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Diel vertical interactions between Atlantic cod *Gadus morhua* and sprat *Sprattus sprattus* in a stratified water column

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ABSTRACT: Information about species interactions at a spatial scale comparable to the perceptive abilities of the involved species is crucial for establishment of predictive food consumption models at the population level. Nevertheless, such information is sparse due to methodological constraints. We studied the diel vertical dynamics of species interactions between Atlantic cod *Gadus morhua* and its major clupeid prey, sprat *Sprattus sprattus*, at a location in the Bornholm Basin of the central Baltic Sea during late winter. This was accomplished by combining acoustic information on diel vertical fish distribution, time of ingestion of individual sprat estimated from cod stomach content data and observed vertical profiles of salinity, temperature and oxygen content. Predation by cod took place primarily at dusk and dawn during ascent and descent of sprat associated with school dissolution and formation, respectively. Cod resided close to the bottom outside these temporal predation windows. Sprat schools were located at the same depth as cod in the daylight hours, whereas at night dispersed sprat were situated higher in the water column. These vertical dynamics could be explained by fitness optimization using bioenergetics and trade-offs between temperature, oxygen saturation of the water and predation risk. This study forms a first step towards providing a mechanistic background for the predatory impact of cod at the basin scale and beyond.

KEY WORDS: Baltic Sea · Stomach content dynamics · Diel feeding cycle · Bioacoustics · Hydrography · Winter situation · Bioenergetics · Fitness optimization

INTRODUCTION

The predator–prey interactions between piscivorous and forage fishes are structuring elements in the dynamics of the ecosystem through trophic cascades (Paine 1980, Frank et al. 2005, Casini et al. 2009). A basic understanding of these interactions is therefore a prerequisite for studying ecosystem functioning in general, and an essential part of ecosystem-based fisheries management (Link 2010). Key variables in the marine environment such as light, temperature, salinity and oxygen are highly heterogeneous in space and time, which in turn influence the spatial distribution patterns of fish populations and their

spatial overlaps. This creates spatial and temporal heterogeneity in small-scale predator–prey interactions that eventually produce the observed dynamics on population, community and ecosystem levels (Hunsicker et al. 2011).

Small-scale studies of species interactions *in situ* are sparse (Turesson & Brönmark 2007, Kaartvedt et al. 2009), and it is in general difficult to obtain direct observations of interactions at the individual level in the sea with available technologies (Hunsicker et al. 2011). Information about prey composition obtained from sampled predator stomachs together with estimates of prey densities in the environment based on trawl catches have been used extensively to infer

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feeding behaviour and functional response of predators (Floeter & Temming 2003, Rindorf et al. 2006). The geographic scale at which this information should be compared has been discussed by several authors (Rose & Leggett 1990, Englund & Leonardsson 2008). Usually, the applied scale is much larger than the perceptive ability of the species involved. The biological mechanisms behind the findings of these studies are therefore open for liberal interpretation. As long as the small-scale mechanisms that give rise to a specific observed functional response at a larger scale are unknown, the results obtained from large-scale sampling are hardly useful for extrapolations to new situations such as future scenarios enforced by climate changes.

The central Baltic Sea is among the largest brackish waters in the world and consists of a number of deep basins, all of which show pronounced vertical stratification of the water column. Low salinity surface water is separated by a halocline from deep water of higher salinity. Irregular inflows of saline water from the North Sea renew the deep water. Hypoxia is prominent after longer stagnation periods without inflow events, and the level of dissolved oxygen is an important driver of fish stock dynamics. The fish community in the Baltic Sea is dominated by Atlantic cod *Gadus morhua* and its 2 major prey species, herring *Clupea harengus* and sprat *Sprattus sprattus*, making predator–prey interactions relatively easy to study — especially because since its outburst in the late 1980s, sprat has become by far the most important planktivorous fish there (Köster et al. 2001).

Neuenfeldt & Beyer (2006) considered the effects of the vertical spatial overlaps of cod and its clupeid prey on the aggregate diet of cod in the Bornholm Basin of the Baltic Sea. They showed that the ratio of herring to sprat consumed by cod decreased more slowly than did the abundance ratio in the environment during the decline of the cod stock in the 1980s, and concluded that without understanding the cod–clupeid overlaps, the observed diet composition dynamics could be misinterpreted as a situation of negative switching. Neuenfeldt & Beyer (2006) only considered the vertical distribution during daytime and disregarded the diel vertical migration (DVM) of the clupeids with schooling close to the bottom during daytime, ascending and dispersing at dusk, and descending and aggregating again at dawn (Cardinale et al. 2003, Nilsson et al. 2003).

Three major mechanisms involving foraging, predator avoidance, and bioenergetics have been hypothesized to explain adaptation of the DVM behaviour in pelagic planktivorous fish (Clark & Levy 1988). The foraging hypothesis suggests that planktivorous fish follow the DVM of zooplankton to optimize their feeding conditions. According to the predator avoidance hypothesis, DVM of both planktivores and zooplankton is believed to be the outcome of the evolutionary race between predator and prey, where the prey follow the 'antipredation window' at levels of light intensity occurring at dusk and dawn (Clark & Levy 1988, Scheuerell & Schindler 2003). Here, the visual searching ability of their predators (and so predation mortality) is reduced and the ratio of predation risk to food consumption rate minimized (Eggers 1978, Levy 1990a, Rosland & Giske 1994). The bioenergetics hypothesis has been used to explain vertical behaviour under different feeding conditions as a motivation to migrate to water temperatures where energy conservation or accretion is optimized. In cases of food limitation, colder water is preferred to reduce metabolic rate and maximize food conversion efficiency (Brett 1971). Alternatively, under favourable feeding conditions the fish are expected to seek warmer water to accelerate food processing and, thus, growth rate (Wurtsbaugh & Neverman 1988, Levy 1990a,b, Neverman & Wurtsbaugh 1994, Orlowski 2000).

Cardinale et al. (2003) found that clupeids in the Bornholm Basin performed DVMs during the feeding season. They related this behaviour to all 3 hypotheses. Cod predation on the clupeids was, however, inferred but not observed. Using hydroacoustics information, Nilsson et al. (2003) found that sprat also performed DVMs in late winter, when they are food limited or do not feed at all (Arrhenius 1998).

Due to limited knowledge about the dynamics of predator–prey interactions, a mechanistic understanding of cod predation on clupeids at small temporal and spatial scales needs to be addressed in the Baltic Sea. The aim of this study was to examine the vertical predator–prey interactions between cod and sprat, and to identify the possible drivers. Attention was restricted to a water column examined during a vessel survey in late winter in the Bornholm Basin of the central Baltic Sea (Nilsson et al. 2003). This should ensure almost constant environmental conditions; the challenge was how the diel light conditions together with other physical and biological variables influenced the behaviour of both species and their interactions in the stratified water column (Blaxter 1975, Lampert & Sommer 2007). The observed behavioural dynamics and interactions of predator and prey are explained in terms of fitness optimization using bioenergetics and trade-offs between temperature, oxygen saturation of the water, food acquisition and predation risk (e.g. Rosland & Giske 1994).

