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SETTLEMENT, SEASONAL SIZE DISTRIBUTION, AND GROWTH OF THE INVASIVE BIVALVE *MYTILOPSIS LEUCOPHAEATA* (CONRAD, 1831) (DREISSENIDAE) IN RELATION TO ENVIRONMENTAL FACTORS

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ABSTRACT Conrad's false mussel (*Mytilopsis leucophaeata*) is an invasive alien bivalve species causing severe biofouling problems in cooling water systems of power and industrial plants. Settlement, seasonal shell size distribution, and growth of this bivalve species were analyzed in relation to relevant environmental factors, using monitoring data from a brackish canal over a period of 4 y. Salinity at the sampling site ranged from 3.2 to 9.2, water temperature from 4.5°C to 23.9°C, and chlorophyll *a* content from 2 to 56 µg l⁻¹. Once a month one short-term exposed panel (1 mo exposed) and one long-term exposed panel (exposed from February 1989 to the month of sampling) were collected. Settled spat and attached mussels were collected monthly from these polyvinylchloride panels and from stones in the littoral zone. The short-term exposed panels were used to determine the period of spat fall. The long-term panels were used to study growth, shell length-frequency distribution, and densities of the mussel population after settlement. To study maximum age, *M. leucophaeata* were kept in cages in the canal. The highest recorded settlement was 204,000 individuals/m². The largest mussel had a shell length of 24.0 mm. Three cohorts of shell length (1–5 mm, 5–15 mm and 15–24 mm) could be distinguished. Data on survival of individual mussel size groups in cages indicated a maximum age of 4.5 y. Shell growth was very low in winter time (average growth less than 1 µm/day in the period of November to April). The average growth rate on the stones during the summer periods (3–4 mo) was 89 µm/day. On the panels, a rapid shell growth to an average shell length of 4 mm was recorded in the period of July until November in their first year, followed by a period of hardly any shell growth from December until May, and a subsequently rapid shell growth to an average shell length of 13 mm during the period of May until August in the second year. Individual mussels grew up to 20.9 mm during a 13-mo period. Growth of shells was significantly correlated with water temperature. The minimum threshold temperature for shell growth stops was 9.1°C (9.1°C–10.1°C) based on monthly measurements. Growth started at a minimum temperature of 9.1°C (9.1°C–14.2°C).

KEY WORDS: *Mytilopsis leucophaeata*, brackish water mussel, dark false mussel, population composition, settlement, shell length growth, shell length-frequency distribution

INTRODUCTION

Conrad's false mussel or dark false mussel *Mytilopsis leucophaeata* (Conrad, 1831) is a dreissenid bivalve species native to the Gulf of Mexico and the southern Atlantic coast of North America (Van der Velde et al. 2010, Kennedy 2011a, 2011b). Its permanent occurrence is restricted to brackish waters. In the period 1800 to 1835, a few records of this species were made in Western Europe (Kickx in Nyst 1835, Oliver 2015). Since then and also recently, *M. leucophaeata* has dispersed over brackish waters in coastal areas along the European coasts and is nowadays widely spread (Zhulidov et al. 2015 and literature therein; Forström et al. 2016). In The Netherlands, *M. leucophaeata* was first recorded near the port of Amsterdam (Amstel) in 1895 (Maitland 1897, Scholten 1919, Van Benthem Jutting 1943 and literature therein). In Belgium, in the harbors of Antwerp, where the species was recorded since 1835, *M. leucophaeata* was studied by Verween et al. (2005, 2006, 2007a, 2007b).

The species was most likely introduced by ship transport (Kennedy 2011a). Dry ballast was replaced by ballast water from the late 1870s onward (Carlton 1985). Ballast water, water tanks, and cooling water systems for ship engines and ship cleaning equipment likely play a role in the dispersal of *Mytilopsis leucophaeata* (Mackie & Claudi 2010, Van der Gaag et al. 2016). At a local scale, the species can spread through the

attachment of adults to boat hulls using byssus threads, transport in live wells or bilge systems, or by transport of water containing their larvae. Adults are more tolerant of fresh water than of sea water (Verhofstad et al. 2013, Van der Gaag et al. 2016). Larvae seem to be only tolerant for brackish conditions (Salinity 3–22) (Verween et al. 2007b). This invasive alien bivalve can cause severe biofouling problems in cooling water systems of power and industrial plants (Mackie & Claudi 2010).

