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### 3. *Mytilopsis leucophaeata*: The brackish water equivalent of *Dreissena polymorpha*? A review

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#### Abstract

European brackish waters have been invaded in recent times by the brackish water mussel, *Mytilopsis leucophaeata*. Although the genus *Mytilopsis* originated from Europe more than 60 million years ago, it disappeared from Europe after its expansion to Central America. In the early 19<sup>th</sup> century, *M. leucophaeata* invaded Europe with a first record in the harbour of Antwerp, Belgium, but it is only when the species became a biofouling problem in the 1990s that attention was brought back to this relatively unknown species. The systematic classification, evolution, ecology and biogeographical expansion of *M. leucophaeata* in European waters are discussed. Because of the morphological resemblance with the zebra mussel, *Dreissena polymorpha*, and the fact that both species have overlapping habitat tolerances, both species were compared whenever possible and a clear identification guide is proposed. Although invasion by *M. leucophaeata* in Europe seems rather slow, its fouling problems are even more severe than those of *D. polymorpha*, underpinning the statement that *M. leucophaeata* is becoming the brackish water equivalent of *D. polymorpha* in Europe. Expansion along European brackish waters is still taking place and speeding up, especially by means of ballast water and hull fouling of ships, with very recent discoveries in the Black Sea, the Guadalquivir in Spain and the Baltic Sea in Finland.

#### Introduction

The brackish water mussel *Mytilopsis leucophaeata* (Conrad, 1831), also known as Conrad's false mussel (Mondadori, 1980) or the dark false mussel, is a mytiliform bivalve, which originates from the U.S. and was first detected in European waters in 1835 in the harbour of Antwerp (Belgium). *Mytilopsis leucophaeata* is a typical estuarine species, and thus resistant to a wide range of oligo- to mesohaline conditions (Siddall, 1980).

In the 1990s, *M. leucophaeata* was detected as a robust fouling species in industrial cooling water systems along estuarine rivers, and as such became an economic problem. This fact, and the apparent rapid recent spread of *Mytilopsis* throughout Europe brought the attention back to this relatively unknown species.

In this paper, current information on the biology of *M. leucophaeata* is reviewed and because of its resemblance to the much better known *Dreissena polymorpha* (Pallas, 1771), comparison with this fresh-water zebra mussel is considered in all aspects of this review.

To maximize the accessibility of the review, this chapter can be approached from different angles in point of view. Readers interested in baseline information on *M. leucophaeata* on e.g. biogeography, developmental biology or identification will find this information in the different sections, which provide an overview of existing knowledge. Readers interested in new insights (on biofouling) on *M. leucophaeata* resulting from this literature review are redirected to the last, concluding section, in which an overview of the lessons learned is provided.

#### Systematic classification and evolution

The genus *Mytilopsis* (Bivalvia, Veneroidea, Dreissenidae) (Fig. 1) was generally considered to include nine recent species: *Mytilopsis adamsi* (Morrison, 1946); *M. africana* (Van Beneden, 1835); *M. allyneana* (Hertlein and Hanna, 1949); *M. cochleata* (Kickx, 1835); *M. domingensis* (Récluz, 1852); *M. leucophaeata* (Conrad, 1831); *M. sallei* (Récluz, 1849); *M. trautwineana* (Tryon, 1866) and *M. zeteki* (Hertlein and Hanna, 1949). However, Marelli and Gray

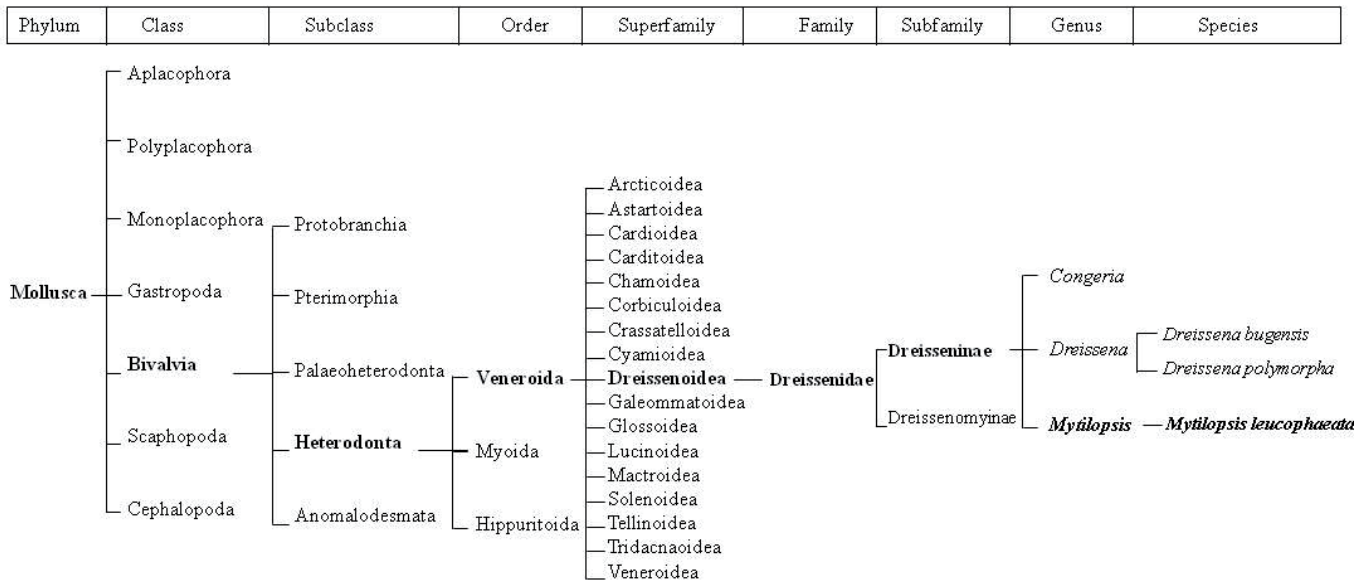


Figure 1. Taxonomical tree of *Mytilopsis leucophaeata* after Nuttall (1990).

(1983) concluded that *M. cochleata* and *M. leucophaeata* are synonyms. All members of the genus *Mytilopsis* inhabit tropical brackish waters, except for *M. leucophaeata*, which also occurs in temperate regions.

The superfamily Dreissenoidae arose in Europe more than 60 million years ago through the genus *Mytilopsis* (Fig. 2) and underwent a broad Eurasian expansion during the next 50 million years. About 5 million years ago, the genus disappeared completely out of Europe. The invasion of the New World occurred more than 30 million years after its first appearance in Europe and *Mytilopsis* spread throughout North and Central America. The currently living species *M. leucophaeata*, sometimes referred to as *Congeria cochleata* (Kickx, 1835) is not known before 5 million years ago. By means of *M. leucophaeata*, *Mytilopsis* re-invaded European waters in recent times.

*Dreissena* did not exist in Europe until 7 million years ago (Steininger et al., 1985). Much of its dispersal throughout Europe, North and Central America occurred since the late 19<sup>th</sup> century. Because *Mytilopsis* was considered a subgenus of *Congeria*, it was suggested that *Dreissena* and *Mytilopsis* evolved from extincted branches of the genus *Congeria* (Babak, 1983; Mackie et al., 1989). The evolutionary development according to Nuttall (1990), who elevated *Mytilopsis* to the genus level, now shows that *Dreissena* and *Congeria* both arose from *Mytilopsis* (Marelli, 1994; Theriault et al., 2004).

The evolutionary history of the dreissenids illustrates the success of the high salinity-tolerant *Mytilopsis*, which has survived since the early Tertiary. Nevertheless, its invasion of the New World during the Oligocene appears to have been luck and its natural disappearance from Europe, about 5 mil-

lion years ago, shows its vulnerability to changing conditions. Both *Mytilopsis* and *Dreissena* seem to be very slow colonizers, unless influenced by man (Nuttall, 1990).

