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The diel vertical migration patterns and individual swimming behavior of overwintering sprat *Sprattus sprattus*

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ABSTRACT

We addressed the behavioral patterns and DVM dynamics of sprat overwintering in a 150 m Norwegian fjord with increasing hypoxia by depth. An upward-facing echosounder deployed at the bottom and cabled to shore provided 4 months of continuous acoustic data. This enabled detailed studies of individual behavior, specifically allowing assessment of individual vertical migrations at dusk and dawn in relation to light, analysis of so-called rise-and-sink swimming, and investigation of the sprat's swimming activity and behavior in severely hypoxic waters. Field campaigns supplemented the acoustic studies. The acoustic records showed that the main habitat for sprat was the upper ~ 65 m where oxygen concentrations were $\geq 0.7 \text{ mL O}_2 \text{ L}^{-1}$. The sprat schooled at ~ 50 m during daytime and initiated an upward migration about 1 hour prior to sunset. While some sprat migrated to surface waters, other individuals interrupted the ascent when at ~20-30 m, and returned to deeper waters ~ 20-50 min after sunset. Sprat at depth was on average larger, yet individuals made excursions to- and from upper layers. Sprat were swimming in a "rise and sink" pattern at depth, likely related to negative buoyancy. Short-term dives into waters with less than $0.45 \text{ mL O}_2 \text{ L}^{-1}$ were interpreted as feeding forays for abundant overwintering *Calanus* spp. The deep group of sprat initiated a dawn ascent less than 1 hour before sunrise, ending at 20-30 m where they formed schools. They subsequently returned to deeper waters about ~20 min prior to sunrise. Measurements of surface light intensities indicated that the sprat experienced lower light levels in upper waters at dawn than at dusk. The vertical swimming speed varied significantly between the behavioral tasks. The mixed DVM patterns and dynamic nocturnal behavior of sprat persisted throughout winter, likely shaped by individual strategies involving optimized feeding and predator avoidance, as well as relating to temperature, hypoxia and negative buoyancy.

Key words; sprat, DVM, dusk and dawn, hypoxia, diving behavior, nocturnal behavior, swimming speed

1. INTRODUCTION

The diel cycle of light commonly influences the behavior and swimming activity of fish (Westin & Aneer 1987, Helfman 1993). Diel vertical migration (DVM) is an important example of such light impacted behavior displayed by a variety of fish as well as other marine and freshwater taxa (Ringelberg 1991, Watanabe et al. 1999, Pearre 2003). The normal DVM mode is ascent to shallower waters at dusk followed by descent to the deeper daytime habitat at dawn. However, a reverse pattern with the organism seeking a deeper nocturnal than diurnal distribution may also occur (Neilson & Perry 1990, Hardiman et al. 2004, Jensen et al. 2011).

While changes in light intensity are considered the main proximate driver for this recurring habitat shift (Neilson & Perry 1990, Cohen & Forward 2009), the adaptive significance is debated, yet generally explained by three hypotheses; bioenergetic efficiency (Wurtsbaugh & Neverman 1988), predator avoidance (Clark & Levy 1988, Lampert 1993), and foraging (Levy 1990a). Predator avoidance and foraging are furthermore integrated in the hypothesis of an “anti-predation window”. This model predicts migration and optimized feeding in upper layers during the crepuscular periods, when ambient light levels are sufficient for visual foraging, yet low enough to provide relative protection against own predators (Clark & Levy 1988, Scheuerell & Schindler 2003). Some fish forage in the dark using tactile stimuli, yet less efficiently since the detection range is shorter (Janssen 1997, Sørnes & Aksnes 2004).

Most studies assessing DVM behavior have focused on establishing large scale patterns, such as comparing the overall diurnal and nocturnal distribution of a population (Cardinale et al. 2003, Orłowski 2005, Gjelland et al. 2009). However, fine scale DVM dynamics like interchange of individuals between deeper and shallow layers throughout night (Simard et al. 1985, Pearre 2003, Sourisseau et al. 2008), or variations in migration speed and timing of migration (Busch & Mehner 2012) are overlooked by only tracking mass movements. Previous research has therefore outlined the importance of assessing individual variability when addressing ultimate causes of DVM (Pearre 2003, Busch & Mehner 2012, Mehner 2012). Such studies have been hampered by methodological constraints. Yet, *in situ* assessment of individual behavior has recently been carried out for both macroplankton and fish by the use of stationary echosounders (e.g. Mehner 2006, Kaartvedt et al. 2007, 2015, Solberg et al. 2012, Vestheim et al. 2014) which provide records of individual trajectories through the acoustic beam.

The European sprat (*Sprattus sprattus*) is a small clupeid fish that commonly displays DVM (Cardinale et al. 2003, Solberg et al. 2012, 2015). It is a visual feeder and a schooling fish (Arrhenius 1998, Cardinale et al. 2003). Hence, the behavior of sprat is characterized by the typical rhythmicity of schooling (Pavlov & Kasumyan 2000). Schools disintegrate at night when light levels drop below a certain threshold and reform at dawn when illumination increases (e.g. Nilsson et al. 2003, Knudsen et al. 2009, Solberg & Kaartvedt 2014). Previous studies on overwintering sprat have shown that various distinct behavioral modes may be predominant at nighttime. This includes surfacing for gulping of atmospheric air and subsequent gas-release (Solberg & Kaartvedt 2014), interrupted migrations at dusk, asynchronous vertical migrations and dawn ascent in the morning (Kaartvedt et al. 2009a, Solberg et al. 2012, 2015). However, apart from surfacing, such behavior has not been analyzed in detail, and time budgets in relation to light conditions as well as associated swimming speeds and patterns, are largely unknown.