MATERIALS AND METHODS

The vertical distribution dynamics of cod and sprat were described by use of hydroacoustics data sampled during a trawl survey of the Baltic Sea in 2002. The diel feeding pattern of cod was established using information about contents in sampled stomachs, input into a gastric evacuation rate (GER) model that enabled estimation of ingestion times of individual sprat. To run the GER model, specimens of the main prey of cod were sampled for measurements of length, mass and energy density. The cod energy balance was assessed using the GER model to prey and stomach data for estimation of food consumption rate. Also, the energy balance of sprat was evaluated by examination and quantification of stomach contents of sampled sprat. The physical variables salinity, temperature and oxygen saturation were described by data from CTD profiling.

Field sampling

Study area

The ~5 km^2 sampling area was located in the northeastern part of the Bornholm Basin (55° 45.000′ to 55° 48.457′ N, 16° 20.210′ to 16° 20.980′ E), at depths of 61.5 to 65.5 m (Fig. 1). The typical depth of the Bornholm Basin is 60 to 80 m with a maximum depth of 105 m.
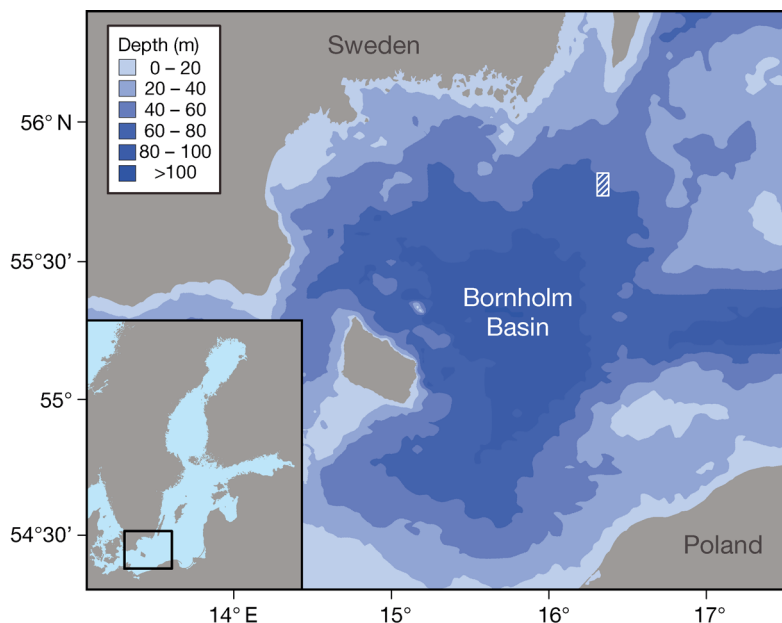

Fig. 1. Sampling site (white, hatched rectangle) in the northeastern area of the Bornholm Basin, central Baltic Sea

Sampling of biological materials

In continuance of the first of the 2 annual international trawl surveys in the Baltic Sea (BITS) in 2002, cod, herring and sprat were obtained from 16 trawl hauls undertaken every 3 h from 12 to 14 March onboard the Danish RV 'Dana' (see Table 1). The BITS gear setup and fishing procedure were followed (http://doi.org/10.17895/ices.pub.2883), using a TV3 bottom trawl with 16 mm cod-end, fishing speed of ~2.5 knots and towing time of ca. 30 min. The vertical gap of the trawl was 5.4 ± 0.4 m (mean ± SD) and the (horizontal) spread between the otter boards ~100 m. The catch from each haul was processed to obtain total number and size distribution by fish species as specified in the BITS protocol. In addition, 4 pelagic 1 h hauls were carried out in the dark hours between 17:00 h on 14 March and 02:00 h on 15 March by use of an EXPO trawl that covered the depth interval of 37 to 50 m. The environmental conditions during this night were comparable to those of the 2 preceding nights, and it is therefore assumed that the results were as well.

On 13 March, local civil twilight started at 04:39 h, sunrise and sunset times were 05:16 and 16:54 h, and civil twilight ended at 17:30 h (UTC). Moonrise and moonset times were 05:46 and 16:00 h (new moon) (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). The sky was clear most of the time.

From each bottom trawl catch, 15 to 51 stomachs of cod within the length range of 38 to 54 cm (most 38 to 48 cm) were excised (see Table 1), individually packed in plastic bags and transferred to a tunnel freezer (−18°C). Invalid stomachs (with signs of regurgitation according to the criteria set up by ICES 1991) were discarded and replaced by valid non-empty stomachs. Otherwise, estimation of food consumption rates would be underestimated due to overrepresentation of empty stomachs (Hislop et al. 1991). In addition, 20 sprat (length range 9 to 13 cm) were selected from each trawl haul and frozen for later examination of their stomach contents. Individuals of sprat (n = 294; 10 to 14 cm), herring (n = 147; 15 to 22 cm) and the isopod *Saduria entomon* (n = 60; 2.8 to 5.4 cm), evenly distributed within the body length ranges, were collected and frozen for later measurements of length, body mass and energy density. Finally, to correct lengths of prey recovered from the cod stomachs when comparing length distributions of prey in the stomachs with

those in the trawl hauls, 20 sprat (11 cm) and 20 herring (18 cm) were measured for length, individually bagged and frozen. The lengths of these individuals were measured once again after thawing to calculate shrinkage due to the freezing procedure.

Hydrography

A total of 9 vertical profiles of salinity, temperature and oxygen saturation were obtained immediately before or after most trawl stations with a Sea-Bird 911 CTD system that recorded conductivity, temperature, pressure (depth) and oxygen partial pressure. The CTD system was mounted on a SBE 32 bottle sampler with 4 l bottles used to collect water at different depths. Subsamples were transferred to specially designed salinity and oxygen bottles according to standard procedures, and oxygen concentrations were measured onboard by the Winkler titration method (Ducklow & Dickson 1994) to calibrate the CTD measurements. Salinity samples were stored and conductivity measured after the cruise using a Portasal 8410B salinometer (Guildline; www.guildline.com/oceanography/salinometers/salinity-measurement/8410a-portasal-portable-salinometer) to check the salinity measurements (Ducklow & Dickson 1994). CTD raw data were processed by use of the SBE Data Processing package version 7.20g (Sea-Bird Scientific; www.seabird.com/sbe911plus-ctd). The Sea-Bird system was furthermore equipped with a light sensor (Biospherical/Licor) to measure photosynthetically active radiation (PAR).

Hydroacoustics

Hydroacoustics data were collected continuously during the cruise period using a Simrad EY500 echosounder with 38 kHz transmit frequency, which was connected to the ES38B transducer (7° beam width) mounted at ~6 m depth in a transducer blister on the hull of the vessel. External power supply was used to increase the transmit pulse power to 2000 W; the pulse rate was 1 ping s^{-1}, and pulse length was set at 1.0 ms. The echosounder was run by the Simrad EY500 software and stored in the Simrad EY DG-file format (Simrad EY500 Instruction Manual). The echosounder was calibrated using a standard 60.0 mm diameter copper sphere in June 2001 at a location near Bornö Island in Gullmar Fjord, Sweden, and again at the same location in June 2002. The measured transducer gain decreased by <2% (from

25.1 to 24.6 dB), indicating that the performance of the echosounder had been stable between calibrations.

