CHAPTER V

Growth patterns of *Mytilopsis leucophaeata*, an invasive biofouling bivalve in Europe

Paper published as:

VERWEEN A, VINCX M, DEGRAER S (2006)

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Biofouling 22 (4): 221 – 231

ABSTRACT

For the first time, growth in *Mytilopsis leucophaeata* (Conrad), an important fouling species in Europe, was investigated. By means of growth cages, individual shell growth of three cohorts - with respectively initial shell length ≤ 5 mm, 10 mm and 15 mm - was monitored in the harbour of Antwerp (Belgium) during 2003 – 2004. *Mytilopsis leucophaeata* followed an oscillatory growth pattern with a single summer growing period per year (May – August). Growth decreased during wintertime, but never ceased completely. *Mytilopsis leucophaeata* has an average growth rate of less then 3 to 6 mm/year. Temperature was found to be the main environmental factor affecting growth. Von Bertalanffy growth function was used to model growth of individuals ≤5 mm, resulting in L_∞ = 16.7 mm and K = 0.56. Based on a combination of growth of all three cohorts, hypothetical growth of an average individual mussel could be modeled over a 5 year period, resulting in a maximum length > 19 mm with a growth constant of 0.41. Its longevity (more than five years) and positive effect of higher water temperatures on growth, combined with its high resistance to chlorination, provides *M. leucophaeata* a high potential for severe and long-lasting biofouling.

KEYWORDS

Mytilopsis leucophaeata, growth, Westerschelde, temperature

INTRODUCTION

The brackish water mussel, *Mytilopsis leucophaeata* (Conrad, 1831) (syn. *Congeria cochleata* Kickx in Nyst, 1835), a mytiliform bivalve (Mollusca, Bivalvia, Veneroida, Dreissenidae), is resistant to a wide range of oligo- to mesohaline conditions (1 – 18 PSU (Practical Salinity Units)). *Mytilopsis leucophaeata* originates from the southern coast of the U.S. to Tampico, Mexico and was first detected in European waters in 1835 in the harbour of Antwerp (Belgium). In North America the species invaded the Hudson River in New York in the 1930s (Rehder, 1937) and was recently found in the Upper Mississippi River (Koch, 1989) and Southern New England (Smith and Boss, 1996). In Europe, it has been found in brackish water bodies along the North Sea coasts from Germany (Therriault et al., 2004) through the Netherlands (Rajagopal et al., 2002b) and Belgium (Verween et al., 2005) into France (Bamber and Taylor, 2002) and in the UK (Oliver et al., 1998) and has recently been reported in the Guadalquivir river in Spain (Escot et al., 2003), the Black Sea basin (Therriault et al., 2004) and the northern Baltic Sea (Laine et al., 2006) (**Fig. 1**). Although *M. leucophaeata* is known in Europe for over 170 years, it is recently spreading rapidly throughout this part of the world mainly by means of ballast water discharges from transoceanic shipping (Oliver et al., 1998). *Mytilopsis leucophaeata* is invading Europe more slowly than *Dreissena polymorpha* in the U.S. (Verween et al., in press) with dispersal being mainly human-induced.

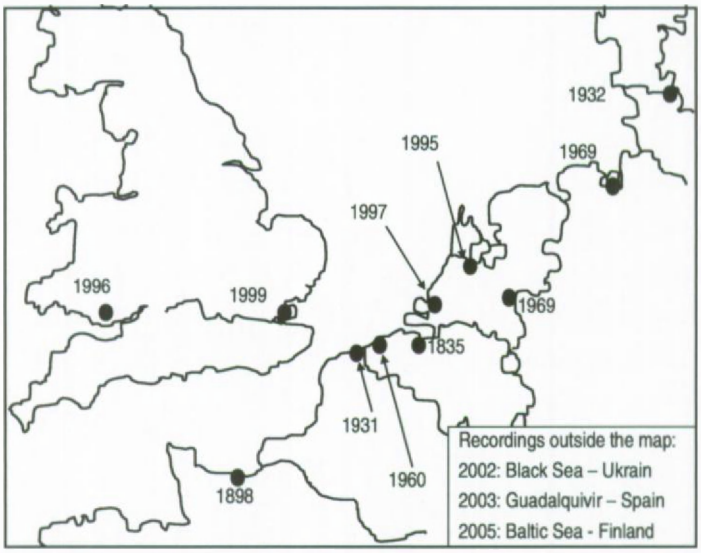

Fig. 1: Distribution of *Mytilopsis leucophaeata* in Europe, with data of first recordings.

Mytilopsis leucophaeata and the freshwater zebra mussel, *D. polymorpha* (Pallas, 1771) are both Dreissenidae with a very similar life cycle. Especially the free-swimming larvae are an important invasion tool for both species. The planktonic D-shaped veligers stay in the water column for about two weeks before settlement (Ackerman et al., 1994) and as such can easily survive transportation from one region to another. Furthermore, being a brackish water species, *M. leucophaeata* larvae and post-larvae are euryhaline and capable of development to metamorphosis at 10 to 32 PSU (Siddall, 1980). After settlement, the post-larvae develop a protective shell, which grows stronger as the individuals become larger. Because of this protective shell, they become highly resistant to external circumstances, including anti-fouling agents. The fact that they inhabit brackish waters makes them far more resistant to environmental changes than freshwater species, being a significant fouling pest in cooling water systems of numerous industrial plants (Rajagopal et al., 1997; Verween et al., 2005) and in potable and service-water pipes (Bamber and Taylor, 2002). Since individuals become more resistant to anti-fouling agents, such as chlorine, as they grow larger (Rajagopal et al., 2002b), knowledge on the growth of *M. leucophaeata* as a function of environmental conditions is indispensable in developing efficient control measures.

