Missing values: see main text.



floor, comparable to aggregations observed further north in April. In August, the 1 mL L^{-1} oxycline had shifted upwards to depths between approximately 70 m in the northern area of the Basin, increasing in depth towards the south and meeting the sea floor in approximately 85 m depth slightly north of 55°N . Cod distribution followed the salinity 11 halocline and the 1 mL L^{-1} oxycline marking the upper and lower boundaries of the observed depth range (38–82 m), respectively, with only a few individuals observed above the halocline and none observed in oxygen concentration levels $<1 \text{ mL L}^{-1}$. North of 55°N , distribution was restricted to pelagic layers well above the sea floor, with the distance to the sea floor well exceeding 15 m in the northern area. In the southern part of the Bornholm Basin, oxygen concentrations exceeded 1 mL L^{-1} throughout the water column. There, cod were observed close to the sea floor. However, no clear aggregation patterns were found along the transect.

The results of the effect modeling are graphically presented in the correlation matrix in Fig. 5. In all cases, significant correlations with $R > |0.441|$ ($P < 0.0001$) exist. However, the high correlations not only occur between observed endogenous (vertical distribution of cod) and exogenous variables (abiotic factors such as temperature, salinity, oxygen) in the Bornholm Basin but also among the exogenous variables temperature, salinity and oxygen. The latter observation requires careful variable selection and removing the correlation (trends) between those exogenous variables that are finally included into the model. It can be inferred from the shifting patterns of the colored dots in Fig. 5 that the strength and type of correlation also depend on the month. A similar graphic pattern can be observed when using years instead of months while plotting the correlation matrix (not shown here). This obvious interaction between year

and month is also confirmed by Fig. 2. Whereas Fig. 2a shows that the lines for years 2006 and 2009 intercross, in Fig. 2b the lines follow non-parallel tracks. Testing the year–month effect on the vertical distribution of cod either as a nested (or an interaction) term using an ANOVA-type approach also leads to significant results ($P < 0.0001$), indicating a strong interaction between both. Given all this, we ended up with the following ANCOVA-type GLM model for cod depth (Z) in relation to oxygen concentration (O), salinity (S) and year (Y) as well as month (M):

$$Z = b_0 + b_1 \times O + b_2 \times S^{(\text{calibrated})} + \sum_j c_j \times Y(M)_j^{(\text{nested})} \quad (2)$$

for the months April, June and August as well as years 2006–2009. To avoid multi-collinearity between salinity and oxygen, in the case of salinity we used the ‘calibrated’ residuals in which the trend is removed, instead of the original values, referred to as residual salinity in the following. This led to orthogonal factors with $R_{O \times S} = 0$ ($P = 1.0$). To include the year–month effect, the nested term version ‘ $Y(M)$ ’ was used, although the result would be exactly the same when specifying the term as interaction version ‘ $Y \times M$ ’. It should be noted that not only does the entire model appear to be significant ($P < 0.0001$), but also the three factors oxygen, salinity plus the year–month interaction term ($P < 0.0001$). The model explains 76% of the variation of the cod depth which is graphically confirmed when plotting observed and predicted cod depth values against each other (Fig. 6a). Parameter estimates and P values are given in Table 1. Figures 6b,c indicate that the model’s residuals are normally distributed. However, Fig. 6a also shows that a hidden factor may play a role, as 24% of residual variance is left unexplained.