Sprat is widely distributed in coastal zones where bottom-water hypoxia is a natural and frequent phenomenon, such as the Baltic, Kattegat, Black Sea and some Norwegian fjords (Parmanne et al. 1994, Daskalov 2003, Kaartvedt et al. 2009a). Fishes in such hypoxic areas face various challenges, including compression of their vertical habitat, which may affect exposure to predators and access to prey. One consequence of hypoxic zones at depth can be reduced overlap with potential prey, as some zooplankton species might take advantage of oxygen depletion and seek refuge in the hypoxic zone (Taylor et al. 2007, Webster et al. 2015). Copepods of the genus *Calanus*, which are ecological key species and important food source for sprat (Solberg et al. 2015), may spend their diapause phase in basins with low oxygen contents (Osgood & Checkley 1997, Bagøien et al. 2000). During the unproductive winter months when zooplankton abundance is low (Cushing 1975), such deep-living copepods may represent the main potential food for zooplanktivores (Solberg et al. 2015). Thus, how sprat deal with hypoxic waters is potentially important for winter growth and stock productivity (Ojaveer & Kalejs 2010, Voss et al. 2012). Hypoxia is a growing phenomenon in coastal environments (Diaz & Rosenberg 2008) and the frequency of ventilation of hypoxic water bodies may change with future climate changes, as indicated in the Baltic where number of deep-water renewal events the last 30 years has pronouncedly decreased (Matthäus et al. 2008).

Sprat is a thermophilic species (Peck et al. 2012), living at the northernmost edge of its geographical range in Norwegian fjords and in the Baltic where surface waters may reach freezing temperatures in winter. It apparently avoids temperatures below five degrees (Stepputtis 2006), and this can create the challenge of evading low temperatures in shallow waters concurrently with staying above a hypoxic layer (Stepputtis et al. 2011, Ojaveer & Kalejs 2010). Since the physostome sprat lack gas secretion organs for adjustment of swimbladder volume, buoyancy may decrease with depth due to swimbladder compression (Huse & Ona 1996, Nero et al. 2004), affecting their swimming activity and consequently their energy budgets in deep waters. In sum, overwintering sprat must trade-off their vertical distribution, swimming- and DVM behavior in heterogeneous water bodies with respect to light, buoyancy alteration, hypoxia and temperatures, as well as distribution of prey and potential predators.

The overall objective of this study was to assess the behavioral patterns and DVM dynamics of overwintering sprat in a high-latitude fjord characterized with hypoxia in bottom waters, cold waters at the surface and potential prey distributed both in shallow and deep-including hypoxic - waters. This involved testing the hypotheses; 1) Corresponding and reciprocal behavior at dusk and dawn relate to corresponding light conditions. i.e. twilight vertical migrations are carried out at similar light thresholds. To address this hypothesis, we establish timing, depth and swimming speed of dusk descent and dawn ascent in relation to surface light intensities. (2) Sinking rate of “rise and sink” swimming among sprat (Kaartvedt et al. 2009a, Solberg et al. 2012) is positively correlated with depth, which would be in line with the assumption of a swimbladder compression. We approach this hypothesis by comparing *in situ* descent speeds of sprat from a previous winter (when absence of hypoxia allowed deeper overwintering) with *in situ* descent speeds from the current winter. Finally, we examine sprat’ individual response to hypoxia by assessing swimming behavior in waters with less than 0,7 mL O₂ L⁻¹, a value documented as the general minimum threshold for oxygen tolerance by overwintering sprat in the field (Kaartvedt et al. 2009a, Solberg et al. 2015). We establish swimming speed, time budgets and maximum tolerance time spent in waters categorized as severely hypoxic; < 0.5 mL O₂ L⁻¹ (Diaz & Rosenberg 2008).

2. MATERIALS AND METHODS

An upward-facing echosounder deployed at the bottom and cabled to shore provided continuous acoustic data throughout an entire winter into early spring. The acoustic records were supplemented with field campaigns to incorporate environmental and biological parameters in the assessment. The stationary acoustic set-up enabled detailed assessment of assemblages of sprat as well as individual behavior.

2.1 Study site

The study took place in the 150 m deep Bunnefjord, which is the innermost branch of the Oslofjord (Figure 1 in Klevjer & Kaartvedt 2011). The deep basin of the Bunnefjord is often characterized by hypoxic conditions due to the presence of two sills that restrict water exchange. One sill (19 m) is located in the sound that connects the inner Oslofjord to outer waters, and the other (~ 50 m) is located at the inlet of the Bunnefjord. The natural tendency of hypoxia has been further enhanced by anthropogenic influence. Still, water renewal normally occurs every 2-3 years, resulting in periods with an oxygenated water column.

2.2 Sampling

Incoming irradiance were continuously measured at the Norwegian University of Life Sciences which is located ~ 15 km south of the study site. Visible light, PAR (Photosynthetic Active Radiation), was measured with a LI-COR quantum sensor in air. The data were integrated over 10 minutes' intervals and all measurements from 07 December to 17 April were kindly made available for this study. Intermittent field campaigns for assessment of environmental factors and sampling of acoustic targets were conducted in December 2007 and January, February and April (2008) using the research vessel of the University of Oslo, *RV Trygve Braarud*. Vertical profiles of temperature and salinity were measured by a Falmouth Scientific Instruments CTD (Conductivity, Temperature and Depth) equipped with Niskin bottles. Water samples were analyzed for oxygen content using the standard Winkler method.

Vertical net tows for mesozooplankton (potential prey) were made over six depth intervals (bottom – 100 m, 100 – 80 m, 80 – 60 m, 60 – 40 m, 40 – 20 m, 20 – 0 m) using a WP-2 net with 200 μ m mesh size (Solberg et al. 2015). The samples were fixed in 4 % formalin and later counted and identified to species or lowest possible taxon level. Post-processing of samples

was performed under a stereo microscope in the lab by personnel specialized in zooplankton identification. Fish were sampled with a pelagic trawl with an aperture of $\sim 100 \text{ m}^2$ and mesh size of 20 cm near the opening, declining to $\sim 1 \text{ cm}$ at the rear part and 3 mm in the cod-end. In total 33 pelagic tows were conducted throughout the winter, mostly at daytime as ship time only permitted limited nocturnal sampling. The echosounders on the research vessel (Simrad EK 500, 38 kHz and 120 kHz) identified acoustic scattering layers during trawling. A Scanmar depth sensor located at the head rope of the $\sim 10 \text{ m}$ deep trawl provided real-time information on trawl depth, and a multisampler cod end enabled vertically stratified sampling (Engås et al. 1997).

