CHAPTER 4

SPATIAL DISTRIBUTION AND POPULATION DYNAMICS OF *SPISULA SUBTRUNCATA* IN A SHALLOW MARINE HABITAT

Steven Degraer (*), Magda Vincx (*) and Patrick Meire (**)

(*) University of Gent, Department of Biology, Marine Biology Section
K.L. Ledeganckstraat 35, 9000, Gent, Belgium

(**) University of Antwerpen, Department of Biology
Universiteitsplein 1, 2610 Wilrijk, Belgium

paper in preparation

ACKNOWLEDGEMENTS

This study is financed by the Flemish administration responsible for environment, nature, land and water management, department Nature (AMINAL, contracts BNO/NO/Wh.94.12 and AN/1995/nr.3) and the Coastal Waterways Division (AWK, contract of 24.07.1997) of the Flemish Government. The first author was financed by the Flemisch Institute for the Promotion of the Scientific – Technological Research in Industry (IWT). Valuable comments on the manuscript are retrieved from Jan Mees. The authors want to thank Johan Van de Velde, Annick Van Kenhove, Myriam Beghyn, Vera Van Lancker and Froukje Clinck for their assistance in the field and the laboratory.

ABSTRACT

Bivalves are important in shallow marine habitats, not at least being the major food resource of the common scoter (*Melanitta nigra*), thousands of which are wintering on the western Coastal Banks, near the Belgian – French border. Next to this ecological importance, one of these bivalves, *Spisula subtruncata*, occurs in fishable stocks in the area and shellfisheries become interested in the commercial harvesting of these stocks. In order to provide information for a sustainable management of the *S. subtruncata* stocks on the western Coastal Banks, this study aimed at (1) the description *S. subtruncata*'s spatial distribution and population dynamics and (2) understanding the implications for future *Spisula*-fishery in the area. The spatial distribution of *S. subtruncata* was studied in 1994 and 1997 in 40 stations in two areas of the western Coastal Banks. The population dynamics were investigated by monthly sampling of two stations between April 1995 and April 1996 and a seasonal sampling between April 1996 and April 1998.

Spisula subtruncata had a patchy distribution in the deeper (6 m), fine sandy (200 ± 20 µm) sediments of the *Lanice conchilega* community, mainly found in the most western part of the Coastal Banks. In July '95, an overwhelming and successful recruitment was observed in this area. Local densities were as high as 150000 ind m^{-2}. Minor, non-successful recruitments were detected in August '96 and August '97. Growth could be described by a seasonally oscillating version of the von Bertalanffy growth function: a growth stop was observed from late autumn till early spring. Probably because of differences in environmental conditions, the growth parameters K and L_∞ differed slightly between the two stations (0.7 and 32 – 33 mm for one stations and 0.9 and 31 – 32 mm for the other station. A combination of length and individual biomass increment shows: (1) a faster length increment of smaller individuals during the second growing period (catching-up phenomenon), (2) a constant length combined with a decreasing individual biomass during the suboptimal winter periods (except for the first one, when the individual biomass slightly increased), (3) a positive relation between the individual biomass decrease and the seawater temperature during the winter periods, and (4) a strong increase of the individual biomass in early spring (April '97 and April '98) because of gametogenesis, followed by a decrease because of spawning (August '97). The total production of the cohort '95 in the tidal gully (Potje) during the study period is estimated at about 1500 g AFDW m^{-2}.

Shellfishery on the ecologically important western Coastal Banks should not be considered since: (1) the food resource for the common scoter will decrease and will possibly lead to the disappearance of the seaducks in the area, (2) the ecologically most diverse and rich macrobenthic *Lanice conchilega* community will be destructed, and (3) the economical

rendability of *Spisula*-fishery is doubtful, because of the highly variable recruitment along the Belgian coastline.

INTRODUCTION

Bivalves are an ecologically important component of the macrobenthos of coastal marine ecosystems. Although their densities are generally low in comparison to other taxa (e.g. polychaetes) their biomass generally constitutes a large proportion of total macrobenthic biomass (Van Steen, 1978; Brey *et al.*, 1990). This high bivalve biomass is a food resource by a variety of demersal fish species (Rainer, 1985; Brey *et al.*, 1990) and by diving seaducks, e.g. the common scoter (*Melanitta nigra*) (Cramp and Simmons, 1977; Meissner and Bräger, 1990; Meire, 1993).

Because of the large number of wintering common scoters on the Belgian western Coastal Banks (Maertens *et al.*, 1988, 1990; Devos, 1990), this area is designated as an 'area of international importance for waterfowl', according to the Ramsar convention (Kuijken, 1972). Furthermore, the western Coastal Banks fulfill the criteria of the EC Bird Directive, although the area is not in the final list of the Belgian EC Bird Directive areas. The presence of the scoters can partly be explained by the undisturbed character of the western Coastal Banks (Degraer *et al.*, in press a), but food availability, mainly bivalves (Cramp and Simmons, 1977; Meissner and Bräger, 1990; Meire, 1993), plays an important role as well (Kirchoff, 1981). The relation between the spatial distribution of the common scoter and the presence of extensive bivalve beds, especially *Spisula subtruncata*, has already been demonstrated (Van Assche and Lowagie, 1991; Leopold *et al.*, 1995).

Since the early nineties, fishermen are interested in the commercial exploitation of *S. subtruncata* stocks and large amounts of the bivalve have already been harvested in the Netherlands, north of the area of investigation. Due to the competition between the *S. subtruncata* fishery and the common scoter, major shifts in the spatial distribution and a decrease of the density of the common scoter are observed (Leopold *et al.*, 1995). At this moment, *S. subtruncata* fishery does not occur in the Belgian coastal waters, but preliminary research to the possibility of harvesting *S. subtruncata* in Belgium already revealed the presence of a fishable standing stock of the bivalve in the area of the western Coastal Banks (Vanhee *et al.*, 1998). The conflicting situation, between the ecological and socio-economical interests in *S. subtruncata*, stresses the need for knowledge on the life history, population dynamics and production of *S. subtruncata*. Although necessary in order to set up a sustainable harvesting management strategy for *S. subtruncata*, this information is largely lacking at this moment. So far, only Davis (1923, 1925) provided some information on the life history and population dynamics of *S. subtruncata* on the Doggerbank.

The aims of this study are: (1) to describe the spatial distribution, population dynamics and production of *S. subtruncata* on the western Coastal Banks during a 2.5 yr study period and (2) to use this newly gathered information in the frame of the sustainable management of *S. subtruncata* in the area.

MATERIALS AND METHODS

STUDY AREA

The western Belgian Coastal Banks extend from the Belgian – French border in the West to Oostende in the East and from the low water line to about 8 m depth (Figure 1). Between Koksijde and Middelkerke, the banks are just a subtidal extension of the beach, whereas the areas 1 and 2 comprise a large range of geomorphological features. The Stroom- and Balandbank (area 1) are linear sandbanks, oriented parallel to the coastline and separated from the beach by a gully, the Kleine Rede. Their depth ranges from 3 to 8 m below mean low water spring level (MLWS). Area 2 comprises three sandbanks (Den Oever, Broersbank and Trapegeer) and a tidal gully (Potje), of which the depth ranges from about 0.5 to 8 m below MLWS. Due to this geomorphogically and, consequently, hydrodynamically diverse character of the area, a large variety of sediments (median grain size from over 500 to 160 µm) are present (Degraer *et al.*, in press a).

