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Growth and reproduction of the bivalve *Spisula subtruncata* (da Costa) in Dutch coastal waters

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Abstract

The bivalve *Spisula subtruncata* is usually abundant in shallow coastal waters along the Dutch coast. However, its biomass has been decreasing since 1995. In order to assess whether reproductive failure may be the cause of the observed decline over the last decades, the energy investment in reproduction of a population of *S. subtruncata* from central Dutch coastal waters was studied. The population studied consisted of individuals of up to four years old. Shell length reached maximum values of around 32 mm and individual total body, somatic and gonadal ash-free dry mass reached maximum values of about 278 mg AFDM, 252 mg AFDM and 76 mg AFDM, respectively. A clear seasonal cycle in somatic and gonadal mass was observed. Somatic and gonadal mass indices increased in early spring and reached maximum values during summer, followed by a decrease to minimum values at the beginning of the following year. Spawning was in June–July and settlement of spat seems to have occurred in July–August. Mean oocyte diameter was 57.43 ± 0.03 μm, corresponding to a volume of 98972 μm^3. These results suggested that reproductive failure was not the cause of the current population decline. Most likely, unsuccessful settlement of spat and/or severe predation during the first months of life were responsible for the observed patterns.

Keywords: Growth; Reproductive investment; Age determination; Oocyte diameter; *Spisula subtruncata*; Dutch coastal waters

Article Outline

1. Introduction

The bivalve *Spisula subtruncata* is a common species occurring in shallow coastal waters from Norway to the Mediterranean and the Canary Islands (Tebble, 1966 and Hayward and Ryland, 1995). In Dutch waters, it occurs along the entire coast (Tebble, 1966, Daan and Mulder, 2005 and Craeymeersch and Perdon, 2006). *S. subtruncata* lives in shallow soft bottoms, where it may reach densities of thousands of adults per m^2 and tens of thousands of spat per m^2 (Leopold et al., 1998). It is an important food source for shrimps and demersal fishes (Braber and De Groot, 1973, Møhlenberg and Kiørboe, 1981 and Pihl and Rosenberg, 1984) and a staple diet of diving sea ducks (Offringa, 1991, Durinck et al., 1993, Leopold et al., 1995 and Fox, 2003).

Although there is substantial information on the stock size of *S. subtruncata* during the last decade (Craeymeersch et al., 2001, Craeymeersch and Perdon, 2003, Craeymeersch and Perdon, 2004a, Craeymeersch and Perdon, 2004b and Craeymeersch and Perdon, 2006), limited information is available on its life-history. The first records on recruitment and growth of *S. subtruncata* are found in Davis, 1923 and Davis, 1925 on the Dogger Bank (North Sea). Petersen (1977) confirmed its presence in this area in the 1970s, but more recently no *S. subtruncata* were seen ont the Dogger Bank (Wieking and Kröncke, 2003 and Daan and Mulder, 2005). *S. subtruncata* was found off the German Wadden Sea coast by Hagmeier (1930) and Ziegelmeier (1978). Degraer et al. (1999) described a population of *S. subtruncata* along the Belgian coast. Although the species sometimes also occurs offshore, in general it seems to be most abundant in coastal waters (Daan and Mulder, 2005; Degraer et al., 2006). In Dutch waters, the biomass of *S. subtruncata* is now the lowest since 1995 (Craeymeersch and Perdon, 2006). The fact that densities of 1-y-old individuals have been very low for the last 5 years (Craeymeersch and Perdon, 2006) suggests that failure in successful spatfall or in subsequent recruitment may be the problem.

Rueda and Smaal (2004) observed ripe gonads in *S. subtruncata* during the summer and related the variation in body condition in the field to gametogenesis. However, the contribution of gonadal mass to the total body mass variation along the year is unknown since the evaluation of gametogenesis was done in a qualitative way by visual inspection of the gonads. Therefore, in the present paper, the energy investment in reproduction of a population of *S. subtruncata* from Dutch coastal waters is studied in a quantitative way to assess whether reproductive failure may be the cause of the observed decline in biomass over the last decades. To this end, seasonal variability in growth (in terms of shell length and somatic mass) and reproductive output (in terms of gonadal mass and oocyte size) of *S. subtruncata* were followed during a 1.5-y period. In addition, since it is still unknown whether a correct age determination of *S. subtruncata* can be done by analysing the shell surface, external shell surface growth rings were compared with internal growth lines in shell cross-sections in the same shells, as done earlier for *Spisula solida* (Gaspar et al., 1995) and *Spisula solidissima* (Jones et al., 1978).

