Temperature dependent larval occurrence and spat settlement of the invasive brackish water bivalve *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae)

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ABSTRACT

Mytilopsis leucophaeata, an invasive bivalve species, causes fouling problems by settling on submerged constructions and in cooling water circuitsin brackish water. To predict spat fall we studied the larval occurrence and settlement of this species in the brackish Noordzeekanaal canal in the Netherlands for several years (1989-1992), while measuring water temperature, salinity and chlorophyll a levels. Larvae were collected monthly by means of a plankton net which was drawn across the whole width of the canal. Settled spat was collected from PVC panels exposed for one month. Larvae appeared for the first time in May or June, and reached maximum numbers in June or July, before disappearing in October, November or even December. The larval period started at a water temperature of 14 °C, reached maximum numbers at 19-23 °C and ended when the water temperature fell below 9 °C. No larvae were observed anymore until the temperature rose to 14 °C in the spring of the next year. Spat fall (June-November) was related to the water temperature in April. If the water temperature in April was lower than 12.5 °C, spat fall started in July, while if temperature was already higher in April, it started a month earlier. The spat fall period started at 15 °C, with maximum numbers at 20-24 °C, and ended when the water temperature dropped below 5 °C. Redundancy Analysis (RDA) demonstrated a strong relationship between larval and spat densities and water temperature.

Key words: dark false mussel, Conradôs false mussel, population dynamics, larvae, settlement, biofouling.

1. Introduction

Mytilopsis leucophaeata (Conrad, 1831), a highly euryhaline dreissenid bivalve species, is native to the Gulf of Mexico and the southern Atlantic coast of North America (Van der Velde et al., 2010a, Kennedy, 2011a,b). It is occurring at salinities of 0.2 to 22 (Practical Salinity Scale) (Verween et al., 2010).

The first record of the species in Western Europe was in the port of Antwerp (Belgium) by Kickx (in Nyst, 1835), and was described as *Mytilus cochleatus*. Thereafter the species was found near the port of Amsterdam (River Amstel, The Netherlands) in 1895 by R.F. Maitland (Scholten, 1919; Van Benthem Jutting, 1943). Although the first presence of the species in Antwerp is most likely due to shipping activities, introduction via ballast water is not likely as at that time dry ballast was used. Ballast water became in practice in the late 1870s (Carlton, 1985). Ballast water could have played a role in the population stocking and further dispersal of *M. leucophaeata*. The species can disperse by fouling on boats or transport in live wells or bilge systems, or veliger larvae surviving in transported water.

For a long time the distribution of *M. leucophaeata* in Western Europe was restricted to France, Belgium, the Netherlands and Germany (Van der Velde et al., 2010b). The species is currently expanding its range at accelerating rate from the North Sea to the British Isles (Oliver et al., 1998, Bamber and Taylor, 2002) the Baltic Sea (Laine et al., 2006, Dziubinská, 2011), the Mediterranean (Girardi, 2003), the Black Sea (Therriault et al., 2004) and the Caspian Sea (Heiler et al., 2010). The species does not show a continuous distribution along these coasts but is restricted to the brackish water areas in estuaries, ports, canals and lagoons where they can survive pollution (Van der Velde et al., 1992, Busch et al., 1995).

Mytilopsis leucophaeata is colonising all hard substrates such as ropes, boats, piles, pontoons etc. (Bergstrom, 2004) causing also problems in industrial cooling water systems (Rajagopal et al., 2002, Verween, 2007).

In view of the fouling problems caused by *M. leucophaeata*, we studied its larval and spat occurrence, densities and variability over several years in the brackish Noordzeekanaal Canal near the Velsen Power Station in the Netherlands, to get insight in this important part of the life cycle and to find indicators useful for prediction, prevention of mitigation in the cooling water circuits of power plants and industries.

2. Material and methods

2.1 Study area and environmental measurements

The Noordzeekanaal Canal connects the North Sea with the port of Amsterdam. The monitoring site was situated at 3 km distance from the sea (coordinates 52^0 27´ 51´´ North, 4^0 39´ 0´´ East). Water temperature (°C) was measured with a thermometer to the nearest 0.1 °C. Salinity (Practical Salinity Scale) was measured by a YSI model 33 S-C-T salinity meter. Chlorophyll a (µg l^{-1}) was measured according to procedures described by Parsons et al. (1984). These parameters were measured monthly in the surface water.

