**ICES CM 2004/K:10**

# Are introduced oysters (*Crassostrea gigas*) hampering the recruitment of indigenous bivalve filter feeders?

Karin Troost, Pauline Kamermans, Eize J. Stamhuis, Wim J. Wolff

Since their first introduction in 1964, Japanese oysters (*Crassostrea gigas*) are spreading rapidly throughout Dutch estuaries. They may affect Dutch ecosystems profoundly. One way in which they might affect indigenous filter-feeding bivalves is by filtering their pelagic larvae, thereby hampering their recruitment. We studied the ability of adult oysters to filter bivalve veliger larvae of different species. Inhalant feeding current velocities of Japanese oysters and blue mussels (*Mytilus edulis*) were assessed using Digital Particle Image Velocimetry. These velocities were compared with average swimming speeds of bivalve veligers from literature. Inhalant feeding current velocities of both oysters and mussels were higher than swimming speeds of bivalve veligers, indicating that both species might be able to filter large amounts of veliger larvae. However, fluid deformation rate profiles revealed inhalant oyster feeding currents to be more diffuse than inhalant mussel feeding currents. This may cause veligers to be less able to detect feeding currents of oysters in time, increasing the chances of being filtered. Additionally, in the Oosterschelde estuary larval numbers in the water column above an oyster bed were compared with larval numbers above a reference site. Significantly less mussel larvae were found above the oyster bed than on the reference site. This supports the theory that adult oysters filter veliger larvae. Larval numbers of oysters however showed completely the opposite. More oyster larvae were present above the oyster bed than above the reference site.

Keywords: introduced species, bivalves, veliger larvae, particle image velocimetry

Karin Troost and Pauline Kamermans: Netherlands Institute for Fisheries Research - Centre for Shellfish Research of Wageningen University and Research centre, PO box 77, 4400 AB, Yerseke, the Netherlands [tel: +31 113 672300, fax: +31 113 573477, e-mail: Karin.Troost@wur.nl and Pauline.Kamermans@wur.nl]. Eize Stamhuis and Wim Wolff: University of Groningen, Department of Marine Biology, PO box 14, 9750 AA, Haren, the Netherlands [tel: +31 50 3632259, fax: +31 50 3632261, e-mail: E.J.Stamhuis@biol.rug.nl and W.J.Wolff@biol.rug.nl].

## Introduction

After nearly a century of European flat oyster (*Ostrea edulis*) farming in the Netherlands, this industry nearly came to an abrupt end in the severe winter of 1963, when the majority of oysters froze to death. Enterprising as ever, Dutch oyster farmers started to look for alternative species to culture. In 1964 they introduced an exotic species in the Oosterschelde estuary in the southwestern part of the Netherlands (fig. 1): the Japanese cupped oyster (*Crassostrea gigas*). This species was well known for its fast growth and not considered a threat since it was assumed not to be able to reproduce in the relatively cold Dutch waters. Additionally, plans for closing the Oosterschelde estuary from the North Sea were in progress that would turn the Oosterschelde estuary into a brackish lake, unsuitable for oyster growth (Drinkwaard, 1999). But plans were changed. Instead of closing the Oosterschelde from the North Sea, between 1979 and 1986 a storm-surge barrier was built that could be closed during episodes of extremely high water levels (Smies and Huiskes, 1981). The Oosterschelde estuary remained a salt-water system. Additionally, against expectations, *Crassostrea gigas* managed to reproduce successfully. In 1976 a first natural spatfall occurred and ever since it has been spreading rapidly throughout Dutch estuaries (Drinkwaard, 1999). By means of stock assessments and reconstructions, the Netherlands Institute for Fisheries Research (Centre for Shellfish Research) estimated that intertidal beds in the Oosterschelde estuary increased from 0.25 $km^2$ in 1980 to 6.40 $km^2$ in 2002 (Kater *et al.*, 2002).

