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How do Currents Influence the Settlement of Zebra Mussels (*Dreissena polymorpha*) in the Szczecin Lagoon?

Christiane Fenske

Ernst-Moritz-Arndt Universität Greifswald, Zoologisches Institut & Museum,
J.S. Bachstraße 11-12, D-17489 Greifswald

Abstract

Unlike most freshwater bivalves, zebra mussels *Dreissena polymorpha* PALLAS) have free swimming larvae and are thus dependent on water currents to guarantee the spreading of their offspring. Although planktonic, the larvae are able to carry out some directed movements. This paper presents investigations carried out in the Szczecin Lagoon, testing the settlement of larvae on different materials at three sites. Zebra mussel larvae preferred the central part of the lagoon for settlement and favoured horizontal over vertical orientation. The rank order referring to number of settled mussels was net > wood > stones > mussel shells > PVC.

Water current velocity in the crucial phase was usually very low (<10 cm/s), i.e. not above the limit for settlement. Therefore, other parameters must be involved as well. Two factors are discussed in particular: 1) salinity, and 2) sensory capacities of larvae, linked to the question of their capability of choosing where they settle.

1. Introduction

Zebra mussels (*Dreissena polymorpha* PALLAS) live in aggregates ("mussel beds") and attach themselves to conspecifics or other materials with the help of their sticky byssus threads. These have a diameter of approx. 150 μm and consist mainly of 3.4 dihydroxyphenylalanine. The mussel clumps form an important habitat for a variety of invertebrate species living in the Szczecin Lagoon as most of the ground is covered with mud in which only very few species can live. The highest biodiversity as regards macrofauna in the Szczecin Lagoon is found on mussel beds.

The map in Fig. 1 shows the distribution of zebra mussels, estimated by videographic recording (Andres 1993) and bottom sampling over several years (Günther 1998). Altogether, they cover approximately 20% of the bottom, mostly on the sandy slopes at about 2 m deep, near the shore. Only one mussel bed is situated in the central basin. The mussels there were probably able to settle at that point because of a peak in the prehistorical bottom. Most of this is covered with mud that reaches a thickness of 3–4 m. Zebra mussels usually prefer hard substrates. However, recent investigations show that American populations of *Dreissena polymorpha* also invade muds (Berkman et al. 1998).

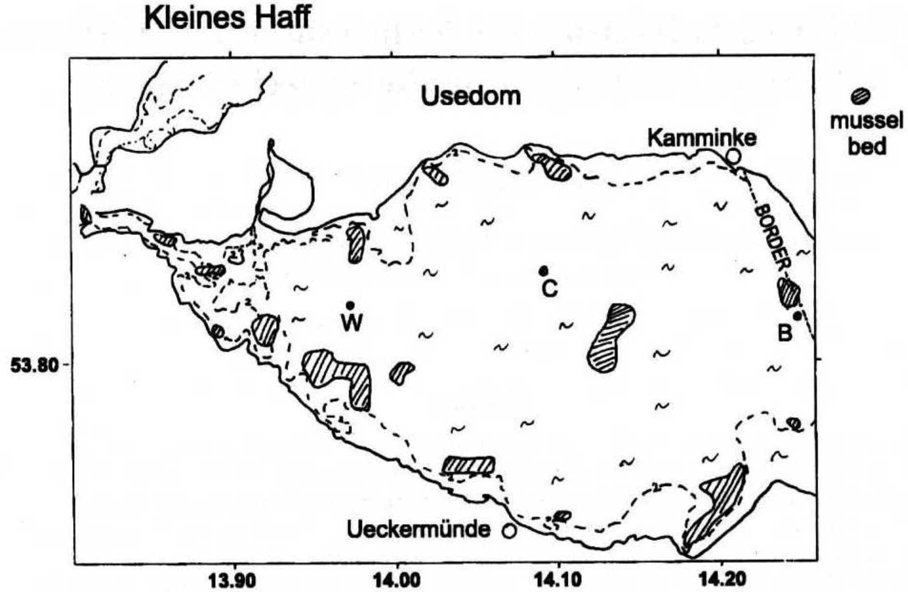


Fig. 1. Investigation area: Kleines Haff (part of the Szczecin Lagoon), three experimental sites: W = western station, C = central station (Meta platform), B = border station. Hatched areas indicate mussel beds

Before their sedentary life, mussels start as free-swimming larvae and spend about 5–6 weeks in the plankton (Fig. 2). When they have developed a little shell they start to search for a suitable substrate and attach themselves with their byssus threads (Korschelt 1891, 1892, Meisenheimer 1899, 1901, Sprung 1987, 1989, 1993).

