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Understanding the life of a sandy beach polychaete of functional importance – *Scolelepis squamata* (Polychaeta: Spionidae) on Belgian sandy beaches (northeastern Atlantic, North Sea)

Jeroen Speybroeck*, Lotte Alsteens, Magda Vincx, Steven Degraer

Marine Biology Section, Ghent University, Krijgslaan 281, Building S8, 9000 Ghent, Belgium

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Abstract

The cosmopolitan sandy beach polychaete *Scolelepis squamata* constitutes an important food resource for juvenile flatfish and wading birds in the northeastern Atlantic, thus playing an important role in sandy beach ecosystem functioning. However, its population dynamics and life history in this part of the world have gone widely uninvestigated. Eight beach transects on Belgian sandy beaches were sampled monthly from October 2003 until October 2004, in order to investigate seasonal trends in the species' abundance, biomass, secondary production, and patterns in reproduction and zonation.

Average density, modal density and modal biomass (ash-free dry weight) (mean average density = 169 ± 9 SE ind/m^2; mean modal density = 505 ± 38 SE ind/m^2; mean modal biomass = 0.25 ± 0.02 SE g/m^2) did not exhibit major seasonal changes, whereas average biomass (0.081 ± 0.005 SE g/m^2) and individuals and biomass per strip transect (IST = 16286 ± 1330 SE ind/m; BMST = 7.8 + 0.7 SE g/m) did, peaking in May 2004. Production was calculated at 1.9 g/(m^2*year) (size-frequency method, SFM) and 0.88 g/(m^2*year) (mass specific growth rate method, MSGR) and mean annual biomass was 0.797 g/m^2; resulting in a P/B ratio of 2.40/year (SFM) and 1.11/year (MSGR), which is intermediate to moderately low compared to other polychaete species. Gravid individuals were found from February until August and a single recruitment period was observed from July until September. An average sex ratio of 1.41 ± 0.08 SE was calculated, with a female predominance. Highest densities (>200 ind/m^2) were mostly found above 3 m above MLLWS and at a median grain size from 190 to 320 μm. Average modal or peak density along each transect was situated from 3.95 m up to 4.40 m above MLLWS, in contrast to some other studies where the species was restricted to mid-tidal levels. Significant differences in elevation of peak density were found between non-gravid (411 ± 4 SE cm) and gravid (402 ± 5 SE cm) animals, but none between gravid males and females. The portion of the tidal range that was occupied by the species in the vertical dimension, just failed to differ significantly between non-gravid and gravid individuals, while gravid males (48.2 ± 5.6 SE cm) occupied a significantly wider range than gravid females (36.8 ± 4.7 SE cm), corresponding with a horizontal range difference of 6–9 m cross-shore. The observed zonation pattern, together with a trend in the difference of peak abundance elevation between males and females, are hypothesised to be a result of a strategy of gravid animals to ensure co-occurrence in a narrower zone during reproduction. Observed differences between Brazilian, Moroccan and Belgian populations (e.g. density, biomass, productivity, P/B, life span, body width, period of presence of gravid individuals and recruitment) do not seem to concur with differences in morphodynamics and might be attributed to latitude-associated gradients like climate. Furthermore, the fact that *Scolelepis squamata*, as defined today, might be a superspecies, cannot be ruled out.
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Keywords: *Scolelepis squamata*; population dynamics; ecological zonation; beaches; biological production; polychaetes; NE Atlantic; North Sea; Belgium

1. Introduction

Scolelepis squamata is a cosmopolitan bristle worm, forming a significant part of abundance and biomass of the macrobenthic fauna from sandy beaches of the North and South Atlantic, North Pacific, Indian Ocean, and the Mediterranean Sea (Souza

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* Corresponding author.
E-mail addresses: jeroen.speybroeck@ugent.be (J. Speybroeck), steven.degraer@ugent.be (S. Degraer).

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and Borzone, 2000) and encompassing a latitudinal range from 58°N to 35°S (Bayed et al., 2006). It is known to be abundant on many Atlantic beaches (Eleftheriou and McIntyre, 1976; Withers, 1977; McDermott, 1987; Souza and Gianuca, 1995; Elliott et al., 1997; Degraer et al., 2003). At the Belgian part of the North Sea, it is largely restricted to the upper intertidal zone, around and somewhat above 4 m above the mean lower low water spring level (MLLWS) (Elliott et al., 1997; Degraer et al., 2003; Van Hoey et al., 2004) but elsewhere, including in the neighbouring Netherlands, it has been reported from mid-tidal levels (Knott et al., 1983; Souza and Borzone, 2000; Janssen and Mulder, 2005) and subtidal sediments as well (Knott et al., 1983; Hartmann-Schröder, 1996; Souza and Borzone, 2000).

The species lives in fine, medium or coarse sand in temporary vertical tubes, built up by sand and mucus and it is said to dig occasionally onto a depth of 40 cm below the sediment surface (Hartmann-Schröder, 1996; Van Hoey et al., 2004). In contrast to other spionid polychaetes, this species lacks a sulcus with ciliary food transport (Dauer, 1983). Its sticky palps collect a wide range of suspended food (organic matter, planktonic animals, fragments of algae,…), which is brought to the mouth by complete contraction of these (Dauer, 1983; Pardo and Amaral, 2004). This is clearly an adaptation to the dynamic intertidal environment: wave action would wash food particles from the usual spionid palps before they can reach the mouth.