The most important native bivalve filter feeders in Dutch estuaries in terms of biomass are the blue mussel (*Mytilus edulis*) and the edible cockle (*Cerastoderma edule*). Both are very important as a food source for many marine birds such as the oystercatcher (*Haematopus ostralegus*) and the eider duck (*Somateria mollissima*).
Japanese oysters have been rapidly expanding since the late 1970's. Simultaneously, during the 1980's and 1990's stocks of other bivalve filter feeders have been declining in the Oosterschelde estuary and the brackish Lake Grevelingen (fig. 1) (anonymous, 1999; Bult *et al.*, 2000; Bult and Kesteloo, 2001; Craeymeersch *et al.*, 2000; Schaub *et al.*, 2002). Additionally, in the Dutch Wadden Sea oyster reefs are observed to take over mussel beds (Dankers *et al.*, 2004). Reise (1998) observed in the German Wadden Sea that Japanese oysters mainly settle on intertidal mussel beds.

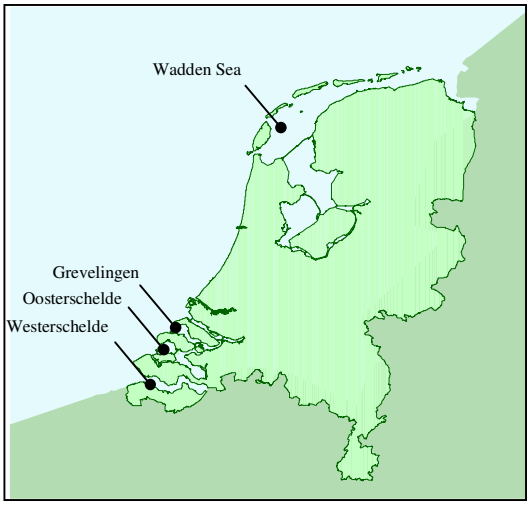



Figure 1: Location of the Wadden Sea, Lake Grevelingen, Oosterschelde and Westerschelde estuaries in the Netherlands.

*Crassostrea gigas* is expected to affect native bivalve filter feeders by competing for the same resources, and/or by competing for space, and/or by filtering their veliger larvae. In this paper we concentrate on the effect of Japanese oysters on the concentration of veliger larvae in the watercolumn. By analysing their filter-feeding characteristics we try to find evidence for their ability to filter significant amounts of bivalve larvae.
Predation on pelagic larvae is not uncommon in benthic communities. Free swimming and settling pelagic larvae of bottom invertebrates and their spat are heavily preyed upon by adult benthic invertebrates (Galtsoff and Loosanoff, 1939; Korringa, 1940; Thorson and Jørgensen, 1946; Hiddink, 2002). Many adult filter-feeding bivalves can be voracious predators. For the American oyster *Crassostrea virginica*, Tamburri and Zimmer-Faust (1996) showed that adults consume larvae of many taxonomic groups; bivalve veligers (including their own), gastropod veligers, cirripeds, decapod zoeae and polychaete trochophores, ranging in size from 172 ± 4 to 1510 ± 22 µm. Cowden *et al.* (1984) showed that *Mytilus edulis* is capable of consuming larvae from several taxonomic groups (polychaete trochophores, crustacean nauplii, asteroid bipinnaria, echinopluteus larvae and nudibranch veligers) and Bayne (1969) and Quayle (1964) showed that *M. edulis* also filters its own larvae. Kristensen (1957) reported on ingestion of bivalve larvae by adult *Cerastoderma edule* and André *et al.* (1993) showed that *C. edule* inhales its own conspecifics. Taking into account prodigous feeding rates measured in laboratory experiments, it is easily expected that *Crassostrea gigas*, like *C. virginica*, is capable of consuming large amounts of pelagic bivalve larvae, thereby hampering the recruitment success of certain species.
Filtration of veliger larvae by adult Japanese oysters can be dependent on many factors. Differences in filtration of larvae of different species may be due to differences in larval swimming speeds or differences in their ability to detect adult feeding currents (has been shown for different species of copepod nauplii escaping mussel filtration by Green *et al.* (2003)). The amount and species

composition of the larvae filtered may be dependent on different filter-feeding flow characteristics, such as velocity and diffuseness of their inhalant feeding current (see Green *et al.*, 2003).
The aim of this study was to determine inhalant feeding current characteristics of adult Japanese oysters and blue mussels in relation to swimming speeds of bivalve veliger larvae. Inhalant feeding current velocities of adult oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) were determined using Digital Particle Image Velocimetry (DPIV). Obtained values were compared with swimming speeds of different bivalve veliger larvae, as found in literature. Fluid deformation rate plots, indicating the diffuseness of the inhalant currents, were created for the inhalant feeding currents and compared between oysters and mussels. Additionally, field observations were made on bivalve larval numbers in the water column in presence and absence of oyster beds. Because of the high filtration capacity of such beds, we expected to find fewer larvae in presence of oysters.