The goal of the present study was to obtain insights into the life history of *Mytilopsis leucophaeata* in relation to key environmental factors for their growth and survival. This paper analyses the settlement, shell length-frequency distribution, shell growth rate, and survival of this invasive species by using data from individuals attached to stones, settled on polyvinylchloride (PVC) panels (short- and long-term exposure), and kept in cages (long-term exposure) in the littoral zone of a large brackish canal.

MATERIAL AND METHODS

Study Area

The study on the population structure of *Mytilopsis leucophaeata* was carried out in the Noordzeekanaal (translated: North Sea canal) at 3 km from the sluices indicated along the canal (coordinates 52° 27' 57" N, 4° 37' 56" E) near Velsen in The Netherlands. This canal connects the fresh and brackish water harbors of the Port of Amsterdam with the North Sea (Fig. 1).

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Therefore, a brackish water gradient is present in the North Sea canal extending from high salinities locations near the sluices at IJmuiden to fresh water locations in harbors near the City of Amsterdam.

Sampling of Water Quality Parameters

Physicochemical properties of the surface water of the canal were measured monthly, viz. water temperature ($^{\circ}\text{C}$) with a mercury thermometer, and salinity with an YSI model 33 S-C-T meter. Water samples were collected for measuring chlorophyll *a* ($\mu\text{g l}^{-1}$) at the laboratory with a Vitatron MCP spectrophotometer.

Collecting Mussels from the Stones for Determination of the Population Structure

Two to five stones were collected monthly from the littoral zone of the North Sea canal near the ferry of Velsen (Fig. 1) at depths of 40–80 cm during the period 1989 to 1992. Care was taken that sufficient mussels were attached to stones, allowing population structure analysis based on shell length-frequency distributions. All stones were transported to the laboratory. Subsequently, all mussels were removed, counted, and their shell lengths were measured using a Vernier caliper with an accuracy of 0.05 mm. The stones were measured on all colonized sides to enable sampled surface area calculations.

Sampling of Mussels from PVC Panels

Polyvinylchloride panels ($32.0 \times 14.2 \times 0.2$ cm) were used to study the settlement of spat, density, and growth of the mussels. The panels were stuck directly into PVC tubes (length 71.0 cm, inside diameter 14.3 cm). The PVC tubes were used to protect the panels against water turbulence, waves by passing ships, and storms that may have caused damage through scouring by the stones. This mimics the settlement and growth of mussels in littoral habitats with low exposure to turbulence and in the pipes of cooling water systems. Crabs and fish could freely enter the tubes so predation was not prevented. Both sides of the panels within the tube could be colonized (total surface area: 900 cm^2). In total, 29 clean tubes each containing two panels for colonization were placed at the stony bottom at a depth of about 75 cm and fixed with stainless steel cables to the jetty near the ferry on February 22, 1989. Subsequently, once a month one short-term exposed panel (1 mo exposed) and one long-term exposed panel (exposed from February 1989 to the month of sampling) were collected. This experiment from February 22, 1989 lasted until August 23, 1990. A second series of 14 clean tubes with the same design were laid out at April 5, 1990. This experiment lasted until August 28, 1991. After each sampling event, the two panels harvested were replaced by new ones.

The collected panels were transported to the laboratory and subsequently examined visually and by a stereomicroscope.

Figure 1. Location of the North Sea canal in The Netherlands with the sampling site at Velsen (at 3 km from the sluices indicated along the canal; this study) and at Amsterdam used by Vorstman (both indicated by an arrow). Insert: black dots indicate the sampling sites in the North Sea canal and Antwerp (Belgium).

The spat and the mussels were counted and their shell length was measured. Depending on the density of mussels and spat, 48–900 cm² of the panel area was inspected. If high densities of mussels were observed, three areas of 16 cm² were inspected (front, middle, and rear of the side with the highest density). When the density was low, the entire panel was inspected (900 cm²). The shell length along with the anterior–posterior axis of each mussel was measured to an accuracy of 0.05 mm. Densities of spat and mussels were expressed as numbers per square meter. The short-term exposed panels were used to determine the period of spat fall (Van der Gaag et al. 2014). The long-term panels were used to study growth, shell length-frequency distribution, and densities of the mussel population after settlement.