SAMPLING

To investigate the spatial distribution and habitat preferences of *Spisula subtruncata* on the western Belgian Coastal Banks, 40 and 39 stations were sampled in October 1994 and October 1997, respectively (Figure 1). At each station, one sample was taken with a Van Veen grab (sampling surface area: 0.1026 m^2) The samples were washed over a sieve, with a 1 mm mesh size, before fixation, and then fixated and preserved in an 8% formaldehyde-seawater solution.

To study the population dynamics of *S. subtruncata*, two of the 40 stations, P2 and P20, were selected because of the high numbers of bivalves observed in October 1994. At each station, five Van Veen grabs were taken on 17 occasions: monthly, between April 1995 and April 1996, and seasonally, between April 1996 and April 1998. After fixation, the samples were sieved through a 0.5 mm and 1 mm sieve and preserved in an 8% formaldehyde-seawater solution. Yet, no individuals of *S. subtruncata* were found in the 0.5 mm fraction.

From each sample, a subsample for sediment analysis was taken with a 1.5 cm diameter core.

LABORATORY PROCEDURES

All individuals of *Spisula* were sorted and identified to species level. Only two species of the genus, *Spisula subtruncata* and *Spisula solida*, were found, of which *S. solida* only occurred in small numbers (< 20 ind m^{-2}) in three stations sampled in 1994. *Spisula solida* was not detected in the stations P2 nor P20. The number of *S. subtruncata* was counted. To study the population dynamics of *S. subtruncata*, 150 to 400 individuals from the stations P2 and P20 were randomly selected for biometrical analyses. Length, width and height were measured with a drawing mirror and dissecting microscope of individuals shorter than 1 cm and by means of a vernier caliper (precision: 0.01 mm) for individuals longer than 1 cm. At station P2, the individual biomass (ash-free dry weight, AFDW) of 30 to 50 individuals was measured by loss of mass on ignition (500°C ± 50 °C for 2 h) of whole oven-dried individuals (70°C for 48 h), giving a good estimate of the individual biomass (Palmerini and Bianchi, 1994). Because all individuals were preserved in a formaldehyde-seawater solution, a decrease of the AFDW, stabilizing after about 3 months, is expected (Brey, 1986). In order to diminish the differences in individual biomass estimates between different sampling months, at least three months were left between fixation and determination of the AFDW. Yet, an underestimation of the individual biomass and, consequently, also standing stock and production, is expected.

The reproductive condition of *S. subtruncata* was studied by dissecting 20 individuals of station P2 for all months from April '96 till April '98. Because of the use of Bengal rose (darkening the gonads), gametogenesis could only clearly be detected when the gonads covered at least half of the visceral mass. In all other situations, the gonadal development could not be assessed with certainty. The subjective rating of gonadal development into five classes from fully to non-developed gonads (Caddy, 1967), could not be used and a discrimination of the individuals' reproductive condition was only made into two classes: (1) well-developed, with more than half of the visceral mass covered by the gonads and (2) poorly or non-developed, with the gonads covering less than half of the visceral mass or being undetectable.

The grain size distribution of sediment sample is analyzed with a laser COULTER LS. The seawater temperature during the sampling period is provided by the Division of Waterways and Coast of the Flemish Government.

DATA ANALYSIS

The biometric relations (length, width, height, individual biomass) are studied by regression analysis. The statistical significance of density differences between two consecutive sampling months are analyzed by means of the non-parametric Mann-Whitney U-test.

The length increment is described by the von Bertalanffy growth function (VBGF) with incorporation of winter growth stop. The mathematical equation is given by:

$$L_t = L_\infty \left\{ 1 - e^{-K(t-t_0) + \frac{CK}{2\pi}\sin\left[2\pi(t-t_s)\right]} \right\}$$

with	L_t	the predicted length at age t
	L_∞	the asymptotic length
	K	the growth constant
	t_0	the (theoretic) age at zero length
	C	determining the amplitude of the seasonal growth oscillation
	t_s	the starting point of the oscillation

The values of the five parameters (L_∞, K, t_0, C, and t_s) were estimated by means of non-linear estimation, with the least squares method, as provided by the statistical software package STATISTICA 5.1 (StatSoft, 1996). The cohort '95 could easily be distinguished from other cohorts by means of monthly length-frequency distributions, as other cohorts were only present in very low numbers. The input data points, in order to retrieve the VBGF, are the average lengths of the cohort '95 of each sampled month. Next to the estimation of the parameters' averages, STATISTICA 5.1 also provides the standard error and the level of significance of each estimate.

The values of K and L_∞ were also estimated using the Ford-Walford method in which age – length data are rearranged as length at a specific time L_t and length at a succeeding time L_{t+dt} data pairs. If the time differences between the consecutive length measurements is constant, the intercept and slope of the linear regression (y = ax + b) of the data pairs can be used for the estimation of K and L_∞, by $K = -1/dt \ln(a)$ and $L_\infty = b / (1 - a)$. In order to fulfill the requirement of constant time differences between two consecutive length measurements, age – length data were only used from all August and January samples (five data pairs).

Production is estimated with the growth and removal summation methods (Crisp, 1984). The growth summation method estimates the production as the increment of biomass from one sampling month to the next for the whole sampling period. The removal summation method sums the loss in weight between consecutive sampling months during the whole sampling period.

RESULTS

SPATIAL DISTRIBUTION

With maximum densities of up to 5000 ind m^{-2}, *Spisula subtruncata* was abundant on the western Belgian Coastal Banks (Figure 1). The species occurred in 25 and 41 % of the stations in October 1994 and October 1997, respectively. A clear preference for area 2 was observed: it was present in 35 % (1994) and 58 % (1997) of the stations in area 2 as compared to 15 and 20 % in area 1. Densities in area 2 were generally higher than in area 1. Overall, the density of *S. subtruncata* in 1997 was higher than in 1994.