## Methods

### *Experimental animals*
Oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) were collected from an intertidal oyster bed in the Oosterschelde estuary in November 2003. The oyster bed is located in the Zandkreek area at a tidal height of about 1.1 to 1.7 meters below mean tide level (close to NAP, the Dutch Ordnance level). Oysters ranged in shell-length from 72 to 280 millimetres, mussels from 54 to 60 millimetres. They were transported dry, in an isolated box with cooling elements to the laboratory where they were placed in tanks with running artificial seawater (temperature 15°C, salinity about 30‰). They were fed with Instant Algae® (Special Blend - Shellfish post-set, premium: *Isochrysis sp.*, *Tetraselmis sp.*, *Pavlova sp.*, *Thalassioseira weissflogii*) from Reed Mariculture (Campbell, California, USA; www.reed-mariculture.com).

### *Conditioning of the animals*
At the beginning of the experiments, the animals were starved for approximately 16 hours and kept dry for approximately 3 hours before putting them in the experimental set-up, to simulate an extended low-tide foddless period and induce a rapid appearance of feeding activity.

### *Digital Particle Image Velocimetry – set-up*
The experiments were carried out in November 2003. Per experiment, one animal was placed in a still-water tank. In order to determine maximum velocities locally and to ensure that the main inhalant current was filmed, the laser sheet was projected to cross-sect the plane between valves, at a location along the shell-edge of interest. Small oysters (78 – 82 mm) were placed upright in black grid of a non-light-reflecting material. Larger oysters were placed horizontally, lying on their cupped valve. Mussels were placed horizontally, supported by two glass strips to ensure that their feeding currents remained unobstructed. A diluted food solution was added to stimulate feeding.
To visualize water movement generated by the bivalve, the water was seeded with neutrally buoyant white particles (PVC, 50 - 125 µm). A laser sheet with adjustable thickness (0.1 to 5.0 mm) was projected in the still-water tank, to create a 2D plane in which particles were illuminated and thus visualized (Stamhuis & Videler, 1995). In our experiments, a CW Krypton laser (Coherent Innova K, Coherent Lasers Inc., Santa Clara, Calif., USA, wavelength = 647 nm, $P_{max}$ = 1 W) was used. The light was delivered through an optical fibre to a sheet probe. A high resolution digital camera (Kodak ES 1.0, 30 fps at 1K x 1K resolution) was mounted perpendicular to the illuminated plane and used to record the movement of illuminated particles in the 2D laser-sheet plane. The camera was linked to a digital acquisition system. Recording started immediately upon placement of an animal in the still-water tank.

### *Digital Particle Image Velocimetry – analysis*
All analyses of recorded images were performed with the DPIV analysis software Swift 4.0 (Dutch Vision Systems, Breda, The Netherlands). Image pairs were analysed, after enhancing them by removing unevenly illuminated backgrounds, using convolution filtering with interrogation areas of 65 x 65 pixels. To locate convolution peaks, the COGW (centre of gravity, weighed to grey value)

was used. Results of the PIV analyses were displayed as velocity vector fields or colour maps of velocity magnitude and shear rate (which will be further referred to as fluid deformation rate).

***Inhalant and exhalant feeding currents of oysters***

Many bivalves have very distinct inhalant and exhalant apertures. But in Japanese oysters, no morphological features can be identified as such. To find the locations of inhalant and exhalant apertures, the entire flow field of one oyster was mapped using DPIV. Because shell edges of a Japanese oyster are highly irregular and undulating, it was not possible to identify in- and exhalant currents in one 2D plane. To overcome this difficulty, multiple 2D maps were created, with the laser sheet projected at slightly different locations parallel to the sagittal plane (fig.2). After analysing image pairs at these different locations, maximum velocity vectors were combined manually in one picture. The oyster that was used to create this overview was 78 millimetres in length. Based on this overview, maximum flow velocities were determined at the top of the shell. In total, inhalant feeding currents were mapped for eight oysters and two mussels. Their maximum inflow velocities were derived from these maps. We decided not to concentrate on the outflow because all particles were removed from the out-flowing water due to the filtration activity of the bivalves. Interpolation would only result in rough estimates (Stamhuis et al., 2002).