2. Materials and methods

2.1. Field sampling

Samples were collected, if possible every month, from December 2001 to June 2003 offshore Grote Keeten (52° 52′ N, 4° 38′ E) in the Dutch coastal zone of the North Sea (Fig. 1).

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Fig. 1. Sampling location (black circle) of *Spisula subtruncata*.

Locally, water depth was around 10 m and the silt content of the sediment was about 3% (Cardoso et al., subm. ms). At each sampling occasion, about 100 individuals evenly distributed over the entire size range were collected over an area of a few km^2, by using a Van Veen grab and a 2.9 m beam trawl with a mesh size of 1 × 1 cm. Samples were sorted out immediately and taken to the laboratory, stored in seawater at 5 °C and processed within the next 48 h.

2.2. Data analysis

Of each individual, shell length was measured to the nearest 0.01 mm with electronic callipers. Subsequently, the bivalves were opened and all flesh (body) was removed. Gonads were separated from somatic tissue under a microscope (6.4×). The ash-free dry mass (AFDM) of each part was determined as the difference in dry mass after drying for 4 d at 60 °C and ash mass after incinerating for 4 h at 560 °C. The investment in somatic and gonadal mass was determined by estimating the Somatic Mass Index (SMI) and the Gonadal Mass Index (GMI). SMI was calculated as the AFDM of the soma divided by cubic shell length and GMI was expressed as the AFDM of the gonad divided by cubic shell length. GMI was determined only for animals that had gonadal mass. The extent to which variability in condition could be accounted for by seasonal variability and by differences among age classes was examined by using ANOVA. Subsequently, the model was used to correct somatic and gonadal mass indices for seasonal and age differences. In order to obtain normality, GMI data were transformed using a squared root transformation.

For the validation of the method of age determination, shells of 126 individuals distributed over the sampling year were selected. Two independent observers analysed both valves of each individual and aged each shell based on the external growth rings. Subsequently, left valves were placed face down in a plastic mould and embedded in epoxy resin (Poly Service, THV-500 epoxyhars and Harder 355), following Ropes (1985). Once hardened, the blocks were sectioned longitudinally through the hinge (Witbaard, 1997 and Witbaard et al., 1999). The cut surfaces were then ground flat, wet polished and examined under a microscope. The pattern of light and dark zones was then analysed by both observers, as done for *Spisula solida* by Gaspar et al. (1995), for *S. solidissima* by Jones et al. (1978), and for *S. solidissima similis* by Walker and Heffernan (1994). That is: thin dark lines, running parallel to the growing edge of the shell (growth lines), alternate with larger white zones, which were called growth increments. In seasons with low growth, lines are closer together, forming a larger and darker band (annual growth band). The distance between two annual growth bands tends to be shorter as the shell grows. For each individual, the number of external surface growth rings was compared with the number of internal growth lines from the shell's cross-section. The year of birth of each individual was determined for both methods.

Von Bertalanffy growth (VBG) curves were fitted to length-at-age data from both the internal growth lines and the surface rings, according to the expression:

$$L_t = L_\infty * (1 - e^{-k * t})$$

where L_∞ is the estimated maximum length (mm), k is the growth rate constant (d^{-1}), t is age in days and L_t is the observed length and mass at age t. VBG parameters L_∞ and k were iteratively estimated.

2.3. Laboratory experiments

From the seasonal cycle of gonadal mass index in 2002, the period of spawning was determined. Before the expected spawning period in 2003, 100 animals were collected once at the study site. Subsequently, they were transported to the laboratory and forced to spawn. Spawning was induced by thermal shock with added fluoxetine as described by Honkoop et al. (1999).

Freshly spawned eggs were collected separately from each female, placed on a microscope slide and digital photographs were made with a Pixera View Finder digital camera fitted to a Zeiss stereo microscope with a final resolution of 1510 pixels per mm. Subsequently, sharply focussed eggs were measured using the ImageJ™ software package (http://rsb.info.nih.gov/ij/). Egg size of at least 50 round eggs per female was measured according to Thorsen and Kjesbu (2001).