Laboratory analyses of sampled biological materials

Cod stomachs were thawed in the laboratory on land, their contents identified to the lowest taxonomic level possible. Each prey item was dabbed with a moistened paper towel, and weighed and measured for length. Length measurements of fish included total length, standard length and reduced standard length (standard length − head = length of vertebral column). Fish prey that could not be measured due to advanced state of digestion were given the mean lengths of their measured conspecifics. Total length and length of the pleotelson of *S. entomon* as well as total length of mysids were measured. The mass of detached prey remains that could not be assigned to any particular prey were allocated to the identified prey items in proportion to their respective surface contributions to total stomach contents according to the GER model used here (see the Supplement at www.int-res.com/articles/suppl/m583p195_supp.pdf) to estimate prey ingestion times and food consumption rates (Andersen & Beyer 2008a).

The fresh sprat, herring and *S. entomon* prey collected for morphometric measurements were thawed in the laboratory, length measured (same as above) and individually weighed. The energy densities of all *S. entomon* together, and sprat and herring grouped in 8 length classes (0.5 and 1 cm intervals, respectively), were thereafter determined by bomb calorimetry in an IKA-7000 bomb calorimeter (www.ika.net) following the procedures described in Pedersen & Hislop (2001). Values were corrected for carbonate content (Paine 1966) as well as nitric acid produced during combustion (Golley 1961). The 20 sprat per trawl haul used for stomach content examination were thawed, the stomachs excised and the recovered contents identified to the lowest possible taxonomic level and weighed.

Data processing and analyses

Hydroacoustics

The editable lines facility in Echoview version 4.6 (https://www.echoview.com) was used to select valid data. An upper limit line was initially set at 3 m below

the near-field of the transducer corresponding to 9 m from the surface. This line was then edited manually to exclude invalid data due to propeller noise or bubbles generated by bow thrusters, other vessels or breaking waves. According to standard procedure to avoid inclusion of bottom echoes, a lower limit line was created with a safety margin of 0.5 m above the bottom line generated by the echosounder. This line was then edited manually to correct errors where the echosounder had included soft bottom or excluded fish schools. The near-bottom dead zone of the echosounder was approximately 0.11 m at 60 m depth and with a 7° beam width. Data recorded while the vessel was stationary during CTD-profiling operations were discarded.

The data preprocessed by Echoview were shown as echograms in 3 different display modes. The first mode (20 log R) displays volume backscattering strength, S_v, at different depths (distances R) (see Fig. 5). The second mode (40 log R) shows data used for single target detection by the Single-targets Method 1 operator in Echoview. The third mode shows the resulting target strength (TS) data and was used to visually inspect detected single targets for further elimination of invalid data overlooked in the previous process.

TS values, compensated for the angular position of each target in the beam, together with the variables time, GPS data, echo depth and bottom depth were exported to Excel. Here, the single targets representing sprat and cod were used to examine their diel vertical distribution dynamics. Data were grouped in 40 min intervals and the distance to the bottom of the 20th, 50th and 80th percentiles was calculated. Using the standard slope 20 (Foote 1987), TS ranges representing the 2 species were estimated as TS = 20 log L + b_{20} (dB) where L (cm) is total fish length, and the species-specific parameter b_{20} is the TS of a 1 cm long fish. The general value −71.2 dB of b_{20} for sprat and herring obtained in high-saline waters and used in the Baltic International Acoustic Survey (ICES 2009) is probably too low for fishes in the eastern Baltic Sea. This is primarily because the fish need a larger swimbladder volume to obtain neutral buoyancy due to the lower salinity here, which implies that the value of b_{20} is higher (Didrikas & Hansson 2004, Fässler et al. 2008). To estimate b_{20}, the distribution of TS in the dark hours with dispersed fish was related to the length distribution of sprat as the dominant species in the trawl catches. No distinct peak in the TS distribution could be obtained from cod. The commonly used value −67.4 dB of b_{20} for cod (Foote 1987) was therefore displaced by the same value as

the difference between −71.2 dB and the estimate of b_{20} obtained for sprat in this study.

Estimation of prey ingestion times and food consumption rates

The time between sampling and ingestion of each prey in the cod stomach was estimated using a GER model to hindcast the recovered prey mass to its original body mass (Griffith 1976), the latter being estimated from observed prey length and the relationship between prey length and fresh body mass. Sampling time was set at the middle of the trawl haul period, because digestive processes are likely to stop in the trawl due to the struggling behaviour of the fish (Farrell et al. 2001). The mechanistic, surface-dependent cylinder GER model advanced by Andersen & Beyer (2005a,b) and validated in a suite of experiments (see references in Andersen et al. 2016) was used here. This implies that the GER of each individual prey at any time is proportional to its exposed surface for the present prey composition in the stomach. In addition, apart from temperature and cod length, the GER depends on the prey item's resistance to the digestive processes, prey length and remaining prey body mass, and the energy density of the currently evacuated prey materials. Model parameter values for cod (Andersen 2012) as well as prey morphometry and energy densities achieved in the present study were used in the hindcasting procedure, which also allows for estimation of the variances of the ingestion times obtained. All details are provided in the Supplement at www.int-res.com/articles/suppl/m583p195_supp.pdf.

Two approaches were used to estimate food consumption rates and feeding levels of cod based on the cylinder GER model. First, total GER (kJ h^{-1}) was estimated for each stomach by summing all individual prey GER (g h^{-1}) contributions at the time of sampling multiplied by the prey-specific energy densities (see the Supplement). Following the principle that, averaging over time and population, mean consumption rate equals mean GER (e.g. Pennington 1985), the daily ration was estimated as the mean total GER (kJ h^{-1}) multiplied by 24 h. Second, estimating the number of prey ingested within a predefined period of time prior to stomach sampling by use of a GER model to stomach content data, Johansen et al. (2004) quantified the consumption of herring by cod in the Barents Sea. In the present study, the output from the estimation of prey ingestion times was used to estimate the amount of prey

energy ingested by each sampled cod during the latest full feeding period (dusk–night–dawn) prior to stomach sampling. This also represents the daily ration, and the mean value was calculated from all cod. The 2 approaches can be considered independent methods because of the shift in focus from instantaneous GER at one point in time to the number of prey consumed over a period of time, which has been chosen independently of the number of prey observed in the stomach at sampling. Thus the methods not only use different parts of the data for each stomach, but they also use them differently. Different results would therefore indicate possible inconsistences in data or violations of respective assumptions.

To evaluate the energy balance status of the sampled cod, and to standardize the daily ration, C, with regard to cod size, the latter was expressed by the feeding level $f = CC_{max}^{-1}$, where the maximum sustained consumption rate, $C_{max} = 0.223 \exp(0.104T - 0.000112T^3) \, M^{0.802}$ (kJ d^{-1}), was established by Jobling (1988) from data on satiation rations of capelin *Mallotus villosus* fed to a cod of body mass M (g) at temperature T (°C) (Johnsen 1981, Braaten 1984).

The 95% CIs of the mean f obtained from the 2 approaches were estimated, and the difference between the means was tested for significance in R (R Core Team 2016). The means were considered equal if $p > 0.05$ (Basic, non-parametric bootstrapping cf. Efron & Tibshirani 1993) .