This paper describes experiments to discover the preferences of larvae to settle on specific materials or at special places within the Szczecin Lagoon.

Currents are one very important factor in determining the settlement of *Dreissena polymorpha*, however, other parameters such as salinity and substrate also play a role.

2. Material & Methods

The investigations were carried out in the western part of the Szczecin Lagoon, also called Oderhaff or Kleines Haff (53.80°N, 14.10°E). Settlement was tested over two years (1998 & 99) at three different sites (Fig. 1). Five different materials were tested: wood, stone (bricks), mussel shells, fishing net, solid PVC.

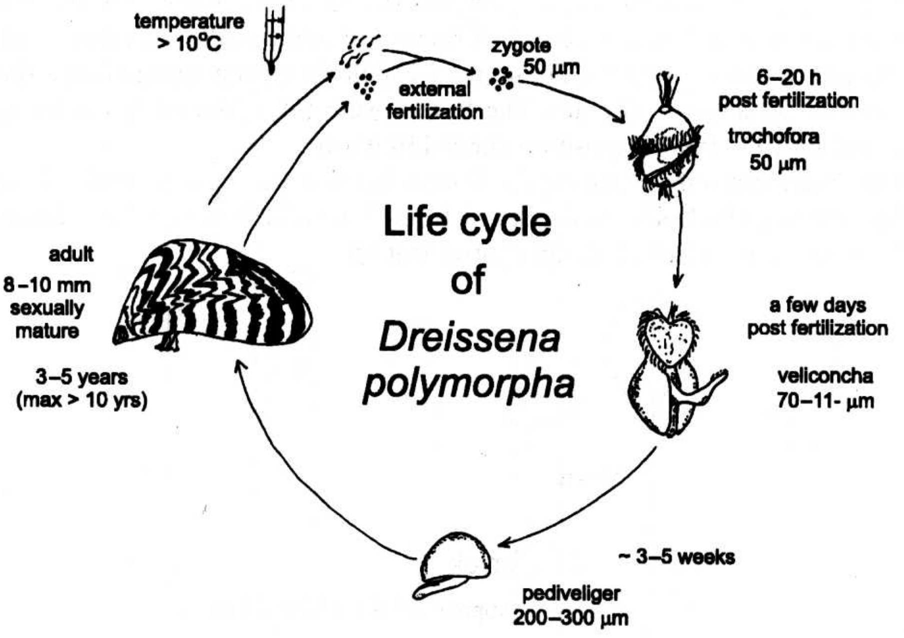


Fig. 2. Life cycle of the zebra mussel (*Dreissena polymorpha*)

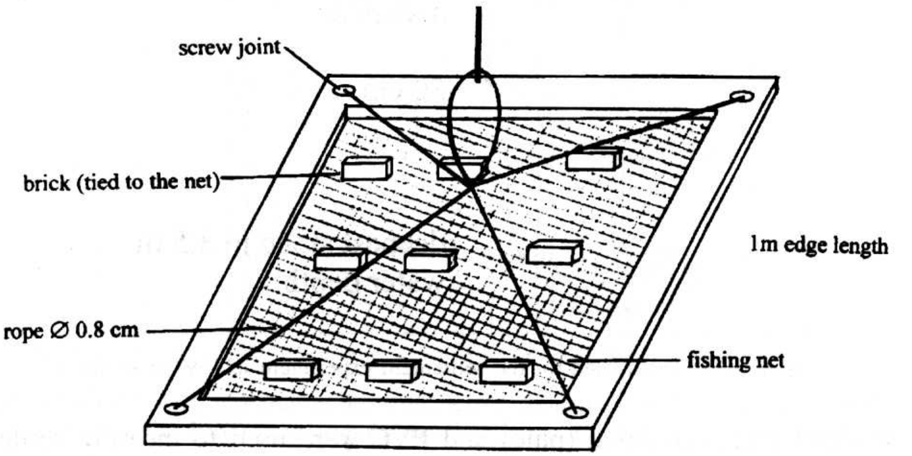


Fig. 3. One of 10 wooden frames used for the settlement experiment in 1998 at stations B and C

On July 23, 1998 10 wooden frames (Fig. 3) were deployed in the lagoon: 2 at the border station, 8 at the Meta platform (station centre). The area in the middle of the 1 m^2 large frames was covered with fishing nets, and on these, 9 bricks were attached with strong dederon (nylon) threads in each frame. On one of the frames at the border station, there were only 4 bricks but additionally, 622 mussel shells from *Arenomya (Mya) arenaria*. These mussel shells had been stringed on a thread that was then attached to the net. The frames were taken out of the water again on November 10th, 1998 (exposition time: 110 days).