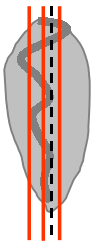


Figure 2: Frontal view of an oyster, showing both valves and undulating shell edges. The dashed line indicates the sagittal plane. Different projections of the laser-sheet, parallel to the sagittal plane, are indicated in red.

When studying large oysters, the movement of particles inside the shell (until they enter the mantle cavity) could also be filmed and analysed. Mussels and small oysters would not permit a view inside the shell-cavity since their valve gape was too narrow for that. Therefore, a comparison between oyster and mussel current velocities was conducted using velocities measured at the shell-edge. It is also the most informative value when studying whether or not larvae are actually sucked into the shell by an adult oyster or mussel.

Immediately after completing all measurements, the experimental animals were killed and their bodies were removed from the shells. Ash-free dry weights were obtained by drying the flesh for 72 hours at 70°C and incinerating it at 550°C for four hours.

***Filtration activity***

The total volume of water passing through the individual oysters and mussels, as a reference for the animal's activity, was calculated as follows.

$$FR = G \times L \times V \times C \qquad (1)$$

FR = filtration rate = volume filtered (l/h)
G = valve gape (mm)
L = length along edge where inflow occurs (mm)
V = flow velocity (mm/s)
C = conversion factor ($mm^3/s$ to l/h) = 0.0036

The relationships between estimated filtration rate and body mass and between maximum inflow velocity and body mass were investigated. In general, filtration rates of filter feeding bivalves are related to their body weight according to the following allometric equation (Foster-Smith, 1975;

Jones *et al.*, 1992; Møhlenberg and Riisgård, 1979; Riisgård, 1988; Riisgård. and Møhlenberg, 1979; Walne, 1972; Winter, 1978):

$$FR = a \times W^b \quad (2)$$

FR = filtration rate (l/h)
a = allometric constant
W = body weight (either dw or afdw)
b = allometric constant

The relationship between filtration rate and body mass offers a second opportunity to check the activity of all animals. If all animals filtered actively, the relationship between filtration rate and the logarithm of body ash-free dry weight should be linear.

***Field observations***

From March 14th until August 25th, in the northern part of the Oosterschelde estuary (fig. 3), bivalve veliger larvae were counted in samples taken above an oyster bed and above a nearby (2000 m) bare tidal flat. Plankton samples were taken with nets (∅ 10 cm, mesh 60 µm, 4 per site) that can rotate freely on a pole, thereby collecting larvae passively during a submersion period (see figure 1E in Armonies, 1994). These nets were placed on the tidal flats during low tide, 30 centimetres above the substrate, and collected during the following low tide period. Samples were preserved in seawater with 4% buffered (borax) formaldehyde (37%). Bivalve veliger larvae were counted using an inverted microscope (magnification x100).

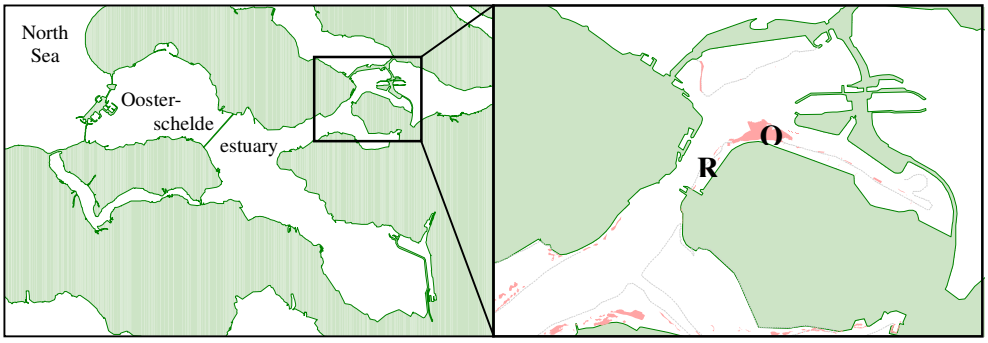



Figure 3: Locations of the sampling sites in the Oosterschelde estuary. Oyster beds in the intertidal (dashed line) are depicted in red. O: sampled oyster bed, R: sampled reference site.

