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Ecology of overwintering sprat (*Sprattus sprattus*)

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ABSTRACT

We used moored upward-facing echosounders in combination with field campaigns to address the overwintering ecology of the clupeid sprat (*Sprattus sprattus*) throughout four separate winters in a Norwegian fjord. The stationary echosounders were cabled to shore and provided continuous measurements at a temporal resolution of seconds. The long-term coverage of several winters enabled study of the sprat behavior in relation to different biotic parameters like abundance, vertical distribution and taxonomic composition of potential prey and predators, as well as environmental conditions like ice-free vs. ice-covered waters and hypoxic- vs. normoxic conditions. Also the size distribution of the sprat differed significantly between years. The majority of the large-size classes had empty stomachs, particularly prominent in one winter. Otherwise, the diet of the sprat seemed to vary according to the fluctuating mesozooplankton community, yet with calanoid copepods being the most common prey in the sprat stomachs all winters. Krill were not common prey apart for the largest sprat in one winter, but particularly large concentrations of krill appeared to mitigate predation pressure from gadoids, which then preferred krill as prey. During daytime, sprat distribution and swimming behavior varied according to the oxygen conditions. Solitary swimming in near-bottom-waters (~150 m) prevailed in moderate hypoxia (30% O_2 saturation) as opposed to schooling in mid-waters when the deep waters were oxygen depleted (0–7% O_2 saturation). Nevertheless, a bimodal vertical distribution with an additional part of the sprat population distributed in upper waters was common in all years. The sprat carried out diel vertical migration (DVM) in all winters, but the patterns varied, and included both normal and asynchronous DVM, including fish with a somewhat deeper nocturnal than daytime distribution. Moreover, individual sprat carried out short and rapid excursions to the surface during the night in all years, likely for gulping atmospheric air. Ice conditions imposed a behavioral response with the sprat moving to shallower depths after the ice covering. The varied ecology and behavior observed throughout the course of four consecutive years underlines the importance of conducting long-term studies for the understanding of overwintering strategies. Overall, this study provided unique insight into the dynamic conditions that a population of fish may encounter while overwintering, providing novel information on a scarcely described phase in the life history of fish at high latitudes.

1. Introduction

The sprat (*Sprattus sprattus*) is a schooling clupeid fish that is widely distributed in the coastal waters of Europe, covering the Mediterranean, the Black Sea, the Baltic and the North Sea including Norwegian fjords (Limborg et al., 2009). It is a relatively small fish with a short life-span (maximum 16 cm and ~ 5 years, respectively) (Bailey, 1980). Gonadal and reproductive growth normally starts when the sprat has reached 95–100 mm (Peck et al., 2012; De Silva, 1973), a size that the fish may reach after its first or second year depending on growth conditions. The sprat plays an important role in the trophic structure of pelagic ecosystems being a major predator on zooplankton and an abundant prey for piscivorous fish like cod and whiting (Daan et al., 1990; Casini et al., 2008, 2011; Kaartvedt et al., 2009). It is also commercially harvested. In Kattegat and in the North Sea, annual catches of sprat comprised 100,000–200,000 t from 1996 until 2011 (ICES, 2011).

Due to its abundance and ecological and commercial importance, the sprat is widely studied (Wahl and Alheit, 1988; Last, 1987; Möllmann et al., 2004; Casini et al., 2011). Major efforts have been on addressing their echophysiology at different life-stages (see review Peck et al., 2012). This encompasses incubation studies of sprat eggs (Thompson et al., 1981; Nissling, 2004), laboratory experiments on endogenously- and exogenously first-feeding stages (Petereit et al., 2008), as well as field investigations of the

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diet of larval, juvenile and adult sprat (Voss et al., 2003; Dickmann et al., 2007; De Silva, 1973; Arrhenius and Hansson, 1993; Arrhenius, 1996). Physiologically- and individual-based models developed on the background of such laboratory- and field research are utilized to predict sprat recruitment and to explain/examine the constraining factors that may impact the population dynamics (Daewel et al., 2008; Baumann et al., 2006). Among the abiotic factors, temperature has a major impact on growth, reproduction and survival of sprat (Grauman and Yula, 1989; Parmanne et al., 1994). However, despite the broad knowledge that already exists on the physiology of sprat, there are still gaps in this species life-history that need to be addressed in order to better understand the processes that affect sprat condition and survival, and to make the projecting models more robust.

The overwintering period likely plays an important role in shaping the life strategy of sprat (particularly for sprat populations at high latitudes). Peck et al. (2012) pointed toward the lack of knowledge that exists on overwintering dynamics for the majority of small pelagic fishes in the North Sea and in the Baltic, with special reference to the little information that is available about potential feeding, size-specific survival and overwintering zooplankton populations.

