
Chapter 5

Population – dynamics of subtidal *Lanice conchilega* (Pallas, 1766) populations at the Belgian Continental Shelf



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Abstract

The paper at hand describes population dynamics, recruitment and persistence of the *Lanice conchilega* populations in subtidal soft – bottom sediments along the Belgian coastline. An intensive sampling campaign (monthly – biweekly from March 2002 until September 2003), the discrimination of different benthic stages and cohort analysis of the adult population enabled the discrimination of trends in recruitment patterns of *L. conchilega*. Three recruitment periods were defined based on the occurrence of peaks of aulophore larvae in the water column and peaks of recently settled individuals in the benthos: (1) spring recruitment period (April – July), (2) summer recruitment period (July – September), and (3) autumn recruitment period (September – November). The spring recruitment period was the most intense and was characterized by high densities of recently settled individuals and juveniles. These high densities resulted in an adult population, which consisted of different cohorts and which was characterized by a high turn over. The summer and autumn recruitments were less intense and did not occur at every station or in every year. Spatial and temporal variations in timing and intensity of settlement and recruitment were observed and described. Results indicate that *L. conchilega* is an opportunistic species, characterized by a long pelagic phase, high settlement of larvae and a high turn over in the adult population. Due to this recruitment strategy and the preferential settling of the larvae in adult patches, the studied *L. conchilega* population was able to maintain high abundances in moderately stable patches.

Keywords

Lanice conchilega, population-dynamics, life-cycle, aulophora larvae, growth, Belgian Continental Shelf

Introduction

Lanice conchilega (Pallas, 1766), a tube-building terebellid polychaete, is a wide-spread species commonly encountered in European intertidal and shallow subtidal sands (< 100m), where it reaches densities of up to several thousands of individuals per m² (Buhr & Winter, 1976; Ropert & Dauvin, 2000; Callaway, 2003). The tubes of adult *L. conchilega*, made from cemented sand grains and shell breccia, have a diameter of about 0.5 cm and are up to 65 cm in length (Ziegelmeier, 1952). The anterior end of the tube protrudes above the sediment surface by 1 - 4 cm and is crowned with a sand-fringe. *Lanice conchilega* prefers surface deposit feeding when occurring in low densities and switches to suspension feeding in the case of high densities (Buhr & Winter, 1977). The species is of high ecological importance since (1) its dense populations affect sediment properties (Jones & Jago, 1993) and oxygen transport (Forster & Graf, 1995), (2) it alters the composition of benthic communities (Zühlke, 2001), and (3) it is an important food item for birds and fish (Petersen & Exo, 1999).

Lanice conchilega has a complex life cycle that includes separate larval (planktonic), juvenile and adult phases. The planktonic larval stage of *L. conchilega* was termed aulophore by Kessler (1963) and is characterized by the presence of a transparent tube, which is used as a floating device. The aulophore looks like a juvenile individual, but has a number of larval characteristics (Bhaud & Cazaux, 1990). The aulophore stage succeeds an intermediate benthic stage (1 - 2 days), which in turn follows a short-lived planktonic trochophore and metatrochophore phase (5 days) (Bhaud, 1988; Marcano & Bhaud, 1995). Since aulophore larvae spend up to 60 days in the plankton, they have the ability to disperse over large distances, depending on the hydrodynamical regime. According to Heuers et al. (1998), settling aulophores prefer tubes of adult *L. conchilega*, shell fragments or other hard epibenthic structures. During the settlement of aulophore larvae, the tentacles glue the anterior end of the larval tube to the substratum and extend the width and length of the tube by gathering sediment particles (Heimler, 1981). A *L. conchilega* individual grows and stabilizes its tube into the sediment during its benthic life, but maintains the capability to re-establish its tube after being washed out (Nicolaidou, 2003). Even though the life span of this species is estimated to be 1-2 years (Beukema et al., 1978) or up to 3 years (Ropert & Dauvin, 2000), there is no information on the age at maturity. A lot of processes can affect the duration of each stage and the transition between stages (e.g. the availability of food, intra- and interspecific competition for space and food, mortality due to factors such as predation and physiological stress (e.g. intolerable temperatures, salinities or oxygen concentrations), disease or parasites (Eckman, 1996)).

A lot of studies have described the planktonic larval phase of *L. conchilega* (Bhaud, 1988; Belgrano et al., 1990; Bhaud & Cazaux, 1990; McHugh, 1993; Marcano & Bhaud, 1995), but fewer investigations studied the benthic settling and population structure (e.g. intertidal studies of Ropert & Dauvin, 2000 and Callaway, 2003). Up till now, none of the studies about *L. conchilega* combined information on the planktonic and benthic stages.

The present study aims to disentangle the population dynamics of a subtidal *L. conchilega* population through observation of the larval phase (aulophore larvae), benthic settling and the adult population structure on three sites in the coastal area of the Belgian Continental Shelf (BCS) during a 1.5 year

period (March 2002 – September 2003). The main research questions are the following: (1) How strong are the turnover and the spatial and temporal variability within a *L. conchilega* population, and (2) Is there temporal stability of the patch locations of *L. conchilega* in subtidal environments?

Materials and Methods

Study area

Three sampling stations in the Belgian coastal zone, which is a part of the Southern Bight of the North Sea (Figure 1), were investigated concerning the population dynamics of *Lanice conchilega*. Station O1 (51° 28.16'; 3° 09.11') is situated in the northeastern coastal zone (NCZ), north of the 'Vlakte van de Raan', whereas WK1 (51° 09.13'; 2° 37.25') and WK2 (51° 09.13'; 2° 32.72') are situated in the southwestern coastal zone (SWZ), in the 'westdiep' gully at the slopes of the Broersbank and Smalbank, respectively (Van Hoey et al., 2005). The three stations are situated at a depth below MLWS of 14 m for station O1, 15 m for station WK2 and 12 m for station WK1. The coastal zone of the BCS is characterized by turbulent, nutrient rich inshore-waters and a dominance of muddy sands. The NCZ is further strongly influenced by the Westerschelde estuary (Van Hoey et al., 2005).

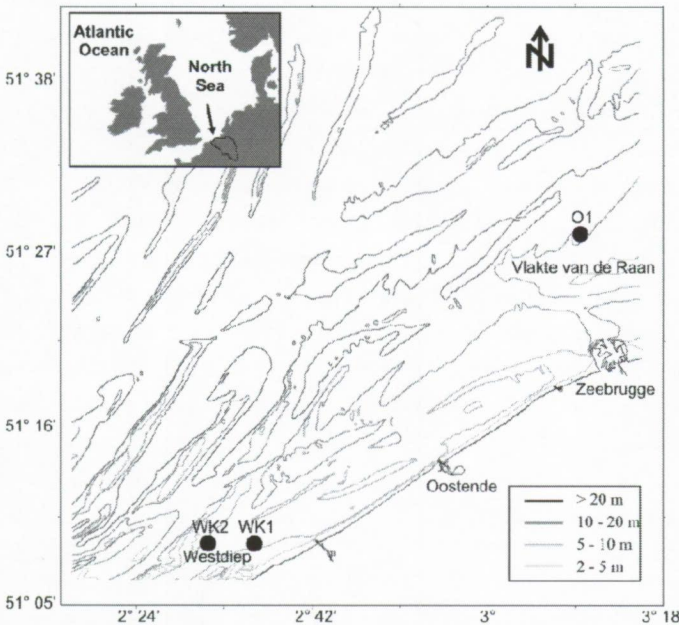


Figure 1. Map of the Belgian Continental Shelf with the location of the three stations (WK1, WK2 and O1).

Data origin

The three stations were sampled monthly (September – April) or biweekly (May-August) during the period March 2002 - September 2003. Such a frequent sampling is seldomly found in population dynamical studies (Thompson and Schaffner, 2001 and the study at hand), but is usually monthly or bimonthly (Garcia-Arberas & Rallo, 2002; Roubah & Scaps, 2003; Garcia-Arberas & Rallo, 2004; Plyushceva et al., 2004; Kevrekidis, 2005). At every sampling occasion and at every sampling station, macrobenthos and plankton samples were taken. There are, however, some gaps in the sampling period due to logistic problems.