Age Determination of Mussels in Cages

Two perforated stainless steel cages (40 × 40 cm, height 15 cm, mesh size 2 mm [all mesh 30% of the surface]) made heavier by a tile at the bottom, with nine perforated compartments measuring 13 × 13 cm were each filled with 280 individuals (35 individuals per compartment) and were placed at the sampling site in the North Sea canal at a depth of about 75 cm on August 18, 1992. Every month the mussels in these cages were checked and dead mussels removed. After cleaning the cages and returning the living mussels, the cages were returned to the canal. The results of this cage experiment were used to determine the maximum age of these mussels.

Statistics

All samples have to be treated as independent as individuals were only measured once. Therefore, growth was estimated by comparing the average and maximum shell lengths of samples of the population. Pearson product moment correlations, significance testing, and Kruskal–Wallis one way analysis of variance on ranks were carried out by means of SigmaPlot for Windows version 11.0. The Kruskal–Wallis variance test was used because all number–shell length distributions did not show a normal distribution. Mean, standard deviation, and standard error were calculated using Excel for Windows.

RESULTS

Environmental Factors

Water temperature varied with seasons and years (Fig. 2A). Minimum and maximum temperature over the years 1989 to 1992 were 4.5°C and 23.9°C, respectively. Lowest temperatures were measured in the periods December to February. Water temperature increased from February to July, was highest during July and August, and decreased afterward. Salinity fluctuated between 3.2 and 9.0 (mean 5.4, SD 1.7) during the period 1989 to 1992. Salinity was not significantly correlated with day length and water temperature. Chlorophyll *a*, mean shell length, maximum shell length, and mean shell growth did not correlate with salinity (Pearson product moment correlation $P > 0.1$). Chlorophyll *a* showed high values before the temperature peak in 1989 and 1992 and during or after the temperature peak in 1990 and 1991; the water temperature, day length, and chlorophyll *a* showed significantly positive Pearson

Figure 2. (A) Water temperature, chlorophyll *a*, and shell growth of *Mytilopsis leucophaeata* in the North Sea canal (at 3 km). (B) Mean shell lengths of six generations of *Mytilopsis leucophaeata* harvested monthly from the stones of the North Sea canal.

product moment correlations. Lowest concentrations were observed during 1991 (Fig. 2A).

The high chlorophyll *a* peaks in the North Sea canal occurred in 1989, 1990, and 1992, before rapid growth of the mussels on the stones. In 1991, the chlorophyll *a* peak occurred after the growth period of *Mytilopsis leucophaeata* (Fig. 2A, B).

Shell Length Growth on the Stones

Shell growth was highest in the summer months (end of April to September) (Table 1). For the summer period 1989 to 1992 (100 days), the mean shell growth was 8.5 mm (SD 1.5 mm) resulting in a mean growth rate of 88.9 µm/day (SD 24.5 µm/day) based on 4,659 individuals.

The relationship between the mean shell length of the 2nd y class of the mussels on the stones and the water temperature was positive, demonstrated by a significant Pearson product moment correlation coefficient (0.381, $P = 0.0076$, $n = 48$; Fig. 2A, B). Over the sampling period of four years, mean shell growth was significantly correlated with day length (correlation coefficient 0.465, $P = 0.0009$, $n = 48$).

No significant correlation was found between the mean shell growth and the chlorophyll *a* concentration (Pearson product moment correlation coefficient 0.0874, $P = 0.555$, $n = 48$).

Spat Fall, Settlement, and Shell Length Growth on the Panels

Spat fall on the panels in 1989 and 1990 started in both the study periods in June and ended in November with high

TABLE 1.

Average shell growth of the second year class during the fast growing season of *Mytilopsis leucophaeata* on the stones in the littoral zone of the North Sea canal.