3. Results

3.1. Internal shell lines vs. external shell marks

Fig. 2 shows shell sections of 2 and 3 y old individuals. Growth lines and an annual growth band are seen in detail in Fig. 2a. Until an age of 2, the number of external rings usually equalled the number of internal growth lines, that is, the two methods nearly always resulted in the same estimate of the age (Table 1). From the age of 3 onwards, the number of mistakes made by using the external reading was substantial. From the 126 individuals analysed, in 21% of the cases, age determination by using external rings was different from the age determined from internal growth lines. In most of these differences, age determined by external rings was lower than the one from internal lines (78% was lower and 22% higher).

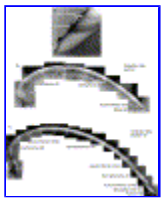

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Fig. 2. Photograph of shell sections of *Spisula subtruncata* showing the narrow growth lines corresponding to the autumn/winter season and the broad growth bands corresponding to the spring/summer season. Growth bands represent the area between two growth lines. (a) Growth lines and growth band (6.6×), (b) 2-y-old individual (16 mm shell length), and (c) 3-y-old individual (21 mm shell length).

Table 1.

Numbers of individuals of *Spisula subtruncata* allotted to an age class by two methods: analysis of the external surface rings or analysis of internal growth lines

	Age from internal lines

		0	*1*	*2*	*3*	*4*
Age from external marks	*0*	**26**	0	0	0	0
	1	1	**17**	4	0	0
	2	0	2	**22**	11	0
	3	0	0	1	**29**	6
	4	0	0	0	2	**5**

Numbers in bold correspond to the number of individuals in which the two methods led to the estimation of an identical age.

VBG curves fitted for length-at-age data for the internal lines and external rings resulted in similar growth curves (Fig. 3). The estimated VBG parameter L_∞ (asymptotic length) resulted in a maximum length of 33.5 ± 1.4 mm for the external rings and 31.1 ± 1.0 mm for the internal lines (Table 2). Nevertheless, no significant differences were found between the two curves (*F*-test, $F_{(2,248)} = 1.55$, $p = 0.214$). In addition, comparison of L_∞ and *k* between the two methods by using the t-test did not result in significant differences (see Table 2).

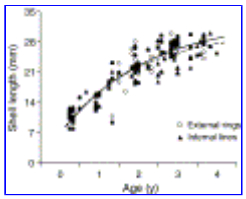

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Fig. 3. Growth rate of *Spisula subtruncata* determined from the analysis of external surface rings (○, —) and internal lines (▲ ---). The transition between two age groups is considered to be on the first of January.

Table 2.

Parameters of the Von Bertalanffy growth curve for shell length (mm) of *Spisula subtruncata*, using the age determined by both the analysis of internal growth lines and external surface rings

	n	L_∞ (mm)	*k* (y^{-1})	r^2
Internal growth lines	126	31.12 ± 1.04	0.46 ± 0.038	0.86
External growth rings	126	33.48 ± 1.40	0.52 ± 0.039	0.86
p (of difference)		> 0.05	> 0.05	

Probability values result from a t-test.

3.2. Body mass cycles and growth

In the following analysis, sexes were treated together because no differences were found between them (ANOVA, p > 0.05). Body, somatic and gonadal mass indices showed clear seasonal trends (Fig. 4). BMI and SMI increased in early spring, showed a peak around May and minimum values around January. GMI increased

from December to May, and decreased from June onwards. Significant differences in indices were found between months but not between age groups (ANOVA, $p > 0.05$). Most individuals developed gonads in May. The gonadosomatic ratio, used as a measure of reproductive investment, showed that in May the total body mass of *S. subtruncata* consisted for about 20% of gonads (not shown).

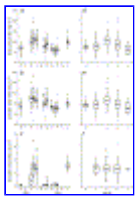

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Fig. 4. (a, d) Body mass index (mg cm^{-3}), (b, e) somatic mass index (mg cm^{-3}) and (c, f) gonadal mass index (mg cm^{-3}) of *Spisula subtruncata* plotted against month (a to c) and age (d to f). GMI values are square-root transformed.