### Identification

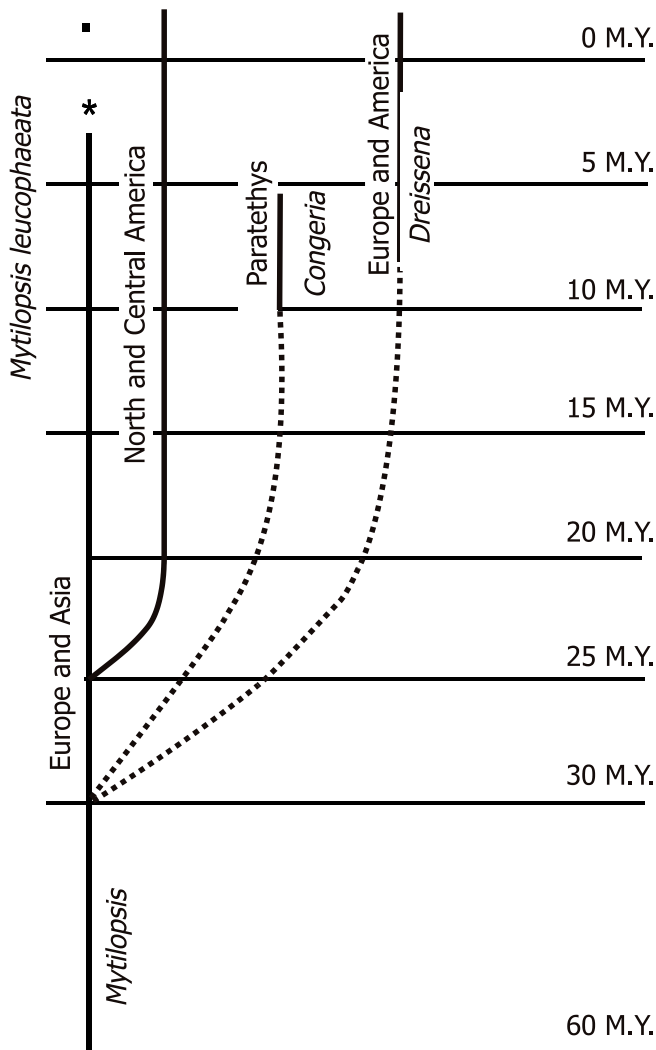
The basic developmental pattern of all gastropod and bivalve molluscs shows a great uniformity, whether they inhabit marine or freshwater environments (Conn et al., 1993). Specifically for bivalves, the life cycle can be roughly divided into two periods: (1) from egg till settling larva, they are pelagic and only protected by a larval soft shell and (2) after settlement, the individuals become benthic and develop a hard mytiliform shell.

Much confusion in identification arises between *M. leucophaeata* and *D. polymorpha*. Since *D. polymorpha* is far better known than *M. leucophaeata* and both species are very much alike, *M. leucophaeata* is often misidentified as *D. polymorpha*. The life history patterns are quasi identical for both species and distinguishing between both in their larval phase is more difficult than for the adult mussels. Therefore a good identification tool for adults and larvae is summarized and differences between both species are emphasised.

### Adults

The shell morphology of *M. leucophaeata* was originally described by Conrad (1831) as follows (Marelli and Gray, 1983):

“Shell incurved, white, with very rugose epidermis; anterior side much depressed; hinge margin excavated, with the teeth obsolete; on the posterior side, under the beaks is a



**Figure 2.** Evolutionary review of the appearance and spread of the Dreissenidae, based on Steininger et al. (1985). (\*: reintroduction in Europe after extinction).

pointed laminar tooth directed inwards. Cab. Academy, No. 1453. Inhabits the southern coast of the U.S.”

This poor description made it impractical to distinguish *M. leucophaeata* from other Dreissenidae.

In 1835, Nyst redescribed the species, which he named *Mytilopsis cochleatus* Kickx, much clearer with detailed drawings of the shell:

“Oblong, subcylindric shell curved, a little depressed posteriorly, a little compressed towards the upper edge and slightly dilated at the posterior end of the cardinal ligament, covered with cob-webby threads which make it appear finely and transversely striated and which meet with the age in some species of curved lamellibranchs.

The beaks are pointed and slightly curved, the shell is covered inside with a septiformous lamina, such as in several species of this kind, but it is moreover provided with an appendix in the shape of a spoon, placed under the septiformous lamina on the side of the upper edge.

The right valve of this species is larger than the left; this character is most perceptible on the lower edge. This shell is usually brown, ashen, and crossed by whitish zones; the young individuals appear sometimes striped.”

From current detailed knowledge on conchological redescrptions of *M. leucophaeata*, we can summarize that the shell is mytiliform and byssate. The exterior periostracum is creamlike coloured in young *M. leucophaeata* to dark brown in adults, with fine to medium rough concentric lines. For juveniles, it is very common to have the same distinct stripes or zigzag patterns as *D. polymorpha*. General appearance is long and wide, ventrally rounded and dorsally flattened, although juveniles seem more elongated and rectangular because of very smoothly curving margins. Body shape of *D. polymorpha* is much broader with flattened ventral margin and more rounded dorsally (MacNeill, 1991) (Fig. 3).

Much of the species confusion between *M. leucophaeata* and *D. polymorpha* occurs because of overlapping shell colouring. *Dreissena polymorpha* has in general a brownish-white zigzag pattern, but not all zebra mussels are striped (Pathy and Mackie, 1993).

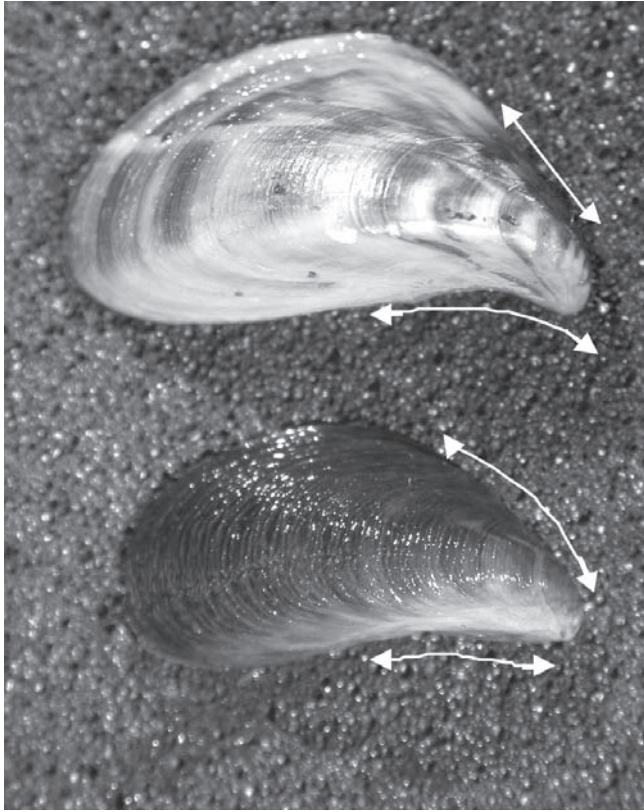
The interior shell of *M. leucophaeata* is coloured grey, with porcelain pallial and extra-pallial regions, and a narrow septum (myophore plate). The pallial line is very short and a pallial sinus is present, though very weakly developed (Fig. 4). The posterior retractor muscle scar is situated directly besides the posterior limit of the nymph. The main and most reliable distinguishing characteristic however is the presence of an apophysis near the umbo, a small triangular or rounded tooth, which serves as an attachment point for anterior retractor muscles, which are quite large in *M. leucophaeata* and visible with a binocular or even with the bare eye in larger individuals.

*Dreissena polymorpha* has a white shell interior with a broad septum with an entire pallial line, but without pallial sinus. In *D. polymorpha*, both anterior adductor and anterior retractors attach to the septum and an apophysis is absent. The fact that *Dreissena* would have evolved from *Mytilopsis* could indicate a reduction of the apophysis during the late Miocene (Panā, 1962). However, there is no evolutionary explanation for the disappearance of this characteristic, since *Mytilopsis*, with an apophysis, appeared 40 million years before *Dreissena* and is still successful (Nuttall, 1990).