Sprat may occur in habitats with hypoxia in deep waters (like in the Baltic, the Black sea and in fjords). This may exclude sprat from the lower parts of the water column, but Kaartvedt et al. (2009) suggested that overwintering sprat also may exploit oxygen depleted waters as a refuge from predators. The sprat may furthermore inhabit waters that become ice covered during winters (e.g. some Norwegian fjords). There is in general little knowledge about how ice may impact fish distribution and behavior in marine waters, largely for logistic reasons. However, echo sounders deployed in fjords and cabled to shore provide the opportunity of conducting non-intrusive long-term studies of both individuals and populations. Such approach enabled Solberg et al. (2012) and Solberg and Kaartvedt (2014) to study sprat behavior in relation to ice covering, revealing that the overwintering strategy of sprat was dynamic and that the sprat had a flexible behavioral repertoire. Yet, limited information exists on how *both* abiotic- and biotic factors may interact in controlling the overwintering ecology of sprat, including variations between years.

The main objective of this study was to assess the ecology of overwintering sprat throughout four separate winters. Long-term coverage using deployed echosounders cabled to shore enabled study of how sprat responded to varying environmental conditions, like ice-free waters versus ice-covered waters, hypoxic conditions versus well-oxygenated waters. By combining intermittent field campaigns with high resolution acoustic data, the sprat behavior was also studied in relation to different biotic parameters, like abundance, taxonomic composition and vertical distribution of its potential prey and predators.

2. Materials and methods

2.1. Study site

The study took place in Bunnefjorden (150 m) which is the innermost part of the Oslofjord, oriented as a parallel branch to the main fjord axis (Fig 1 in Klevjer and Kaartvedt, 2011). The deep waters of the Bunnefjord are usually characterized by hypoxic or even anoxic conditions. Water exchange of the basin water is restricted by two sills, one (~50 m) at the inlet of the Bunnefjord, and one (19 m) that is located in the sound that connects the inner Oslofjord to outer waters. Yet, water renewals normally occur every 2–3 yr resulting in periods with well-oxygenated waters extending to the bottom. Bunnefjorden often becomes ice covered during the winter.

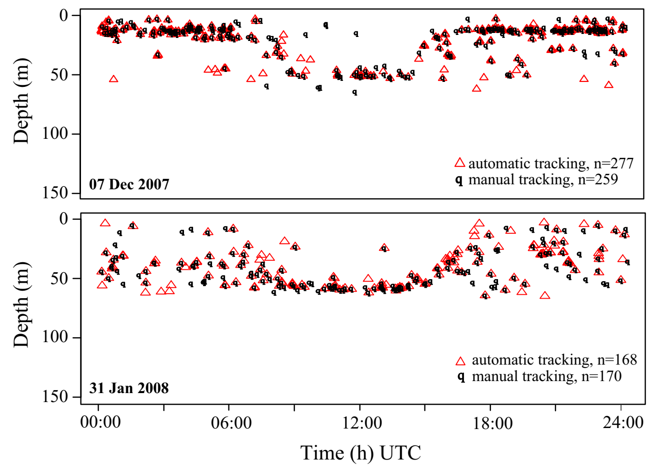

Fig. 1. Tracks of potential predators plotted against time and depth of 07 December 2007 and 31 January 2008. The black and red plots show the results of manual vs. automatic target tracking, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Sampling

Intermittent sampling campaigns were conducted by the research vessel of the University of Oslo "Trygve Braarud" (Table 1). CTD measurements (Conductivity, Temperature and Depth) were made by a Falmouth Scientific Instruments CTD equipped with Niskin bottles to obtain water samples for oxygen measurements. Oxygen content was analyzed by the standard Winkler method. Pelagic trawling was performed day and night using a 100 m^2 trawl towed horizontally (or sometimes obliquely) at ~2 knots. The trawl is equipped with a multisampler codend (Engås et al., 1997) enabling vertically stratified sampling. The two echosounders onboard the research vessel (Simrad EK 500, 38 kHz and 120 kHz) were used for targeting acoustic scattering layers during trawling, and a Scanmar depth sensor measured the trawling depth during each tow. In total 122 successful pelagic tows were conducted in the course of the four study periods (47 in 05/06, 33 in 07/08, 9 in April 09 and 33 in 09/10) (Table 1). Two hauls with bottom trawl (30 min each) were additionally carried out in December 05.

All fish were sorted by species for each trawl catch and larger fish (potential predators on sprat) were counted and measured for weight and length before being frozen for later analyzes. The total volume of the remaining catch was measured and a subsample of 30 sprat per tow (or per depth in the cases of repeated trawl depths) were frozen for stomach analyses and length measurements. The trawl catches of sprat were standardized as number of sprat "per 10 min of trawling". The volume of krill (*Meganyctiphanes norvegica*) was noted for each catch.

The stomachs of 1355 sprat, 238 whiting (*Merlangius merlangus*), and 6 other piscivorous fishes (haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and saithe *Pollachius virens*) were analyzed for potential prey. The stomachs were dissected out and the contents were analyzed under a stereo microscope. Stomach contents were identified to the lowest possible taxon. For the sprat, the degree of stomach fullness was classified into five categories from 0 to 1, where 0 = empty, 0.25 = a bit of content, 0.5 = half full, 0.75 = nearly full, 1 = bursting full. Degree of digestion was noted for each food item per stomach, classified in the same way as stomach fullness with five categories from 0 to 1 (0 = fresh, 1 = fully digested/unrecognizable mass). A portion of the sprat stomachs contained only unidentifiable content (category 1) and were not included when calculating the frequency of occurrence of prey categories among the stomach contents.