Since no significant differences were found in growth curves estimated from internal lines and external rings, age was determined for all individuals sampled based on external shell rings, to allow a direct comparison of growth patterns with results from other authors. This resulted in individuals from 0 to 4 y old. The largest observed individual sizes were 32.4 mm shell length, 278.2 mg AFDM total body mass, 252.1 mg AFDM somatic mass and 76.0 mg AFDM gonadal mass. A general pattern was found of periods of growth in total body, somatic and gonadal mass alternating with periods of decrease in mean values (Fig. 5). Growth in shell length and mass occurred in spring, in general from about February to June. Weight loss occurred in winter (from around October to February) as suggested by the decrease in mean total body mass and somatic mass values. The sometimes observed decreases in mean shell length between successive sampling occasions were probably caused by sampling errors. Growth in gonadal mass occurred from February to June, after which gonadal mass decreased rapidly due to spawning. From about September to January most individuals were empty of gonads.

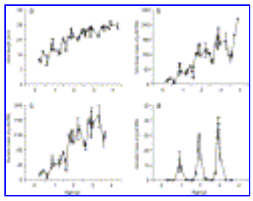

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Fig. 5. Means of (a) shell length (mm ± SE), (b) total body mass (mg AFDM ± SE), (c) somatic mass (mg AFDM ± SE), and (d) gonadal mass (mg AFDM ± SE) of *Spisula subtruncata* plotted against age (years). The transition between two age groups is considered to be on the first of January.

3.3. Spawning and oocyte size

The drop in GMI observed between June and August 2002 (Fig. 4) indicated spawning in June or July. All individuals above 12 mm shell length developed gonads during the spawning season. From a total of 100 individuals, 90 spawned, half of which were females and the other half males. Oocyte size of 45 females was measured and the mean oocyte diameter was 57.43 ± 0.03 μm (mean ± SE). No significant relationship was found between egg diameter and female shell size.

4. Discussion

4.1. Age determination

Growth marks on shells are usually related to cessation of growth during winter months, due to low food availability and low temperatures. In Dutch waters, growth of bivalves stops during winter and their soft parts usually lose weight in autumn/winter (Lammens, 1967, Pieters et al., 1979, Beukema et al., 1985, Zwarts, 1991 and Honkoop and Beukema, 1997). In Belgian waters, Degraer et al. (1999) found that growth of *Spisula subtruncata* stopped between autumn and spring. However, sudden changes in temperature or food conditions, spawning, and other stressing factors may also lead to a temporary cessation of growth. This may cause errors in age determination by examining growth bands (both externally and internally). Since the shell structure of *S. subtruncata* is similar to those of *S. solida* and *S. solidissima*, we analysed the internal growth lines as described by Jones et al. (1978) and Gaspar et al. (1995) for those two species. However, a validation of the use of internal growth marks for age determination in *S. subtruncata* is required. This can be achieved by marking experiments (Jones et al., 1978, Richardson, 1988 and Gaspar et al., 1995) or by carbon and oxygen isotope analysis (Witbaard et al., 1994) to confirm the seasonality of the bands.

The present study shows some discrepancies between external reading of shell marks and internal lines from shell sections but these hardly affect the obtained growth curves. In *S. solida* and *S. solidissima* (Jones et al., 1978 and Gaspar et al., 1995), age determined from external surface rings resulted in an overestimation of growth in comparison with internal reading. The fact that the variability in growth parameter estimates was higher when external reading was used instead of internal suggests that the use of internal lines may be a more accurate method. If so, the external reading led to a systematic underestimation of the number of growth marks, especially in individuals over 2 y old, resulting in an overestimation of growth. Nevertheless, since maximum age observed in the present study was only 4 y, differences in growth between the two methods were very small. In other years, older animals (up to 5 y old) were found in a nearby area (Leopold, 1996). Therefore, in older populations it may be important to analyse the internal shell lines to obtain a more accurate estimation of age.

4.2. Body mass cycles and growth

Seasonal variation in indices of body, somatic and gonadal mass showed increases in early spring, reaching maximum values around May, followed by a decline until the beginning of the following year. The decrease in body condition during summer seems to be a consequence of both the release of gametes and increased water temperature, leading to higher metabolic costs (Rueda and Smaal, 2004). In fact, a small increase in somatic mass index (SMI) was seen in October, at the end of the spawning season, suggesting that the drop in SMI during the summer months is partly due to spawning. The variation of total individual mass (soma plus gonad) on the Belgian coast followed the same trend with maximum values between April and July and minimal ones in January–February (Degraer et al., 1999). Body mass index (BMI) values found in the present study are in the same order of magnitude as the results of Bodoy (1980) off the Mediterranean coast, although the seasonal trend is different since peak values there occur in March.