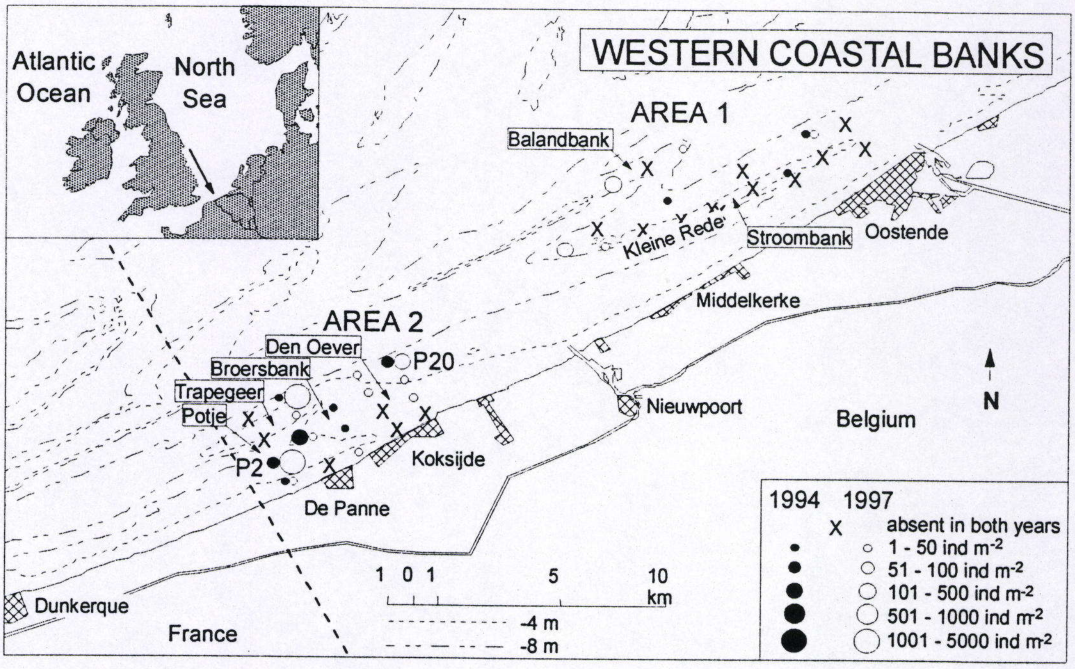


Figure 1. The geographical situation of the study area and the spatial distribution of *Spisula subtruncata* over the western Belgian Coastal Banks in 1994 and 1997, with indication of the two areas under consideration.

Spisula subtruncata was mainly found in the *Lanice conchilega* community (Table 1), where it occurred with an average density of 48 and 549 ind m^{-2} in 1994 and 1997, respectively. Whereas *S. subtruncata* is found in less than 40 % of the stations of the two other macrobenthic Coastal Bank communities, it was present in at least 55 % of the stations of the *L. conchilega* community in 1994 and 1997.

	1994			1997		
	Density	Occ.	n°	Density	Occ.	n°
Lanice conchilega community	48 ± 29	55	6	549 ± 328	63	5
Nephtys cirrosa community	<1 ± <1	10	2	5 ± 2	29	7
'Mytilus edulis' community	7 ± 4	40	2	3 ± 3	33	1

Table 1. The distribution of *Spisula subtruncata* over the three macrobenthic Coastal Bank communities in 1994 and 1997, as defined in chapter 3, with the average density ± standard error (ind m^{-2}), together with the percentage of occurrence (Occ.) in the stations of the three communities (%) and the number of stations with *S. subtruncata* (n°).

During the whole sampling period, the variance of the density of *S. subtruncata* was always much higher than the mean. Thus, the spatial dispersion of *S. subtruncata* was contagious (Elliott, 1977).

DENSITY FLUCTUATIONS

All individuals of *Spisula subtruncata* were retained on a 1 mm sieve; no individuals were found in the 0.5 mm fraction. Between April and July 1995, the maximal density of *Spisula subtruncata* in the stations P2 and P20 was 20 ind m^{-2} (Figure 2). In August '95, the species became very abundant in both stations, with densities up to 150000 ind m^{-2}. Between August '95 and January '96, the density decreased to about 10000 ind m^{-2} in both stations. After January '96, the density of *S. subtruncata* in P20 continued to decrease and never exceeded some hundreds of ind m^{-2}, while in P2 the density also continued to decrease, but was never lower than about 1000 ind m^{-2}.

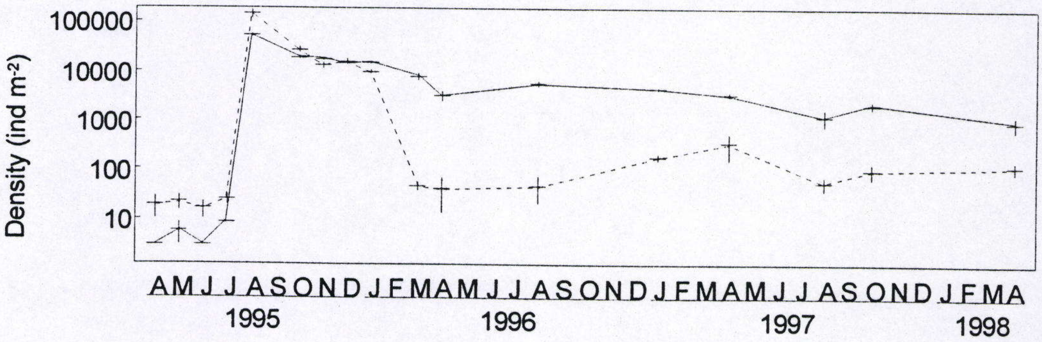


Figure 2. The temporal variation of the density (ind m^{-2}) of *Spisula subtruncata* in the stations P2 (solid line) and P20 (dashed line), with indication of the standard error (vertical lines)

BIOMETRICS

The relation between length and biomass of *Spisula* subtruncata during the study period is presented per month and for all months together in Table 2. Except for August '96 and October '97, when regressions were non significant, highly significant ($p < 0.0001$) regressions were found. The same applies for regressions between length and height and width (p always < 0.0001).

	N	a		b	
		Mean	S.E.	Mean	S.E.
Aug '95	23	2.93	0.49	-5.19	0.90
Oct '95	48	3.10	0.20	-5.54	0.49
Nov '95	20	3.72	0.43	-7.07	1.07
Dec '95	20	2.59	0.44	-4.29	1.09
Jan '96	47	3.00	0.18	-5.23	0.45
Mar '96	30	2.44	0.21	-3.58	0.53
Apr '96	17	2.95	0.42	-4.39	1.11
Aug '96	49	-0.03	0.73	4.69	2.20
Jan '97	49	2.38	0.29	-2.72	0.87
Apr '97	49	3.73	0.70	-5.86	2.23
Aug '97	46	5.18	0.78	-11.25	2.55
Oct '97	50	1.73	1.12	0.94	3.72
Apr '98	49	2.34	0.26	-2.01	0.86
All months	508	4.36	0.05	-8.43	0.16
Length – Height	439	0.73	< 0.01	-0.76	0.11
Length – Width	415	0.49	0.01	-1.14	0.12
Height – Width	415	0.67	0.01	-0.66	0.10

Table 2. The parameters (a and b) of the correlation : $\ln(\text{biomass}) = a * \ln(\text{length}) + b$), as defined for each sampling date and for all months together and the parameters of the biometric correlations between length, height, and width (Height or Width = a * Length + b) for all months together. S.E., standard error; N, number of observations.

During most of the sampling period *S. subtruncata* had a 'normal' shape (Figure 3). From August '96 till August '97, some aberrant shapes, with a clear ventral indentation, occurred next to the 'normal' forms. Except for January '97, a generally increasing percentage of aberrant forms with increasing density was detected (Figure 4). This trend was especially obvious in August '96 and April '97, whereas in January '97 the general trend was disturbed by the high percentage of aberrant forms (80 %) at the lowest density (3300 ind m^{-2}). No data are available for August '97. After August '97, no clear aberrant forms were detected anymore.

