Mar Biol (2007) 152:863–875
DOI 10.1007/s00227-007-0740-y

RESEARCH ARTICLE

Spatial distribution, population dynamics and productivity of *Spisula subtruncata*: implications for *Spisula* fisheries in seaduck wintering areas

Steven Degraer · Patrick Meire · Magda Vincx

Received: 3 December 2004 / Accepted: 24 May 2007 / Published online: 16 June 2007
© Springer-Verlag 2007

Abstract Bivalves are important in shallow marine habitats, not at least being the major food resource for seaducks such as the common scoter (*Melanitta nigra*), thousands of which are wintering on the Western Coastal Banks, near the Belgian-French border (North Sea). Next to this ecological importance, fishable stocks of one of these bivalves, *Spisula subtruncata*, occur in the area. This study aimed at investigating *S. subtruncata*'s spatial distribution, population dynamics and productivity and its implications for a sustainable *Spisula* fishery in seaduck wintering areas. The spatial distribution of *S. subtruncata* was studied in 1994 and 1997 in two areas of the Belgian Western Coastal Banks. The population dynamics and production 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 *Abra alba* community, mainly found in the western most part of the Western Coastal Banks. In August 1995, an overwhelming and successful recruitment was observed in this area: local densities were as high as 150,000 ind m^{-2}. Minor, non-successful recruitments were detected in August 1996 and 1997. Due to space limitation, high densities of *S. subtruncata* are hypothesized to be responsible for the occurrence of aberrant shapes as observed from August 1996 onwards. Growth was described by a seasonally oscillating version of the von Bertalanffy growth function (VBGF): a growth stop was observed from late autumn till early spring. The VBGF parameters K (growth constant) and L_∞ (asymptotic length) were estimated at 0.7–0.9 and 31–33 mm. A combination of length and individual biomass increment showed: (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 winter, when the individual biomass slightly increased), (3) a positive relationship 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 1997 and 1998) because of gametogenesis, followed by a decrease because of spawning (August 1997). The extremely high total production of the 1995 year class in the tidal gully (Potje) during the study period was estimated at approximately 1,500 g ash-free dry weight (ADW) m^{-2} or 600 g ADW m^{-2} on average per year. Shellfisheries for *S. subtruncata* within seaduck wintering areas, such as the Western Coastal Banks, should be carefully deliberated since (1) an important food resource for the seaducks will decrease, (2) the ecologically most diverse and rich macrobenthic *A. alba* community will be heavily affected, and (3) the recovery of *Spisula* populations after depletion is expected to be erratic.

Introduction

Bivalves are an ecologically important component of the macrobenthos of coastal marine ecosystems. Although their

---

Communicated by O. Kinne.

S. Degraer (✉) · M. Vincx
Biology Department, Marine Biology Section, Ghent University,
Krijgslaan 281-S8, 9000 Ghent, Belgium
e-mail: Steven.Degraer@UGent.be

P. Meire
Department of Biology, University of Antwerp,
Universiteitsplein 1, 2610 Wilrijk, Belgium

densities in the southern North Sea 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 for a variety of demersal fish species (Rainer 1985; Brey et al. 1990) and for diving seaducks, e.g. the common scoter (*Melanitta nigra*) (Cramp and Simmons 1977; Meissner and Bräger 1990; Meire 1993). The presence of wintering scoters at the Western Coastal Banks can partly be explained by its undisturbed character (Degraer et al. 1999a), 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, inclusive *Spisula subtruncata* next to several other shallowly living and medium sized bivalves, such as *Abra alba*, has already been demonstrated (Van Assche and Lowagie 1991; Leopold et al. 1995; Kaiser et al. 2006).

Since the early 1980s, fishermen are interested in the commercial exploitation of *S. subtruncata* stocks and, as an alternative to the declining *Cerastoderma edule* fisheries, large amounts of the bivalve have already been harvested in the Netherlands, north of the area of investigation (Craeymeersch et al. 2001). The consequent competition for food (i.e. shellfish) and space (i.e. disturbance by shipping) between the *S. subtruncata* fishery and the common scoter, is currently believed to be the major threat for the common scoter in the Netherlands, causing shifts in the spatial distribution and a decrease of the number of wintering common scoters (Leopold et al. 1995). 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) and Fraschetti et al. (1997) provided information on the life history and population dynamics of *S. subtruncata*.

The aims of this study are (1) to investigate the spatial distribution, population dynamics and productivity of *S. subtruncata* in a seaduck wintering area during a 2.5 year study period and (2) to use this information in the frame of a sustainable fisheries of *S. subtruncata*.

Materials and methods

Study area

The selected seaduck wintering area, the Belgian Western Coastal Banks, extend from the Belgian-French border to Oostende and from the low water line to about 8 m depth (Fig. 1). Between Koksijde and Middelkerke, the banks are merely 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 geomorphologically and, consequently, hydrodynamically diverse character of the area, a large variety of sediments (median grain size from 160 to 500 µm) is present (Degraer et al. 1999a).

Because of the large number of wintering common scoters on the Belgian Western Coastal Banks (Maertens

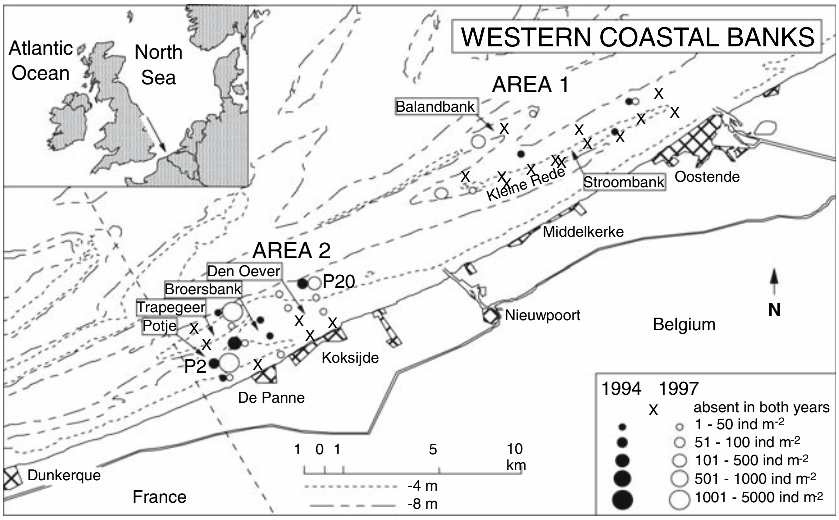


Fig. 1 Spatial distribution of *Spisula subtruncata* at the Belgian Western Coastal Banks in 1994 and 1997, with indication of the two areas under consideration

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). The area is designated as a Special Protection Area (SPA), implementing the European Habitat Directive (92/43/EEG). Parts of the area are further designated as SPA, implementing the European Bird Directive (79/409/EEG).