RESULTS

Hydrography

The vertical profiles of salinity, temperature and oxygen saturation obtained from the 9 CTD stations were similar, and therefore averaged into a generalized profile (Fig. 2) for comparison with the species-specific vertical fish distributions obtained from hydroacoustics. The profile showed a typical winter situation in a stagnant period with no recent intrusion of saline water from the North Sea. The top layer of water extended down to ~8 m above the bottom
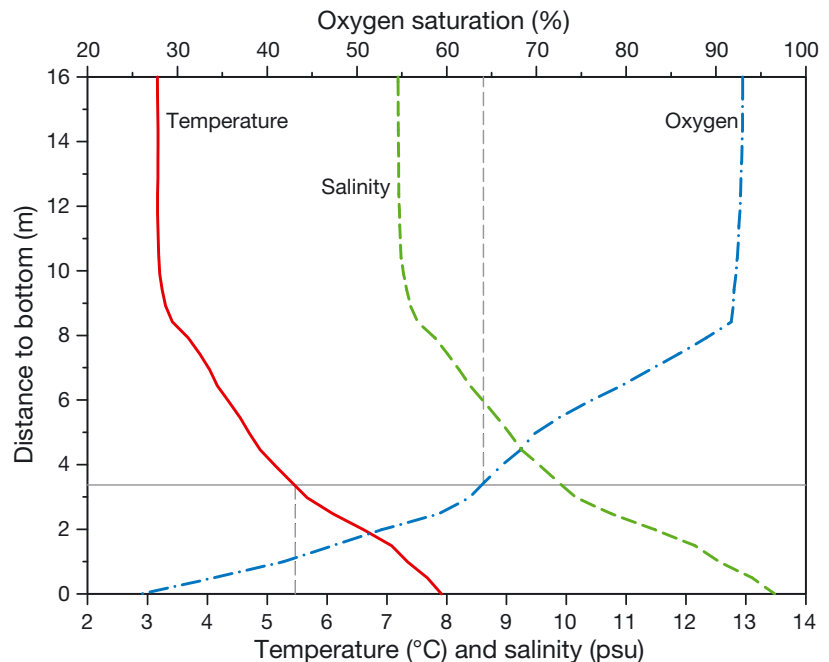

Fig. 2. Generalized vertical profiles of temperature, salinity and oxygen saturation in the lower part of the ~64 m water column obtained from 9 CTD stations (conditions are constant above this part of the water column). Horizontal line: mean of the daytime vertical distribution of Atlantic cod *Gadus morhua* (detected single target echoes of strengths between −30 and −24 dB); dashed lines: corresponding temperature and oxygen saturation of the water

and was uniform with low temperature (3°C) and salinity (7 psu) and high oxygen saturation (93%). Towards the bottom in the combined halo-, thermo- and oxycline, the salinity and temperature increased to 13.5 psu and 8°C, and oxygen saturation decreased to below 25%.

From the Sea-Bird PAR data, Nilsson et al. (2003) estimated the diffuse attenuation coefficient to vary between 0.131 and 0.167 m^{-1}, and used a value of 0.16 m^{-1} together with a model for surface illuminance to calculate local light intensities in the water column. At dusk, the schools of sprat detected by hydroacoustics ascended following the lines of equal light levels between 2×10^{-2} and 2×10^{-3} μmol quanta m^{-2} s^{-1} and gradually dissolved below these lines causing a widening of the vertical dispersed distribution of fish (see Nilsson et al. 2003 for details).

Trawl catches

In the daylight hours, when the fishes were situated close to the bottom and thus within reach of the trawl, sprat was the dominant fish in the trawl catches comprising 96.7% of the total number of fish
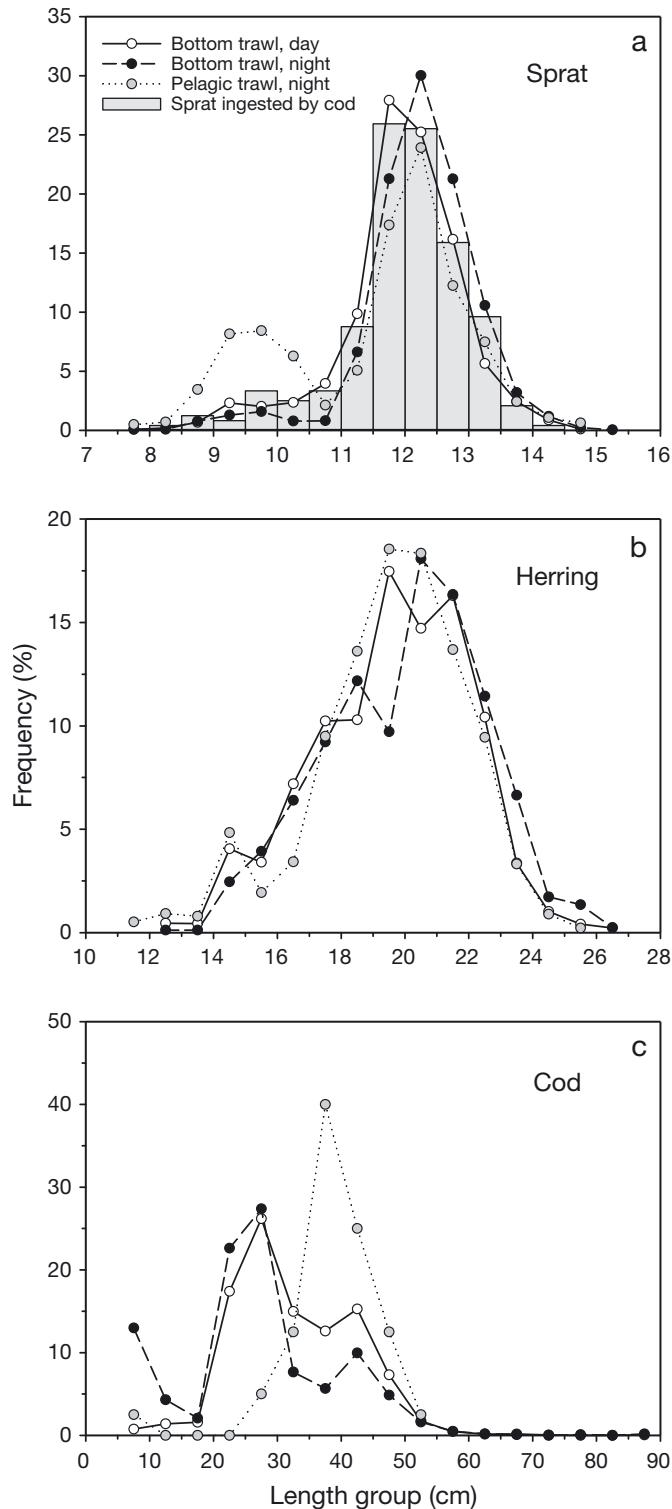
Fig. 3. Size distributions of (a) sprat *Sprattus sprattus*, (b) herring *Clupea harengus* and (c) Atlantic cod *Gadus morhua* caught by bottom trawling in the light hours (n_a = 259 941, n_b = 7080, n_c = 2024) and dark hours (n_a = 19 779, n_b = 813, n_c = 1256), and by pelagic trawling in the dark hours (n_a = 86 967, n_b = 4033, n_c = 40). Columns in (a) indicate the size distribution of sprat ingested by the sampled cod (n = 249)

caught, whereas herring and cod only comprised 2.6 and 0.7%, respectively (Fig. 3). Converted to biomass, sprat still accounted for 80% and herring and cod amounted to 10% each. The share of other species was consequently insignificant.

The trawled sprat ranged in length from 7.5 to 14.5 cm with a peak at 12 cm (Fig. 3a). The size distribution of sprat obtained by bottom trawling did not differ between night and day. In the dark hours, however, the pelagic catches above the halocline displayed another peak composed of smaller individuals (9 to 10 cm) representing young-of-the-year (YOY) sprat, which was consistent for all pelagic hauls. As a result, the proportions of sprat <11 cm in catches obtained from pelagic and bottom trawling at night were significantly different (*z*-test for 2 population proportions, z = 70.8, p < 0.0001).

