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Can bivalve veligers escape feeding currents of adult bivalves?

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Abstract

While the stock of introduced Pacific oysters (*Crassostrea gigas*) increased in the Oosterschelde estuary (SW Netherlands), so did the filtration pressure of all bivalve species together. In the same period, stocks of native bivalves declined slightly. The expansion of Pacific oysters in Dutch estuaries might be partially due to better abilities of their larvae to avoid or escape filtration, compared to larvae of native bivalves. In this context, escape and swimming abilities of Pacific oyster larvae and the larvae of the native blue mussel (*Mytilus edulis*) were compared.

Swimming behaviour of *C. gigas* larvae and larvae of *M. edulis* was recorded in still water and in a suction current mimicking a bivalve feeding current, in a horizontal and in a vertical plane. Larval swimming behaviour in a suction flow field was reconstructed by subtracting local water movement vectors from the total movement of larvae, yielding movement paths due to larval swimming alone.

Swimming speeds and the rate of displacement in vertical direction of *C. gigas* and *M. edulis* larvae were related to larval shell length, and to the pitch of up- or downward swimming.

Larvae of both species did not show escape reactions in a suction flow field. With increasing shell length, larval swimming speeds of both species increased significantly. Swimming speeds of *C. gigas* larvae were significantly higher than swimming speeds of *M. edulis* larvae, resulting in a faster vertical displacement. The ability to migrate to more favourable water layers faster may offer *C. gigas* an advantage over native bivalves with slower swimming larvae.

Keywords: Bivalve larvae; *Crassostrea gigas*; Digital particle image velocimetry; Escape response; Larval swimming; Larviphagy; *Mytilus edulis*

1. Introduction

1.1. Introduced oysters

Pacific oysters (*Crassostrea gigas* (Thunberg)) were introduced in the Netherlands in the Oosterschelde estuary in 1964 (Drinkwaard, 1999a,b). They spread rapidly throughout all Dutch estuaries (Bruins, 1983; Drinkwaard, 1999b; Wolff and Reise, 2002; Smaal et al., 2005; Dankers et al., 2006) and are now a potential threat to native bivalve filter feeders. While Pacific oyster stock increased, stocks of native bivalves slightly declined. As a consequence, the total filtration pressure in the Oosterschelde estuary was estimated to have increased from 289 million m^3 water day^{-1} in 1990 to 398 million m^3 day^{-1} in 2000. All filter feeding bivalves together are estimated to filter a volume equal to that of the estuary in one week. Of this total filtration capacity, roughly 2/3 can be ascribed to the Pacific oysters while they contribute 'only' 50% to the total filter feeder biomass (Geurts van Kessel et al., 2003; Kater, 2003). The strong increase of *C. gigas*, the increase of total bivalve filter feeder biomass, and the slight decrease of biomass of native filter feeders may have been brought about or at least stimulated by different responses of the larvae of the various bivalve species to larviphagy, i.e. the filtering of bivalve larvae by adults of their own and other species.

1.2. Larviphagy

During the first one to four weeks of their lives, many bivalve species are part of the zooplankton. This is their pelagic larval

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stage, after which they search for a suitable substrate to settle (Wildish and Kristmanson, 1997). During this pelagic stage, bivalve larvae experience very high mortality rates due to various factors (e.g. Thorson, 1950; Rumrill, 1990; Gosselin and Qian, 1997). It has been demonstrated that bivalve larvae are filtered by adult bivalves (Bayne, 1964a; Quayle, 1964; André and Rosenberg, 1991; Tamburri and Zimmer-Faust, 1996; Jasprica et al., 1997; Lehane and Davenport, 2002, 2004). Since adult bivalves filter all particles above a certain threshold size non-selectively (Møhlenberg and Riisgård, 1978), they may also filter their own larvae. This has indeed been demonstrated for several species: the blue mussel *Mytilus edulis* (Bayne, 1964a; Cowden et al., 1984), the edible cockle *Cerastoderma edule* (André and Rosenberg, 1991), the American oyster *Crassostrea virginica* (Tamburri and Zimmer-Faust, 1996) and the zebra mussel *Dreissena polymorpha* (MacIsaac et al., 1991). Once filtered, bivalve larvae are either ingested or rejected in pseudofaeces. If ingested they most likely die in the digestion process or in the faeces (Mileikovsky, 1974; Lehane and Davenport, 2004; Troost et al., submitted for publication). Larvae that are rejected in pseudofaeces are also likely to die (Mileikovsky, 1974; Tamburri and Zimmer-Faust, 1996; Lehane and Davenport, 2004). Bivalve larvae are not likely to reach a size refuge from bivalve filtration before settlement, since *C. gigas* larvae with a shell length of 241 μm were readily filtered and ingested by adult *C. gigas*, *M. edulis* and *C. edule* (Troost et al., submitted for publication). Furthermore, (parts of) zooplankton species with widths up to 300 μm and lengths of up to even 1000 μm were commonly found in stomachs of *C. gigas* and *M. edulis* (unpublished field observations, KT). Many bivalve larvae settle at sizes of 200-350 μm (see Hendriks et al., 2005).

Larvae of some species might be better in avoiding or escaping bivalve filtration than larvae of other species. This may lead to different mortality rates and, potentially, to differences in recruitment success. Kimmerer et al. (1994) already suggested that selectivity caused by differences in escape responses could make bivalve predation an important factor influencing biomass and species composition of inshore zooplankton. In extension, bivalve predation of larvae could influence stocks of macrobenthic species with pelagic larvae (such as bivalves).

1.3. Escape abilities

Since aggregations of filter feeding bivalves can be a serious threat to conspecific larvae, one would expect filter feeding bivalve species to have evolved some kind of survival strategy. One strategy can be the production of an excess of larvae, allowing them to cope with high losses due to predation. Most bivalves produce large amounts of larvae (Helm et al., 2004). Another strategy can be to provide their larvae with means to avoid or escape predation. Although bivalve larvae do have sensory abilities (LaBarbera, 1974; Hidu and Haskin, 1978; Cragg, 1980; Prael et al., 2001; review by Kingsford et al., 2002), it is still unknown if they are able to detect and act on hydromechanical signals created by, for instance, a filtering bivalve. Behavioural reactions to hydromechanical signals (rheotaxis) have been observed in several zooplanktonic species (e.g. Singarajah, 1975; Jakobsen, 2001; Kingsford et al., 2002) and studied extensively in copepods and their nauplii (e.g. Fields and Yen, 1997; Kiørboe et al., 1999; Titelman, 2001; Green et al., 2003; Titelman and Kiørboe, 2003), but not in bivalve larvae. In the copepod studies, shear rate (or shear deformation, see Kiørboe et al., 1999) turned out to be the strongest cue for escape jumps. Bivalve larvae may respond to the same cue, or they may be triggered to escape by other properties of a suction current such as acceleration or strain rate (or longitudinal deformation rate, see Kiørboe et al., 1999). The direction of potential escape reactions in bivalve larvae is most likely to be orientated vertically, because of their swimming mode and the spatial position of bivalve filter feeders. Most bivalve veliger larvae alternately swim upward and sink. When swimming upward, they typically do so in a helical pattern (Fig. 1) (Cragg, 1980). Upon encountering a disturbance they may either increase their swimming speed in vertical direction (Hidu and Haskin, 1978; Cragg, 1980; Prael et al., 2001), e.g. by increasing their absolute swimming speed along the helix or by increasing the pitch of upward or downward swimming, or they may close their shell valves and sink rapidly (LaBarbera, 1974; Hidu and Haskin, 1978; Cragg, 1980). It is also possible that bivalve larvae are able to detect hydromechanical signals, but unable to escape inhalant feeding currents, or they may not be able to do either.

