



Sprat *Sprattus sprattus* can exploit low oxygen waters for overwintering

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ABSTRACT: Acoustic studies and sampling during 4 winters in a Norwegian fjord showed that the clupeid fish sprat *Sprattus sprattus* inhabited severely hypoxic waters. Their lower tolerable oxygen content was at ~7% O₂ saturation (~0.5 ml O₂ l⁻¹ at 7°C), and they occurred as deep as this limit allowed in the 150 m water column. Sprat in this hypoxic habitat were foraging on dormant copepods *Calanus* spp. in the daytime, or did not feed at all. Use of hull-mounted, submerged and bottom-mounted echosounders allowed observations of *in situ* swimming behavior of individual sprat, revealing that they were continuously moving up and down. This behavior can likely be ascribed to negative buoyancy, compensated for by repetitive upward swimming. A large portion of the sprat population occurred in deep water during both day and night, yet the sprat did undertake both synchronous and asynchronous nocturnal vertical migrations. Some individuals swam all the way to the surface, apparently to refill their swimbladder, before immediately diving. Gadoid predators seemed to avoid waters with oxygen contents below ~15 to 20% O₂ saturation so that few predators occurred in the deep, low-oxygen sprat habitat. However, gadoids were foraging on the vertically migrating sprat at night. We hypothesize that overwintering sprat may take advantage of low oxygen waters due to higher tolerance for hypoxia than their predators.

KEY WORDS: Sprat · Hypoxia · Overwintering · Predators · Feeding

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INTRODUCTION

Hypoxic and anoxic marine environments have existed through geological time, but their occurrences are increasing, and oxygen budgets of many coastal ecosystems are now adversely affected by eutrophication (Diaz 2000). Hypoxia has direct influence on the fauna through exclusion of non-tolerant species, and many species disappear when oxygen values approach ~2 ml l⁻¹ (Diaz 2000). There are also more subtle effects generated by hypoxia, such as on the interaction between predators and prey with different oxygen tolerances (e.g. Breitbart et al. 1997, Nestlerode & Diaz 1998, Keister et al. 2000, Robb & Abrahams 2003). Upwelling regions and other coastal ecosystems sustain large fish stocks, and these regions are where hypoxic waters are most likely to occur (Helly & Levin 2004). To understand and manage marine ecosystems it is necessary to unveil the effect of hypoxia on individual species as well as predator–prey interactions.

Oxygen concentrations often decrease with depth, and hypoxia in deeper layers can strongly affect the vertical distribution of fish species (Domenici et al. 2007). Hypoxia may limit the inhabitable water column, enhancing vertical overlap between predator and prey with resulting higher prey mortality (e.g. Keister et al. 2000). On the other hand, hypoxic waters may provide refuges for prey that are more tolerant than their predators. In the absence of such hypoxic refuges, the predators can reduce or completely wipe out the prey population (Horppila et al. 2000, Klumb et al. 2004). Therefore, whether hypoxia shifts the balance in favor of the predator or the prey depends on their relative tolerance to hypoxia (Domenici et al. 2007).

Robb & Abrahams (2003) argued that within and between species, smaller fish were the most tolerant of hypoxic environments since their gill areas and red blood cells are larger relative to body volume. Hypoxic environments therefore have the potential of serving

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as a refuge from the bigger predators (Robb & Abrahams 2003). However, Nilsson & Östlund-Nilsson (2008) concluded that body size, *per se*, has little or no impact on the ability to take up oxygen during hypoxic conditions, and that natural selection is more important in determining fish hypoxia tolerance than scaling of physiological functions.

Gadoids and clupeids are the major fish resources of the North Atlantic, with gadoids being primary predators on clupeids. Clupeids often occur in dense schools and, expectedly, are adapted to hypoxia, which may occur in the center of the schools (e.g. Domenici et al. 2002, Herbert & Steffensen 2006). This might suggest higher tolerance to hypoxia than their gadoid predators, which may avoid low-oxygen waters (e.g. Baden et al. 1990). Nevertheless, there are reports on cod occurring in less oxygenated waters than their clupeid prey (in the hyposaline waters of the Baltic; Neuenfeldt 2002, Neuenfeldt & Beyer 2006). Therefore, how oxygen contents affect the predator–prey relationship between gadoids and clupeids is not established.

The clupeid sprat *Sprattus sprattus* is a widely distributed and commercially exploited fish in coastal environments, including habitats characterized by hypoxia in deep waters like some fjords and the Baltic and Black Seas (Daskalov 2003, Harvey et al. 2003, Casini et al. 2006). A clupeid relative, the herring *Clupea harengus*, may inhabit low-oxygen water during winter (Lie et al. 1978, Dommasnes et al. 1994), but to our knowledge, no assessment of the overwintering strategies of sprat has been published. In the present study, we evaluate the distribution and behavior of sprat and their gadoid predators in a hypoxic Norwegian fjord during 4 winters characterized by different oxygen conditions. We establish the vertical distributions of overwintering sprat and their potential predators in relation to the vertical profile of water oxygen content and other environmental parameters. We also assess the *in situ* behavior of individual sprat and establish the feeding conditions and their feeding behavior in the overwintering habitat.

MATERIALS AND METHODS

The present study took place in the ~150 m deep Bunnefjorden, which historically has sustained fisheries for sprat. Bunnefjorden constitutes the innermost part of Oslofjorden, Norway (Fig. 1), and is characterized by an oxygen deficit in the deep water. This is due to very limited water exchange of the basin water, and the consequent natural tendency for hypoxia has been enhanced by anthropogenic influence. Oslofjorden is connected to outer waters through a narrow sound with a 19 m deep sill (inside Drøbak; Fig. 1), with an

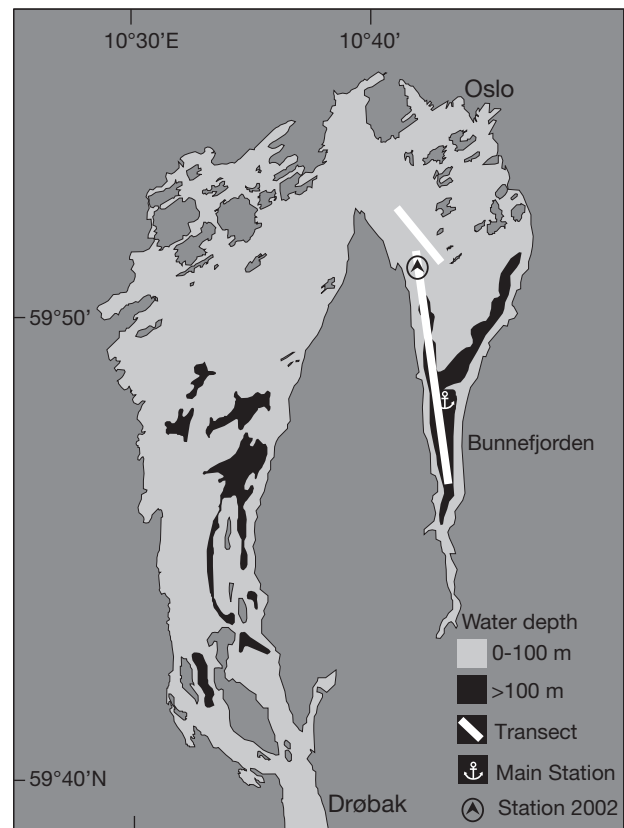


Fig. 1. Study sites. The anchor depicts the main sampling and CTD station in the deepest part of Bunnefjorden, and the arrowhead the deployment location of the bottom-mounted, upward-facing transducer (2002). Lines depict tracks of acoustic transects and trawling (short line: 1995; long line: 2002, 2004, 2005)

additional ~50 m sill at the inlet to Bunnefjorden. The parallel orientation of this branch with the main fjord axis further hampers exchange from these backwaters. Still, the deep water is normally renewed every ~3 yr, resulting in periods with oxygenated waters extending to the bottom (Baalsrud & Magnusson 2002).

