

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

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31 **ABSTRACT**

32 We addressed the behavioral patterns and DVM dynamics of sprat overwintering in a 150 m
33 Norwegian fjord with increasing hypoxia by depth. An upward-facing echosounder deployed at
34 the bottom and cabled to shore provided 4 months of continuous acoustic data. This enabled
35 detailed studies of individual behavior, specifically allowing assessment of individual vertical
36 migrations at dusk and dawn in relation to light, analysis of so-called rise-and-sink swimming, and
37 investigation of the sprat' swimming activity and behavior in severely hypoxic waters. Field
38 campaigns supplemented the acoustic studies. The acoustic records showed that the main habitat
39 for sprat was the upper ~ 65 m where oxygen concentrations were ≥ 0.7 mL O₂ L⁻¹. The sprat
40 schooled at ~ 50 m during daytime and initiated an upward migration about 1 hour prior to sunset.
41 While some sprat migrated to surface waters, other individuals interrupted the ascent when at ~20-
42 30 m, and returned to deeper waters ~ 20-50 min after sunset. Sprat at depth was on average larger,
43 yet individuals made excursions to- and from upper layers. Sprat were swimming in a "rise and
44 sink" pattern at depth, likely related to negative buoyancy. Short-term dives into waters with less
45 than 0.45 mL O₂ L⁻¹ were interpreted as feeding forays for abundant overwintering *Calanus* spp.
46 The deep group of sprat initiated a dawn ascent less than 1 hour before sunrise, ending at 20-30 m
47 where they formed schools. They subsequently returned to deeper waters about ~20 min prior to
48 sunrise. Measurements of surface light intensities indicated that the sprat experienced lower light
49 levels in upper waters at dawn than at dusk. The vertical swimming speed varied significantly
50 between the behavioral tasks. The mixed DVM patterns and dynamic nocturnal behavior of sprat
51 persisted throughout winter, likely shaped by individual strategies involving optimized feeding
52 and predator avoidance, as well as relating to temperature, hypoxia and negative buoyancy.

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

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58 **1. INTRODUCTION**

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

66 While changes in light intensity are considered the main proximate driver for this recurring
67 habitat shift (Neilson & Perry 1990, Cohen & Forward 2009), the adaptive significance is debated,
68 yet generally explained by three hypotheses; bioenergetic efficiency (Wurtsbaugh & Neverman
69 1988), predator avoidance (Clark & Levy 1988, Lampert 1993), and foraging (Levy 1990a).
70 Predator avoidance and foraging are furthermore integrated in the hypothesis of an “anti-predation
71 window”. This model predicts migration and optimized feeding in upper layers during the
72 crepuscular periods, when ambient light levels are sufficient for visual foraging, yet low enough
73 to provide relative protection against own predators (Clark & Levy 1988, Scheuerell & Schindler
74 2003). Some fish forage in the dark using tactile stimuli, yet less efficiently since the detection
75 range is shorter (Janssen 1997, Sørnes & Aksnes 2004).

76 Most studies assessing DVM behavior have focused on establishing large scale patterns,
77 such as comparing the overall diurnal and nocturnal distribution of a population (Cardinale et al.
78 2003, Orłowski 2005, Gjelland et al. 2009). However, fine scale DVM dynamics like interchange
79 of individuals between deeper and shallow layers throughout night (Simard et al. 1985, Pearre
80 2003, Sourisseau et al. 2008), or variations in migration speed and timing of migration (Busch &
81 Mehner 2012) are overlooked by only tracking mass movements. Previous research has therefore
82 outlined the importance of assessing individual variability when addressing ultimate causes of
83 DVM (Pearre 2003, Busch & Mehner 2012, Mehner 2012). Such studies have been hampered by
84 methodological constraints. Yet, *in situ* assessment of individual behavior has recently been
85 carried out for both macroplankton and fish by the use of stationary echosounders (e.g. Mehner
86 2006, Kaartvedt et al. 2007, 2015, Solberg et al. 2012, Vestheim et al. 2014) which provide records
87 of individual trajectories through the acoustic beam.