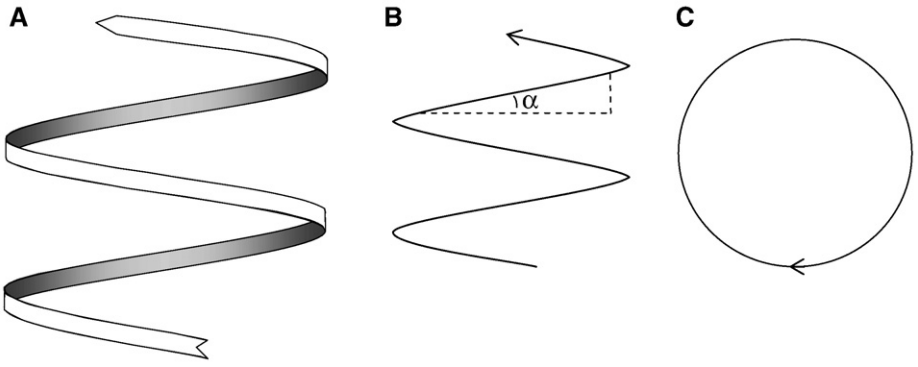

Fig. 1. Upward helical swimming pattern of a bivalve veliger larva. A: overview, B: side-view (α = pitch of upward swimming), C: view from above.

Table 1
Larvae used in the experiments on escape reactions (Exp. 1 and 2)

Exp.	Species	Date	Age (*days*)	Length (*μm*)	Concentration (*n ml*$^{-1}$)	Plane	Suction	Larvae *n*	Frames *n*
1	*C. gigas*	July 13, '05	4	123±11	115			*	
	M. edulis	Oct. 17, '05	21	120±18	50			*	
2	*C. gigas*	March 16, '07	8	173±25	30	vertical	yes	42	100
	″	″	″	″	″	″	no	35**	100
	″	″	″	″	″	horizontal	yes	23	100
	″	″	″	″	″	″	no	20	100
	M. edulis	March 14, '07	14	166±12	10	vertical	yes	47	100
	″	″	″	″	″	″	no	23**	100
	″	″	″	″	″	horizontal	no	27	100

The age and average length (with standard deviation) are given, as well as larval concentrations, numbers of larvae digitized, and numbers of filmed frames analysed.
* these larvae were also used to study swimming speeds in a horizontal plane (§ 2.4.1.).
** these larvae were also used to study swimming speeds and pitch in a vertical plane (§ 2.4.2.).

1.4. Hypothesis

Regarding the expansion success of *C. gigas* in Dutch estuaries, and the parallel decline of native bivalves, we expect *C. gigas* to have a competitive advantage over native bivalves. In this context, we investigated whether *C. gigas* larvae are better able to escape or avoid filtration by adult bivalves than the larvae of the native *M. edulis*.

We hypothesized that both *C. gigas* and *M. edulis* larvae are able to detect adult bivalve feeding currents, and we studied escape responses of *C. gigas* and *M. edulis* larvae in an artificial flow field simulating a bivalve feeding current to test this hypothesis. In addition, we hypothesized that *C. gigas* larvae have higher swimming speeds than *M. edulis* larvae. If both are able to detect fluid disturbances, this may enable oyster larvae to escape faster and therefore more successfully. Additionally, higher swimming speeds and faster vertical displacement may increase survival chances in general. So firstly, we determined mean and maximum absolute swimming speeds for *C. gigas* and *M. edulis* larvae of different sizes. Secondly we compared absolute swimming speeds and vertical rate of displacement in relation to the pitch of upward and downward swimming between larvae of *C. gigas* and *M. edulis* of the same size.

2. Materials and methods

2.1. Experimental larvae

C. gigas larvae were purchased from a commercial hatchery (Seasalter Shellfish (Whitstable) Ltd., U.K.), and shipped to the laboratory at Haren, the Netherlands. They had been reared at 27 °C and 30 psu salinity. During transport they were kept in moist filtration paper in a plastic Petri-dish, cooled at 4 – 5 °C with ice packs. Transport took no more than 24 hours. *M. edulis* larvae were transported in a similar manner from the experimental *M. edulis* hatchery of Wageningen IMARES at Yerseke, the Netherlands. These larvae had been reared at 18 °C and 30 psu salinity. Different age groups were used (Tables 1 and 2), which were ordered and shipped separately. Upon arrival the larvae were suspended in seawater with a temperature of 4 – 5 °C and salinity of 30 psu. They were then placed in a climate chamber, at a concentration between 10 and 50 ml^{-1}, to reach a temperature of 17 °C over a period of at least three hours (see Helm et al., 2004 for protocols for transporting and acclimatizing larvae). After reaching 17 °C, the larvae were left for another hour before using them in the experiments. During the experiments, the larvae were fed with the same algae as they had been reared on (*M. edulis*: *Isochrysis galbana* and *Pavlova lutherii*; *C. gigas*: *Pavlova* sp., *Isochrysis* sp., *Chaetoceros muelleri* and *Tetraselmis sp.*). All experiments were carried out in natural seawater with a salinity of 30 psu and completed within 4 hours. Across all size groups, the size of *C. gigas* larvae ranged from 68 to 279 μm shell length (measured as the longest distance from anterior to posterior, parallel to the hinge), and the size of *M. edulis* larvae ranged from 73 to 166 μm shell length. All larvae in one size group were of the same age.

2.2. Suction current

A constant suction flow field was created with an automatic pipette (Eppendorf Multipette® pro). A tube with an inner diameter of 7 mm led from the tip of the pipette horizontally into

Table 2
Larvae used in the horizontal swimming speed experiment

Species	Date (*2005*)	Age (*days*)	Average length (*μm*)	n larvae filmed	n frames analysed
Crassostrea gigas	April 6	8	166±23	3	18-41
″	April 7	2	68±17	1	42
″	April 12	14	279±18	2	13-31
″	July 1	7	183±25	12	15-85
″	July 13	4	123±11 *	11	19-87
″	July 20	10	214±19	17	13-55
″	July 22	12	246±17	14	22-37
Mytilus edulis	March 30	6	87±7	3	18-40
″	April 5	14	153±18	3	42-79
″	April 5	12	157±14	1	19
″	June 2	2	101±5	2	50-62
″	June 6	2	103±5	4	21-61
″	June 14	14	73±5	9	29-204
″	October 17	21	120±18 *	8	21-117

The age and average length (with standard deviation) are given, as well as numbers of larvae used in the experiment, and numbers of filmed frames that were analysed.
* these groups were used to visualize swimming tracks (by super-imposing filmed frames) in Experiment 1 (§ 2.3.1.).