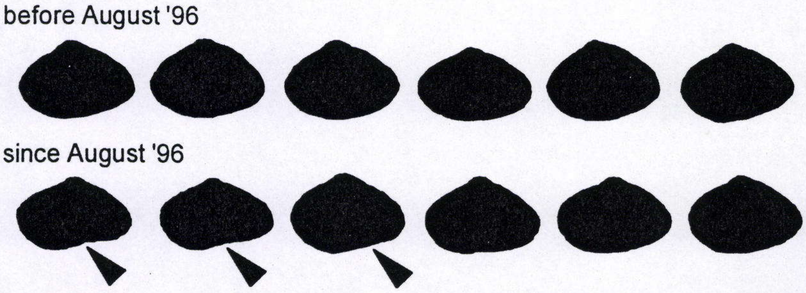


Figure 3. The variability in outline of *Spisula subtruncata* before August '96 and from August '96 on. The arrows are pointing to the ventral indentation.

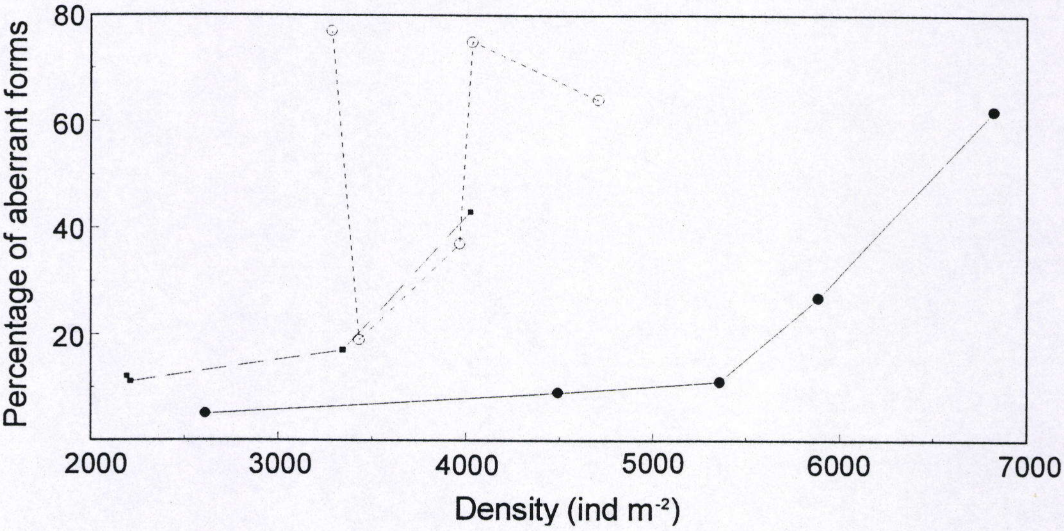


Figure 4. The relation between the density and the percentage of aberrant forms of *Spisula subtruncata* in station P2. ●, August '96; ○, January '97; ■, April '97.

GROWTH

Between April and July '95, a low number of larger individuals of *S. subtruncata* (17 – 33 mm) were found in both stations (Figure 5). Such large individuals were present till January '96 in station P20. The length-frequency distributions show the appearance of a high number of small individuals (P2: 3 – 10 mm; P20: 2 – 6 mm) in August '95. These double their length by October '95. Between October '95 and March '96, individuals, belonging to this cohort, were still present in large numbers, but they ceased growing. After March '96, the cohort could still be detected in high densities in station P2, while their density decreased steeply in station P20, their density steeply decreased. Still, in both stations, periods of growth (March '96 – January '97 and April '97 – October '97) alternated with periods of more or less zero growth (August '96 – January '97 and October '97 – April '98). In both stations, the length-frequency distribution of the cohort, appearing in August '95, remained unimodal during the whole study period. Furthermore, the appearance of small individuals of *S. subtruncata* (3 – 6 mm) was also found in station P20 in August '96 and in August '97. On both occasions, their density remained low and they growed till April of the next year. The small individuals of August '96 were not detected again in 1997.

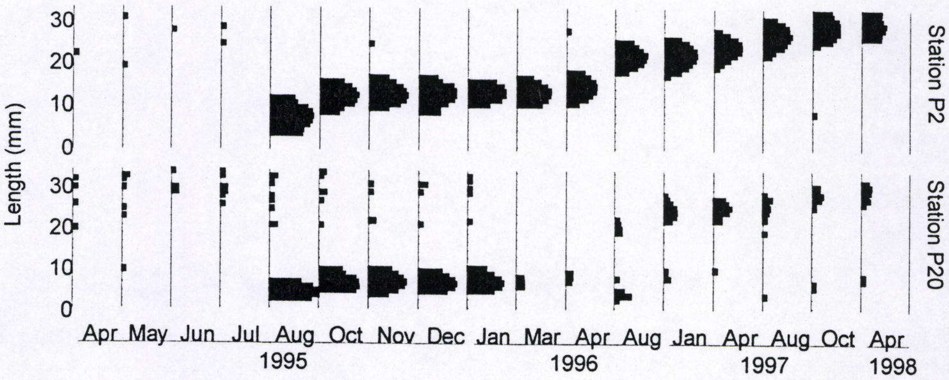
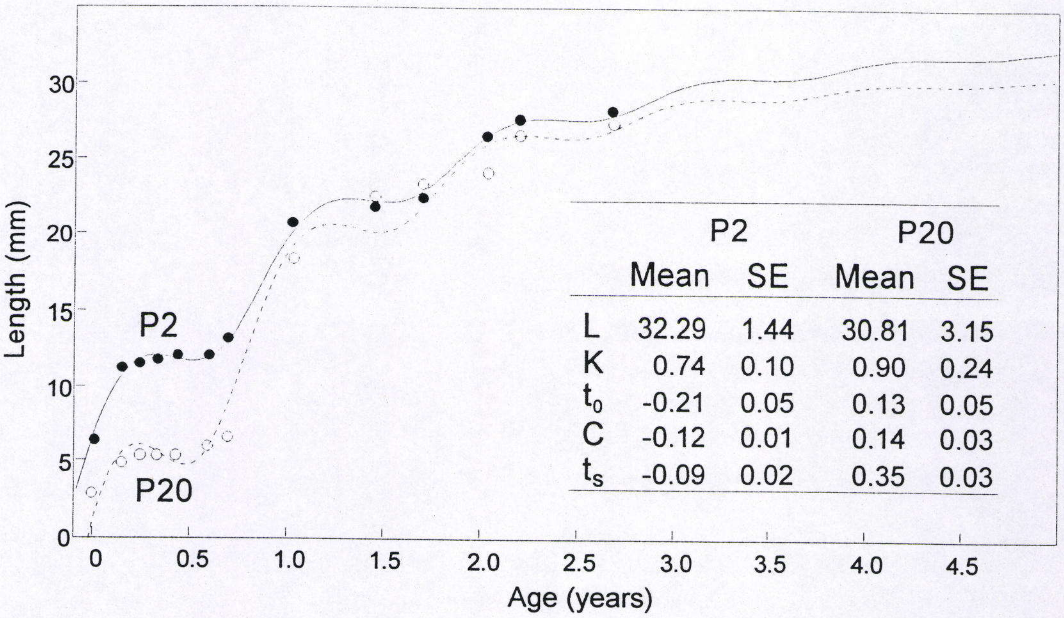


Figure 5. The length – frequency distributions of the stations P2 and P20 during all sampling months. X-axis (logarithmic): density (ind m^{-2}) with a maximum of 74000 ind m^{-2}; Y-axis (linear): length of *Spisula subtruncata* (mm).

