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Seasonal variability of fecundity and spawning dynamics of Baltic sprat

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ABSTRACT

Seasonal variability in fecundity has been observed in a number of marine fishes and is important towards understanding the reproductive potential of a fish stock. However, the seasonal dynamics of egg production of Baltic sprat (*Sprattus sprattus balticus* S) have not been well described to date. We present data on the timing of spawning, and the seasonal variability in batch fecundity, number of developing oocytes, oocyte dry weight, spawning fraction, fish condition and atresia for this species in the Bornholm Basin, Baltic Sea. Histological techniques in combination with image analysis were applied to investigate those variables based upon material sampled in 2005 and 2008. Sprat were reported to be in spawning condition from January to June in each year plus in 2008 signs of ovarian maturation were also observed in November. Relative batch fecundity was found to vary two-fold with 85 eggs g^{-1} ovary free body weight observed early in the spawning season (January 2005) and 165 eggs g^{-1} ovary free body weight late in the spawning season (June 2008). Variability in batch fecundity during peak spawning was rather low. A seasonal decrease in oocyte dry weight was related to an increase in batch fecundity. Spawning fraction varied over the course of the spawning period with values ranging from 0.29 in March to 0.18 in June. Stereometric analyses confirmed the indeterminate fecundity of Baltic sprat. Prevalence of atresia was low during peak spawning in April to June (1.0–4.0%) but considerably higher during the early spawning period in March (16.4%) and highest in November (38.5%). Female sprat condition was low during the spawning period and increased sharply after spawning ceased. Our study provides a better understanding of fecundity and spawning dynamics of Baltic sprat which will aid to improve the assessment of reproductive potential of this ecologically and economically important fish species.

1. Introduction

Seasonality in marine fish spawning activity plays a critical role in reproductive success and varies in terms of its timing, duration, and degree of synchronisation among individuals within a population (Lowerre-Barbieri et al., 2011). For successful reproduction, it is essential that the produced early life stages are released into an environment where conditions favour survival, but a trade-off with other selective forces acting on parental spawning time may exist (Wright and Trippel, 2009). The phenology of environmental features of marine habitats is highly variable and this influences optimum spawning time. Thus, batch spawning over an extended spawning season has evolved in many marine fish species producing pelagic eggs (Murua and Saborido-Rey, 2003). This spawning strategy increases the probability that at least some offspring overlap with optimal conditions for growth and survival (Sherman et al., 1984; Alheit, 1988), increasing the probability of successful recruitment.

Multiple-batch spawners often release eggs over a prolonged period. In this time frame, changes in environmental conditions can cause variability in the reproductive output in terms of batch fecundity, spawning fraction and frequency, as well as egg quality (Alheit, 1993; Trippel et al., 1997). This seasonal variability may be due to changes in food availability and the resulting scope of individual fish to allocate energy either to reproduction or to somatic growth and maintenance. For a better understanding of mechanisms which potentially drive the reproductive potential of a stock, it is important to characterise the aforementioned seasonal variability in spawning parameters.

The spawning season of Baltic sprat (*Sprattus sprattus balticus* S.), a multiple batch spawner with indeterminate oocyte recruitment, lasts from approximately February to August in the Baltic Sea (Ojaveer and Kalejs, 2010). Timing of spawning may be dependent on temperature conditions, with extremely low winter temperatures causing a delay in the onset of spawning (Karasiova, 2002). It

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Table 1
Sampling details for determination of sprat ovary developmental stages and batch fecundity for the years 2005 and 2008. DA = research vessel (RV) "Dana", AL = RV "Alkor", WH = RV "Walther Herwig III". P: pelagic trawl; B: bottom trawl; *n*: number of 2-kg sub-samples taken.

Cruise	Gear	Date	*n*	Size range (cm)	Number of females analysed	
					Ovarian development phase	Fecundity
AL 251	P	26–28th January 2005	None	11.4–14.0	n.a.	25
AL 255	P	20–23th April 2005	None	10.1–14.9	n.a.	45
WH 275	P	16–19th May 2005	None	9.6–15.3	n.a.	102
AL 262	P	22d–25th July 2005	None	n.a.	n.a.	0
DA 0208	B	13–15th March 2008	5	9.9–14.5	110	54
AL 318	P	19–21th April 2008	5	10.5–13.4	104	44
WH 312	P	12–18th May 2008	5	10.6–14.4	101	55
AL 320	P	7–10th June 2008	3	11.2–14.2	60	31
AL 324	P	27th August 2008	None	13.3–13.8	5	0
DA 0808	B	15th November 2008	1	9.8–14.6	26	0

has been shown that batch fecundity increases during the spawning season (Heidrich, 1925; Alekseev and Alekseeva, 2005) and the only observation of spawning fraction for several consecutive months is given by Kraus and Köster (2004), who reported quite high variability in this parameter over the peak spawning season for the Bornholm Basin. Some observations on the oogenesis of Baltic sprat exist (Haslob et al., 2012; Alekseev and Alekseeva, 2005), but the seasonal dynamics and resulting consequences for spawning fraction and/or batch fecundity are still unknown.