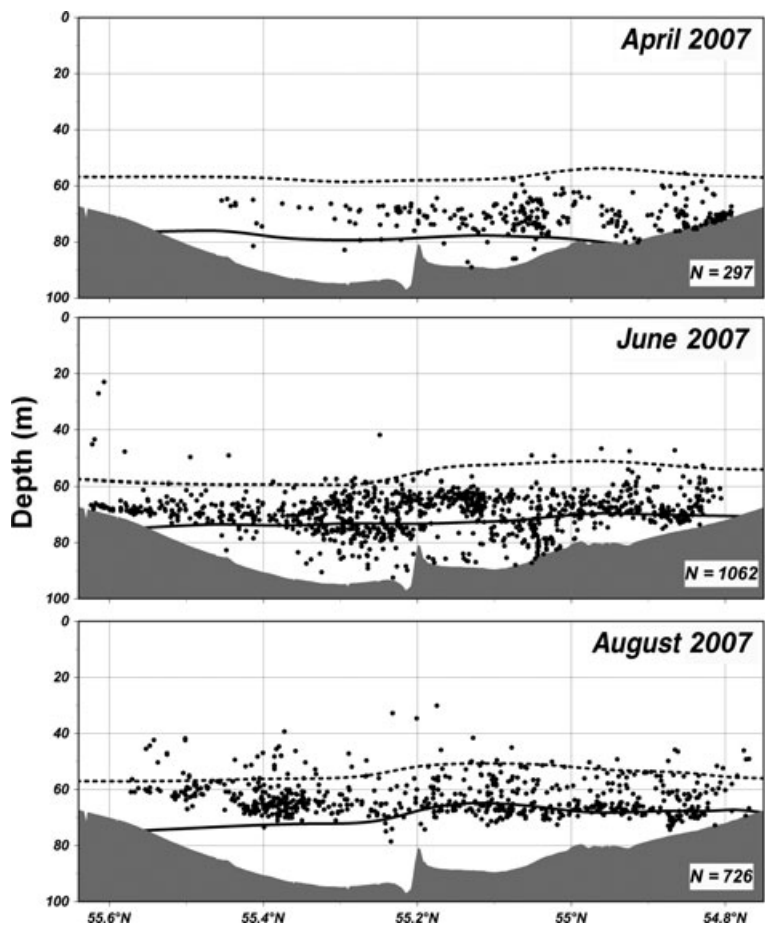


Figure 3. Horizontal and vertical distribution patterns of adult cod (*Gadus morhua*) along hydroacoustic transect T1 (15°45'00"E) in the central Bornholm Basin in April (top panel), June (middle panel) and August (lower panel) 2007. Black dots represent individual cod identified by hydroacoustic single-fish tracking. Dotted line, salinity 11 halocline; solid line, 1 mL L⁻¹ oxycline.

DISCUSSION

Based on *in situ* spatial distribution data of cod (*Gadus morhua*) as well as corresponding hydrographic variables, a GLM effect model explaining 76% of cod depth variation was established. Apart from a significant year-month effect, salinity and oxygen concentration were identified as the most significant factors influencing vertical distribution of cod.

The 24% of variation in depth distribution of cod remaining unexplained by the model applied could be caused by either a hidden factor (see below) or deviations from linearity in the response of individuals to environmental stressors, which is indicated by the inferior performance of the model for regions above the permanent halocline (i.e. above approximately 50 m depth, see Fig. 6a). The transects sampled did not cover regions where bottom depth was shallower than halocline depth, i.e. where cod could have remained demersal in oxygenated layers of low salinity. Therefore it is possible that factors other than salinity determine vertical distribution patterns of cod in that

area. As cod are physoclists, a swimbladder-defined limitation in free vertical range could be a possible factor. However, previous studies revealed that cod show a high plasticity in vertical movement and swimbladder capacity (Harden Jones and Scholes, 1985; Righton *et al.*, 2001) and in the Baltic Sea even do not display equilibration after capture and release but immediately return to the depth to which they were originally adapted (Van der Kooij *et al.*, 2007). Therefore, swimbladder-related limitations in the vertical range of cod are considered unlikely.