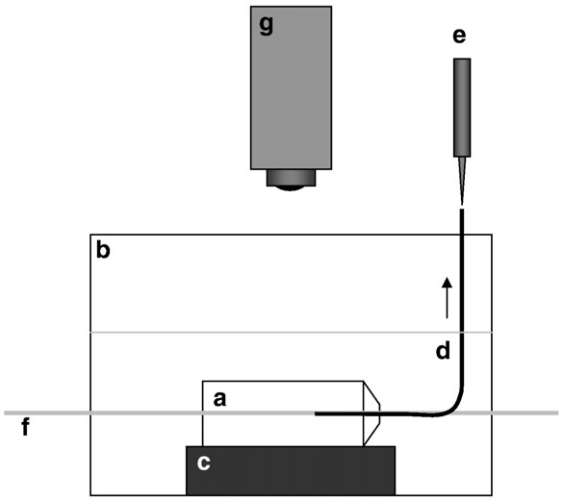

Fig. 2. Schematic drawing of the experimental horizontal set-up for mapping the suction current velocity profile using digital particle image velocimetry and recording larval behaviour in the flow field. The experimental chamber (a) was placed in an aquarium (b), elevated on a black block (c) that also provided a black background for high contrast. The suction tube (d) was connected to an automatic pipette (e). A 2D laser sheet (f) was projected horizontally through the centre of the suction tube for observations in a horizontal plane (this figure), and vertically through the centre of the suction tube for observations in a vertical plane. After placing larvae in the experimental chamber, their movements were filmed with a high-resolution digital camera (g) that was mounted perpendicular to the laser sheet.

the experimental chamber (Fig. 2). We used the lowest possible suction speed of 2199.41 $mm^3\ s^{-1}$. In the resulting flow field, flow velocities similar to those that occur in a natural bivalve feeding flow field (Troost et al., in prep.) were present at a short distance from the tube inflow.

The experimental chamber was a Plexiglas flask (150 × 110 × 36 mm). The chamber was submerged in a glass aquarium filled with seawater: water removed from the flask by suction was immediately replaced through the flask opening, and water temperature changes and advection or convection currents were practically absent. By using a small experimental volume, we reduced the observation area and the amount of larvae necessary to create a sufficiently high concentration during swimming speed measurement experiments.

To characterize the suction flow field, we used neutrally buoyant synthetic white particles (Pliolyte, BASF, diam. 25 – 50 μm) to visualize the water movement. In the darkened room we then projected a laser sheet with 0.5 ± 0.2 mm thickness through the experimental vessel towards the centre of the suction tube. We used a CW Krypton laser (Coherent Innova K, Coherent Lasers Inc., USA; $\lambda = 647$ nm, $P_{max} = 1$ W), projected through an optical lens. Only the particles in the laser sheet were illuminated, and their movement was recorded using a high resolution digital camera (Kodak MEGAPLUS ES 1.0, 30 fps at

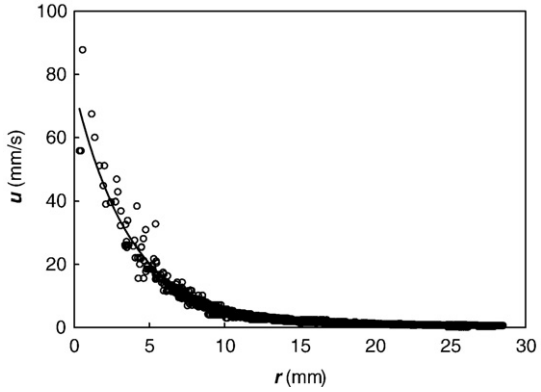

Fig. 3. Velocity profile of the suction current, resulting from the tracing of single synthetic particles in Didge©. The suction current velocity u follows an exponential decay function of the distance r from the suction tube aperture (at $r = 0$ mm) (non-linear regression, $R^2 = 0.95$, $p < 0.05$).

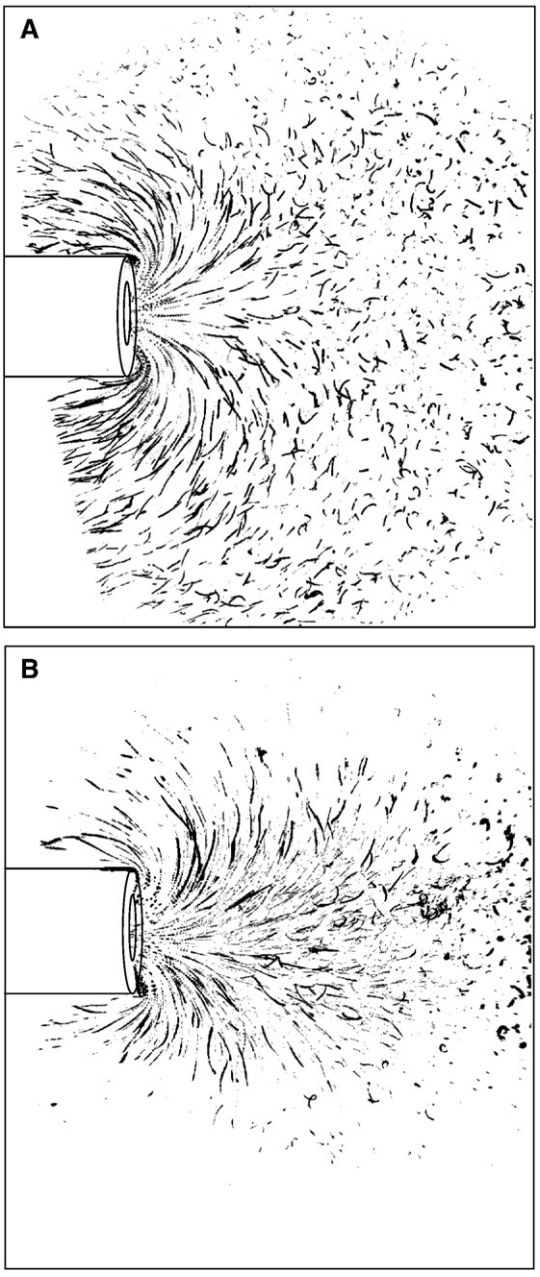

Fig. 4. Movement paths of individual *C. gigas* larvae (A) and *M. edulis* larvae (B) in the suction flow field. A is an succession of 44 filmed frames in 1.47 seconds and B of 100 frames in 3.33 seconds. The suction tube (indicated in the left) is 12.8 mm in outer diameter.