2.2 Collection of larvae

Larvae were collected monthly using a plankton net (diameter 29 cm, length 54 cm, mesh size 45 µm), which was drawn by a ferry across the whole width (275 m) of the canal during the 1989-1992 period. The plankton samples were fixed by adding formaldehyde to the canal water until a concentration of 0.8 % had been reached, transported to the laboratory in jars, and stored until analysis. Three larval subsamples were counted with a Sedgwick-Rafter counting cell. Average values were used to calculate the densities of larvae per cubic metre of water. All larvae could be ascribed to *M. leucophaeata* as at 3 km distance from the sea in the Noordzeekanaal Canal *M. leucophaeata* is the single bivalve species present occurring in high densities at all hard substrates. In this section of the canal the salinities (3-9) were too low for *Mytilus edulis* L., 1758, which is present at the North Sea side of the sluices (Van Haaren and Tempelman, 2006) and too high for *Dreissena polymorpha* (Pallas, 1771) which is present in the canal near the harbours of Amsterdam (Peeters, 1988, Van Couwelaar and Van Dijk, 1988, 1989, Directoraat-Generaal Rijkswaterstaat, 1993). During our investigations we identified more than 30,000 specimens of bivalves in all stages from the stones and panels near Velsen and all belonged to *M. leucophaeata*. Except for turbulence when ships pass by there is almost no current in the canal which makes it unlikely that larvae of *Dreissena polymorpha* or other bivalves occurring in very low numbers in other sections of the canal and side canals can drift to this place. In our tubes with permanent panels in the same years no other bivalve species than *M. leucophaeata* was found. The publications of Conn et al. (1993) and Ackerman et al. (1994) describing all larval stages of *M. leucophaeata* and *Dreissena* spp. were used for identification.

2.3 Collection of spat from PVC panels

Spat settlement was studied using 2 mm thick PVC panels (14.3 x 35 cm). Each settlement panel was placed in a 70 cm long PVC tube (open at both sides, diameter 14.3 cm) to create a less turbulent environment and to protect the panel from scouring and damage caused by large waves due to ships and storms. Both sides of the panel within the tube could be colonized (combined surface area 900 cm^2). The tube containing one panel for colonization, was attached with a stainless steel cable to the jetty near the ferry at a depth of about 75 cm, and was laid down on the stony bottom, on February 22nd 1989. Each month the panel that had been exposed for one month was collected and replaced by a new one during the period February 22nd 1989 until August 23rd 1990. A similar second tube with a panel was laid out on April 5th 1990 and this exposure experiment lasted until 28 August 1991. Individuals were counted in the laboratory on 16-900 cm^2 of panel area depending on the density of the spat and were expressed as numbers per square metre. Removed PVC panels were cleansed of overgrowth and reused on the next sampling date.

2.4 Statistical analysis

Larval and spat densities recorded during the years of observation were related to environmental parameters (chlorophyll a concentration, water temperature, salinity) and the sampling dates, comparing years, months and day length (time between sunrise and sunset, in hours), using Canoco for Windows v4.5 (ter Braak et al, 2002). To cope with the zero-values (no mussel larvae or spat found), data were log-transformed according to $y= \log(x+1)$. Redundancy analysis (RDA), a direct gradient analysis based on a linear response model (as the gradient length was found to be short: i.e. 1.41), was used to ordinate larval and spat densities and occurrences to the environmental parameters and to identify year-to-year variation. SigmaPlot for Windows 11.0 (2008) was used to calculate and plot figures and regression lines.

3. Results

Water temperature varied with the seasons and years (Figure 1A)(minimum temperature for the 1989-1992 period was 4.5 °C, maximum temperature was 23.9 °C). Day length and water temperature showed a linear correlation (regression line: $y = 6.874 + 0.402x$; N=48; $R^2=0.563$; $P<0.001$). Salinity fluctuated between 3.2 and 9.0 (Figure 1A). We found no influence of salinity fluctuations on larval appearance or spat fall. Chlorophyll a showed large peaks before the peak temperatures in 1989 and 1992 and after or during the peak temperatures in 1991, while low values were observed in 1990 (Figure 1A). Chlorophyll a peaks preceded the larval density peaks by one month. Shifting the chlorophyll a values foreward by one month resulted in a linear correlation between chlorophyll a and larval numbers (regression line: $y = 6.806 + 0.00111x$; N=47; $R^2=0.126$; P=0.014). Temperature and chlorophyll a showed a direct relation (regression line: $y = -0.473 + 0.674x$; N=48; $R^2=0.180$; P=0.003) just as day length and chlorophyll a content (regression line: $y = 10.948 + 0.158x$; N=48; $R^2=0.220$; P<0.001).

Larvae were first found in May (1989, 1990, 1992) or June (1991) (Table 1), and disappeared in October (1990, 1992) or November (1989, 1991). Peaks were observed in June (1989) and July (1990, 1991 and 1992) (Figure 1B). Day length and appearance of larvae were linearly correlated (regression line $y =11.316 + 0.000587x$; N=48; $R^2=0.307$; P<0.001). There was a correlation between the relative increases in the number of larvae (as a percentage of the maximum peak number in each year) and the temperature rise (linear regression line: $y= -105.3 + 8.7x$; n=14; $R^2 = 0.551$; P=0.002). Larval densities started to increase from temperatures of 14-19 °C, reaching maximum values at 19-23 °C. The percentages of larvae observed after the temperature peak were also correlated to falling temperatures in the 23-16 °C range (linear regression line: $y= -58.69 + 5.7x$; n=21; $R^2 = 0.384$; P=0.003). Below 16 °C, the numbers dropped rapidly, and between 13 and 9 °C the number of larvae remained at very low densities (Figure 2A). No larvae were observed below a temperature of 9 °C.