Period	Days	Growth (mm)	Growth rate ($\mu\text{m/day}$)	Number of mussels measured
May 22–September 11, 1989	112	8.0	71.4	1,196
April 23–July 16, 1990	84	10.5	125.0	1,062
April 22–August 12, 1991	112	8.5	75.9	1,302
April 21–July 14, 1992	84	7.0	83.3	1,099

numbers in the period July to September. On the shortly exposed panels, newly settled spat in the months August to September resulted in high mean densities of mussels (highest mean $\pm$ SD: $171,000 \pm 17,000$ individuals/m²; $n = 3$). This spat fall occurred after the high chlorophyll *a* peak in 1989, 1990, and 1992; in 1991 an early summer chlorophyll *a* peak did not occur (Fig. 2A). The highest mean density ($114,000$ individuals/m², SD $34,000$, $n = 3$) of *Mytilopsis leucophaeata* on long-term panels placed in February 1989 was observed in August 1989 after the first spat fall. After this event, the density decreased significantly during the next 3 y (Fig. 3). The settlement and growth of *M. leucophaeata* on the long-term panels starting in 1989 and 1990 showed that the mean shell length increased from July to November in 1989 (July until October in 1990), followed by a pause extending from November 1989 to April 1990 (October 1990 until May 1991) followed by a further growth period from April 1990 to July 1990 (May 1991 until July 1991). The individuals on the long-term panels showed rapid growth from spat (0.3 – 1.3 mm) to an average 5 -mm shell length during July to November (Fig. 5A–E). Hardly any growth occurred from December to May (Fig. 5F–K) followed by renewed rapid growth from May to July (Fig. 5K–M) in the next year

Figure 3. Mean densities of *Mytilopsis leucophaeata* in relation to exposure time of panels that were placed in the littoral zone of the North Sea canal. A linear regression line ($Y = 100.4 \cdot 10^3 - 74.8 X$; $R^2 = 0.476$; $P < 0.001$; $n = 18$) with 95% confidence level lines is outlined.

(Table 2). The percentage frequencies of the summation of shell-length frequency percentages for 1989 and 1990 were not significantly different (Kruskal–Wallace test) (Fig. 5N). There was also no statistically significant difference between the shell-length frequencies measured in the same months during these two years (Kruskal–Wallace test). No statistically significant difference was found between the frequencies of all subsequent months in each experiment (Kruskal–Wallace test). In July 1990 and 1991, the mean shell length reached was 13.5 mm (SD 2.56 mm) (1990) and 11.4 mm (SD 2.31 mm) (1991), respectively. During a 13-mo period, the fastest growing mussels reached a maximum shell length of 20.9 mm in 1990 and 20.8 mm in 1991. Shell length of the small-sized mussels increased in the same period from 0.5 to 3.9 mm in 1990 and from 0.5 to 4.1 mm in 1991 (Fig. 4). There was a significant linear correlation between maximum and mean shell length (mm) of individuals on the long-term exposed panels (Fig. 6).

Figure 4. Box plots of shell length distributions (A: 1989 to 1990; B: 1990 to 1991) of *Mytilopsis leucophaeata* on the panels in the North Sea canal. Boxes showing the 25 and 75 percentile lines and the median line together with whiskers extending to the 10 and 90 percentile lines are shown, outliers are presented as dots. The spat fall per month is presented as an insert expressed as the number of individuals per square meter.

Figure 5. (A–M) Monthly shell length frequency distribution of *Mytilopsis leucophaeata* on panels in the North Sea canal. (N) Summation of frequencies of all shell lengths of (A)–(M) on these panels.

Mean shell length and mean shell length growth on the panels were both significantly correlated with each other and with maximum shell length growth. Mean shell growth on the stones was significantly correlated with the day length (Pearson product moment correlation 0.465; $P < 0.001$; $n = 48$) and mean shell growth on the panels with water temperature. Other

correlations were not significant (Table 3). We observed a minimum threshold temperature for growth of 9.1°C (Table 4). Growth started in spring at a temperature of 11.2°C (SD 1.94°C) and stopped on both stones and panels in autumn when temperatures fell to 9.4°C (SD 0.39°C) (Figs. 2A and 4). During the winter time and early spring, a period of eight months, there

TABLE 2.

Average shell growth of the first year class of *Mytilopsis leucophaeata* on the long-term panels in the littoral zone of the North Sea canal.