1018×1008 px resolution) that was mounted perpendicular to the laser sheet. The camera was linked to a digital acquisition system, and all filmed frames were saved in uncompressed tiff format. We recorded particle movement in a vertical as well as a horizontal plane. Digital Particle Image Velocimetry (Stamhuis and Videler, 1995; Stamhuis et al., 2002) was used to obtain an overview of the entire velocity field. Image pairs were analyzed with the DPIV analysis software Swift 4.0 (developed at the University of Groningen) using convolution filtering with interrogation areas of 65×65 pixels, after image enhancement to remove unevenly illuminated backgrounds and increase contrast. To locate convolution peaks, the COGW (centre of gravity, weighed to grey value, Stamhuis et al., 2002) was used. To obtain more detailed velocity vectors, movement of single particles was traced using the image digitizing software program Didge© 2.3b1 (A.J. Cullum, Creighton University, Omaha, NE, USA). Changes in direction in x (dx) and y (dy) direction were calculated, and from these, particle velocities that represent water current velocity.

2.3. Larval movements in suction flow

To study escape reactions of larvae, the experimental chamber and aquarium were filled with filtered seawater of 17 °C. In stead of synthetic particles, bivalve larvae were added. We performed two separate experiments.

2.3.1. Experiment 1

In the first experiment, we used *C. gigas* larvae of 123±11 µm and *M. edulis* larvae of 120±18 µm in high concentrations (resp.

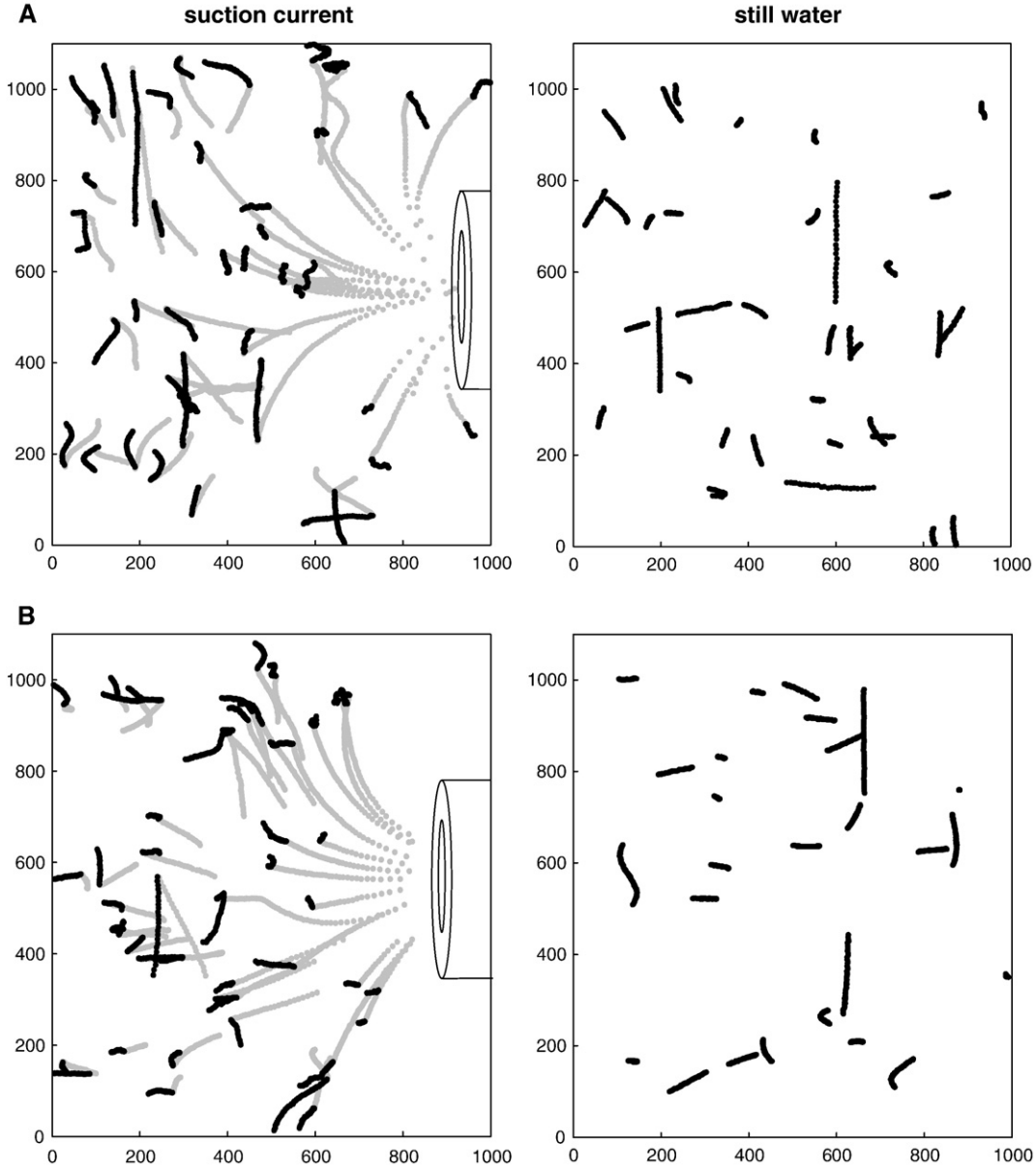

Fig. 5. Total movement paths (grey) and (reconstructed) swimming paths (black) in a vertical plane, of individual larvae in a suction current and in still water: A) *C. gigas* larvae in a vertical plane (1000 px = 30 mm); B) *M. edulis* larvae in a vertical plane (1000 px = 30 mm). Values on the axes are in pixels (px). The suction tube (indicated in the right) is 12.8 mm in outer diameter.

115 and 50 ml^{-1}) in separate experiments (Table 1). We used an experimental chamber with dimensions 100×77×36 mm. After introducing the larvae, they were left for one hour before a suction current was applied. For both species, movements of illuminated larvae in the suction current were recorded in a horizontal laser sheet. After this first experiment, we visualized the movement tracks of the larvae, by super-imposing a succession of 44 −100 filmed frames (after thresholding to monochrome black/white values) in Adobe Photoshop. We examined these movement paths in search for movements that could indicate escape behaviour.

2.3.2. Experiment 2

In the second experiment, we used *C. gigas* larvae and *M. edulis* larvae from one size group. In separate experiments, *C. gigas* larvae of 173±25 µm and *M. edulis* larvae of 166±12 µm shell length were used in respective concentrations of 30 and 10 ml^{-1} (Table 1). After introducing the larvae we waited for one hour to start the experiment. For both larval species, movements of illuminated larvae in a vertical and a horizontal laser sheet were recorded in separate experiments. Larval movements were first recorded in still water for approximately 10 minutes. Then, recording continued as a suction current was applied. We traced the positions of 20 − 47 *C. gigas* and *M. edulis* larvae using Didge©, in both still water and in a suction flow field throughout 50-100 filmed frames. Movement paths of larvae in a suction flow, and swimming paths of larvae in still water, were visualized by plotting the digitized *x* and *y* coordinates of the paths in a 2D map. To study swimming behaviour of larvae in a suction flow field, velocity vectors (d*x* and d*y*) of synthetic particles, representing