***Statistical analysis***

After log-transformation of body ash-free dry weights and maximum inhalant current velocities, the relationships between estimated filtration rates and body mass and between maximum current velocities and body mass were tested with a linear regression analysis. Differences between larval numbers above the oyster bed and larval numbers at the reference site were tested with an ANOVA. All statistical analyses were carried out with SYSTAT®9.

**Results**

***Inhalant feeding current velocity***

To locate inhalant and exhalant currents, velocities from the different analyses of the flow field of one oyster were combined manually in an overview picture (fig. 4). Locally, current velocities fluctuated highly. This is probably partially due to the undulating form of the shell edges, which causes the valve gape to fluctuate in width along the shell edge.

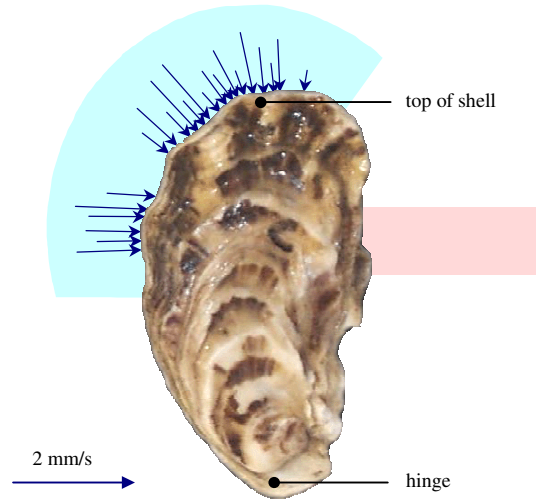



Figure 4: Different velocity analyses of the flow field of one oyster combined in one picture. Inhalant current velocities are depicted with arrows. In this picture, the flat valve is positioned in front. The light blue area along the shell edge indicates particle movement directed towards the shell. The pink area shows roughly where particle movement was directed from the shell.

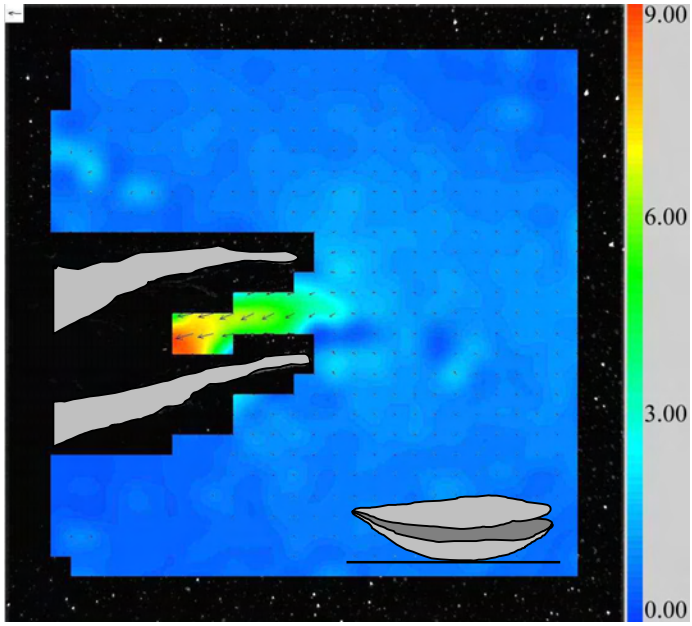



Figure 5: A magnitude plot of the velocities of an inhalant feeding current, as created in *Swift 4.0*. Velocities range from 0.00 mm/s in blue to 9.00 mm/s in red. The picture of 1000 x 1000 pixels was divided in 65 x 65 pixels interrogation areas. Per interrogation area, a velocity vector was calculated, as shown in this plot. Both shell valves are depicted in grey. The oyster is lying horizontally on its cupped valve (see inset in lower-right corner). Maximum current velocity (red) occurs inside the shell.