88

89 The European sprat (*Sprattus sprattus*) is a small clupeid fish that commonly displays DVM
90 (Cardinale et al. 2003, Solberg et al. 2012, 2015). It is a visual feeder and a schooling fish
91 (Arrhenius 1998, Cardinale et al. 2003). Hence, the behavior of sprat is characterized by the typical
92 rhythmicity of schooling (Pavlov & Kasumyan 2000). Schools disintegrate at night when light
93 levels drop below a certain threshold and reform at dawn when illumination increases (e.g. Nilsson
94 et al. 2003, Knudsen et al. 2009, Solberg & Kaartvedt 2014). Previous studies on overwintering
95 sprat have shown that various distinct behavioral modes may be predominant at nighttime. This
96 includes surfacing for gulping of atmospheric air and subsequent gas-release (Solberg & Kaartvedt
97 2014), interrupted migrations at dusk, asynchronous vertical migrations and dawn ascent in the
98 morning (Kaartvedt et al. 2009a, Solberg et al. 2012, 2015). However, apart from surfacing, such
99 behavior has not been analyzed in detail, and time budgets in relation to light conditions as well
100 as associated swimming speeds and patterns, are largely unknown.

101 Sprat is widely distributed in coastal zones where bottom-water hypoxia is a natural and
102 frequent phenomenon, such as the Baltic, Kattegat, Black Sea and some Norwegian fjords
103 (Parmanne et al. 1994, Daskalov 2003, Kaartvedt et al. 2009a). Fishes in such hypoxic areas face
104 various challenges, including compression of their vertical habitat, which may affect exposure to
105 predators and access to prey. One consequence of hypoxic zones at depth can be reduced overlap
106 with potential prey, as some zooplankton species might take advantage of oxygen depletion and
107 seek refuge in the hypoxic zone (Taylor et al. 2007, Webster et al. 2015). Copepods of the genus
108 *Calanus*, which are ecological key species and important food source for sprat (Solberg et al.
109 2015), may spend their diapause phase in basins with low oxygen contents (Osgood & Checkley
110 1997, Bagøien et al. 2000). During the unproductive winter months when zooplankton abundance
111 is low (Cushing 1975), such deep-living copepods may represent the main potential food for
112 zooplanktivores (Solberg et al. 2015). Thus, how sprat deal with hypoxic waters is potentially
113 important for winter growth and stock productivity (Ojaveer & Kalejs 2010, Voss et al. 2012).
114 Hypoxia is a growing phenomenon in coastal environments (Diaz & Rosenberg 2008) and the
115 frequency of ventilation of hypoxic water bodies may change with future climate changes, as
116 indicated in the Baltic where number of deep-water renewal events the last 30 years has
117 pronouncedly decreased (Matthäus et al. 2008).

118

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

130 The overall objective of this study was to assess the behavioral patterns and DVM
131 dynamics of overwintering sprat in a high-latitude fjord characterized with hypoxia in bottom
132 waters, cold waters at the surface and potential prey distributed both in shallow and deep- including
133 hypoxic - waters. This involved testing the hypotheses; 1) Corresponding and reciprocal behavior
134 at dusk and dawn relate to corresponding light conditions. i.e. twilight vertical migrations are
135 carried out at similar light thresholds. To address this hypothesis, we establish timing, depth and
136 swimming speed of dusk descent and dawn ascent in relation to surface light intensities. (2)
137 Sinking rate of “rise and sink” swimming among sprat (Kaartvedt et al. 2009a, Solberg et al. 2012)
138 is positively correlated with depth, which would be in line with the assumption of a swimbladder
139 compression. We approach this hypothesis by comparing *in situ* descent speeds of sprat from a
140 previous winter (when absence of hypoxia allowed deeper overwintering) with *in situ* descent
141 speeds from the current winter. Finally, we examine sprat’ individual response to hypoxia by
142 assessing swimming behavior in waters with less than 0,7 mL O₂ L⁻¹, a value documented as the
143 general minimum threshold for oxygen tolerance by overwintering sprat in the field (Kaartvedt et
144 al. 2009a, Solberg et al. 2015). We establish swimming speed, time budgets and maximum
145 tolerance time spent in waters categorized as severely hypoxic; < 0.5 mL O₂ L⁻¹ (Diaz & Rosenberg
146 2008).