Bricks were not only tested on the frames but also on separate chains (Fig. 4) thereby exposing the bricks at depths of from 2 m to 3.50 m at 50 cm distances. 5 such chains were attached at the central station.

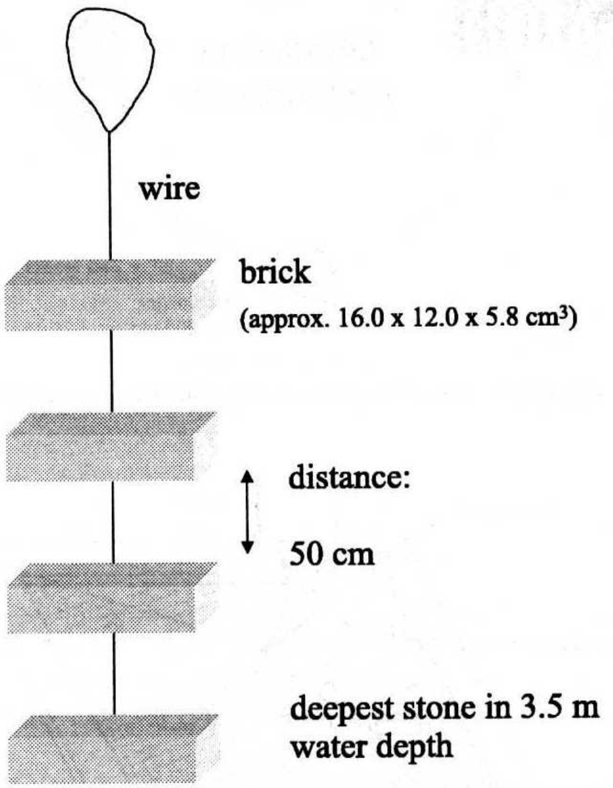


Fig. 4. Stone chain used for the settlement experiment in 1998 at station C

In 1999, plates of wood (pine) and PVC were used to measure settlement. Altogether, 36 wooden plates and 72 PVC plates were brought in. The plates were arranged in horizontal and vertical chains by sewing them to the cords. Three chains with horizontal plates and three with vertical plates were exposed in depths of from 1 m down to 3.50 m at a distance of 50 cm (Fig. 5). The plates were deployed near the western end of the lagoon (PVC) and at the central station (PVC and wood) (Fig. 1). The experiment started on July 16th, 1999 and ended on November 8th, 1999 (exposition time: 115 days).