In Belgium, *Scolelepis squamata* is a species indicative for the upper intertidal *Eurydice pulchra*–*S. squamata* community, of which it comprises a large part in abundance and biomass (500 ind/m^2: Degraer et al., 2003; 343 ind/m^2 on a total of 983 ind/m^2: Van Hoey et al., 2004). Similar communities have been found in the upper intertidal parts of many beaches all over the world (McLachlan and Jaramillo, 1995). In northwestern Europe, the species also plays an important functional role, being an important food item for wading birds, especially Sanderling (*Calidris alba*) (Glutz Von Blotzheim et al., 1984), and juvenile flatfish, mainly Plaice (*Pleuronectes platessa*) (Beyst et al., 1999, 2002), but also, e.g. the syntopic occurring isopod *E. pulchra* (Hayward and Ryland, 1995) and the predacious polychaete *Eteone longa* (Hartmann-Schröder, 1996; Michaelis and Vennemann, 2005).

Early studies from the northeastern Atlantic, focusing mainly on reproductive biology and larval development, established *Scolelepis squamata* to be gonochoric, its reproduction and spawning spread over a long period consisting of pelagic fertilisation. The species is a ‘broadcast spawner’, in contrast to several other spionids exhibiting brooding (e.g. Gudmundsson, 1985). Broadcast spawning can be interpreted as an evolutionary valuable feature for an intertidal species, allowing hydrodynamically facilitated dispersal. Its development involves planktotrophic larvae being found from June to October, possibly even until January (Hannerz, 1956; Joyner, 1962; also adopted by Giangrande, 1997; Blake and Arnofsky, 1999). One study from Barbados surprised by showing that the species’ reproduction involves spermatophores (Richards, 1970), which are likely to be washed off the female body of intertidal polychaetes by waves and tidal currents. However, it has strongly been questioned that this relates to the species *S. squamata* (Blake and Arnofsky, 1999) and therefore we will not consider the results of Richards (1970). An unpublished study from the northern Netherlands was one of the first to assess benthic biomass, seasonal variation and secondary production of the species and suggested a 2-year life cycle with a single recruitment every year, resulting from the reproduction of the 2-year-old (and afterwards dying) animals (Mooij, unpublished data). More recently, two studies on the population dynamics of the species were published from other parts of the Atlantic (Brazil: Souza and Borzone, 2000; Morocco: Bayed et al., 2006). The results show some remarkable differences, stressing the need for additional research in other parts of the world. Therefore, population dynamics, local life history and zonation patterns of *S. squamata* were investigated.

2. Material and methods

2.1. Sampling

Eight cross-shore transects were sampled on the Belgian shore from October 2003 until October 2004, January 2004 excluded. Sampling started each time at high tide and continued until low tide was reached, taking a sample every half hour just above the swash zone. Sampling dates related to a fixed point in the lunar spring tide-neap tide cycle. While sampling at spring tide would have been optimal, this would have involved monthly night time sampling. Due to this practical limitation, we scheduled sampling just in between spring and neap tides. Each sample consisted of a 0.1026 m^2 rectangle, being dug out to a depth of 20 cm and sieved over a sieve with a 1 mm mesh width. An additional, adjacent sample was taken for analysis of granulometry. Elevation of sampling stations and the entire beach profile were measured using a leveller and corroborated afterwards with results of the M2 tidal reduction model (Coastal Waterways Division of the Flemish Community).

2.2. Lab procedures

To obtain a length–biomass regression, allowing calculation of biomass from measurement data, 100 undamaged specimens of all sizes were randomly collected from March and September samples. Four parts of the animal’s body were measured: (1) width of prostomium, (2) length of prostomium, (3) width of third setiger, and (4) width of tenth setiger. All 100 specimens were dried (4 h at 110 °C) and dry weight was established. Subsequent combustion (2 h at 550 °C) delivered the specimen’s ash weight and subtraction of both weights delivered ash-free dry weight (AFDW). After square root transformation of AFDW, linear regression analyses between the individual biomass and all four body measurements were executed. Comparison of level of significance (p) and explicatory power (R^2) between the five obtained equations, urged selection of width of the third setiger (S3) as the best length proxy ((1) prostomial width: $R^2 = 0.74$; $p = 0.01$; (2) prostomial length: $R^2 = 0.61$; $p = 0.02$; (3) S3; $R^2 = 0.91$; $p < 0.01$; (4) S10: $R^2 = 0.88$; $p = 0.01$), and a mathematical relationship between S3 and AFDW was established (sqrt(AFDW) = 2.84 × (width S3) −0.92; intercept: −0.92 ± SE 0.072; slope: 2.84 ± SE 0.096; $R^2 = 0.91$; $F = 870.37$; $p < 0.01$; SE of predicted y-values = 0.23).

Subsequently, S3 was measured on all collected specimens (11,958 ind.), allowing calculation of the individual biomass (AFDW). Individuals were counted and attributed to four groups: gravid (ovigerous) females, gravid males, non-gravid animals, and a group of damaged specimens for which reproductive status and sex could not be determined.