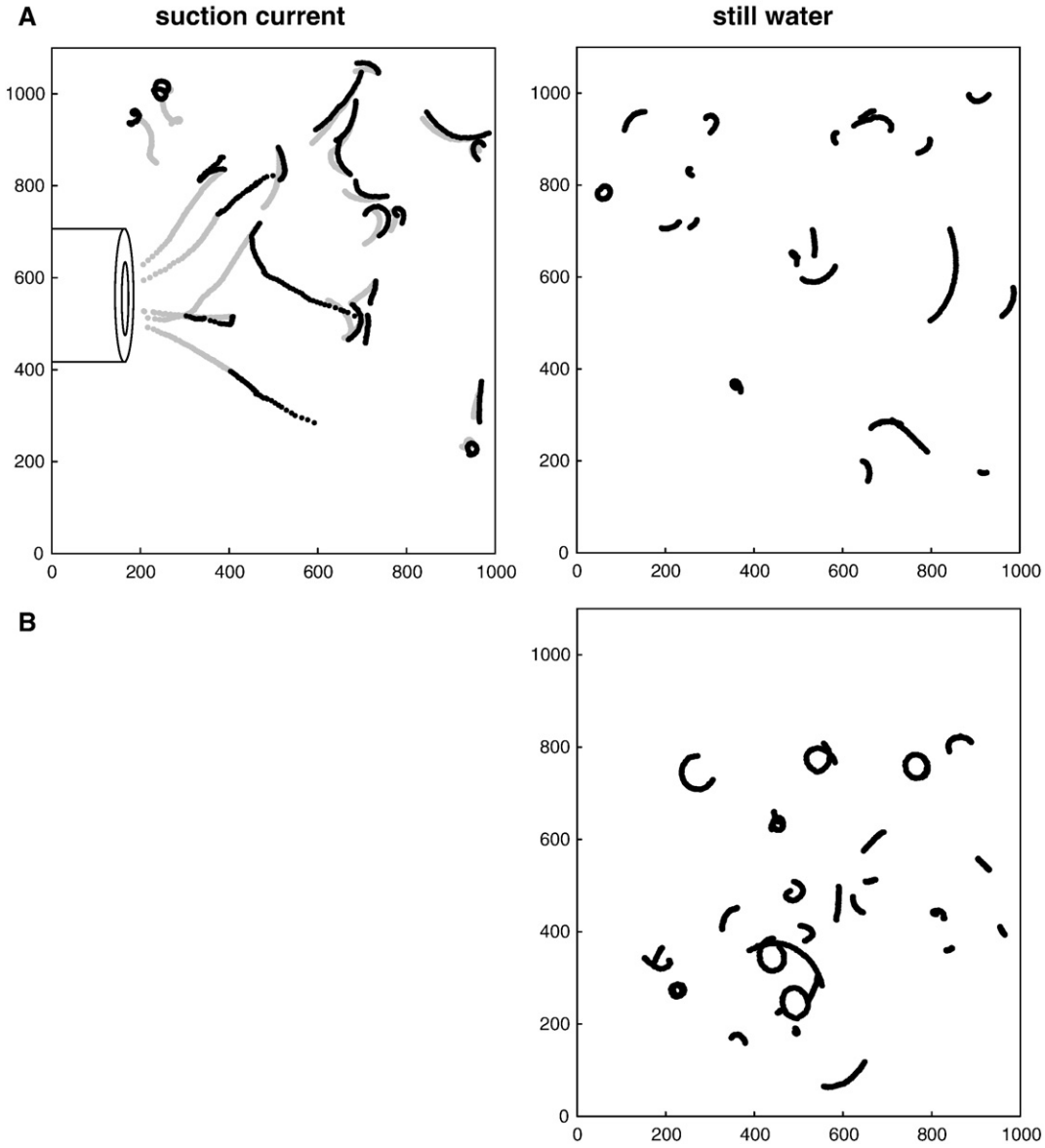

Fig. 6. Total movement paths (grey) and (reconstructed) swimming paths (black) in a horizontal plane, of individual larvae in a suction current and in still water: A) *C. gigas* larvae in a horizontal plane (1000 px=45 mm); B) *M. edulis* larvae in a horizontal plane (1000 px=42 mm; no suction current observations). Values on the axes are in pixels (px). The suction tube (indicated in the left) is 12.8 mm in outer diameter.

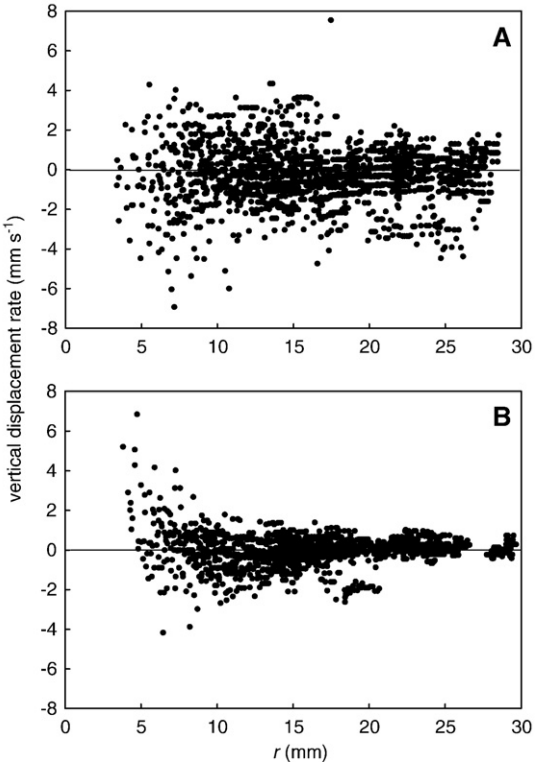

Fig. 7. Rate of vertical displacement (in mm s^{-1}) plotted against the distance from the suction tube (r in mm), for: A) *C. gigas* larvae and B) *M. edulis* larvae. Complete sets of running averages of each individual larva are plotted. For both species, there was no relationship between vertical displacement rate and distance from the suction tube (linear regression $p > 0.05$).

water current vectors, were subtracted from larval movement vectors to calculate velocity vectors caused by the swimming activity of the larvae alone. In order to subtract water current vectors, the image area of 1018 × 1008 px was subdivided in cells of 20 × 20 px. Per cell, average dx and dy of single synthetic particles (traced using Didge©) were calculated from frame to frame. Per cell, these values were subtracted from all dx and dy from frame to frame of digitized movement paths of *C. gigas* and *M. edulis* larvae in the suction flow field. This yielded dx and dy net swimming vectors of the larvae. Using these swimming vectors, swimming paths of larvae in a suction flow field were reconstructed and plotted in a 2D map. In vertical planes, displacement in vertical direction was calculated from net dy. Rates of vertical displacement in a suction flow field were related to the distance from the suction tube aperture.