Not taking into account the larger individuals present in both stations till August '95 and probably belonging to several cohorts, one cohort, appearing in August '95 (cohort '95), was detected in station P2. In station P20, three cohorts were distinguished: cohort '95, '96, and '97, first detected in August '95, August '96, and 'August '97, respectively. The growth curves of all cohorts showed a general pattern of periods of growth alternated with periods of growth stop. As the most succesful cohort was cohort '95, the parameters of the von Bertalanffy growth function (VBGF) were estimated for this cohort only (Figure 6).

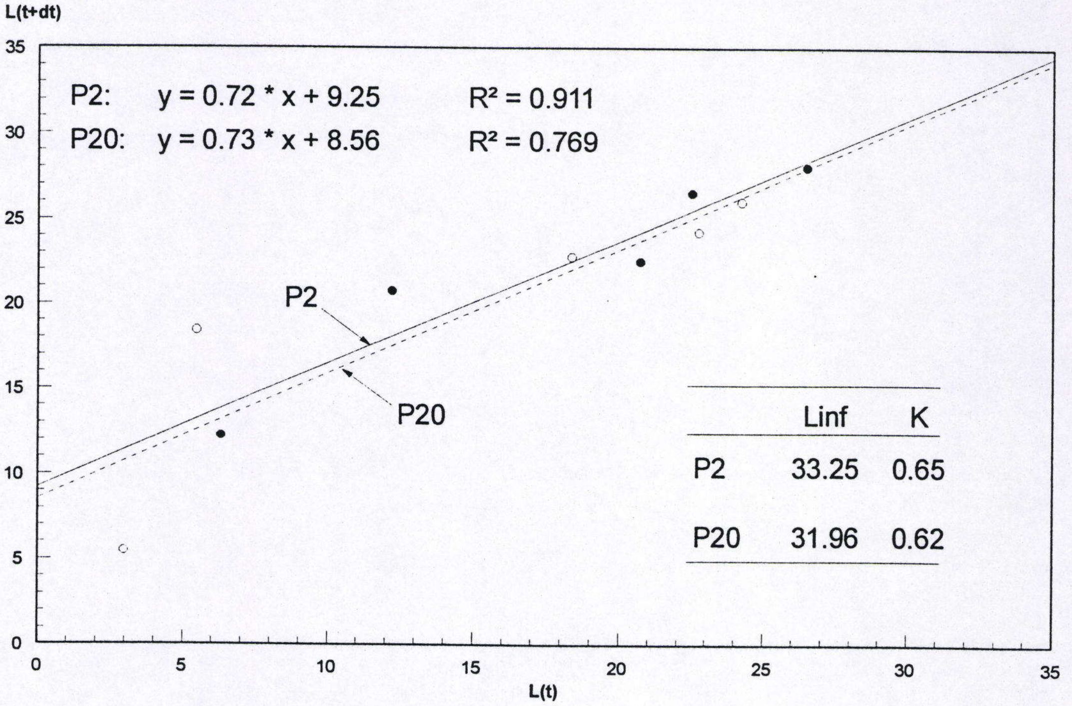
The VBGF of station P2 coincides very well with the observed data points: 99.7 % of the variance in the data points is explained by the VBGF. Furthermore, the standard errors on the estimated growth parameters were all very small ($p < 0.002$). In station P20, the VBGF coincided less clearly with the data points, especially during the second year, when the VBGF was generally below the observed data points. In P20, the VBGF predicts a clear decreasing length during the winter periods. Even though the standard errors of the estimated VBGF parameters are higher than in station P2 ($p < 0.0283$), 98.08 % of the variance is explained by the VBGF. According to the VBGF, L_∞ is higher in P2 (32.29 mm) than in P20 (30.81 mm), while K is higher in P20 (0.90) than in P2 (0.74).

Estimates of K and L_∞ by means of the Ford-Walford method (Figure 7), yielded comparable values for both stations (L_∞: 33.25 and 31.96 mm; K: 0.65 and 0.62, in P2 and P20, respectively).



	P2		P20	
	Mean	SE	Mean	SE
L	32.29	1.44	30.81	3.15
K	0.74	0.10	0.90	0.24
t_0	-0.21	0.05	0.13	0.05
C	-0.12	0.01	0.14	0.03
t_s	-0.09	0.02	0.35	0.03

Figure 6. The graphical presentation of the von Bertalanffy growth function, together with the estimates of the five parameters of the function (L_∞, K, t_0, C, and t_s) and the standard error (SE). P2, • and solid line; P20, ○ and dashed line.



P2: $y = 0.72 * x + 9.25$ $R^2 = 0.911$

P20: $y = 0.73 * x + 8.56$ $R^2 = 0.769$

	Linf	K
P2	33.25	0.65
P20	31.96	0.62

Figure 7. The graphical presentation of the Ford-Walford method for the estimation of L_∞ and K, with L_∞ = intercept / (1 – slope) and K = (-1 / dt) * ln(slope).

PRODUCTION

In August '95, the individual weight of cohort '95 individuals in station P2 ranged from 0.1 to 2.1 mg (mean: 0.5 mg ind^{-1}) (Figure 8). During their first winter (October '95 – January '96) the average individual weight was 9 mg ind^{-1}, slightly increasing over winter. Between January and August '96, the individual weight steeply increased to more than 100 mg ind^{-1}. During the second winter period, it decreased slightly to about 90 mg ind^{-1} (January '97). After the second winter period, individual weight increments were detected between January and April '97 (90 to 400 mg ind^{-1}) and between August and October '97 (250 to 900 mg ind^{-1}). Individual weight losses were observed between April and August '97 (400 to 250 mg ind^{-1}) and between October '97 and April '98 (= third winter period) (900 to 250 mg ind^{-1}).