Spat fall occurred in the months of June, July, August, September, October and November (Figure 1B). The timing of the spat fall start was related to the water temperature in April (Table 1). If water temperature in April rose above 12.5 °C, spat fall occurred in June, while if water temperature remained below 12.5 °C in that month, spat fall was delayed to July. Spat appeared for the first time in June in 1990 and 1992, and in July in 1989 and 1991 (Table 1), and usually ended in November (1990, 1992). Spat fall appeared for the first time at a water temperature of 15 °C, reached a maximum level at a temperature range of 20-24 °C and stopped at a water temperature of 5 °C (Figure 2B). With rising temperatures, spat fall showed a sudden increase at 20 °C, while showing an irregular decrease with decreasing temperatures.

A RDA relating the densities of larvae and spat to the environmental characteristics demonstrated that both mussel larvae and spat densities were closely related to temperature (Fig. 3), while relations were also observed with chlorophyll a and day length, particularly for the larval densities. Spat densities were highly correlated with the month of August, but were also high in July and September, while larval densities were already increasing in June. The figure shows the differences between the years, with higher spat densities in 1990, a year with higher salinities in summer and autumn, whereas 1992 was a year with relative low spat densities.

4. Discussion and Conclusions

We found a water temperature threshold value for maturation of 12.5 °C in April. If the water temperature was higher in April, spat fall occurred in June, while at lower April temperatures, spat fall was delayed to July indicating that the water temperature in April was predictive of the timing of spat fall. Verween et al. (2005) mentioned 12 °C as the lowest threshold value for allowing gonad maturation, which is close to our predictive 12.5 °C.

Verween (2009) found that the chlorophyll a concentration was a significant determinant of gametogenesis when a time delay of two months was taken into account; this made chlorophyll a a significant factor governing the gametogenetic index and spawning. We found that the chlorophyll a peak preceded the larval density peak by one month. After correcting for a lag time we found a significant correlation. The availability of phytoplankton seems to be a trigger for the final maturation of the gonads and subsequent release of the larvae. The correlation between day length and the appearance of the larval peak is most probably a result of the availability of phytoplankton as food for the larvae, which in turn depends on the length of the day.

We found a high year-to-year variability in larval densities, with the highest values recorded in 1991, lower ones in 1989 and 1990 and the lowest in 1992. In 1992, these low values resulted in very low spat densities, while the highest ones were also recorded in 1991. Spat densities in 1989 were, however, unexpectedly low, while those in 1990 were very high. Larval densities were correlated to the rising and falling water temperatures. According to Siddall (1980), abundant settlement of spat in natural populations in Florida takes place two weeks after gamete release, when the temperature reaches 26 °C during spat fall. However, such high temperatures are normally not reached in temperate zones except in cooling water discharge areas.

Verween et al. (2005) found at Antwerp that spawning generally started at the end of May or early June and lasted five months. Water temperatures at the time the first larvae were detected ranged from 16.2 °C to 19.5 °C, and salinity from 2.6 to 4.9. According to these authors, no threshold condition for spawning seems to exist for *M. leucophaeata*. However, they suggest that a threshold temperature for gamete maturation may be 13 ± 1 °C, as larval presence ended at that temperature in November. We found that the first larvae appeared at a water temperature of 14 °C, while larvae were sometimes still present in Autumn at a temperature of 9 °C.

We sampled the larvae in the Noordzeekanaal on a monthly basis and found only one peak for each year over the 1989-1992 period, with first appearance in May or June and the last larvae present in October or November. Larval densities appeared to be related to day length, which suggests synchronization with food availability as indicated by the chlorophyll a content.

Our observations enabled us to prepare a schematic overview summarizing gonad development, larval occurrence, spat fall and relevant water temperatures during the year (Fig. 4). Our conclusion is that water temperature and day length are the driving forces behind the reproductive system of *M. leucophaeata*, where the day length is important for the production of the food (chlorophyll a) and the water temperature for all biological activities, like gonad development, larval appearance, spat fall and food production (chlorophyll a).

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References

Ackerman, J.D., Sim, B., Nichols, S.J., Claudi, R., 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves. Canadian Journal of Zoology 72, 1169-1179.

Bamber, R.N.,Taylor, J.D., 2002. The brackish water mussel, *Mytilopsis leucophaeta* (Conrad, 1831) (Bivalvia: Dreissenidae) in the river Thames. Journal of Conchology 37, 403-404.