2.4. Swimming speeds

2.4.1. Horizontal

Swimming speeds of 60 *C. gigas* larvae and 30 *M. edulis* larvae were analysed, for both species in 7 size groups (Table 2). Larvae were filmed in a Petri-dish in seawater of 17 ± 1 °C against a black background, lit by cold light from the side. The larvae were filmed from above with the digital camera described above. A recording was considered successful when during playback a significant displacement was observed. The water column in the Petri-dish was approximately 1 cm high, and the depth of sharpness of the camera was narrower than that, resulting in recordings of swimming in a horizontal plane only. The filmed images were saved frame by frame in uncompressed tiff format to prevent digital compression artefacts that might affect swimming speed measurements. Swimming speeds were analysed frame by frame. To filter out noise, running means were calculated by averaging each swimming speed per frame with the previous and next swimming speed in the swimming trajectory of each larva. For both species, mean swimming speeds of measured larvae were related to the mean shell length per size group.

2.4.2. Vertical

To determine and compare rates of vertical displacement of *C. gigas* and *M. edulis* larvae, and relate these to the pitch of upward or downward swimming (Fig. 1), we used the digitized swimming trajectories of larvae of both species in vertical planes without suction (§ 2.3.2.). Per swimming trajectory per larva, we identified and isolated sections with a constant pitch. Resulting trajectory sections with constant pitch were plotted as y against x coordinates of the separate digitized locations of the larvae per filmed frame. The pitch of upward or downward swimming was determined from the slope of a fitted linear regression line. The slope was converted to a pitch in degrees by taking the inverted tangent function (pitch (°) = $\tan^{-1}$(slope)). Rates of vertical displacement encountered along these trajectories with constant pitch were calculated from dy, and running means were calculated as described in the previous section. Rates of vertical displacement were related to the pitch of upward and downward swimming (ranging from −90° to 90°), and a comparison was made between *C. gigas* and *M. edulis* larvae. Sinking velocities were removed from the analyses by excluding all vertical displacement rates at negative angles larger than −85°. This was done because some sinking velocities were exceptionally large, in comparison to other swimming speeds, likely caused by a complete closure of the shell valves (Cragg, 1980).

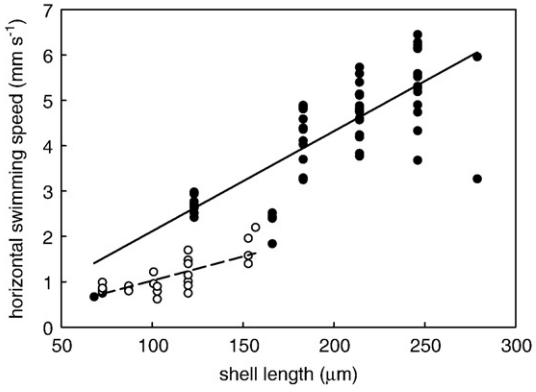

Fig. 8. Mean swimming speeds per larva (● = *C. gigas*, ○ = *M. edulis*) in mm s^{-1}, plotted against the mean shell length in µm. Both data sets fit a linear regression (*C. gigas*, solid line, $R^2 = 0.65$, $p < 0.05$; *M. edulis*, dashed line, $R^2 = 0.56$, $p < 0.05$). After ln-transformation (not shown in this figure), intercepts were significantly different (GLM, $p < 0.05$) but slopes were not (GLM, $p > 0.05$).

2.5. Statistical analysis

Curve-fitting and non-linear regressions were performed with Sigmaplot® 2001. All other statistical tests were performed with SPSS® 12.0.1. Data were visually checked for normality using a Q-Q plot, and for equality of variances by plotting studentized residuals against predicted values. If the prerequisites were not met, the data were ln-transformed before testing. A significance level of $\alpha = 0.05$ was maintained.

3. Results

3.1. Suction current

The suction flow field was radially symmetrical, and the velocity profile (Fig. 3) closely fitted an exponential decay function

$$U_W(r) = u_{max} \cdot e^{-br} \quad (1)$$

that relates the water current velocity U_w (mm s^{-1}) to the distance from the tip of the suction tube r (mm), with a maximum current velocity at the tip of the suction tube u_{max} of 75.85 mm s^{-1} and constant b of 0.26 (non-linear regression: $R^2 = 0.95$, $p < 0.05$).

3.2. Escape reactions

The movement paths of larvae in a suction field, as visualized by the super-imposed filmed frames in experiment 1, did not indicate any escape reactions (Fig. 4). Movement paths were clearly circular at the outer margins, at longer distances from the suction tube. This reflects the helical swimming behaviour of bivalve veliger larvae (Fig. 1). Coming closer to the suction tube, movement paths became more elongated as their motion was distorted by the increasing super-imposed water current. No escape jumps were observed, neither were the larvae observed to turn and swim against the current. Also in experiment 2, where we included observations on movement in a vertical plane, no escape reactions were observed in the larvae of both species. This can be seen in the digitized movement paths and the reconstructed swimming paths of larvae in a suction current (water movement subtracted), in comparison to swimming paths of larvae in still water in both vertical (Fig. 5) and horizontal (Fig. 6) planes. The larvae of both species clearly did not show escape jumps, nor were they observed to turn to swim against the current. They continued their helical swimming behaviour. As the larvae were being sucked towards the suction tube, their swimming behaviour appeared to remain the same. In a suction flow field only 2 *M. edulis* and 4 *C. gigas* larvae were observed to sink (Fig. 5). These were not regarded as escape reactions since in still water similar low numbers of sinking larvae were observed (3 larvae per species; Fig. 5). Results for sucked *M. edulis* larvae in a horizontal plane are lacking because the filmed frames were lost in a computer hard-disk failure.

Larvae recorded in a vertical laser sheet did not show escape responses in the form of suddenly increased rates of vertical displacement (either upward or downward due to sinking) at a certain distance from the suction tube (Fig. 7). Rates of vertical displacement showed no relationship with distance from the suction aperture (linear regression $p > 0.05$). Coming closer to the suction aperture, the variance in vertical displacement rate increased, especially in *M. edulis* larvae. This is likely due do methodological artefacts, and not to larval behaviour. This will be explained in Section 4.3.

Table 3
Mean swimming speeds of bivalve larvae

Species	Size (*μm*)	mean/*max.* swimming speeds					Source
		Horizontal (*mm* s^{-1})	Up (*mm* s^{-1})	Down (*mm* s^{-1})	Sinking (*mm* s^{-1})	Any direction (*mm* s^{-1})	
Arctica islandica	170 - 202	-	0.3 – 0.4	-	-	0.5 – 0.8	1
Cerastoderma edule	280	-	0.9	1.3	1.7	-	2
Crassostrea gigas	68 - 279	0.7 – 6.5 *r*	-	-	-	-	*TS*
″	173	-	0.9	1.4	3.2	-	*TS*
Crassostrea virginica	75 - 300	*0.3 – 0.8*	*0.8 – 2.3*	-	*1.7 – 8.3*	-	3
″	65 - 160	-	0.4 – 1.0	-	-	-	4
″	120 - 300	-	-	-	1 - 4	-	4
″	77 - 290	-	*1.4 - 5.0*	-	-	-	13
Ostrea edulis	-	-	1.2	-	-	-	6 (in 5)
Mercenaria mercenaria	-	-	*1.3*	-	-	-	9 (in 8)
″	-	-	1.2 – 1.3	-	-	-	7 (in 5)
Mytilus edulis	255	-	-	-	-	1.1	10
″	226 - 261	1.3 – 3.3	-	-	-	-	11
″	73 - 157	0.6 – 2.2 *r*	-	-	-	-	*TS*
″	166	-	0.7	0.4	1.4	-	*TS*
Pecten maximus	(3-41 days)	-	0.2 – 0.5	-	-	*2.2*	5
Spisula solidissima	96 - 196	-	0.2 – 0.5	0.2 – 0.4	0.6 – 2.2	-	12