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150 **2. MATERIALS AND METHODS**

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

156

157 **2.1 Study site**

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

165

166 **2.2 Sampling**

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

177 Vertical net tows for mesozooplankton (potential prey) were made over six depth intervals
178 (bottom – 100 m, 100 – 80 m, 80 – 60 m, 60 – 40 m, 40 – 20 m, 20 – 0 m) using a WP-2 net with
179 200 µm mesh size (Solberg et al. 2015). The samples were fixed in 4 % formalin and later counted
180 and identified to species or lowest possible taxon level. Post-processing of samples was performed

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

189

190 ***2.3 Continuous acoustic studies***

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

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

208

209 ***2.4 Analysis of individual vertical migrations during dusk and dawn***

210 Behavioral patterns of “dusk descent” and “dawn ascent” (individual vertical migrations observed
211 during the two twilight periods) were analyzed using the acoustic post processing software

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

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

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

237 Calculations of sunrise, sunset and twilight phases were obtained from the website
238 www.timeanddate.com. Sunrise was defined as the time when the upper part of the sun is visible
239 at the horizon, and sunset when the last part of the sun is about to disappear below the horizon.
240 Civil twilight, which is the brightest of the three twilight phases (prior to sunrise and after sunset),
241 was defined as the period when the center of the sun is between 0 and 6 degrees below the horizon.

242

243 ***2.5 Automatic Target Tracking of rise-and-sink swimming***

244 The sinking rate (vertical descent speed) of the characteristic “rise and sink” swimming in sprat
245 and herring (Huse & Ona 1996, Kaartvedt et al. 2009a) was assessed by Target Tracking [TT] in
246 Sonar_5. TT combines single echoes recognized by the pulse-length-based single echo detector
247 (SED) of Sonar_5 into tracks, and provides data on the swimming speed and the acoustic size
248 (Target Strength, TS). For a more accurate representation of echo strength that is independent of
249 range, the echoes displayed in the SED-echogram are calibrated according to the TVG-function
250 (Time Varied Gain) $40 \text{ Log } R$ (See chapter 3, MacLennan & Simmonds 1992), and also
251 compensated for any off-axis position in the beam. In automatic TT, individual tracks are selected
252 based on algorithms that utilize information on the proximity of sequential echoes. Descent rate
253 was measured by automatic tracking and the settings applied correspond to those used in Solberg
254 et al. (2012) from a previous winter in Bunnefjorden (see that study for further details). Five dates
255 were chosen for analyses (08 December 2007, 12 January 2008, 10 February 2008, 10 March 2008,
256 08 April 2008). Tracking results were used from the depth range 55 – 64 m where “rise and sink”
257 swimming prevailed. Only descending tracks were included in the results. Sinking rates from
258 Solberg et al. (2012), $n = 395\ 520$, were statistically compared with sinking rates from the current
259 study, $n = 12\ 084$.

260

261 ***2.6 Manual Target Tracking of diving behavior in hypoxic waters***

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

267 The threshold was set at - 65 dB to sort out weak echoes related to any organisms smaller
268 than sprat. Periods of 6 – 7 days were chosen for this manual tracking (07–12 December 2007, 11–
269 17 January 2008 and 09–15 February 2008), selected since oxygen content was measured at the
270 study site during these weeks (Solberg et al. 2015). Diving individuals appeared as distinct targets
271 (lines) making short-term excursions ~ 5 – 15 meters into waters below the lowermost part of the
272 scattering layer (see section 3.3.4). The following data were extracted from the tracking; TS,
273 frequency of dives, diving speed (i.e. vertical swimming speed), maximum depth of the dive and

274 dive duration. TS-values of ascending sprat tracks are commonly relatively weak related to change
275 in tilt angle (Røstad 2006), and the returning ascent was not always detectable in the echogram.
276 All descending tracks were therefore used to calculate the average maximum depth of the dives
277 registered for each period, whereas vertical swimming speeds and total time spent diving, were
278 analyzed only for diving events where *both* downward- and upward swimming traces could be
279 tracked. Only tracks registered deeper than 65 m (the lowermost limit of the acoustic
280 backscattering layer) were included in the results.