The plankton samples were taken with a trawl plankton net with a net aperture of 1 m diameter and a mesh size of 200 μm . Sampling the entire water column and especially the part nearby the bottom was ensured by taking the plankton net down, holding it passively during a period of 1 (in plankton bloom periods) to 2 minutes nearby the bottom and then pulling it up. After cleaning the net, the plankton was sieved on a 200 μm mesh sieve and fixed in a 4% formaldehyde seawater solution. The sampled water volume was calculated using the following equation: water volume filtered (m^3) = $\pi \times (0.5\text{m})^2 \times$ the sampling distance in meter. The sampling distance was measured by an electronic flow meter, which was fitted in the net aperture.

In the lab, the aulophore larvae of *L. conchilega* were counted by taking subsamples of 10 ml out of a fixed volume (depending on the size of the sample) that was continuously homogenized. This procedure was repeated until a volume was reached, that contained minimally 100 aulophore larvae (Thiébaud et al., 1992). Afterwards, the amount of aulophore larvae was standardized to numbers per m^3 . Aulophore larvae were recognized by a slimy, transparent tube and a morphological organization clearly marked by numerous segments (Bhaud, 1988).

The macrobenthic samples were taken with a Van Veen grab (sampling surface area: 0.1026 m^2) and sieved after fixation (with 8% formaldehyde seawater solution) over a 1 and 0.5 mm sieve. The amount of *L. conchilega* individuals retained on these two sieves was combined in the final dataset. On each sampling occasion and location three replicate samples were taken.

While processing the benthos samples, a distinction was made between the following developmental phases of *L. conchilega*: (1) recently settled individuals (morphological features similar to aulophore larvae, without transparent tube); (2) juveniles (recently settled individuals with prolongation of the abdomen, building a small tube); (3) young adults (*L. conchilega* individuals with a tube diameter < 1 mm); (4) adults (*L. conchilega* individuals with a tube diameter > 1 mm, therefore not mature) and (5) tubes with intact sand fringes (Figure 2). No discrimination between mature and immature individuals was made. Counting tube tops with intact sand fringes has been previously used to estimate the densities of *L. conchilega* (Ropert & Dauvin, 2000; Strasser & Pieloth, 2001; Callaway, 2003; Van Hoey et al., submitted).

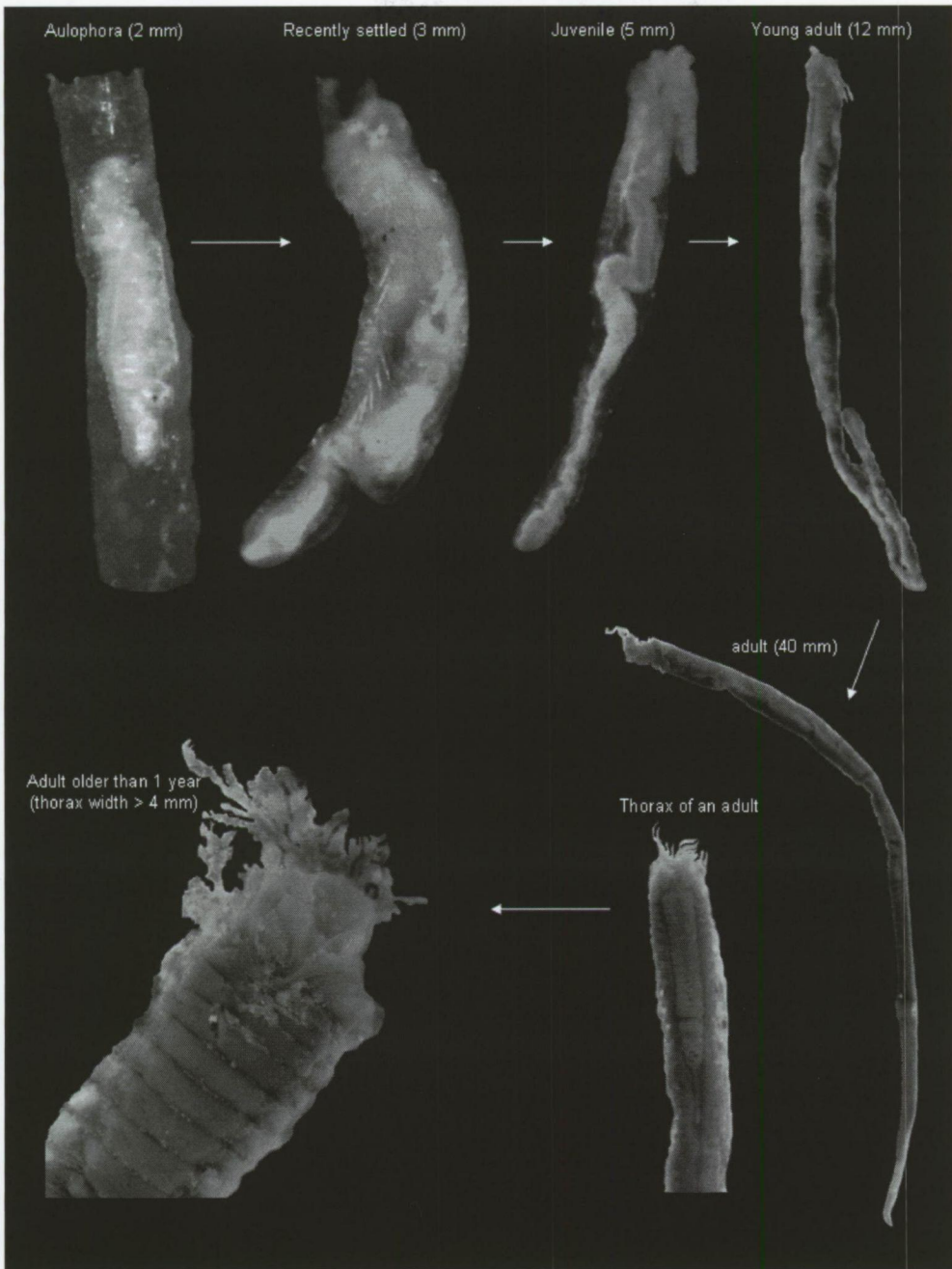


Figure 2. Picture of the different developmental phases of *L. conchilega*

Data analysis

Buhr (1976) and Ropert & Dauvin (2000) used the internal diameter of the *Lanice* tube as a proxy for biomass, whereas Callaway (2003) found a significant correlation between the width of the tubes and the thorax width. The use of partial size measurements is highly extended in studies on the population dynamics of polychaetes in order to estimate biomass and production (Garcia-Arberas & Rallo, 2002). The diameter of the tube was measured by introducing a cone-shaped stainless steel gauge into the opening of the tube. The diameter of the instrument varied from 0 to 5 mm with steps of 0.01 mm. The relationship between the individual ash free dry weight, assessed firstly by drying for 4 hours by 110°C (Dry weight) and then burning at 550°C for 4 hours (Ash weight), and the inner diameter of the sand tube was linearly shaped and expressed as:

$$\text{Sqrt}(\text{AFDW}) = 0.0612 * \text{diameter} - 0.0366 \quad (N = 61; r^2 = 0.9186, p < 0.001)$$

with D the inner diameter of the sand tube (mm) and W the ash free dry weight (g) (Figure 3).