It has been shown that during the course of almost all years investigated, cod in the (central) Bornholm Basin obviously suffered from loss of favorable habitat due to deteriorating oxygen concentrations in the deep parts of the Basin. Progressive oxygen depletion induced an upward shift of cod distribution as characterized by a significant upward shift of mean cod depth. The upper boundary of overall vertical distribution remained nearly constant and was related to the upper layers of the permanent halocline. Cod generally concentrated near or at the sea floor if

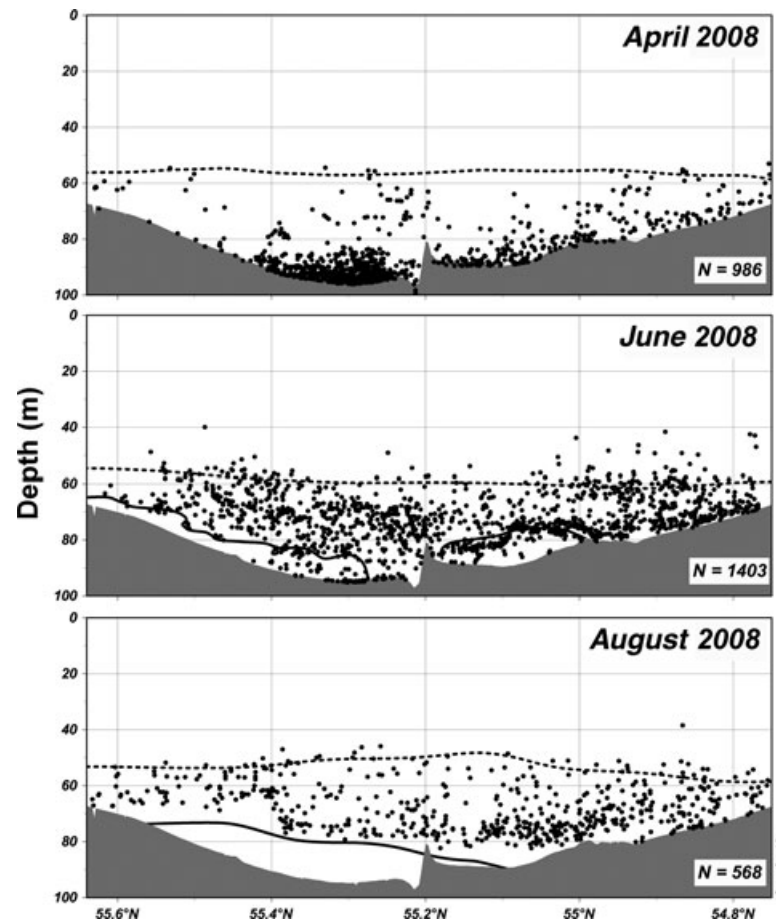


Figure 4. Horizontal and vertical distribution patterns of adult cod (*Gadus morhua*) along hydroacoustic transect T1 (15°45'00"E) in the central Bornholm Basin in April (top panel), June (middle panel) and August (lower panel) 2008. Black dots represent individual cod identified by hydroacoustic single-fish tracking. Dotted line, salinity 11 halo-cline; solid line, 1 mL L⁻¹ oxycline.

oxygen concentrations permitted and only migrated upward when the oxygen level near the sea floor decreased below acceptable conditions. This seasonal upward migration is consistent with observations of decreasing oxygen levels in the bottom layers of the Bornholm Basin in subsequent quarters of the year after the winter months due to a lack of atmospheric forcing events (Hinrichsen *et al.*, 2002).

Echorecordings were conducted almost exclusively during nighttime to avoid misidentification of echoes originating from clupeids. Irregular diurnal vertical migration behavior of cod has been observed in different regions and has been related, among other considerations, to prey availability and buoyancy equilibration (Godø and Michalsen, 2000; Strand and Huse, 2007). However, vertical distribution patterns derived from data storage tags did not indicate any specific diurnal migration behavior of cod in the central Baltic Sea (Neuenfeldt *et al.*, 2007). Hence we consider our conclusions to be also valid for daytime distribution.