Sampling

To investigate the spatial distribution, habitat preferences and density fluctuations of the *S. subtruncata* population at the Belgian Western Coastal Banks, 40 and 39 stations were sampled in October 1994 and 1997, respectively (Fig. 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 1 mm mesh sized sieve before fixation and then fixated and preserved in an 8% formaldehyde–seawater solution.

To study the population dynamics (i.e. growth, production and gonad development) of *S. subtruncata* two stations (P2 and P20) were selected because of the high numbers of bivalves observed in October 1994. At each station, 5 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 1 and 0.5 mm sieve and preserved in 8% formaldehyde–seawater solution. In contrast to Fraschetti et al. (1997), who found an important fraction of a Mediterranean *S. subtruncata* population smaller than 1 mm, 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, *S. subtruncata* and *Spisula solida*, were found, of which *S. solida* only occurred in low numbers (<20 ind m^{-2}) in three stations sampled in 1994. *Spisula solida* was not detected in the stations P2 nor P20. Hence, although species identification of small (<0.5 cm) *Spisula* specimens is perilous, *S. solida* juveniles were not expected to bias the population dynamical aspects of *S. subtruncata* within this study.

The number of *S. subtruncata* was counted. To study the population dynamics of *S. subtruncata*, 150–400 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 with a vernier caliper (precision: 0.01 mm) for individuals longer than 1 cm. At station P2, the individual biomass (ash-free dry weight, ADW) of 30–50 individuals per sampling occasion was measured by loss of mass on ignition (500 ± 50°C for 2 h) of complete, oven-dried individuals (70°C for 48 h) (Palmerini and Bianchi 1994). Because all individuals were preserved in a formaldehyde–seawater solution, a decrease of the ADW, 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 3 months were left between fixation and determination of the ADW. Yet, an underestimation of the individual biomass and standing stock might thus be expected.

The reproductive condition of *S. subtruncata* was studied by dissecting 20 individuals of station P2 for each month from April 1996 to April 1998. 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 cases, the gonad development could not be assessed with certainty. The rating of gonad 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 made only 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.

Data analysis

The detailed spatial distribution of *S. subtruncata* was investigated by calculating its density and frequency of occurrence in each of the macrobenthic communities, detected in the area. Based on a multivariate community analysis of the macrobenthos at each sampling station, Degraer et al. (1999c) discerned between three distinct communities: (1) the density- and species-rich *A. alba* community and (2) the density- and species-poor *Nephtys cirrosa* and *Ophelia limacina–Glycera lapidum* communities, following Van Hoey et al. (2004).

The biometric relationships between (1) length and biomass and (2) length, height and width were investigated by regression analysis (least squares method), using the following equations:

$$\text{Biomass} = a \times \text{Length}^b$$

$$\log_{10} Y = a + b \times \log_{10}\text{Length}$$

with Y = height or width.

The deviation of the b value of the regression function from the isometric value (i.e. length-biomass relation: b = 3; length–height–width relation: b = 1) was analyzed by means of a *t*-test, as advised by Sokal and Rohlf (1987) and applied by Gaspar et al. (2002). A significant deviation indicates a negative ($b < 3$ or $b < 1$) or positive ($b > 3$ or $b > 1$) allometric relationship.

The length increment was described by the von Bertalanffy growth function (VBGF) with incorporation of winter growth stop. The equation, calculating the predicted length at age t (L_t), is given by:

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

with L_t the predicted length at age t. The values of the five parameters (L_∞, asymptotic length; K, growth constant; t_0, theoretic age at zero length; C, amplitude of the seasonal growth oscillation and t_s, starting point of the oscillation) were estimated by means of non-linear estimation (least squares method), as provided by the statistical software package STATISTICA 5.1 (Anonymous 1996). The 1995-year class could easily be distinguished from other year classes by means of monthly length-frequency distributions, as other year classes were only present in very low numbers and clearly differed in size. The input data points to develop the VBGF, were the average lengths of the 1995 year class at each sampling occasion. Next to the estimation of the parameters, STATISTICA 5.1 also provided 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 $L_{t+\mathrm{dt}}$ 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 $K = -1/\mathrm{dt}\ \ln(a)$ 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 used only from all August and January samples (five data pairs).

Productivity was estimated with the growth and removal summation methods (Crisp 1984). The daily mean weight specific growth rate (Winberg 1971) was calculated.

Growth summation:

$$P = \sum_{1}^{i} \left(\bar{D} \times \Delta \mathrm{IW}\right)$$

Removal summation:

$$P = \sum_{1}^{i} \left(\Delta D \times \overline{\mathrm{IW}}\right)$$

Daily mean weight specific growth rate:

$$\Delta_w = \frac{\ln\left(\mathrm{IW}_{j+1}\right) - \ln\left(\mathrm{IW}_j\right)}{d}$$

with i, period; j, time; D, density, IW, individual weight and d, number of days.

Results

Spatial distribution and density

With maximum densities of up to 5,000 ind m^{-2}, *S. subtruncata* was abundant on the Western Coastal Banks (Fig. 1). The species occurred in 25 and 41% of the stations in October 1994 and 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. The density of *S. subtruncata* in 1997 was higher than in 1994.

Spisula subtruncata was mainly found in the *Abra alba* community, as defined by Van Hoey et al. (2004), where it occurred with an average density of 48 and 549 ind m^{-2} in 1994 and 1997, respectively. Whereas *S. subtruncata* was found in maximum 40% of the stations of the two other subtidal macrobenthic communities, it was present in at 55 and 63% of the stations of the *A. alba* community in 1994 and 1997, respectively.

All individuals of *S. subtruncata* were retained on a 1 mm sieve; no individuals were found in the 0.5 mm fraction. From April till July 1995, the maximal density of *S. subtruncata* in the stations P2 and P20 was 20 ind m^{-2} (Fig. 2). In August 1995, the species became very abundant in both stations, with densities up to 150,000 ind m^{-2}. Between August 1995 and January 1996, the density decreased to about 10,000 ind m^{-2} in both stations. After January 1996, the density of *S. subtruncata* in station P20 continued to decrease to some hundreds of ind m^{-2}, while in station P2 the density also continued to decrease, but was never lower than about 1,000 ind m^{-2}.

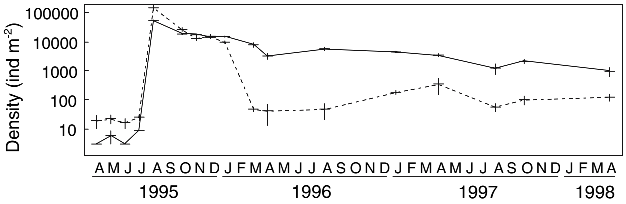


Fig. 2 Temporal variation of the density (ind m^{-2}) of *Spisula subtruncata* in the stations P2 (*solid line*) and P20 (*dashed line*), with indication of the standard error (*vertical lines*)

Biometrics

Except for August 1996 and October 1997, when regressions were not significant, highly significant ($P < 0.0001$) regressions between length and biomass of *S. subtruncata* during the study period were found per month and for all months together (Table 1). During the first half year of their life, the biomass of *S. subtruncata* showed an isometric relationship with length. During the next 2 years of its life however, isometric (33%) as well as positive (17%) and negative (50%) allometric relationships were found; no clear seasonality could be observed. An overall positive allometry between length and biomass was found when combining all months. A very highly significant positive allometric relationship was found for both height and width in relation to length (Table 2).