Next to its economic impact, the invasion of pest bivalves, such as *M. leucophaeata* can also have important ecological consequences. *Dreissena polymorpha* invasions for instance may lead to decreased plankton biomass resulting in decreased turbidity and increased growth of benthic plants, while some benthic invertebrates may be adversely affected, with an altered food web and shifted ecosystem as result (MacIsaac, 1996).

Although *M. leucophaeata* is known to cause major biofouling problems throughout Europe, there is a large discrepancy with the information on the species. We do for example not have information on the potential magnitude of fouling problems, caused by *M. leucophaeata*, as well on a temporal as on a spatial scale. Basic knowledge on the autecology of such biofouling species is a first step in comprehending its ecology, thus forming a baseline for a successful future biofouling treatment. We hypothesize that *M. leucophaeata* has definitely the potential of becoming the brackish water equivalent of *D. polymorpha* in Europe.

The aims of this study were therefore:

- To investigate growth rate of different size classes of *M. leucophaeata;*
- To analyse the influence of environmental factors on the growth of *M. leucophaeata;*
- To model shell growth of *M. leucophaeata.*

MATERIALS AND METHODS

1. STUDY SITE AND EXPERIMENTAL SETUP

All field work was conducted at the site of BASF, Antwerpen N.V. (Belgium), along the Schelde river. The industrial plant is situated at the right bank in the harbour of Antwerp, near the Dutch border (**Fig. 2**), and receives water of intermediate salinity (1 – 12 PSU) coming from the Westerschelde river and from the Rijn-Schelde channel.

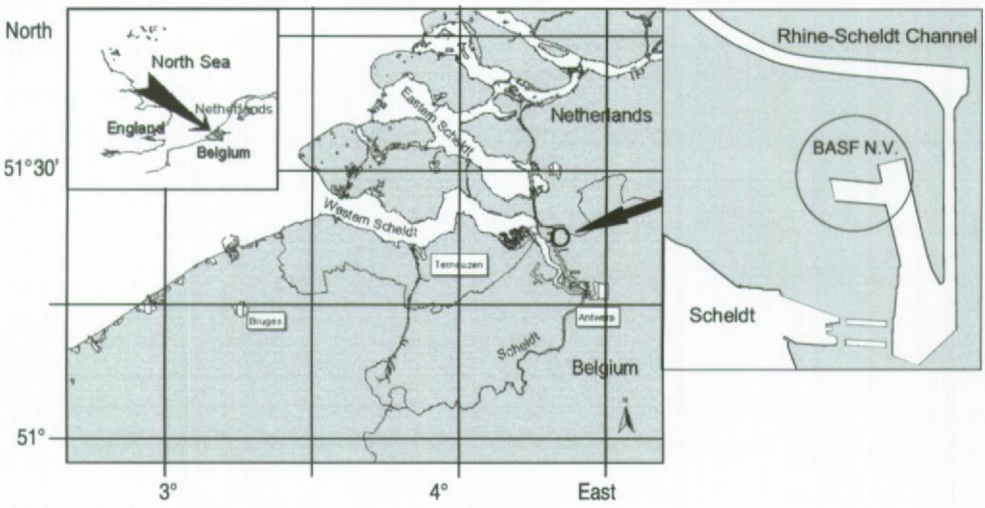

Fig. 2: Map of Westerschelde river with indication of the study site.

Biofouling problems with the brackish water mussel at BASF Antwerpen N.V. were first detected in 1998. During summer, the cooling water conduits of the industrial plant take in up to 80 000 m³ of 1 mm-filtered, but untreated river water per hour and in wintertime, an average flow of 30 000 m³ of water per hour occurs. Larvae can thus enter the system together with the extracted water, where they may attach onto substrates, such as the heat exchangers and the tubes in the conduits. Peak larval densities exceeded 1500 individuals per m³ (Verween, unpublished data).

Water is pumped into the cooling water system at two intake points, at a distance of one kilometre from each other. At each intake point, a control installation for biofouling hazard was built. These installations received water from the dock, but were disconnected from the biocide-usage in the rest of the system, as such making it possible to study growth of *M. leucophaeata* under non-toxicological circumstances.

Each installation consisted of three PVC-tanks in which an average water flow of 1 m^3 h^{-1} was generated. In each of the PVC-tanks, growth cages were suspended in such a way that full water circulation through the cages was allowed. Each growth cage was divided into twenty individual growth chambers. To prevent individuals from escaping and to allow water circulation through the cage, the top and bottom of each chamber consisted of a plastic net with mesh size of 1 mm.