Vertical movements of cod and emerging vertical aggregation structures described as columns have been

observed before and have been related to spawning behavior (Rose, 1993; Lawson and Rose, 2000). The sampling conducted in this study was not capable of resolving small-scale individual vertical migration behavior. The extended vertical range observed during peak spawning time in June and August could be related at least partly to spawning and courtship activity. However, the reduced vertical range of the largest fraction of cod observed, for example, in April 2008 would seem to indicate that hydrographic influences are the main cause, with cod possibly having a natural preference for demersal residence if unrestricted by physical environment (e.g., Van der Kooij *et al.*, 2007). Additionally, spawning columns indicating instantaneous courtship and spawning behavior were not detected during nighttime hydroacoustic recording but were in some instances detected in the area during dawn/daylight (M. Schaber, unpublished data).

Based on data storage tag data, Neuenfeldt *et al.* (2009) could show that cod in the Bornholm basin undertook frequent short migrations into water layers of extremely low oxygen content, most likely for feeding or to reduce osmotic stress. This observation

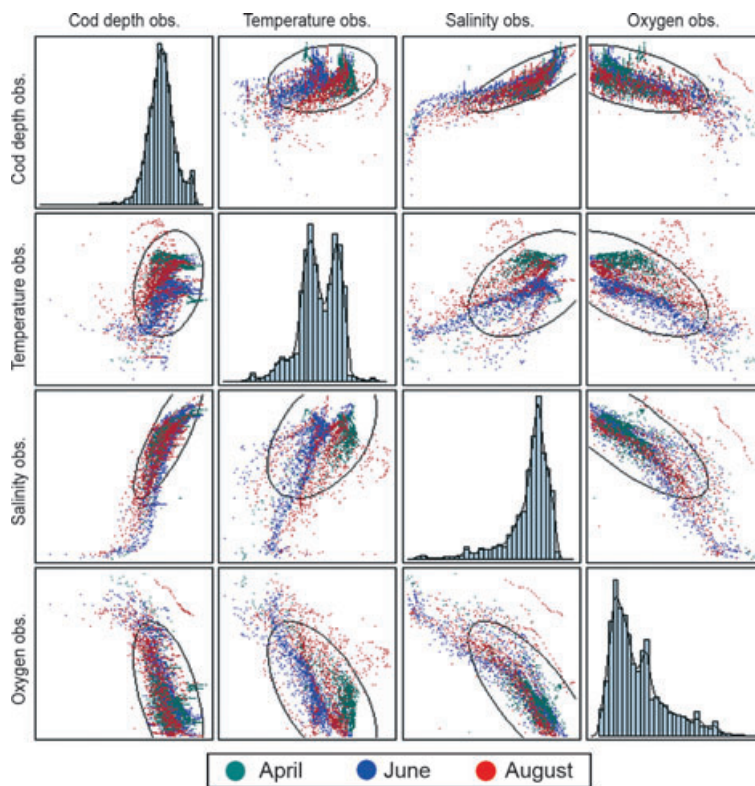


Figure 5. Correlation matrix between observed endogenous (cod *Gadus morhua* vertical distribution) and exogenous variables in the Bornholm Basin. Ellipses indicate confidence of prediction around the center of the data cloud (95%, $\alpha = 0.05$) assuming a bi-variate normal distribution.

may explain why in our data a few cod were always detected in extremely unfavorable oxygen conditions near the bottom, whereas the majority of the fish were detected in layers with higher oxygen content. Alternatively, Stepputtis *et al.* (2011) showed small-scale horizontal variation in the depth of the oxygen minimum layer, which may not have been resolved by the hydrographic grid measurements and subsequent interpolation of hydrographic data between point measurements.