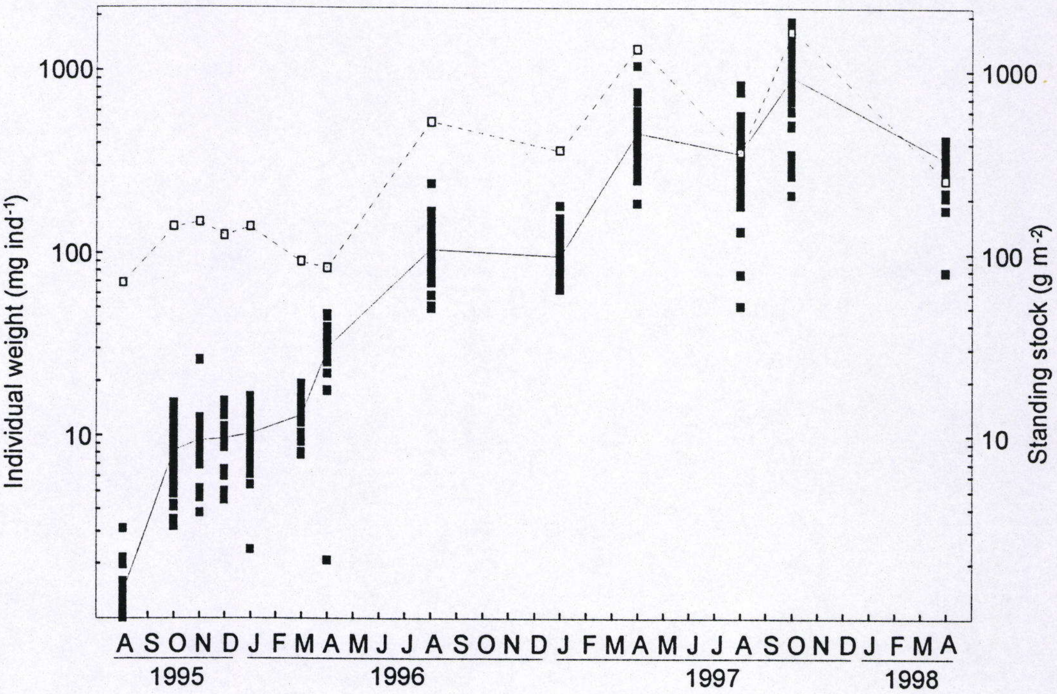


Figure 8. The temporal variation of the individual weight (mg AFDW ind^{-1}) and the standing stock (g AFDW m^{-2}) of the cohort '95 of *Spisula subtruncata* in station P2.

The standing stock of the cohort '95 in station P2 generally followed the same pattern as the individual weight, with a minimum of 65 g m^{-2} (August '95) and a maximum of 1500 g m^{-2} (October '97) (Figure 8). The main difference with the individual weight was found during the first winter: the standing stock decreased (150 to 80 g m^{-2}), while the individual weight increased slightly.

The gonadal development of *S. subtruncata* was studied from April '96 till April '98. A clear peak in the reproductive condition was found in April '97 and in April '98, with the gonads covering at least half of the visceral mass. Though it was difficult to discriminate between the gonadal and visceral mass, all other months revealed non-developed or only slightly developed gonads.

Except for the negative production between December '95 and January '96 according to the removal summation method, a positive production was assessed by both methods between August '95 and April '96 (Table 3). During this period, the total production was estimated at 366 (growth summation method) and 354 g m^{-2} (removal summation method). About half of this production was found between August and October '95. After April '96, both methods yielded different production estimates with a maximum of 1214 g m^{-2} between January and April '97 (growth summation method) and a minimum of –765 g m^{-2} between October '97 and April '98 (growth summation method). The two production estimates (growth and removal summation methods) of the cohort '95 in station P2 yielded similar results of 1657 and 1473 g m^{-2} during the study period (979 d).

The daily mean weight specific growth rate was maximal between August and October '95 (0.033 mg mg^{-1} d^{-1}). High values (minimal 0.017 mg mg^{-1} d^{-1}) were also found during the periods March – April '96, January – April '97, and August – October '97. During the first winter period, low, but positive daily mean weight specific growth rates were observed (maximal 0.004 mg mg^{-1} d^{-1}). Negative values (down to -0.006 mg mg^{-1} d^{-1}) were found during the second and third winter period (August '96 – January '97 and October '97 – April '98) and between April and August '97.

DISCUSSION

SPATIAL DISTRIBUTION AND RECRUITMENT

The bivalve, *Spisula subtruncata* is known to be an abundant species in shallow coastal waters of the Southern North Sea (Van Urk, 1959; Tebble, 1966). In this study, the bivalve is found to be abundant and widespread on the western Coastal Banks. Within this area, *S. subtruncata* is not distributed uniformely: its highest densities were found in the macrobenthos-rich *Lanice conchilega* community. This community occurs in the, relative to other Coastal Bank zones, deeper lying (about 6 m), fine sandy sediments (median grain size: 200 ± 20 µm), mainly of the gully, Potje (P2), and the northern flank of a sandbank, Den Oever (P20), both situated in area 2 (Degraer *et al.*, in press a). Still, *S. subtruncata*

Sampling date	Period	N° of days	Individual weight	Density	Average I.W.	Average Density	Increment I.W.	Decrement Density	Production G.S.	Production R.S.	$\overline{C}_w$
August '95	---		1.4	50117							
October '95	1	54	8.1	16848	4.8	33483	6.8	33269	224	158	0.033
November '95	2	36	9.3	15749	8.7	16299	1.1	1099	20	10	0.004
December '95	3	30	9.5	13006	9.4	14378	0.3	2743	3	26	0.001
January '96	4	38	10.1	13702	9.8	13354	0.6	-696	8	-7	0.002
March '96	5	58	12.8	6925	11.5	10314	2.7	6777	28	78	0.004
April '96	6	37	29.9	2770	21.4	4848	17.1	4155	83	89	0.023
August '96	7	124	104.0	5035	67.0	3903	74.1	-2265	289	-152	0.010
January '97	8	154	94.8	3885	99.4	4460	-9.2	1150	-41	114	-0.001
April '97	9	90	449.8	2955	272.3	3420	355.0	930	1214	253	0.017
August '97	10	126	347.1	1033	398.5	1994	-102.7	1922	-205	766	-0.002
October '97	11	57	909.2	1807	628.2	1420	562.1	-774	798	-486	0.017
April '98	12	175	320.6	791	615.0	1299	-588.6	1016	-765	625	-0.006
TOTAL	---	979	---	---	---	---	---	---	1657	1473	

Table 3. Calculation of the production of the cohort '95 of *Spisula subtruncata* in station P2, according to the growth summation and the removal summation method (Crisp, 1984) and the daily mean weight specific growth rate (Winberg 1971), with: N° of days: the number of days between two consequent sampling dates or during one period; Individual Weight in mg ind^{-1}; Density in ind m^{-2}; Average I.W. and Density: the average individual weight and density; Increment I.W.: the individual weight increment, in mg ind^{-1} period^{-1}; Increment Density: in ind period^{-1}; Production G.S. and R.S.: production estimates, in g m^{-2}, according to the growth summation method, $P = \Sigma$ (Average Density$_i$ * Increment I.W.$_i$) and the removal summation method, $P = \Sigma$ (Average I.W.$_i$ * Increment Density$_i$); $\overline{C}_w$: daily mean weight specific growth rate, in mg mg^{-1} d^{-1}, $\overline{C}_w$ = (ln(individual weight$_2$) – ln(Individual Weight$_1$)) * N° of days^{-1}.

was absent in a rather large proportion (37 %) of the stations of the *L. conchilega* community. Together with the contagious small scale spatial distribution, these facts support the idea of a patchy distribution of the bivalve, even within the optimal habitat, and the existence of *Spisula* banks (Davis, 1923; Van Assche and Lowagie, 1991; Meire, 1993).