### Larvae

Within 24 hours after the external fertilisation of gametes, released in the water column, a short-living trochophora stage is identified. Although rarely seen in plankton samples, this stage is frequently observed in laboratory induced fertilisation studies (Fig. 5). The trochophora has a ring of cilia, a prototroch, important for a direct swimming motion and transforms into a veliger stage. Veligers already have a soft

bilateral symmetric bivalve shell, but they feed and move with their larval organ, a ciliated velum. Early veligers have a straight, dorsal hinge and rounded ventral margins. These first larval shells (prodissoconch I) are free of ornaments and D-shaped in profile, which is referred to as D-shaped



**Figure 3.** Exterior right valve of (1) *Dreissena polymorpha* and (2) *Mytilopsis leucophaeata*.

veligers. Later a second, more ornamented larval shell (prodissoconch II) is secreted and gives the larva a clam-like profile: veliconcha, which is the last larval pelagic stage. Just before the larvae will become benthic, they grow considerably and develop new organs, like a muscular foot used for swimming near the bottom and crawling on surfaces. This pediveliger stage also forms gill filaments in the mantle cavity, which do not reach maturity until after metamorphosis. Primary settlement occurs by secreting a byssal thread onto a filamentous surface and is, once anchored, accompanied by loss of the velum leading to the postveliger stage. Young individuals, morphologically similar to adult mussels, but still immature, are referred to as juveniles (Fig. 5).

Since there is some synonymy in literature concerning the larval stages of mussels, an overview of the possible names is given in Table 2.

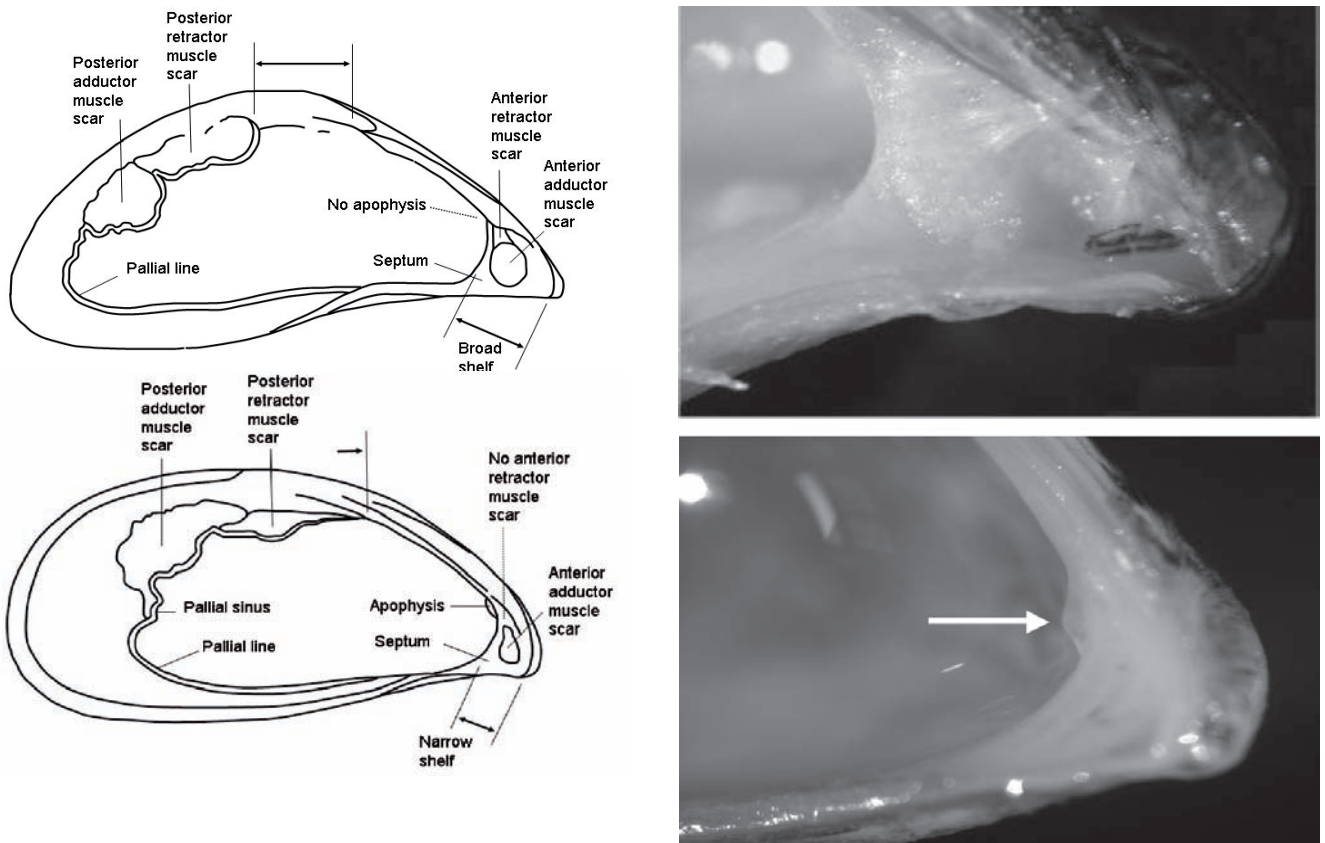
Although adult Dreisseninae become much larger than *M. leucophaeata* adults, size is not a distinguishing larval characteristic (Conn et al., 1993; Ackerman et al., 1994; Verween, unpublished data) (Table 3). The overall size of each developmental stage for each of the two species is overlapping, and these sizes differ for different individuals of one species. There is however a difference in shape which becomes more explicit as the individual develops.

No comparative study has been conducted for the trochophora stage. The other stages however have been studied intensively and differences between both species were summarized per species.

The D-shaped veliger in *M. leucophaeata* has a typical straight dorsal hinge and rounded ventral valve margins

**Table 1.** Comparison of characteristics of adult *Mytilopsis leucophaeata* and *Dreissena polymorpha* (according to Pathy and Mackie, 1993). (+: present; -: absent)

	<i>Mytilopsis leucophaeata</i>	<i>Dreissena polymorpha</i>
<b>Exterior</b>		
shell colouring	adult: dark brown, possible stripes juvenile: striped patterns	striped patterns, all black or white sometimes without stripes
ventral margin	convex, rounded ventro-lateral shoulder	concave, acute ventro-lateral shoulder
dorsal margin	flattened	rounded
umbo	rounded	pointed
posterior end	rounded	angled
<b>Interior</b>		
septum	narrow	broad
apophyse	+	-
pallial line	indented posterior in pallial sinus	entire, rounded
pallial sinus	+ (very weak)	-



**Figure 4.** Interior left valve of (1) *Dreissena polymorpha* and (2) *Mytilopsis leucophaeata* with a detailed view of the apex (1) without and (2) with apophyse indicated by a white arrow.