2.3. Data analysis

Counts were used for abundance-related analysis. Biomass calculation allowed calculation of secondary production, using two methods (cf. Souza and Borzone, 2000): size-frequency method (SFM: Hynes and Coleman, 1968) and mass specific growth rate method (MSGR: Crisp, 1984). Growth (von Bertalanffy growth function − parameters estimated by: (1) preliminary estimation of L_{inf} with Powel−Wetherall plot (Wetherall, 1986) and (2) using the obtained value as seeding value for growth curve fitting), mortality (instantaneous mortality rate Z, calculated assuming a single negative exponential model and applying a size-converted catch curve with the ELEFAN II routine (Pauly, 1990; Gayanilo et al., 1996)) and a cohort analysis (decomposition of size-frequency distributions into Gaussian components with Bhattacharya's method (Bhattacharya, 1967) and NORMSEP (Hasselblad, 1966; Tomlinson, 1971)) were conducted with FiSat II Software (Gayanilo et al., 1996), using ELEFAN routines (Pauly and David, 1981; Pauly, 1986). The growth function was determined by its parameters, being L_{inf}, maximum asymptotic width of third setiger; K, growth curve parameter; C, parameter reflecting the strength of the seasonal growth oscillation; WP, wintering point, moment of minimal growth; R_n, index for the goodness of fit provided by the ELEFAN I routine. If similar units and definitions are used, growth performance parameters have been shown to be remarkable constant between different populations of the same species (Munro and Pauly, 1983). For the first time to our knowledge, values for marine invertebrates are presented; both the weight-related phi (ϕ) and size-related phi prime (ϕ').

Due to its more descriptive rather than predictive capacity (Short, 1999), the beach index (BI) was preferred over the more conventional omega and RTR parameters for characterisation of morphodynamics (BI = log(((−log 2(media grain size in μm)+ 1) tidal range)/slope) (McLachlan and Dorvlo, 2005).

Given the spatially (intra-transect comparisons − zonation) and temporally (monthly sampling at the same transect locations) dependent nature of the data, statistical tests were chosen accordingly.

3. Results

3.1. Physical environment

All sampled beaches were wide and macrotidal with an average spring tide tidal range of more or less from 4.5 to 4.7 m. Beach slope was weak (0.75−1.15°) though regular, while along some transects, the small-scale relief displayed a seasonal change in morphology concerning the presence of beach runnels. Sediment analysis showed the median grain size to range from 171 to 347 μm (including lower intertidal stations were the species was absent) and the sediment to be well to moderately well sorted (SD = 1.29−1.58 μm). Values for BI of 2.7−3.0 indicate the highly dissipative morphodynamic nature of all sampled transects, as has been shown to be the case for many Belgian beaches (Degraer et al., 2003).

3.2. Life cycle, demography, reproduction and recruitment

No difference between the overall pattern and patterns per transects or per beach was observed. Four cohorts could be observed (Fig. 1; Table 1). The oldest one (C1) was only observed in samples of the first sampling month (October 2003). Most likely, specimens belonging to this cohort died subsequently. Two other cohorts were present throughout the entire sampling period (larger, older C2 and younger, smaller C3). The decrease

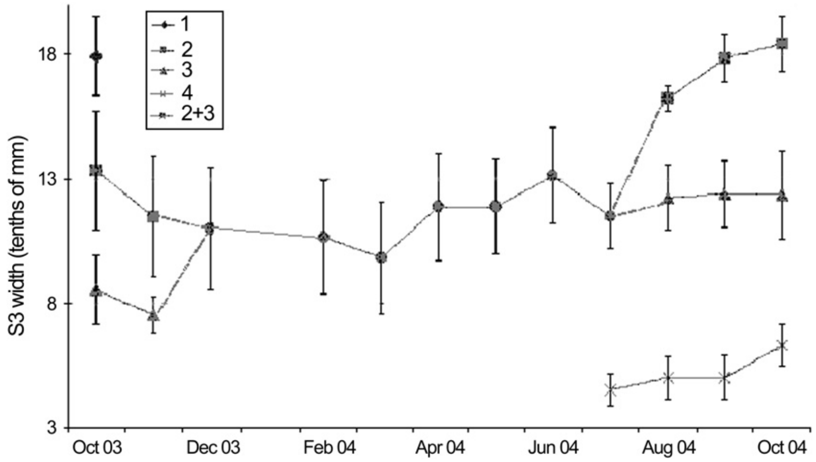

Fig. 1. Variation of S3 width of each cohort over time, as differentiated by Bhattacharya's method and consolidated by NORMSEP; dotted lines indicate fusion (November 2003−December 2003) and split (July 2004−August 2004) of cohorts 2 and 3.

Table 1
Total number (n), relative number (n %; percentage of total), average S3 width (average; tenths of mm) and standard deviation to that width (SD; tenths of mm), as obtained from the cohort analysis; C1, cohort 1, oldest cohort, C2, cohort 2, C3, cohort 3; C4, cohort 4, youngest cohort, C2 + C3 relates to the sum of the joint second and third cohorts; see also Fig. 2

	Oct 03	Nov 03	Dec 03	Feb 04	Mar 04	Apr 04	May 04	Jun 04	Jul 04	Aug 04	Sep 04	Oct 04
n												
C1	27	0	0	0	0	0	0	0	0	0	0	0
C2	580	1174	0	0	0	0	0	0	0	7	3	3
C2 + C3	0	0	1198	1111	773	1154	1381	805	701	0	0	0
C3	229	151	0	0	0	0	0	0	0	433	178	452
C4	0	0	0	0	0	0	0	0	126	183	185	253
n %												
C1	3.2	0	0	0	0	0	0	0	0	0	0	0
C2	69.4	88.6	0	0	0	0	0	0	0	1.1	0.8	0.42
C2 + C3	0	0	100	100	100	100	100	100	84.8	0	0	0
C3	27.4	11.4	0	0	0	0	0	0	0	69.5	48.6	63.8
C4	0	0	0	0	0	0	0	0	15.2	29.4	50.6	35.7
Average												
C1	17.9											
C2	13.3	11.5								16.2	17.9	18.4
C2 + C3			11.0	10.6	9.8	11.9	11.9	13.1	11.5			
C3	8.5	7.5								12.2	12.4	12.4
C4									4.5	5.0	5.0	6.3
SD												
C1	1.6											
C2	2.4	2.4								0.5	1.0	1.1
C2 + C3			2.5	2.3	2.2	2.1	1.9	1.9	1.3			
C3	1.4	0.7								1.3	1.3	1.8
C4									0.7	0.8	0.9	0.9