	Exposure time (days)	Growth (mm)	Growth rate ($\mu\text{m/day}$)	Number of mussels measured
Period 1				
July 20 to November 23, 1989	126	5.2	41	1,832
November 23, 1989 to March 22, 1990	119	0.4	3	1,492
March 22 to July 25, 1990	125	8.2	66	1,302
Period 2				
July 25 to November 22, 1990	120	5.5	46	1,459
November 22, 1990 to May 25, 1991	185	-0.5*	0	2,449
May 25 to July 17, 1991	51	6.4	125	247

* Negative length growth value is caused by cohort sampling approach.

was no significant shell growth (Figs. 2A and 4). In spring, water temperature can rise so fast that monthly temperature measurements result in overestimations of the threshold water temperature.

Size Cohorts on the Stones

In most cases, two size cohorts and sometimes one or three cohorts in the population on the stones could be distinguished (Fig. 7). Next generations of mussels indicated by length class 0–5 mm always appeared in July or August. This size class could be easily followed until July next year by the presence of two cohorts. The average shell length of various generations observed over time showed rapid growth (Fig. 2B). Mussels with an average shell length below 5 mm, the first cohort, grew in the second year from April/May in 3 mo by 7–10.5 mm (Table 1) to 10–15 mm. This rapidly growing cohort contributed most to the population until the next cohort was settling in August/September (Fig. 7). A third cohort of a few individuals was also determined with shell lengths of 15–23 mm. Analysis of all individuals collected from the stones (12,556 individuals) showed two bends at 4 and 12 mm, respectively indicating the presence of two cohorts (Fig. 8). A possible third cohort

(expected to be approximately 20 mm in shell length) is hardly visible because of very low numbers (Fig. 7).

Age Determination in the Cages

At least two mussels in the cages belonging to the shell length class 16–18 mm and 8–10 mm (already at least 1 y old) at the start of the experiment survived 3 and 3.5 y, indicating a maximum age of 4–4.5 y. Their shell lengths at mortality were 18.9 and 17.3 mm, respectively.

DISCUSSION

Settlement, Shell Length, and Age

Spat fall was very high in the North Sea canal resulting in densities of up to 204,000 individuals/m². These high densities in the canal produce many larvae resulting in densities of up to 142,500 larvae/m³ (Van der Gaag et al. 2014), causing severe biofouling problems in cooling water circuits of power stations and industries in the area (Rajagopal et al. 1997, 2002, 2005a, 2005b, 2010a, 2010b, Jenner et al. 1998).

A maximum shell length of 24.0 mm was found in the North Sea canal. Large mussels were rare. Of 12,556 individuals collected in the littoral zone, only 25 individuals (0.2%) potentially belong to a third size cohort with shell lengths varying from 17.5 to 22.5 mm, indicating high mortality after the second cohort. Verween et al. (2006) recorded a maximum shell length of 17–22 mm in the Scheldt (Belgium). For The Netherlands, Gittenberger et al. (1998) reported a maximum shell length, height, and width of 23, 11, and 9 mm, respectively. On occasion, shell lengths of up to 27.0 mm have been recorded (Gittenberger et al. 1998, Kennedy 2011a).

Two cohorts based on shell length measurements with high numbers and a third one with very low numbers could be distinguished on stones from the North Sea canal. Results show that prudence is called for when interpreting cohorts to define year classes or different generations. In cages, a maximum age of 4.5 y was recorded indicating the existence of 5 y classes. Verween et al. (2006) made a hypothetical calculated graphical presentation of 5 y classes with the Von Bertalanffy growth function using data from experiments carried out in the harbor of Antwerp and concluded that *Mytilopsis leucophaeata* could become older than 5 y (lengths). Exceptionally large specimens with shell lengths of 23–24 mm were observed by Vorstman (1933b) in November to December. According to her observations,

Figure 6. The relation between maximum and mean shell length (mm) on the panels in the North Sea canal. The linear regression line with 95% confidence level line is displayed ($Y = 5.8023 + 0.8946X$; $R^2 = 0.6884$; $P < 0.0001$; $n = 26$).

TABLE 3.

Pearson product moment correlation of day length, mean shell length, mean shell growth, maximum shell growth, chlorophyll *a*, and water temperature for the long term panel field experiments 1989 to 1990 (A) and 1990 to 1991 (B).