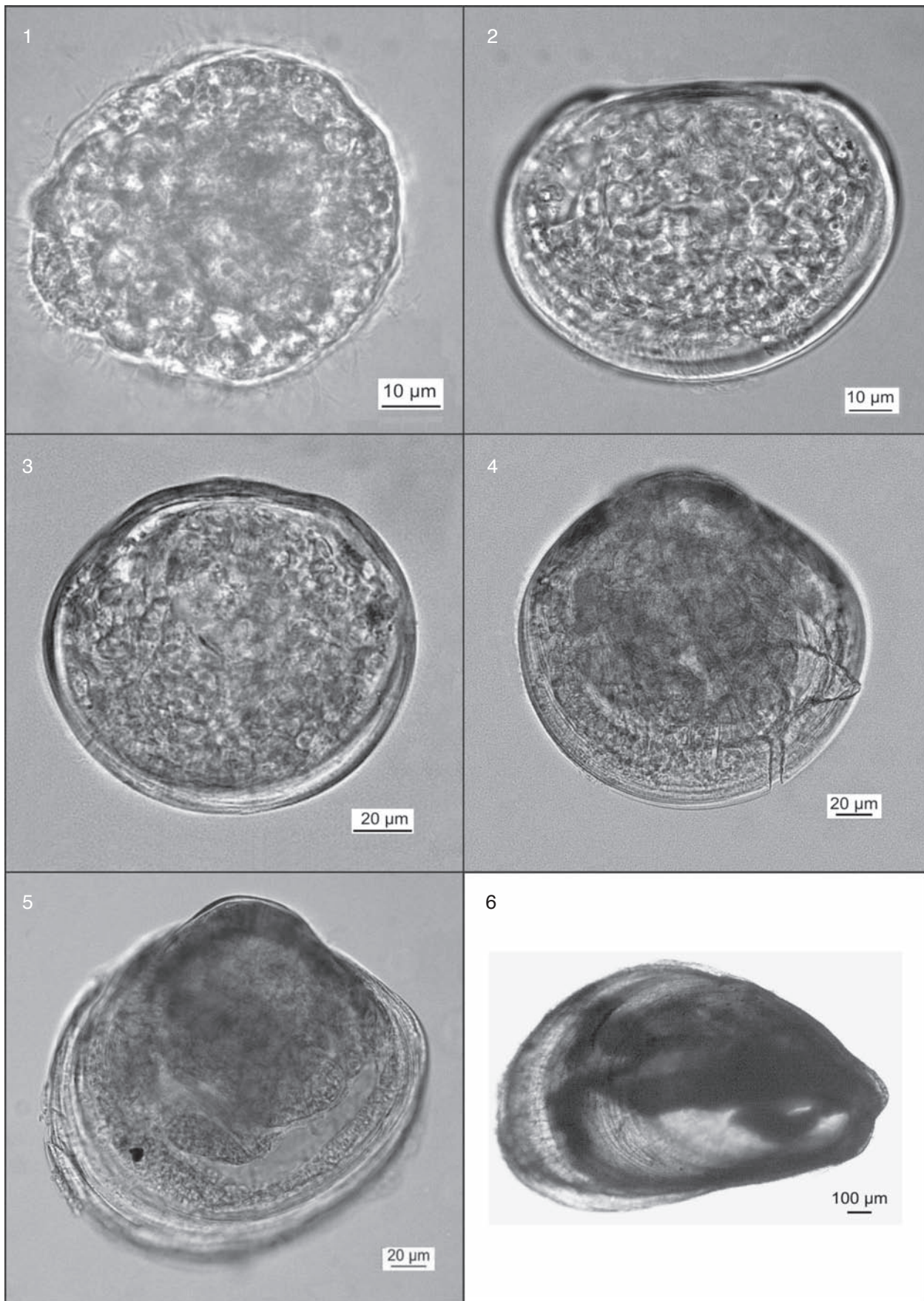
(Fig. 6a). The hinge has a subtle rounded lateral profile and becomes angular at the ends. The veliconcha develops an umbo, which makes it look clam-like and shows a uniform pigmentation. The asymmetry of the shell becomes clearer as the anterior side is slightly elongated and less rounded compared to the posterior side. The body shape of the pediveliger is highly asymmetric with the anterior being markedly elongated and less rounded than the posterior. A high concentration of pigment is visible near the umbonal region. Development and growth of the larval shell continues in posteroventral direction in the postveliger stage. The anterior shoulder is more pronounced and dorsally a well devel-

oped umbo is visible. The pigment stays concentrated near the umbo and a pigment spot is posteroventrally visible. The juveniles have a rounded posterior and a rather pronounced anterior shoulder and will continue developing mytiliform. The pigmentation is less concentrated and fills almost the entire shell.

In general, the shell valves of the D-shaped veliger and the veliconcha of *D. polymorpha* are more ovoid. The veliconcha has a velum pigment at the anterior side (Fig. 6b). The pediveliger has a highly pronounced anterior side, which is rather angulated. The pigment is rather randomly spread in the larvae. The velum pigment is mostly still present, but not

**Table 2.** Synonymy in life history stages of *Dreissena polymorpha* and *Mytilopsis leucophaeata* (Ackerman, 1995)

Pelagic larvae	<b>trochophora</b>	
	veliger	<b>D-shaped</b> or straight-hinged veliger
		<b>veliconcha</b> or umbonal veliger
Benthic mussels	<b>pediveliger</b> or settling veliger	
	<b>postveliger</b> or spat or plantigrade mussel	
	<b>juvenile</b> of siphon-forming mussel	
	<b>adult</b> or branchi-siphonal mussel	



**Figure 5.** Larval stages of *Mytilopsis leucophaeata*: (1) trochophora; (2) D-shaped veliger; (3) veliconcha; (4) pediveliger; (5) postveliger; (6) juvenile.

**Table 3.** Developmental sizes of *Mytilopsis leucophaeata* and *Dreissena polymorpha* (Rajagopal, personal communication; Verween, unpublished data; Conn et al., 1993; Ackerman et al., 1994)

	<i>Mytilopsis leucophaeata</i>	<i>Dreissena polymorpha</i>
egg	> 32 $\mu\text{m}$	40-96 $\mu\text{m}$
trochophora	< 63 $\mu\text{m}$	57-121 $\mu\text{m}$
D-shaped veliger	50-91 $\mu\text{m}$	70-160 $\mu\text{m}$
veliconcha	109-150 $\mu\text{m}$	120-280 $\mu\text{m}$
pediveliger	145-220 $\mu\text{m}$	167-300 $\mu\text{m}$
postveliger	220-480 $\mu\text{m}$	158-500 $\mu\text{m}$
juvenile	> 580 $\mu\text{m}$	> 500 $\mu\text{m}$

in all pediveligers. The postveliger is randomly pigmented. Development occurs in a rather ventral way, with a much longer and straighter anterior shoulder. The anterior margin in juveniles is straight. The umbo is well developed, but less pronounced than in *M. leucophaeata*. No specific pigmentation is present. In Table 4 the main distinguishing characteristics of larval and postlarval stages between *M. leucophaeata* and *D. polymorpha* are summarized. However, it needs to be emphasised that gut content can easily be misidentified as pigment spots, so Fig. 6a and 6b should be additionally used to distinguish between both species.

### Ecological characteristics

*Mytilopsis leucophaeata* has been detected in rather isolated waters, like the Black Sea (Therriault et al., 2004) as well as in very open regions, like the river Schelde (Verween et al., 2005) at very different ranges in temperature and salinity. This leads to the hypothesis that the habitat preferences and environmental limits of this species are very broad, and that the species may tolerate a wide variety of environmental circumstances in its newly invaded habitat.

Overlapping tolerances of *M. leucophaeata* and *D. polymorpha* in habitat and food preferences, temperature and salinity allow a sympatric distribution of both species, especially in estuaries. An estuary is a semi-enclosed coastal water body in which sea water mixes with fresh water. The consequent gradient in salinity and temperature leads to possible sympatric distribution of both species, as already observed in the estuarine delta of the Rhine, Meuse and Schelde Rivers (Wolff, 1969; Marelli and Gray, 1983) and the Noordzeekanaal (Van der Velde et al., 1998).

### Substratum preferences

One of the most principal factors affecting the distribution and abundance of *D. polymorpha* is a suitable substrate for attachment (Karatayev et al., 1998a). Primary settlement merely happens on filamentous structures, such as bys-

sus threads of adults. Secondary settlement occurs mostly on hard surfaces, particularly rocks and stones, and macrophytes. Highest abundances however have been recorded on artificial substrates.

Although no specific research has been conducted on habitat preferences of *M. leucophaeata*, the species has been found merely attached on artificial substrates such as the conduits of the cooling water installation in Antwerp and The Netherlands (Verween et al., 2005; Rajagopal et al., 1995b), large, stone walls at Cardiff Docks (Oliver et al., 1998) and wooden posts and piling in the River Thames (Bamber and Taylor, 2002). In the Delta area in The Netherlands, mussels have been found attached to natural occurring stones and wood, but only in scarce densities (Wolff, 1969).