in S3 from October to November 2003 might be attributed to early winter conditions and associated loss of body weight. Unfortunately, the applied methods did not allow separation of these two cohorts from December 2003 until July 2004. Erratic positive and negative growth, as observed for the combined group of both cohorts, is most likely to be attributed to shifts in the relative abundance measures of both cohorts. Comparison of there numbers just before (November 2003: C2 = 89%; C3 = 11%; ($n_{C2} = 1174$; $n_{C3} = 151$)) and after (August 2004: C2 = 1%; C3 = 70%; ($n_{C2} = 7$; $n_{C3} = 433$)) the period during which they cannot be told apart, suggests a gradual decrease of dominance of the older C2, whereas the opposite can be observed for the younger C3. Settlement of recruits could be observed first in July 2004, and subsequent increase of average S3 relates to growth of this C4 cohort.

Highest numbers of gravid adults were present from the end of April until early June (Fig. 2). By September, gravid adults had disappeared from the data (Fig. 2) and only very low numbers of the reproducing C2 cohort were left (Table 1). The start of appearance of gravid adults was situated in the period of merged C2 + C3 cohorts (Table 1, Figs. 1 and 2). On average, more females than males could be found (sample averaged sex-ratio = 1.41 females/male). Some samples contained up to seven times more females than males.

3.3. Abundance and biomass patterns

Mean average density was 169 ± 9 SE ind/m^2. Due to the species being restricted to an upper intertidal zone, this figure comprises many samples of lower elevations where the species is absent. Therefore, also the mean maximum (or modal) density along each transect is given: 505 ± 38 SE ind/m^2; one sample represented a maximal abundance value of 1880 ind/m^2. A different way to express abundance is as individuals per strip transect or running (long-shore) meter: $\mathrm{IST}_r = (w_r/n_r)\sum q_i$ [ind/m], which is the sum of all ind/m^2 (q_i) from all n samples of transect r, multiplied by the horizontal width of the species distribution (w) on the beach (Defeo and Rueda, 2002). Average IST_r was 16286 ± 1330 SE ind/m and displayed significant

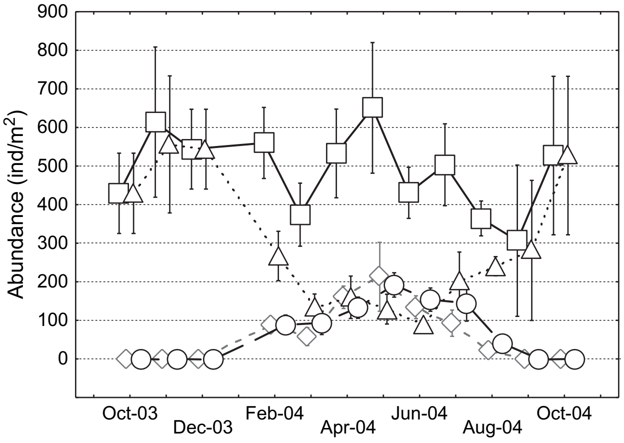

Fig. 2. Variation of total and partial abundance (ind/m^2) over time; squares and solid line, total abundance; triangles and dotted line, non-gravid animals abundance; diamonds and short-dashed line, gravid male abundance; circles and long-dashed line, gravid female abundance; error bars are standard errors.

seasonal variation (Friedman Chi Square ($N = 8$, df $= 10$) $=$ 22.6; $p = 0.013$) with lower values being apparent from June until October (Fig. 3).

Mean average biomass was 0.081 ± 0.005 SE g AFDW/m^2; mean maximum biomass along each transect was 0.25 ± 0.02 SE g AFDW/m^2. Like with IST, a biomass-related BMST was calculated. On average, this was 7.8 ± 0.7 SE g AFDW/m. BMST also displayed significant temporal variation (Friedman Chi Square ($N = 8$, df $= 10$) $= 26.98$; $p = 0.0026$), peaking simultaneously with the above estimated period of reproduction.

3.4. Growth and mortality

A von Bertalanffy growth curve was fit to the S3 width-frequency distributions (Fig. 4): $L_{\mathrm{inf}} = 2.489$ mm; $K = 0.51$/year; $C = \mathrm{WP} = 0.00$; $R_n = 0.343$. Growth performance indices were also calculated: weight-related phi (ϕ) $= 0.166$; size-related phi prime (ϕ') $= 2.5$. Instantaneous mortality rate Z was 4.08/year.

3.5. Mean annual biomass, secondary production and P/B ratio

Mean annual biomass was 0.797 g/m^2. As with Souza and Borzone (2000), values for the secondary production and P/B ratio as obtained with the SFM were higher than those estimated with the MSGR method. Annual production was 1.9 (SFM) and 0.88 (MSGR) g/(m^2*year). Deduced P/B ratio's were 2.40 (SFM) and 1.11 (MSGR)/year.

3.6. Zonation

Densities of more than 500 ind/m^2 occurred in sand with median grain size ranging from 210 to 320 µm (Fig. 5a).

Maximum density of *Scolelepis squamata* along each transect was usually encountered between 3.95 and 4.40 m above MLLWS (Fig. 5b). No significant seasonal variation in the elevation of the maximum density was detected (Friedman Chi Square ($N = 7$, df $= 9$) $= 11.23178$; $p = 0.26$).