Bergstrom, P., Carey, R., Hornor, S., Judy, C., 2004. Water quality & SAV improved in mesohaline Chesapeake Bay in 2004: Was this due to abundant dark false mussel? Poster presentation available at http://longislandsoundstudy.net/wp-content/uploads/2010/02/Bergstrom_DFMPOSTER120309FINAL.pdf
Accessed Sept 22nd 2010.

Busch, D., Schuchardt, B., Kettler, J., Steinweg, B., 1995. Die Verbreitung der Muschelarten *Dreissena polymorpha* und *Congeria leucophaeata* in der Weser und ihre Eignung für ein passives Schwermetallbiomonitoring. In: Gerken, B., Schirmer, M. (Eds.), Die Weser. Zur Situation von Strom und Landschaft und Perspektiven ihrer Entwicklung. Gustav Fischer Verlag, Stuttgart. Limnologie aktuell 6, 109-122.

Carlton, J.T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology, Annual Review 23, 313-371.

Conn, D.B., Lutz, R.A., Hu, Y.-P., Kennedy, V.S., 1993. Guide to the identification of larval and postlarval stages of Zebra mussels *Dreissena* spp. and the dark false mussel *Mytilopsis leucophaeata*. Publication New York Sea Grant Institute, State University of New York and Cornell University. 22 pp.

Directoraat-Generaal Rijkswaterstaat, 1993. Het Noordzeekanaal. Beschrijving toestand en ontwikkelingen 1976-1991. Nota nr. 93.017. 67 pp.

DziubiŒska, A., 2011. *Mytilopsis leucophaeata*, an alien dreissenid bivalve discovered in the Gulf of GdaŒsk (southern Baltic Sea). Oceanologia 53, 651-655.

Girardi, H., 2003. *Mytilopsis leucophaeata* (Conrad, 1831) (Bivalvia Dreisseniidae) dans le canal maritime dôAigues-Mortes au port du Grau du Roi (Gard). Documents Malacologiques 4, 47-48.

Heiler, K.C.M., Nahavandi, N., Albrecht, C., 2010. A new invasion into an ancient lake ï the invasion history of the dreissenid mussel *Mytilopsis leucophaeata* (Conrad, 1831) and its first record in the Caspian Sea. Malacologia 53, 185-192.

Kennedy, V.S., 2011a. The invasive dark false mussel *Mytilopsis leucophaeata* (Bivalvia: Dreissenidae): a literature review. Aquatic Ecology 45, 163-183.

Kennedy, V.S., 2011b. Biology of the uncommon dreissenid bivalve *Mytilopsis leucophaeata* (Conrad, 1831) in central Chesapeake Bay. Journal of Molluscan Studies 77, 154-164.

Laine, A.O., Mattila, J., Lehikoinen, A., 2006. First record of the brackish water dreissenid *Mytilopsis leucophaeata* in the northern Baltic Sea. Aquatic Invasions 1, 38-41.

Nyst, P.H.,1835. Mollusques. Bulletins de lôAcadémie Royale des Sciences et belles-lettres de Bruxelles II, 235-237.

Oliver, P.G., Holmes, A.M., Mettam, C., 1998. *Mytilopsis leucophaeta* (Conrad, 1831) [Bivalvia: Dreissenoidea]. A species new to the British fauna. Journal of Conchology 36, 13-18.

Parssons, T.R., Yoshiaki, M., Lalli, C.M.,1984. A manual of chemical and biological methods for seawater analysis. Pegamon Press, Oxford, pp. 1-173.

Peeters, E.H.H.M., 1988. Bodemfauna onderzoek in het Noordzeekanaal-komplex 1988. Rijkswaterstaat Directie Noord-Holland Nota ANW 88.27.

Rajagopal, S., Van der Gaag, M., Van der Velde, G., Jenner, H.A., 2002. Control of brackish water fouling mussel, *Mytilopsis leucophaeata* (Conrad) with sodium hypochlorite. Archives of Environmental Contamination and Toxicology 43, 296-300.

Scholten, J., 1919. Eenige aanteekeningen over de land- en zoetwater-molluskenfauna van Nederland. Bijdragen tot de Dierkunde 21, 67-71.

Siddall, S.E., 1980. Early development of *Mytilopsis leucophaeta* (Bivalvia: Dreissenacea). The Veliger 22, 378-379.

SigmaPlot for Windows Version 11.0 (Build 11.0.0.77) Copyright © 2008 Systat Software, Inc. 1735 Technology Drive Suite 430 San Jose, CA95110, U.S.A.

Ter Braak, C.J.F., Smilauer, P., 2002. CANOCO reference manual and CanocoDraw for Windows Userǿs guide: Software for Canonical Community Ordination (ver.4. 5), Microcomputer Power, Ithaca, N.Y., 500 pp.