The present study was designed to assess the distribution and *in situ* behavior of overwintering sprat, as well as their physical/chemical environment, potential food sources and predators. The approach consisted of a combination of ship-mounted and submerged echosounders and sampling. We provide results from 4 winters (1995, 2002, 2004 and 2005), with the major part of the study carried out in January and February 2004 and 2005.

Salinity and temperature were measured by a CTD equipped with 12 Niskin water bottles, from which samples for oxygen content were obtained. Dissolved oxygen was quantified using the standard Winkler procedure. Additional data on hydrography and oxygen were made available by the Norwegian Institute

for Water Research (NIVA). Mesozooplankton (potential prey) was sampled by a WP2 plankton net (200 μm mesh size) at 4 depth intervals day and night (bottom to 85/80 m, 85/80 to 40 m, 40 to 20 m and 20 to 0 m). Samples were fixed in 4% formalin for later analysis and enumeration.

To identify acoustic targets and get samples for size distributions and stomach contents, pelagic trawling was conducted day and night using a 100 m² trawl towed at ~2 knots. Mesh size near the opening was 20 cm, declining to 1 cm at the rear end. In total, 22 pelagic tows were performed (see Tables 1 & 2), with trawling depth selected from acoustic structures. Sampling depth was monitored during trawling using a Scanmar trawl sensor. In winter 2002, when oxygenated waters extended all the way to the bottom, we also applied a bottom trawl (1 tow).

All larger fish (piscivores) from the trawl catches were enumerated, weighed and measured for length. Stomachs were frozen for later identification of contents. The total volume of the remaining catch (sprat) was measured, and subsamples of 30 individuals were frozen for later length measurements and stomach analyses. Fishing for piscivores was also performed by lure from the ship to provide a qualitative check on stomach contents for which cod-end feeding in the trawl could be excluded.

Acoustic transects to assess fish distribution were made both day and night. The ship was surveying at 8 knots, continuously logging acoustic data at 38 kHz (SIMRAD EK500 echosounder, 12° beam width) and 120 kHz (data not shown). For winter 1995, an echogram (night) was provided by the Institute of Marine Research, Flødevigen. This echogram is included since it documents the vertical distribution of fish in a winter when hypoxic conditions occurred particularly shallow in the water column.

For more detailed studies of vertical distributions and swimming behavior, acoustic records were made with the ship (RV 'Trygve Braarud', 22 m) kept stationary. This was done to follow the movements of individual fish through a non-moving acoustic beam. The ship was moored with 3 anchors, which assured that registrations were made from a fixed position in the calm fjord environment. The major part of the fjord was ice-free during the investigations, but registrations one afternoon were made with the ship kept stationary at the ice edge in the inner part of the fjord. Stationary research vessels function as fish aggregation devices (FADs; Røstad et al. 2006), but we do not believe that the enhanced concentrations of fish beneath the moored vessel affect the conclusions presented here.

The ship-mounted echosounders were used in combination with submerged 120 kHz and 38 kHz (the latter only in 2005) SIMRAD EK 60 echosounders, built

into a pressure case and using 7° beam width, pressure-proof transducers. The system was powered from the ship through 300 m of cable, which also conducted digital data back to a PC on board. This submerged equipment was deployed to get high resolution information on individual fish in the deeper part of the water column. We also applied a bottom-mounted, upward-facing transducer in 2002 (38 kHz, 7° beam width), which enabled records from near-surface waters. This upward-facing transducer was connected to the EK500 onboard the RV 'Trygve Braarud' by 300 m of cable. Studies of individual fish swimming behavior were made by observing echo traces on echograms (plotted in Matlab) and by using acoustic target tracking (TT). By applying software allocating subsequent echoes to the same target (Sonar5-pro, Balk & Lindem 2002), TT provides data on individual size (target strength [TS]) and swimming behavior. Raw acoustic data were stored for later analysis.

The large trawl aperture and lack of a closing device prevented sampling with sufficient resolution to unveil the relative vertical distribution of sprat and their predators in the sharp oxycline of the fjord. Acoustic analyses were therefore made to assess the fine-scale vertical distribution of potential predators in relation to the sprat. We first performed TT on data from the hull-mounted transducer to establish the distribution of individuals with an average TS > -38 dB; this value corresponded to that of the prevailing predators and was ~10 dB stronger than the peak for the sprat TS-distribution (Røstad 2006). However, fish in deep water were too densely distributed to be resolved individually at range. Trawl catches suggested that this backscatter could be ascribed to sprat. This assumption was tested using the submerged echosounders which could resolve both the strong targets (representing larger fish) and smaller fish (sprat) individually even in dense, deep concentrations. Targets with TS between -60 and -40 dB were allocated to sprat, and targets > -38 dB to predatory gadoids.

The selection criteria for the tracking were a minimum of 10 echoes, accepting a maximum of 1 missing ping. We did not account for the expanding acoustic beam with range in this analysis, which could lead to an overestimation of predators by depth in data from the hull-mounted transducer. This would also be the case if multiple targets of sprat were accepted as predators. These biases are not problematic as they would make our conclusions (on reduced numbers of large fish in deep water; see 'Results') conservative. On the other hand, if high densities of sprat in deep waters swamps echo detection of predators, their abundance becomes underestimated. This would not relate to the high resolution data from the submerged transducers. Additionally, the expanding acoustic beam would imply an

increased registration volume by depth, but this would relate to both predators and prey, and would not prevent reliable results on their relative vertical distributions.

RESULTS

Fish vertical distributions in relation to water column properties

The deep water of Bunnefjorden was devoid of backscatter (fish) in 3 of the 4 winters (Fig. 2). An acoustic scattering layer (SL) that can be ascribed to sprat (see below) was then situated in a steep oxycline in ~mid-water day and night. The depth of the lower edge of the SL varied between winters, in concert with the varying depth for oxygen concentrations of ~7% ($0.5 \text{ ml O}_2 \text{ l}^{-1}$ at 7°C ; Fig. 2). The highest concentrations of sprat occurred between 7 and 15% O_2 . The oxycline was steeper in 2004 than in 2005, resulting in a smaller depth interval with these oxygen concentrations in 2004 (7 to 10 m compared to 15 m). This coincided with a more compressed vertical distribution of sprat at night (Fig. 2). A strong SL (sprat) occurred along the bottom in winter 2002, when minimum oxygen values in the fjord were ~22% (Fig. 2). These vertical distributions did not correlate with profiles of salinities and temperatures. The hydrography was largely homogeneous below 60 to 70 m, with temperatures and salinities of 7 to 8°C and 32 to 33, respectively, and modest variations between winters.

