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Spatial and seasonal variability in reproductive investment of Baltic sprat

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ABSTRACT

Fecundity of marine fish species is highly variable, but trade-offs between fecundity and egg quality have rarely been observed at the individual level. We investigated spatial differences in reproductive investment of individual European sprat *Sprattus sprattus* (Linnaeus 1758) females by determining batch fecundity, condition indices (somatic condition index and gonadosomatic index) as well as oocyte dry weight, protein content, lipid content, spawning batch energy content, and fatty acid composition. Sampling was conducted in five different spawning areas within the Baltic Sea between March and May 2012. Spawning sprat from the Kiel Bight were in a better nutritional condition compared to sprat from the Arkona Basin, Bornholm Basin, and the Gdansk Deep. These females were also producing up to twice as many oocytes, and invested significantly more energy in reproduction, than their counterparts sampled in the eastern part of the Baltic Sea. Still, oocytes produced by Kiel Bight sprat contained significantly lower fractions of the essential fatty acids 20:4 (n-6) and 22:6 (n-3). A seasonal trade-off between oocyte weight/lipid content and fecundity was found for Baltic sprat, albeit the gross energy invested into spawning remained constant. Observed spatial and seasonal differences in sprat reproductive investment may be linked to hydrographic conditions and food availability and will impact the survival probability of yolk-sac and first feeding larvae. These findings indicate that Baltic sprat is able to adapt its reproductive tactics to the highly variable pelagic habitat of the Baltic Sea.

1. Introduction

The European Sprat *Sprattus sprattus* (Linnaeus 1758) is a key species in the pelagic food web of the Baltic Sea (Rudstam et al., 1994). Within the Baltic Sea sprat occur from the Belt Sea and Kiel Bight in the West to the Gulf of Finland in the East (Parmanne et al., 1994). Due to the hydrographic characteristics of the Baltic, sprat encounter a large range of environmental conditions within their pelagic habitat. The Baltic is a semi-enclosed brackish sea with a steep temperature and salinity gradient decreasing from West to East (Janssen et al., 1999). It is further characterized by a stable thermohaline stratification in the deep basins. The depths of the halocline and the oxycline depend primarily on the frequency of inflow events of oxygenated, saline water from the adjacent North Sea through the shallow Danish straits (Leppäranta and Myrberg, 2009). Recruitment in sprat is salinity dependent; salinities below 8 impair sprat egg survival (Petereit et al., 2009). Thus spawning mainly takes place in the Western Baltic and the deep basins of the central Baltic (Aro 1989; Karasiova and Zezera 2005; Baumann et al., 2006).

Like many other clupeid fish species, sprat is an indeterminate batch spawner releasing a number of successive egg batches during a protracted spawning season (Alheit, 1988; Heidrich, 1925). The spawning season of sprat within the Baltic generally ranges from February to August (Grauman et al., 1987; Ojaveer and Kalejs, 2010), but spawning individuals have been observed in the South-Central Baltic as early as January (Haslob et al., 2013). Peak spawning typically occurs between May and June (Heidrich, 1925; Karasiova, 2002), although extremely cold winter temperatures may cause a delay (Karasiova, 2002).

Rechlin (1975) showed significant differences in morphology and life history traits of sprat from the Bight of Mecklenburg and sprat from the central part of the Baltic. Thus, the western Baltic sprat population may be more closely related to the Kattegat-Skagerrak population. While, Debes et al. (2008) did not observe differences in the mitochondrial DNA of Baltic and North Sea sprat populations, Limborg et al. (2009) was able to detect genetic differences among sprat sampled in the Baltic Proper using a DNA microsatellite approach. Limborg et al. (2009) showed that sprat populations from the Arkona Basin, the Gdansk Deep, and the Bornholm Basin are all genetically distinct. However, the migration behaviour of sprat leads to an extensive mixing of different stock components in some areas, which hampered clear

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identification and separation of sprat sub-populations in the Baltic Sea so far (Aro, 1989). Because of this Baltic sprat have been assessed and managed as a single stock unit since 1989 (ICES, 2015; Ojaveer and Kalejs, 2010).

Local adaption is a common phenomenon in dominant marine species of the Baltic Sea ecosystem (Johannesson et al., 2011). Studies of sprat populations within the central Baltic lead to the conclusion that the species is locally adapted in regard to its morphology, growth, reproductive traits, and recruitment patterns (Kraus and Köster, 2001; Parmanne et al., 1994; Rechlin, 1975). Previous fecundity studies on sprat revealed spatial, interseasonal and interannual variability in batch fecundity in different spawning areas in the Baltic (Alekseev and Alekseeva, 2005; Alheit, 1988; Haslob et al., 2011; Müller et al., 1990). In addition, Haslob et al. (2011) found that Baltic sprat batch fecundity was positively related to ambient temperature and salinity in the Central Baltic.

The individual investment into reproduction includes both the number of spawned eggs and the properties of the oocytes. Egg quality, often expressed as hatching success or viability of early larvae stages (Morgan, 2008), is related to many factors, e.g. the size or weight of the oocyte (Blaxter and Hempel, 1969); the amount of nutrients, lipids and proteins deposited into the oocyte (Brooks et al., 1997); and the fatty acid composition of the oocyte (Wiegand, 1996). Oocyte protein and lipid content are directly related to the nutritional condition of the larvae and the length of the time window between hatching and first feeding (Guisande et al., 1998). Castro et al. (2009) showed that an increase in egg lipid and protein content enhanced hatching success for Anchoveta (*Engraulis ringens*). Thus, knowledge of egg composition is essential, since it has direct consequences on early life stage survival.