The distribution patterns presented in this study, characterized by the halocline as upper, and oxygen concentration as lower habitat boundary, are consistent with these findings, as generally only a small fraction of all cod detected were distributed outside the referring boundary layers. Given that cod are considered euryhaline and do not experience severe osmotic disturbances in salinities as low as 7 (Dutil *et al.*, 1992; Claireaux *et al.*, 1995), it seems surprising that the permanent halocline mainly constituted the upper distribution boundary in this study, especially as cod outside their spawning activities are distributed over most parts of the Baltic, including areas with reduced salinities (e.g., Aro, 1989). However, Baltic cod during spawning tolerate less variability in salinity and prefer salinities >11 below the permanent halo-

cline (Tomkiewicz *et al.*, 1998; Wieland *et al.*, 2000; Schaber *et al.*, 2009).

In June 2007 and, to a lesser extent in June 2008, a rather high proportion of cod have been detected in O_2 concentrations of $<1 \text{ mL L}^{-1}$. As hydroacoustic observations represent a real-time *in situ* snap-shot of fish distribution, the cod observed in low oxygen layers could either have been on brief vertical foraging excursions, as described by Neuenfeldt *et al.* (2009), or displaying courtship and mating behavior, as indicated by extended vertical movements (Rose, 1993; Lawson and Rose, 2000). These behavioral patterns could possibly contribute to the 24% of unexplained variance in the GLM. Whether cod actively seek oxygen-depleted layers for spawning or for relief from osmotic stress and thus eventually jeopardize the successful development of eggs and larvae, however, remains questionable.

Both during peak spawning (also see Schaber *et al.*, 2009) and in preceding months, ambient temperature obviously had no pronounced effect on the vertical distribution of cod in the Bornholm Basin. This is in accordance with recent descriptions of a broad thermal niche of European cod stocks that includes the Baltic Sea. Even though the thermal niche is narrower during spawning, cod observed in this study were on average

Figure 6. Effect modeling of cod (*Gadus morhua*) vertical distribution in the Bornholm Basin. (a) Plot of observed versus predicted depth distribution of individual cod (circles) with correspondence line (middle solid line) plus 95% confidence limits (outer solid lines). (b) Statistical distribution of the residuals: Histogram (vertical bars) with solid curve indicating the expected normal distribution and dashed curve representing the associated kernel distribution (normal kernel). (c) Probability-probability plot of the residuals.

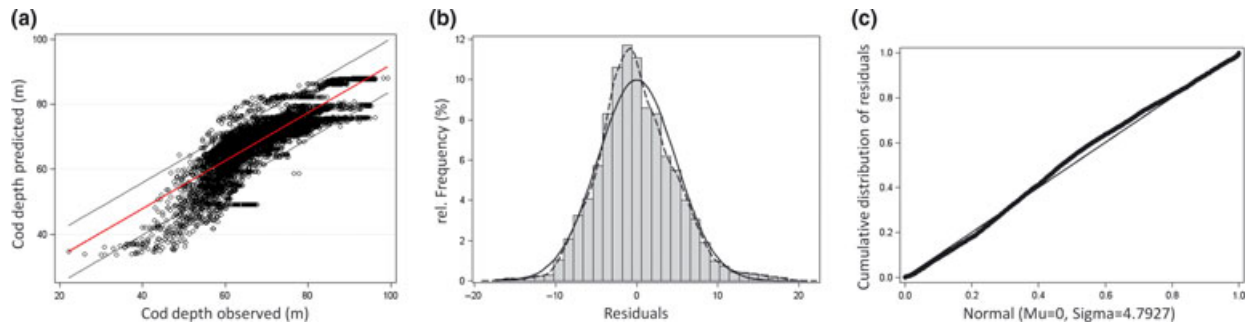


Table 1. Parameter estimates and *P* values from ANCOVA (GLM).