Catches in the deep SL oxycline were dominated by sprat day and night, exceeding other components by orders of magnitude, both by numbers and volume (Table 1). Catches above this SL were low, apart from reasonably high catches of sprat in upper waters at night in 2004. Gadoids, mainly whiting *Merlangius merlangus* and cod *Gadus morhua*, were captured at most trawl depths (Table 2). The bottom trawling in 2002 resulted in large catches of sprat and no gadoids (Tables 1 & 2).

The acoustic analysis (nighttime) showed that the larger fish (predators) generally stayed shallower than the concentration of smaller fish (sprat) that accumulated in the oxycline, the gadoids largely being confined to waters with oxygen contents above ~15 to 20% (Figs. 3 & 4). The volume backscatter (S_v) below the individually resolved fish (Fig. 3) can largely be ascribed to sprat, as supported from data obtained by the submerged echosounder in 2005, where acoustic data are sorted according to TS (i.e. size classes). The vertical separation of the predators from the lower part of the sprat-SL was largest in 2005, when the oxycline was less sharp than the previous year.

Behavior of sprat

The sprat were schooling during the daytime, apart from the fish near-bottom in 2002. Schools dispersed in darkness, and the sprat-SL spread out vertically, including a slight deepening of its lower edge (Figs. 2 & 5). Sprat ascended in the afternoon, and a part of the population apparently carried out normal diel migrations, as suggested by acoustic records and nocturnal catches in upper layers. However, many individuals left the upwardly migrating assemblage of fish upon initiation of or early in the afternoon ascent. The downward pulse of individuals (descending at $\sim 10 \text{ cm s}^{-1}$) next formed the deep nocturnal SL (Fig. 5). Sprat in this SL were continuously swimming up and down, yet generally remaining at the same depth over time (Fig. 5). Descent rates in this setting were $\sim 3 \text{ cm s}^{-1}$, which was interpreted as sinking, followed by compensatory ascent. Additionally, asynchronous vertical migrations were recorded, and echo traces of individual fish could be followed as they migrated between the lower and upper part of the water column and vice versa (Fig. 6). The upward-facing transducer (2002) unveiled individuals that were swimming all the way to the surface and immediately diving thereafter (Fig. 7).

Food and feeding

Copepods dominated the net samples, and all taxa were more abundant in 2004 than in 2005 (Fig. 8). *Oithona* was the prevailing copepod genus. It was most abundant in the upper 20 m, which also was the case for most calanoid copepods (Fig. 8). *Calanus* spp. revealed an opposite trend in their vertical distribution, with the highest concentrations in the deepest depth interval. The population of overwintering *Calanus* spp. was by far dominated by copepod stage V. There were no differences in vertical distribution between day and night.

Sprat had little, and mainly unidentifiable, stomach contents in 2004 (Table 1). *Oithona* spp. was the most common among the few identified prey organisms, and a few *Temora longicornis* were also recorded. Feeding was frequent in 2005 (Table 1), when only deep-living prey occurred among the stomach contents. Foraging took place during the day and *Calanus* spp. occurred in most of the stomachs from sprat collected in the daytime (Table 1). Some *Oncea* spp. were also recorded among the stomach contents, while other prey species barely occurred. Food was well digested at night, some *Calanus* spp. being the only recognizable prey.

Sprat was the main food item of the gadoids (Table 2; also derived from fishing with lures). Whiting also for-

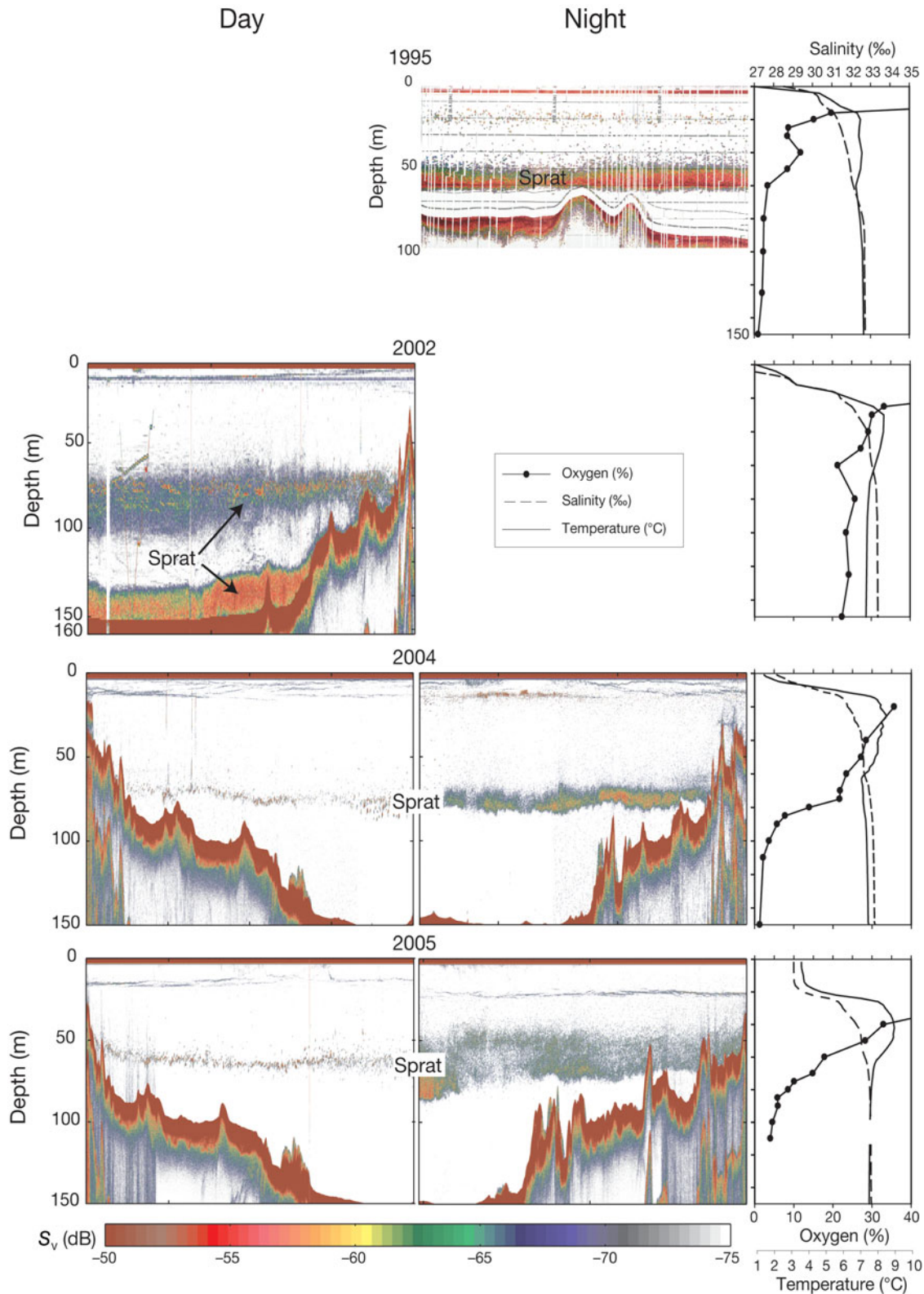


Fig. 2. Acoustic transects (38 kHz) and vertical profiles of hydrography and oxygen in Bunnefjorden during 4 winters. Locations of transects and CTD stations are depicted in Fig 1. The northernmost transect is from 1995, and is from a shallower station than the oxygen measurements. Color scale refers to acoustic backscatter (S_v ; dB). The acoustic results in 2002 include records during stop at a sampling station