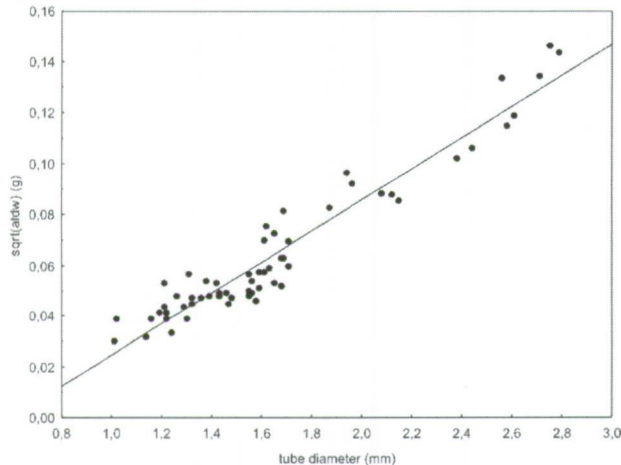


Figure 3. The relationship between the individual ash free dry weight (mg) and the inner diameter of the sand tube (mm).

The tubes were subjected to diameter measurements and were classified into 0.1 mm classes. In order to detect and separate cohorts, the length-frequency distributions were subjected to modal analysis with the help of the software NORMSEP (Tomlinson, 1971), which is based on the means detected in the analysis of the histograms with the Bhattacharya method (Bhattacharya, 1967). This method splits composite length-frequency distributions into separate normal distributions. The normal components (mean, theoretical number per group, standard deviation) of frequency size distributions were identified for each date with an adequate number of individuals. The means of the normal distributions for all sampling dates were then linked to trace the modal length progression of the cohorts. The growth rates were estimated as the differences in mean tube width values of the individuals of identified cohorts between successive samplings. The secondary production was

calculated by means of the weight increment method, which estimates the production as the increment of biomass from one sampling date to the next for each cohort separately, and for the whole sampling period (Crisp, 1984). All these analyses were done with the program FISAT II (FAO-ICLARM Fish Stock Assessment Tools).

Results

Environmental data

The stations O1, WK2 and WK1 were characterized by fine muddy sand, with an average median grain size of 197 ± 39.4 (SD), 196 ± 5 (SD) and 177 ± 2.4 (SD) μm , respectively, and an average mud content of 17.9 ± 12.47 (SD), 7.12 ± 3.28 (SD) and 5.7 ± 4.75 (SD) % (Figure 4). The median grain size was quite stable at stations WK1 and WK2, whereas at station O1, there were considerable fluctuations including three periods of lower median grain size (July - August 2002; May - July 2003 and after August 2003). These oscillations were caused by increases in the mud content during July - August 2002 (17 and 21%) and during May - July 2003 and after August 2003 (above 20%, up to 47.6%).

The water temperature at the three stations reached its highest values in August 2002 and 2003 (19.1°C - 20.0°C and 21.2°C - 22.0°C) and the lowest values in February 2003 (4.3°C - 4.4°C). The temperature increase after the winter of 2002-2003 was detected much faster at station WK2 (March - April 2003: 7.2 - 10.6°C) compared to station O1 (March - April 2003: 6.0 - 9.6°C).

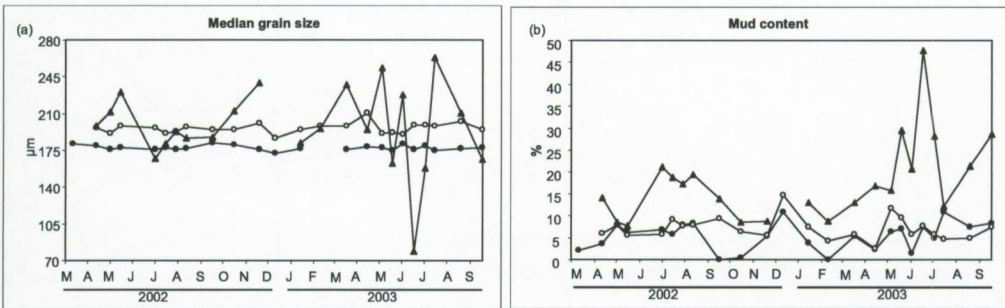


Figure 4. Distribution of the median grain size (a) and mud content (b) during the sampling period at the three stations (station WK1: black points; Station WK2: open points; Station O1: black triangle).

Life cycle and demography

Periods of recruitment

General pattern

In this section, the general recruitment pattern of *L. conchilega* is described based on the observations of 2002. Three peaks in the density of aulophore larvae could be observed: (1) a peak of very high densities in early May (O1: 859 ind/m³; WK2: 437 ind/m³), (2) a very small peak at the end of July (O1: 62 ind/m³; WK2: 41 ind/m³), and (3) a small peak in autumn (September – October) (Figure 5). During winter, aulophore larvae were scarcely found (< 2 ind/m³). The three peaks in the planktonic density of aulophore larvae (spring, summer, autumn) were also detected in the benthos samples, in which the different successive stages (recently settled, juvenile, young adults and adults) followed each other in their density peaks (Figure 6). The three periods, in which increased densities of aulophore larvae and benthic stages were found, will further be referred to as (1) spring recruitment period (April – July), (2) summer recruitment period (July - September) and (3) the autumn recruitment period (September – November).

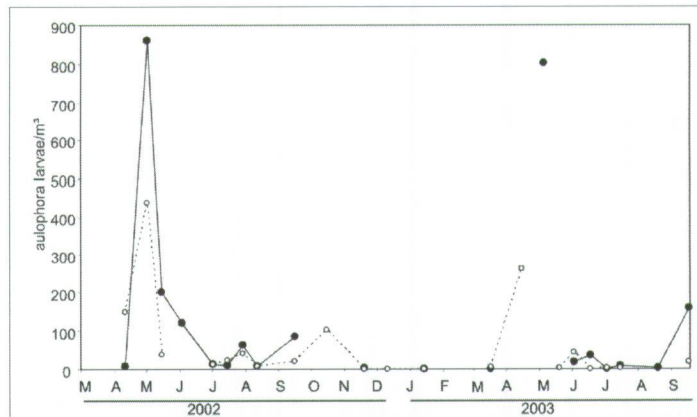


Figure 5. Density distribution of the aulophore larvae in the water column at station WK2 (open points, dotted line) and station O1 (black points, black line).

During the spring recruitment period, the settling phase of *L. conchilega* (recently settled individuals) was found from April 2002 onwards at the three stations and reached its highest densities in early May (1855 ind/m² at station O1, 2651 ind/m² at station WK2, 5292 ind/m² at station WK1). Hereafter, early July, the densities declined to < 10 ind/m² at stations WK2 and WK1, and to 64 ind/m² at station O1. The older stages of *L. conchilega* (juvenile and young adult) showed a similar pattern, though with a time lag of about two weeks. Juveniles and young adults from the spring recruitment were found until half of July, but this pattern was not clearly defined due to the partial overlap with the summer recruitment period. Due to the spring recruitment, the adult densities started to increase from half of May – June 2002 and reached their highest densities in early July (2495 ind/m² at station O1, 1439 ind/m² at station WK2, 1059 ind/m² at station WK1).