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

284

285 **3. RESULTS**

286 **3.1 Hydrography**

287 Solberg et al. (2015) describe environmental conditions during the winter of 07-08, with a brief
288 description of results here. Severe hypoxia prevailed in the lower half of the water column
289 throughout winter. Dissolved oxygen values were 7 mL L⁻¹ in surface waters, approximately 2 mL
290 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
291 temperature was 2-3 °C in December to February and ~ 7 °C in April. From January to April, a
292 thermocline fluctuated between 15-20 m depth where the temperature increased from ~3 °C to ~
293 9 °C with depth. This maximum temperature of the water column extended down to ~ 60 m.
294 Salinity ranged from ~ 23 to 32 from 0 – 25 m before it stabilized around 33 in the lower half of
295 the water column (Figure 2).

296

297 **3.2 Trawl and net catches**

298 The catches of fish were dominated by sprat with approximately 10350 sprat caught in total (results
299 from all tows combined). The other most abundant fish species were herring (*Clupea harengus*)
300 (~ 800), gobiids (230) and whiting (*Merlangius merlangus*) (214). In December, January and
301 February, the majority of the overwintering sprat were caught at 40-60 m, with low catches above
302 and below (Figure 3). In total 7 tows just below a hypoxic interface of 0.7 mL O₂ L⁻¹ (Figure 3, 4)

303 gave virtually zero catches. In April, by the end of the overwintering period, sprat were only caught
304 at depths shallower than 40 m.

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

311 Krill (*Meganyctiphanes norvegica*) were abundant in the trawl catches, with a total of 84.5
312 liters caught. Krill were captured in deep waters at day (~ 60 m) and in the shallow nocturnal tows
313 in February (not shown). The large diurnal catches of krill were generally below the sprat schools.
314 The copepod *Calanus* was the prevalent mesozooplankton. The vast majority of *Calanus*
315 overwintered in the severely hypoxic waters below the sprat, occurring in concentrations up to
316 500-1000 individuals m^{-3} (Figure 3). Abundance increased by depth in early winter and became
317 shallower in the course of winter, then with some vertical overlap with the vertical distribution of
318 sprat (Figure 3). Other mesozooplankton taxa were most abundant in the upper 20 m, occurring in
319 abundances of 100-200 individuals m^{-3} , abundance decreasing by depth (Figure 3).

320

321 ***3.3 Acoustic studies: general overview of DVM behavior***

322 The sprat schooled during day. Most schools occurred at ~50 m depth, just above a scattering layer
323 of krill, which in turn stayed close to oxygen-depleted waters below (Figure 1, 4). Some schools
324 also appeared in shallow waters. At night, schools dispersed, some fish carried out normal DVM
325 and migrated all the way to the surface, crossing the thermo- and halocline so that the nocturnal
326 distribution was in colder and fresher waters (Figure 4). Others populated deeper waters, including
327 a deeper distribution at night than during daytime. These accumulated as deep as 65 m depth,
328 where the oxygen content was ~ 0.7 mL L^{-1} . (Figure 4). Krill carried out normal DVM with a
329 shallower distribution at night than during day (Figure 4). The vertical paths of the dielly migrating
330 sprat and krill crossed in the afternoon and morning, as further outlined below.

331

332 ***3.4 Ascent and descent at dusk***

333 The sprat schools started ascending ~ 45 min prior to sunset. Some individuals interrupted this
334 ascent by leaving the ascending school and returning to deeper waters, termed “dusk descent”. The
335 first records of an interrupted vertical migration were generally made ~ 20 min after sunset, at a
336 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
337 dusk descent (Table 1). The close relation of the first dusk descent with the timing of sunset is
338 depicted in Figure 5 together with corresponding surface light intensities, showing how timing
339 changed throughout the winter in accordance with the seasonal change in daylength. The last
340 descent was initiated ~ 50 min after sunset by individuals that had reached depths of 15-20 m
341 (Table 1). This event occurred nearly parallel to conclusion of civil twilight, which ended 47 ± 5.5
342 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).