The use of growth cages could reduce growth as a result of a reduced water circulation due to clogging of the cage perforation and as such limiting food (Karatayev et al., pers comm). In the present study, meshes were cleaned biweekly to avoid clogging and ensuring a continuous water flow, similar to that outside the cages. Garton and Johnson (2000) have proven that changing the mesh size and the design of the growth cages had no significant effect on the individual shell growth. This implies that the mussels in the cages are not negatively influenced by their cloistering and that they experience about the same circumstances as 'free' individuals.

2. GROWTH MEASUREMENTS

To determine growth and the influence of the environment, two factors need to be considered: (1) size dependency of shell growth rate and (2) individual variation of shell increment (Jantz and Neumann, 1998). To include this variation, mussels from three different cohorts were collected. In February 2003 mussels with various sizes were collected from the dock and gently rinsed. The mussels were kept in a mesh bag suspended in the control installation, before being placed in the growth cages. Shell length (i.e. maximum dimension along the anterior-posterior shell axis) was measured to the nearest 0.01 mm using an electronic vernier calliper. Based on their initial shell length (ISL), individuals were allocated to three size classes: smaller than or equal to 5 ± 1 mm ($ISL_{\leq 5}$), equal to 10 ± 1 mm (ISL_{10}) and equal to 15 ± 1 mm (ISL_{15}). Growth was monitored for one hundred twenty mussels: two installations, each with three PVC-tanks, leading to six growth cages, each filled with 20 mussels. Each cohort was initially represented by 40 individuals. Length of all individuals was measured monthly between February 28th 2003 and December 21st 2004. Growth is expressed as shell length increment (SLI) and calculated from following equation:

$$SLI\ (\mu m/day) = (SL_{t+1} - SL_t) / dt \quad \text{(Jantz and Neumann, 1998)} \qquad (1)$$

with SL_{t+1} as the final shell length (µm), SL_t the initial shell length (µm) and dt the time (in days) between t and $t + 1$. Average SLI within each size class was expressed as the average of the individual SLIs of the size class (µm/day).

Water temperature (°C), salinity (PSU) and oxygen content (mg/l) of the incoming water were monitored weekly, by means of field sampling devices. A Profiline conductivity meter LF 197 was used for salinity and temperature measurements, while oxygen content was measured by an Oxi 320 microprocessor oxygen meter. Chlorophyll a concentration (µg/l), from 2003 on was measured from a 500 ml water sample through filtering onto a Whatman GF/F filter and analysing with a HPLC-sampler according to Jeffrey et al. (1997). Chlorophyll a data from 1999 until 2002 were derived from Schaar van Ouden Doel, nearby the monitored dock (chemical measuring network MWTL). ANOVA indicated no significant difference in chlorophyll a concentrations between both sample points.

3. GROWTH ANALYSIS

Growth (SLI) between years and installations was compared using the Mann-Whitney U-test, between mussel groups by means of Kruskal-Wallis test. Regression analysis between SLI and ISL was conducted and univariate Pearson correlation analysis was used to search for correlations between environmental variables at time t and SLI at time $t+1$. Multiple regression was conducted to examine the relationship between the environmental variables at time t and SLI at time $t+1$. Because of its highest growth rates and consequent most obvious growth pattern, the growth class with $ISL_{\leq 5}$ was considered to determine the influence of the environmental factors on the individual growth rate. Regression and correlation analysis were conducted with the statistical software SAS 9.1 (SAS Institute Inc., 2004). Because of the same reasons, the maximal length and growth rate were determined for growth class with $ISL_{\leq 5}$. The length increment for *M. leucophaeata*, as for other species showing seasonal oscillations in growth, was described by the Von Bertalanffy growth function (VBGF):

$$L_t = L_\infty * (1 - e^{-K(t-t_0) + (CK/2\pi)\sin[2\pi(t-t_s)]}) \quad \text{(Gayanilo et al., 1989, modified from von Bertalanffy, 1938)} \qquad (2)$$

where L_t is the predicted length at age t, L_∞ is the asymptotic length, K is the growth rate, C determines the amplitude of the seasonal growth oscillation, t_s is the starting point of the oscillation and t_0 the theoretical age at zero length. The values of the five parameters were estimated by means of non-linear

estimation with the least squares method as provided by the statistical software package STATISTICA 5.5 (Statsoft, 2000).

An independent estimate of L_∞ and K was obtained using the Ford-Walford method in which length and age were rearranged as data pairs consisting of length at a specific time $t = n$ and length at a succeeding time $t = n + 1$ (Gulland, 1983). The time difference between the length measurements (dt) was kept constant. Based on the linear regression equation $y = ax + b$, L_∞ and K were estimated as $L_\infty = b / (1 - a)$ and $K = (-1 / dt) * ln(a)$.

Since there was no significant difference in growth rate between years (see results), hypothetical shell growth of an average individual mussel could be modeled over five year classes (last 6 months of year class 0 to year class 5), in which $ISL_{\leq 5}$ was considered to represent growth in the last 6 months of the year classes 0 to year class 2, ISL_{10} the last 6 months of year classes 1 to year class 3 and ISL_{15} the last 6 months of year classes 3 to year class 5. The first 6 months of year class 0 could not be included because our investigation was initiated in February, while year class 0 individuals can only be found from July onwards. To avoid a bias due to the minor growth and high mortality in ISL_{15} (see results), Von Bertalanffy parameters were also calculated without this cohort.