Table 1. Trawl catches and sprat stomach contents (length and stomach contents for 30 individuals sample⁻¹). Blanks: no data

Date (d.mo.yr)	Time	Depth (m)	Sprat (l)	Sprat mean length (cm)	Stomachs containing prey (%)	Mean no. <i>Calanus</i> spp.	Mean no. other copepods	% containing undigested contents
20.02.02	Day	40–50	2	7.6 ± 0.6				
		80–90	37	7.6 ± 0.7				
		130–140	140	9.5 ± 1.8				
		Bottom trawl (90)	>1000	11.3 ± 1.9				
14.01.04	Day	70–80	0.5					
		75–90	65	8.3 ± 1.4	23	0	0.4	7
14.01.04	Night	20–26	1	8.2 ± 1.6	30	0	0.2	3
		75–85	16	8.2 ± 1.0	41	0	0.2	13
28.01.04	Day	20–26	0.1					
		40–50	0					
		60–70	13	8.0 ± 1.0	37	0	0.5	7
		70–80	220	9.8 ± 1.4	0	0	0	0
28.01.04	Night	15–21	20	10.8 ± 2.0	30	0	0	0
		40–50	4	10.6 ± 1.7	20	0.2	0.1	3
		75–85	70	9.0 ± 1.6	7	0	0.1	3
08.02.05	Day	60–80	40	7.9 ± 1.0	57	1.4	0.1	10
10.02.05	Day	20–27	0					
		31–46	0					
		55–68	1	9.3 ± 1.2	93	4.7	0.6	60
		72–85	60	9.5 ± 1.3	93	5.6	0	37
10.02.05	Night	27–21	0.1	10.1 ± 1.9				
		65–30	6	8.9 ± 1.3	53	0	0	0
		85–65	50	11.3 ± 1.8	47	0.3	0	0

Table 2. Trawl catches and stomach contents of gadoids. Blanks: no data

Date (d.mo.yr)	Time	Depth (m)	Whiting				Other gadoids								
			No.	Mean length (cm)	Stomachs containing prey (%)	Mean no. prey				No.	Stomachs containing prey (%)	Mean no. prey			
							Sprat	Gobies	Krill	Shrimp					
20.02.02	Day	40–50	0								0				
		80–90	4								3				
		130–140	0								0				
		Bottom trawl (90)													
14.01.04	Day	70–80	11	32.3 ± 4.8	60	0.73	0	0.27	0	1	100	1	1		
		75–90	16	30.7 ± 5.0	77	1.46	0	0.38	0	0					
14.01.04	Night	20–26	4	27.8 ± 5.3	50	0.5	0	0	0	0					
		75–85	5	36.1 ± 3.3	75	1	0	0	0	0					
28.01.04	Day	20–26	0							0					
		40–50	0							0					
		60–70	1	39.5	100	2	0	0	0	0					
		70–80	2	27.3	0	0	0	0	0	1	100	4		3	
28.01.04	Night	15–21	8	31.6 ± 3.6	64	1.25	0	0.38	0	8	100	2.5	0.88	0.38	
		40–50	8	33.4 ± 3.5	75	1	0	0	0	1	100	3	0	0	
		75–85	9	35.1 ± 3.2	89	1.44	0	0.22	0.11	3	100	2.66	0	0	
08.02.05	Day	60–80	13	29.5 ± 4.2	42	0.33	0.17	0.17	0	0					
10.02.05	Day	20–27	0							0					
		31–46	0							0					
		55–68	22	33.0 ± 4.1	45	0.65	0.1	0	0	0					
		72–85	1							0					
10.02.05	Night	27–21	13	32.7 ± 5.2	50	0.33	0	0.08	0	0					
		65–30	30	31.1 ± 5.1	68	0.76	0	0	0.12	1					
		85–65	8	32.4 ± 4.5	72	0.86	0	0	0.14	1					