Type	Variable	Parameter	Estimate	Partial <i>P</i> value	Overall <i>P</i> value per factor
Intercept	Intercept	b_0	4.32279009	<0.0001	<0.0001
Hydrographical covariates	Oxygen residual	b_1	0.04715755	<0.0001	<0.0001
	Salinity	b_2	0.07968214	<0.0001	<0.0001
Year (Month) interaction	2007 (4)	c_{level1}	0.01890009	<0.0001	<0.0001
	2008 (4)	c_{level2}	0.11567843	<0.0001	<0.0001
	2009 (4)	c_{level3}	0.00368297	0.0825	<0.0001
	2006 (6)	c_{level4}	-0.0189703	<0.0001	<0.0001
	2007 (6)	c_{level5}	0.03025222	<0.0001	<0.0001
	2008 (6)	c_{level6}	0.05921711	<0.0001	<0.0001
	2006 (8)	c_{level7}	0.02317519	<0.0001	<0.0001
	2007 (8)	c_{level8}	0.05100519	<0.0001	<0.0001
	2008 (8)	c_{level9}	0.02994956	<0.0001	<0.0001
	2009 (8)	$c_{level10}$	0		

well within the known thermal limits both during growth and feeding as well as maturation and spawning (Righton *et al.*, 2010).

A distinct fraction of cod is distributed in the pelagic, and so far this fraction is not taken into account in cod stock assessment. Baltic cod stock assessment is tuned with a survey index derived from bottom trawl surveys. Extreme environmental conditions in the deep basins with cod exclusively distributed pelagically in areas with oxygen depletion as observed, for example, in August 2007 and 2008 could lead to a distinct bias in the stock assessment tuning indices (ICES, 2009). This is especially obvious as the present survey strategy regulates sampling in a way that trawl hauls are omitted if the ambient oxygen concentration in the region of vertical net opening is below 1.5 mL L^{-1} , based on the assumption that due to

oxygen deficiency no cod are distributed in this area and 'zero catches' are to be expected (ICES, 2008). Possible consequences of neglecting the pelagic fraction of cod in the central Baltic basins are underestimations of stock size in predictive runs for assessment.

Although the survey manual restricts sampling to the first and fourth quarter of each year (March and November), therefore ruling out biases resulting from spawning aggregation behavior etc., and the sampling for this study was conducted outside the period of regular stock assessment surveys, we consider our findings expandable to other seasons. Avoidance of oxygen-depleted zones will persist, even if spawning aggregations disperse after the main spawning season (Aro, 1989).

We consider that our sampling on hydroacoustic transects is not capable of resolving large-scale lat-

eral migration behavior of cod as a reaction to deteriorating oxygen concentrations as the two transects sampled did not cover the whole Bornholm Basin including the basin rims. Lateral dispersion of cod above areas of oxygen depletion has been suggested by Hjelm *et al.* (2004) based on catch rates and has also been discussed in relation to biases in stock assessments. However, as their sampling was based on (bottom) trawl surveys, it can be concluded that a pelagic component of the population over oxygen-depleted zones would not have been caught by their gear and would thus have remained undetected.

Decreasing salinity levels in the Baltic proper as predicted for future years together with low oxygen concentrations in deep layers (BACC Author Team, 2008) could lead to further deterioration of the stock situation of eastern Baltic cod already challenged by adverse reproduction conditions and intense fishing pressure. As a result, the overall vertical range of favorable habitat available is likely to diminish further, which on the one hand can lead to a further reduction of successful spawning opportunities by vertical compression of the reproductive volume and on the other hand can increase susceptibility of the vertically more condensed cod aggregations to fishing pressure. This has also to be taken into account when incorporating the pelagic fraction into stock assessment indices, as a possible corresponding increase in catch per unit effort may lead to the false impression of an increase in stock size.

The present study has shown that hydroacoustic methods, which are widely and mostly used for fish abundance estimation (see Simmonds and MacLennan, 2005), can also be applied to assess the interaction of fishes and their environment. Limitations imposed by sampling gear (e.g., trawl nets, see Tomkiewicz *et al.*, 1998; Hjelm *et al.*, 2004) or a reduced number of samples (data storage tags, see Neuenfeldt *et al.*, 2007) can be overcome by this non-invasive method due to a high spatial resolution that allows for scaling of results to a population level. Thus, corresponding studies can further contribute to our knowledge on the environmental ecology of different fish species, which is especially important in terms of the implementation of an ecosystem-based fishery management.