In addition to total lipid content, fatty acid composition is important in marine fish embryo development (Tocher and Sargent, 1984). Essential fatty acids cannot be synthesised *de novo* by fish or most other heterotrophic consumers in significant quantities (Sargent et al., 1995) but are crucial for development (e.g. neuronal development). Lane and Kohler (2006) stated that elevated levels of docosahexaenoic acid (DHA, 22:6 (n-3)) and Eicosapentaenoic acid (EPA, 20:5 (n-3)) accounted for an increased hatching success in White bass (*Morone chrysops*) larvae. Additionally, hatching success was positively linked to high ratios of DHA to EPA and high levels of Arachidonic acid (ARA, 20:4 (n-6)) in Baltic cod (*Gadus morhua*) (Pickova and Dutta, 1997).

The aim of the present study was to investigate Baltic sprat reproductive investment on the level of individual females, in terms of egg production (batch fecundity), oocyte composition, oocyte energy content, and oocyte quality with regard to fatty acid composition. The data allowed for a spatial and seasonal comparison of the energy invested into spawning and for investigating the capacity of individual sprat to reproduce within the Baltic. The study also examines the trade-offs between reproductive investment and oocyte quality. This is also the first study since Heidrich (1925) to determine fecundity data for sprat from the western Baltic. Furthermore, the present study is the first to highlight spatially and seasonally resolved spawning energetics in *S. sprattus*. Presented results may serve as input parameters for bioenergetic modelling of sprat on the population or individual level, taking into account the energy invested into spawning.

2. Material and methods

2.1. Sampling

Sampling was conducted in the Baltic Sea during three cruises of the German RV "Alkor" in March, April, and May 2012. Five different areas were sampled: KB, AB, Bornholm Basin (BB), Gdansk Deep (GD), and Gotland Basin (GB) (from West to East, Fig. 1).

Fish were caught with a pelagic trawl. Trawling time was in general 30 min per haul. After each haul a CTD cast was conducted to record water temperature, salinity, and oxygen content. The total lengths (*TL*, ± 0.1 cm) of at least 200 sprat per haul were measured for length frequency analysis. Only female sprat with ovaries containing fully hydrated oocytes were sampled, running ripe females were rejected to avoid possible loss of oocytes, as this would lead to an underestimation of batch fecundity. Sprat were sampled immediately after the haul was on deck and stored on crushed ice. The sampled fish were weighed (wet weight *WW*, ± 0.1 g) and measured (*TL*, ± 0.1 cm), and their ovaries were dissected carefully.

Oocytes were extracted from a single ovary lobe, rinsed with deionized water, and counted under a stereo microscope (Leica MZ 8). A counted number of oocytes (around 50 oocytes per fish) were transferred to pre-weighed tin-caps (8*8*15 mm). These samples were used to determine the oocyte dry weight, lipid content, and fatty acid composition. In addition, a counted number of oocytes (around 10 oocytes per fish) were sampled in Eppendorf caps for determination of protein content. Oocyte samples were stored at −80 °C for subsequent fatty acid and protein analysis in the laboratory. Finally, both ovary lobes were stored in 4% buffered formaldehyde solution for further fecundity analysis.

2.2. Batch fecundity, condition index, and gonadosomatic index

Ovary free body weight (*OFBW*, ± 0.1 g) of sampled frozen fish and fixed ovary weights (*OW*, ± 0.1 g) were measured (Sartorius, 0.01 g) in the laboratory on land, to avoid imprecise measurements due to the ship's motion at sea. Absolute batch fecundity (*ABF*) was determined gravimetrically using the hydrated oocyte method suggested by Hunter et al. (1985) for indeterminate batch spawners. For ascertainment of the relative batch fecundity per unit body weight (*RBF*), *ABF* was divided by *OFBW* (Alheit, 1988). Further, a condition index (*K*) was determined (Eq. (1)), and a gonadosomatic index (*GSI*) was calculated (Eq. (2)) with the following formulas:

$$K = \left(\frac{OFBW}{TL^3}\right) \times 100 \quad (1)$$

$$GSI = \left(\frac{OW}{OFBW}\right) \times 100 \quad (2)$$

2.3. Oocyte dry weight

Oocyte dry weight (*ODW*) was determined to the nearest 0.1 mg (Sartorius SC 2 micro-scale), using the samples stored in pre-weighed tin caps, after freeze-drying (Christ Alpha 1–4) for at least 24 h. After subtracting the weight of the empty tin cap, the average *ODW* was then calculated by dividing the total weight by the number of oocytes contained in the tin cap.

2.4. Total lipid content per oocyte and fatty acids analysis

The fatty acid signature of oocytes was determined by gas chromatography (GC). Lipid extraction of the dried oocytes was performed using a 1:1:1 solvent mix of dichloromethane:methanol:chloroform. A five component fatty acid methyl ester Mix (13:0 – 21:0, Restek, Bad Homburg, Germany; c = 8.5 ng component ml^{-1}) was added as an internal standard and a 23:0 fatty acid standard (Restek, Bad Homburg, Germany, c = 25.1 ng ml^{-1}) was added as an esterification efficiency control. Esterification was performed over night at 50 °C in 200 ml 1% H_2SO_4 and 100 ml toluene. The solvent phase was transferred to 100 ml *n*-hexane and a 1 ml aliquot measured in a Thermo Fisher Trace GC Ultra with a Thermo Fisher TRACE™ TR-FAME column (10 m*0.1 mm*0.2 mm). For more details on sample preparation and GC settings, see Hauss et al. (2012). The total lipid content per oocyte was determined by adding up the weights of all detected fatty acids.