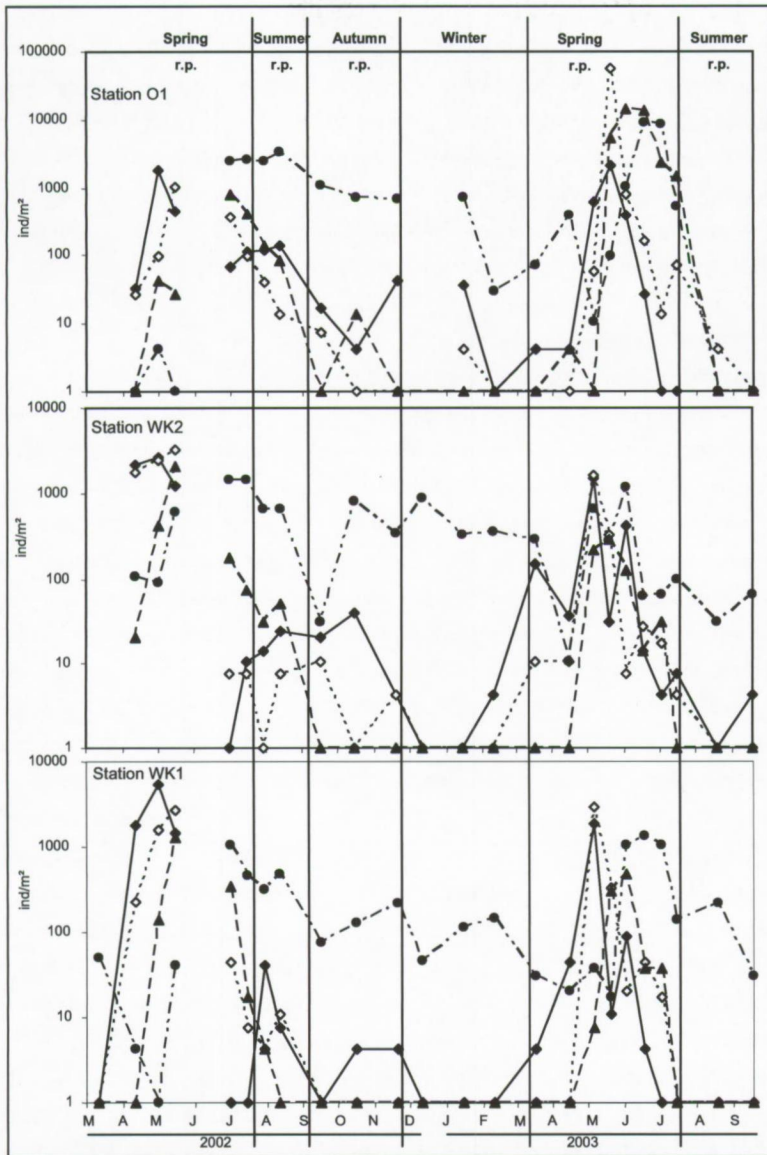


Figure 6. Density distribution of the different benthic stages of *Lanice conchilega* for the three stations: recently settled individuals (black rhombus, black line), juvenile individuals (open rhombus, dotted line), young adults (black triangle, interrupted – dotted line), adults (black points, interrupted – dotted line). Sampling points with a time lag of more than one month were not connected. (r.p.: recruitment period)

During the summer recruitment period, an increase of the density of recently settled individuals could be found from half of July until August (64 – 136 ind/m² at station O1, 10 – 22 ind/m² at station WK2 and 39 – 6 ind/m² at station WK1). The densities of the juveniles and young adults decreased at the three stations or remained stable at low densities (± 10 ind/m²). The adult densities remained high at

station O1 (to 3434 ind/m²) or but decreased at stations WK2 (to 650 ind/m²) and WK1 (to 478 ind/m²) during the summer period.

During the autumn recruitment period, a small density increase of recently settled individuals was detected at stations O1 (42 ind/m²) and WK2 (40 ind/m²), in some cases followed by small peaks of successive stages. At station WK1, only low densities (3 ind/m²) of recently settled individuals were found, but no following successive stages and therefore no autumn recruitment.

During the winter, recently settled (max 36 ind/m² at station O1) and juvenile individuals (3 ind/m²) were scarce. In autumn-winter, the densities of adult individuals declined (1105 - 72 ind/m² at station O1, 794 - 284 ind/m² at station WK2, 215 - 30 ind/m² at station WK1).

Spatial and temporal variability

Within this generally observed recruitment pattern of *L. conchilega*, spatial differences in timing and intensity, and year-to-year variations were detected. On a small spatial scale (stations WK2 and WK1 - hundred of meters), the same recruitment patterns were observed, except for the absence of a successful autumn recruitment (at station WK1) and differences in intensity of the density peaks (e.g. density of recently settled individuals in May: 5293 ind/m² at station WK1 and 2652 ind/m² at station WK2). On a larger spatial scale (stations WK2 - WK1 and O1 - kilometres), differences in timing and intensity were observed. In 2003, a time lag of about two weeks was observed in the recruitment pattern between station O1 and stations WK2 - WK1 and the density peaks of recently settled individuals (< 100 ind/m² at station O1, > 1000 ind/m² at stations WK2 - WK1) and aulophore larvae (149 ind/m³ at station WK2, 7 ind/m³ at station O1) were already higher in April 2002 at stations WK2 - WK1 compared to station O1.

Next to spatial differences between stations WK2, WK1 and O1, a temporal difference was observed between the two investigated years (2002 and 2003). The most obvious temporal difference between the two years concerned the recruitment intensity. For stations WK2 - WK1, the densities of the *L. conchilega* stages (e.g. total density half May at station WK2: 640 ind/m² in 2003 and 6608 ind/m² in 2002), were lower in the spring recruitment period of 2003 than in 2002, resulting in lower adult densities in 2003 compared to 2002 (e.g. adult density for station WK2 in the beginning of July: 66 ind/m² in 2003, 1440 ind/m² in 2002). The inverse pattern was observed at station O1, with lower densities of the benthic stages of *L. conchilega* in 2002 (1030 ind/m²) compared to 2003 (juveniles, 57017 ind/m²). The spring recruitment at station O1 in 2003 was not successful, due to the disappearance of adult *L. conchilega* individuals in the summer. In 2003, no summer recruitment period was detected for the three stations (density of recently settled individuals <10 ind/m²).

Adult population structure

The size frequency histograms clearly show that small individuals (\varnothing 1 - 1.5 mm) were only found during the period April - October, which indicates a long period of recruitment (Figure 7). During the winter period (November - March), no obvious new recruitment was detected and the size frequency distribution remained rather stable. During the prolonged recruitment period, the densities of the small individuals decreased in time. In June - July, the majority of the large individuals (\varnothing > 3 mm) disappeared, and older solitary individual (\varnothing > 4 mm) were only occasionally found.

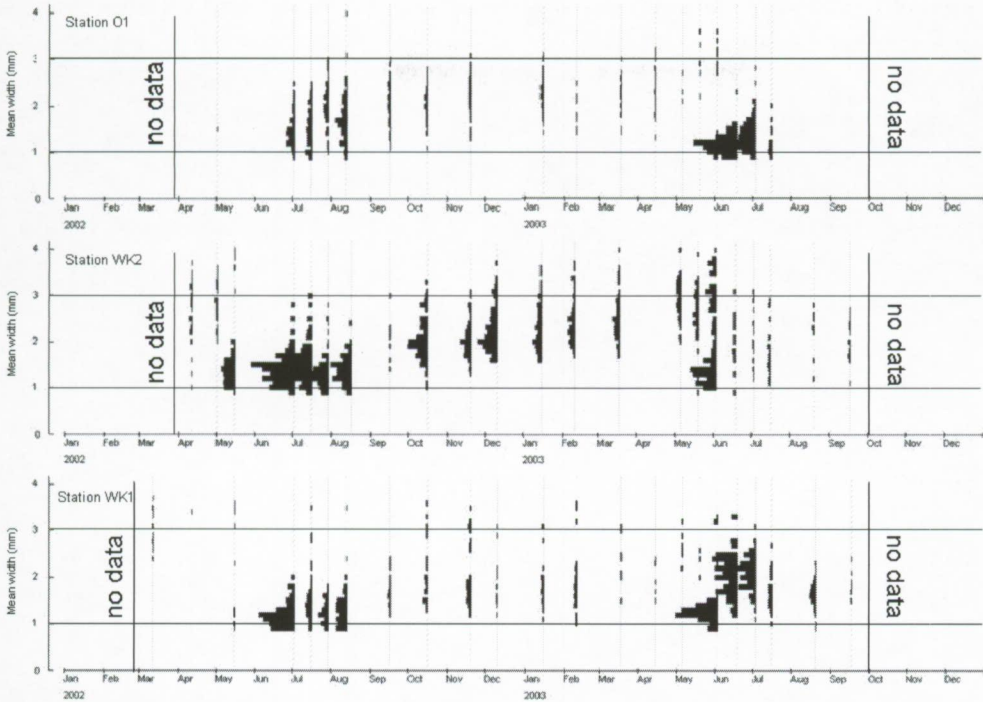


Figure 7. Size-frequency distribution of the adult *Lanice conchilega* individuals for the three stations

Cohorts

Based on the size frequency distributions, different cohorts were objectively distinguished using the Bhattacharya method and were afterwards validated by NORMSEP (see Material and Methods) (Figure 8). A cohort is defined as the individuals originating from a well outlined recruitment moment. In the present study, almost on every sampling date, a new cohort could be distinguished, which was due to the constant presence of *L. conchilega* individuals of the smaller size classes during April - October. Based on the presence and abundance of aulophore larvae and recently settled stages of *L. conchilega*, three periods of recruitment were defined. The different identified cohorts were lumped into groups representing the individuals originating from the respective recruitment periods. The cohort - groups reflect the growth and population structure of the individuals originating from a certain recruitment period.