2.3 Continuous acoustic studies

A bottom-mounted upward-facing 200 kHz echosounder (Simrad EK60) was deployed at 150 m depth (59.7921° N , 10.7267° E) on 06 December 2007 and retrieved 17 April 2008. Due to equipment failure, there are no records from 14 – 20 December 2007 and 28 December to 10 January 2008. The acoustic transceiver (GPT) was kept in a pressure-proof casing and the echosounder was mounted in a steel frame with gimbal couplings to ensure a horizontal orientation of the transducers surface (ES 200-7CD). The echosounder was connected to land with a cable that provided electricity and transmitted digitized signals to a computer on shore where all raw data were stored for later post-processing. Calibration of the echosounder was performed with a standard 13.7 mm copper sphere near the surface prior to deployment (Foote et al. 1987). The temporal resolution of data (ping rate) was $1\text{-}2 \text{ pings s}^{-1}$ and the pulse length was set to 0.256 ms.

Post-processing of acoustic data was initially performed in MATLAB in which echograms displaying acoustic records with a time resolution of 1 and 24 hours were made. These echograms provided an overview of vertical distributions and DVM-patterns of acoustic targets used as basis for further analyses. Acoustic targets were identified as mainly representing sprat based on trawl results from the present and previous studies in the fjord (e.g. Røstad 2006, Paulsen 2008, Kaartvedt et al. 2009a, Solberg et al. 2012) and on comparison of TS measurements of sprat from the same location (Røstad 2006, Solberg & Kaartvedt 2014).

2.4 Analysis of individual vertical migrations during dusk and dawn

Behavioral patterns of “dusk descent” and “dawn ascent” (individual vertical migrations observed during the two twilight periods) were analyzed using the acoustic post processing software Sonar_5 (version 5.9.9, Balk & Lindem 2005). Single traces of migrating fish were visible in the echograms. However, at this long range from the echosounder, it was not possible to successfully record these single trajectories by Target Tracking [TT] (see section 2.5.2), which requires higher quality of the acoustic returns than is the case for many echoes displayed in an echogram (Ehrenberg & Torkelson 1996). Therefore, migrating individuals were registered manually by the use of “a mouse tip monitor” in Sonar_5 (by double clicking with the mouse in the echogram, date, time and depth were listed for each click). In order to describe the process and assess timing and speed of these migration patterns, ten “events” symbolized as letters (A-J) were registered for each day around sunset/dusk and sunrise/dawn. The registration of events is illustrated in the echogram example in Figure 1 and further explained below:

Sunset/dusk; (A) timing when the sprat schools start an upward migration (i.e. initiation of normal DVM), (B) when the first individuals interrupt the upward migration and swim downwards, (C) when the first individuals end their descent, (D) when the last individuals interrupt the upward migration and swim downwards, (E) when the last individuals end their descent. The events of D and E only refer to individuals leaving the ascending group in the course of the migration (not to individuals that carried out normal DVM and alternatively descended later at night). The following sequences were listed for dawn/sunrise; (F) timing when the first individuals start migrating upwards, (G) when the first individuals end their ascent, (H) when the last individuals start upward migration, (I) when the last individuals end their ascent, (J) when schools establish during daytime after returning from upper waters.

Surface light measurements of time intervals with the closest correspondence to the timing of the events B – E and F – I was extracted for each day during the study period, and average light intensity was calculated for each migration event. Average swimming speeds for dusk descent and upward swimming speed for dawn ascent were calculated based on all data, (i.e. for each day, two dusk descent speeds and two dawn ascent speeds were calculated).

Calculations of sunrise, sunset and twilight phases were obtained from the website www.timeanddate.com. Sunrise was defined as the time when the upper part of the sun is visible at the horizon, and sunset when the last part of the sun is about to disappear below the horizon. Civil twilight, which is the brightest of the three twilight phases (prior to sunrise and after

sunset), was defined as the period when the center of the sun is between 0 and 6 degrees below the horizon.

2.5 Automatic Target Tracking of rise-and-sink swimming

The sinking rate (vertical descent speed) of the characteristic “rise and sink” swimming in sprat and herring (Huse & Ona 1996, Kaartvedt et al. 2009a) was assessed by Target Tracking [TT] in Sonar_5. TT combines single echoes recognized by the pulse-length-based single echo detector (SED) of Sonar_5 into tracks, and provides data on the swimming speed and the acoustic size (Target Strength, TS). For a more accurate representation of echo strength that is independent of range, the echoes displayed in the SED-echogram are calibrated according to the TVG-function (Time Varied Gain) $40 \log R$ (See chapter 3, MacLennan & Simmonds 1992), and also compensated for any off-axis position in the beam. In automatic TT, individual tracks are selected based on algorithms that utilize information on the proximity of sequential echoes. Descent rate was measured by automatic tracking and the settings applied correspond to those used in Solberg et al. (2012) from a previous winter in Bunnefjorden (see that study for further details). Five dates were chosen for analyses (08 December 2007, 12 January 2008, 10 February 2008, 10 March 2008, 08 April 2008). Tracking results were used from the depth range 55 – 64 m where “rise and sink” swimming prevailed. Only descending tracks were included in the results. Sinking rates from Solberg et al. (2012), $n = 395\,520$, were statistically compared with sinking rates from the current study, $n = 12\,084$.

2.6 Manual Target Tracking of diving behavior in hypoxic waters

A diving behavior where fish dived into the hypoxic layer was detected by manual target tracking (TT) in the SED-echogram of Sonar_5. In manual TT, echoes based on criteria for a well-defined single target are selected from the SED-echogram and combined into tracks by the researcher. This manual method was chosen to ensure that descending and ascending tracks originating from the same fish were kept together.

The threshold was set at - 65 dB to sort out weak echoes related to any organisms smaller than sprat. Periods of 6 – 7 days were chosen for this manual tracking (07–12 December 2007, 11–17 January 2008 and 09–15 February 2008), selected since oxygen content was measured at the study site during these weeks (Solberg et al. 2015). Diving individuals appeared as distinct

targets (lines) making short-term excursions ~ 5 – 15 meters into waters below the lowermost part of the scattering layer (see section 3.3.4). The following data were extracted from the tracking; TS, frequency of dives, diving speed (i.e. vertical swimming speed), maximum depth of the dive and dive duration. TS-values of ascending sprat tracks are commonly relatively weak related to change in tilt angle (Røstad 2006), and the returning ascent was not always detectable in the echogram. All descending tracks were therefore used to calculate the average maximum depth of the dives registered for each period, whereas vertical swimming speeds and total time spent diving, were analyzed only for diving events where *both* downward- and upward swimming traces could be tracked. Only tracks registered deeper than 65 m (the lowermost limit of the acoustic backscattering layer) were included in the results.