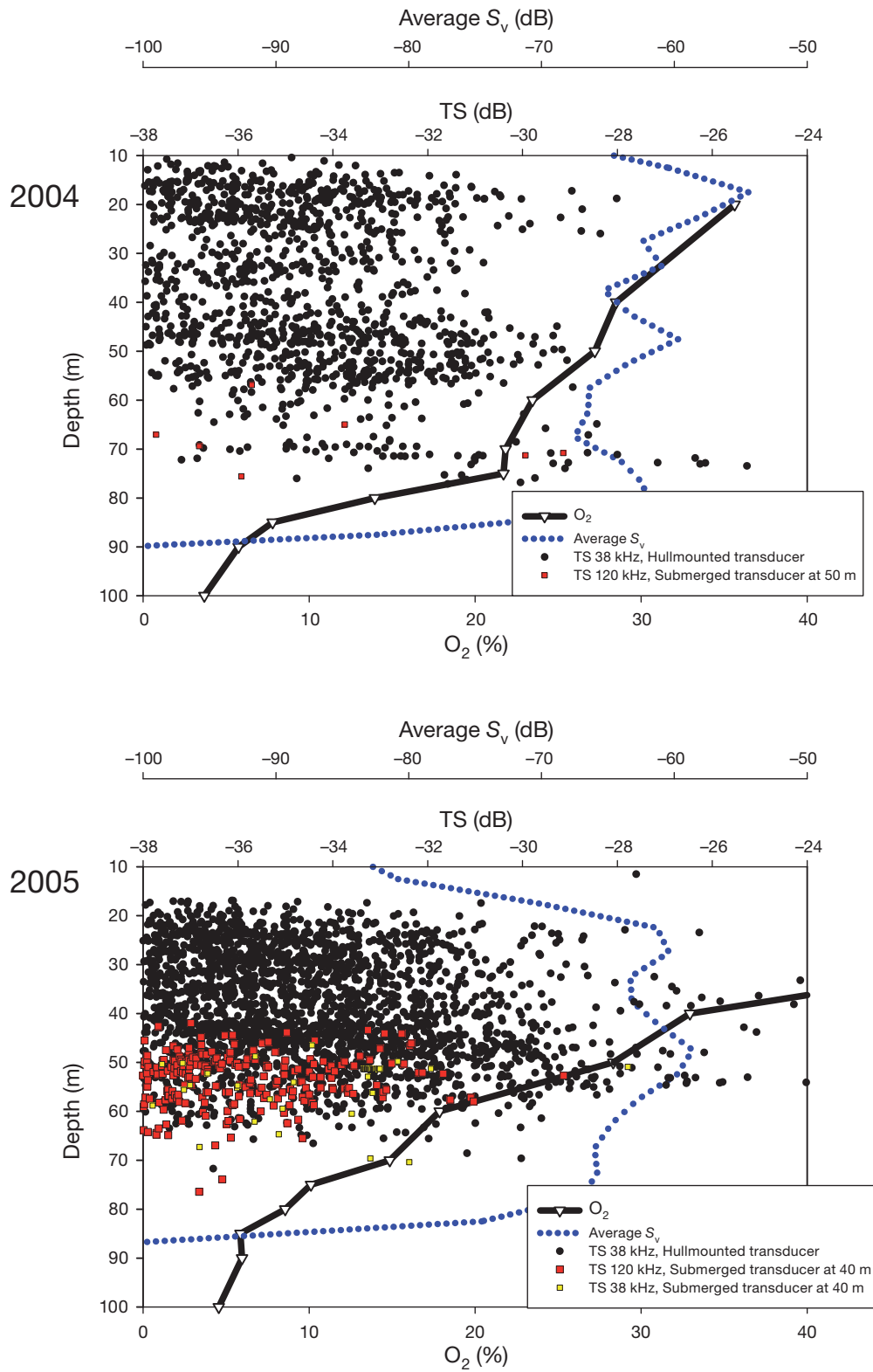


Fig. 3. Vertical distributions of individual large fish (target strength [TS] > -38 dB; predators) and total acoustic backscatter (S_v , a proxy for total fish biomass) on 14 January 2004 and 09 February 2005. Each dot represents the depth of a single tracked fish (min. 10 ping) and its average TS. Registration periods for single fish detections were 4.5 h in 2004 and ~15 h in 2005 (except with the submerged 38 kHz echosounder, 1.5 h). The oxygen profile is superimposed on the acoustic representation of individual fish and fish biomass

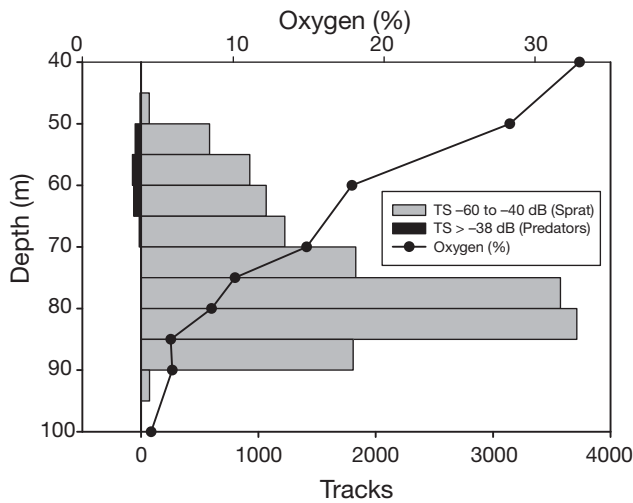


Fig. 4. Vertical distribution of individual fish targets (2005) as derived from the 120 kHz echsounder, submerged at 40 m. Results are from tracking of targets >−38 dB (interpreted as predators) and <−40 dB (interpreted as sprat). The oxygen profile is superimposed

aged on krill, and some well-digested benthic prey were recorded among stomach contents of cod collected at night (2004).

DISCUSSION

Distribution and behavior of sprat

Sprat accumulated in hypoxic waters. The lower tolerable level seemed to be at ~7% saturation ($0.5 \text{ ml O}_2 \text{ l}^{-1}$ at ~7°C), which is below previous reports from hypoxic habitats of clupeids (Dommasnes et al. 1994, Domenici et al. 2002, Neuenfeldt & Beyer 2006). The average oxygen concentrations encountered by an individual fish was somewhat higher due to vertical relocations within the steep oxycline and excursions into upper waters at night might involve periodic relief from the most severe oxygen stress. Spicer et al. (1999) showed that the krill *Meganyctiphanes norvegica* inhabiting low oxygen water by day would die if

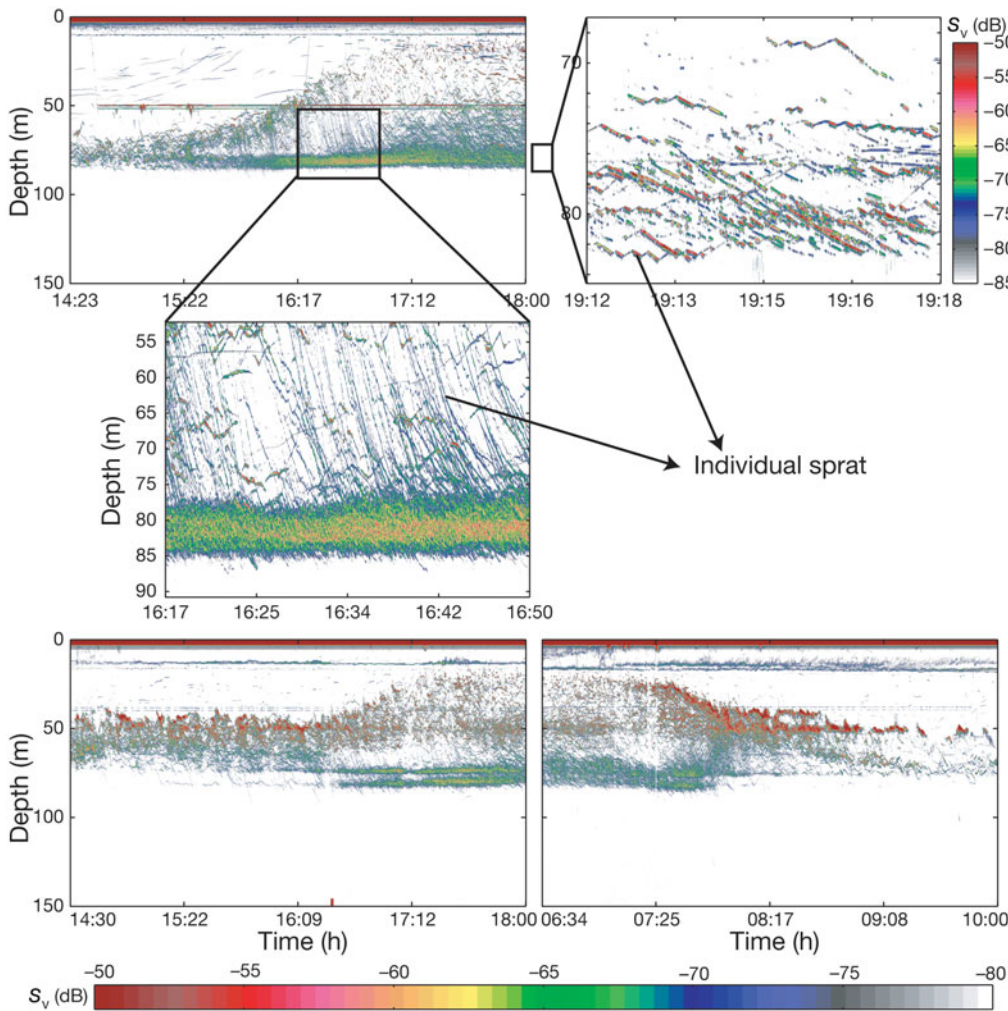


Fig. 5. Diel vertical migration and individual sprat behavior recorded with the vessel kept stationary on 14 January 2004 (upper) and 9–10 February 2005 (lower). In both years, the lower edge of the scattering layer is at ~7% oxygen saturation, the more severely hypoxic water below being devoid of acoustic backscatter. Records are from a hull-mounted 38 kHz transducer, except for the upper right panel showing individual fish in the deep scattering layer, which are from a submerged 120 kHz echosounder. Individual sinking fish appear as oblique downward lines (many subsequent echoes are received from each descending fish over time); ascending individuals appear as oblique rising lines. The submerged echosounder is seen at 50 m in 2004 and at 40 m in 2005