	Mean shell length		Mean shell growth		Maximum shell growth		Water temperature	
	A	B	A	B	A	B	A	B
Day length	0.387	0.164	0.739	0.483	0.0691	-0.0678	0.750	
	0.191	0.593	0.006	0.111	0.823	0.826	<0.001	
	13	13	12	12	13	13	48	
Mean shell length	—	—	0.742	0.716	0.918	0.908	0.0618	-0.0562
			0.006	0.009	<0.001	<0.001	0.841	0.855
			12	12	13	13	13	13
Mean shell growth	—	—	—	—	0.654	0.641	0.586	0.608
					0.021	0.025	0.045	0.036
					12	12	12	12
Maximum shell growth	—	—	—	—	—	—	-0.136	-0.180
							0.659	0.557
							13	13
Chlorophyll <i>a</i>	—	—	—	—	—	—	0.329	
							0.0224	
							48	

Day length, chlorophyll *a*, and water temperature values are used from the years 1989 to 1992. The correlation is regarded as significant at *P* value < 0.05 (indicated in bold figures). The cell contents include, in order of appearance, the correlation coefficient, *P* value, and number of samples.

these individuals had died and were never older than 1 y and a few months (Vorstman 1933a, 1933b).

Settlement, Shell Length Growth, and Reproduction

Vorstman (1933a, 1933b, 1934) used glass slides as settlement plates and collected spat replacing the glass slides fortnightly during the period 1932 to 1934 at Oosterdock in the Mesohaline harbor of Amsterdam (Fig. 1). These publications did not contain quantitative data, graphs, and statistics. Only a general description of the results by Vorstman was presented. These results can be confirmed by the present quantitative study. Fourteen-day-old spat had a shell length of 0.85 mm and a shell height of 0.70 mm. A new generation settled in July to October and grew until the month November. Growth began again in May the next year. During winter time, the shell length of the young generation varied between circa 2 and 10 mm. The winter pause was visible as a clear mark on the shell followed by further growth. The fully grown shells were

circa 19–20 mm long, a length reached by the next autumn. This fully grown generation started to die off in November. In the subsequent months, this generation decreased in numbers until the generation was extinct by April the next year. Therefore, the maximum age at this site was 18 mo.

Vorstman (1933b) observed no large living specimens in April and May, recording only specimens ranging from 1 to 9 mm. According to Vorstman (1933b), specimens were on an average 4 mm in length in winter time. At the end of July and at an average shell length of 8 mm, a resting period of about 14 days occurred followed by recommencement of shell growth. In July mussels were on average 11 mm long, by the end of August 15 mm long and half way through September 17 mm long including a resting period of a few weeks, reaching by the end of October 19 mm in length. Kennedy (2011a) noted that the sizes recorded by Vorstman (1933b) may not be typical of first year maximum sizes as sizes of 10–15 mm have also been reported. Schütz (1969) compared Vorstman's results with those she obtained from the Nordostseekanal in Germany and found similar results with respect to the life cycle.

According to Rajagopal et al. (1995), the sexes of *Mytilopsis leucophaeata* in the North Sea canal could be distinguished from a shell size of 2.4 mm and reproductive maturity was reached at about 7 mm. Spawning took place from July–September based on the reproductive tissue cycle and gonad index leading to a lower tissue dry weight in the period July–October. Vorstman (1933b) observed reproductively mature specimens (from 10 mm) in mid-July and observed young mussels occurring from the end of July until November.

According to Verween et al. (2006), *Mytilopsis leucophaeata* shell growth rate was most rapid in June to July, decreasing in September and further decreasing in October to November with no growth occurring in winter time.

Relation of Shell Length Growth and Environmental Factors

We found that salinity had no significant correlation with day length, chlorophyll *a*, water temperature, mean shell length,

TABLE 4.

Threshold values of water temperature for shell growth of *Mytilopsis leucophaeata* on panels and stones in the North Sea canal.

Substrate	Year	Shell growth	
		Start (°C)	Halted (°C)
Panels	1989	n.d.	9.1
	1990	10.0	9.2
	1991	9.1	n.d.
Stones	1989	10.0	9.1
	1990	12.8	9.2
	1991	11.0	10.1
	1992	14.2	9.5

n.d., not determined.