To compare the acoustic size between the individuals diving into hypoxic waters and the diel migrating sprat (i.e. for corroboration of target identity), also TS values of sprat performing dusk descent one afternoon (09 December 2007) were established.

3. RESULTS

3.1 Hydrography

Solberg et al. (2015) describe environmental conditions during the winter of 07-08, with a brief description of results here. Severe hypoxia prevailed in the lower half of the water column throughout winter. Dissolved oxygen values were 7 mL L⁻¹ in surface waters, approximately 2 mL L⁻¹ at 30 m, less than 1 mL L⁻¹ at 60 m and nearly 0 mL L⁻¹ below 100 m (Figure 2). The surface temperature was 2-3 °C in December to February and ~ 7 °C in April. From January to April, a thermocline fluctuated between 15-20 m depth where the temperature increased from ~3 °C to ~ 9 °C with depth. This maximum temperature of the water column extended down to ~ 60 m. Salinity ranged from ~ 23 to 32 from 0 – 25 m before it stabilized around 33 in the lower half of the water column (Figure 2).

3.2 Trawl and net catches

The catches of fish were dominated by sprat with approximately 10350 sprat caught in total (results from all tows combined). The other most abundant fish species were herring (*Clupea harengus*) (~ 800), gobiids (230) and whiting (*Merlangius merlangus*) (214). In December,

January and February, the majority of the overwintering sprat were caught at 40-60 m, with low catches above and below (Figure 3). In total 7 tows just below a hypoxic interface of $0.7 \text{ mL O}_2 \text{ L}^{-1}$ (Figure 3, 4) gave virtually zero catches. In April, by the end of the overwintering period, sprat were only caught at depths shallower than 40 m.

Available ship-time restricted nocturnal sampling to February and priority then was on comparing sprat in shallow and deep waters. The nocturnal tows in the interval $\sim 15 - 25 \text{ m}$ (3 replicates) and $\sim 50 - 60 \text{ m}$ (3 replicates) revealed a significant size difference between sprat from deep and shallow tows (Mann-Whitney-Wilcoxon test (MWW), $W=1882.5$, $n=98$, $p < 0.001$), with a higher proportion of large sizes in the deep tows. The average lengths from the shallow and deep samples were 8.8 ± 1.5 (mean $\pm$ sd, $n = 57$) and 10.9 ± 1.9 ($n = 41$), respectively.

Krill (*Meganyctiphanes norvegica*) were abundant in the trawl catches, with a total of 84.5 liters caught. Krill were captured in deep waters at day ($\sim 60 \text{ m}$) and in the shallow nocturnal tows in February (not shown). The large diurnal catches of krill were generally below the sprat schools.

The copepod *Calanus* was the prevalent mesozooplankton. The vast majority of *Calanus* overwintered in the severely hypoxic waters below the sprat, occurring in concentrations up to 500-1000 individuals m^{-3} (Figure 3). Abundance increased by depth in early winter and became shallower in the course of winter, then with some vertical overlap with the vertical distribution of sprat (Figure 3). Other mesozooplankton taxa were most abundant in the upper 20 m, occurring in abundances of 100-200 individuals m^{-3} , abundance decreasing by depth (Figure 3).

3.3 Acoustic studies: general overview of DVM behavior

The sprat schooled during day. Most schools occurred at $\sim 50 \text{ m}$ depth, just above a scattering layer of krill, which in turn stayed close to oxygen-depleted waters below (Figure 1, 4). Some schools also appeared in shallow waters. At night, schools dispersed, some fish carried out normal DVM and migrated all the way to the surface, crossing the thermo- and halocline so that the nocturnal distribution was in colder and fresher waters (Figure 4). Others populated deeper waters, including a deeper distribution at night than during daytime. These accumulated as deep as 65 m depth, where the oxygen content was $\sim 0.7 \text{ mL L}^{-1}$. (Figure 4). Krill carried out normal

DVM with a shallower distribution at night than during day (Figure 4). The vertical paths of the dielly migrating sprat and krill crossed in the afternoon and morning, as further outlined below.

3.4 Ascent and descent at dusk

The sprat schools started ascending ~ 45 min prior to sunset. Some individuals interrupted this ascent by leaving the ascending school and returning to deeper waters, termed “dusk descent”. The first records of an interrupted vertical migration were generally made ~ 20 min after sunset, at a depth of ~ 30 m (Table 1). Average surface light intensity was $\sim 2 \pm 4 \mu\text{mol m}^{-2} \text{s}^{-1}$ at initiation of dusk descent (Table 1). The close relation of the first dusk descent with the timing of sunset is depicted in Figure 5 together with corresponding surface light intensities, showing how timing changed throughout the winter in accordance with the seasonal change in daylength. The last descent was initiated ~ 50 min after sunset by individuals that had reached depths of 15-20 m (Table 1). This event occurred nearly parallel to conclusion of civil twilight, which ended 47 ± 5.5 min after sunset. The average surface light intensity was then $\sim 0.1 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 1).

3.5 Rise-and-sink swimming and hypoxic diving behavior

Individual sprat performed rise-and-sink behavior (swimming repeatedly up and down) close to the seemingly limiting hypoxic interface (Figure 6). Average descent speed was $\sim 0.025 \pm 0.01 \text{ m s}^{-1}$ (automatic tracking, $n = 12269$). This sinking speed was significantly slower than the sinking rate of the data from Solberg et al. (2012) which was $\sim 0.035 \text{ m s}^{-1}$ (MWW-test, $W = 3615012795$, $p < 0.001$, $n = 407\ 604$).

Individual fish occasionally dived into more oxygen depleted waters (Figure 6). These diving individuals apparently belonged to the deep-living group of sprat, and in some cases, it was possible to observe fish switching from rise-and-sink behavior to hypoxic diving (Figure 6b). In March and April, diving tracks were detected near a weak acoustic layer within the hypoxic waters (Figure 6 c,d).