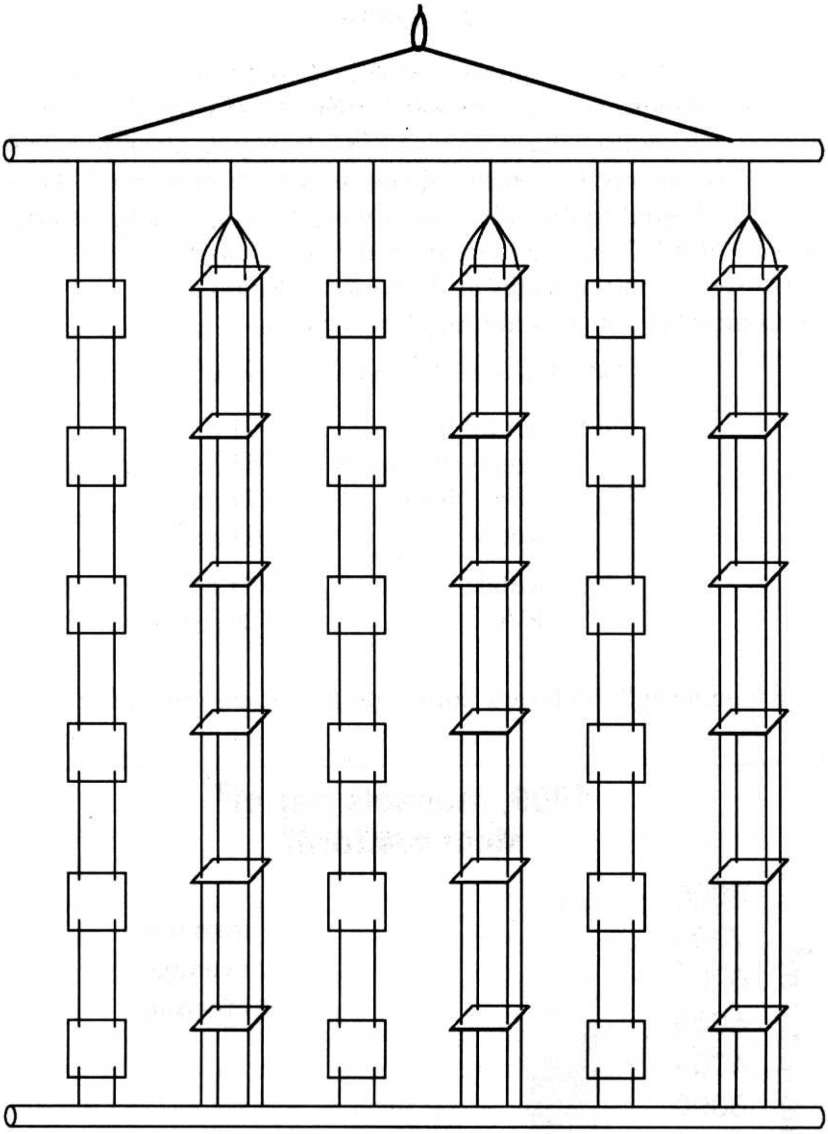


Fig. 5. Plates (15 × 15 cm) used in the settlement experiment in 1999 at stations W and C. Plates (either wood or PVC) were arranged between heavy iron bars and deployed in depths of from 1.00 to 3.50 m

After retrieving the materials offered for settlement, mussels that had settled on them were counted and measured.

3. Results

Not only numerous *Dreissena* mussels had settled on the materials but also another species: *Cordylophora caspia*, a hydrozoan polyp. This polyp also finds it difficult to attach to very smooth surfaces such as PVC. It may be a competitor for space, but it could also enhance settlement of *Dreissena* by "roughening" the surface.

The counts showed that in both years mussels preferred the central station. In the year 1999, 8277 mussels settled on the plates at the central station while none (zero!) settled on the plates at the western station.

The maximum abundances are listed in Table 1.

Table 1. Maximum abundances of mussels

1998	net on frames	15771 /m^2
	stones on frames	7955 /m^2
	stone chains	4574 /m^2
	wood	9021 /m^2
1999	wood	7873 /m^2
	PVC	4526 /m^2

Mussels significantly preferred horizontal to vertical orientation (Fig. 6)

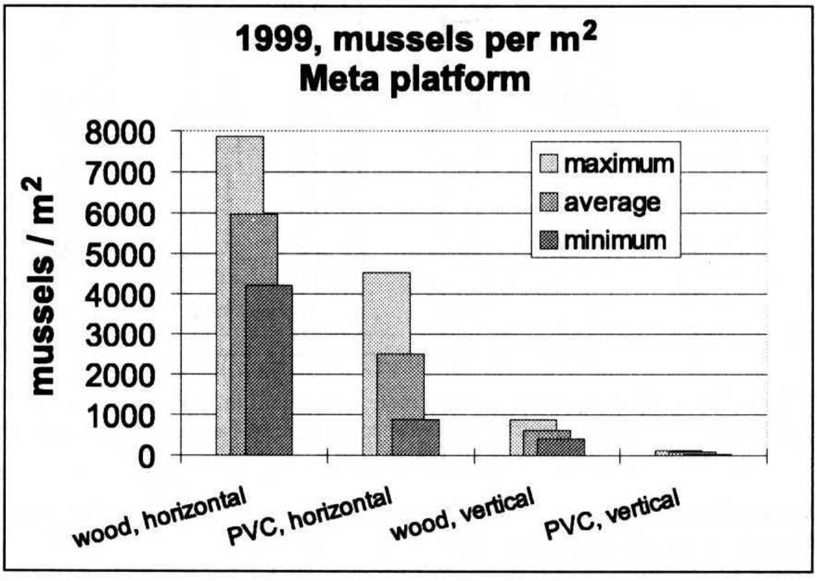


Fig. 6. Settlement at the central station (Meta platform) in 1999. Horizontal wooden plates were most attractive for *Dreissena polymorpha*

Settlement was highest on the fishing nets in the frames (average of 7358 mussels/m^2) This might have been enhanced by concomitantly settling of hydroid polyps (*Cordylophora caspia*).

As regards the material, there was a significant preference for wood over PVC (Table 1). They settled preferably on the upper side of plates or stones.

In both years, there was no significant difference between the depths (Tables 2 & 3).