Especially within area 2, an increase in occurrence and density of *S. subtruncata* is detected between 1994 and 1997: an overwhelming recruitment, with densities up to 150000 ind m^{-2}, has been taking place during July '95 (first detected at 10 August 1995). The recruitment not only took place in the stations P2 (Potje) and P20 (Den Oever), but probably over a large range of the western Coastal Banks and certainly of area 2, where the small individuals formed a dense mat of about 1 cm on top of the sediment in at least two more stations (personal observation). One of these two other stations was situated in the *Nephtys cirrosa* community, occurring in shallower (about 4 m), coarser (median grain size: about 250 µm) sediments (Chapter 3). This, together with the higher densities and occurrence of *S. subtruncata* in the *N. cirrosa* community in 1997, compared to 1994, suggests that the recruitment also occurred in suboptimal environments. Yet, a succesful recruitment, followed by fair survival of the individuals, was only noticed in the *L. conchilega* community. As post-settlement mortality often operates as a density regulation of soft-sediment invertebrates (Olafsson *et al.*, 1994), it probably explains the steep density decrease between August and October '95 in both stations. In October '95, both stations had a similar density of 15000 - 20000 ind m^{-2}. Due to this mortality of *S. subtruncata*, small (at maximum 1 cm), dead and dying individuals of *S. subtruncata* formed large banks at the high water line of the beach of De Panne, situated in area 2, in September '95 (personal observation).

Furthermore, after January '96, a drastic decrease in density (to less than 100 ind m^{-2}) occurs in station P20, while the density in P2 was never below 1000 ind m^{-2}. This high mortality of *S. subtruncata* coincided with an increase of the sediment's mud concentration: till December '95 a mud concentration of maximal 5 % was found, while this concentration started to increase from January '96 on to reach up to 30 % in March '96. This sedimentological change was not detected in P2, where the mud concentration was never higher than 6 %. This sedimentological change may be responsible for the high mortality of *S. subtruncata* in P20 between January and March '96. High mortality of *Spisula*, related to mud deposition, has also been demonstrated in Swansea Bay (U.K.) (Shackley and Collins, 1984)

Next to the succesful recruitment, detected in August '95 in both stations, two other recruitments were detected in August '96 (cohort '96) and August '97 (cohort '97) in P20 (Den Oever). The appearance of the three cohorts all point towards a period of recruitment in July – August. This coincides with the recruitment of many other bivalve species in temperate regions, as *Abra alba* (Rainer, 1985). On the Doggerbank, recruitment of *S. subtruncata* was also assessed to take place between June and the beginning of August, followed by a mean date of settlement not many weeks or even days later (Davis, 1923, 1925). The recruitments revealed a low number of individuals and were found till at least April of the following year. In the case of cohort '96, the few surviving individuals possibly survived for a longer period, but they could not be discriminated from the cohort '95 by means of the length-frequency distributions since August '97. A successful recruitment of the cohort '96 and the cohort '97, increasing the occurrence and density of the bivalve, is thus doubtful and certainly minor to the cohort '95. The highly variable recruitment, common in many benthic organisms with planktonic life stages (Fogarty *et al.*, 1991), is responsible for the high temporal variability within the spatial distribution and density of *S. subtruncata*. On the western Coastal Banks, the bivalve was only present in low densities in 1977 (Van Steen, 1978), whereas high densities (more than 1000 ind m^{-2}) were found in 1991 in the eastern part of area 2 (Van Assche and Lowagie, 1991), where *S. subtruncata* was almost absent during this study.

GROWTH AND PRODUCTION

Like *Macoma balthica* (Bachelet, 1980) and *Scrobicularia plana* (Bachelet, 1981), the growth curve (length increment) of *S. subtruncata*, comprizing periods of growth (early spring till early autumn) interrupted by periods of growth cessations (late autumn and winter), can be described by the von Bertalanffy growth function (VBGF) with incorporation of a winterpoint, explaining 99.7 % of the total variance within the data of P2 and 98 % in P20. The growth constant (K), estimated at 0.74 and 0.90 (VBGF) and 0.65 and 0.62 (Ford-Walford method) in P2 and P20, respectively, is generally high respective to many populations of other bivalves, with K-values generally below 0.5 and maximum 0.9 (Bachelet, 1980; Urban and Campos, 1994; Walker and Heffernan, 1994; Kock, 1995; Ramón *et al.*, 1995). L_∞, the length of an individual of maximal age, was estimated at 32.3 and 30.8 mm (VBGF) and 33.3 and 32.0 mm (Ford-Walford method) in P2 and P20, respectively, while the longest individual of this study measured 33.14 mm. The comparable estimation of L_∞ by means of the three methods confirms the reliability of L_∞. Yet, a slightly lower L_∞ is expected for individuals inhabiting the sediments of P20. Though relatively small, the different K and L_∞ values may be caused by the differences in the habitat of P2 and P20, as already shown for *M. balthica* (Bachelet, 1982; Harvey *et al.*, 1993).

Yet, growth is a combined length and individual biomass increment. Shortly after the recruitment of cohort '95 (August '95), an obvious difference in length between P2 (6 mm) and P20 (3 mm) is detected. This difference in length may be the result of (1) a higher density of recruits in P20, causing an increased competition for food and space, (2) a later settlement of the planktonic larvae out of the water column, decreasing the duration of the growing period, and/or (3) environmental differences between the two stations, favouring growth of the individuals in P2. Only the higher density in P20 could be detected, but the two other may play a role as well. Davis (1923), who found two separable (length-frequency distributions) length classes of recently settled individuals of *Spisula subtruncata* on the Doggerbank, stated: "*...This appears to indicate a double spawning season, not necessarily the result of two spawnings of the same adult group, but more probably the result of two adult groups maturing at different seasons...*". The differential maturation and spawning of two adult groups, will create a time lag between the presence and settlement of planktonic larvae of the two groups. If this explains the difference in length of recently settled individuals of *S. subtruncata* between P2 and P20, the populations in both stations are probably originating from two different adult populations or patches of *S. subtruncata*. Taking into account the prevailing residual currents along the Belgian coastline, causing a northeastern flow of the water masses, including planktonic organisms (e.g. larvae of *S. subtruncata*), these adult populations should be found southwest of the study area (northern France). Distances of several tens of kilometers between the geographical position of the adult population and the place of settlement of juvenile *S. subtruncata* are already described for the Doggerbank (Davis, 1923)

Till October '95, the newly settled recruits had a short growing period, during which their length almost doubled (P2: 11 mm; P20: 5 mm) and the individual biomass (Ash-Free Dry Weight, AFDW) in P2 increased from 0.5 to 8 mg. An average length of *S. subtruncata* of 5 – 6 mm on the Doggerbank (October 1922) has already been demonstrated by Davis (1923). A similar fast length and biomass increment during the first growing period has already been demonstrated for the bivalve *Macoma balthica* (Ankar, 1980; Bachelet, 1980).