TS-values of the diving fish resembled the TS-values for sprat measured during dusk descent, having medians of -46.7 dB ($n = 220$) and -45.7 dB, respectively (tracking from 09 December 2007, $n = 39$). The median TS of the upward swimming tracks were -56.5 dB ($n = 220$). Records of dives into the oxygen-depleted waters below 65 m were made every night in all

the three weeks this phenomenon was quantified, with more frequent diving records made in February than in December and January (Figure 7). Dives occurred exclusively between sunset and sunrise. The average depth of dives did not change in the course of winter (68.8 ± 3.2 , $n = 126$; 68.1 ± 2.4 m, $n = 137$; 68.4 ± 1.8 m, $n = 244$ in December, January and February, respectively). Oxygen content declined with time and the O_2 concentrations at 70 m depth was 0.70 mL L^{-1} in December, 0.53 mL L^{-1} in January and 0.45 mL L^{-1} in February. Duration of dives into the severely hypoxic waters (e.g. time spent below 65 m) was on average 3.4 ± 1.5 min in December ($n=26$), 2.1 ± 0.8 min in January ($n=49$) and 2.0 ± 0.7 min in February ($n=145$), being significantly longer in December than for the two other months (Two-sample t-test: $t=4.16$, $df=34.10$ $p < 0.001$ and $t=4.78$, $df=26.85$, $p < 0.001$).

Asynchronous migrations involving individuals switching between the lower and upper group of sprat occurred throughout night, here briefly presented by an example of descending targets in the early morning (Figure 8). Vertical migrations ascribed to surfacing (interpreted as gulping of air) were always predominant early at night, but are not further dealt with here since treated in detail elsewhere (another winter; Solberg & Kaartvedt 2014).

3.6 Dawn ascent

“Dawn ascent”, in which sprat from deep water swam upwards for a short period in the morning, was always part of the DVM-pattern. Individual sprat started their ascent ~ 50 min prior to sunrise, closely corresponding to the beginning of civil twilight (46.5 ± 5.5 min to sunrise) and while surface light intensities were still $< 0.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Table 1). The last individual left depth ~ 20 minutes later. The ascending individuals formed schools at 20-30 m depth before returning to deeper waters (e.g. Figure 1). The schools normally began descending ~ 20 min before sunrise, following the seasonal change in time of sunrise, although slightly later during the latter half of March (Figure 5). Average surface light intensities were $0.8 \pm 1.8 \mu\text{mol m}^{-2}\text{s}^{-1}$ when the sprat left upper waters and descended in schools, yet, in mid-March the levels were higher during this event (Figure 5).

Light intensities at beginning of dusk descent (B) and end of dawn ascent (I) (*i.e.* the maximum light levels sprat experienced in upper waters at dusk and dawn) were significantly different (MWW-test, $W = 6420$, $n = 202$, $p < 0.001$), also if removing four outliers of values $> 10 \mu\text{mol m}^{-2}\text{s}^{-1}$ at dusk descent in February (MWW-test, $W = 6024$, $n = 198$, $p = 0.007$).

3.7 Vertical swimming speed

Swimming speed differed between the various behavioral tasks. Individual downward swimming speed during dusk descent ranged from $\sim 0.06 - 0.15 \text{ m s}^{-1}$ with an average of $\sim 0.10 \text{ m s}^{-1}$, whereas average ascent speed during dawn ascent was $\sim 0.06 \text{ m s}^{-1}$ (speed estimated for two fish tracks per day, $n = 202$) (Figure 9). Comparing vertical speed of these corresponding swimming modes at dusk and dawn revealed significant higher speed during dusk descent (MWW-test, $W = 35321$, $n = 404$, $p < 0.001$). For the hypoxic diving events, average downward swimming speed was $0.06 \pm 0.01 \text{ m s}^{-1}$. Downward speed was significantly slower than upward swimming speed (MWW-test, $W = 43423$, $n = 220$, $p < 0.001$), of which the average speed was twice as high; $0.12 \pm 0.02 \text{ m s}^{-1}$ (manual tracking, $n = 220$) (Figure 9). Migration speeds of schools were low. The ascent of the sprat schools in the afternoon (prior to dusk descent) and descent in the morning (subsequent to dawn ascent) were generally carried out at a speed of $\sim 0.005 \text{ m s}^{-1}$ (approximate speed derived from echograms, $n=101$) (Figure 9).

4. DISCUSSION

This study has assessed diel vertical migration, nocturnal distribution and individual swimming behavior of sprat. The study represents the first account on statistics of timing, depth and swimming speed of dusk descent and dawn ascent in relation to light, and complements findings from previous winters on nocturnal “rise and sink” swimming. Novel results on hypoxic diving are described and the study provides data on maximum exposure time in waters of oxygen content as low as 5-7 % saturation. The study furthermore adds information on asynchronous DVM and relations to potential prey organisms and thermoclines. Since trawl catches comprised some herring (about 10 % of sprat with respect to numbers), and sprat and herring may form mixed species schools (Maes & Ollevier 2002), herring records likely have been included in the acoustic results. We anyway reason that such limited inclusion of herring will not affect conclusions presented here because overall behavioral patterns observed this winter concur with other years sprat were studied in this location and herring were barely captured (Solberg et al. 2012, 2015, Solberg & Kaartvedt 2014). The inability to classify targets with absolute certainty

is nevertheless a limiting factor and the possibility that herring represented some of the analyzed single targets cannot be ruled out.

4.1 DVM-Patterns

4.1.1 Potential relations to food

A summary of the DVM patterns and behavioral modes displayed by the overwintering sprat at night is schematically outlined in Figure 10, together with schematic distributions of potential prey. The initiation of normal diel vertical migration by the schooling fish in the afternoon resembled the migration behavior found in other studies (Cardinale et al. 2003, Orlowski 2005). DVM is common in planktivorous fish (Pearre 2003, Hrabik et al. 2006, Kaartvedt et al. 2009b), and often explained by feeding opportunities in surface waters at night (Levy 1990a). Some sprat migrated into the upper ~ 20 m, overlapping with the distribution of shallow-living copepods like *Temora* sp. and *Acartia* sp. (in total ~ 200 ind. m⁻³) and these copepods occurred among the stomach contents of sprat (Table 4 in Solberg et al. 2015). Others interrupted their ascent. Interrupted ascents in the afternoon have also been reported in winter for the small mesopelagic fish *Maurolicus muelleri* (Staby et al. 2011, Prihartato et al. 2015). Staby et al. (2011) suggested that these planktivores foraged during ascent and returned to depth according to state of satiation. Feeding during upward migrations at dusk and dawn would be in accordance with the “anti-predation window” hypothesis (Clark & Levy 1988, Scheuerell & Schindler 2003).