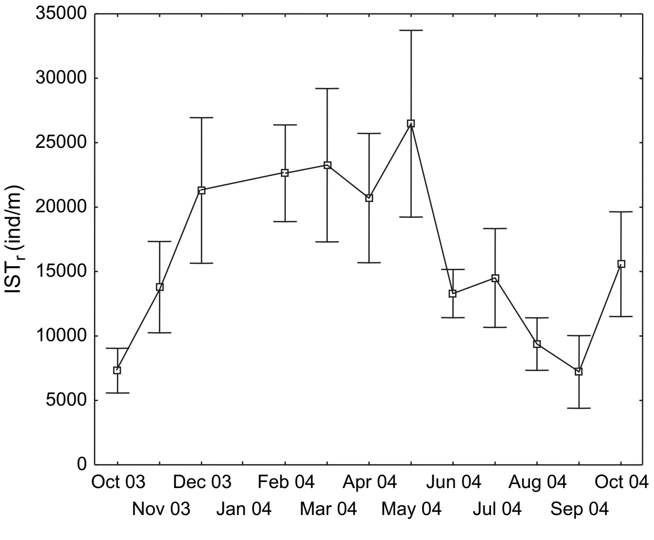

Fig. 3. Variation of individuals per strip transect (ind/m) over time; error bars are standard errors.

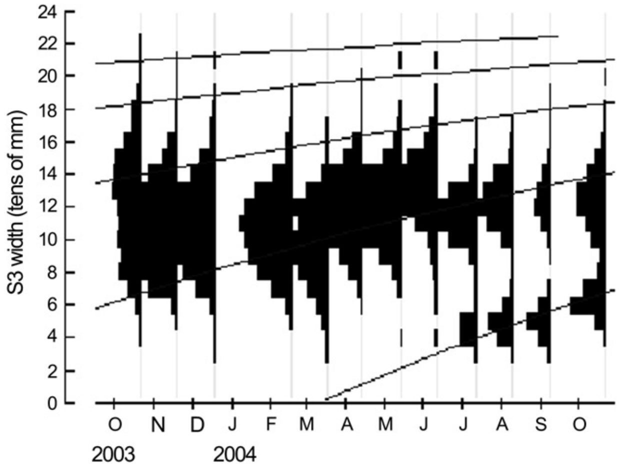

Fig. 4. Available length-frequency distributions with fitted von Bertalanffy growth curves.

Maximum density of non-gravid animals (i.e. mainly younger, pre-gravid animals) was located significantly higher on the beach than that of gravid animals (Wilcoxon's Matched Pairs Test: $p = 0.026$), with peak abundances of non-gravid animals located at 411.15 ± 4.19 SE cm above MLLWS and those of gravid animals at 401.71 ± 4.95 SE cm above MLLWS. No significant year-round difference was found between males and females (Wilcoxon's Matched Pairs Test: $p = 0.59$). Yet,

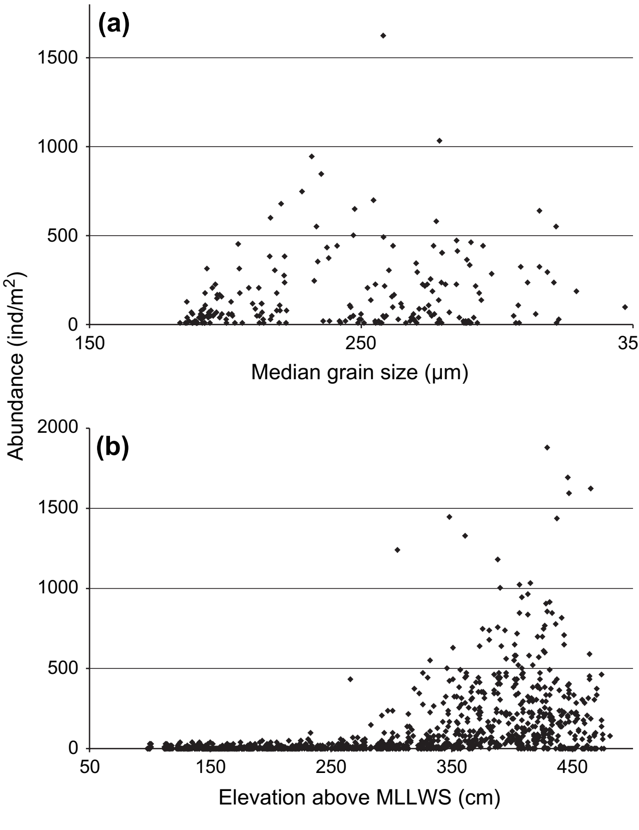

Fig. 5. Abundance (ind/m^2) as a function of (a) median grain size (µm) ($n = 214$) and (b) height above MLLWS (m) ($n = 1229$).

looking at the different months, the difference in elevation between peak densities of both sexes seemed to display a trend (Fig. 6), by which this difference is minimal at the (deduced) time of reproduction.

In contrast to earlier studies, the occupied width of the vertical intertidal range was investigated. This zone width is defined as the difference in elevation between both the lowest and highest sample containing at least five specimens (~50 ind/m^2) and was 68.0 ± 4.1 SE cm on average. Males (48.2 ± 5.6 SE cm) occupied a significantly wider range than females (36.8 ± 4.7 SE cm) (Wilcoxon's Matched Pairs Test: $p = 0.02$). In view of the beach slope, this seemingly small difference corresponds to a horizontal range difference of 6–9 m cross-shore. Gravid animals seemed to tend to occupy a wider range than non-gravid animals, being significant at the 10% level (Wilcoxon's Matched Pairs Test: $p = 0.08$).