New cohorts were detected from April until October, with small differences between the three stations; no new cohorts were observed during winter (Figure 8). At station WK2, some cohorts originating from 2001 could be defined. The spring cohort - group contained different cohorts appearing from April until July and disappeared within the same year or in the following year. The cohorts, which disappeared within the same year, reached a maximum tube width of 3 mm, whereas the survivors of the winter period reached a maximum tube width of up to 3.5 mm. The summer cohort - group consisted of 1 or 2 cohorts originating from August - September, and disappeared in the following year.

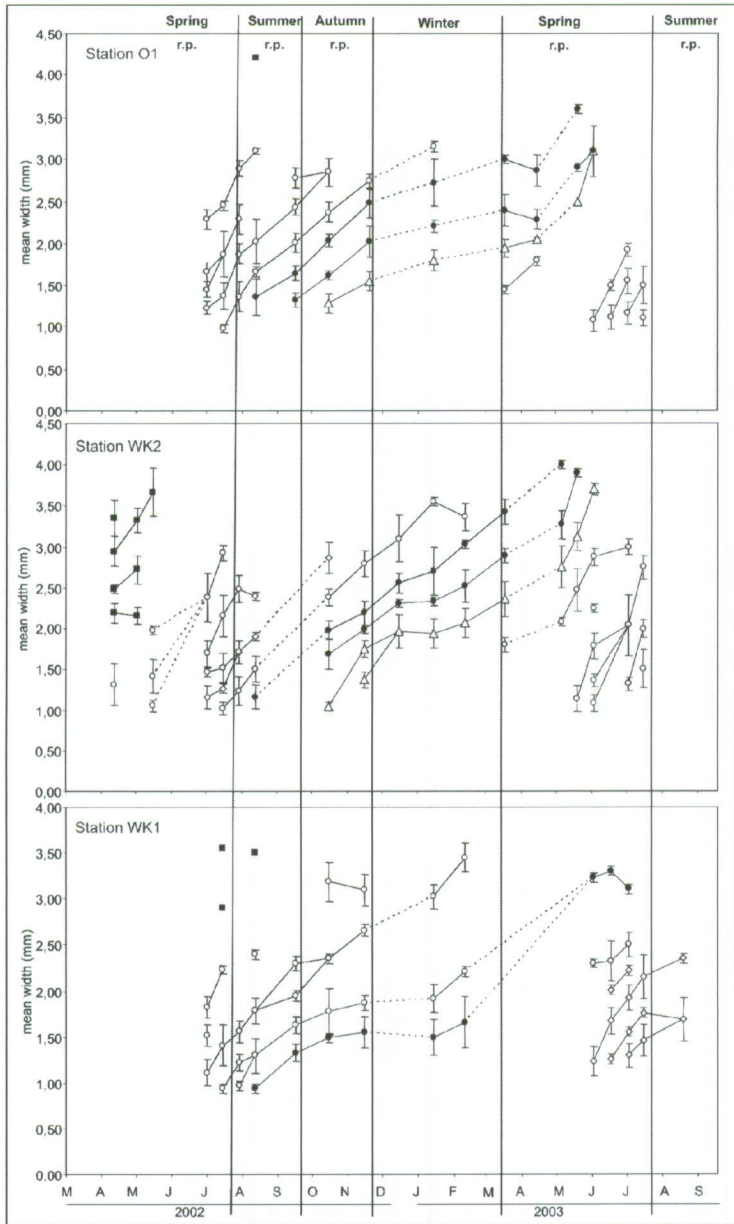


Figure 8. Variations of the mean tube width (in mm) of each *Lanice conchilega* cohort differentiated by Bhattacharya and validated by NORMSEP during the sampling period for the three stations with indication of the recruitment periods (r.p.). Cohorts of 2001 (black square); cohorts of the spring recruitment period (open points); cohorts of the summer recruitment period (black points); cohorts of the autumn recruitment period (open triangles). Sampling points with a time lag of more than one month were connected with a dotted line.

Finally, the autumn cohort – group, originating from October – November, survived until spring of the following year. The individuals of the summer and autumn cohorts reached a maximum tube width of

3.5 to 4 mm. Mean widths were sometimes characterised by a relatively large standard deviations, due to the overlap between some cohorts.

Population size

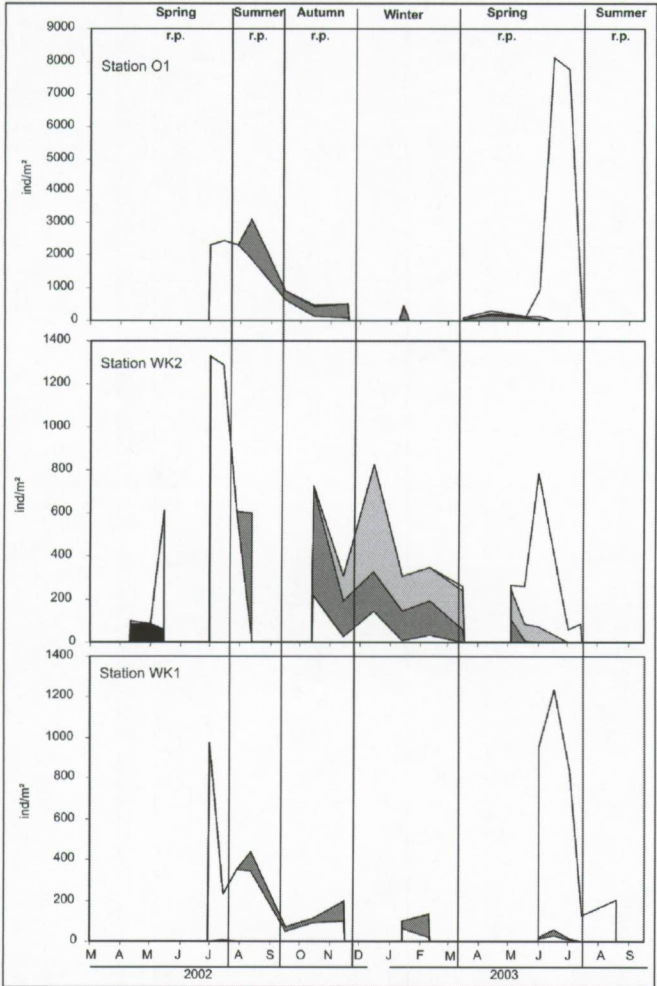


Figure 9. *Lanice conchilega* adult population structure (density of each cohort - group originating from a defined recruitment period) during the study period for the three stations with indication of the recruitment periods (r.p.). Population of 2001 (black), spring recruitment (white), summer recruitment (grey), autumn recruitment (light grey). Sampling points with a time lag of more than one month were connected with a dotted line.