### Food resources

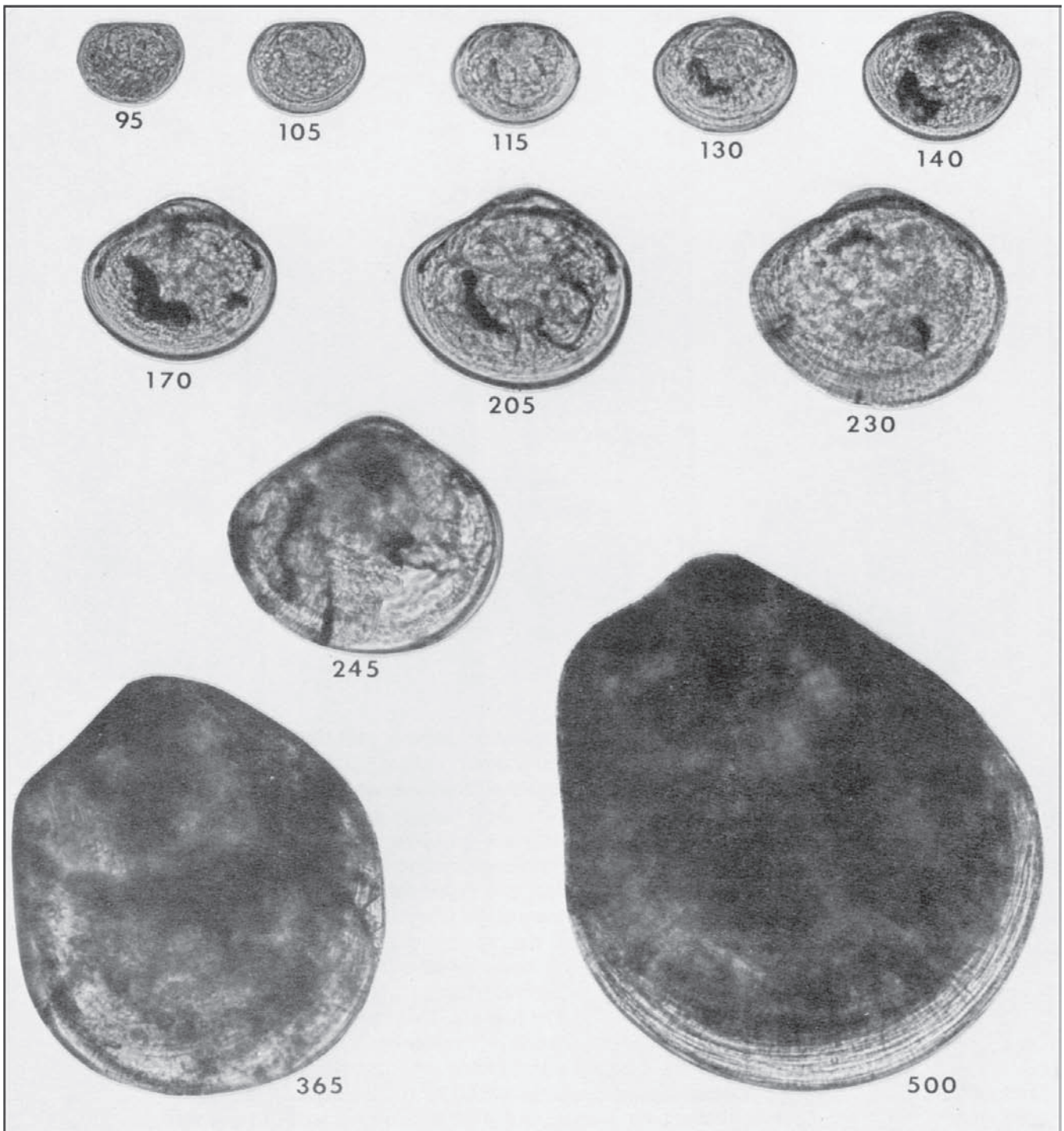
Mussels filter-feed primarily on planktonic algae and zooplankton. Other nutritional sources are bacteria, detritus, and organic matter, though less ingested. The filtration rate of *D. polymorpha* is affected by size, turbidity, temperature and certain concentrations of specific sizes and kinds of algal and bacterial cells (Mackie and Schloesser, 1996).

*M. leucophaeata* is a filter feeder with phytoplankton as major food source. They are able to ingest particles as small as 4  $\mu\text{m}$ , and can feed on *Isochrysis galbana* in laboratory cultures (Verween, unpubl. data).

### Salinity tolerances

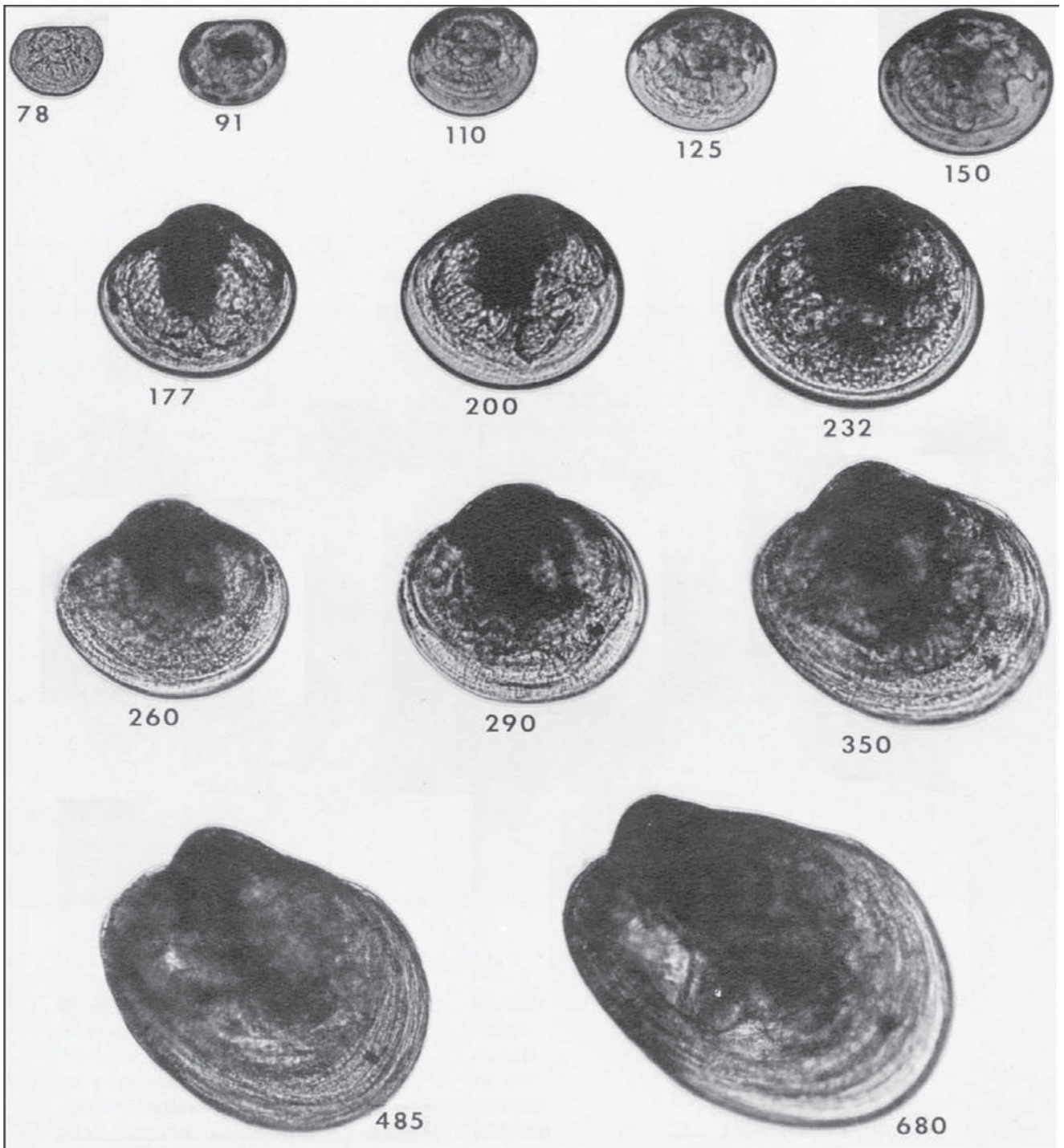
The salinity tolerance limits of *M. leucophaeata* are mostly described in combination with data on *D. polymorpha*. Because the hyperosmotic regulation of body fluids, which is a universal adaptation of brackish water animals, can enlarge the salinity tolerance of a species, literature data concerning *M. leucophaeata* vary greatly (Table 5).