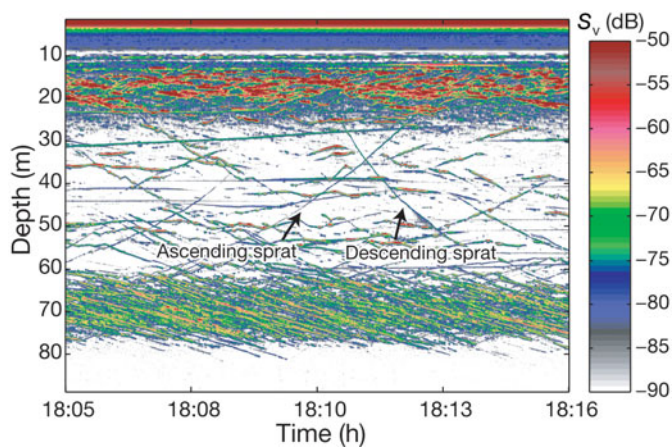


Fig. 6. Acoustic registrations showing asynchronous diel vertical migration. Individual fish appear as individual lines. Interchange of individual fish between the lower and upper layers is documented both for ascending and descending echo traces ascribed to sprat. The echogram is from 28 January 2004 (night)

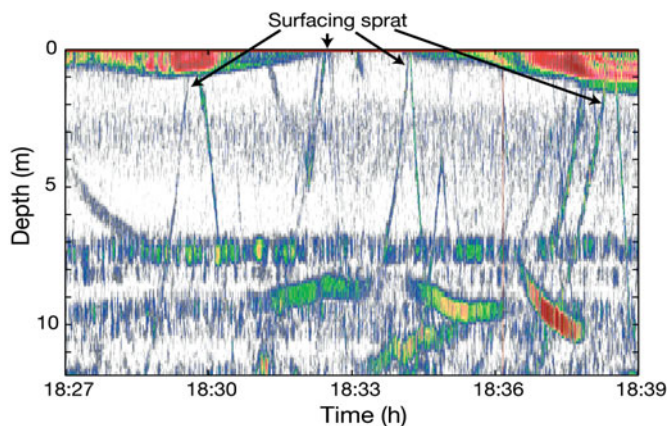


Fig. 7. Fish ascending to the surface. Individual fish appear as individual lines. Echo traces are ascribed to sprat that rise all the way to the surface before immediately descending. The echogram is from a bottom-mounted, upward-facing 38 kHz transducer on 19 February 2002 (night)

prevented from carrying out nocturnal migrations to upper, more oxygenated layers.

There was a deepening of the lower edge of the sprat distribution when schools dispersed in darkness, i.e. non-schooling fish occurred in the least oxygenated waters. Fish are able to tolerate lower oxygen levels individually as respiratory distress in hypoxic waters may be more severe in schooling fish; for example, schools of herring break up at low oxygen values (Domenici et al. 2000, 2002).

Water temperature had no explanatory power for the stratified vertical distribution of sprat in the oxycline. Below ca. 50 m, temperatures were fairly homogenous, without gradients associated with the sprat-SL. How-

ever, low oxygen can better be tolerated in low temperatures (e.g. Wood 1995), so the actual temperature would affect the absolute oxygen level the sprat could tolerate.

Low activity helps tolerate hypoxia, and fish occurring in hypoxic waters often reduce their swimming to lower metabolic demands (e.g. Herbert & Steffensen 2005, Domenici et al. 2007). Yet swimming seemed to be necessary for sprat to keep afloat in their overwintering habitat. We explain the continuous descent/ascent cycle as sinking due to negative buoyancy, followed by compensatory ascent. Our findings on sprat parallel results by Huse & Ona (1996) on non-feeding, overwintering herring: the negatively buoyant herring appeared to adopt a rise and glide swimming strategy. Such swimming behavior is considered to be energetically favorable (Huse & Ona 1996), thus reducing oxygen consumption. Nevertheless, with an average sinking velocity of 3 cm s^{-1} , time spent sinking and ascending apparently being about 50% each (Røstad 2006), a sprat would ascend 1300 m each day just to stay at the same depth.

Buoyancy regulation in most teleosts is accomplished by swimbladder volume regulation (Horn 1975). The physostome swimbladder of clupeids lacks a gas gland and apparently has to be filled through air gulping at the surface (Blaxter & Batty 1984). The swimbladder compresses and expands with ambient pressure according to Boyle's law. At a depth of 80 m, the swimbladder volume would be only one-ninth that at the surface, strongly reducing its contribution to buoyancy. Accordingly, the swimbladder seems to play a rather small part in buoyancy control among clupeids, fat content often being more important (Blaxter & Batty 1984).

The records of sprat swimming all the way to the surface at night and immediately returning to deeper water suggest they refilled their swimbladder. Besides buoyancy purposes (which may be limited), this points at the possibility that the swimbladder functions as a scuba tank, allowing them to spend an extended time in hypoxic water (G. E. Nilsson pers. comm.). The oxygen level in the swimbladder of herring *Clupea harengus* is generally much below atmospheric levels at the surface, which can only be explained by consumption of the oxygen in the bladder (Blaxter & Batty 1984). Love et al. (2004) reported on mesopelagic fish which migrated into anoxic waters at day, where they survived by use of oxygen in the swimbladder. The cephalopod *Nautilus* utilizes oxygen in its gas-filled shell to extend the periods it can escape predators in hypoxic water layers in tropical oceans (Boutillier et al. 1996). However, to what extent sprat use oxygen stored in its air-filled swimbladder for respiration remains to be examined.

Feeding of sprat

The feeding of sprat varied between winters and apparently was not related to availability of prey. Copepods were most abundant in 2004, when the

majority of sprat had empty stomachs. Feeding was common the subsequent winter, when abundance of prey was lower. The primary prey, overwintering *Calanus* spp., were moderately abundant compared to results from previous studies of overwintering *Calanus*