Table 2. Pearson correlation for the settlement experiment at the central station in the Kleines Haff in 1999 (PVC plates vs. wooden plates, horizontal vs. vertical orientation, different depths; $n = 71$)

Material	Correlation result	Significance level
PVC vs. wood	−0.382 ∗ ∗	$p<0.001$
horizontal vs. vertical	−0.639 ∗ ∗	$p<0.0001$
depth (1.00 m to 3. 50 m)	0.072	$p = 0.551$ (not significant)

Table 3. Pearson correlation for the settlement experiment at the central station and border station in the Kleines Haff in 1998 (different depths (2–4 m); $n = 13$)

Material	Correlation result	Significance level
stones on chains ($n = 13$)	−0.061	$p = 0.843$ (not significant)
stones on frames ($n = 46$)	0.233	$p = 0.120$ (not significant)
wood ($n = 8$)	0.067	$p = 0.874$ (not significant)

For 1999, only the central station could be taken into account, as there were no mussels on the PVC plates at the western station. Figure 8 shows the settlement in different depths. The average settlement was highest at 2.00 m (wood) or 2.50 m (PVC).

The *Mya*-mussel chain, offered as a "pseudo-natural surface" at depth of 2 m in 1998 did not seem to be very attractive for *Dreissena polymorpha* larvae (Fig. 7). The total area of *Mya* mussels was estimated using the equation of an ellipse, doubling the result in order to take into account the inner and outer surface of the shell (length * height * 0.7854 * 2). Random samples of 50 *Mya* mussels (out of 622) were measured for shell length and height, leading to an average area of 1825.72 mm^2 per shell. The whole mussel chain therefore offered 1.14 m^2. We found 1211 newly settled *Dreissena* mussels on the *Mya* shells, which equals 1066/m^2.

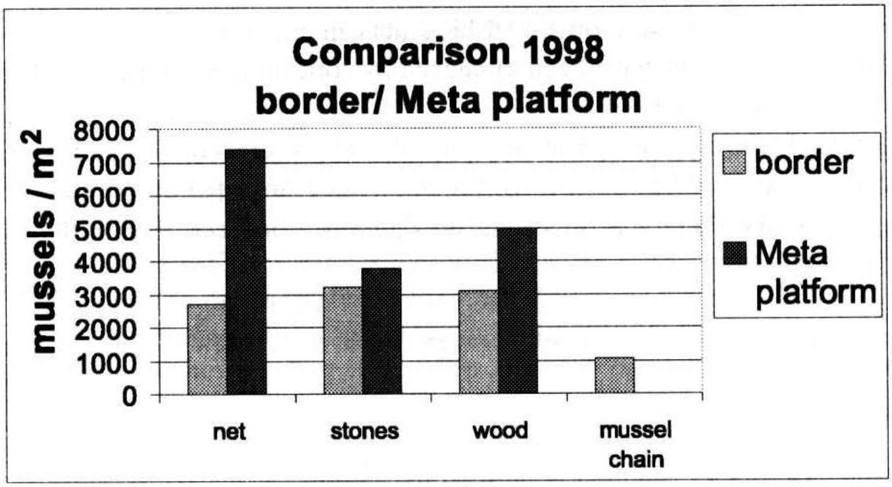


Fig. 7. Average settlement in 1998, comparing stations B (border) and C (Meta platform)

4. Discussion

Besides the main question "How do currents influence the settlement of *Dreissena polymorpha*?" the following questions should be addressed in brief:

- Where do the larvae come from?
- Are they able to choose where they settle?
- What is the current velocity?
- Which current directions prevail in the phase of potential settlement?
- Does wind play an important role?
- Where are the larvae - near the bottom, at the surface, everywhere in the water?
- Do the larvae influence each other in the process of settlement (can they attract conspecifics)?)
- Is salinity the most important factor for settlement in the Szczecin Lagoon?

The mussel larvae have a size of approx. 200–300 μ before settling (Fig. 2). They are then about 5–6 weeks old and have to find a suitable substrate to settle on. Many factors are known to influence the settlement of invertebrate larvae:

- water currents
- sediment, surface texture, contour
- salinity
- oxygen conditions
- colour of the underground