Therriault, T.W., Docker, M.F., Orlova, M.I., Heath, D.D., MacIsaac, H.J., 2004. Molecular resolution of the family Dreissenidae (Mollusca: Bivalvia) with emphasis on Ponto-Caspian species, including first report of *Mytilopsis leucophaeata* in the Black Sea basin. Molecular Phylogenetics and Evolution 30, 479-489.

Van Benthem Jutting, T.,1943. *Congeria* Partsch (1836). In: Fauna van Nederland. Afl XII. Mollusca C11 Lamellibranchiata. pp. 210-214.

Van Couwelaar, M., Van Dijk, J., 1988. Onderzoek oeverfauna Noordzeekanaal 1987. Stichting Ecotest, Amsterdam; Rijkswaterstaat Directie Noord-Holland, Haarlem. nota ANW 88.10. 42 pp.

Van Couwelaar, M., Van Dijk, J.. 1989. Onderzoek oeverfauna Noordzeekanaal, zijkanalen en havens ï 1988. Stichting Ecotest, Amsterdam. Rijkswaterstaat Directie Noord-Holland afd. Waterhuishouding (ANW). nota ANW 89.17. 50 pp.

Van der Velde, G., Hermus, K., Van der Gaag, M., Jenner, H.A., 1992. Cadmium, Zinc and Copper in the body, byssus and shell of the mussels, *Mytilopsis leucophaeta* and *Dreissena polymorpha* in the brackish Noordzeekanaal of the Netherlands. In: Neumann D, Jenner HA (Eds.), The Zebra Mussel *Dreissena polymorpha*. Ecology, biological monitoring and first applications in the water quality management. Gustav Fischer Verlag, Stuttgart. Limnologie aktuell 4, 213-226.

Van der Velde, G., Rajagopal, S., Bij de Vaate, A., 2010a. From Zebra mussels to Quagga mussels: an introduction to the Dreissenidae. Chapter 1. In: Van der Velde, G., Rajagopal, S., Bij de Vaate, A. (Eds.), The Zebra Mussel in Europe. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim. pp. 1-10.

Van der Velde, G., Rajagopal, S., Bij de Vaate, A. (Eds.), 2010b. The Zebra Mussel in Europe. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim.

Van Haaren, T., Tempelman, D., 2006. De tweekleppigen van het Noordzeekanaal (Mollusca: Bivalvia). Nederlandse Faunistische Mededelingen 24: 89-115.

Verween, A., 2007. Biological knowledge as a tool for ecologically sound biofouling control: a case study of the invasive bivalve *Mytilopsis leucophaeata* in Europe. Thesis,University of Gent.

Verween, A., Vincx, M., Degraer, S., 2007. The effect of temperature and salinity on the survival of *Mytilopsis leucophaeata* (Mollusca, Bivalvia): The search for environmental limits. Journal of Experimental Marine Biology and Ecology 348, 111-120.

Verween, A., Vincx, M., Degraer, S., 2009. Seasonal variation in gametogenesis and spawning of *Mytilopsis leucophaeata*, an invasive bivalve in Europe. Journal of Molluscan Studies 75, 307-310.

Verween, A., Vincx, M., Degraer, S., 2010. *Mytilopsis leucophaeata*: the brackish water equivalent of *Dreissena polymorpha*? A review. Chapter 3. In: Van der Velde, G., Rajagopal, S., Bij de Vaate, A. (Eds.), The Zebra Mussel in Europe. Backhuys Publishers, Leiden/Margraf Publishers, Weikersheim, pp. 29-43.

Verween, A, Vincx, M., Mees, J., Degraer, S., 2005. Seasonal variability of *Mytilopsis leucophaeata* larvae in the harbour of Antwerp: implications for ecologically and economically sound biofouling control. Belgium Journal of Zoology 135, 91-93.

Figure legends

Fig. 1 A. Water temperature (°C), chlorophyll a (ε g l^{-1}), salinity in the surface water of the Noordzeekanaal and day length (hrs) near Velsen (km 3) in the 1989-1992 period. **B.** Numbers of larvae of *Mytilopsis leucophaeata* collected per cubic metre of water each month and spat (0-2 mm) of *Mytilopsis leucophaeata* settled each month per square metre of the PVC panels in the Noordzeekanaal near Velsen during 1989-1992.

Fig. 2. Relative increase in the number of larvae (**A1**) and spat (**B1**) of *Mytilopsis leucophaeata* with rising water temperatures, and decrease in the number of larvae (**A2**) and spat (**B2**) with falling water temperatures over the years 1989-1992 in the Noordzeekanaal near Velsen. Peak maximum occurrences of larvae or spat for each year were set at 100%.