Analysis of flow velocities inside the shell cavity of larger oysters revealed higher velocities than at the shell-edge, where the water enters the shell-cavity (fig. 5).
Feeding current velocities at the shell-edge of oysters and mussels were in the same range, from 3.0 to 5.6 millimetres per second (table 1). The highest flow velocity found in oysters was 1.5 times higher than the highest flow velocity found in mussels. Maximum velocities of oyster feeding

currents increased significantly with individual oyster ash-free dry weights (fig. 6). The highest maximum velocity recorded inside the shell of a large oyster was 11.1 millimetres per second, approximately two times the maximum velocity recorded at the shell-edge.

Table 1: Maximum current velocities of inhalant feeding currents of oysters (*C. gigas*) and mussels (*M. edulis*).

| **species** | **length** | **afdw** | **max. velocity** | | | **n** |
|---|---|---|---|---|---|---|
| | | | *shell entrance* | *inside shell* | *range* | |
| | *(mm)* | *(mg)* | *(mm/s)* | *(mm/s)* | *(mm/s)* | |
| *C. gigas* | 81 | 428 | 3.2 | | 0.8 - 3.2 | 5 |
| " | 72 | 461 | 1.3 | | 0.7 - 1.3 | 9 |
| " | 163 | 1970 | 3.4 | 8.2 | 3.4 | 1 |
| " | 265 | 2991 | 3.2 | | 3.0 - 3.2 | 2 |
| " | 248 | 3580 | 4.5 | 9.0 | 2.2 - 4.5 | 3 |
| " | 153 | 4121 | 5.3 | | 1.2 - 5.3 | 3 |
| " | 280 | 4287 | 5.0 | 7.8 | 2.9 - 5.0 | 2 |
| " | 197 | 4666 | 5.6 | 11.1 | 1.7 - 5.6 | 8 |
| *M. edulis* | 60 | 221 | 3.0 | | 1.1 - 3.0 | 7 |
| " | 54 | 324 | 4.0 | | 1.2 - 4.0 | 4 |

Maximum inhalant feeding current velocities of oysters were significantly related to body mass according to a logarithmic formula (fig. 6). Plotting the maximum current velocity (mm/s) against body mass (g afdw) on a double logarithmic scale resulted in a positive linear relationship (linear regression analysis: $p<0.05$).

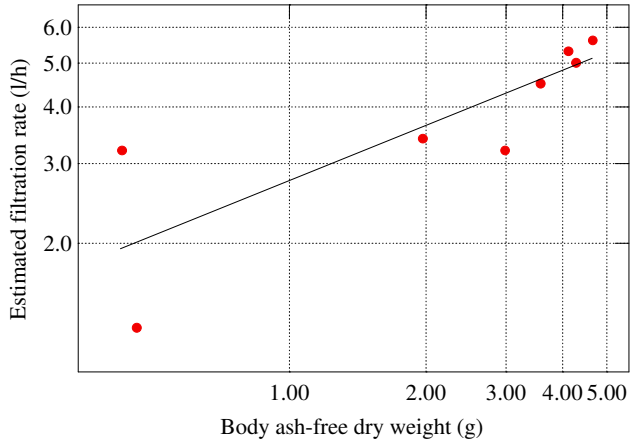



Figure 6: The logarithm of maximum inhalant current velocity was significantly and positively linearly related to the logarithm of body mass (linear regression: n=8, $p<0.05$).

### *Filtration activity*

Estimated oyster filtration rates ranged from 1 to 5 litres per hour per gram ash-free dry tissue weight (table 3). Estimated mussel filtration rates were 4.5 and 4.6 litres per hour. Estimated filtration rates of oysters were linearly and positively related to the logarithm of body mass (in grams ash-free dry weight) (fig. 7) according to the formula $FR=aW^b$ (eq. 1).