It has been stated that *M. leucophaeata* can live and establish in salinities ranging from almost freshwater (0.1



**Figure 6a.** Photomicrographic sequence showing lateral views of various developmental stages of *Dreissena* spp. and maximum shell length ( $\mu\text{m}$ ) indicated by the numerical value below each specimen (Conn et al., 1993).





**Figure 6b.** Photomicrographic sequence showing lateral views of various developmental stages of *Mytilopsis leucophaeata* and maximum shell length ( $\mu\text{m}$ ) indicated by the numerical value below each specimen (Conn et al., 1993).

PSU) over oligo- to mesohaline conditions, with a maximum of 26.4 PSU, which indicates that this species can be found across nearly the whole estuarine gradient. Although *M. leucophaeata* can survive even in freshwater (0 PSU) and in highly saline water (31 PSU), these are well above the levels preferred for propagation (Wolff, 1969). Only true seawater (35 PSU) is outside its reach of survival. There is however still disagreement about the optimal salinity level for *M. leucophaeata*, ranging in literature from 0.75 PSU to 20.9 PSU, which could indicate that *M. leucophaeata* is able to adapt to circumstances more derogatory from its original habitat.

The larvae and postlarvae of *M. leucophaeata* are capable of development at even higher salinities, ranging to 32 PSU. This characteristic makes it possible for *M. leucophaeata* to transfer the oceans as larvae in ballast water with high salinities and as such colonise a new, isolated estuarine habitat (Siddall, 1980).

Since *D. polymorpha* is a typical fresh water species, its capability to adapt to different salinity levels is much smaller than for *M. leucophaeata*. The euryhaline capacities of *M. leucophaeata* however lead to a possible habitat overlap in salinity between the two species. According to MacNeill (1991), salinity tolerances appear to overlap greatly between 0.2 and 3 PSU. Both species are dominant in sessile communities of the Noordzeekanaal connecting Amsterdam harbour with the North Sea, where salinity ranged from 1.7 to 9.2 PSU (Van der Velde et al., 1998). As a general rule it is accepted that *D. polymorpha* tolerates salinities up to 6 PSU, which leads to a possible habitat overlap for both species between 0.1 and 6 PSU.

### Temperature tolerances

Although almost all members of the genus *Mytilopsis* inhabit tropical and subtropical waters, *M. leucophaeata* is restricted to warm, more temperate waters (Marelli and Gray,

1983). At its place of origin, the Gulf of Mexico, yearly water temperature fluctuates between 24 and 27°C, but in European waters, the species endures much lower temperatures (Table 6).

Its resistance to temperatures as low as 6.8°C, makes *M. leucophaeata* a potentially very suitable inhabitant of all temperate waters throughout Europe. Since *Dreissena polymorpha* tolerates temperatures up to 29°C, water temperature is not a characteristic to distinguish between possible *M. leucophaeata* and *D. polymorpha* habitats.

However, temperature is an important, species-specific factor in the initiation of spawning (De Vooy, 1999). Spawning in *Mytilus edulis* only occurs when the water temperature exceeds 10°C (Chipperfield, 1953; Wilson and Seed, 1974). For *D. polymorpha*, 12°C is the minimum temperature allowing gonad maturation and as a general rule is accepted that no veligers will appear in the water column at lower temperatures (Ram et al., 1996), although Mantecca et al. (2003b) found a spawning population at 25 m depth, where temperature stayed below 10°C most of the year. Monitoring data show that for *M. leucophaeata*, this threshold temperature for gamete maturation may be 13°C ± S.E. 1°C (Verween et al., 2005). Other studies indicate that reproduction usually starts at a temperature higher than 15°C (Schütz, 1969) or even higher than 20°C (Rajagopal et al., 1995b).

### Life history

Since almost no literature is available on the life history patterns of *M. leucophaeata*, population dynamics of *M. leucophaeata* in relation to environmental factors were investigated in the cooling system of BASF, Antwerp along the River Schelde during the period 2000–2004, determining (1) the yearly period of larval presence in the water column and (2) the growth rate of juvenile and adult mussels.

### Recruitment

In all years spawning of *M. leucophaeata* began end of May early June and lasted for about four months (Fig. 7). Temperature and salinity at first detection ranged between 16.2–19.5°C, and from 2.6 to 4.9 PSU, respectively. Two or more distinct larval peaks could be observed per year. Different peaks were probably due to different spawning periods (Borcherding, 1991), but although major differences in densities between months and years were found, the period of larval occurrence was markedly similar (Verween et al., 2005).

Dreissenidae are sequential spawners (Borcherding, 1991), and the seasonal flexibility in larval production patterns indicates that adults carry ripe gametes for a very long time. After initial spawning, the exposure to ripe eggs and

**Table 4.** Comparison of characteristics of larval and postlarval stages of *Mytilopsis leucophaeata* and *Dreissena polymorpha* (according to Conn et al., 1993) (+: present; -: absent)

	<i>M. leucophaeata</i>	<i>D. polymorpha</i>
gut pigment	+	+
velar pigment	-	+
posterior-ventral pigment	+	-
general shape	rounded	ovoid
anterior vs posterior shoulder	slightly lower	markedly lower

**Table 5.** Overview of salinity ranges where presence of *Mytilopsis leucophaeata* is recorded, according to literature

Min. salinity (PSU)	Max. salinity (PSU)	Optimal salinity (PSU)	Region	References
	26.4		The Netherlands	Otto and Wielinga, 1933
0	12.7		Laboratory	Castagna and Chanley, 1973; Deaton et al., 1989
0.2	2.7	1.4	The Netherlands	Janssen and Janssen-Kruit, 1967
3.5	9.2		The Netherlands	Van Benthem-Jutting, 1943
8.0	22.0		Virginia Keys, U.S.	Siddall, 1980
0.5	2.0		Southern England, U.S.	Smith and Boss, 1996
	15.0		Cardiff Docks, England	Oliver et al., 1998
6.0	14.0		Thames, England	Bamber and Taylor, 2002
0.5	5.0		Black Sea, Ukraine	Therriault et al., 2004
	0.9		Gaudalquivir, Spain	Escot et al., 2003
0.1	11.7		Schelde, Belgium	Verween et al., 2005
Development of larvae				
10.0	32.0			Siddall, 1980

sperm in the water column often triggers gamete release by other ripe mussels, thereby creating periodic synchronisation in larval production, resulting in different larval peaks. For *D. polymorpha* interannual differences in recruitment success are most likely influenced by environmental factors, e.g. weather conditions, abundance and timing of phytoplankton blooms, wind currents, etc. (Garton and Haag, 1993), although the specific influence on variation in larval abundance in the water column is still poorly understood (Nichols, 1996). However, an increase in adult density could lead to increasing recruitment success (Sprung, 1993), as monitored for 2003, which could indicate that the adult stock

of *M. leucophaeata* in the dock of BASF, Antwerp is still expanding.

The release of gametes in *D. polymorpha* is highly variable (Nichols, 1996) throughout its range in Europe, Russia and North America and can be a very synchronized event, focused over 1 or 2 weeks, or can be completely non-synchronized, occurring throughout the year, depending on the site where the species is found. In some localities, zebra mussels start spawning at water temperatures of 12°C, but do not start until water reaches 22°C at other areas. On average, peak larval densities in the water column are reached very rapidly and then gradually decline over a 6-8 week period.