During most of the sampling period *S. subtruncata* had a regular shape. From August 1996 till 1997 however, an aberrant shape, with a clear ventral indentation, occurred next to regularly shaped individuals (Fig. 3). Except for January 1997, a generally increasing percentage of aberrant shapes with increasing density was detected. This trend was especially obvious in August 1996 and April 1997, whereas in January 1997 the general trend was disturbed by the high percentage of aberrant shapes (80%) at the lowest density (3,300 ind m^{-2}). No data were available for August 1997. After August 1997, no clear aberrantly shaped individuals were detected anymore.

Length increment

Between April and July 1995, a low number of larger individuals of *S. subtruncata* (17–33 mm) was found in both stations (Fig. 4). Such large individuals were present till January 1996 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 1995. These individuals doubled their length by October 1995. Between October 1995 and March 1996, individuals, belonging to this year class, were still present in large numbers, but they ceased growing. After March 1996, the year class could still be detected in high densities in station P2, while their density steeply decreased in station P20. Still, in both stations, periods of growth (March 1996–January 1997 and April 1997–October 1997) alternated with periods of more or less zero growth (August 1996–January 1997 and October 1997–April 1998). In both stations, the length–frequency distribution of the year class, appearing in August 1995, 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 1996 and in August 1997. Yet, on both occasions, their density remained low and they growed till April of the next year.

Not taking into account the larger individuals present in both stations till August 1995 and probably belonging to several year classes, one year class, appearing in August 1995 (1995-year class), was detected in station P2. In station P20, 3 year classes were distinguished: the 1995, 1996 and 1997 year classes, first detected in August 1995, August 1996, and August 1997, respectively. As the 1995-year class was most succesful, the parameters of the VBGF were estimated for this year class only (Fig. 5).

The VBGF of station P2 coincided very well with the observed data points: 99.7% of the variance in the data points was explained by the VBGF. Furthermore, the

Table 1 The parameters (a and b) of the regression function Biomass = $a \times \text{Length}^b$, as defined for each sampling occasion (non-significant regressions for August 1996 and October 1997 not given) and for all months together

	N	a		b		*P*	Biometric relationship
		Mean	SE	Mean	SE		
August 1995	23	0.006	0.006	2.887	0.548	0.839	Isometry
October1995	48	0.011	0.006	2.667	0.206	0.619	Isometry
November 1995	20	<0.001	0.001	3.984	0.833	0.111	Isometry
December 1995	20	0.036	0.036	2.223	0.397	0.066	Isometry
January 1996	47	0.009	0.007	2.801	0.294	0.503	Isometry
March 1996	30	0.030	0.019	2.407	0.241	0.020	– Allometry
April 1996	17	0.049	0.130	2.425	0.996	0.572	Isometry
January 1997	49	0.128	0.160	2.169	0.406	0.046	– Allometry
April 1997	49	0.003	0.008	3.747	0.808	0.302	Isometry
August 1997	46	0.009	0.023	3.236	0.806	0.008	+ Allometry
April 1998	49	2.210	3.149	1.493	0.426	0.001	– Allometry
All months	508	0.002	0.001	3.840	0.267	<0.001	+ Allometry

N number of observations; *SE*, standard error; *P*, significance level of *t*-test for allometry (H_0: $b = 3$)

Table 2 Summary parameters of the regression analysis of the relationships between length (L), height (H) and width (W) of *Spisula subtruncata*

Biometric equation	N	R^2	SE	P	Relationship
$\log H = -0.270 + 1.084 \log L$	439	0.99	0.006	<0.001	+ allometry
$\log W = -0.562 + 1.149 \log L$	415	0.97	0.009	<0.001	+ allometry

N number of observations; R^2 determination coefficient; *SE* standard error of slope estimate; *P* significance level of *t*-test for allometry (H_0: $b = 1$)

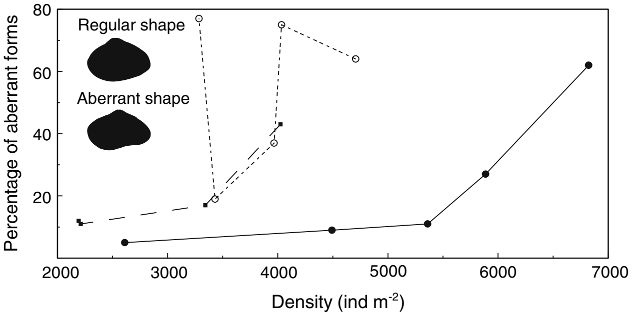


Fig. 3 The relation between the density and the percentage of aberrant shapes of *Spisula subtruncata* in station P2. *filled circle* August ‘96; *open circle* January ‘97; *filled square* April ‘97

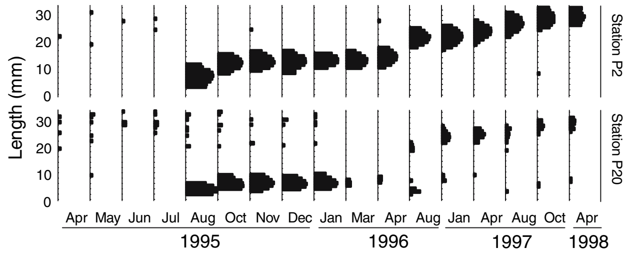
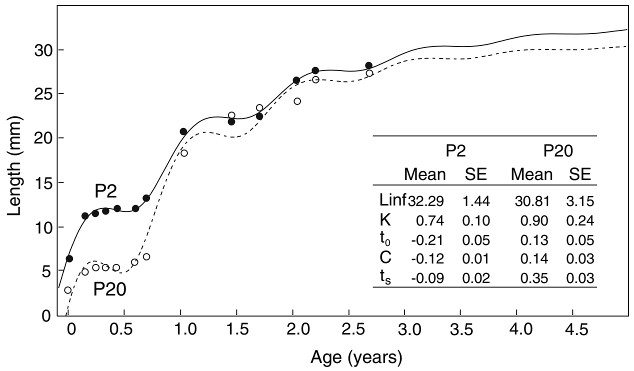


Fig. 4 Length–frequency distribution of *Spisula subtruncata* at the stations P2 and P20 during all sampling months. *x*-axis (logarithmic): density (ind m^{-2}) with a maximum of 74,000 ind m^{-2}; *y*-axis (linear): length of *Spisula subtruncata* (mm)