Atresia plays a role in down regulating the realised fecundity in a number of marine fish species when conditions turn unfavourable in terms of food availability or hydrographic conditions. This is especially the case for determinate spawners, e.g. cod (*Gadus morhua*; Kraus et al., 2008), plaice (*Pleuronectes platessa*; Kennedy et al., 2007), and sole (*Solea solea*; Witthames and Greer Walker, 1995). These species are capital breeders (Jönsson, 1997), in which the cost of reproduction is supported by energetic reserves stored prior to the spawning season. Hence, potential fecundity is determined before the onset of spawning. In fish species with indeterminate oocyte recruitment, atresia might also play an important role to re-allocate surplus production of oocytes at the end of the spawning season (Murua et al., 2006; Korta et al., 2010). For Baltic sprat, no prior studies have investigated atresia; however, its occurrence and seasonality is an important aspect in fecundity studies of other species.

Knowledge of fecundity traits is essential to understand recruitment processes in exploited fish stocks (Rickman et al., 2000). Thus, there is a need to monitor fecundity (Lambert, 2008) and to understand its seasonal dynamics due to environmental variability. In this context, the main objective of this study was to investigate the seasonal variability in a number of fecundity traits to gain better knowledge of the spawning dynamics of this ecologically and economically important fish species. For this purpose, ovaries were sampled over the entire spawning season and were analysed with histological and image analysis methods. Moreover, a stereometric approach was applied to assess the number of developing oocytes and to quantify atretic oocytes. The presented results will enable a better evaluation of the reproductive potential of this stock.

2. Methods

Sprat were sampled in 2005 and 2008 during several research cruises conducted in the Bornholm Basin, Baltic Sea (Fig. 1 and Table 1). For the year 2005, determination of sex and maturity was conducted macroscopically immediately after the haul was on board. For this purpose at least 10 sprat per 1 cm length class were staged. Additionally, females with hydrated oocytes were sampled and preserved in a buffered 8% formaldehyde solution in January, April and May 2005 for subsequent batch fecundity analyses. To assure a proper fixation, the body cavity of each fish was slit open. Samples for the year 2008 were taken in March, April, May, June, August and November (Table 1). In this year, up to five 2-kg sub-samples of sprat were taken from pelagic fishery hauls and fixed as described above. In the laboratory, at least 20 female sprat were then sampled randomly from the sub-samples for subsequent quantitative determination of ovarian development phases by histology. To increase the sample size for batch fecundity analysis, additional females with hydrated ovaries were collected from the same sub-samples when available. From all sampled females, the ovaries were removed for histological processing. One histological cross-section of one of the ovary lobes (tissue embedded in paraffin; 3 μm sections; haematoxylin staining) was produced from each sampled ovary. The ovary lobe (left or right) was chosen randomly. During the cruise in August 2008, only a few sprat were caught, and only five females could be collected for histological analysis. Only one sprat sub-sample was available for November 2008. A total of 406 ovaries were analysed histologically for the year 2008, plus 65 additionally collected hydrated ovaries (Table 1).

For all females analysed in the laboratory, total weight (±0.1 g), gutted weight (±0.1 g), total length (*TL*, ±0.1 cm), and ovary weight (*OW*, ±0.1 mg), and ovary free body weight (*OFBW*, ±0.1 g) were determined. Condition index (*K*) was calculated taking into account *TL* and *OFBW*:

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

The gonadosomatic index (*GSI*) was calculated taking into account *OW* and *OFBW*:

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

2.1. Ovarian developmental phases

All histological sections were viewed to assess the ovarian developmental phase based on the presence of the most advanced oocyte stage (Table 2) according to Brown-Peterson et al. (2011). Five oocyte developmental stages were distinguished: (i) primary growth (PG), (ii) cortical alveolar (CA), (iii) vitellogenesis (VIT), (iv) germinal vesicle migration (GVM), and (v) hydrated oocytes (HYD). Moreover, the presence of recent post ovulatory follicles (POFs) was recorded. Recent POFs (<24 h) were identified using histological criteria published for Baltic sprat (Haslob et al., 2012). Additionally, each ovary section was checked for the presence of α-atretic oocytes and based on that, the prevalence of atresia was estimated as the proportion of females with oocyte atresia.

2.2. Stereology

The number of developing oocytes (*NDO*) and atretic oocytes were estimated stereometrically for a subsample of ovaries ($n = 98$)