The size distribution of herring ranged from 12 to 25 cm with the most abundant sizes between 17 and 23 cm; the size overlap with sprat was slight (Fig. 3b). The size range of cod caught by bottom trawl was 7 to 85 cm with only few individuals above 55 cm. The distributions displayed 2 peaks at 20 to 30 cm and 40 to 45 cm, as well as a third one for the smallest cod in the dark hours (Fig. 3c). In contrast, smaller cod were almost absent in the pelagic catches and the distribution of the cod obtained from pelagic trawling peaked at 35 to 45 cm.

Hydroacoustics

The echograms primarily reflected the behavioural dynamics of sprat that dominated by number and biomass. The daytime situation was characterized by schools of fish located close to the bottom (Fig. 4a). The dense layer of fish seemed, however, to stay clear of the bottom at larger depths. At dusk between 17:00 and 18:00 h, fish schools ascended whilst other schools left below dispersed, resulting in a gradual extension of the vertical distribution well above the halocline into the upper uniform water layer (Fig. 4b) (see also Nilsson et al. 2003). The fish remained dispersed in the water column throughout night until dawn between 04:25 and 05:25 h, where the reversed process of school formation and descent re-established the daytime pattern.

The frequency distribution of TS of all single targets displayed a distinct peak at −42 dB (Fig. 5), which was consistent between sub-sections of the acoustic track. Related to the 12 cm peak of the length distribution of sprat caught by trawling (Fig. 3a), this TS peak provided b_{20} = −63.9 dB
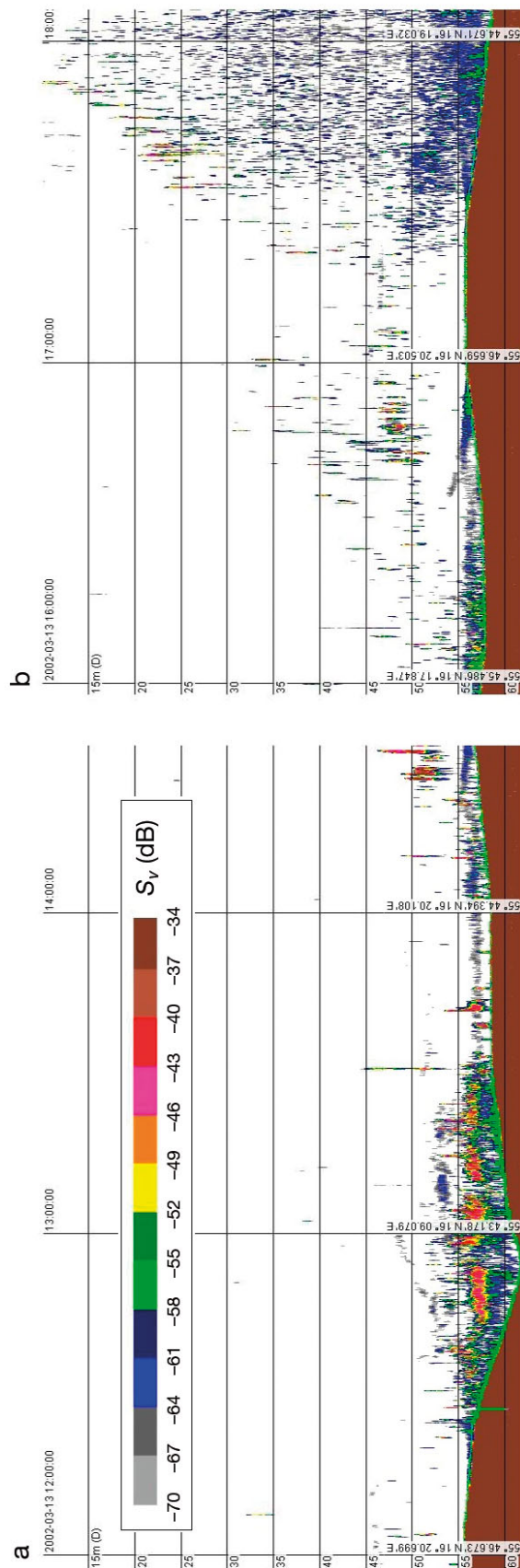
Fig. 4. Echograms produced by the Echoview software in 20 log *R* display mode for (a) day and (b) dusk

from the *L*–TS relationship (i.e. a displacement of 7.3 dB from the value of −71.2 dB used in ICES 2009). This b_{20} value implies TS = −38 dB for the ~20 cm peak of the herring length distribution (Fig. 3b), which may explain the hump on the distribution curve just to the right of the sprat peak in the TS distribution (Fig. 5). For cod, b_{20} = −60.1 dB was obtained by use of the same displacement as for sprat. Using the species-specific values obtained, the single targets of strengths from −46 to −41 dB representing 7.5 to 14 cm sprat, and from −30 to −24 dB covering 30 to 60 cm cod were selected to describe the diel vertical distribution dynamics of these 2 species. The peak at −60 dB (Fig. 5) within the TS range of small organisms, which also was consistent between sub-sections of the acoustic track, probably represents mysids that form layers close to the bottom.

Based on the observed single targets, the vertical distribution of sprat showed a distinct diel pattern (Fig. 6a). They stayed close to the bottom below the uniform surface layer during daytime and ascended in the period between 17:00 and 18:00 h to cover more than half the water column throughout the dark hours before descending again between 04:25 and 05:25 h. These vertical distribution dynamics of sprat reflected the pattern appearing on the 20 log *R* echograms (Fig. 5).

Like sprat, cod stayed close to the bottom during the daylight hours and made ascents at dusk synchronously with sprat, but apparently of short dura-
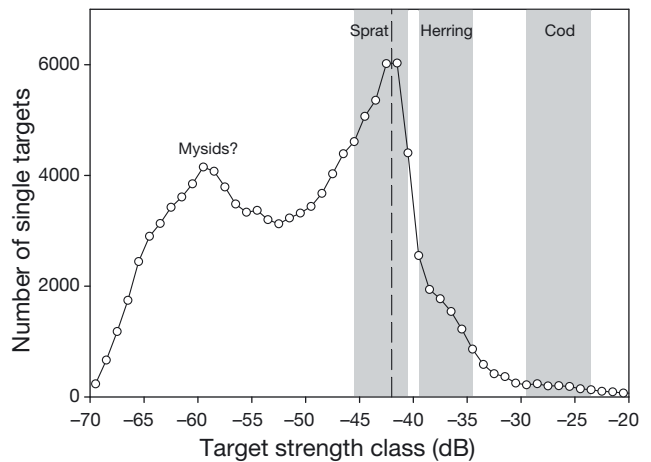