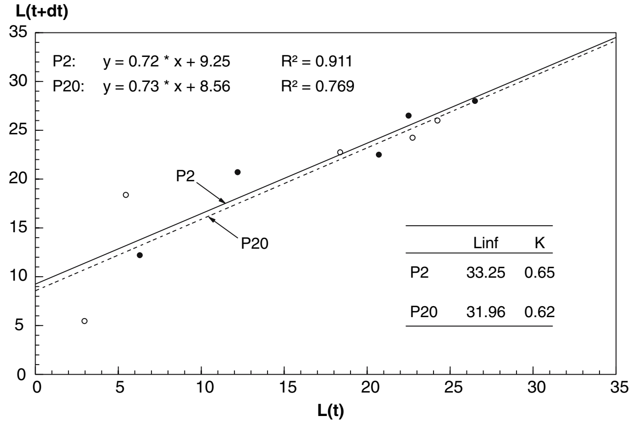
standard errors on the estimated growth parameters were very small. In station P20, the VBGF coincided less clearly with the data points, especially during the second year, when the VBGF was generally below the observed data points. In station P20, the VBGF predicted a clear decreasing length during the winter periods. Even though the standard errors of the estimated VBGF parameters were higher than in station P2, 98.1% of the variance was explained by the VBGF. According to the VBGF, L_∞ was higher in station P2 (32.29 mm) than in station P20 (30.81 mm), while *K* was higher in station P20 (0.90) than in station P2 (0.74).

Estimates of *K* and L_∞ by means of the Ford–Walford method (Fig. 6), yielded comparable values for both stations (L_∞: 33.25 and 31.96 mm; *K*: 0.65 and 0.62, in station P2 and station P20, respectively).



	P2		P20	
	Mean	SE	Mean	SE
Linf	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

Fig. 5 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 their standard error (SE). Station P2 *filled circle* and *solid line*; station P20 *open circle* and *dashed line*



	Linf	K
P2	33.25	0.65
P20	31.96	0.62

Fig. 6 Ford–Walford plot for the estimation of L_∞ and *K*, with L_∞ = intercept/(1 – slope) and $K = (-1/\mathrm{d}t) \times \ln(\text{slope})$

Production

In August 1995, the individual weight of the 1995-year class (only measured for station P2) ranged from 0.1 to 2.1 mg ADW (mean 0.5 mg ADW ind^{-1}) (Fig. 7). During their first winter (October 1995–January 1996) the average individual weight was 9 mg ADW ind^{-1}, slightly increasing over winter. Between January and August 1996, the individual weight steeply increased to more than 100 mg ADW ind^{-1}. During the second winter period, it

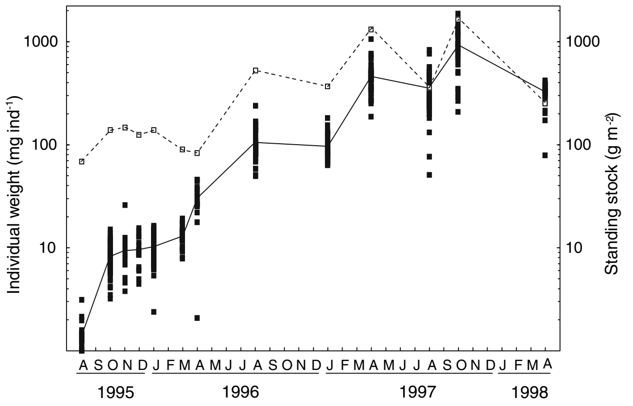


Fig. 7 Temporal variation of the individual weight (*filled square*, mg ADW ind^{-1}) and the standing stock (*open square*, g ADW m^{-2}) of the 1995 year class of *Spisula subtruncata* in station P2

slightly decreased to about 90 mg ADW ind^{-1} (January 1997). After the second winter period, individual weight increments were detected between January and April 1997 (90–400 mg ADW ind^{-1}) and between August and October 1997 (250–900 mg ADW ind^{-1}). Individual weight losses were observed between April and August 1997 (400–250 mg ADW ind^{-1}) and between October 1997 and April 1998 (=third winter period) (900–250 mg ADW ind^{-1}).

The standing stock of the 1995-year class in station P2 generally followed the same pattern as the individual weight, with a minimum of 65 g ADW m^{-2} (August 1995) and a maximum of 1,500 g ADW m^{-2} (October 1997) (Fig. 7). The main difference with the individual weight was found during the first winter: the standing stock decreased (150–80 g ADW m^{-2}), while the individual weight slightly increased.

The gonad development of *S. subtruncata* was studied from April 1996, when gonad development could first take place in the 1995-year class, till April 1998. A clear peak in the reproductive condition (i.e. gonad development) was found in April 1997 and 1998, with the gonads covering at least half of the visceral mass in all individuals. All other months revealed non-developed or only slightly developed gonads.

Except for the negative production between December 1995 and January 1996 according to the removal summation method, both methods calculated a positive production between August 1995 and April 1996 (Table 3). During this period, the total production was estimated at 366 (growth summation method) and 354 g ADW m^{-2} (removal summation method). About half of this production was found between August and October 1995. After April 1996, both methods yielded different production estimates with a maximum of 1,214 g ADW m^{-2} between January and April 1997 (growth summation method) and a minimum of –765 g ADW m^{-2} between October 1997 and April 1998 (growth summation method). The two production estimates (growth and removal summation methods) of the 1995-year class in station P2 yielded similar results of 1,657 and 1,473 g ADW m^{-2} during the study period (979 days).

The daily mean weight specific growth rate was maximal between August and October 1995 (0.033 mg mg^{-1} day^{-1}). High values (minimal 0.017 mg mg^{-1} day^{-1}) were also found during the periods March–April 1996, January–April 1997, and August–October 1997. During the first winter period, low, but positive daily mean weight specific growth rates were observed (maximal 0.004 mg mg^{-1} day^{-1}). Negative values (down to –0.006 mg mg^{-1} day^{-1}) were found during the second and third winter period (August 1996–January 1997 and October 1997–April 1998) and between April and August 1997.