343

344 ***3.5 Rise-and-sink swimming and hypoxic diving behavior***

345 Individual sprat performed rise-and-sink behavior (swimming repeatedly up and down) close to
346 the seemingly limiting hypoxic interface (Figure 6). Average descent speed was $\sim 0.025 \pm 0.01 \text{ m}$
347 s^{-1} (automatic tracking, $n = 12269$). This sinking speed was significantly slower than the sinking
348 rate of the data from Solberg et al. (2012) which was $\sim 0.035 \text{ m s}^{-1}$ (MWW-test, $W = 3615012795$,
349 $p < 0.001$, $n = 407\ 604$).

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

355 TS-values of the diving fish resembled the TS-values for sprat measured during dusk
356 descent, having medians of -46.7 dB ($n = 220$) and -45.7 dB, respectively (tracking from 09
357 December 2007, $n = 39$). The median TS of the upward swimming tracks were -56.5 dB ($n = 220$).
358 Records of dives into the oxygen-depleted waters below 65 m were made every night in all the
359 three weeks this phenomenon was quantified, with more frequent diving records made in February
360 than in December and January (Figure 7). Dives occurred exclusively between sunset and sunrise.
361 The average depth of dives did not change in the course of winter (68.8 ± 3.2 , $n = 126$; 68.1 ± 2.4
362 m, $n = 137$; 68.4 ± 1.8 m, $n = 244$ in December, January and February, respectively). Oxygen
363 content declined with time and the O_2 concentrations at 70 m depth was 0.70 mL L^{-1} in December,

364 0.53 mL L⁻¹ in January and 0.45 mL L⁻¹ in February. Duration of dives into the severely hypoxic
365 waters (e.g. time spent below 65 m) was on average 3.4 ± 1.5 min in December (n=26), 2.1 ± 0.8
366 min in January (n=49) and 2.0 ± 0.7 min in February (n=145), being significantly longer in
367 December than for the two other months (Two-sample t-test: $t=4.16$, $df=34.10$ $p < 0.001$ and
368 $t=4.78$, $df=26.85$, $p < 0.001$).

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

374

375 **3.6 Dawn ascent**

376 “Dawn ascent”, in which sprat from deep water swam upwards for a short period in the morning,
377 was always part of the DVM-pattern. Individual sprat started their ascent ~ 50 min prior to sunrise,
378 closely corresponding to the beginning of civil twilight (46.5 ± 5.5 min to sunrise) and while
379 surface light intensities were still $< 0.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Table 1). The last individual left depth ~ 20
380 minutes later. The ascending individuals formed schools at 20-30 m depth before returning to
381 deeper waters (e.g. Figure 1). The schools normally began descending ~ 20 min before sunrise,
382 following the seasonal change in time of sunrise, although slightly later during the latter half of
383 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
384 upper waters and descended in schools, yet, in mid-March the levels were higher during this event
385 (Figure 5).

386 Light intensities at beginning of dusk descent (B) and end of dawn ascent (I) (*i.e.* the
387 maximum light levels sprat experienced in upper waters at dusk and dawn) were significantly
388 different (MWW-test, $W = 6420$, $n = 202$, $p < 0.001$), also if removing four outliers of values >10
389 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at dusk descent in February (MWW-test, $W = 6024$, $n = 198$, $p = 0.007$).