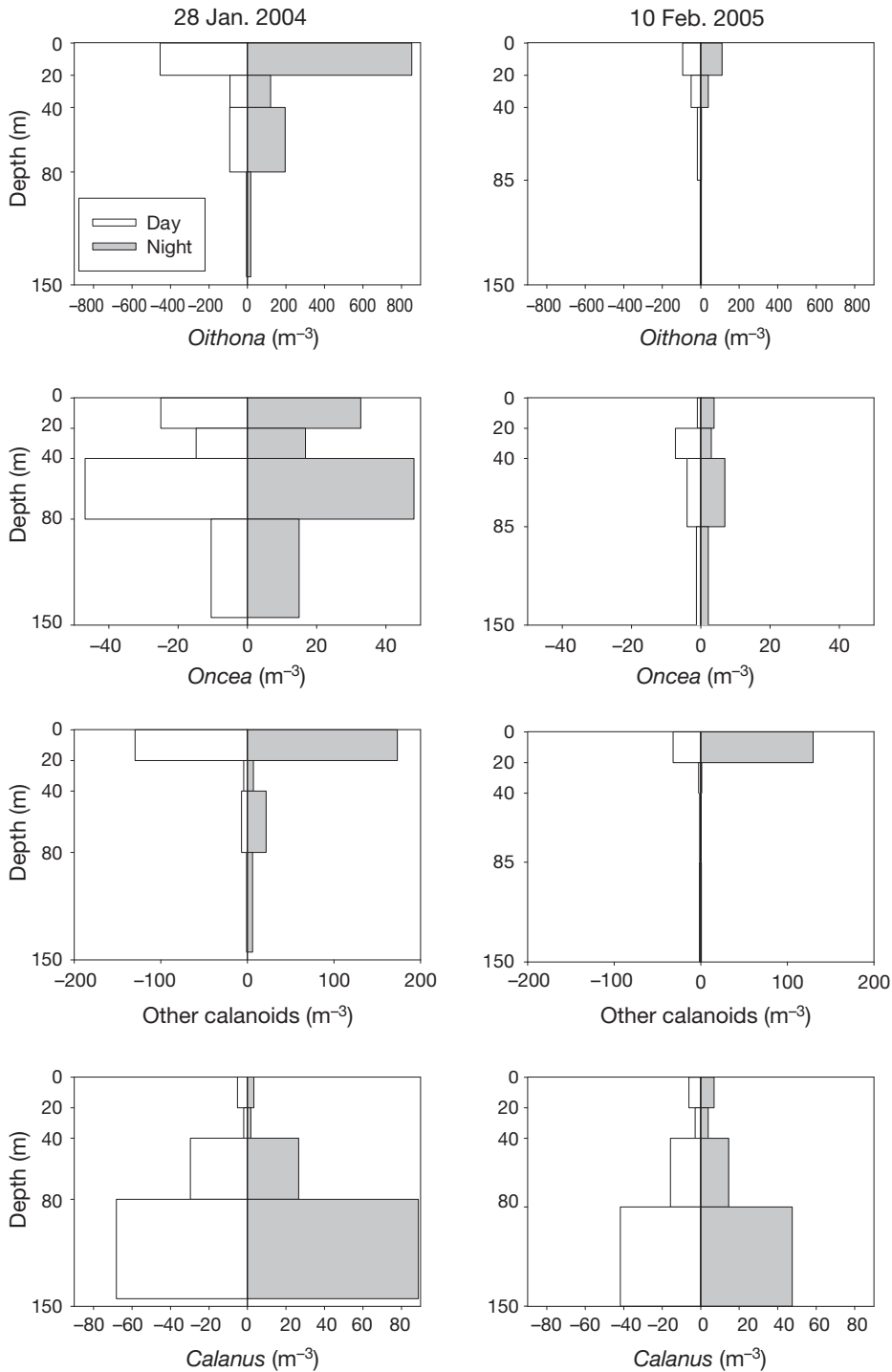


Fig. 8. Vertical distribution of copepods on 28 January 2004 and 10 February 2005 (day and night). Note different scales on x-axes

spp. in the Oslofjord and other fjord locations (Bagøien et al. 2000, 2001), but dormant *Calanus* spp. may occur in dense microlayers just above oxygen-depleted waters (Osgood & Checkley 1997).

The sprat in the oxycline were feeding on *Calanus* spp. in deep water during the day. The transient and short vertical migrations in the evening of individuals that next formed the deep nocturnal SL might have extended the time and water volume for feeding at light conditions, representing antipredation windows (cf. Clark & Levy 1988), before swimming back to deep waters. These fish also carried out subsequent asynchronous nocturnal vertical migrations. Asynchronous vertical migrations are normally explained in terms of the hunger satiation hypothesis, i.e. organisms leave the upper layers once fed (see Pearre 2003 for a review). However, this may not apply in our case, since foraging of sprat constituting the SL was basically restricted to deep-living copepods during the day. These migrations possibly rather relate to refilling of the swimbladder or for repaying oxygen debts.

The population apparently also contained a component carrying out normal nocturnal vertical migrations. We do not have sufficient data to distinguish these fish from those in deep water or to establish to what extent these individuals were foraging in upper layers at night, but some shallow-living copepods were identified among sprat stomach contents. Different parts of a population may make different choices due to factors such as age (Giske & Aksnes 1992), stored resources (Hays et al. 2001), hunger (Pearre 2003) or parasites (Barber et al. 2000), or because the population splits into risk-seeking and risk-averse individuals (Wolf et al. 2007).

The scarce feeding by sprat in the fjord, particularly when copepod abundance was highest (and the oxycline steepest), suggests that the overwintering habitat was not selected based on feeding conditions. Digestion requires oxygen (e.g. Reinhardt 2002), and fish may reduce foraging when oxygen concentrations become low (Jordan & Steffensen 2007), as in the steep oxycline recorded in 2004. So life in hypoxic water has its costs, but for the sprat in Bunnefjorden, some benefits evidently also exceed the costs. We suggest that predator avoidance is a major benefit to sprat overwintering in hypoxic waters.

Distribution and behavior of predators

Predatory fish, primarily whiting, were located shallower than most sprat, occurring in waters with oxygen concentrations above ~15 to 20% O₂ saturation. This is in accord with tolerable oxygen contents reported for gadoids from previous field studies (Petersen & Pihl

1995, Herbert & Steffensen 2005), as well as from experimental data (Schurmann & Steffensen 1997, Plante et al. 1998, Herbert & Steffensen 2005). Plante et al. (1998) showed that cod can make short incursions in waters as hypoxic as 15% O₂ saturation with good chances of survival. While a few larger fish dived into such hypoxic waters in Bunnefjorden, sprat were primarily captured during their migrations to upper waters at night, and was then the primary prey for whiting and cod. This was evident from stomach contents analysis of both gadoids captured in trawls and fish captured by lure from the ship, which had freshly eaten sprat in their stomachs.

A few of the predators (cod) had remains of benthic prey in their stomachs. Benthic prey could not have been collected at the study site due to the nearly anoxic bottom waters. This suggests that some predators performed horizontal, diel migrations, feeding along the shallower shore of the fjord at day and migrating into deep waters to prey on vertically migrating sprat at night.

CONCLUSIONS

The present study has shown that sprat tolerate severely hypoxic waters and a hypoxic fjord-basin represents a suitable overwintering habitat. Negatively buoyant sprat adopted an energetically favorable rise and glide swimming behavior, thus reducing oxygen consumption in the hypoxic habitat. Dormant copepods provided a food resource in deep water, but the feeding of sprat was unrelated to copepod abundance. Digestion requires oxygen, and varying hypoxic conditions rather than availability of prey may explain the variation in feeding. The population of sprat attracts gadoid predators, which are less tolerant to hypoxia and hence stay shallower in the water column. We therefore hypothesize that the sprat can exploit hypoxic waters as a predator refuge. However, the sprat in the present study undertook both synchronous and asynchronous nocturnal vertical migrations, possibly to alleviate oxygen debt, refill their swimbladder or forage. Vertically migrating sprat to some extent became vulnerable to predators, even though they ascended in the shelter of darkness. This scenario suggests that a hypoxic water column facilitates co-occurrence of these prey and predator populations. The ability of sprat to tolerate—and potentially exploit—low oxygen waters may be crucial for its continued success in coastal habitats exposed to both natural and anthropogenic hypoxia.