4. Discussion

4.1. Life cycle, demography, reproduction and recruitment

Compared to spionid family averages, as calculated by McHugh and Fong (2002), Belgian *Scolelepis squamata* especially differs regarding its elevated age at first (and single) reproduction (Table 2). Also egg size (as determined by Joyner, 1962) and life span attain higher values, whereas body size is identical to McHugh and Fong's calculated family average, even though it has been mentioned that the species may reach 80–138 mm elsewhere (Hartmann-Schröder, 1996).

The discontinuous presence of gravid adults (February–August) suggests discontinuous reproduction, coinciding with discontinuous recruitment. Bayed et al. (2006) also found discontinuous reproduction, albeit gravid animals were found over a longer period (10 months instead of seven) and four different peaks of recruitment (instead of one), whereas Souza and Borzone (2000) found continuous reproduction (with two recruitment peaks) to be highly probable. Taking into account a duration of larval development of about 1–2 months (Hannerz, 1956; Joyner, 1962), the (maximum) reproductive effort can be estimated to run from the end of April until early June. This coincides with the highest observed relative abundance of gravid adults.

The observed predominance of females is in contrast to the findings of Bayed et al. (2006) but not exceptional among polychaetes (e.g. Fidalgo e Costa, 2003).

4.2. Abundance and biomass

Significant seasonal variation in IST, with lower values from June until October, suggests that the number of recruits settling in that period, is too low to compensate for the mortality among the C1 cohort, which most likely gave birth to these recruits. Whether this is a recurrent phenomenon on Belgian beaches has to be addressed with a multi-annual study, allowing assessment of interannual variation. However, we cannot rule out that this observed pattern is generated by the choice of sieving mesh width. Possibly, a bottle-neck effect for recruit abundance is at hand during the period that they are too small to be retained by a 1 mm mesh width sieve. On the other hand, demonstration of different zonation of adults and non-gravid animals (as discussed below), was possible, despite potential loss of the smallest individuals.

Concerning biomass, the only previously available assessment from Belgian beaches concerns a beach at De Panne, with total macrobenthic biomass ranging from 0.040 to 0.800 g AFDW/m^2 (Elliott et al., 1997). Thus, with considerable reservation, we might estimate *Scolelepis squamata* to be able to build up one-third of total biomass.

Despite the results from this study and earlier work, it is still not possible to identify *Scolelepis squamata*'s population size controlling factors and the role of stochasticity at different geographical scales remains poorly understood.

4.3. Growth and mortality

Remarkably, growth does not seem to be seasonally oscillating, whereas the cohort analysis suggested a decrease of S3 and biomass from October 2003 to November 2003. The goodness of fit value is slightly higher than those of Souza and Borzone

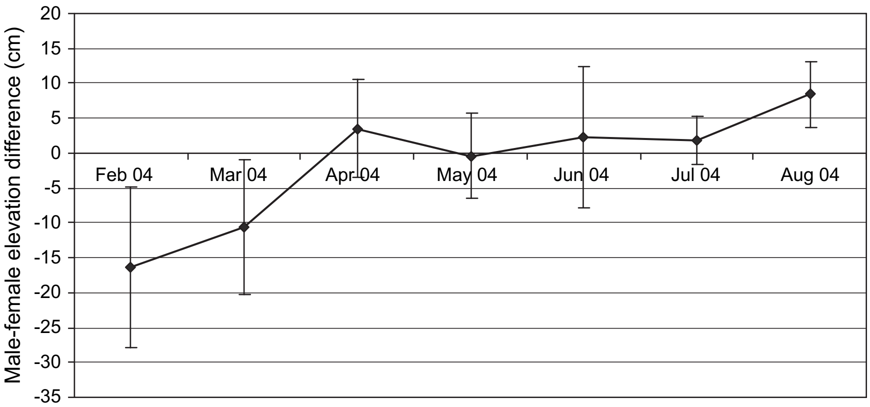

Fig. 6. Average difference between gravid males and females regarding the elevation of their maximum abundance (in cm; male peak abundance minus female peak abundance) displayed over time; error bars are standard errors.

Table 2
Comparison of Belgian *Scolelepis squamata* to family averages, as calculated by McHugh and Fong (2002). Spionidae error values are standard deviations; *n* = number of species

	Spionidae	*Scolelepis squamata*
Age at first reproduction (years)	0.5 ± 0.4 (*n* = 12)	1.8
Life span (years)	1.8 ± 0.7 (*n* = 11)	2.2
Body size (mm)	40 ± 22 (*n* = 8)	40
Fecundity (# eggs/embryos)	3676 ± 9597 (*n* = 20)	?
Egg size (diameter in μm)	145 ± 60 (*n* = 29)	192–280 μm × 106–142 μm (from UK: Joyner, 1962)

(2000) (0.28 and 0.29). Unfortunately, no previously obtained growth performance indices of the species or related animals are available. We advocate the use of these more species-specific parameters in growth studies, in order to allow better a comparison across different studies.

The observed mortality value ($Z = 4.08$/year) is of the same order of magnitude as those obtained by Souza and Borzone (2000) ($Z = 2.52$/year and 5.52/year).

4.4. Mean annual biomass, secondary production and P/B ratio

The observed P/B ratio of 1.76/year (average of SFM and MSGR) and by previous research (2.1–2.5/year in Mooij, unpublished data; 2.7/year in Souza and Borzone, 2000; 2.03/year in Bayed et al., 2006), is intermediate to moderately low in comparison with other polychaetes and other spionids (e.g. Heip and Herman, 1979; Méndez et al., 1997; Abrantes et al., 1999; Thompson and Schaffner, 2001; García-Arberas and Rallo, 2002, 2004; Kevrekidis, 2005; see also compilation of 16 spionid species in Souza and Borzone (2000)) (Table 3).