Fig. 5. Total number of single targets in each 1 dB target strength class obtained from backscatter data by use of hydroacoustics. The dashed vertical line at −42 dB indicates sprat *Sprattus sprattus* of total length 12 cm (Fig. 3). Grey shading: target strength ranges of sprat (7 to 14 cm), herring *Clupea harengus* (17 to 23 cm) and Atlantic cod *Gadus morhua* (30 to 60 cm)

tion (Fig. 6b). Further ascents appeared to be going on during the night, though at times the data here were sparse. Cod made a brief ascent again at dawn in the period where the sprat moved downward. At daytime, the mean distance from cod to bottom was 3.4 m at 5.5°C and 64.2% O_2 saturation (Fig. 2). Assuming that digesting cod were residing here, this local temperature was used to estimate prey ingestion times and food consumption rates by use of the GER model to stomach content data.
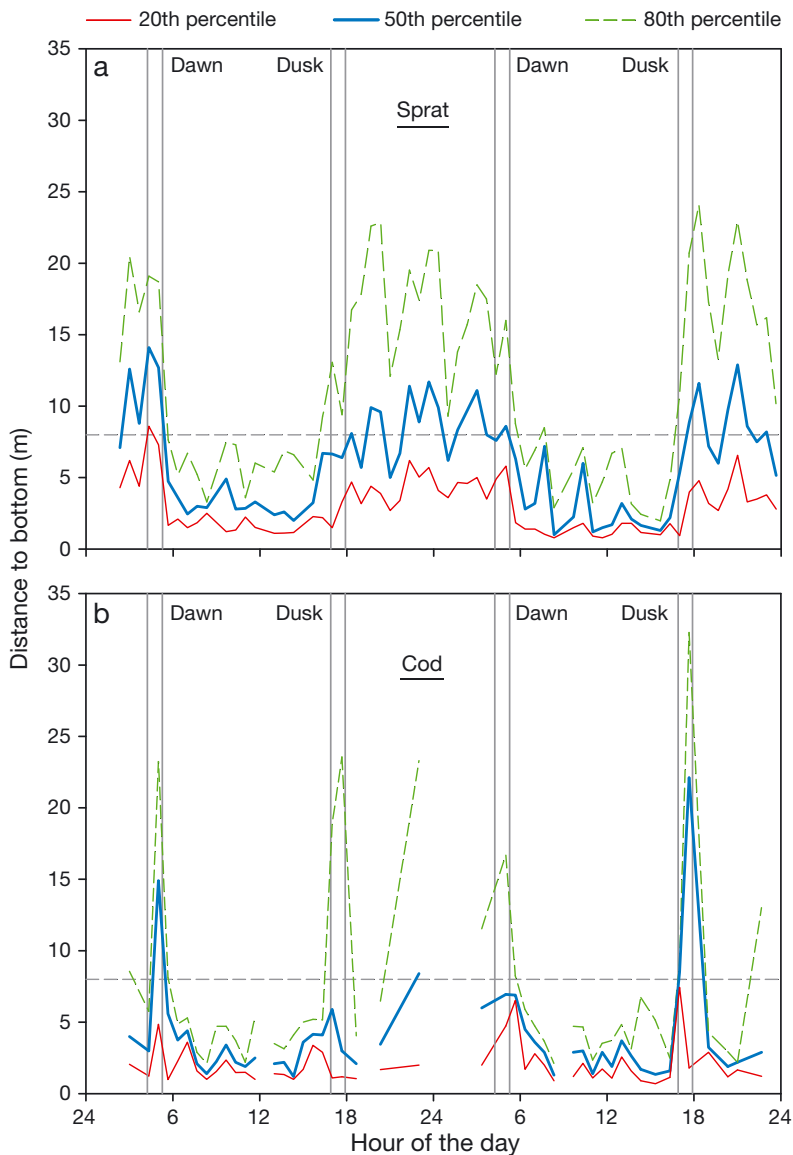

Fig. 6. Diel dynamics of the vertical distribution of single targets of strengths between (a) −46 and −41 dB interpreted as sprat *Sprattus sprattus* (n = 27 430) and (b) −30 and −24 dB interpreted as Atlantic cod *Gadus morhua* (n = 1208). Curves are 20th, 50th and 80th percentiles for each 40 min period. The gaps for cod indicate missing or few (<10) observations in a period. Horizontal dashed line: bottom of the uniform top layer of the ~64 m water column; pairs of vertical lines define dawn and dusk

Cod stomachs

The number of cod stomachs differed between sample times (Table 1), and to avoid bias when examining the diel feeding pattern, the period hindcasted for each cod stomach should represent a multiple of 24 h. Also, it is a prerequisite for an unbiased result (and without excessive uncertainties) that all ingestion times in the period are based on prey with observable lengths (Andersen & Beyer 2008b). These conditions restricted the hindcasted period to 24 h, and the diel feeding pattern obtained from the estimated ingestion times of sprat (n = 194) showed a distinct pattern with peaks at dusk and dawn (Fig. 7). Using 95% CIs of the estimated ingestion times, it could not be rejected that 87.1% of the sprat were ingested at dusk (39.7%) or dawn (47.4%). Similarly, 12.4% were ingested during night and one sprat during daytime.

The feeding level *f* obtained from the mean GER was 0.40 (95% CI: 0.37 to 0.43; 492 stomachs). The fractions made up by sprat, herring, *Saduria entomon*, *Mysis mixta* and other prey in the diet of cod were 93.0, 5.3, 1.0, 0.4, and 0.2% energy. Other prey were sandeel *Ammodytes tobianus* and sand goby *Pomatoschistus minutus*.

The indicated feeding pattern of cod that included a feeding pause during daytime (Fig. 7), enabled the alternative estimate 0.39 (0.32 to 0.45; 492 stomachs) of *f* by accounting for the energy contained in all the prey ingested by each sampled cod during the latest full feeding period (dusk–night–dawn) prior to stomach sampling. This value was close to the estimate based on mean GER (p > 0.74). A total of 162 stomachs, equivalent to 33% of the total number of stomachs, contained prey ingested during this period. The fractions constituted by sprat, herring, *S. entomon*, *M. mixta* and other prey in the diet of cod were 90.0, 8.7, 1.2, 0.1 and 0% energy.

Correcting for shrinkage of 4.9% ± 0.9 (SD) due to the freezing procedure, the size distribution of ingested sprat with observable lengths matched the distribution of sprat obtained by bottom trawling (Fig. 3a). The size range of in-

Table 1. Total number of cod stomachs (empty stomachs in parentheses) and associated cod total body length and mass (mean ± SD) by bottom trawl station, sampled in the Bornholm Basin of the Central Baltic Sea (30 min trawl haul with indicated date, start time and water depth)