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REFERENCES

- Aro, E. (1989) A review of fish migration patterns in the Baltic. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **190**:72–96.
- BACC Author Team (2008) *Assessment of Climate Change for the Baltic Sea Basin*. Heidelberg: Springer-Verlag, pp. 474.
- Bagge, O., Thurow, F., Steffensen, E. and Bay, J. (1994) The Baltic cod. *Dana* **10**:1–28.
- Claireaux, G., Webber, D.M., Kerr, S.R. and Boutilier, R.G. (1995) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating salinity and oxygenation conditions. *J. Exp. Biol.* **198**:61–69.
- Dutil, J.D., Munro, J., Audet, C. and Besner, M. (1992) Seasonal variations in the physiological response of the Atlantic cod *Gadus morhua* to low salinity. *Can. J. Fish. Aquat. Sci.* **49**:1149–1156.
- Fässler, S.M. and Gorska, N. (2009) On the target strength of Baltic clupeids. *ICES J. Mar. Sci.* **66**:1184–1190.
- Foote, K.G. (1987) Fish target strengths for use in echo integrator surveys. *J. Acoust. Soc. Am.* **82**:901–987.
- Foote, K.G., Aglen, A. and Nakken, O. (1986) Measurement of fish target strength with a split-beam echosounder. *J. Acoust. Soc. Am.* **80**:612–621.
- Godø, O.R. and Michalsen, K. (2000) Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. *Fish. Res.* **48**:127–140.
- Harden Jones, F.R. and Scholes, P. (1985) Gas secretion and resorption in the swimbladder of the cod *Gadus morhua*. *J. Comp. Physiol. B.* **155**:319–331.
- Hinrichsen, H.-H., Lehmann, A., St. John, M. and Brüggel, B. (1997) Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Cont. Shelf Res.* **17**:187–201.
- Hinrichsen, H.-H., St. John, M., Lehmann, A., MacKenzie, B.R. and Köster, F.W. (2002) Resolving the impact of short-term variations in physical processes impacting on the spawning environment of eastern Baltic cod: application of a 3-D hydrodynamic model. *J. Mar. Syst.* **32**:281–294.
- Hinrichsen, H.-H., Voss, R., Wieland, K., Köster, F., Andersen, K.H. and Margonski, P. (2007) Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. *Mar. Ecol. Prog. Ser.* **345**:245–254.
- Hjelm, J., Simonsson, J. and Cardinale, M. (2004) Spatial distribution of cod in the Baltic Sea in relation to abiotic factors – a question of fish-age and area. *ICES C. M.* 2004/L:16, pp. 35.
- ICES (2001) Manual for the Baltic international acoustic surveys (BIAS). *ICES C. M.* 2001/H:02 (Annex 2), pp. 25.
- ICES (2007) Report of the Baltic International Fish Survey Working Group (WGBIFS). *ICES C. M.* 2007/LRC:06, pp. 84.
- ICES (2008) Manual for the Baltic international trawl surveys (BITS). *ICES C. M.* 2008/LRC:08 (Addendum 1), pp. 72.