Given the harsh nature of the sandy beach environment, a higher secondary production and turnover as well as a shorter life span, would be expected. Although not visibly substantiated by data (i.e. comparable median grain size, slope and morphodynamics), it is possible that Belgian beaches provide a more benign habitat than, e.g. the Brazilian ones (Souza and Borzone, 2000), the latter inducing higher secondary production and shorter life span (P/B ratio, as average of SFM and MSGR output, 2.7) and life span of about 6 months, in contrast to 1.76 and 1.8 here). It is noted that the use of different biomass assessment techniques may hamper objective comparability of results (4 h at 110 °C and 2 h at 550 °C (AFDW) in this study; 24 h at 80 °C in Bayed et al. (2006) (DW); 6 h at 500 °C in Souza and Borzone (2000)).

4.5. Zonation

Peak abundance elevation seems to concur with Moroccan observations (Bayed et al., 2006) but not to Brazilian (Souza and Borzone, 2000) nor Dutch (Mooij, unpublished data) results. Sedimentology, slope and morphodynamics of Belgian, Dutch and Brazilian beaches seem comparable, in contrast to those of the Moroccan beach. Opposite to the results of Souza and Borzone (2000) at a local scale, no clear explanation for global differences seems to reside within these abiotic factors. Due to the relatively low number of sampled transects, local variability of abundance of *Scolelepis squamata* on Belgian beaches can for now not be attributed to grain size diameter nor to clear morphodynamic differences.

In contrast to observations made on some other macrobenthic animals, like the syntopic occurring amphipod *Bathyporeia pilosa* (Persson, 1982; as *Bathyporeia* sp. in Degraer et al., 1999), no seasonal cross-shore migration could be demonstrated and presumed limited adult mobility (Joyner, 1962), is thereby partially confirmed.

The established segregation of younger specimens and adults, with the latter situated lower on the beach than the former, has already been observed for other macrobenthic species (McLachlan and Jaramillo, 1995; Gaspar et al., 2002) and, although it was also proven for *Scolelepis squamata* by Mooij (unpublished data), it seems – to our knowledge – to have gone unpublished so far for polychaetes (Defeo and McLachlan, 2005). This segregation might be explained by smaller specimens being poorer intraspecific competitors than adults (de Alava and Defeo, 1991), but also easier water maintenance of a smaller animal body and preference for lower levels of predation found at higher elevation might explain the observed zonation of smaller individuals. Water maintenance is likely to be more restrictive for soft-bodied polychaetes than, e.g. for more

Table 3
Some examples of the P/B ratio of polychaete species

Family	Species	P/B ratio (/year)	Author
Spionidae	*Scolelepis squamata*	1.76 (average)	This study
Spionidae	*Scolelepis squamata*	2.03	Bayed et al. (2006)
Spionidae	*Scolelepis squamata*	2.7 (average)	Souza and Borzone (2000)
Spionidae	*Streblospio benedicti*	4.46	García-Arberas and Rallo (2004)
Spionidae	*Streblospio shrubsolii*	2.14 and 2.23	Kevrekidis (2005)
Spionidae	16 species, compiled by Souza and Borzone (2000)	1–12.9	Various (see Souza and Borzone, 2000)
Nereididae	*Nereis* (*Hediste*) *diversicolor*	2.5	Heip and Herman (1979)
Nereididae	*Nereis* (*Hediste*) *diversicolor*	1.97	García-Arberas and Rallo (2002)
Nereididae	*Nereis* (*Hediste*) *diversicolor*	4.4–7.9	Abrantes et al. (1999)
Capitellidae	*Capitella capitata*	23.7 and 36.7	Méndez et al. (1997)
Chaetopteridae	*Chaetopterus* cf. *variopedatus*	1.0–3.5	Thompson and Schaffner (2001)

robustly built crustaceans. The main predators of *S. squamata* are birds (especially Sanderling) and submerged predators (e.g. epibenthic fish and larger crustaceans but also other infauna species, especially *Eurydice pulchra*). Whereas the former are visual predators, likely to detect larger specimens more easily, submerged predators will have more difficulty reaching more shallow zones. The observed segregation goes accompanied by a difference in vertical tidal range zone width significant at the 10% level, with adults occupying a somewhat wider zone, suggesting that intraspecific competition for space might indeed be at work here. Additionally, the omnivorous nature of the adult animals might hamper settlement through cannibalism on their recruits. Intraspecific segregation in *Arenicola marina* has been attributed to a negative response of settling juveniles towards the presence of adults (Hardege et al., 1998; Reise et al., 2001). However, sandy beaches, in contrast to more stable muddy environments such as tidal flats, exhibit far less biological interactions and are essentially physically driven ecosystems (Defeo and McLachlan, 2005).

The observed trend in difference of elevation of peak abundance might indicate cross-shore aggregation of males and females during reproduction, in order to minimise distances to be travelled by their spawn prior to successful fertilisation. Aggregation should, however, be tested both in the cross-shore and long-shore direction involving sampling at an adequate scale, smaller than the scale at which we sampled.

In contrast to most studies on intertidal fauna, width of the vertical intertidal range was considered and showed significant differences between males and females, with males being distributed wider in the cross-shore direction than gravid females. Therefore, it seems valuable to us to include zone width in sandy beach fauna research.