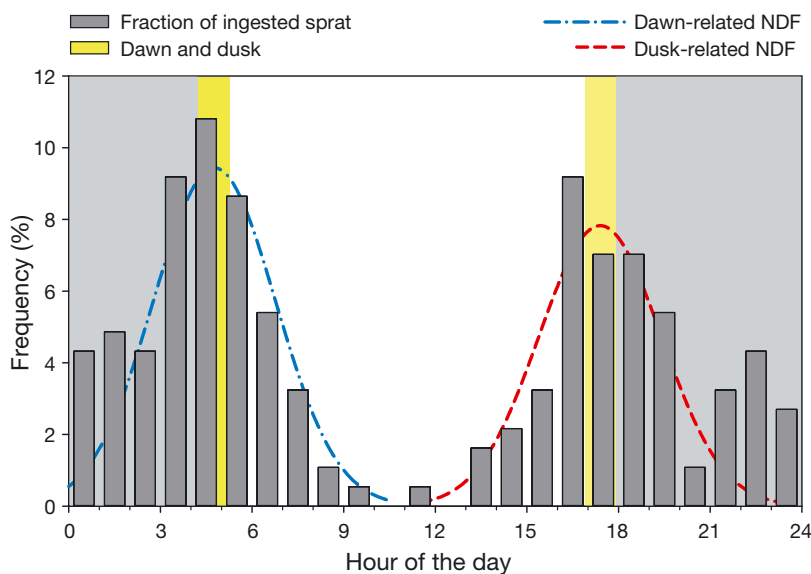| Station	Start time (UCT)	Mean depth (m)	Length (cm)	Mass (g)	Stomachs (n)
12 March 2002					
1	02:36	65.5	43.0 ± 2.9	783 ± 160	40 (6)
2	05:18	65.5	42.3 ± 2.4	780 ± 161	38 (7)
3	08:23	65.0	41.9 ± 2.7	739 ± 156	35 (10)
4	11:18	64.5	41.4 ± 2.4	713 ± 134	17 (4)
5	14:20	63.5	41.7 ± 2.3	748 ± 138	50 (17)
6	17:15	61.5	41.5 ± 2.4	730 ± 151	28 (6)
7	20:12	62.5	41.9 ± 2.8	748 ± 177	17 (4)
8	23:22	64.5	42.4 ± 2.4	753 ± 151	15 (5)
13 March 2002					
9	02:27	65.5	43.2 ± 2.9	829 ± 143	22 (2)
10	05:18	64.5	45.8 ± 4.7	995 ± 325	42 (13)
11	08:15	64.5	42.0 ± 2.4	756 ± 141	40 (8)
12	11:17	64.5	42.1 ± 2.7	746 ± 131	36 (9)
13	14:17	64.5	42.3 ± 3.0	759 ± 198	51 (12)
14	18:21	64.5	42.6 ± 2.5	754 ± 141	21 (8)
15	21:14	64.5	41.8 ± 2.9	729 ± 159	23 (9)
14 March 2002					
16	00:34	63.5	41.9 ± 2.3	744 ± 144	17 (4)
Total			42.5 ± 3.0	776 ± 188	492 (124)

Fig. 7. Diel dynamics of Atlantic cod *Gadus morhua* feeding on sprat *Sprattus sprattus*. Columns represent the distribution of all estimated ingestion times (n = 194 sprat) within a 24 h period prior to sampling of the individual cod. The 2 curves display the normal distribution functions (NDF) for all dawn- and dusk-related ingestion times, respectively, assuming that the actual ingestion takes place in the middle of the dawn and dusk periods and using the mean SD of the estimates. The rest of the sprat were ingested during the day (1 sprat) or at night. Dawn and dusk are indicated by the transitions between white (day) and grey (night) background

gested herring with measured length (only 14 fish) and corrected for estimated shrinkage of 4.5% ± 0.7 (SD) ranged from 14 to 20 cm (mean of 16.4 cm). This range constituted only the lower half of size distribution of trawled herring (Fig. 3b).

Sprat stomachs

Almost all 320 sampled sprat stomachs were empty. The exceptions were fish from trawl Stn 2, with 10 out of 20 stomachs containing small amounts of adult *Pseudocalanus* sp. remains (mean wet content mass: 0.011 g; 0.14% body mass) and trawl Stn 12, with 6 of 20 stomachs containing copepod remains (0.002 g; 0.02% body mass). Estimation of food consumption rates by use of a GER model (e.g. Bernreuther et al. 2009) to these small amounts of stomach contents therefore gives no meaning.

DISCUSSION

The crepuscular feeding of cod with ~90% of the sprat being ingested around dusk or dawn is a general characteristic of piscivorous fishes preying on pelagic, planktivorous fishes performing DVMs (e.g. Hrabik et al. 2006, Jensen et al. 2006). Sprat in the area sampled in the present study also performed DVMs in the feeding season and were distributed in the upper part of the water column at night, where a secondary thermocline at this time of year provided high temperatures above the halocline (Cardinale et al. 2003). This behaviour was explained by maximization of the food processing rate and thus the growth rate (Wurtsbaugh & Neverman 1988, Levy 1990a,b, Neverman & Wurtsbaugh 1994, Orlowski 2000). The timing of their DVM with the zooplankton movements was attributed to optimization of the feeding conditions.

Feeding and vertical distribution dynamics of sprat

With nothing (or occasionally small remains of food) in their stomachs, the sprat in the present study appeared to starve in late winter because their

main food, planktonic copepods, were still overwintering and at the lowest densities of their annual cycle during the study period (Peters et al. 2006, 2013). This is consistent with the findings of Arrhenius (1998), that sprat in the Baltic Sea feed little and lose body energy during the winter months (November to March), and of Kaartvedt et al. (2009), that sprat in a Norwegian fjord feed on dormant copepods during daytime, or do not feed at all. It furthermore fits in with the general tendency that planktivorous fishes in the temperate zone are food-limited during overwintering (Byström et al. 2006).

Previous laboratory work has shown that a number of fishes on low ration, or starved, select colder temperatures compared to well-fed individuals (Comeau et al. 2002). A generally accepted Q_{10} value of ~2.2 for metabolic rates (Schmidt-Nielsen 1983, Willmer et al. 2000) provides a reduction in metabolic rate of 33% when sprat are located above the thermocline at 3°C, compared to the bottom at 8°C in the present study. There is consequently a bioenergetic incentive for the starving sprat to stay high in the water column during the winter to minimize energy expenditures by performing DVMs into the upper uniform layer of low temperature in the dark hours when predation risk is reduced (Brett 1971, Méndez & Wieser 1993).

Being a physostome fish, the vertical distribution of sprat may be affected in 2 ways. These fish lack gas secreting glands for adjustment of the swimbladder at different depths, so the swimbladder becomes successively compressed at increasing depth making the fish negatively buoyant in deeper water (Solberg & Kaartvedt 2014). Using bottom mounted, upward facing echosounders during wintertime in Bunnefjorden, Norway, Kaartvedt et al. (2009) tracked individual sprat and showed that the fish continuously swam up and down at depths >55 m, and this way maintained the same depth over time. This was interpreted as sinking due to negative buoyancy followed by compensatory ascent, which implies extra metabolic costs compared to a situation of neutral buoyancy (Huse & Ona 1996, Speers-Roesch et al. 2004). In the present study, the ascent of sprat from depths of 55 to 60 m at dusk when predation risk is reduced may therefore also be due to a strategy of minimizing swimming costs by reducing negative buoyancy. Secondly, Kaartvedt et al. (2009), Solberg & Kaartvedt (2014) and Solberg et al. (2015) tracked individual sprat performing short excursions to the surface at night and ascribed this swimming behaviour to refilling the swimbladder by gulping atmospheric air. However, even in situations of inverse DVM, with sprat aggregating in deep water at night, surfacing

did not seem to impact the vertical distribution pattern at large (Solberg & Kaartvedt 2014). It is therefore doubtful whether surfacing behaviour can explain the vertical distribution dynamics observed in the present study in the Baltic Sea.

The probability of suffering winter starvation mortality increases with decreasing fish size (Schultz & Conover 1999, Byström et al. 2006). This is because the relationship between body mass and the energy reserve accumulated during spring, summer and autumn is hyperallometric (power >1), but hypoallometric (power < 1) between body mass and metabolic rate, implying that larger fish are able to subsist longer on their reserves compared to their smaller conspecifics at a given temperature (Schultz & Conover 1999). The higher percentage of the small, YOY sprat in the pelagic trawl catches above the halocline compared to the bottom trawl catches in the dark hours (Fig. 3a) may therefore be the result of a higher incentive for the smaller fish to seek and stay at lower temperature.