**Table 6.** Water temperature ranges where presence of *Mytilopsis leucophaeata* is recorded, according to literature

Min. temperature (°C)	Max. temperature (°C)	Region	Reference
13	30	Miami, U.S.	Siddall, 1980
11	26	Noordzeekanaal, The Netherlands	Rajagopal et al., 1995b
6.8	25.8	Schelde, Belgium	Verween et al., 2005

### Growth

By means of growth cages, shell growth was followed in the River Schelde during 2003 and 2004. Monitoring several length classes allowed to model shell growth of a modal mussel, settled at the end of February over a period of nearly 5 years (Fig. 8).

*Mytilopsis leucophaeata* follows an oscillatory growth trajectory similar to many species living in environments with a distinct annual cycle in temperature and/or light conditions (Crisp, 1984), with one summer growing season a year. A negative, linear relation between shell length and shell growth rate was detected. The parameters of the Von Bertalanffy growth curve were estimated and gave an asymptotic length ( $L_{\infty}$ ) of 17 mm, although empty shells larger than 20 mm have been found, and a growth constant  $K$  of 0.56 per year (Verween, unpubl. data).

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 7) 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.

The duration of the growing season of *M. leucophaeata* is mainly restricted to the summer (July - September), similar to that of *D. polymorpha*, when growth also occurs primarily during the summer with little or no growth during wintertime (Bij de Vaate, 1991). In contrast, *D. polymorpha* seems to grow faster ( $K = 0.808$ ) and much larger ( $L = 40.5$  mm), but

has a shorter life span between 2 and 4 years (Conides et al., 1997; Chase and Bailey, 1999a).

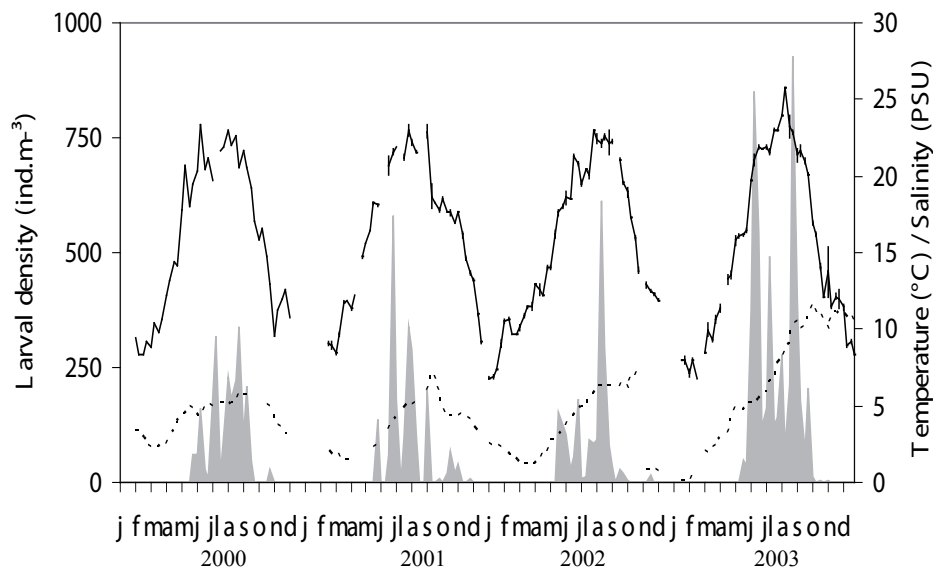
### Biogeographical distribution

Dreissenidae have recently spread throughout the world by means of shipping activities (Nuttall, 1990). Obviously, the ever expanding industrial development, hull fouling and ballast water discharges from transoceanic shipping together with the creation of canals linking isolated water bodies with each other and create an ideal passive transferring method for both aquatic and terrestrial species from one region to another. These phenomena are believed to be responsible for the recent spread of these and other non-indigenous species throughout the world (Coutts, 1999; Therriault et al., 2004). More specifically, it is assumed that the ballast water transfer and hull fouling of industrial ships are very important vectors for the spread of *M. leucophaeata*. Other human-mediated vectors for dispersal of mussels include hull fouling on recreational boats trailered from infested to uninfested water bodies, commercial bait transport, hatchery stocking activities, aquaria releases and navigation and irrigation canals (O'Neill, 1996). However, since European brackish water bodies are seldom recreational and not naturally connected to one another, these other vectors seem unlikely for the spread of *M. leucophaeata*. In Europe, mussels may also disperse naturally by being transported passively as planktonic larvae in water currents and by attaching to other organisms such as crayfish and turtles (Carlton, 1994). They may also attach to the legs and feet of shorebirds, but these are only low-level factors (Johnson, 1994). Water currents can disperse *M. leucophaeata* larvae further downstream in estuaries, but because of saline boundaries, it will never reach the high dispersal capacity of *Dreissena* larvae in freshwater ecosystems. The presence of brackish water stepping stones throughout Europe might however improve the dispersal of *M. leucophaeata* by means of transportation through birds, although no specific research has been conducted.

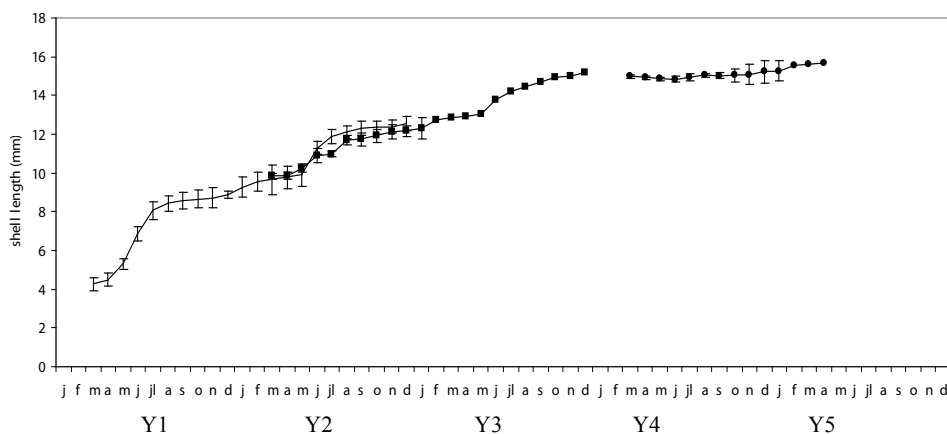
*Mytilopsis leucophaeata* originates along the southern coast of the U.S. and ranges from Tampico, Mexico to the Hudson River estuary (Marelli and Gray, 1983). It invaded Europe with a first record in 1835 in the harbour of Antwerp in Belgium (Nyst, 1835). The species, which Nyst addressed as "original and at least new to Belgian fauna" was found attached in great abundance to piles in a ship repair dock. Since the mussels were accompanied by barnacles and corals, Nyst concluded that they were probably brought there by transoceanic ships. However, it needs to be emphasised that no details on the type of barnacles and corals are mentioned, and as such they do not completely confirm the trans-oceanic crossing theory, although it is most likely it happened this way. In the early 19<sup>th</sup> century the species was also found in France and the Netherlands (Récluz, 1849; Reeve, 1858; Fisher, 1858, all in Marelli and Gray, 1983).

**Table 7.** 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	Noordzeekanaal, The Netherlands	Rajagopal et al., 1995b
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., 2006



**Figure 7.** Seasonal variation in larval arrival of *Mytilopsis leucophaeata* in the cooling water system at BASF, Antwerp (full line: temperature in °C, dashed line: salinity in PSU, grey shaded: larval density in ind m<sup>-3</sup> (adapted from Verween et al., 2005).



**Figure 8.** The extrapolated graphical presentation of the Von Bertalanffy growth function over four years (adapted from Verween et al., 2006).

In 1928, the species was recorded from the Kiel canal in Germany (Boettger, 1933). *M. leucophaeata* was detected in Dunkerque and the Canal of Caen in France (Germain, 1931). In 1960, Adam (1960) shortly described *M. leucophaeata* again in Belgian waters, near Nieuwpoort, as part of listing of Belgian molluscs, and the species also invaded the Rhine River in The Netherlands as mentioned by Wolff (1969).