Discussion

Spatial distribution and recruitment

The bivalve *S. subtruncata* is known to be an abundant species in shallow coastal waters of the Southern North Sea (Van Urk 1959; Tebble 1966; Rueda and Smaal 2004). 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: highest density and frequency of occurrence coincided with the distribution of the *A. alba* community. At the Western Coastal Banks this community occurs in the deeper (about 6 m), fine sandy sediments (median grain size: 200 ± 20 µm), mainly of the gully Potje and the northern flank of the sandbank Den Oever, both situated in area 2 (Degraer et al. 1999a, 1999c). Still, *S. subtruncata* was absent in a rather large proportion (37%) of the stations of the *A. alba* community. This fact supports the idea of a patchy distribution of the bivalve 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* was detected between 1994 and 1997: an overwhelming recruitment, with densities up to 150,000 ind m^{-2}, was first detected on 10 August 1995. Since (1) settling individuals have an average size of 210 µm (Fraschetti et al. 1997) and (2) the collected individuals were 2 mm at minimum (absence of specimens in the 0.5 mm fraction!), the recruitment must have taken place in July 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

Table 3 Calculation of the production of the cohort 1995 of *Spisula subtruncata* in station P2, according to the growth summation (GS) and the removal summation method (RS) (Crisp 1984) and the daily mean weight specific growth rate (Δ_w Winberg 1971)

Date	Period	N of days	IW	Density	Mean IW	Mean Density	IW Increment	Density decrement	Production GS	Production RS	Δ_w
August 1995	–		1.4	50,117							
October 1995	1	54	8.1	16,848	4.8	33,483	6.8	33,269	224	158	0.033
November 1995	2	36	9.3	15,749	8.7	16,299	1.1	1,099	20	10	0.004
December 1995	3	30	9.5	13,006	9.4	14,378	0.3	2,743	3	26	0.001
January 1996	4	38	10.1	13,702	9.8	13,354	0.6	–696	8	–7	0.002
March 1996	5	58	12.8	6,925	11.5	10,314	2.7	6,777	28	78	0.004
April 1996	6	37	29.9	2,770	21.4	4,848	17.1	4,155	83	89	0.023
August 1996	7	124	104.0	5,035	67.0	3,903	74.1	–2265	289	–152	0.010
January 1997	8	154	94.8	3,885	99.4	4,460	–9.2	1,150	–41	114	–0.001
April 1997	9	90	449.8	2,955	272.3	3,420	355.0	930	1,214	253	0.017
August 1997	10	126	347.1	1,033	398.5	1,994	–102.7	1,922	–205	766	–0.002
October 1997	11	57	909.2	1,807	628.2	1,420	562.1	–774	798	–486	0.017
April 1998	12	175	320.6	791	615.0	1,299	–588.6	1,016	–765	625	–0.006
Total	–	979	–	–	–	–	–	–	1,657	1,473	

N of days: the number of days between two consequent sampling dates or during one period; IW: individual weight (mg ADW ind^{-1}); Density (ind m^{-2}); Mean IW and Density: the mean individual weight and density during one period; IW and Density increment: individual weight and density increment during one period (mg ADW ind^{-1} period^{-1} or ind m^{-2} period^{-1}, respectively); Production (g m^{-2}); Δ_w daily mean weight specific growth rate, in mg mg^{-1} day^{-1}

two other stations was situated in the *Nephtys cirrosa* community, occurring in shallower (about 4 m), coarser (median grain size: about 250 µm) sediments (Degraer et al. 1999a). Similar to Møhlenberg and Kiørboe (1981), this fact, 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, while a successful recruitment, followed by a fair survival of the individuals, was only noticed in the optimal habitat of the *A. alba* community (e.g. stations P2 and P20).

As post-settlement mortality often operates as a density regulation of soft-sediment invertebrates (Olafsson et al. 1994; Fraschetti et al. 2003), it probably explains the steep density decrease between August and October 1995 in both stations. In October 1995, both stations had a similar density of 15,000–20,000 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 strandline of the beach of De Panne, situated in area 2, in September 1995 (personal observation).

Furthermore, after January 1996, a drastic decrease in density (to less than 100 ind m^{-2}) occurred in station P20, while the density in station P2 was never below 1000 ind m^{-2}. This high mortality of *S. subtruncata* coincided with an increase of the sediment's mud content: till December 1995 a mud content of maximal 5% was found, while this content started to increase from January 1996 onwards to reach up to 30% in March 1996 (Degraer et al. 1999b). This sedimentological change was not detected in station P2, where the mud content was never higher than 6%. This sedimentological change may be responsible for the high mortality of *S. subtruncata* in station P20 between January and March 1996. High mortality of *Spisula*, related to mud deposition, has also been demonstrated in Swansea Bay (UK) (Shackley and Collins 1984).

Next to the successful recruitment, detected in August 1995 in both stations, two other recruitments were detected: August 1996 (1996-year class) and August 1997 (1997-year class) in station P20 (Den Oever). The appearance of the 3 year classes all point towards a period of recruitment in July–August. This coincides with the recruitment of many other bivalve species in temperate regions, such as *A. alba* (Rainer 1985). On the Doggerbank (North Sea), recruitment of *S. subtruncata* was also assessed to take place between June and the beginning of August (Davis 1923, 1925). The recruitment events in August 1996 and 1997 both revealed a low number of individuals and were found till at least April of the following year. In the case of the 1996-year class, a low number possibly survived for a longer period, but they could not be discriminated from the 1995-year class by means of the length–frequency distributions from August 1997 onwards. A successful recruitment of the 1996-year class and the 1997-year class, increasing the occurrence and density of the bivalve, is thus doubtful and certainly minor to the 1995-year class. A high year-to-year variability in recruitment success of *S. subtruncata* was already demonstrated in the Mediterranean (Fraschetti et al. 1997). Survival to 1 year dependent on high-density bivalve settlement in the preceding summer was also demonstrated for *Spisula solidissima* (Weissberger and Grassle 2003).

The highly variable recruitment success, common in many benthic organisms with planktonic life stages (Fogarty et al. 1991; Chintala and Grassle 2001; Lewis et al. 2001), is responsible for the high temporal variability within the spatial distribution and density of *S. subtruncata*. On the Western Coastal Banks, the bivalve was present in low densities in 1977 (Van Steen 1978), whereas high densities (more than 1,000 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

Since both height and width showed a positive allometric relationship with length, the bivalve's shape gradually changes from relatively long and slender individuals to more robust (i.e. higher and wider) individuals as they grow bigger. Although also isometry as well as negative allometry can be observed in bivalves, positive allometry clearly prevails and was already observed for *S. subtruncata* in the Algarve region (southern Portugal) by Gaspar et al. (2002). In the latter study, the main reasons for a positive allometry were hypothesized to be (1) the need for active burrowing in the juvenile stage, favouring slender individuals versus (2) the avoidance of involuntary dislodgement in the adult stage, favouring more robust individuals. The isometric relationship between length and biomass ($b = 3$) during the first half year of the bivalve's life indicates an equal increment in length and biomass. After this period, the rather erratic shift between isometry, positive and negative allometry did not allow to deduct any seasonal trend. Hence, it was impossible to hypothesize on the changes in biometric relationships in relation to physiological changes, such as length-dependent starvation or individual productivity. This absence of trend might be due to the rather long-time intervals between the consequent sampling occasions, rather than to the absence of length-dependent physiological changes. It definitely does not mean that (length-independent) starvation nor increased productivity take place, as demonstrated further down the discussion.

Similar to *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 cessation (late autumn and winter), can be described by the VBGF with incorporation of a winterpoint, explaining 99.7% of the total variance within the data of station P2 and 98% in station P20. The growth constant (K), estimated at 0.74 and 0.90 (VBGF) and 0.65 and 0.62 (Ford–Walford method) in station P2 and station P20, respectively, is high, but within the range that of many other bivalve growth constant estimates, with K-values generally below 0.5, but with a maximum 1.0 (Bachelet 1980; Urban and Campos 1994; Walker and Heffernan 1994; Kock 1995; Ramón et al. 1995; Cranfield et al. 1996; Cranfield and Michael 2001). 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 stations P2 and P20, respectively, while the longest individual of this study measured 33.14 mm. The comparable estimations of L_∞ confirm the reliability of L_∞.