390

391 **3.7 Vertical swimming speed**

392 Swimming speed differed between the various behavioral tasks. Individual downward swimming
393 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
394 average ascent speed during dawn ascent was $\sim 0.06 \text{ m s}^{-1}$ (speed estimated for two fish tracks per

395 day, $n = 202$) (Figure 9). Comparing vertical speed of these corresponding swimming modes at
396 dusk and dawn revealed significant higher speed during dusk descent (MWW-test, $W = 35321$, n
397 $= 404$, $p < 0.001$). For the hypoxic diving events, average downward swimming speed was 0.06
398 ± 0.01 m s^{-1} . Downward speed was significantly slower than upward swimming speed (MWW-
399 test, $W = 43423$, $n = 220$, $p < 0.001$), of which the average speed was twice as high; 0.12 ± 0.02
400 m s^{-1} (manual tracking, $n = 220$) (Figure 9). Migration speeds of schools were low. The ascent of
401 the sprat schools in the afternoon (prior to dusk descent) and descent in the morning (subsequent
402 to dawn ascent) were generally carried out at a speed of ~ 0.005 m s^{-1} (approximate speed derived
403 from echograms, $n=101$) (Figure 9).

404

405 **4. DISCUSSION**

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

421 **4.1 DVM-Patterns**

422 *4.1.1 Potential relations to food*

423 A summary of the DVM patterns and behavioral modes displayed by the overwintering sprat at
424 night is schematically outlined in Figure 10, together with schematic distributions of potential prey.

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

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

447 4.1.2 Relations to light

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

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

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

473

474 *4.1.3 Dispersal and aggregations of schools*

475 The transition between the diurnal and nocturnal behavior of sprat involved dispersal- and
476 aggregation of schools. Because vision is generally crucial in the schooling of fish (Pavlov &
477 Kasumyan 2000), it largely occurs at day. Daytime schooling is also in accordance with the notion
478 that schooling is beneficial in terms of predator avoidance (Magurran 1990). Fréon et al. (1996)
479 suggested that dissolution of schools at dusk is slow and likely due to passive dispersion, while
480 fish actively swim together to form schools at dawn. Such patterns have also been suggested based
481 on acoustic data on DVM behavior of sprat and herring (Cardinale et al. 2003, Nilsson et al. 2003).
482 However, a passive dispersal of schools does not concur with the distinctive “dusk descent”
483 behavior detected in this study. The dissolution of schools in the afternoon indeed spanned a longer
484 time window than the formation of schools in the morning (average 30 min vs. 20 min), yet it
485 appeared that the sprat actively left the ascending schools. Such individuals immediately changed
486 swimming direction and descended with a speed of ~ 1 body length per second (~ 10 cm s⁻¹), being

487 four times higher than the apparent passive sinking rates documented in the rise and sink
488 swimming. This descent speed was furthermore significantly higher than the ascent speed (~ 6 cm
489 s^{-1}) during dawn ascent.

490

491 **4.2 Nocturnal distribution**

492 *4.2.1 Potential relation to size*

493 A nocturnal bimodal distribution is seemingly common for sprat in Bunnefjorden (Kaartvedt et al.
494 2009a, Solberg & Kaartvedt 2014). Even though individuals shifted between vertical strata
495 throughout night, the nocturnal trawling revealed a higher proportion of large individuals in deep
496 waters. Average lengths (8.8 and 10.9 cm) of shallow and deep sprat catches generally correspond
497 to late juvenile- and adult stages, respectively, as gonadal growth normally starts from the size of
498 ≥ 9.5 cm (Peck et al. 2012). Adult mesopelagic fish stay deeper than juveniles during overwintering
499 in Norwegian fjords, apparently displaying a more risk-averse behavior to increase survival and
500 their opportunity to spawn (Rosland & Giske 1994). Trawl catches revealed that gadoids were
501 common the current winter (Solberg et al. 2015). Although the gadoids largely distributed
502 vertically to - and were foraging on - the very abundant krill this particular winter, sprat also
503 occurred among the stomach contents (Solberg et al. 2015) and the gadoids did likely represent a
504 perceived predation risk by the sprat.