Mann and Wolf 1983; 2) Jonsson et al. 1991; 3) Hidu and Haskin 1978; 4) Mann 1988; 5) Cragg 1980; 6) Cragg and Gruffydd 1975; 7) Turner and George 1955; 8) Chia et al. 1984; 9) Carriker 1961; 10) Konstantinova 1966; 11) Sprung 1984; 12) Mann et al. 1991; 13) Mann and Rainer 1990; *TS*) this study.
Where maximum values are given, these are expressed in *italics*. Where a range of all recorded speeds is given, in stead of a range in mean or maximum values, this is indicated with an '*r*'. All swimming speeds were determined at salinities between 22 and 33 psu, at 1 bar pressure and at temperatures between 12 and 25 °C (see references). In the cases of swimming in 'any direction', the exact direction was unspecified for *A. islandica* and *M. edulis*.

3.3. Swimming speeds

3.3.1. Horizontal

In both species, recorded in a horizontal plane, mean swimming speeds per larva showed a linear relationship with shell length (Fig. 8; linear regression, *C. gigas* $R^2=0.65$, $p<0.05$, *M. edulis* $R^2=0.56$, $p<0.05$). Swimming speeds of *C. gigas* larvae were significantly higher than swimming speeds of *M. edulis* larvae across all size groups (Fig. 8; GLM after ln-transformation: slopes $p>0.05$, intercepts $p<0.05$, difference between intercepts: 2.4 mm s^{-1} (recalculated from ln-transformed value)). Swimming speeds found in *C. gigas* larvae ranged from 0.7 to 6.5 mm s^{-1} and swimming speeds in *M. edulis* from 0.6 to 2.2 mm s^{-1} (Table 3).

3.3.2. Vertical

Speeds of vertical displacement and absolute swimming speeds were plotted for each trajectory section with a constant pitch (Fig. 9). With an increased pitch of upward and downward swimming, vertical displacement rates of both *C. gigas* and *M. edulis* larvae increased significantly (Fig. 9A; linear regression: *C. gigas* $R^2=0.86$, $p<0.05$; *M. edulis* $R^2=0.91$, $p<0.05$). With an increasing pitch, from −90° to +90°, rates of vertical displacement in *C. gigas* larvae showed a significantly stronger increase than in *M. edulis* larvae (GLM slopes $p<0.05$, intercepts $p>0.05$). On average, larvae of *C. gigas* and *M. edulis* showed a slight downward displacement in experiments without suction. The average rate of vertical displacement was -0.18 ± 1.26 mm s^{-1} for *C. gigas* and -0.20 ± 0.55 mm s^{-1} for *M. edulis*. This deviated significantly from 0.0 (one-sample t-test $p<0.05$).

In both species, absolute swimming speeds were not related to the pitch (Fig. 9B; linear regression, *C. gigas* $R^2=0.02$, $p>0.05$; *M. edulis* $R^2=0.10$, $p>0.05$). Again, sinking velocities were excluded from the analysis.

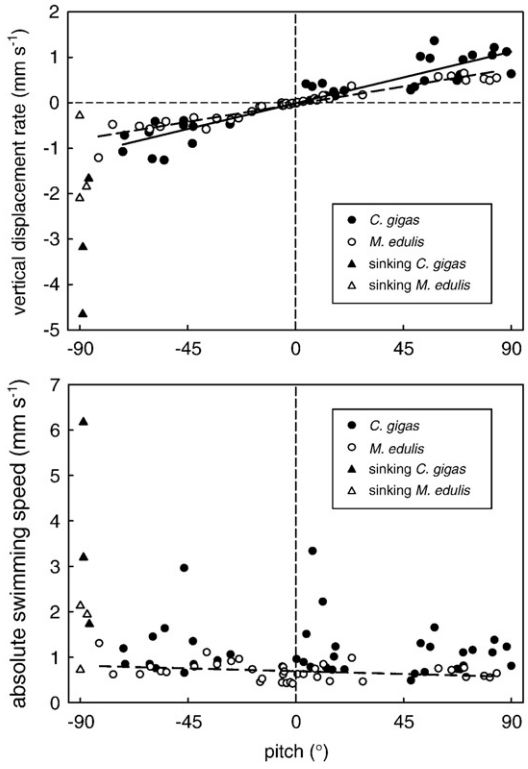

Fig. 9. Mean vertical displacement rate and mean absolute swimming speed per larva, in *C. gigas* and *M. edulis* larvae, plotted against the pitch. Vertical displacement speeds of *C. gigas* and *M.* edulis both fit a linear regression (*C. gigas*: $R^2=0.82$, $p<0.05$, solid line; *M. edulis*: $R^2=0.81$, $p<0.05$, dashed line). Slopes differ significantly (GLM $p<0.05$). Absolute swimming speeds of *C. gigas* do not fit a linear regression ($R^2=0.00$, $p>0.05$), absolute swimming speeds of *M. edulis* do ($R^2=0.05$, $p<0.05$, slope$=-1.3\times10^{-3}$, dashed line). Sinking speeds (filled and open triangles) were not included in the regression analyses on vertical and absolute swimming speeds.

4. Discussion

Both *C. gigas* and *M. edulis* larvae did not show escape responses to the simulated inhalant current. Either they can detect hydromechanical stimuli but cannot react to them, or they are unable to detect the hydromechanical signals created by a filter feeding bivalve. Larvae of *C. gigas* swam faster than larvae of *M. edulis*, resulting in a faster displacement in vertical direction.

4.1. Absence of escape responses

The absence of any escape response suggests that bivalve larvae are not able to detect inhalant current velocities of adult bivalves, or at least that they are not able to induce an escape response after having detected an inhalant current. If larvae were not sensitive enough to detect our simulated feeding current, they are not likely to escape bivalve feeding currents either. In the simulated flow field, higher current speeds were present than in the inhalant flow field of a live filter feeding bivalve. This provided a wide range in values for different possible triggers (e.g. acceleration, shear and strain rate) to respond to. If larvae are able to detect and escape from bivalve inhalant feeding currents, we should at least have seen some escape attempts. Possibly, larvae are physically unable to perform escape swimming, which should at least involve higher swimming speeds than the normal cruising speeds. From the next paragraph it follows that the larvae may already have been swimming at their maximum speeds. The larvae appear not to be equipped with sophisticated sensory organs such as the antennae of copepods to detect hydromechanical signals (e.g. Visser, 2001), or swimming legs to perform quick escape jumps (e.g. Van Duren and Videler, 2003).