At station WK2 only, a population originating from 2001 was still represented in relatively high densities (+ 100 ind/m²) in May 2002 (Figure 9). During the period of investigation, two major density peaks (June – July 2002 and 2003), consisting of individuals of the spring cohort – group, were observed. After the peak, the densities decreased rapidly. The abundant presence of individuals from the summer cohort – group resulted in a second peak in August 2002 at the stations. The

overwintering population of *L. conchilega* mainly consisted of individuals from the spring or summer cohort - group, whereas at station WK2, the densities of the individuals from the autumn cohort - group were similar to those of the other cohort - groups during winter. Generally, the spring cohort - group formed not always the dominant group in the population of the following year, despite its high densities after the spring recruitment.

Biomass

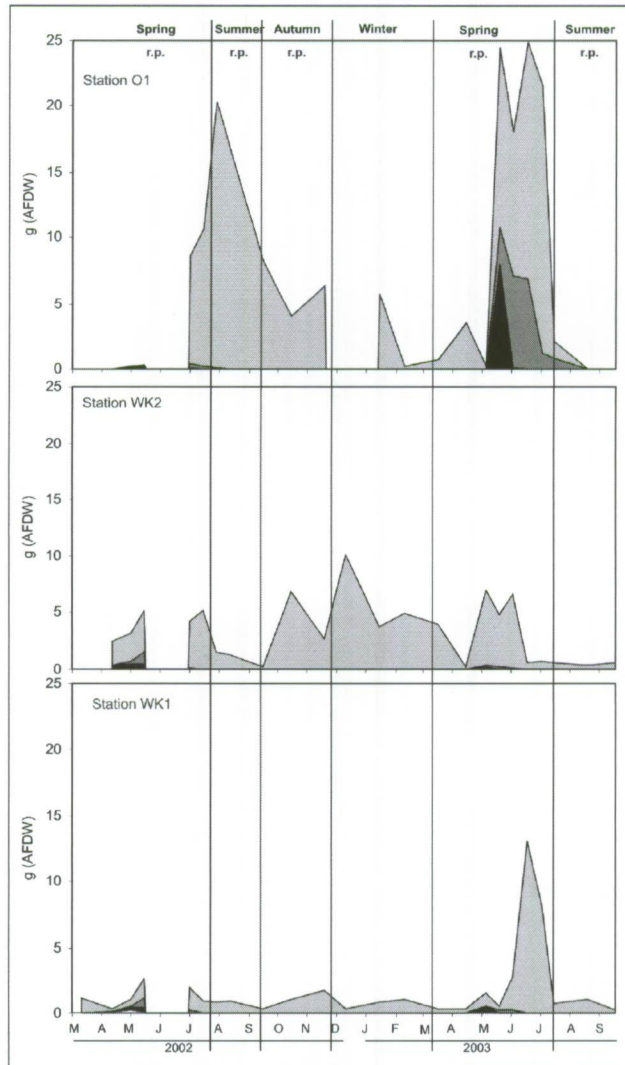


Figure 10. Biomass (g AFDW) pattern of the different benthic stages of *Lanice conchilega* for the three stations with indication of the different recruitment periods (r.p.): recently settled individuals (white), juvenile individuals (black), young adults (grey), adults (light grey). Sampling points with a time lag of more than one month were connected with a dotted line.

The biomass values (expressed as grams AFDW) at the three stations were primarily determined by a high relative contribution of adults in the population (Figure 10). During spring – summer, the high adult biomass resulted from high densities of small individuals, while the high autumn – winter biomass resulted from the presence of bigger individuals (in lower numbers). Only during the spring recruitment, other benthic stages were present in such high numbers that they significantly contributed to the total biomass. The highest biomass values were recorded at station O1 in the summer of 2002 (up to 20.3 g/m²) and in May-June 2003 (up to 24.9 g/m²). These peaks were caused by the high relative contribution of the adult biomass in the summer of 2002, of juveniles and adults in May 2003 and of young adults and adults in June 2003. At station WK2, biomass reached its highest values in July (5.1 g/m²) and in autumn – winter 2002-2003 (up to 10.1 g/m²), due to the high relative contribution of the adult population. At station WK1, the biomass values were low in 2002 (0.2 - 1.8 g/m²) compared to the other stations, due to the smaller adult population. In June 2003, high densities of adults originating from the spring recruitment of 2003 resulted in higher biomass values (maximum 13 g/m²).

Growth

Growth was more distinct at station WK2 (0.0178 mm/day) than at the two other stations (O1: 0.0154 mm/day; WK1: 0.0102 mm/day) (Table 1). The individuals of the spring cohort group were characterised by a relatively faster growth (0.0128 – 0.0191 mm/day), especially in 2003 (0.0118 – 0.0323 mm/day), than the individuals of the summer (0.0061 – 0.0123 mm/day) and autumn (0.0124 – 0.0155 mm/day) cohort groups. When comparing the spring cohorts, growth was faster in 2003 than in 2002 at stations O1 and WK2; values of WK1 were comparable between years.

Production

The total production during the 1.5 year study period was highest at station O1 (64.8 g/m²), followed by stations WK2 (28.2 g/m²) and WK1 (10.3 g/m²) (Table 1). The production was highest for the individuals of the spring cohort group (32.6 g/m² at station O1, 12.4 g/m² at station WK2, 3.3 g/m² at station WK1) compared to the individuals of the summer and autumn cohort group (7.9 – 1.3 g/m² at station O1, 6.8 – 4.5 g/m² at station WK2, 1.7 g/m² at station WK1). The production of the spring cohort group was lower in 2003 than in 2002, except for station WK1 (5.33 g/m²).

In 2002, annual secondary production of *L. conchilega* amounted to 38.34 g/m² at station O1, 22.13 g/m² at station WK2, and 5.00 g/m² at station WK1. The total biomass during this period at the three stations was respectively: 85.59 g/m², yielding a P/B ratio of 0.45 for station O1, 58.67 g/m², yielding a P/B ratio of 0.38 for station WK2, 13.54 g/m², yielding a P/B ratio of 0.37 for station WK1.

Table 1. Production, growth, biomass and P/B – ratio per cohort group during the 1.5 year study period

Station O1	production g/m ²	growth mm/day	biomass g AFDW /m ²	P/B
2001				
2002/1	32,6000	0,0164	58,9162	0,5533
2002/2	7,8620	0,0078	21,8444	0,3599
2002/3	1,3178	0,0124	4,8340	0,2726
2003/1	23,0413	0,0250	31,8544	0,7233
	total	average	total	
	64,8211	0,0154	117,4491	0,5519

Station WK 2	production g/m ²	growth mm/day	biomass g AFDW /m ²	P/B
2001	0,5132	0,0099	3,6583	0,1403
2002/1	12,3929	0,0191	20,9055	0,5928
2002/2	6,7741	0,0123	17,7583	0,3815
2002/3	4,5121	0,0155	16,7148	0,2699
2003/1	4,0352	0,0323	7,0037	0,5762
	total	average	total	
	28,2276	0,0178	66,0406	0,4274

Station WK 1	production g/m ²	growth mm/day	biomass g AFDW /m ²	P/B
2001				
2002/1	3,2937	0,0128	11,7363	0,2806
2002/2	1,6495	0,0061	1,4766	1,1172
2002/3				
2003/1	5,3288	0,0118	21,9255	0,2430
	total	average	total	
	10,2720	0,0102	35,1384	0,2923

Discussion

The family Terebellidae is characterized by a remarkable heterogeneity in terms of developmental strategies and larval ecology. *Lanice* (together with *Loimia*) is separated from other genera, which have a direct or mixed development. *Lanice* is characterized by two planktonic stages separated by a benthic larval stage, the second planktonic stage lasting much longer than the first and having morphological features similar to those of the juvenile worms (Bhaud, 1988; McHugh, 1993).