Figure 7. Monthly shell length-frequency distribution of *Mytilopsis leucophaeata* on stones in the littoral zone of the North Sea canal.

maximum shell length, and mean shell length growth; however, water temperature, day length, and chlorophyll *a* showed a significantly positive correlation with each other. No significant correlation was found between the mean shell length and the chlorophyll *a* concentration. The relationship between the

mean shell length of the second year class of mussels on the stones and the water temperature was positive. During a 4-y period, mean shell length growth was significantly correlated with day length. Mean shell length and mean shell length growth on the panels were both significantly correlated with

Figure 8. Summation frequency of all shell lengths of each size class of the measured individuals of *Mytilopsis leucophaeata* on the stones in the littoral zone of the North Sea canal (1989 to 1992).

maximum shell length growth and with each other. Mean shell growth on the stones was significantly correlated with the day length, and mean growth on the panels was significantly correlated with water temperature. Other correlations were not significant.

Similarly, Verween et al. (2006) found that shell growth was correlated positively with temperature but not with chlorophyll *a* concentration. They found that chlorophyll *a* was only weakly correlated with temperature.

The shell growth on the panels in the North Sea canal was rapid during July to November, followed by a period of almost no growth from December to May, and again rapid shell growth from May to July. Maximum and minimum shell lengths and growth of *Mytilopsis leucophaeata* on the panels followed a typical pattern. Growth was observed to start and stop at a threshold temperature of 9.1°C. Fast growth of some individuals and slow growth of others may be caused by different settling times of larval cohorts. It is unknown whether an individual can spawn only once or several times during a spawning season.

Verween et al. (2005, 2007a) found a series of peaks in larval density during the spawning season by sampling on a weekly basis. Dreissenidae should be sequential spawners, and seasonal flexibility in larval production should indicate that adults can carry gametes for a long time (Verween et al. 2005).

Differential Growth of Individuals

Shell size is often used to estimate the age of a newly discovered colonization (Willing 2015). Individuals settled on the plates in the North Sea canal after the planktonic

phase differed strongly in their growth rate. Within three months after settlement, the fastest growers could reach a shell length of about 12 mm, and after a growth pause during winter and spring, individuals could grow further to a size of over 20 mm within 2 mo. At the same time, other individuals would grow very slowly. This means that shell size of *Mytilopsis leucophaeata* is not a direct reflection of age, but that mussels of the same size should be ascribed to a range of possible ages. Over a period of 13 mo after settlement, animals with shell lengths smaller than 1 mm could be 3–4 mo old; of 1.0–1.5 mm shell length 4–11 mo old; and above 2–4 mm shell length 9–12 mo old. For the most rapidly growing mussels during that period: 2 mm shell length could indicate a mussel is 1 mo old, 3 mm could indicate 2 mo old, 8 mm could indicate 2–3 mo old, 10–12 mm could indicate 3–11 mo old, 14–17 mm could indicate 12 mo old and 20.8–20.9 mm could indicate 13 mo old (Figs. 4 and 5). This may be caused by sequential settlement whereby some early settled individuals experience better conditions for growth than later settlers; however, other factors may also play a role in growth regulation such as genetic differences, food availability, density, and position with respect to other individuals.

CONCLUSION

The present study reports new data on settlement, shell length distribution, and growth of *Mytilopsis leucophaeata* in relation to key environmental factors in the littoral zone of a brackish water canal. At locations where salinity conditions were suitable, settlement and shell length growth, day length, and water temperature showed a positive correlation. The minimum threshold temperature for shell length growth stops was 9.1°C (9.1°C–10.1°C) based on monthly measurements. Growth started at a minimum temperature of 9.1°C (9.1°C–14.2°C). These threshold temperatures are similar with those for the related *Dreissena polymorpha* (Pallas, 1771) (Mackie 1991, Jantz & Neumann 1998). The general pattern of shell growth after settlement was a strong growth to an average shell length of 4 mm by Autumn followed by a growth pause in winter and start of growth in May the next year. Individual shell growth showed a high degree of variation. The cage data proved that a few individuals of *M. leucophaeata* can reach up to 4.5 y old.

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