Shortly after the recruitment of the 1995-year class (August 1995), smaller individuals were found in station P20 (average 3 mm) compared to station P2 (average 6 mm). This difference in length may be the result of (1) a higher density of recruits in station P20 (Walker 2001; Horii et al. 2002), causing an increased competition for food and space, (2) a later settlement of the planktonic larvae, shortening the growing period (Davis 1923), and/or (3) environmental differences between the two stations, favouring growth of the individuals in station P2. Only the higher density in station P20 could be detected, but the two other aspects may play a role as well. Davis (1923), who found two separable (length–frequency distributions) length classes of recently settled individuals of *S. 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 station P2 and station P20, the populations in both stations are probably originating from two different parental stocks 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 1995, 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 in station P2 increased from 0.5 to 8 mg ADW ind^{-1}. An average length of *S. subtruncata* of 5–6 mm in October has already been demonstrated on the Doggerbank (Davis 1923). A similar fast length and biomass increment during the first growing period was found for the bivalve *Macoma balthica* (Ankar 1980; Bachelet 1980).

As expected, a length increment could hardly be noticed during the winter conditions (October 1995 till March 1996). Yet, during this first winter period the individual biomass continued to increase steadily, though slowly. During the second growing season (March 1996 till August 1996) the length and biomass increased to about 22 mm (both stations) and 100 mg ADW ind^{-1} (station P2). This implies a faster length increment of the individuals at station P20. 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—constant in time—growth constant (*K*), the faster length increment of *S. subtruncata* in station 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 station P2, the individual biomass decreased from 100 to 90 mg ADW ind^{-1} during the second winter and from 900 to 300 mg ADW ind^{-1} during third winter. 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 both winter periods, with low temperatures and chlorophyll 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 was fluctuating. The steep increase in biomass between January and April 1997 (from 90 to 450 mg ADW ind^{-1}) in combination with an only minor length increment can be attributed to gametogenesis (gonad production). Similar to many bivalve species in temperate regions (including *S. subtruncata*; Rueda and Smaal 2004), the gametogenesis takes place in spring (well developed gonads in April 1997 and 1998), when food availability increases (Bachelet 1980; Nakaoka and Matsui 1994). A spectacular individual biomass increase, partly as a consequence of the gametogenesis, was also observed in other bivalve species (Bachelet 1982; Zwarts 1991). Between April and August 1997, the drop in individual biomass (from 450 to 350 mg ADW 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 (Bachelet 1980). After August 1997, the increment in individual biomass, from 350 to 900 mg ADW ind^{-1}, probably points towards an increased somatic production in order to survive the next starving period, their third winter period. An increase in condition index in summer and late autumn, due to the accumulation of reserves, was also observed for *Spisula solida* (Gaspar and Monteiro 1999).

Combining the somatic and gonad growth, the 1995-year class of *S. subtruncata* had a net production of about 1.5 kg ADW m^{-2} over a 2.5 year period in station P2 or an average yearly production of the 1995 year class of 600 g ADW m^{-2} year^{-1}. This is very high in comparison to other studies, in which a yearly production of maximum 156 g ADW m^{-2} year^{-1} (*Mytilus edulis*) was assessed (Table 4). This high productivity is attributed to a combination of a high individual productivity, but also to the high population density. These high densities are hypothesized to be directly responsible (space limitation) for the aberrant

Table 4 Yearly production estimates (g m^{-2} year^{-1}) for a variety of bivalves

Species	Area	Yearly production	Type	Source
Spisula subtruncata	North Sea	600	ADW	This study
Spisula subtruncata	Mediterranean	0.1–0.6	ADW	Fraschetti et al. (1997)
Corbicula fluminea	USA (freshwater)	9–23 (max.)	SDW	Stites et al. (1995)
Arctica islandica	Baltic Sea	15	ADW	Brey et al. (1990)
Mytilus edulis	North Sea	156	ADW	Craeymeersch et al. (1986)
Scrobicularia plana	Atlantic ocean	0.6–25.2	ADW	Bachelet (1982)
Macoma balthica	Atlantic ocean	0.7–3.2	ADW	Bachelet (1982)
Macoma balthica	Baltic Sea	62.8	SDW	Ankar (1980)

Biomass type: *ADW* Ash-free dry weight; *SDW*, Shell-free dry weight shape of *S. subtruncata* after August 1996. Although other causes for such shell deformations, such as pollution or fisheries damage, cannot be excluded, these causes are considered unlikely or at least inferior because (1) the Belgian coastal zone is not considered a highly polluted area, as demonstrated by the low levels of trace metals in e.g. *S. subtruncata* (Guns et al. 1999) and (2) both pollution and fisheries damage can be expected to cause irregular (e.g. Sokolowski et al. 2004), rather than the observed regular ventral indentation.

Implications of a possible *Spisula* fishery at the Western Coastal Banks

Although *Spisula* fishery is presently not allowed in Belgium, the legislative prohibition is often pressurized when major stocks are encountered. This section on the implications of *Spisula* fishery should therefore be regarded as a policy support for a careful evaluation of a possible *Spisula* fishery at the Western Coastal Banks and by extension the full Belgian part of the North Sea (BPNS). Several general principles within this section further support *Spisula* fisheries management outside the BPNS.

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 and especially its common *A. alba* community is known to harbour a rich bivalve fauna, with—next to *S. subtruncata*—*A. alba*, *Tellina fabula* and *Ensis* spp. reaching relatively high densities (on average 139, 104 and 62 ind m^{-2}, respectively) (Degraer et al. 1999a). Furthermore, being too shallow for most commercial shipping, the area is fulfilling all demands of the seaducks and, consequently, thousands of common scoter are wintering in the area (Maertens et al. 1988, 1990; Devos 1990; Offringa et al. 1998). The evident decrease of the standing stock of *S. subtruncata* due to shellfisheries might lead to a shortage in food for the seaducks and may lead to the local disappearance of seaducks, as already demonstrated in the Netherlands for the common scoter (Leopold 1993; Leopold et al. 1995) as well as for the common eider (Camphuysen et al. 2002). This local disappearance might further be enhanced by visual disturbance merely due to the presence of the fishing boats. Because the common scoters are mainly wintering in the southern North Sea, such visual disturbance might be minimized if shellfisheries take place from spring to autumn, being the most profitable period for shellfisheries as demonstrated by the high condition index during this period in this study and suggested by Leopold (1993).