Another potential food source available was krill, which were particularly common the current winter (Røstad & Kaartvedt 2013, Solberg et al. 2015). Although they appear to be too large to be preyed upon by most sprat, krill did occur among the stomach contents for the largest individuals the winter of this study (Solberg et al. 2015). Krill mostly stayed below the sprat during day and occupied upper waters above the deep group of sprat at night. However, the larger sprat crossed the path of krill during their reciprocal migrations during dusk descent and dawn ascent. The temporal resolution of sampling was not appropriate to assess if dusk and dawn thus represented time windows where the largest sprat foraged particularly actively on the krill. This may be a hypothesis for future studies, suggesting timing for sampling in upcoming field campaigns.

4.1.2 Relations to light

End of dusk descent and initiation of dawn ascent concurred with the ending and beginning of the brightest form of twilight throughout the season, and the movements were performed within matching depth ranges. Yet, the behavioral modes did not relate to corresponding light levels, as initially hypothesized. Dawn ascent was concluded at light intensities less than $< 1 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas light intensities at beginning of dusk descent was about twice as high. Comparing the maximum light intensities sprat experienced at the shallowest position during dusk and dawn revealed significant differences, and indicated that sprat appears in upper waters at light intensities that are lower during dawn ascent than at dusk. We accordingly reject our hypothesis.

Corresponding to what is indicated for sprat in the current study, the pearlside *Maurolicus muelleri* occupies shallow waters at lower light intensities during dawn ascent than at dusk (Staby & Aksnes 2011, Prihartato et al 2015). To what extent this is adaptive or has a physiological cause remains to be established. The dark-to light adaptation in the retina is more rapid than the light-to-dark adaptation (Ferwerda et al. 1996) so that dark adapted fish possibly are more efficient in detecting prey at low light intensities in the morning.

Surface light intensities at the time sprat left upper waters subsequent to dawn ascent were mostly similar throughout the study period (see Figure 5). Vertical light extinction was likely relative constant through most of the unproductive winter period, typically being one order of magnitude per ~15 m in Oslofjord waters (Jerlov 1968, Onsrud & Kaartvedt 1998, own unpublished results). Yet, an increase in measured light levels was apparent in mid-March, with the sprat leaving upper waters nearer to the upcoming sunrise these days. There was a strong build-up of chlorophyll *a* in mid-March (Røstad & Kaartvedt 2013), so that increased light extinction would cause darker waters relative to surface measurements in this period. The sprat apparently adjusted their timing in upper waters accordingly. They also seemed to respond by schooling at shallower depths during this period (as indicated by shallower weighted mean depth) (Figure 9 in Solberg et al. 2015).

4.1.3 Dispersal and aggregations of schools

The transition between the diurnal and nocturnal behavior of sprat involved dispersal- and aggregation of schools. Because vision is generally crucial in the schooling of fish (Pavlov & Kasumyan 2000), it largely occurs at day. Daytime schooling is also in accordance with the notion that schooling is beneficial in terms of predator avoidance (Magurran 1990). Fréon et al.

(1996) suggested that dissolution of schools at dusk is slow and likely due to passive dispersion, while fish actively swim together to form schools at dawn. Such patterns have also been suggested based on acoustic data on DVM behavior of sprat and herring (Cardinale et al. 2003, Nilsson et al. 2003). However, a passive dispersal of schools does not concur with the distinctive “dusk descent” behavior detected in this study. The dissolution of schools in the afternoon indeed spanned a longer time window than the formation of schools in the morning (average 30 min vs. 20 min), yet it appeared that the sprat actively left the ascending schools. Such individuals immediately changed swimming direction and descended with a speed of ~ 1 body length per second ($\sim 10 \text{ cm s}^{-1}$), being four times higher than the apparent passive sinking rates documented in the rise and sink swimming. This descent speed was furthermore significantly higher than the ascent speed ($\sim 6 \text{ cm s}^{-1}$) during dawn ascent.

4.2 Nocturnal distribution

4.2.1 Potential relation to size

A nocturnal bimodal distribution is seemingly common for sprat in Bunnefjorden (Kaartvedt et al. 2009a, Solberg & Kaartvedt 2014). Even though individuals shifted between vertical strata throughout night, the nocturnal trawling revealed a higher proportion of large individuals in deep waters. Average lengths (8.8 and 10.9 cm) of shallow and deep sprat catches generally correspond to late juvenile- and adult stages, respectively, as gonadal growth normally starts from the size of ≥ 9.5 cm (Peck et al. 2012). Adult mesopelagic fish stay deeper than juveniles during overwintering in Norwegian fjords, apparently displaying a more risk-averse behavior to increase survival and their opportunity to spawn (Rosland & Giske 1994). Trawl catches revealed that gadoids were common the current winter (Solberg et al. 2015). Although the gadoids largely distributed vertically to - and were foraging on - the very abundant krill this particular winter, sprat also occurred among the stomach contents (Solberg et al. 2015) and the gadoids did likely represent a perceived predation risk by the sprat.

4.2.2 Potential relation to temperature

The bioenergetics-efficiency hypothesis predicts a selection of migration depth in accordance to optimal temperatures for growth (Brett 1971), indicated in a variety of fish (Levy 1990b, Bevelhimer & Adams 1993, Mehner et al. 2010). The optimal temperature for growth in Baltic

sprat ranges between $\sim 10\text{-}20\text{ }^{\circ}\text{C}$ (Peck et al. 2012). The highest temperature in Bunnefjorden was $\sim 9\text{ }^{\circ}\text{C}$ at 25-55 m deep with slightly colder waters below (Figure 3) so that temperature cannot explain the nocturnal accumulation of sprat at the hypoxic interface. On the other hand, temperature may have determined the upper depth of the behavioral modes of dusk descent and dawn rise. The deep group of sprat generally returned to deeper waters at $\sim 20\text{ m}$, a depth range that largely corresponded with the presences of temperatures declining from $> 8\text{ }^{\circ}\text{C}$ to $< 4\text{ }^{\circ}\text{C}$ a few meters above. Low temperatures are considered an essential factor for setting the upper limit to the vertical distribution of sprat (Stepputtis et al. 2011), with sprat in the Baltic shown to avoid temperatures below five degrees (Stepputtis 2006). Yet, a possible temperature restriction was in any case not shared by all sprat. The shallow group – presumably juveniles - indeed traversed the thermocline as observed in the acoustic records (Figure 4), and further suggested by nocturnal catches of sprat in February. In the Baltic, adults are found to distribute deeper and warmer than younger age classes during severe wintering conditions (Ojaveer & Kalejs 2010).