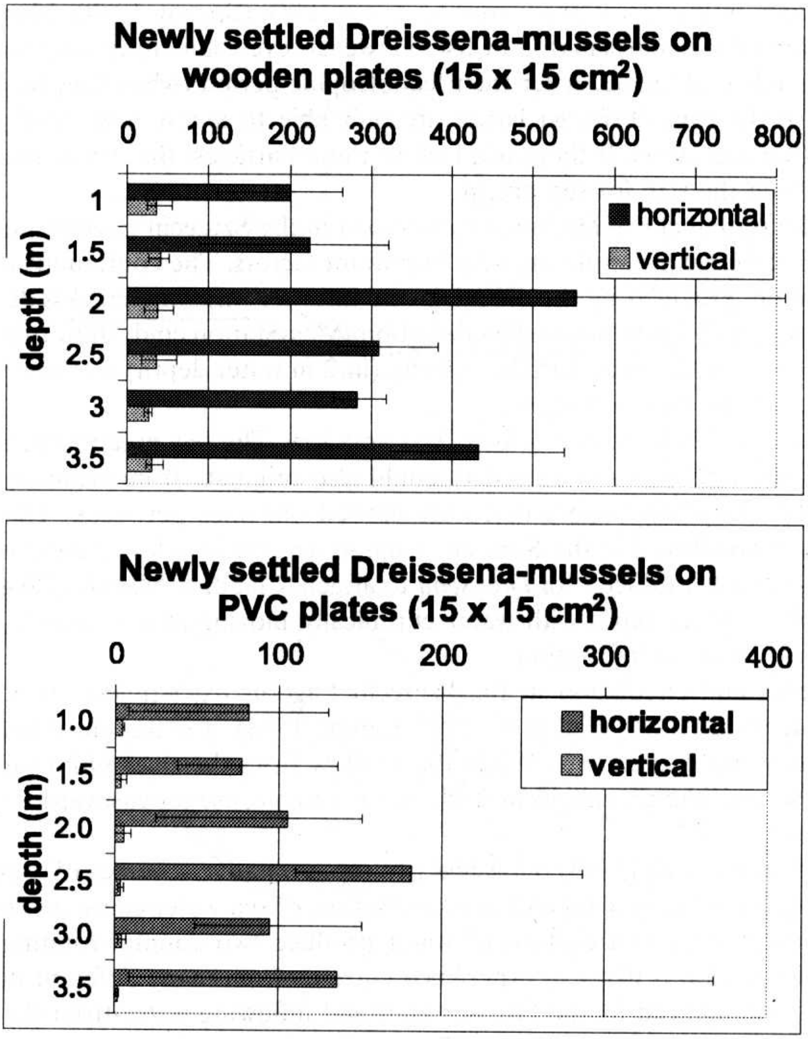


Fig. 8. Comparison of settlement in 1999 at different depths. Bars indicate maximum and minimum settlement (wooden plates: $n = 3$, PVC plates: $n = 6$). Note the different scales of the x-axes!

- (bacterial) films
- light
- gravity
- chemical factors

(Knight-Jones & Crisp 1953, Crisp 1974, Larman & Gabott 1975, Rittschof et al. 1984, Wethey 1984, Yule & Crisp 1983, Mullineaux & Butman, Dineen & Hines 1994, Keough & Raimondi 1996, Chabot & Bourget 1998).

Mortality in the larval phase may be up to 100% (Sprung 1989). Many larvae serve as food for other plankton or fish. However, even starvation may be a factor limiting survival of larvae. After their lecitotrophic period (when they feed on the reserves of the egg) *Dreissena* larvae are only able to ingest very small particles (1–4 μ) (Sprung 1989). If there is a lack of these particles, the larvae may not be able to attain the size for settlement.

For the settlement of *Dreissena polymorpha* in the Szczecin Lagoon, water currents and sediment structure are very important factors. The continuous measurements, kindly provided by the GKSS in the internet http://meteo.gkss.de/cgi_bin/MessStation.cmd http://meteo.gkss.de/cgi-bin/MessStation.cmd, show that in 1999, at both experimental sites, current velocity (in 2 m water depth) was always below 100 cm/s, usually even <10 cm/s.