505

506 *4.2.2 Potential relation to temperature*

507 The bioenergetics-efficiency hypothesis predicts a selection of migration depth in accordance to
508 optimal temperatures for growth (Brett 1971), indicated in a variety of fish (Levy 1990b,
509 Bevelhimer & Adams 1993, Mehner et al. 2010). The optimal temperature for growth in Baltic
510 sprat ranges between ~ 10 - 20 C° (Peck et al. 2012). The highest temperature in Bunnefjorden was
511 ~ 9 C° at 25-55 m deep with slightly colder waters below (Figure 3) so that temperature cannot
512 explain the nocturnal accumulation of sprat at the hypoxic interface. On the other hand,
513 temperature may have determined the upper depth of the behavioral modes of dusk descent and
514 dawn rise. The deep group of sprat generally returned to deeper waters at ~ 20 m, a depth range
515 that largely corresponded with the presences of temperatures declining from > 8 C° to < 4 C° a
516 few meters above. Low temperatures are considered an essential factor for setting the upper limit
517 to the vertical distribution of sprat (Stepputtis et al. 2011), with sprat in the Baltic shown to avoid

518 temperatures below five degrees (Stepputtis 2006). Yet, a possible temperature restriction was in
519 any case not shared by all sprat. The shallow group – presumably juveniles - indeed traversed the
520 thermocline as observed in the acoustic records (Figure 4), and further suggested by nocturnal
521 catches of sprat in February. In the Baltic, adults are found to distribute deeper and warmer than
522 younger age classes during severe wintering conditions (Ojaveer & Kalejs 2010).

523

524 **4.3 Nocturnal behavior**

525 *4.3.1 Rise-and-sink swimming*

526 Sprat at the hypoxic interface performed rise and sink swimming, as also previously documented
527 for individual sprat in deeper waters (Kaartvedt et al. 2009a, Solberg et al. 2012). Sinking speeds
528 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
529 a year when oxygen conditions allowed deeper overwintering. This more than 30 % higher sinking
530 speed for sprat in deeper waters is in line with what we hypothesized. Rise-and-sink swimming
531 has been repeatedly documented for herring and sprat (Huse & Ona 1996, Kaartvedt et al. 2009a).
532 The general interpretation is that this swimming behavior is carried out to counteract for negative
533 buoyancy due to swimbladder compression at depth (Huse and Ona 1996, Nero et al. 2004). A
534 higher sinking rate in deep waters is expected since the physostome sprat will become less buoyant
535 with increasing pressure. The current results therefore support the hypothesis that rise-and-sink
536 swimming is a behavior related to negative buoyancy (Huse and Ona 1996).

537

538 *4.3.2 Hypoxic diving*

539 Concentrations of overwintering *Calanus* spp. inhabited the lower, severely hypoxic part of the
540 water column below the sprat. This relatively large-sized copepod is the preferred prey for sprat
541 (Paulsen 2008, Solberg et al. 2015) and prevailed among the stomach contents this winter (Solberg
542 et al. 2015). Zooplankton net tows were only taken at day, but overwintering *Calanus* does not
543 carry out DVM (e.g. Bagøien et al. 2001), also apparent from acoustic data this winter in
544 Bunnefjorden (c.f. Fig. 5 in Røstad & Kaartvedt 2013). The distribution of overwintering *Calanus*
545 in oxygen-depleted waters may have motivated individual excursions into these deep layers.
546 Taylor et al. (2007) studied swimming behavior of juvenile anchovies (*Anchoa* spp.) in settings
547 comparable to this study. They reported on brief movements into the hypoxic waters, and
548 suggested that the anchovies used this diving behavior for feeding. Such foraging strategy was also

549 indicated in juvenile mud minnows (*Umbra limi*) that contained large numbers of prey that only
550 occurred in oxygen depleted waters (Rahel & Nuntzman 1994). Correspondingly, the sprat may
551 have carried out dives to forage on the high numbers of *Calanus* spp., in accordance with the
552 acoustic records of fish apparently targeting echoes ascribed to *Calanus* spp. (Figure 7cd). The
553 highest *Calanus* abundance was located below 80 m (from Dec-Feb) which was deeper than what
554 sprat generally dived to (average maximum diving depth ~70 m). However, *Calanus* were
555 abundant also between 60-80 m as confirmed by the net tows, and the *Calanus* spp. population
556 moved progressively higher up in the water column in the course of the winter. The concentrations
557 from 60 to 80 m were more than double in February (~250 ind. m⁻³) than in December (~100 ind.
558 m⁻³), and a gradual upward shift was also documented acoustically (Figure 7cd, Røstad &
559 Kaartvedt 2013). The higher number of diving events detected in February might indeed relate to
560 this upward shift of potential prey.