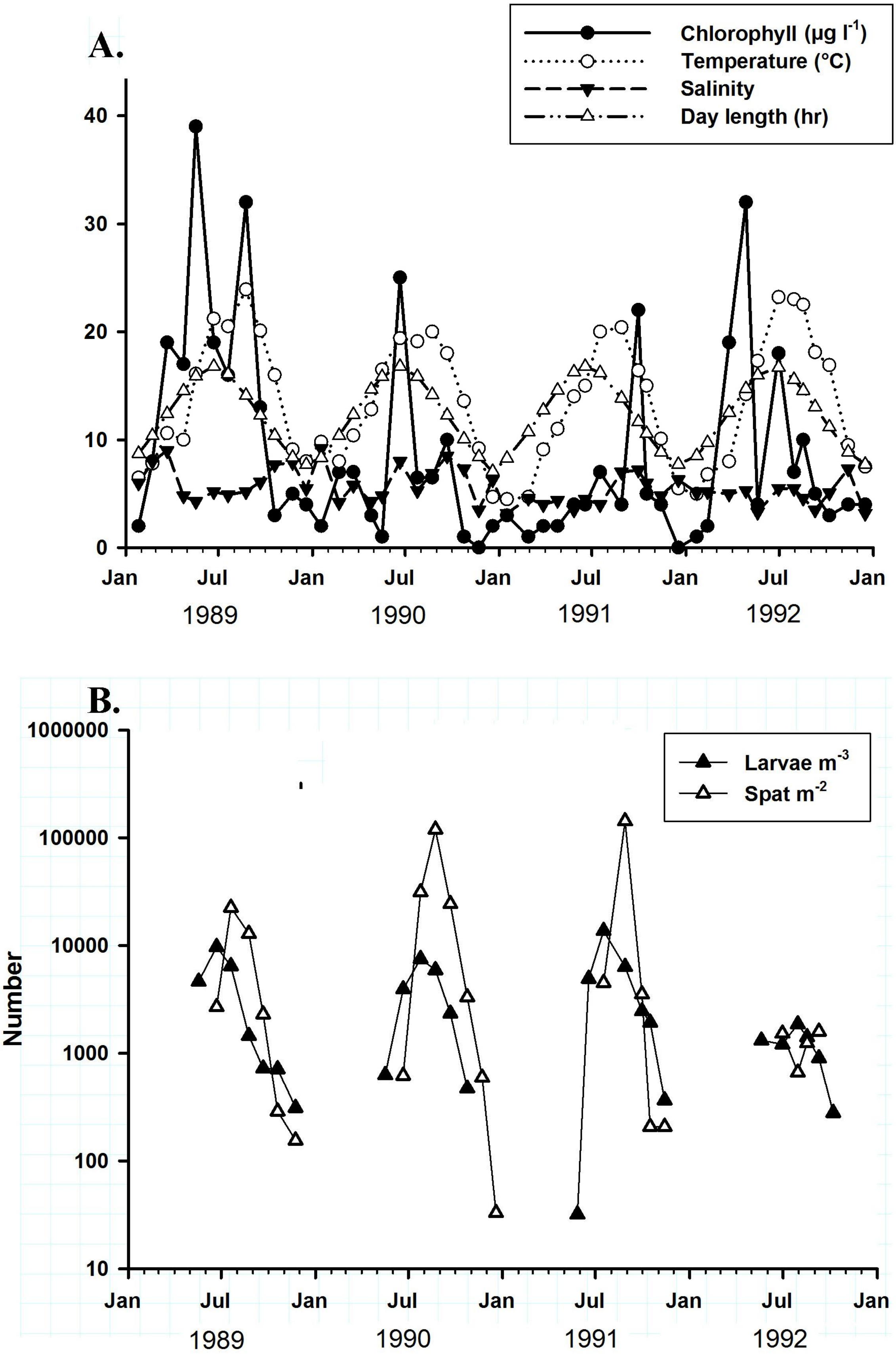
Fig. 3. Ordination (RDA) of *Mytilopsis leucophaeata* larvae and spat densities to environmental parameters (temperature, chlorophyll a, salinity and day length), sampling years and sampling months.

Fig. 4. Schematic overview of larval occurrence and spat settlement of *Mytilopsis leucophaeata* and relevant water temperatures and day length during the year. See also [1]Verween et al. (2005).

Table 1. Water temperature (°C) at the time of arrival and disappearance of *Mytilopsis leucophaeata* larvae in the water column and spat fall on PVC panels in the Noordzeekanaal.