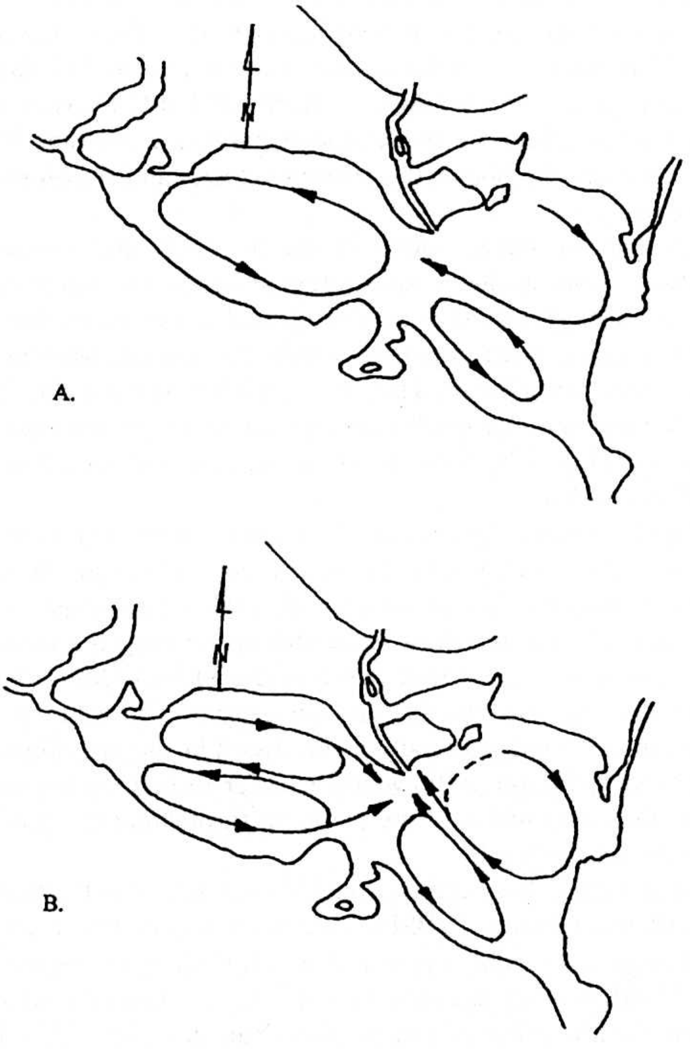
Similarly in 1998, current velocity was very low. The few exceptions, when for a short while 100 cm/s was exceeded, could also originate from cleaning procedures of the measuring probes that were carried out once per week. The current velocities encountered in the Szczecin Lagoon lie clearly below critical velocities that would make it difficult for *Dreissena* to attach. Claudi & Mackie (1994) report that small diameter pipes with water chronically moving at less than 2 m/s, are particularly prone to infestation.

Currents and circulation in the Szczecin Lagoon react quickly to local and small scale wind fields (Wolf et al. 1998, Lampe 1998), it is therefore not easy to model the water movements. While the outflow from the river Odra pushes the water westward, the prevailing westerly winds often cause an eastward movement of the water.

Robakiewicz et al. (1993) published two representative schemes of water circulation (Fig. 9): western wind and intensive inflow of sea water cause one big eddy; while western wind and outflow of water produce two counter-rotating eddies. The border station is likely to experience currents from many different directions as it is also influenced by the Grosses Haff and inflowing water from the Świna.

Moreover, currents can have different directions at the surface and at the bottom. *Dreissena* larvae may start their larval life in "deeper waters", but in the shallow Szczecin Lagoon (average depth 3.7 m (Meyer et al. 1998)) it can be assumed that they are soon well distributed and not located exclusively in one layer. It has been reported that *Dreissena* larvae carry out vertical migrations (Einsle & Walz 1972, Siller 1983, quoted after Sprung 1993). While larvae come to the surface at dusk, they prefer 5 m depth at noon. Although these observations were carried out in deeper waters, these migrations can also be assumed for the Szczecin Lagoon.

However, newly settled mussels can be used as indicators, summing up the recruitment success over the year. It is important to differentiate between settlement and recruitment (definitions based on Mackie & Schloesser 1996):



A.

B.

Fig. 9. Scheme of water circulation in the Szczecin Lagoon (after Robakiewicz et al. 1993)
A – western wind and intensive inflow of sea water, B – western wind and outflow of water

settlement = transition from the pelagic (i.e. free-swimming) to the benthic stage (on the sediment), including attachment and morphological changes;

recruitment = survival after a certain time (settlement combined with post-settlement mortality); the investigator determines time or size for successful recruits.

Supposing that larvae are mainly transported passively one can estimate where they might have come from. But even the low current velocity of 10 cm/s means that larvae could travel as far as 8.64 km per day. Thus, they could traverse the Kleines Haff from the border to the western end in 3–4 days. The typical sinking velocity of planktonic larvae is 0.001–0.01 m/s (Massel 1999), but the actual settlement is influenced by the roughness of the bottom. The rougher the material to settle on, the higher the friction velocity and the shorter the average time of settlement.

The time that the larvae spend in the plankton varies greatly, depending on temperature, food, available substratum etc.; but the minimum time is 1–2 weeks. The animals that settled on the offered materials at the three stations could therefore come from anywhere within the lagoon. Moreover, they could also originate from the Grosses Haff or even River Odra itself. It is planned to carry out calculations for a small scale spread of larvae for short time periods with a model developed by Schernewski et al. from the Institute for Baltic Sea Research, Warnemünde.