Over the distribution range of *S. subtruncata*, populations are characterised by large seasonal and interannual fluctuations in density and biomass values. Along European coasts, values of thousands of individuals per m^2 and high biomasses, observed during the summer of some years, may decline to less than 100 ind m^{-2} and to a few mg AFDM m^{-2} in winter (Cattaneo and Massé, 1983, Ambrogi and Ambrogi, 1985, Ambrogi and Ambrogi, 1987, Fraschetti et al., 1997 and Degraer, 1999), leading in some cases to the almost complete disappearance of the population. Along the Dutch coast, large year-to-year variability in densities and biomasses is also observed (Craeymeersch et al., 2001, Craeymeersch and Perdon, 2004a, Craeymeersch and Perdon, 2004b and Craeymeersch and Perdon, 2006). As a consequence, the role of *S. subtruncata* in structuring the macrobenthic community will vary due to the large spatial and temporal differences in abundance and biomass (Bodoy, 1980, Cattaneo and Massé, 1983, Ambrogi and Ambrogi, 1985, Ambrogi and Ambrogi, 1987, Fraschetti et al., 1997 and Degraer, 1999).

There appears to be a positive trend of both age and shell size with latitude, which might be a reflection of

differences in environmental conditions between areas. In the Mediterranean, *S. subtruncata* was found to reach a maximum size of 14 mm (at the age of 1 y) in the Golf of Marseille (Bodoy, 1980), and in the Ligurian and Adriatic Seas, maximum length observed was around 13 mm. Life-span did not exceed 1 and 2–3 y, respectively (Ambrogi and Ambrogi, 1985 and Fraschetti et al., 1997). During the present study, *S. subtruncata* reached a maximum age of 4 y, corresponding to a length of about 32 mm. However, larger maximum sizes have been reported for the same area (Leopold, 1996), in which the largest individual found was 37.5 mm long (Leopold, pers. comm., 2006).

4.3. Spawning and oocyte size

The drop in GMI shown in Fig. 4 suggests that spawning of *S. subtruncata* in Dutch coastal waters occurs in June or July at a water temperature of about 15–17 °C (Cardoso et al., subm. ms). From macroscopic observations of the gonad, Rueda and Smaal (2004) observed active gonads from April to June, which is in accordance with our observations. During the period of maximum gonadal mass (in May), all individuals above 12 mm shell length (corresponding to the end of the first year of life) developed gonads, suggesting that sexual maturity is a function of size and not of age. Mean oocyte diameter of spawned females was around 57 μm, corresponding to a volume of 98972 μm^3. As far as known, there are no previous records of oocyte diameter in *S. subtruncata* so a comparison with other areas is not possible. Neither is information available on larval-stage duration and timing of settlement. However, the relationship between egg/larval volume and egg/larval development time in bivalves proposed by Cardoso et al., (2006) suggests that for an egg volume of 98972 μm^3, at a mean temperature of 16 °C, egg development time (from fertilization to hatching) is around 3 days. Since the egg volume of *S. subtruncata* and *S. solidissima* is similar (Loosanoff and Davies, 1963), also a similar larval volume at hatching can be assumed. At a temperature of 16 °C and larval volume of 321,392 μm^3 (Loosanoff and Davies, 1963), larval development time is about 24 days. This suggests that it takes about one month after spawning for larvae to settle on the seafloor and that settlement in the studied *S. subtruncata* population occurred around July–August. The fact that 0-y-old individuals were present in the samples from September onwards corroborates these results.

The fact that almost all mature individuals (males and females) developed gonads during the spawning season and the release of gametes did not seem to be a problem (as observed in the experimental set-up) suggests that the current population decline is not caused by reproductive failure. Since commercial fishing on *S. subtruncata* is now regulated (Craeymeersch and Perdon, 2006) and bird predation on adults has not increased over the years (Leopold, pers. comm., 2006) it is most likely that unsuccessful settlement of spat and/or severe predation during the first months of life is responsible for the observed patterns.

A more extensive study, in terms of temporal and spatial differences in growth and reproduction between populations, as well as a larger sampling effort, will be required to fully appreciate the large year-to-year variability in population dynamics and growth of *S. subtruncata*. Nevertheless, although our results are limited to a small area of the Dutch coast, the present study allows insight into the reproductive investment of *S. subtruncata* as a first approach to understanding the cause of the near disappearance of this species along the Dutch coast.

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