	1989	**1990**	**1991**	**1992**
March	10.6	10.4	9.1	8.0
April	10.0	12.8	11.0	14.2
May	16.1	16.5	14.0	17.3
June	21.2	19.4	15.0	23.2
July	20.5	19.1	20.0	23.0
First larvae	Jun 22th	May 17th	May 27th	May 20th
Last larvae	Nov 23th	Oct 24th	Nov 13th	Oct 7th
First spat fall	Jul 20th	Jun 14th	Jul 17th	Jun 30th
Last spat fall	Dec 20th	Nov 22th	Dec 17th	Nov 13th

Figure 1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Chlorophyll (µg l-1)
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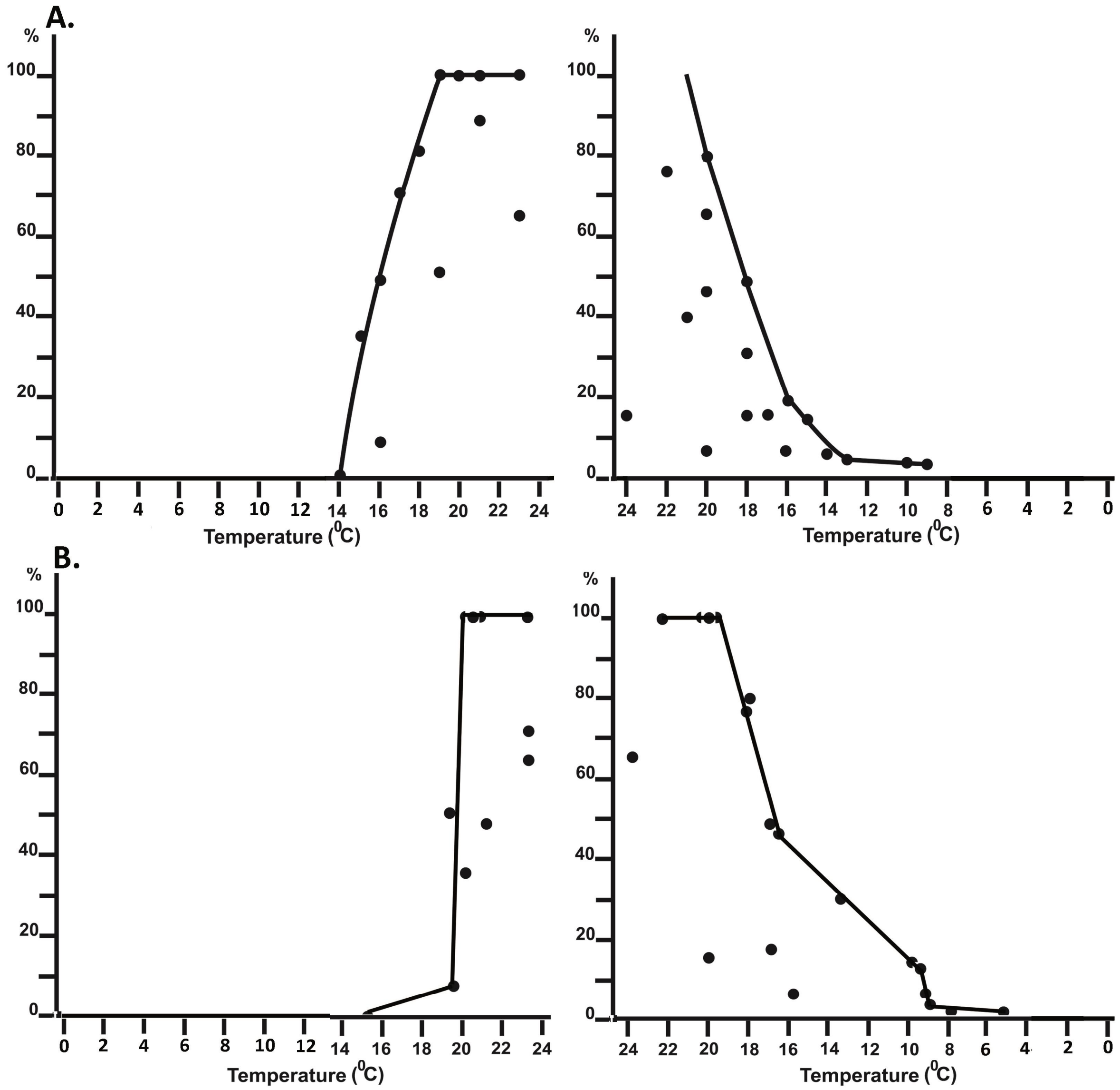
Figure 2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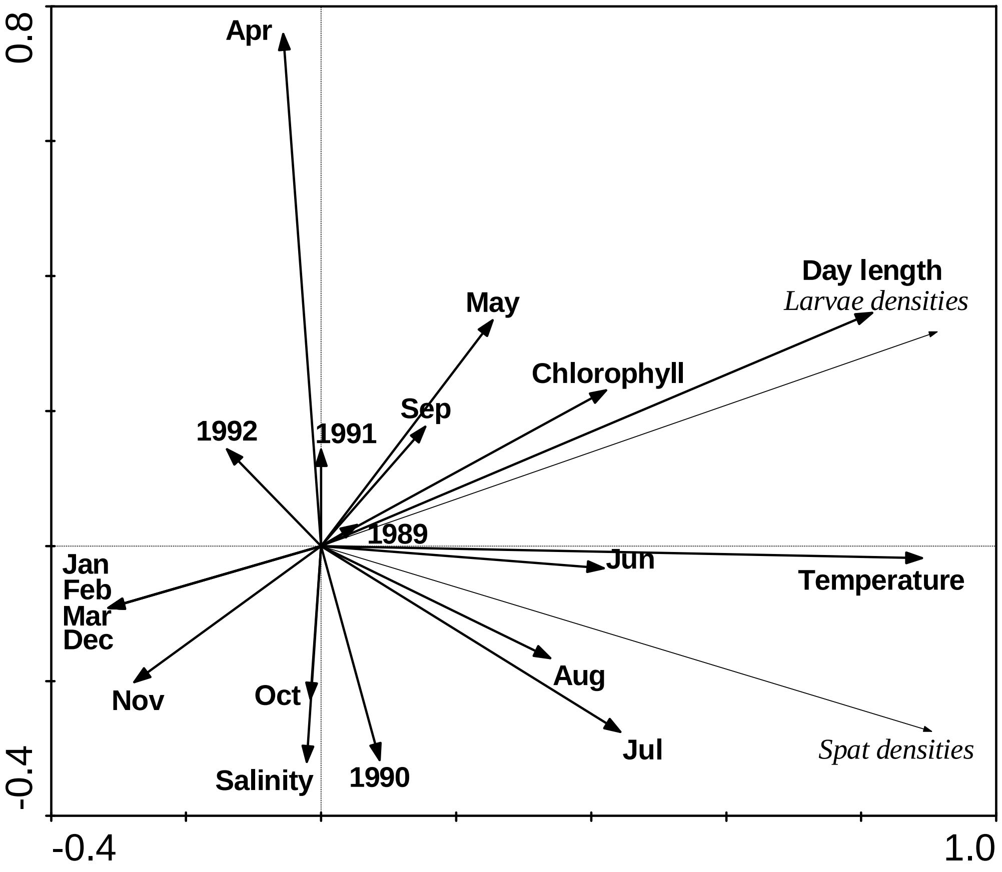
Temperature (0C)