RESULTS

1. GROWTH RATE

Mann-Whitney U-test indicated no significant difference in mussel growth between the two test-installations ($p = 0.11$) and between 2003 and 2004 ($p = 0.37$). Kruskal-Wallis analysis showed a high significant difference in SLI between growth classes ($p = 0.002$).

For cohorts $ISL_{\leq 5}$ and ISL_{10}, the SLI performed a seasonal oscillation, in which a yearly period of peak growth, with average SLI higher than 10 µm/day, could be distinguished. In 2003, this growing season started in May and ended in August (average $SLI_{\leq 5}$ = 30 µm/day, average SLI_{10} = 14 µm/day), while in 2004, peak growth took place from May until July (average $SLI_{\leq 5}$ = 23 µm/day, average SLI_{10} = 15 µm/day). During wintertime, almost no growth was observed, with minimum shell growth of 1 µm/day during November 2004 (2003: average $SLI_{\leq 5}$ = 7 µm/day, average SLI_{10} = 2 µm/day; 2004: average

$SLI_{\leq 5}$ = 4 µm/day, average SLI_{10} = 6 µm/day). Maximum shell growth was recorded in June 2003, with $SLI_{\leq 5}$ = 58 ± 11 µm/day and SLI_{10} = 28 ± 11 µm/day.

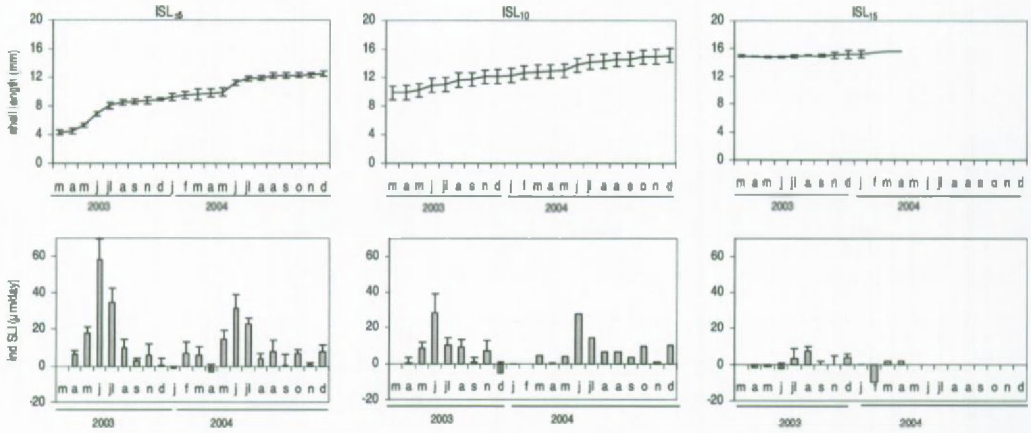

Fig. 3: Seasonal changes in shell length ± SE and SLI ± SE in 2003 – 2004 in three size classes (SLI = shell length increment).

During the entire growth monitoring period individuals with $ISL_{\leq 5}$ grew from an average of 4.2 mm to 12.6 mm in 22 months with an average shell increment (SLI) of 11.4 µm/day, whereas individuals with ISL_{10} grew from 9.8 mm to 15.2 mm with an average SLI of 7.5 µm/day (**Fig. 3**). The larger individuals (ISL_{15}) died within a year. In this length class, no distinct growing periods could be observed, and almost no growth occurred (average SLI_{15} = 0.39 µm/day; maximum value = 3.5 µm/day in June 2003).

Correlation analysis resulted in a negative relationship between ISL and SLI (r = 0.98; p = 0.09), indicating a size-dependency of shell growth. The decrease in shell growth with increasing shell length was linear with the linear regression model explaining 99.9 % of variation in shell growth for the growing season (May – August) and 97.1 % for the yearly average growth.

2. Correlation with the environment

Comparing the results of the shell length increment with the environmental conditions of the water (**Fig. 4**), the start of the growing season (May – June) coincided with the maximal monthly increase in temperature and salinity. Temperature and salinity rose from 16 °C to 21 °C and from 4.8 PSU to 6.0 PSU in May 2003 and from 15 °C to 21 °C and from 6.7 PSU to 8.0 PSU in June 2004. Highest SLI

however did not coincide with the maxima of these variables, but occurred earlier (June). Maximal temperature occurred in August (23.2 °C in 2003, 23.0 °C in 2004), maximal salinity in September – October (11.0 PSU in 2003 and 9.6 PSU in 2004).