561 Sprat normally detect prey visually, which likely does not apply during such night dives.
562 While the clupeid herring may shift to filter feeding at high prey concentrations (e.g. Gibson &
563 Ezzi 1992), sprat are generally considered to be particulate feeders (Bernreuther 2007, Brachvogel
564 et al. 2013). Also, filter feeding usually occurs at higher prey concentrations than recorded here
565 (Brachvogel et al. 2013). However, fish may locate their prey using the lateral-line system when
566 low light renders vision ineffective, also recorded among clupeids (Janssen et al. 1995).
567 Experimental studies have revealed that tactile foraging may involve a tail beat followed by a
568 glide, with all prey detected during the glide phase (Janssen 1997). This might be in accordance
569 with the intermediate swimming speed observed for hypoxic diving, being double the sinking rate
570 in rise-and-sink, and half that of the fish returning from the dive.

571 The dives were carried out in waters with oxygen contents as low as 0.45 mL O₂ L⁻¹. The
572 results suggest maximum exposure time of ~ 2 minutes for sprat at such oxygen concentrations (in
573 waters of ~ 8 °C). The limiting effect at such levels of hypoxia is further indicated by the significant
574 reduction in total diving time between dives from December and dives from January and February,
575 when oxygen levels had declined with only ~ 0.2 mL O₂ L⁻¹. Tactile feeding is less efficient than
576 prey search by sight (Sørnes & Aksnes 2004). Yet the lipid reserves *Calanus* spp. accumulate
577 during diapause (Heath et al. 2004, Svetlichny et al. 2006, Wilson et al. 2015), would make them
578 attractive prey organisms so that the energy bonus might have justified the short hypoxic
579 excursions.

580 **4.4 Conclusion**

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

589

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597

598

599 **FIGURE LEGENDS**

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

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

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

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

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

622 **Figure 5.** Timing of migration events relative to sunset (upper red line) and sunrise (lower red
623 line) during the period 08 Dec 2007-16 Apr 2008. The letters represent events depicted in Figure
624 1: **B**; initiation of dusk descent and **I**; end of dawn ascent (last individual appears in upper waters).
625 Light measurements corresponding to the timing of the migration events are indicated with black
626 lines. Local time is UTC + 1 h (December – March) and UTC + 2 h (April).

627

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

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

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

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

644 **Figure 10.** Schematic overview of the DVM- and nocturnal behavior of sprat. Sprat schools
645 initiated normal DVM ~ 1 hour prior to sunset. While some sprat migrated all the way to surface
646 waters, other individuals interrupted the ascent and returned to deep waters, (“*dusk descent*”).
647 Descending sprat accumulated near the interface of oxygen depleted waters (depicted in red) where
648 they continued with solitary “*rise and sink*” swimming. A “*surfacing behavior*” was dominant 1-
649 2 hours after sunset. One group of sprat occurred in surface waters while other specimen distributed
650 from below ~ 30 to ~ 65 m. Interactions between the surface and deep group occurred as the sprat
651 occasionally migrated between the two groups “*interchanges*”. Sprat close to the minimum
652 oxygen boarder occasionally dived into the highly oxygen depleted waters followed by an
653 immediate return to the interface (“*hypoxic diving*”). All sprat from the deep layer initiated an
654 upward migration ~ 1 h prior to sunrise (“*dawn ascent*”), with a subsequent return to deeper waters,
655 then while schooling. Abundance and distribution of krill, small copepods and overwintering
656 *Calanus* spp. are denoted in the figure. Occurrence of potential predators of sprat is not included,
657 but their distribution is shown in Figure 2 in Solberg et al. (2015).

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