4.3 Nocturnal behavior

4.3.1 Rise-and-sink swimming

Sprat at the hypoxic interface performed rise and sink swimming, as also previously documented for individual sprat in deeper waters (Kaartvedt et al. 2009a, Solberg et al. 2012). Sinking speeds were $\sim 2.5\text{ cm s}^{-1}$. In comparison, Solberg et al. (2012) measured sinking speeds of $\sim 3.5\text{ cm s}^{-1}$ in a year when oxygen conditions allowed deeper overwintering. This more than 30 % higher sinking speed for sprat in deeper waters is in line with what we hypothesized. Rise-and-sink swimming has been repeatedly documented for herring and sprat (Huse & Ona 1996, Kaartvedt et al. 2009a). The general interpretation is that this swimming behavior is carried out to counteract for negative buoyancy due to swimbladder compression at depth (Huse and Ona 1996, Nero et al. 2004). A higher sinking rate in deep waters is expected since the physostome sprat will become less buoyant with increasing pressure. The current results therefore support the hypothesis that rise-and-sink swimming is a behavior related to negative buoyancy (Huse and Ona 1996).

4.3.2 Hypoxic diving

Concentrations of overwintering *Calanus* spp. inhabited the lower, severely hypoxic part of the water column below the sprat. This relatively large-sized copepod is the preferred prey for sprat (Paulsen 2008, Solberg et al. 2015) and prevailed among the stomach contents this winter (Solberg et al. 2015). Zooplankton net tows were only taken at day, but overwintering *Calanus* does not carry out DVM (e.g. Bagøien et al. 2001), also apparent from acoustic data this winter in Bunnefjorden (c.f. Fig. 5 in Røstad & Kaartvedt 2013). The distribution of overwintering *Calanus* in oxygen-depleted waters may have motivated individual excursions into these deep layers. Taylor et al. (2007) studied swimming behavior of juvenile anchovies (*Anchoa* spp.) in settings comparable to this study. They reported on brief movements into the hypoxic waters, and suggested that the anchovies used this diving behavior for feeding. Such foraging strategy was also indicated in juvenile mud minnows (*Umbra limi*) that contained large numbers of prey that only occurred in oxygen depleted waters (Rahel & Nuntzman 1994). Correspondingly, the sprat may have carried out dives to forage on the high numbers of *Calanus* spp., in accordance with the acoustic records of fish apparently targeting echoes ascribed to *Calanus* spp. (Figure 7cd). The highest *Calanus* abundance was located below 80 m (from Dec-Feb) which was deeper than what sprat generally dived to (average maximum diving depth ~70 m). However, *Calanus* were abundant also between 60-80 m as confirmed by the net tows, and the *Calanus* spp. population moved progressively higher up in the water column in the course of the winter. The concentrations from 60 to 80 m were more than double in February (~250 ind. m⁻³) than in December (~100 ind. m⁻³), and a gradual upward shift was also documented acoustically (Figure 7cd, Røstad & Kaartvedt 2013). The higher number of diving events detected in February might indeed relate to this upward shift of potential prey.

Sprat normally detect prey visually, which likely does not apply during such night dives. While the clupeid herring may shift to filter feeding at high prey concentrations (e.g. Gibson & Ezzi 1992), sprat are generally considered to be particulate feeders (Bernreuther 2007, Brachvogel et al. 2013). Also, filter feeding usually occurs at higher prey concentrations than recorded here (Brachvogel et al. 2013). However, fish may locate their prey using the lateral-line system when low light renders vision ineffective, also recorded among clupeids (Janssen et al. 1995). Experimental studies have revealed that tactile foraging may involve a tail beat followed by a glide, with all prey detected during the glide phase (Janssen 1997). This might be in

accordance with the intermediate swimming speed observed for hypoxic diving, being double the sinking rate in rise-and-sink, and half that of the fish returning from the dive.

The dives were carried out in waters with oxygen contents as low as $0.45 \text{ mL O}_2 \text{ L}^{-1}$. The results suggest maximum exposure time of ~ 2 minutes for sprat at such oxygen concentrations (in waters of $\sim 8^\circ\text{C}$). The limiting effect at such levels of hypoxia is further indicated by the significant reduction in total diving time between dives from December and dives from January and February, when oxygen levels had declined with only $\sim 0.2 \text{ mL O}_2 \text{ L}^{-1}$. Tactile feeding is less efficient than prey search by sight (Sørnes & Aksnes 2004). Yet the lipid reserves *Calanus* spp. accumulate during diapause (Heath et al. 2004, Svetlichny et al. 2006, Wilson et al. 2015), would make them attractive prey organisms so that the energy bonus might have justified the short hypoxic excursions.

4.4 Conclusion

The use of a stationary echosounder cabled to shore enabled continuous long-term studies with high temporal resolution of both individuals and assemblages of the small pelagic fish *Sprattus sprattus*. The overwintering sprat displayed highly varied DVM behavior and nocturnal swimming behavior, likely shaped by individual strategies involving optimized feeding and predator avoidance, as well as relating to temperature, hypoxia and negative buoyancy. The results document that stationary, submerged echosounders provide a powerful tool for non-intrusively studies of fish in situ. The findings further underline that studies of individuals may provide novel information on behavioral traits that do not appear from population studies.

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FIGURE LEGENDS

Table 1. Summary of the timing (in relation to sunset and sunrise) and depth of the vertical migration modes registered during dusk and dawn with corresponding surface light intensities (PAR $\mu\text{mol m}^{-2} \text{s}^{-1}$). Mean values with standard deviations are based on 101 days of registrations.