As expected, a length increment could hardly be noticed during the winter conditions (October '95 till March '96). Yet, during this first winter period the individual biomass steadily, though slowly, continued to increase. During the second growing season (March '96 till

August '96) the length and biomass increased to about 22 mm (both stations) and 100 mg ind^{-1} (P2). This implies a faster length increment of the individuals of P20, starting at a lower length in March '96. This differential growth of *S. subtruncata* during the second growing season, also observed by Davis (1923), may be explained by the 'catching up phenomenon', describing a faster growth of individuals starting at a smaller size (Lammens, 1967; Bachelet, 1980). Because the VBGF is based on a single, and thus constant in time, growth constant (K), the faster length increment of *S. subtruncata* in P20 during this second growing period, in comparison with other growing periods, explains the underestimation of the length of the individuals at the end of the growing period. During the second and third winter period, *S. subtruncata* had a relatively constant length of about 22 – 24 and 27 – 28 mm, respectively, in both stations. In P2, the individual biomass twice decreased from 100 to 90 mg ind^{-1} and from 900 to 300 mg ind^{-1}. Because the growth of different bivalves show a positive correlation with the seawater temperature and the chlorophyll a-content of the watercolumn (Ankar, 1980), suboptimal growing conditions are expected during these winter periods, with low temperatures and chlorophyl a-content along the Belgian coast (Moll, 1998). The most obvious biomass decrease during the third winter (decreasing 65 %), may be related with the relatively high seawater temperatures during the winter 1997 – 1998 (minimum 4 C°), when bivalves need to spend more energy at their basic metabolism than at lower temperatures (winter 1996 – 1997: minimum – 0.5°C, with 1.5 months below 4 °C) (Zwarts, 1991). Yet, an age-dependent increase of basic metabolism rates may play an important role as well.

Finally, during the third growing period, the length steadily increased to about 27 – 28 mm in both stations, whereas the individual biomass is fluctuating. The steep increase in biomass between January and April '97 (from 90 to 450 mg ind^{-1}) in combination with an only minor length increment, may be attributed to gametogenesis (gonadal production). Just like many other bivalve species in temperate regions, the gametogenesis takes place in Spring (well developed gonads in April '97 and April '98), when food availability increases (Bachelet, 1980; Nakaoka and Matsui, 1994). A spectacular individual biomass increase, partly as a consequence of the gametogenesis, is also observed in other bivalve species (Bachelet, 1982; Zwarts, 1991). Between April and August '97, the less spectacular drop in the individual biomass (from 450 to 350 mg ind^{-1}) in combination with a new length increment (from about 22 to 25 mm), may be explained by the release of the gametes and new somatic production, respectively, drastically decreasing and slightly increasing the individual biomass (Bachelet, 1980). After August '97, the increment in individual biomass, from 350 to 900 mg ind^{-1}, probably points towards an increased somatic production in order to survive the next starving period, their third winter period. Combining the somatic and gonadal growth, the cohort '95 of *S. subtruncata* had a net production of about 1.5 kg AFDW m^{-2} over a 2.5 yr period in station P2 or an average yearly production of the cohort '95 of 600 g AFDW. This is very high in comparison with many other studies on the production of bivalves, where a yearly production, expressed in g AFDW m^{-2} yr^{-1}, of maximum 156 found (Table 4).

Species	Site	Yearly production (g m^{-2} yr^{-1})	Biomass type	Source
Arctica islandica	Western Baltic Sea	15	AFDW	Brey *et al.*, 1990
Corbicula fluminea	Georgia, USA (freshwater)	9 – 23 (max.)	SFDW	Stites *et al.*, 1995
Macoma balthica	Southwestern France	0.71 – 3.24	AFDW	Bachelet, 1982
Macoma balthica	Northern Baltic Sea	62.8	SFDW	Ankar, 1980
Mytilus edulis	Southwestern Netherlands	156	AFDW	Craeymeersch *et al.*, 1986
Scrobicularia plana	Southwestern France	0.62 – 25.21	AFDW	Bachelet, 1982

Table 4. Yearly production estimates of a variety of bivalves, with biomass type: AFDW, Ash-free Dry Weight and SFDW, Shell-free Dry Weight.

IMPLICATIONS OF SHELLFISHERY ON THE WESTERN COASTAL BANKS

Spisula subtruncata is known to be an important food resource for the common scoter (*Melanitta nigra*) (Leopold *et al.*, 1995). Within its wintering area, the common scoter prefers shallow coastal waters, with a lack of disturbance and a fair density of bivalves (Kirchoff, 1981), being its major food resource (Cramp and Simmons, 1977; Meissner and Bräger, 1990). The western Coastal Banks, being too shallow for commercial shipping and having high densities of bivalves, as *S. subtruncata*, are fulfilling all demands of the seaducks and, consequently, thousands the common scoter were staying in the area during some winter periods (Maertens *et al.*, 1988, 1990; Devos, 1990; Offringa *et al.*, 1998). As the fishery of *S. subtruncata* will evidently lead to a decrease in the standing stock of the bivalve in the area, the food resources for the common scoter may not be fulfilling the seaduck's demands anymore and can lead to the disappearance of the common scoter in the area, as already demonstrated in the Netherlands (Leopold, 1993; Leopold *et al.*, 1995). Furthermore, though being the most abundant bivalve in all macrobenthic communities of the western Coastal Banks, certainly in 1997, *Spisula subtruncata* is only found in high densities in the *Lanice conchilega* community. This ecologically, highly important community is only encountered in the deeper parts of area 1, as the tidal gully, Potje, and the northern flank of Den Oever and a few spots of area 2 (Degraer *et al.*, in press a). In comparison with the shallow parts of the western Coastal Banks, these relatively deeper areas create a hydrodynamically more benign situation for the macrobenthos, strongly increasing the density and diversity of the macrobenthos. Shellfishery in the most important areas (*L. conchilega* community), can lead to an impoverishment (density, biomass and diversity) of the macrobenthos (Craeymeersch, 1997).

Finally, because the occurrence of fishable stocks of *Spisula subtruncata* (86000 ton) is concentrated in small areas, mainly situated in area 2 (Potje and northern flank of Den Oever and Trapegeer) (Vanhee *et al.*, 1998), this stock can be depleted within a short period of time. In Belgium, where no shellfishery occurs at this moment, first of all large investments within the shellfishery are necessary to harvest the bivalve. On the other hand, as the relatively small stock of *S. subtruncata* may be depleted quickly and no other fishable stocks of this species are present along the Belgian coastline (only 65 km!), the investments will only render for one season. After the depletion of the stocks, the natural recovery of the stocks may take several years, as demonstrated by highly variable recruitment of *S. subtruncata*. It is thus doubtful whether the Belgian *Spisula*-fishery can render over a longer period of time.