From trawl catches in the feeding season, Cardinale et al. (2003) found differences in the length frequency distribution of herring at different water depths during the day as well as at night, with larger individuals being more abundant near the bottom. However, in contrast to the results of the present study, they did not report any differences for sprat. Still, Fig. 8 of Cardinale et al. (2003) indicates that the percentage of small sprat in the pelagic catches during the night is higher compared with the size composition of the catches close to the bottom. If statistically significant, it might be argued that during the night when predation risk is reduced, the sprat seek warmer water to accelerate food consumption or processing and maximize their energy stores for the coming winter (e.g. Levy 1990a,b). Busch & Mehner (2012) observed a similar pattern for coregonids and estimated that small fish profit from a faster and earlier ascent at dusk by increasing their daily ration by ~8% relative to fish that would migrate together with the main population. On this basis, Busch & Mehner (2012) recommended that the size-specific variability in individual migration trajectories must be considered in future studies addressing ultimate causes of DVM.

During wintertime in Bunnefjorden, the hydroacoustics showed a bimodal vertical distribution of sprat (Solberg et al. 2015). In the winters during which the sprat were actually feeding, this distribution was reflected in their size range in that body size increased with depth. Supported by observed stomach contents, this distribution was partly explained by the smaller, YOY individuals being more active

feeders in the intermediate waters compared to their older conspecifics. The Bunnefjorden is a deep fjord with a thick, hypoxic bottom layer, the upper part of which probably works as a refuge from gadoid predators. The intermediate water is warmer than bottom and surface waters. The distribution pattern could therefore be explained by 2 different fitness optimization strategies, with the YOY sprat benefiting most by maximizing growth rate, and the adults by minimizing mortality rate. These different strategies were used in a stochastic dynamic optimization model developed by Rosland & Giske (1994) for the depth distribution of juveniles and adults of the small mesopelagic planktivorous fish *Maurolicus muelleri* in a winter situation. The distribution pattern could, however, also be explained by different internal states such as hunger coupled with the energy storage for overwintering (Solberg et al. 2015), the latter generally increasing with body size cf. the discussion above. The studies on sprat in Bunnefjorden thus demonstrate how biotic and abiotic variables may interact in controlling the overwintering ecology of sprat (Solberg et al. 2015).

Feeding and vertical distribution dynamics of cod

The narrow diet niche width of the sampled cod reflected the low diversity of appropriate prey in the Baltic Sea. Sprat constituted >90% of the ingested energy, and herring most of the remaining part, leaving other prey (including invertebrates) as an almost insignificant portion of the diet. Smaller cod (<25 cm) probably fed mostly on bottom-dwelling invertebrates. At least, they were almost absent in the pelagic catches (Fig. 3c), indicating that they did not forage on sprat and therefore did not participate in the vertical foraging movements.

The size range and frequency distribution of sprat ingested by the sampled cod matched well that of sprat caught by bottom trawl (Fig. 3a). In contrast, the size range (14 to 20 cm) of ingested herring covered only the lower half of the length distribution of herring in the trawl catches (Fig. 3b). The latter observation is in accordance with field studies on prey size preference of cod, where the maximum prey fish length in stomachs of cod of the same size range as in the present study was ~20 cm for a mixture of prey, including clupeids (Lilly & Fleming 1981, Scharf et al. 2000, Pinnegar et al. 2003). Cod longer than 50 cm were rare, so herring above 20 cm appeared to have been at least partly released from predation pressure by cod.

The estimated feeding level $f \sim 0.40$ for cod was obtained irrespective of methodology and subset of data by use of the GER model to cod stomach content data. This level is close to the median value 0.43 (SD = 0.07) estimated by Armstrong & Schindler (2011) across 66 populations of 38 fish species. It is well above a typical maintenance level of ~0.20 (Hanson et al. 1997) and 0.20 to 0.25 estimated from laboratory experiments on the 2 gadoids whiting *Merlangius merlangus* and saithe *Pollachius virens* fed natural prey fishes (Andersen & Riis-Vestergaard 2003).

Thus, in contrast to sprat, the energy balance of cod appeared to be positive and the feeding conditions therefore favourable during wintertime. If so, the optimal behaviour between feeding events should be to stay at high temperature to maximize the food processing rate (e.g. Levy 1990a,b). However, higher temperatures imply lower levels of dissolved oxygen (Fig. 2) and chronic hypoxia is known to depress food consumption and growth rates of fish (Chabot & Dutil 1999), probably by reducing the aerobic scope (maximum metabolic rate − standard metabolic rate) (Jordan & Steffensen 2007). The optimum conditions for food processing are therefore believed to have been determined by a trade-off between temperature and oxygen saturation in the environmental settings of the Bornholm Basin. In laboratory experiments at 10°C on cod of body size similar to the present study, significant effects of dissolved oxygen on growth were observed below 65% saturation, with the estimated critical level between 65 and 73% (Chabot & Dutil 1999). Also, the GER was unaffected or only marginally affected at 65% saturation (Brach 1999) whereas it was significantly slower at 55 and 40% saturation as compared with normoxia (Chabot et al. 2015).

Considering the positive energy balance and the trade-off between temperature and oxygen saturation, the estimated position in the water column of cod at 64% oxygen saturation and 5.5°C, apart from (feeding) raids upwards in the water column (Figs. 2 & 6b), appears optimal in terms of maximizing the food processing rate. Higher temperatures would imply lowering of the oxygen saturation to levels that significantly depress the physiological processes in the fish.

SUMMARY AND CONCLUSIONS

The different energy balances of the 2 species explained their respective temperature preferences. Also, there appeared to be a trade-off between temperature and oxygen saturation for cod profiting from the accessibility of sprat prey by staying at the tem-

perature–oxygen combination that maximizes food processing (e.g. Claireaux et al. 2000). Schooling of sprat at the same depth as cod in the daytime appeared to be an effective method of protection against predation, as cod were not successful in capturing sprat during this period (Fig. 7) (Magurran 1990, Pitcher 1993, Pitcher & Parrish 1993). Reduction of standard metabolic costs of the starving sprat may constitute the adaptive background for moving to the upper water layers of lower temperature during the dark hours, when predation risk is reduced. The reduction of swimming costs by staying high in the water column and reducing the negative buoyancy at night further contribute to lowering total metabolic costs. Hence, a trade-off between predation and winter starvation mortality may explain the DVM behaviour of sprat under these environmental conditions.

Through a focus on a typical winter situation, it has been possible to acquire new mechanistic knowledge about vertical predator–prey interactions in the most important basin of the Baltic Sea. The adaptive behaviour of predator and prey was explained by combining diel predation patterns with vertical fish distribution dynamics, the setting of the physical environment, and fitness optimization based on bioenergetics and relevant trade-offs. In this way, the present study presents an avenue to unveil the biological mechanisms on a small scale that give rise to specific observed predator–prey interactions on a large scale. Use of the integrated methodologies applied here to obtain information from other seasons and locations in the basin and beyond should ultimately contribute to establishment of aggregate functional response of cod in the Baltic Sea. This approach should prove useful for forecasting the upper trophic dynamics in scenarios enforced by climate changes, and further provide important trade-offs for fitness optimization in life history models.

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