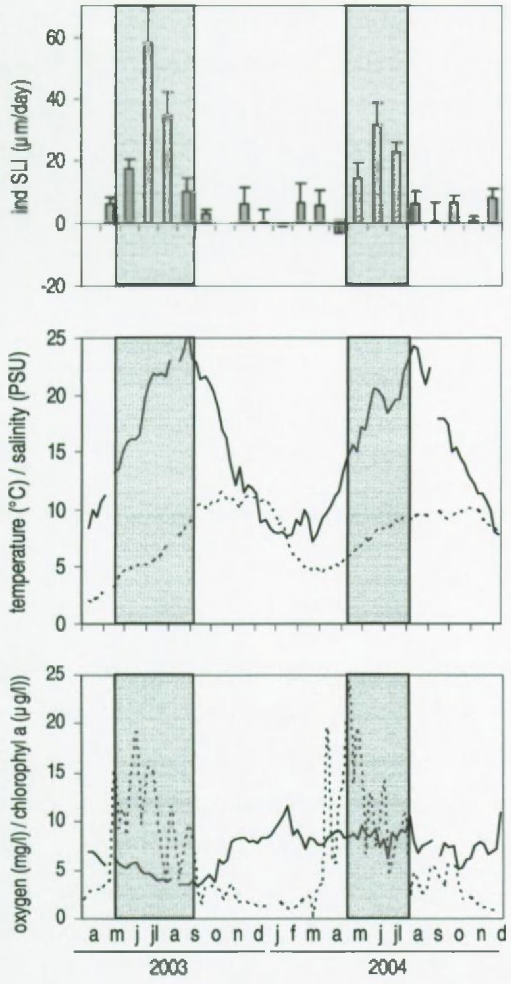

Fig. 4: Seasonal changes in SLI in *Mytilopsis leucophaeata* ± standard errors and the corresponding changes in environmental factors (dark squares: growing season; full line: temperature and oxygen content; dashed line: salinity and chlorophyll a).

When statistically comparing the average individual growth rate with the conditions of the water, a highly significant positive correlation of SLI with temperature (Pearson r = 0.69; p = 0.0008) was detected (**Table I**), however not with salinity (r = - 0.01; p = 0.97) nor with the oxygen content of the water (r = -

0.39; $p = 0.09$). The duration of the growing season further seemed to be correlated with the quantity of algal food in the water: growth did not occur before a first chlorophyll a peak in the water column (maximum of 15.6 µg/l on 15th April 2003; maximum of 24.4 µg/l on 27th April 2004) and ceased directly after the last chlorophyll a peak (7.6 µg/l on 19th August 2003; 10.9 µg/l on 27th July 2004). However, there was no significant relationship between SLI and chlorophyll a content ($r = 0.22$; $p = 0.34$) and none of the variables were significantly intercorrelated (max. correlation coefficient: 0.39). Multiple regression was significant ($p = 0.02$) with one significantly contributing variable, temperature ($p = 0.006$).[1]

Table I: Results of Pearson correlation analysis with indication of the significance level (*** $p < 0.001$).

	Temperature	Salinity	Oxygen content	Food	SLI
Temperature		0.27	- 0.30	0.39	0.69***
Salinity			0.20	- 0.36	- 0.01
Oxygen content				- 0.30	- 0.39
Chlorophyll a					0.22

3. SHELL GROWTH MODELING

The Von Bertalanffy growth function, modeled on the growth cohort $ISL_{\leq 5}$ gave a maximum length (L_∞) of 16.7 ± 1.2 mm with a growth constant (K) of 0.56 ± 0.09. Seasonal growth oscillation is rather small (C = 0.11). The function coincided well with the observed data points: 98.7 % of the variance in data points of the cohort was explained by the growth function. All parameters of the Von Bertalanffy growth function were highly significant ($p < 0.0001$). The Ford-Walford method yielded slightly different values for L_∞ and K for growth cohort $ISL_{\leq 5}$ (L_∞ = 14.5 mm; K = 1.09) (**Fig. 5**) and explained 96.9 % of the variance in the data points.

Because after 12 months (March 2004) growth of cohort $ISL_{\leq 5}$ showed a great overlap with cohort ISL_{10} at the start of the monitoring (March 2003), and no significant difference in length between both years was detected (Mann-Whitney U-test: $p = 0.36$), both cohorts could be merged and growth could be modelled continuously over a period of 34 months. Since a gap is present when merging cohorts ISL_{10} and ISL_{15} and cohort ISL_{15} showed little or no growth and these individuals died within a year, merging

[1] Multiple regression with only one significant variable does not give any extra information in this study and is thus unnecessary.

this cohort was approached with prudence. As such, we reproduced the hypothetical minimal growth of *M. leucophaeata* spanning 5 year classes of its life cycle.