4.2. Swimming speeds

In a horizontal plane, *C. gigas* larvae swam significantly faster than *M. edulis* larvae across all size groups. We also found that *C. gigas* larvae increase their rate of vertical displacement faster with increasing pitch (either upward or downward). Since absolute swimming speeds of both species were not related to the pitch, we can say that the positive relationship between vertical rate of displacement and pitch is due to an increase in the pitch itself and not due to an increase in absolute swimming speeds. The observed pitch, however, will be lower than the actual pitch

of swimming because of the gravitational force on the larva (Jonsson et al., 1991). Thus, the higher increase in vertical displacement with increasing pitch of *C. gigas* larvae is a direct result of their higher swimming speeds. This means that the difference between absolute swimming speeds of *C. gigas* and *M. edulis* larvae that we measured for different size groups in a horizontal plane, is directly reflected in differences in vertical displacement rates. Although we did not compare rates of vertical displacement for a whole size range of *C. gigas* and *M. edulis* larvae, we can conclude from our results that *C. gigas* larvae move faster in vertical directions than *M. edulis* larvae. Since larvae swim with pitches of up to 90°, we can estimate that the maximum rate of vertical displacement is likely about 2 mm s^{-1} for *M. edulis* larvae and about 6 mm s^{-1} for *C. gigas* larvae, based on the results of swimming speeds in a horizontal plane and the size range of the larvae.

The double function of the velum in bivalve veliger larvae, propulsion and feeding (Widdows, 1991), may explain why these larvae regulate their vertical displacement rate by changing the pitch: It allows them to continue swimming at maximum speed, thereby maximizing food intake (Jonsson et al., 1991).

Considering the above, we can say that our horizontal swimming speeds are actually swimming speeds in 'any direction', that are classified as horizontal swimming speeds because the water column was merely 1 cm high, forcing the larvae to swim in a horizontal plane and not allowing them to swim upward.

Observed swimming speeds of *M. edulis* larvae were in the same range as swimming speeds of bivalve larvae found in earlier studies (Table 3). *C. gigas* larvae swam significantly faster than all previously studied bivalve larvae except for one species: observed swimming speeds of *C. gigas* larvae were comparable to swimming speeds of the larvae of *Crassostrea virginica*. The values for upward and downward swimming, as well as sinking, were comparable to the values found by Hidu and Haskin (1978) and Mann (1988). Mann and Rainer (1990) recorded an upward maximum vertical displacement of 5.0 mm s^{-1} in *C. virginica* larvae of 290 µm, which is much higher than our 0.9 mm s^{-1} for *C. gigas*, but agrees well with the maximum swimming speed of around 6 mm s^{-1} we estimated above. Wood and Hargis (1971) reported an observed absolute swimming speed of 10 mm s^{-1} for larvae of *C. virginica*, but this is an anecdotal remark and the authors do not elaborate on methodology and results.

Although linear functions described the relationship between larval length and swimming speed most accurately (Fig. 8), the swimming speeds likely reach a plateau or an optimum at a certain shell length, such as found by Cragg (1980) for larvae of *Pecten maximus* and by Hidu and Haskin (1978) for larvae of *C. virginica*. The largest size group of *C. gigas* larvae indeed show decreased swimming speeds, although only in two observations, indicating a cessation in the increase in swimming speeds or even a decrease. *M. edulis* larvae do not show a plateau or an optimum at all. An optimum was likely not yet reached in *M. edulis* larvae because we did not include the largest larval stages (up to pediveliger stage).

The difference in swimming speed between *M. edulis* and *C. gigas* is not only caused by a difference in size or size range used. Also at comparable shell lengths, *C. gigas* larvae swam faster than *M. edulis* larvae. Regarding swimming speeds in a horizontal plane (Petri-dish), *C. gigas* larvae from all size groups swam on average with a speed of 18.0 body lengths (bl=shell lengths) s^{-1} and *M. edulis* larvae with a speed of 10.5 bl s^{-1}, both independent of shell length or age (linear regression, $p>0.05$).

4.3. Methodological considerations

Due to the limited imaging frequency of our camera (30 fps) and the linear approximation of the particle and larval velocities, we might have underestimated particle displacement and larval swimming velocities close to the suction tube aperture. This is, however, expected to have had minor consequences for our results since the underestimation can be assumed to be the same for both particles and larvae at the same location in the flow field.

Observations and measurements on particles and on larvae were made in separate experiments. Minor differences in e.g. the position of the suction tube in the transparent measurement chamber may have decreased the fit of water movement (synthetic particles) and larval movement. This may have increased the variances in the resulting data, especially closer to the suction tube opening, as e.g. shown in the vertical displacement rates towards the suction tube (Fig. 7). The conclusions based on the experimental data do, however, hardly suffer from this increase in variance.

Furthermore, we do not expect differences in larval concentrations (Table 1) to have affected swimming speeds or inhibited escape reactions. In Pacific oyster hatcheries, concentrations of 5 up to 57 ml^{-1} are generally used without significant negative effects on larval health (Helm et al., 2004). Therefore, significant effects on larval behaviour were also not expected. During the experiments, collisions between larvae were observed only occasionally.

From hatchery to experiments *C. gigas* larvae experienced a change from 27° to 5° to 17 °C. *M. edulis* larvae experienced a change from 18° to 5° to 17 °C. This falls within the limits of, a protocol for transport and acclimatization that is generally used in hatchery practice (Helm et al., 2004). On visual inspection the larvae appeared to be healthy and behaving normally. Therefore, we do not expect serious effects on swimming performance.

The larvae showed no reaction to the laser light; no attraction, nor avoidance.

4.4. Ecological implications

Since larvae of both species showed no escape responses, the expansion of *C. gigas* in Dutch waters, seemingly at the cost of native bivalves, cannot be explained by better escape abilities of their larvae in comparison to the larvae of native bivalves. The absence of escape responses in bivalve larvae theoretically makes them an easy prey for bivalve filter feeders. Besides various other sources of high natural mortality (e.g. Thorson, 1950; Rumrill, 1990; Gosselin and Qian, 1997), bivalve larvae might suffer substantial mortality due to bivalve filtration. High mortality rates are, however, a natural phenomenon for planktonic larvae that are produced in very high numbers (see Helm et al., 2004).

Additionally, larvae may not have shown direct escape responses to a suction current, but they might avoid filtration by benthic suspension feeders in a more indirect manner through regulation of their vertical position in the water column. Bivalve larvae have been shown to migrate in vertical directions and to respond to directional indicators such as pressure, gravity and light (Bayne, 1963, 1964b; Mann and Wolf, 1983). For instance, young *M. edulis* larvae are reported to occupy higher water levels through phototaxis and negative geotaxis, thereby possibly avoiding benthic filter feeders (Thorson, 1950; Bayne, 1964b). In this respect, the significantly higher swimming speeds of Pacific oyster larvae can be speculated to offer them competitive advantages over larvae of native bivalves. Theoretically, *C. gigas* larvae can move faster vertically to other water layers than *M. edulis* larvae, enabling them to either avoid benthic predators, find layers with more food (Raby et al., 1994) or to transport themselves with the tides in favourable directions (Shanks and Brink, 2005). Whether they actually do so in the field remains open for further research.

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