Figure 3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Spat densities
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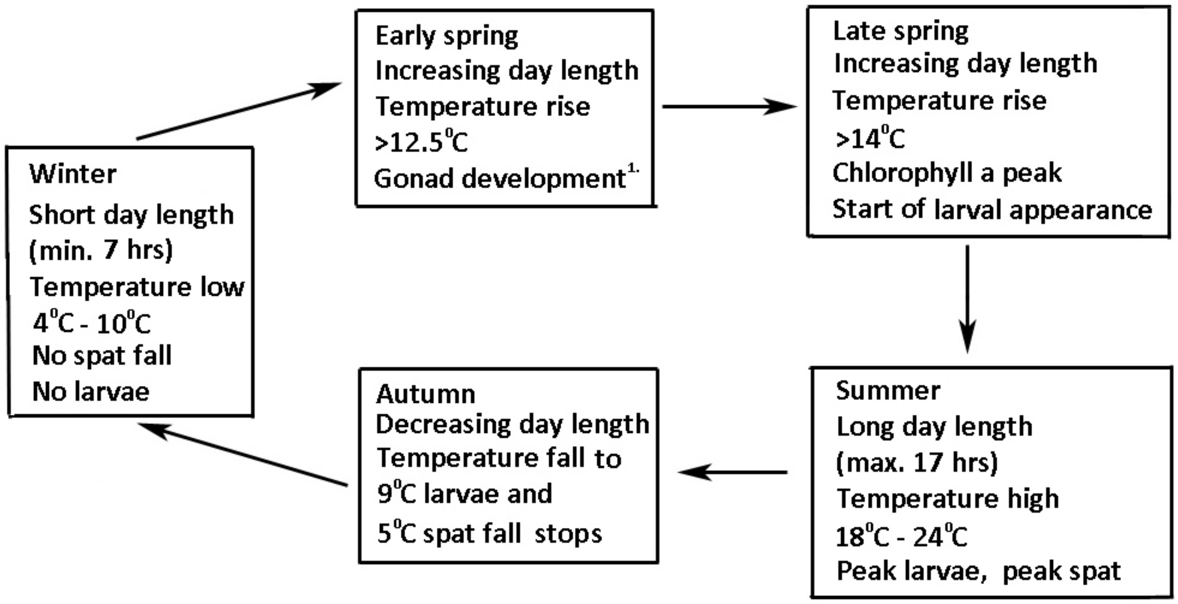
Figure 4


Winter
Short day length
(min. 7 hrs)
Temperature low
4°C - 10°C
No spat fall
No larvae
Early spring
Increasing day length
Temperature rise
>12.5°C
Gonad development1.
Late spring
Increasing day length
Temperature rise
>14°C
Chlorophyll a peak
Start of larval appearance
Summer
Long day length
(max. 17 hrs)
Temperature high
18°C - 24°C
Peak larvae, peak spat
Autumn
Decreasing day length
Temperature fall to
9°C larvae and
5°C spat fall stops