Because Thorson (1966) suggested that recruitment and early-life stages play an important role in bottom population dynamics, we made a detailed study about the recruitment patterns of *L. conchilega*. To this end, we detailedly discriminated between the first benthic stages (recently settled individuals, juveniles and young adults), based on a high sampling frequency. This enabled us to observe the settlement and recruitment patterns of *L. conchilega*. The detailed population structure of the subtidal *L. conchilega* patches was disentangled with the method of Bhattacharya and validated with NORMSEP. Due to the rather subjective way of this method, the obtained results of the population structure were handled and discussed with caution. Unfortunately, the patchiness of *L. conchilega*, especially in subtidal locations, makes it difficult to differentiate the trends in recruitment patterns of the successive sampling occasions. Nevertheless, we believe that the patterns of settling, recruitment and population structure of *L. conchilega* obtained and discussed in this paper provide a good

estimate of the population dynamics of *L. conchilega* populations in fine muddy sands along the Belgian Coast.

Life cycle and demography

Fertilization

A step which was not directly investigated in this study, but which is important to address in closing the larval loop is the success of fertilization and larval production. Egg fertilization and larval production are controlled by both behavior (reproductive synchrony, aggregation or swarming) and the external physical environment (Eckmann, 1996). Reproductive synchrony in temperate regions, for example, is controlled by insolation, water temperature and stratification, with resultant effects on primary and secondary production. For sexually mature benthic organisms, a fertilization probability of 70-80% can be assumed if density exceeds several individuals per m² (as is the case for *L. conchilega* in this study). In the case of lower densities, a probability of 20% is expected (Eckman, 1996). The maximum fecundity of *L. conchilega* is estimated at 90000 - 160000 oocytes per individual of 125-150 µm (Bhaud, 1988; McHugh, 1993). Eckman (1996) mentioned that the degree of uncertainty about the fertilization is not of major importance, due to the increased losses in later stages (high rates of mortality of planktonic larvae) and the influences of advection on their fate.

Sexually mature males and females of *L. conchilega* can be found from April to the end of June according to Kessler (1963) in the German Bight. However, this period is probably longer along the Belgian coast, as larval release was detected until October in the present study.

Larval phase

After a short planktonic (trochophore and metatrochophore) and benthic phase (metamorphose I) of a few days, the second planktonic stage (the aulophore larva) stays in the water column for up to 60 days (Bhaud, 1988). In our study, aulophore larvae were found during almost the whole year (mainly March – November), with three peaks: one mean peak in spring and two smaller peaks in summer and autumn. The most important larval density peak (spring) coincided with the period of increase of temperature and primary production (April – May). The hypothesis that the timing of the occurrence of larvae and settling is linked to temperature and primary production is supported by the observations in the present study. The occurrences of aulophore larvae and the timing of settlement, together with the increases in temperature and primary production (pers. observation), were observed approximately one month later at station O1, compared to stations WK2 and WK1. Similarly, it can be hypothesized that the autumn peak of aulophore larvae coincided with an autumn plankton bloom, which regularly occurs in temperate regions (Rousseau, 2000). The increase in larval density in summer cannot be linked to such an event. The few larvae found in December – February were older aulophore stages (more than five tentacles; personal observation), indicating that there was no obvious new recruitment during winter. Normally, aulophore larvae have the ability to settle as soon as they have five tentacles, but older aulophore larvae were frequently found in the water column (Marcano & Bhaud, 1995), due to the resuspension ability of the larvae (Bhaud & Cazaux, 1990). In other studies, the aulophore

larvae were also found during the whole year, with variations in the timing of periods with marked abundance (e.g. June – September in Arcachon and Roscoff; April – October in Plymouth; March – April + July in Helgoland) (Marcano & Bhaud, 1995).

The occurrence of planktonic larvae is related to temperature and primary production increases, but the distribution of the larvae in the southern Bight of the North Sea is also influenced by hydrodynamics (Belgrano et al., 1990) and, to a large extent, larval behavior (Bhaud, 2000). The position of the autophore larvae in the water column depends on the secretion of a mucus trail, while the sinking rate depends on the behavior of the larvae, which can quickly loosen their connection with the mucus trail and secrete another one (Bhaud & Cazaux, 1990). The success of the settling of these planktonic larvae to the benthos is unpredictable, because the transition is complex and affected by many variables (Feller et al., 1992).

Periods of recruitment

Settlement is defined as the successful transition from the larval stage to benthic life, whereas the term recruitment represents the success of the life cycle, resulting in the appearance of new classes of adult individuals (Bhaud, 2000).

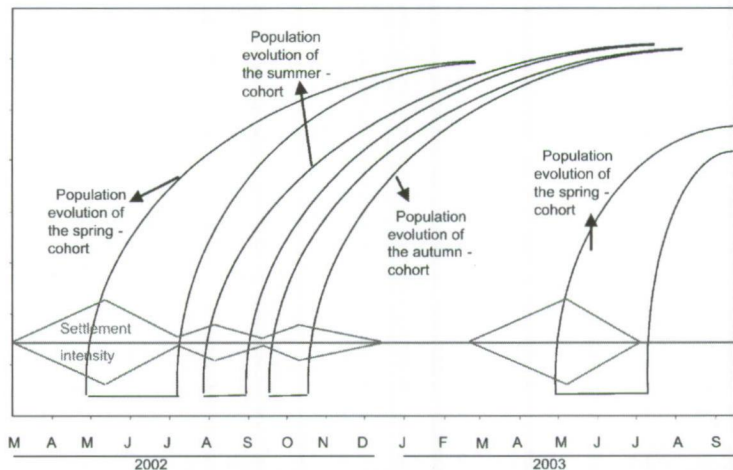


Figure 11. Schematic overview of the general trends in settlement and recruitment and evolution of the populations originating from the different recruitment periods.

General pattern of settlement and recruitment

In general, the settling of autophore larvae was visible from March – April onwards, while recruitment was clearly visible from May - June onwards (cf. size frequency distributions). The settling and recruitment of *L. conchilega* can be situated continuously from March until November and can be divided into three periods (Figure 11). These three periods were defined based on the occurrence of peaks of autophore larvae in the water column and peaks of recently settled individuals in the benthos. Consequently, following periods were distinguished: (1) spring recruitment period (April – July), (2) summer recruitment period (July – September), and (3) autumn recruitment period (September –

November). Each period was characterized by a peak in recently settled individuals, followed by recruitment to the adult population. The evolution of the adult population, consisting of different cohorts, was visualized in Figure 10. The transition from settling to final recruitment was investigated in the present study by distinguishing different developmental stages in the benthos (recently settled individuals, juveniles and young adults). These stages succeeded each other in time, with declining densities from the settling phases towards the adult population. The time lapse between settling and detection of the individuals in the adult population is not more than one month, as juveniles started to detach and re-settle in the sediment one month after attachment to adults (Callaway, 2003). This transition period was characterized by a high mortality (from 1000-s ind/m² to <1000 ind/m²). Cohort analysis indicates that the densities of the individuals of the small size classes (< 2 mm width) rapidly decreased in time and that they were replaced by high densities of newly recruited individuals by the time the following sampling occasion took place. This high mortality and turn over of individuals could mainly be due to competition for space and food, erosion, predation, mechanical damage, disease or other physiological stress (Eckman, 1996).

The three defined recruitment periods in the present study were characterized by variations in intensity and duration. The spring recruitment period was the most intense and prolonged recruitment period, with a lot of new cohorts resulting in high adult densities in the beginning of the summer. Some of the cohorts disappeared in the same year, without reaching the maximal tube width of older *L. conchilega* individuals. It is not clear if those individuals were sexually mature, because there is no information on the age of maturity of *L. conchilega*, but they could be responsible for new recruitment in the same year. Others survived the winter and were, together with the individuals from the summer and autumn recruitment period, responsible for the spring recruitment of the following year. The summer and autumn recruitment periods were less intense and could not always be detected in the adult population structure. It can be concluded that *L. conchilega* is characterized by a pattern of constant recruitment with one or more definite periods of acute increase. This pattern has already been reported for a lot of other polychaete species (e.g. Spionidae spp., *Hediste diversicolor*, *Capitella* spp) (Méndez et al., 1997; Bolam, 2004; Garcia-Arberas & Rallo, 2004). The population structure of *Hediste diversicolor*, for example, showed different cohorts, originating from a varying recruitment rate, and which were lumped into two periods (Garcia-Arberas & Rallo, 2002).