Acknowledgements. This study was funded by the Research Council of Norway.

LITERATURE CITED

- Baalsrud K, Magnusson J (2002) Indre Oslofjord: Natur og miljø. Fagrådet for vann og avløpsteknisk samarbeid i indre Oslofjord, Oslo
- Baden SP, Loo LO, Phil L, Rosenberg R (1990) Effects of eutrophication on the benthic communities including fish: Swedish west coast. *Ambio* 19:113–122
- Bagøien E, Kaartvedt S, Øveraas S (2000) Seasonal vertical migration of *Calanus* spp. in Oslofjorden. *Sarsia* 85: 299–311
- Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. *Limnol Oceanogr* 46:1494–1510
- Balk H, Lindem T (2002) Sonar4 and Sonar5-Pro post processing systems. Operator manual. Lindem Data Acquisition, Oslo
- Barber I, Hoare D, Krause J (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. *Rev Fish Biol Fish* 10:131–165
- Blaxter JHS, Batty RS (1984) The herring swimbladder: loss and gain of gas. *J Mar Biol Assoc UK* 64:441–459
- Boutillier RG, West TG, Pogson GH, Mesa KA, Wells J, Wells MJ (1996) *Nautilus* and the art of metabolic maintenance. *Nature* 382:534–536
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* 67:489–507
- Casini M, Cardinale M, Hjelm J (2006) Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: What gives the tune? *Oikos* 112:638–650
- Clark CW, Levy DA (1988) Diel vertical migration by juvenile sockeye salmon and the antipredation window. *Am Nat* 131:271–290
- Daskalov GM (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. *Mar Ecol Prog Ser* 255:259–270
- Diaz RJ (2000) Overview of hypoxia around the world. *J Environ Qual* 30:275–281
- Domenici P, Steffensen JF, Batty RS (2000) The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. *J Fish Biol* 57:1526–1538
- Domenici P, Ferrari RS, Steffensen JF, Batty RS (2002) The effect of progressive hypoxia on school structure and dynamics in Atlantic herring *Clupea harengus*. *Proc R Soc Lond B Biol Sci* 269:2103–2111
- Domenici P, Lefrancois C, Shingles A (2007) Hypoxia and the antipredator behaviours of fishes. *Philos Trans R Soc Lond B Biol Sci* 362:2102–2121
- Dommasnes A, Rey F, Røttingen I (1994) Reduced oxygen concentrations in herring wintering areas. *ICES J Mar Sci* 51:63–69
- Giske J, Aksnes DL (1992) Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. *Sarsia* 77:253–261
- Harvey CJ, Cox SP, Essington TE, Hansson S, Kitchell JF (2003) An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES J Mar Sci* 60:939–950
- Hays GC, Kennedy H, Frost BW (2001) Individual variation in diel vertical migration of a marine copepod: why some individuals remain at depth when others migrate. *Limnol Oceanogr* 46:2050–2054
- Helly JJ, Levin LA (2004) Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Res Part I* 51:1159–1168
- Herbert NA, Steffensen JF (2005) The response of Atlantic cod, *Gadus morhua*, to progressive hypoxia: fish swimming speed and physiological stress. *Mar Biol* 147: 1403–1412
- Herbert NA, Steffensen JF (2006) Hypoxia increases the behavioural activity of schooling herring: A response to physiological stress or respiratory distress? *Mar Biol* 149: 1217–1225
- Horn MH (1975) Swimbladder state and structure in relation to behavior and mode of life in stromateoid fish. *Fish Bull* 73:95–109
- Horppila J, Malinen T, Nurminen L, Tallberg P, Vinni M (2000) A metalimnetic oxygen minimum indirectly contributing to the low biomass of cladocerans in Lake Hiidenvesi: a diurnal study on the refuge effect. *Hydrobiologia* 436:81–90
- Huse I, Ona E (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES J Mar Sci* 53:863–867
- Jordan AD, Steffensen JF (2007) Effects of ration size and hypoxia on specific dynamic action in the cod. *Physiol Biochem Zool* 80:178–185
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59
- Klumb RA, Bunch KL, Mills EL, Rudstam LG and others (2004) Establishment of a metalimnetic oxygen refuge for zooplankton in a productive Lake Ontario embayment. *Ecol Appl* 14:113–131
- Lie U, Dahl O, Østvedt OJ (1978) Aspects of the life history of the local herring stock in Lindåspollene. *Fiskeridir Skr Ser Havunders* 16:369–404
- Love RH, Fisher RA, Wilson MA, Nero RW (2004) Unusual swimbladder behavior of fish in the Cariaco Trench. *Deep-Sea Res I* 51:1–16
- Nestlerode JA, Diaz RJ (1998) Effects of periodic environmental hypoxia on predation of a tethered polychaete, *Glycera americana*: implications for trophic dynamics. *Mar Ecol Prog Ser* 172:185–195
- Neuenfeldt S (2002) The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. *Fish Oceanogr* 11:11–17
- Neuenfeldt S, Beyer JE (2006) Environmentally driven predator-prey overlaps determine the aggregated diet of the cod *Gadus morhua* in the Baltic Sea. *Mar Ecol Prog Ser* 310:151–163
- Nilsson GE, Östlund-Nilsson S (2008) Does size matter for hypoxia tolerance in fish? *Biol Rev Camb Philos Soc* 83:173–189
- Osgood KE, Checkley KE Jr (1997) Seasonal variations of a deep aggregation of *Calanus pacificus* in the Santa Barbara basin. *Mar Ecol Prog Ser* 148:59–69
- Pearre S Jr (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol Rev Camb Philos Soc* 78:1–79
- Petersen JK, Pihl L (1995) Responses to hypoxia of plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth. *Environ Biol Fishes* 43:311–321
- Plante S, Chabot D, Dutil JD (1998) Hypoxia tolerance in Atlantic cod. *J Fish Biol* 53:1342–1356
- Reinhardt UG (2002) Asset protection in juvenile salmon: how adding biological realism changes a dynamic foraging model. *Behav Ecol* 13:94–100
- Robb T, Abrahams MV (2003) Variation in tolerance to hypoxia in a predator and prey species: An ecological

- advantage of being small? *J Fish Biol* 62:1067–1081
- Røstad A (2006) Fish behavior and implications for acoustic abundance estimates and ecological research. PhD thesis, University of Oslo
- Røstad A, Kaartvedt S, Klevjer TA, Melle W (2006) Fish are attracted to vessels. *ICES J Mar Sci* 63:1431–1437
- Schurmann H, Steffensen JF (1997) Effects of temperature, hypoxia and activity on the metabolism of juvenile cod. *J Fish Biol* 50:1166–1180
- Spicer JI, Thomasson MA, Strömberg JO (1999) Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters. *Mar Ecol Prog Ser* 185: 181–187
- Wolf M, van Doorn GS, Leimar A, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584
- Wood SC (1995) Interrelationships between hypoxia and thermoregulation in vertebrates. In: Heisler N (ed) *Advances in comparative and environmental physiology: mechanisms of systematic regulation in lower vertebrates*. Springer Verlag, Berlin, p 209–231

*Editorial responsibility: Andrew Brierley,
St. Andrews, UK*

*Submitted: August 7, 2008; Accepted: July 2, 2009
Proofs received from author(s): September 7, 2009*