Furthermore, though being the most abundant bivalve in all macrobenthic communities of the Western Coastal Banks (Degraer et al. 1999b), certainly in 1997, *S. subtruncata* is only found in high densities in the *A. alba* community (Degraer et al. 1999a). At the Western Coastal Banks this ecological highly important community (Van Hoey et al. 2004) 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. 1999a). 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. Because shellfisheries can lead to a general impoverishment (density, biomass and diversity) of the whole macrobenthic system (Craeymeersch 1997), in case of *S. subtruncata* fisheries severe damage to the ecologically important macrobenthic *A. alba* community might be expected.

Finally, because the occurrence of fishable stocks of *S. subtruncata* (86,000 ton in 1998) is concentrated in small areas, mainly the Western Coastal Banks (Vanhee et al. 1998), this stock can be depleted within a short period of time. Though having a high productivity, the natural recovery of the stocks after stock depletion may take several years, as demonstrated by the highly variable recruitment of *S. subtruncata* found in this study.

Because of (1) the direct resource competition between shellfisheries and seaducks, (2) the damage to the ecologically important macrobenthic *A. alba* community and (3) the expected erratic recovery *Spisula* populations after depletion, a continuous deliberation about the spatial allocation of *Spisula* fisheries is advised. Such deliberation is already in use in the Netherlands where the spatial allocation of *Spisula* fisheries is licensed from year to year, based on a thorough yearly investigation of the spatial distribution and standing stock of *S. subtruncata* (Craeymeersch and Perdon 2003).

Acknowledgments 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), the Coastal Waterways Division (AWK, contract of 24.07.1997) and Ghent University (contracts GOA 120.503.98 and GOA 01G00705: http://www.biology.ugent.be/bbsea). The first author was financed by the Flemish 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. This publication contributes to the EU Network of Excellence *MarBEF* (contract GOCE-CT-2003-505446; http://www.marbef.org).

References

Ankar S (1980) Growth and production of *Macoma balthica* (L.) in a northern Baltic soft bottom. Ophelia (Suppl 1):31–48

Anonymous (1996) Statistica for WINDOWS (Computer program manual). StatSoft, Inc., Tulsa

Bachelet G (1980) Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde estuary (SW France). Mar Biol 59:105–117

Bachelet G (1981) Application de l'équitation de von Bertalanffy à la croissance du bivalve *Scrobicularia plana*. Cah Biol Mar 22:291–311

Bachelet G (1982) Quelques problèmes liés à l'estimation de la production secondaire. Cas des bivalves *Macoma balthica* et *Scrobicularia plana*. Oceanol Acta 5:421–431

Brey T (1986) Formalin and formaldehyde-depot chemicals: effects on dry weight and ash free dry weight of two marine bivalve species. Meeresforsch 31:52–57

Brey T, Arntz WE, Pauly D, Rumohr H (1990) *Arctica* (*Cyprina*) *islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. J Exp Mar Biol Ecol 136:217–235

Caddy JF (1967) Maturation of gametes and spawning in *Macoma balthica* (L.). Can J Zool 45:955–965

Camphuysen CJ, Berrevoets CM, Cremers HJWM, Dekinga A, Dekker R, Ens BJ, van der Have TM, Kats RKH, Kuiken T, Leopold MF, van de Meer J, Piersma T (2002) Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biol Conserv 106:303–317

Chintala MM, Grassle JP (2001) Comparison of recruitment frequency and growth of surfclams, *Spisula solidissima* (Dillwyn, 1817) in different inner-shelf habitats of New Jersey. J Shellfish Res 20:1177–1186

Craeymeersch JA (1997) Effekten van de schelpdiervisserij op het bodemleven in de Voordelta. Report Nederlands Instituut voor Oecologisch Onderzoek, pp 63

Craeymeersch JA, Perdon J (2003) De halfgeknotte strandschep, *Spisula subtruncata*, in de Nederlandse kustwateren in 2003. RIVO Report C040/04, Yerseke

Craeymeersch JA, Leopold MF, van Wijk MO (2001) Halfgeknotte strandschelp en Amerikaanse zwaardschede: een overzicht van bestaande kennis over visserij, economische betekenis regelgeving, ecologie van de beviste soorten en effecten op het ecosysteem. RIVO Report C033/01, Yerseke

Cramp S, Simmons KEL (eds) (1977) The birds of the western Palearctic, vol. I. Oxford University Press, Oxford

Cranfield HJ, Michael KP (2001) Growth rates of five species of surf clams on a southern North Island beach, New Zealand. NZ J Mar Freshw Res 35:909–924

Cranfield HJ, Michael KP, Francis RICC (1996) Growth rates of five species of subtidal clam on a beach in the South Island, New Zealand. Mar Freshw Res 47:773–784

Crisp DJ (1984) Energy flow measurements. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. Blackwell, Edinburgh, pp 197–279

Davis FM (1923) Quantitative studies on the fauna of the sea bottom. N° 1. Preliminary investigation of the Dogger Bank. Fishery Investigations, Ser. II, vol 6, N 2

Davis FM (1925) Quantitative studies on the fauna of the sea bottom. N° 1. Results of the investigations in the southern North Sea, 1921–1924. Fishery Investigations, Ser. II, vol 8, N° 4

Degraer S, Vincx M, Meire P, Offringa H (1999a) The macrozoobenthos of an important wintering area of the Common scoter (*Melanitta nigra*). J Mar Biol Assoc UK 79:243–251

Degraer S, Vincx M, Meire P (1999b) Temporal changes within the *Lanice conchilega* community (North Sea, Belgian coast). In: Degraer S (ed) Macrobenthos of shallow marine habitats (Belgian coast) and its use in coastal zone management. PhD thesis, Ghent University, Department of Biology, Marine Biology Section, Gent, pp 41–55

Degraer S, Vincx M, Meire P (1999c) Macrobenthic community changes: dynamics versus stability and their importance in coastal zone management. In: Degraer S (ed) Macrobenthos of shallow marine habitats (Belgian coast) and its use in coastal zone management. PhD thesis, Ghent University, Department of Biology, Marine Biology Section, Gent, pp 56–74

Devos K (1990) Opmerkelijke aantallen watervogels op de Vlaamse Banken (Noordzee) tijdens het winterhalfjaar 1988–1989. Oriolus 56:1–11

Fogarty MJ, Sissenwine MP, Cohen EB (1991) Recruitment variability and the dynamics of exploited populations. Trends Ecol Evol 6:241–246

Fraschetti S, Covazzi A, Chiantora M, Albertelli G (1997) Life-history of the bivalve *Spisula subtruncata* (da Costa) in the Ligurian Sea (North-Western Mediterranean): the contribution of newly settled juveniles. Sci Mar 61(Suppl 2):25–32

Fraschetti S, Giangrande A, Terlizzi A, Boero F (2003) Pre- and post-settlement events in benthic community dynamics. Oceanol Acta 25:285–295

Gaspar MB, Monteiro CC (1999) Gametogenesis and spawning in the subtidal white clam *Spisula solida*, in relation to temperature. J Mar Biol Assoc UK 79:753–755