There may be several "generations" of larvae in the plankton. Piesik (1983) recorded three peaks for a river Odra channel. Although the last peak (August/September) had the lowest number of settling postveligers, he found that these "late-settlers" were the most successful in surviving the winter.

Due to its shallowness (average depth of the Kleines Haff: 3.7 m), the lagoon is usually well mixed and contains enough oxygen. The water is eutrophic and should offer enough food, especially as the trend in the last 30 years led to ever smaller plankton (Schiewer 1995) which is easier to take up for mussels.

However, the composition of the plankton throughout the year (predators vs. producers) was not analysed.

Chemical attraction has been thoroughly investigated in barnacles and specific "barnacle settlement factors" (BSF) have been found. But recent experiments showed that high settlement was not always linked to places treated with BSF (Hills et al. 1998). Usually glycoproteins are the substances used in several taxonomic groups for attraction of conspecifics (Yule & Crisp 1983). However, such a specific attractant has not been described for *Dreissena polymorpha*.

Experiments in other places showed that *Dreissena* does not necessarily need a specific substrate for settlement (Stanczykowska 1964), yet they prefer to settle on wood or bricks and avoid toxic material such as zinc or copper.

The larvae must be able to sense surfaces on which they can settle. They probably use both tactile and chemical cues.

But some results are contradictory: Sprung (1993) describes PVC as intensively settled on, while in my experiments, only a few *Dreissena* larvae chose this substrate.

Under natural conditions, however, one has to assume strongly varying results as regards the developing time, choice of substrate etc. One example is given for barnacles by Knight-Jones & Crisp (1953) who describe that the rate of settlement may vary, even if the supply from the plankton is constant.

The preference to settle on horizontal plates, especially on the upper sides, could result from slightly higher current velocities at the vertical plates. If we assume the currents to flow horizontally in general, mussels have more time to attach on upper sides of horizontal plates due to gravity.

As the larval stage is the most sensitive one in the development of *Dreissena polymorpha*, another key factor for settlement is salinity. In the Kleines Haff the average salinity ranges between 0.5 and 1.1 ppt. The incipient lethal salinity for post-veliger larvae is nearly 2 ppt (Kilgour et al. 1994). *Dreissena* originates from the brackish waters of the Caspian and Aral Seas (Babak 1983, Zhadin 1952, quoted after Ludyanskiy 1993) and the adults might even be able to tolerate up to 10 ppt, then again not only salinity is important, but also the ionic composition of the water. The Caspian waters are richer in calcium and sulphate and lower in sodium and chloride than are oceanic waters (Ludyanskiy 1993). However, the usual salinity in the Szczecin Lagoon should not perturb *Dreissena*, but at the border station the water conditions are not stable. Influx of Baltic Sea water temporarily increases the salinity content, especially in deeper layers. It may be these instabilities that make it more difficult for *Dreissena* to settle there as compared with the central station at the Meta platform.

The low attractiveness of *Mya*-mussels as a substrate to settle on may also be due to salinity. The mussels had been collected at Ruegen island at places where dredging material from the Baltic Sea is brought on shore. The Baltic Sea water there has a salinity of 7–8 ppt and if this is slowly washed out from the shells it might be unfavourable for *Dreissena.*

However, at the western station (near Peenepfahl) salinity is not likely to vary greatly. Accurate salinity measurements show that saline water only follows the shipping lane southwards and does not spread out in large fans.

The reason why no mussels settled at the western station may be attributed to the material (PVC), not to currents or salinity. The place itself is not entirely omitted by *Dreissena:* when the pile (Peenepfahl) was lifted in November 2000, many *Dreissena* mussels had settled on its base. Some were even up to 10 mm long (Gerbatsch, pers. comm.).

5. Summary

1) Many factors influence the settlement of Dreissena.
2) Currents at the time in question were usually very slow (< 10 cm/s), making it easy for the larvae to attach themselves.
3) In general, *Dreissena* larvae prefer hard substrates to settle on.
4) However, the artificial substrates offered were not fouled equally:

a) rank order: net > wood > stones > mussel shells > PVC

b) preferred station: Meta (centre of Kleines Haff)

c) more mussels settled on horizontal than on vertical areas

Open questions

Where does the larval supply come from?
How old were the larvae when they settled?

6. Conclusion

Dreissena mussels can be used as indicators of currents, as they have pelagic (= free swimming) larvae. However, as settlement and recruitment depend on many factors, it is difficult to assess the actual effect of currents.

The different settlement rates on the various materials confirm that the larvae do not only go where the currents carry them. They cover long distances in the water currents but are able to choose, on a small scale, where to attach themselves.

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