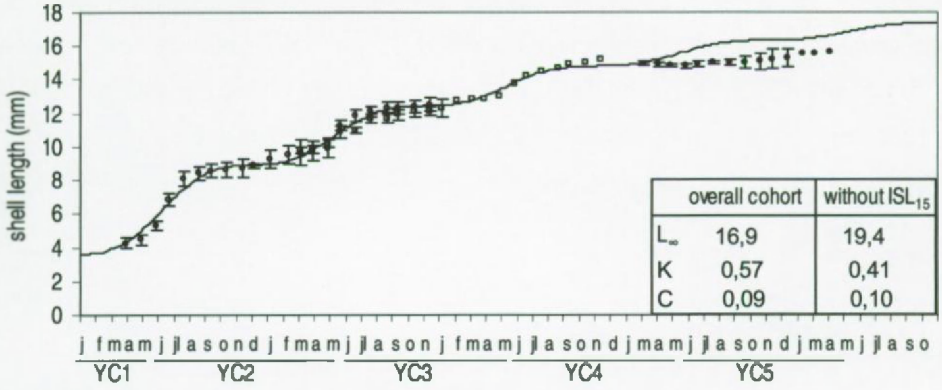

Fig. 5: Graphical presentations of the von Bertalanffy growth function excluding ISL_{15} and measured data points over five year classes ± SE. L_∞: asymptotic length, K: growth constant, C: amplitude of seasonal growth oscillation. The VBGF parameters have been calculated for the overall cohort and the cohort excluding ISL_{15}.

The Von Bertalanffy growth function of the overall benthic growth of *M. leucophaeata* coincided very well with the observed data points, as 98.8 % of the variance in data points of the overall cohort was explained by the growth function. The cohort led to a maximum length (L_∞) of 16.9 ± 0.24 mm with a growth constant (K) of 0.57 ± 0.03. The seasonal growth oscillation is small (C = 0.09). Excluding cohort ISL_{15}, a maximum length of 19.4 mm was calculated with a growth constant of 0.41. The seasonal growth oscillation remained small (C = 0.10) and variation was attributed for 98.8 % by the model.

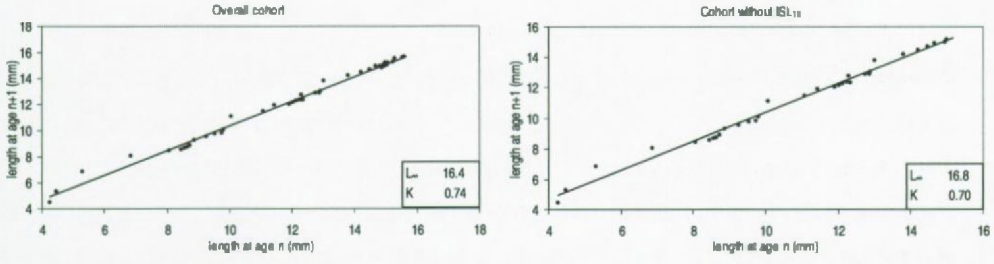

Fig. 6: Graphical presentation of the Ford-Walford method for the estimation of L_∞ and K. L_∞ = intercept / (1 – slope); K = (-1/dt)*ln (slope).

The Ford-Walford method yielded comparable values for L_∞ and K for the overall growth cohort (L_∞ = 16.4 mm; K = 0.74) (**Fig. 6**) and explained 99.2 % of the variance in the data points. Excluding ISL_{15}, estimates showed only minor changes: L_∞ = 16.8 mm, K = 0.70 with 98.7 % of the variance explained.

DISCUSSION AND CONCLUSIONS

1. GROWTH

Growth in mussels is particularly seasonal, with little or no growth during winter (Seed, 1969b), as for numerous species living in environments with a distinct annual cycle in temperature and/or light conditions (Brey, 1999). Similarly in this study, growth of *M. leucophaeata* also occurred oscillatory, comprising a single period of major growth (late spring till summer), identified here as growing season, and a period of minor growth (autumn and winter) per year. During the growing season, SLI showed a unimodal distribution, with maximum growth in June and July. This observation falls well within the range of variation in growth patterns, observed for *D. polymorpha*, in which maximum growth rate was found to vary from the very beginning of the growing season (May-June) (Smit et al., 1992; Garton and Johnson, 2000) to the end of the growing season (Morton, 1969).

Yearly average growth rate for *M. leucophaeata*, measured here, varied from about 3 to 6 mm/year, which is quite low compared to *D. polymorpha* (yearly average growth rate: 15 to 20 mm/year) (Mackie, 1991; Mackie and Schloesser, 1996).

Although *M. leucophaeata* tended to grow more slowly on a yearly basis, it never ceased growing completely, whereas a full growth stop had already been demonstrated for *D. polymorpha* (Morton, 1969; Bij de Vaate, 1991). Because 6 °C (Bij de Vaate, 1991) to 10 °C (Mackie, 1991; Jantz and Neumann, 1992; Smylie, 1994) is considered to be the lower temperature limit for growth and development of the closely related *D. polymorpha*, a full growth stop in this species can be expected during North-western European winters. Being a subtropical species, the slow, though continuous growth in *M. leucophaeata* in winter, when temperature dropped as low as 6.3 °C, should thus be interpreted as a result of its eurytopic nature. Indeed, habitat preferences and environmental limits of *M.*

leucophaeata are proven to be very broad (Smith and Boss, 1996; Oliver et al., 1998; Bamber and Taylor, 2002; Escot et al., 2003).

During our monitoring period, the onset of spawning in *M. leucophaeata* was detected in May 2003 and June 2004 (Verween et al., 2005). The present study indicated that the growing season of *M. leucophaeata*, identified here as a period of growth with SLI higher than 10 µm/day, started after this onset of spawning. This can be explained by availability of an energy-surplus for somatic growth after a period of gametogenesis. Add the high temperature during summer and the large quantity of food available in the water column, and enough energy can be present to induce a (somatic) growth spurt (Dorgelo, 1993).