The continuous recruitment of *L. conchilega* in Belgian Coastal waters is characterized by a high turn over and population renewal, which result in the maintenance of high densities of *L. conchilega* during the year. This type of population renewal was not detected every year in the intertidal *L. conchilega* populations of the bay the Veys (France) to maintain the high adult densities (Ropert & Dauvin, 2000). In that particular case, the population renewal probably resulted from transfer of benthic populations from offshore towards the coast. Population renewal due to a significant recruitment was detected in the intertidal *L. conchilega* population at the sandflat 'Gröninger Plate', which was yearly (1998 – 2000) characterized by a high percentage of juvenile tubes (< 3 mm wide; adults 3 – 8 mm) in May – October (Zühlke, 2001).

Settlement supports temporal stability

The high adult densities are not only maintained due to the recruitment strategy; the settlement strategy plays a major role and determines the temporal stability of the *L. conchilega* patch locations. Epibenthic structures (adult tubes or tube like structures, shells) are needed for the settling and tube building of the *L. conchilega* larvae (Heuers et al, 1998; Callaway, 2003). The success of initial larval settlement, i.e. the number of recruits per adult tube, increases with the density of adult tubes (Heuers et al., 1998). Generally, settling in areas occupied by adult conspecifics increases the probability of adequate survival conditions in terms of food supply, predation pressure and abiotic environmental conditions (Pawlik, 1992). The main advantage for *L. conchilega* individuals attaching to adults is probably the secure anchorage in the sand, because settling directly in the sediment would subject individuals to a higher risk of passive dislodgement. In the present study and in the study of Callaway (2003), averages of 5 to 13 juveniles and a maximum of 72 individuals were found attached to single adult tubes. However, attachment of *L. conchilega* individuals to adults or hard substratum is not obligatory. Strasser & Pieloth (2001) showed that juveniles recolonized a sandflat that had experienced a collapse of the *L. conchilega* population and was devoid of adult tubes. Similarly, settling and recruitment were observed at station O1 in 2002, in spite of the absence of adult tubes. However, the settling and recruitment was more successful at station O1 in 2003, which could be due to the presence of adult tubes. It can be concluded that the presence of adult tubes enhances settling in existing *L. conchilega* patches, but new establishments are possible.

Spatial and temporal variability

Within this generally observed recruitment pattern of *L. conchilega*, spatial differences in timing and intensity, and year-to-year variations were detected. On a small spatial scale, differences in intensity were observed, but there were no significant differences in timing. On a larger spatial scale, however, differences in both intensity and timing were quite pronounced. In 2003, for example, there was a time lag in the recruitment of 2 weeks between station O1 and stations WK2 - WK1. This time lag on a large spatial scale was also observed in the timing of the plankton bloom, which was later at station O1 (pers. obs.). These differences between stations indicate that the larval presence and settling were not synchronized along the Belgian coast, but may mainly be influenced by variations in local factors, like temperature and primary production. Spatial and temporal differences in intensity could also be linked to differences in larval supply (Strasser & Pieloth, 2001). In the present study, the autophore densities were similar in 2002 and 2003 at station O1 (± 800 ind/m²), in spite of unequal recruitment success between the years. The density estimates of the autophore larvae were based on one sample at each sampling occasion, without taking into account the possible short – term tidal (Belgrano et al., 1990) and spatial variability at those locations. Consequently, no conclusions can be formulated about the linkage between the recruitment variability and differences in larval supply.

Temporal differences in settling period of *L. conchilega* were observed in the present study (between 2002 and 2003 and between stations) and in the study of Callaway (2003) (April – May in 1998; May – June in 1999; June in 2000). The three recruitment periods discerned were not detected every year (e.g. summer recruitment period in 2003 at the three stations, autumn recruitment period at station WK1).

Differences in settling and recruitment success can explain part of differences in the adult density in the following year (Buchanan et al., 1986). The extensive adult population in spring 2003 at stations WK2 and WK1 is probably due to successful settling and recruitment in 2002. The recruitment success was lower in 2003, resulting in low adult densities at the end of the summer. The inverse pattern was detected at station O1, with an extremely high settling and recruitment in 2003 compared to 2002. Recruitment and settling, however, were not successful: the adult population completely crashed in August, probably due to a disturbance (e.g. beam – trawling and waves). Despite the lower settling and recruitment in 2002 at station O1, an adult population was present in high densities in 2003. This means that other factors, like natural (storms) or anthropogenic (beam –trawling) disturbances and post – settlement processes can influence the normal temporal pattern in coastal zones, which complicates making predictions on success of settlement and recruitment (Buchanan et al., 1986; Feller et al., 1992).

Life span

In the study of Ropert & Dauvin (2000), a cohort of juvenile individuals needed 17 to 24 months to integrate into a persistent adult population (tube width: 3.4 - 4.2 mm). In our study, the individuals already reached a tube width of 2 - 3 mm after a few months and a persistent adult population was not present (at least not in meaningful densities). Therefore, the life span of the *L. conchilega* individuals in the present study was estimated to be one year, with variations of a few months (individuals with a tube width of more than four mm were seldomly found). In the study of Ropert & Dauvin (2000), however, individuals with a tube width of more than two mm were estimated to be more than one year old. The smaller ones originated from the recruitment in June (samples in October) and in that particular study, *L. conchilega* reached a life-span of three years. In the Wadden Sea area, this species was estimated to live 1 – 2 years (Beukema et al., 1978). Although the differences in life-span between the different locations are considerable, they are commonly found for a lot of other species (Spionidae, *Perinereis cultrifera*) (Roubah & Scaps, 2003; Bolam, 2004).

Growth and production

In the present study, *L. conchilega* was characterized by a high growth rate (average of 0.0102 – 0.0178 mm/day), whereas its growth rate in the Bay the Veys was lower (0.0039 to 0.0053 mm/day) (Ropert, 1999). Most probably, the reduced food availability and feeding time in intertidal areas reduce the growth of *L. conchilega* compared to the subtidal areas. The growth is at its maximum after the integration of the juveniles into the population (Ropert, 1999; the present study). The increased food supply after the spring phytoplankton bloom might be responsible for the high growth rates and the fast development of the individuals to adults in the same year. The high productivity and biomass of *L. conchilega* is also linked to the high and almost constant food availability in the coastal zone of the BCS, which is characterized by turbulent, nutrient rich water and riverine input of the Westerscheldt and Yzer. Rees (1983) stated that spatial differences in production mainly depend on the food availability and quality. Therefore, it can be assumed that the constantly high supply of nutrients via

the Westerscheldt caused for the high production and biomass values observed at station O1. Similarly, the P/B ratio was highest at station O1 (P/B: 0.55) compared to the two other stations (P/B: 0.43, 0.29), but was comparable with the P/B ratios obtained in the study of Ropert (1999) (P/B: 0.55, 0.36). These P/B ratio's deviate from the values expected for a short – living species. Normally, the productivity becomes more important when the life-span is shorter, resulting in higher P/B ratio's (Ménard et al., 1989). This is not the case for *L. conchilega*: the populations of *L. conchilega* (high turn over) do not correspond with a "classic" population.

Conclusion

This study underlined the opportunistic status of the tube - building polychaete *Lanice conchilega*, whose life – cycle is characterized by a long pelagic phase, mass benthic settling with high mortality, rapid growth and a high turn – over in the adult population. It is difficult to predict the adult population density in the long run, based on the settlement and recruitment success in a particular year, due to the high natural and anthropogenic disturbance in coastal areas. Nevertheless, due to the (almost continuous) high recruitment and the preferential settling of the aulophore larvae nearby *L. conchilega* tubes, a temporal stability of the location of the *L. conchilega* population was found, with varying density. Finally, we detected temporal and spatial variability in settling and recruitment patterns of *L. conchilega* along the Belgian Coast.

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