- ICES (2009) Report of the Baltic International Fish Survey Working Group (WGBIFS). ICES C. M. 2009/LRC: 05, pp. 75.
- Killworth, P.D., Stainforth, D., Webb, D.J. and Paterson, S.M. (1991) The development of a free-surface Bryan-Cox-Semtner ocean model. *J. Phys. Oceanogr.* **21**:1333–1348.
- Lawson, G.L. and Rose, G.A. (2000) Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Can. J. Fish. Aquat. Sci.* **57**:1011–1024.
- Lehmann, A. (1995) A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus* **47**:1013–1031.
- Lehmann, A. and Hinrichsen, H.-H. (2000) On the thermal-haline variability of the Baltic Sea. *J. Mar. Syst.* **25**:333–357.
- Matthäus, W. and Franck, H. (1992) Characteristics of major Baltic inflows – a statistical analysis. *Cont. Shelf Res.* **12**:1375–1400.
- McQuinn, I.H. and Winger, P.D. (2003) Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. *ICES J. Mar. Sci.* **60**:575–583.
- Neuenfeldt, S. (2002) The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. *Fish. Oceanogr.* **11**:11–17.
- Neuenfeldt, S. and Beyer, J.E. (2003) Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. *J. Fish Biol.* **62**:168–183.
- Neuenfeldt, S., Hinrichsen, H.-H., Nielsen, A. and Andersen, K.H. (2007) Reconstructing migrations of individual cod (*Gadus morhua* L.) in the Baltic Sea using electronic data storage tags. *Fish. Oceanogr.* **16**:526–535.
- Neuenfeldt, S., Andersen, K.H. and Hinrichsen, H.-H. (2009) Some cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. *J. Fish Biol.* **75**:290–294.
- Nilsson, L.A., Thygesen, U.H., Lundgren, B., Nielsen, B.F., Nielsen, J.R. and Beyer, J.E. (2003) Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. *Aquat. Living Resour.* **16**:317–324.
- Peltonen, H. and Balk, H. (2005) The acoustic target strength of herring (*Clupea harengus* L.) in the northern Baltic Sea. *ICES J. Mar. Sci.* **62**:803–808.
- Righton, D., Metcalfe, J. and Connolly, P. (2001) Different behaviour of North Sea and Irish Sea cod. *Nature* **441**:156.
- Righton, D.A., Andersen, K.H., Neat, F. *et al.* (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Mar. Ecol. Prog. Ser.* **420**:1–13.
- Rose, G.A. (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* **366**:458–461.
- Schaber, M., Hinrichsen, H.-H., Neuenfeldt, S. and Voss, R. (2009) Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua* – habitat choice and limits during spawning. *Mar. Ecol. Prog. Ser.* **377**:239–253.
- Schlitzer, R. (2007) Ocean Data View (ODV). Available at <http://odv.awi.de> [accessed on 21 October 2011].
- Simmonds, J. and MacLennan, D. (2005) *Fisheries Acoustics: Theory and Practice*. 2nd edn. Oxford: Blackwell Publishing, pp. 437.
- Sonardata (2007) Echoview. Available at <http://www.echoview.com> [accessed on 21 October 2011].
- Sparholt, H., Aro, E. and Modin, J. (1991) The spatial distribution of cod (*Gadus morhua* L.) in the Baltic Sea. *Dana* **9**:45–56.
- Stepputtis, D., Hinrichsen, H.-H., Böttcher, U., Götz, E. and Mohrholz, V. (2011) An example of meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat, *Sprattus sprattus balticus* (Schn.). *Fish. Oceanogr.* **20**:82–88.
- Strand, E. and Huse, G. (2007) Vertical migration in adult Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **64**:1747–1760.
- Tomkiewicz, J., Lehmann, K.M. and St. John, M. (1998) Oceanographic influences on the distribution of Baltic cod, *Gadus morhua*, during spawning in the Bornholm Basin of the Baltic Sea. *Fish. Oceanogr.* **7**:48–62.
- Van der Kooij, J., Righton, D., Strand, E. *et al.* (2007) Life under pressure: insights from electronic data-storage tags into cod swimbladder function. *ICES J. Mar. Sci.* **64**:1293–1301.
- Wieland, K., Waller, U. and Schnack, D. (1994) Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana* **10**:163–177.
- Wieland, K., Jarre-Teichmann, A. and Horbowa, K. (2000) Changes in timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES J. Mar. Sci.* **57**:452–464.