It is only when *M. leucophaeata* became an economic problem in the 1990s as an important industrial fouler, that attention was brought back to this, until then, relatively unknown species. In 1994, *M. leucophaeata* was causing fouling problems in the cooling water installation of the Velsen and Hemweg power station in the Netherlands (Rajagopal et

al., 1995b), and was present in the Noordzeekanaal (Van der Velde et al., 1998) and the Waal River (Kelleher et al., 1997). In 1996, *M. leucophaeata* was recorded for the first time from British waters. Clumps of tubeworms, together with *Mytilus* and *Mytilopsis* were found on the walls of Roath Basin, Cardiff Docks in South Wales (Oliver et al., 1998). Given the long time that *M. leucophaeata* has inhabited nearby countries like Belgium and France, it is surprising that no previous records in England existed. The presence of the North Sea Channel with its high salinity acts as a barrier for the natural dispersal of the species. Since ballast water is its main transfer method, and this is less used by the smaller Channel crossing ships, it has been almost impossible for *M. leucophaeata* to cross this barrier. In 1998, the brackish

water mussel was identified for the second time in England, in Cliff Fort Lagoon, first as a high density of dead valves in the sediment, but in 1999, live specimens were found on wooden posts and piles (Bamber and Taylor, 2002). Recently (Therriault et al., 2004), *M. leucophaeata* was identified from the Dniester Liman Black Sea Basin (Moldavia Ukraine) for the first time. Again ballast water discharges are probably responsible for this invasion since canal construction opened corridors between previous disjunct regions of the Black Sea and the Caspian Sea. In 2003, a large population of *M. leucophaeata* was found in the River Guadalquivir of the Iberian Peninsula (Spain) (Escot et al., 2003), where it is causing massive fouling problems in an industrial cooling water system, together with *Cordylophora caspia* and *Corbicula fluminea* among others. Very recently, October 2005, *M. leucophaeata* has been detected in the northern Baltic Sea in Finland, in an area affected by cooling water from a power plant (Laine et al., 2006)

It took almost 30 million years for *Mytilopsis* to expand its range from Eurasia to North America during the Eocene, but considerably less time to re-invade Europe during recent times (Therriault et al., 2004). The fact that the invasion of British waters from mainland Europe seemed almost impossible suggests that *M. leucophaeata* is not an efficient active invader (Oliver et al., 1998). However, the species has found an extremely powerful invasion tool in the use of ballast water in transoceanic ships. This means that as long as shipping activities keep expanding, the invasion of the brackish water mussel will speed up. Although awareness programs are already in full development in North America, and ballast water use is restricted carefully, it is only in 2008 that the European Strategy on Invasive Alien Species (Council of Europe, 2003) will be implemented by the majority of the European member states (Council of Europe, 2004). A worldwide agreement is needed to restrict or minimise invasions by *M. leucophaeata* and many other aquatic invaders.

### In conclusion: lessons learned

Previous chapters summarize literature information on the biology and ecology of *M. leucophaeata*. In this chapter, attention is brought back to the fundamental questions concerning this relatively unknown species. Can *M. leucophaeata* really become the brackish water equivalent of *D. polymorpha*, or is it, although invasive, a rather harmless species?

### Invasion capacities

The habitat preferences and environmental limits of *M. leucophaeata* are very broad, which means that, theoretically, we can expect this species in all European brackish water bodies. To invade into a new area, *M. leucophaeata* has to overcome a major obstacle after human-mediated dis-

persal: although the species has a broad tolerance to salinity, survival with reproduction is impossible in fully fresh or seawater. This makes it almost impossible for the bivalve to cross these natural salinity barriers and as such to naturally invade into new areas. In contrast to *D. polymorpha*, who can expand very rapidly as soon as a new freshwater basis is colonized, *M. leucophaeata* is a rather slow natural colonizer with low dispersal capacities, who is restricted to brackish water bodies.

Transfer from one place to another is thus mainly human-induced. By means of transport as larvae in ballast water or as adults attached to the hull, shipping traffic is the most important vector for dispersal of *M. leucophaeata* (Therriault et al., 2004). The presence of stepping stones of estuaries all over Europe however leaves the possibility of minor dispersal by means of transportation of juveniles through attachment to the legs and feet of waterfowl and shorebirds.

No clear invasion pattern throughout time can be found in Europe, which might indicate that *M. leucophaeata* is present in Western Europe since the early 19<sup>th</sup> century, but may not been identified before because of misidentification of the species as *D. polymorpha* in the past and the lack of interest in the species.

To reverse the spreading of *M. leucophaeata*, public awareness is important, just like for every other invasive species. Especially in Europe, almost no implementations have yet been made to raise the awareness of industrial initiatives and public governments.

### Biofouling capacities

Although *M. leucophaeata* is a slower colonizer than *D. polymorpha*, it is definitely an even severe fouling species. Though, only few biofouling problems have been reported so far for a couple of reasons:

- 1) Misidentification of the species. Along the River Schelde, fouling problems with *M. leucophaeata* have not been reported, because of confusion with *D. polymorpha*. Because of this fact, we can be sure that there are more spots where *M. leucophaeata* fouling has been misidentified, and as such not reported and treated in the proper way. This problem can easily be solved through an enhanced communication between science and industry, as distinguishing between adults of both species is not difficult at all. The most important feature is the apophysis, a small triangular or rounded tooth, only present in *M. leucophaeata*. Identification on larvae-level is more problematic, so in this case, searching for the adult population nearby the problem zone is recommended.
- 2) The unequal proportion between fresh and brackish water. Hundreds of rivers and their tributaries cross

the European continent, with only a couple of estuaries and brackish water seas. Add the fact that few industry is present along these brackish water bodies in contrast to the freshwater rivers, and the less known *M. leucophaeata* fouling problems are a fact.

- 3) No legal framework on biocide dosage. Biofouling is prevented by treatment with biocides, of which chlorination is the most effective and cost effective control measure. The use of biocides is only recently being restricted in Belgium and a lot of European countries still have lack of legislation with respect to discharges of chemicals in cooling water. Because of that, concentrations of used biocides are so high that mussels are killed completely and no observation of species has happened in the past. It was only when the legislation on biocide application became stricter in Belgium, that the magnitude of the biofouling problem caused by *M. leucophaeata* in the harbour of Antwerp became clear.

#### Resistance to anti-fouling techniques

Pathy and Mackie (1993) posed that the ecological and economical threats of *M. leucophaeata* are less severe than those of the zebra mussel. However, the fact that they inhabit brackish waters makes them far more resistant to environmental changes (Siddall, 1980), which makes them potentially an even more robust fouler than *D. polymorpha*. Therefore, *M. leucophaeata* is more resistant to anti-fouling techniques than the freshwater *D. polymorpha*, as proven by Rajagopal et al. (1997a, 2003b, 2005a). A comparison of chlorine toxicity data with *M. leucophaeata*, *D. polymorpha* and *Mytilus edulis* shows that *M. leucophaeata* is the most tolerant species (Rajagopal et al., 2002e).

*M. leucophaeata* adults are smaller than those of *D. polymorpha* adults, which makes the fouling problems less severe in density. On the other hand, *M. leucophaeata* is a long-lived species in comparison to *D. polymorpha*, which means that the adult population will remain a problem in the conduits for a longer time, which can introduce more severe problems in time.

Knowledge on the cyclic presence of mussel larvae provides a basis for an ecologically and economically proper use of biocides (Relini, 1984). The strict timing of *M. leucophaeata* larvae in the harbour of Antwerp is an indication that to prevent new biofouling, a pointed dosage of biocides during the period of larval presence will be as effective as a continuous dosage throughout the year. This saving can lead to the exploration on the use of ecologically less harmful, but more expensive biocides. The long lifespan on the other hand states that even though larvae may be effectively combated, the adult population in the conduits will remain a non-combatable source of larvae for a long time.

In summary, *M. leucophaeata* is a slower invader in Europe (Van der Velde et al., 2010) than *D. polymorpha* in the U.S.. However once invaded, it is an even more severe fouling species than *D. polymorpha*, and as such it has to be taken in account that *M. leucophaeata* has most definitely the potential of becoming the brackish water equivalent of *D. polymorpha* in Europe.

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