Lab experiments have shown *Scolelepis squamata* to be tolerant towards sediments with a wide range of median grain sizes (Speybroeck et al., in preparation). Thus, the role of sediment as a population structuring element seems limited. The detected pattern of abundance as a function of median grain size has to be regarded as largely depending on the "by coincidence" available range of grain sizes at a given site and elevation (Table 4).

4.6. Towards global patterns of intraspecific variation in life history characteristics

It has been suggested that global differences in secondary production might be attributed to sediment stability during

Table 4
Comparison of results on the population dynamics, life history and zonation patterns of *Scolelepis squamata*

	This study	Bayed et al. (2006)	Souza and Borzone (2000)	Mooij (unpublished data)
Material and methods				
Country	Belgium	Morocco	Brazil	The Netherlands
Size proxy; alternatives?	S3 width; yes	l of prostomium; yes	S5 width; no (?)	S10 width; no (?)
Biomass quantifier	AFDW	DW	AFDW	AFDW
Sampling period (years)	1	2.25	1	1
Sampling frequency	Monthly	Monthly	Monthly	6/year
Life cycle and population characteristics				
Reproduction	Discontinuous	Discontinuous	Continuous	Discontinuous
Presence gravid animals	Feb–Aug	Jan–Feb to Nov–Dec	All year; 2 peaks	?
Life span (months)	24–26	12 (summer recruits)	6 and 9	23
Sex ratio	1.41 ♀♀/♂♂	More ♂♂	?	?
Abundance and biomass				
Mean abundance (ind/m^2)	169	130–2800	?	?
Mean modal abundance (ind/m^2)	505	1310–1348	20	?; 4800 ad. and 17000 juvenile peaks
Mean biomass (g/m^2)	0.081	?	?	?
Mean modal biomass (g/m^2)	0.25	?	?	?
Mean IST$_r$ (ind/m)	16286	?	Peaks of 92 and 319	?
Mean BMST$_r$ (g/m)	7.8	?	?	?
Growth and mortality				
Growth – VBGF parameters	$L_{\text{inf}} = 24.89$; $K = 0.51$; $C = \text{WP} = 0$	?	$L_{\text{inf}} = 0.7$ mm; $K = 3$; $C = 0.92$; $\text{WP} = 0.70$ and 0.25	?
Mortality (/year)	4.08	?	2.5 and 5.5	?
Mean annual biomass, production and P/B ratio				
Mean annual biomass (g/m^2)	0.80	5.57	0.21	22.8
P (g/(m^2*year))	1.4	11.28	0.57	56.2
P/B ratio (/year)	1.76	2.03	2.7	2.5
Zonation				
Elevation of modal density	3.95–4.40 m above MLLWS	Retention zone	Mid-tidal	Mid-tidal
Height segregation	Juveniles higher than adults	?	?	Juveniles higher than adults
Width of vertical range (cm)	68	?	?	?

?: no data.

recruitment, environmental stress and differences in successful recruitment (Souza and Borzone, 2000; Bayed et al., 2006), while the global variation in reproductive patterns and zonation cannot (or, at least, not for now) readily be linked to abiotic factors (slope, median grain size, morphodynamics,…). It is not possible to fit the available data to general trends of latitudinal variation in population features, as presented by Defeo and McLachlan (2005) and all available studies are too short termed to allow assessment of the importance of episodic environmental events. A clinal gradient induced by climatology might be at work, yet with only a handful of studies available, a worldwide pattern cannot be drawn, thus, this hypothesis cannot be tested. Disregarding possible taxonomical imperfection, northwestern European populations of *Scolelepis squamata*, like those from this study and those studied by Mooij (unpublished data), are leaning more towards *K*-strategy than the apparently more short-lived, multivoltine populations from Morocco and especially Brazil. An accordingly anticipated, lower P/B ratio is, however, not immediately apparent; the Brazilian ratio is higher, while the Moroccan one is not. As mentioned, comparability of these values might be hampered by differences in applied methodology. Whereas observed differences in abundance and biomass, secondary production, P/B ratio, life span, reproductive patterns and zonation might be attributed to both intraspecific plasticity of life history characteristics and a differential response to morphodynamical variation of the studied beaches, one might ponder upon the limits of intraspecific variation. A remarkable fact is the observed variation in body size between the available studies. Recalculation and comparison of the applied body length proxy measures shows animals from Belgian beaches to be of comparable size as those from the Wadden Sea (Mooij, unpublished data). In contrast, animals from southern Brazil seem to be only half as broad (setiger width) as Belgian one, whereas Moroccan ones would have a prostomium length twice that of the Belgian populations. Without being able to draw any certain conclusions, these differences should at least raise some suspicion. Confusion on whether the same species is being dealt with has already arisen (Richards, 1970; see Blake and Arnofsky, 1999), in part being evoked by propagation of the older name *Nerine cirratulus* (e.g. Bhaud, 1986). Therefore, taxonomical research seems desirable, in order to assess whether *Scolelepis squamata* as defined today might be a superspecies, as already hinted by Pardo and Amaral (2004).

5. Conclusions

Clearly differing to the discussed extent from studies from other parts of the world, Belgian *Scolelepis squamata* are semelparous with a long life span of about 24 months. A single recruitment per year (from July continuing at least until October) is produced by each cohort after about 2 years of growth (although occasional spawning of larger 1-year-old specimens cannot be ruled out) and followed by death, making the species monotelic. Absence of a winter stop in growth can be regarded as a somewhat surprising result. Differences between different studies might be related to taxonomical imperfections and some molecular assessment seems desirable. The – to our knowledge – first evidence of polychaete intraspecific cross-shore size segregation provides a novel result for sandy beach ecology research.

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