Because (1) shell growth was positively correlated with temperature ($r = 0.69$; $p = 0.0008$), (2) no significant correlation between growth rate and chlorophyll a concentration was found ($r = 0.22$; $p = 0.34$) and (3) chlorophyll a concentration was only weakly correlated to temperature ($r = 0.39$; $p = 0.08$), it should be concluded that mainly temperature is regulating shell growth of *M. leucophaeata*. Multiple regression, showing a significant effect, endorsed this pattern with only temperature as significantly contributing variable ($p = 0.006$) in shell growth. Next to temperature, food quantity and quality can however be considered to probably represent the second most important determinants of mussel growth, as already demonstrated for the bivalves *Mytilus provincialis* (Ceccherelli and Rossi, 1984) and *M. edulis* (Frechette and Bourget, 1987). A similar pattern of environmental (somatic) growth control could also be demonstrated for *D. polymorpha*: temperature as the most important controlling variable (Griffiths et al., 1991; Karayücel, 1996; McMahon, 1996) and generally a positive relationship between growth and chlorophyll a concentration (Walz, 1978b; Jantz and Neumann, 1992; Sprung, 1995).

Shell growth rate (SLI) of *M. leucophaeata* was strongly dependent on the initial shell length (ISL), with (1) smaller individuals growing faster than larger individuals and (2) a near complete cessation of growth for individuals larger than 15 mm. Such length-dependency of growth, also detected for other bivalves, such as *D. polymorpha* (Neumann et al., 1993) and *M. edulis* (Seed, 1969b), is believed to be caused by (1) a lower metabolic activity in older individuals or (2) a relatively stronger increase in body mass over body length, which would require longer periods of feeding in order to maintain enough energy to grow (Seed, 1969b).

2. SHELL GROWTH MODELING

Modeling of shell growth cohort $ISL_{\leq 5}$ according to the seasonal Von Bertalanffy growth function indicated a maximum theoretical length of *M. leucophaeata* of 16.7 mm with an average growth constant K of 0.56. Although this L_∞ corresponds with the somewhat lower maximum length of 14 mm of *M. leucophaeata*, found in the nearby North Sea Channel near the Hemweg and Velsen power station (The Netherlands) (Rajagopal et al., 1995), many larger individuals were found in the harbour of Antwerp (personal observations). The different values of the Ford-Walford model (L_∞ = 14.5 mm; K = 1.04) can be explained by the fact that Ford-Walford is a linear model-fitting technique (Sun et al., 2001), being less suitable in modelling seasonal growth. Szypula (1987) also proved that the Ford-Walford model yielded the least reliable results in modelling length growth in various fish species in comparison to other models.

Because only small individuals have been taken into account in this Von Bertalanffy growth modeling, a surplus value was given to the study by means of modeling a hypothesized shell growth of an average individual mussel over 5 year classes in the Schelde river near Antwerp. The overall Von Bertalanffy growth function indicated (1) a maximum theoretical length of 17 mm and (2) an average growth constant K of 0.57. However, when excluding the cohort ISL_{15} from the model, a higher maximal length (19.4 mm), but lower growth constant (0.41) was predicted. Both predictions seem reliable, because measurements of large individuals, collected in the harbour of Antwerp, revealed several individuals with a length of about 17 mm up to a maximum, though rare length of 26 mm.

Table II: Overview of maximum shell length measurements of *Mytilopsis leucophaeata*, according to literature

Max. length (mm)	Region	Reference
10 - 20	U.S.	Abbott, 1974 Emerson and Jacobson, 1976 Pennak, 1978
22	Miami, U.S.	Siddall, 1980
14	North Sea Channel, The Netherlands	Rajagopal et al., 1995
27	The Netherlands	Gittenberger et al., 1998
20	Cardiff Docks, England	Oliver et al., 1998
15.2	Thames, England	Bamber and Taylor, 2002
17-22	Schelde, Belgium	Verween et al., in press

Historic American identification guides on shells describe a size range from 1 to 2 cm for *M. leucophaeata* (Abbott, 1974; Emerson and Jacobson, 1976; Pennak, 1978). More detailed information on the species (**Table II**) shows that the average maximal length indeed is about 20 mm, but generally, smaller individuals (10-15 mm) are found in the field. The larger sizes like 27 mm, described by Gittenberger et al. (1998) can be considered exceptionally large for this species. Compared to *D. polymorpha* ($K = 0.808$; $L_\infty = 40.5$ mm) (Conides et al., 1997), *M. leucophaeata* in the harbour of Antwerp thus seem to grow slower and smaller. However, the growth constant K is not extremely low in comparison to many populations of other bivalves, with K-values ranging from 0.07 to 0.97 (Bachelet, 1980, 1981; Urban and Campos, 1994; Walker and Heffernan, 1994; Ramón et al., 1995), and is average when compared to other mussel species, as *Mytilus edulis* ($0.02 \leq K \leq 1.46$ in Dolmer, 1998), *Perna perna* ($0.31 \leq K \leq 0.7$ in McQuaid and Lindsay, 2000) and *Limnoperna fortunei* ($0.33 \leq K \leq 0.38$ in Maroñas et al., 2003). *Mytilopsis leucophaeata* is however a very small mussel species, respective to other mussels, with L_∞ being 32 - 283 mm, 66 - 117 mm and 36 mm for respectively *M. edulis* (Dolmer, 1998), *P. perna* (McQuaid and Lindsay, 2000) and *L. fortunei* (Maroñas et al., 2003).