Gaspar MB, Santos MN, Vasconcelos P, Monteiro CC (2002) Shell morphometric relationships of the most common bivalve species (Mollusca, Bivalvia) of the Algarve coast (southern Portugal. Hydrobiologia 477:73–80

Guns M, Van Hoeyweghen P, Vyncke W, Hillewaert H (1999) Trace metals in selected benthic invertebrates from Belgian coastal waters (1981–1996). Mar Pollut Bull 38:1184–1193

Horii T, Murakami O, Sakurai I (2002) Effect of density on growth in Skhalin surf clam *Pseudocardium sachalinense*. Nippon Suisan Gakk 68:666–673

Kaiser MJ, Galanidi M, Showler DA, Elliott AJ, Caldow RWG, Rees EIS, Stillman RA, Sutherland WJ (2006) Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. Ibis 148:110–128

Kock M (1995) Über die Biologie der fischereilich genutzten *Spisula solida*-Bestände. Diplomarbeit, Mathematisch-Naturwissenschaftliche Facultät der Christian-Albrechts-Universität, Kiel

Kirchoff K (1981) Zur Verbreitung der uberwinternden Meeresenten auf der Offnen Kieler und Lubecker Bucht (westliche Ostsee). Corax 8:197–207

Kuijken E (1972) Belgian wetlands of international importance for waterfowl. In: Proceedings of the international conference on the conservation of wetlands and waterfowl, Ramsar, pp 179–188

Lammens JJ (1967) Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). Neth J Sea Res 3:315–382

Leopold MF (1993) *Spisula*'s, zeeëenden en kokkelvissers: een nieuw milieuprobleem op de Noordzee. Sula 7:24–28

Leopold MF, Baptist HJM, Wolf PA, Offringa H (1995) De Zwarte Zeeëend *Melanitta nigra* in Nederland. Limosa 68:49–64

Lewis CVW, Weinberg JR, Davis CS (2001) Population structure and recruitment of the bivalve *Arctica islandica* (Linnaeus, 1767) on Georges Bank from 1980–1999. J Shellfish Res 20:1135–1144

Maertens L, Meire P, Kuijken E (1988) Vliegtuigtellingen van watervogels voor de Belgische kust, winter 1986–1987. Oriolus 54:55–60

Maertens L, Meire P, Devos K, Kuijken E (1990) Vliegtuigtellingen van watervogels voor de Belgische kust, winters 1987–1988 en 1988–1989. Oriolus 56:12–19

Meire PM (1993) The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. In: Dame RF (ed) Bivalve filter feeders in estuarine and coastal ecosystem processes. NATO ASI Series, vol G 33, pp 197–243

Meissner J, Bräger S (1990) The feeding ecology of wintering Eiders *Somateria mollissima* and Common scoters *Melanitta nigra* on the Baltic Sea coast of Schleswig-Holstein, FRG. Wader Study Group Bull 58:10–12

Møhlenberg F, Kiørboe T (1981) Growth and energetics in *Spisula subtruncata* (da Costa) and the effect of suspended bottom material. Ophelia 20:79–90

Moll A (1998) Regional distribution of primary production in the North Sea simulated by a three-dimensional model. J Marine Syst 16:151–170

Nakaoka M, Matsui S (1994) Annual variation in the growth rate of *Yoldia notabilis* (Bivalvia: Nuculanidae) in Otsuchi Bay, northeastern Japan, analyzed using shell microgrowth patterns. Mar Biol 119:397–404

Offringa H, Seys J, Van Den Bossche W, Meire P (1998) Seabirds on the Channel doormat. De Giervalk 86:3–74

Olafsson EB, Peterson CH, Ambrose WG (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr Mar Biol 32:65–109

Palmerini P, Bianchi CN (1994) Biomass measurements and weight-to-weight conversion factors: a comparison of methods applied to the mussel *Mytilus galloprovincialis*. Mar Biol 120:273–277

Rainer SF (1985) Population dynamics and production of the bivalve *Abra alba* and implications for fisheries production. Mar Biol 85:253–262

Ramón M, Abelló P, Richardson CA (1995 Population structure and growth of *Donax trunculus* (Bivalvia: Donacidae) in the western Mediterranean. Mar Biol 121:665–671

Rueda JL, Smaal AC (2004) Variation of the physiological energetics of the bivalve *Spisula subtruncata* (da Costa, 1778) within an annual cycle. J Exp Mar Biol Ecol 301:141–157

Shackley SE, Collins M (1984) Variations in sublittoral sediments and their associated macro-infauna in response to inner shelf processes; Swansea Bay, U.K. Sedimentology 31:793–804

Sokal RR, Rohlf FJ (1987) Introduction to biostatistics. WH Freeman, New York

Sokolowski A, Wolowicz M, Hummel H, Smolarz-Gorska K, Fichet D, Radenac G, Thiriot-Quievreux C, Namiesnik J (2004) Abnormal features of *Macoma balthica* (Bivalvia) in the Baltic Sea: alerting symptoms of environmental adversity? Mar Pollut Bull 49:17–22

Tebble N (1966) British bivalve seashells. A handbook for identification. The British Museum of Natural History, London

Urban H-J, Campos B (1994) Population dynamics of the bivalves *Gari solida*, *Semele solida* and *Protothaca thaca* from a small bay in Chile at 36°S. Mar Ecol Prog Ser 115:93–102

Van Assche A, Lowagie H (1991) Het voorkomen van de Zwarte Zeeëend (*Melanitta nigra*) langs de Belgische kust. Thesis Ghent University, Ghent

Vanhee J, Declerck D, De Clerck R, Vyncke W, van Stralen M, Lindenberg E (1998) Onderzoek naar de mogelijkheden van schelpdiervisserij voor de Belgische kust. Mededelingen van het Departement Zeevisserij (CLO-Gent), Oostende

Van Hoey G, Degraer S, Vincx M (2004) Macrobenthic communities of soft-bottom sediments at the Belgian Continental Shelf. Estuar Coast Shelf Sci 59:601–615

Van Steen E (1978) Het macrobenthos van een overwinteringsgebied van *Melanitta nigra* (Linné, 1758) voor de Belgische kust. Thesis Ghent University, Ghent

Van Urk RM (1959) De *Spisula*'s van het Nederlandse strand. Basteria 23:1–32

Walker RL (2001) Effects of stocking density on growth and survival of Atlantic surfclams in bottom cages versus mesh bags. J Shellfish Res 20:1173–1176

Walker RL, Heffernan PB (1994) Age, growth rate, and size of the southern surfclam, *Spisula solidissima similis* (Say, 1822). J Shellfish Res 13:433–441

Weissberger EJ, Grassle JP (2003) Settlement, first-year growth, and mortality of surfclams, *Spisula solidissima*. Estuar Coast Shelf Sci 56:669–684

Winberg GG (1971) Methods for the estimation of production of aquatic animals. Academic, London

Zwarts L (1991) Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. Neth J Sea Res 28:231–224