Figure 1. Acoustic record (200 kHz) from 20 Jan 2008 depicting the different sequences of DVM behavior during dusk (left) and dawn (right). The letters mark the following “events”: **(A)** the sprat schools starting migrating upwards, **(B)** the first individuals interrupting their upward migration and swim downwards, **(C)** the first individuals ending their descent, **(D)** the last individuals interrupting the upward migration and swim downwards, **(E)** the last individuals ending their descent, **(F)** the first individuals migrating upwards, **(G)** the first individuals ending their upward migration, **(H)** the last individuals migrating upwards, **(I)** the last individuals ending their upward migration, **(J)** the schools ending their downward migration. Local time is UTC + 1 h.

Figure 2. Vertical profiles of hydrography data in Bunnefjorden on 13 December 2007, 14 January, 12 February and 17 April 2008. Lines with symbols represent oxygen data, solid lines temperature, and dotted lines illustrate salinity.

Figure 3. Left: diurnal catches of sprat in Bunnefjorden from December 07 – April 08 presented as number of sprat per 10 min of trawling. Error bars are standard deviations and n represents number of trawls per depth interval. Right: vertical concentrations of *Calanus* spp. and other mesozooplankton (individuals m^{-3}) in December 07, February 08 and April 08 in Bunnefjorden. Dotted lines demarcate oxygen contents of 0.70 mL L^{-1} .

Figure 4. Left: acoustic record (200 kHz) from midday 27 until midday 28 January 2008 showing the vertical distribution of sprat and krill throughout 24 h. Right: vertical profiles of salinity, temperature and oxygen content in January 2008.

Figure 5. Timing of migration events relative to sunset (upper red line) and sunrise (lower red line) during the period 08 Dec 2007-16 Apr 2008. The letters represent events depicted in Figure 1: **B**; initiation of dusk descent and **I**; end of dawn ascent (last individual appears in upper waters). Light measurements corresponding to the timing of the migration events are indicated with black lines. Local time is UTC + 1 h (December – March) and UTC + 2 h (April).

Figure 6a) Acoustic record (200 kHz) from 17 Jan 2008 showing a single fish diving ~ 10 m into oxygen depleted waters before returning to the fish layer above **b)** The same acoustic record as a) displayed with a higher S_v -threshold (- 72 dB) where “rise and sink” swimming prior to the dive is visible **c)** and **d)** Acoustic records from March and April 2008 showing fish diving down to a dense layer ascribed to overwintering *Calanus* spp.. Note that the backscattering layer of *Calanus* spp. is shallower in April.

Figure 7. Daily diving events into severely hypoxic waters (x-axis) plotted against hour of the day (y-axis) during the periods 07–12 Dec 2007 (left) 11–17 January 2008 (middle) and 09–15 February 2008 (right). Differently shaded bricks depict number of diving events per hour. Local time is UTC + 1 hour. The horizontal lines mark sunrise (lower) and sunset (upper).

Figure 8. Acoustic record from 22 Dec 2007. Vertical interchange of sprat from the surface group migrating down to the deep group late at night.

Figure 9. The sprat’ average vertical swimming speed during various behavioral modes; upwards swimming in the afternoon (schools), “dusk descent”, sinking in “rise-and-sink” swimming, hypoxic diving, “dawn ascent” and downwards swimming in the morning (schools). Error bars are standard deviations.

Figure 10. Schematic overview of the DVM- and nocturnal behavior of sprat. Sprat schools initiated normal DVM ~ 1 hour prior to sunset. While some sprat migrated all the way to surface waters, other individuals interrupted the ascent and returned to deep waters, (“*dusk descent*”). Descending sprat accumulated near the interface of oxygen depleted waters (depicted in red) where they continued with solitary “*rise and sink*” swimming. A “*surfacing behavior*” was dominant 1-2 hours after sunset. One group of sprat occurred in surface waters while other specimen distributed from below ~ 30 to ~ 65 m. Interactions between the surface and deep group occurred as the sprat occasionally migrated between the two groups “*interchanges*”. Sprat close to the minimum oxygen boarder occasionally dived into the highly oxygen depleted waters followed by an immediate return to the interface (“*hypoxic diving*”). All sprat from the deep layer initiated an upward migration ~ 1 h prior to sunrise (“*dawn ascent*”), with a subsequent return to deeper waters, then while schooling. Abundance and distribution of krill, small

copepods and overwintering *Calanus* spp. are denoted in the figure. Occurrence of potential predators of sprat is not included, but their distribution is shown in Figure 2 in Solberg et al. (2015).

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Ascent and descent at dusk		Dawn ascent	
Timing, light and depth			
Schools start ascending	46 ± 25 min prior to sunset start depth: ~ 40 – 60 m	First initiation of dawn rise (F)	51 ± 18 min prior to sunrise 0.06 ± 0.13 μmol m ⁻² s ⁻¹ start depth: 52 ± 4 m stop depth: 22 ± 5 m
First initiation of dusk descent (B)	23 ± 21 min after sunset 2.09 ± 3.96 μmol m ⁻² s ⁻¹ start depth: 30 ± 7 m stop depth: 60 ± 3 m	Last dawn ascent registration (H)	30 ± 17 min prior to sunrise 0.38 ± 1.03 μmol m ⁻² s ⁻¹ start depth: 56 ± 2 m stop depth: 30 ± 6 m
Last dusk descent registration (D)	52 ± 20 min after sunset 0.13 ± 0.32 μmol m ⁻² s ⁻¹ start depth: 16 ± 6 m stop depth: 52 ± 5 m	Schools start descending (I)	23 ± 17 min prior to sunrise 0.80 ± 1.81 μmol m ⁻² s ⁻¹ start depth: ~ 30 m

HIGHLIGHTS

- Stationary acoustics enabled long-term studies of sprat in a hypoxia-impacted fjord
- Sprat performed normal- and asynchronous DVM, including dawn ascent and dusk descent
- Reciprocal behavior at dusk and dawn did not relate to similar light conditions
- DVM behavior seemed to be size-dependent
- Sprat dived into hypoxic waters ($0.5 \text{ mL O}_2 \text{ L}^{-1}$), proposedly to feed on *Calanus* spp.