The modeling study at hand of the overall growth cohort renders an estimate of the minimum longevity of *M. leucophaeata* in the Schelde river of almost 5 years, when growth starts to decrease dramatically and individuals become rare. Cessation of growth however does not necessarily indicate the maximum longevity: slow growth in larger individuals – almost impossible to measure - together with their rareness thus makes it difficult to estimate the true longevity of *M. leucophaeata* in the harbour of Antwerp. Estimation of mussel longevity has also proven to be very difficult: for *D. polymorpha*, life span estimates varied from 3 to 19 years (Karatayev et al., pers comm). Recent data on European populations however report a maximum longevity between 2 and 4 years (Conides et al., 1997; Chase and Bailey, 1999), while North American populations have a shorter life span of 1.5 to 2 years (Mackie and Schloesser, 1996). It is because of these phenomena that data consisting maximum life span of *M. leucophaeata* presented here are just a first indication, and that further research would be needed to come to definite proof.

3. BIOFOULING CONSEQUENCES

Rajagopal (1997, 2003) carried out shell valve movement experiments using three species of mussels: a freshwater mussel *D. polymorpha*, a marine mussel *M. edulis* and a brackish water mussel *M. leucophaeata*. Adult mussels were subjected to continuous or intermittent chlorination at different concentrations. Their lethal and sublethal responses were compared to those of control mussels and

shell valve activity was monitored. These studies have proven that *M. leucophaeata* is much more tolerant to chlorination than the other mussel species, as such endorsing the fact that *M. leucophaeata* can become a major fouling problem once established. Again, being a brackish water species with broad habitat preferences raises its defensibility against external conditions, such as environmental changes (Verween et al., personal observations) as well as biocides.

This study on the population dynamics of *M. leucophaeata* extends the number of arguments for a severe biofouling potential of *M. leucophaeata*;

1. This study and many others demonstrate that temperature is the most important factor in determining (shell) growth in mussels, with in general, an increase in growth with a rise in temperature over the ecological range of the species (Bayne and Worrall, 1980). By definition, the water temperature within cooling water systems is (slightly) higher than in the surrounding water, resulting in cooling water systems inducing a higher growth rate of *M. leucophaeata*. Similarly, according to Karatayev (1995) the growth of *D. polymorpha* was significantly higher in heated cages than in the unheated zone. Hence, higher temperature waters should be considered as an advantageous environment, implying the presence of an energy surplus for any physiological process in *M. leucophaeata* (Sprung, 1995; Walz, 1978b). This energy surplus should not only be used for somatic growth, but also for gametogenesis, indicating a raise in reproductive capacity in the installation in comparison with the surrounding water. As a result of this increased reproductive capacity, an increased recruitment success, along with its biofouling consequences, might be hypothesized.

2. The study at hand shows that *M. leucophaeata* is a small, slowly growing, invasive bivalve, which seems, by means of these characteristics, a rather harmless fouling species, especially in comparison to the larger, quickly growing *D. polymorpha*. However, very little growth is required before mussels reach the size equal to the interpolate gap of plate heat exchangers, at which point blockage can occur (Jenner et al., 1998). Point blockage is considered a major problem, caused by biofouling mussels. Direct interference with the functioning of the system (cf. definition of biofouling) should thus not be considered strictly correlated with size

3. Its high longevity (more than five years, compare to *D. polymorpha*: 2 – 4 years) indicates that once fouling problems have arisen, these problems might persist for a long time: an adult *M.*

leucophaeata is very tolerant to chlorination, not easily removable and, once established, will keep on producing offspring for a long period of time.

We can conclude that *M. leucophaeata* definitely has the potential of becoming the brackish water equivalent of *D. polymorpha* in Europe. Although fouling problems caused by *M. leucophaeata* are different in nature in comparison to those instigated by *D. polymorpha*, they may be as severe and even more difficult to solve, as already observed in power stations in the Netherlands (Rajagopal et al., 1995), Belgium (Verween et al., 2005), the central Gulf of Finland (Laine et al., 2006) and possibly upcoming in the U.K. (Bamber and Taylor, 2002) and other brackish water related industries.

ACKNOWLEDGEMENTS

The first author was financially supported by a BOF-project (contract 011D13503) of Ghent University and especially appreciates the logistic and financial support of BASF, Antwerpen N.V. and ONDEO Nalco (contract d.d. 21/10/2001). This research is part of the UGent project GOA 01G00705.

Dr. Gheskiere provided constructive comments on the manuscript. We would also like to thank Endis-Risk for the picture of the Schelde river (Figure 1) and the chemical measuring network MWTL (The Netherlands) for the use of their chlorophyll a data.