Table 3: estimated filtration rates for all oysters. Lengths and ash-free dry weights are also given. Filtration rates are shown in litres processed per oyster or per 1 g afdw in one hour.

| **length** | **ash-free dry weight** | **filtration rate** | |
|---|---|---|---|
| *(mm)* | *(g)* | *(l/h/oyster)* | *(l/h/g afdw)* |
| 81 | 0.63 | 2 | 3 |
| 72 | 0.70 | 1 | 1 |
| 163 | 2.67 | 10 | 4 |
| 265 | 4.59 | 14 | 3 |
| 248 | 5.35 | 26 | 5 |
| 153 | 5.48 | 15 | 3 |
| 197 | 5.91 | 16 | 3 |
| 280 | 6.04 | 24 | 4 |

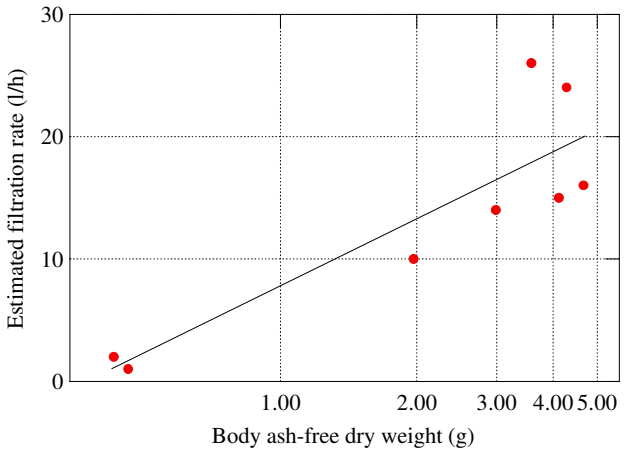



Figure 7: Estimated filtration rates were significantly and positively linearly related to the logarithm of body mass (linear regression: n=8, $p<0.05$).

### *Larval swimming speed*

Larval swimming speeds of various bivalves were obtained from the literature (table 2).

Table 2: Swimming speeds of bivalve veliger larvae.

| **Species** | **size** | **swimming speed** | **reference** |
|---|---|---|---|
| | *(µm)* | *(mm/s)* | |
| *Arctica islandica* | - | 0.75 *(mean)* | Mann & Wolf, 1983 |
| *Crassostrea virginica* | > 240 | 2.3 *(max.)* | Hidu & Haskins, 1978 |
| *Crassostrea virginica* | - | 10.0 *(max.)* | Wood & Hargis, 1971 |
| *Mercenaria mercenaria* | - | 0.13 *(mean)* | Carriker, 1961 |
| *Mytilus edulis* | - | 1.1 *(mean)* | Konstantinova, 1966 |
| *Pecten maximus* | 250 | 2.2 *(max.)* | Cragg, 1980 |
| *Spisula solidissima* | > 150 | 0.5 *(max.)* | Mann *et al.* , 1991 |

Highest swimming speeds were found for *Crassostrea virginica* and *Pecten maximus*. *Mytilus edulis* was found by Konstantinova (1966) to swim with a speed of 1.1 millimetres per second, which will not be enough to be able to escape feeding currents of both *Crassostrea gigas* and *Mytilus edulis*. No swimming speeds were found for *Crassostrea gigas.*

### *Fluid deformation rate*

After analysis of images in *Swift 4.0*, plots of fluid deformation rates were created. This was done for oysters and mussels and the location and magnitude of the highest fluid deformation rates were

compared (fig. 7A-B). For mussels, highest fluid deformation rates can be seen clearly just outside the shell entrance, whereas oysters show highest fluid deformation rates inside the shell.

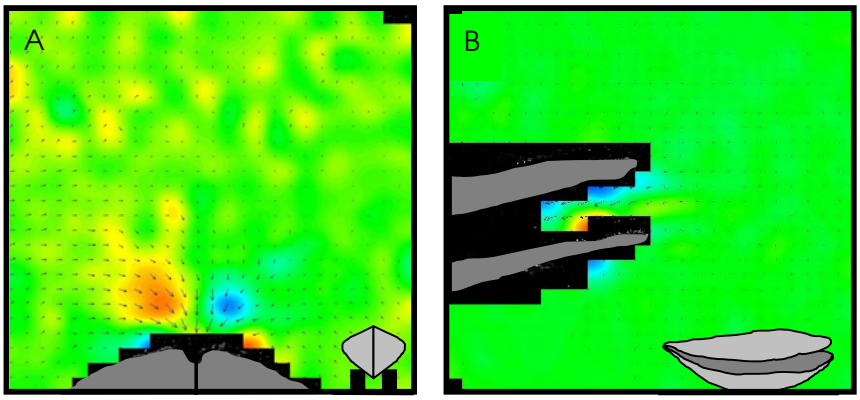
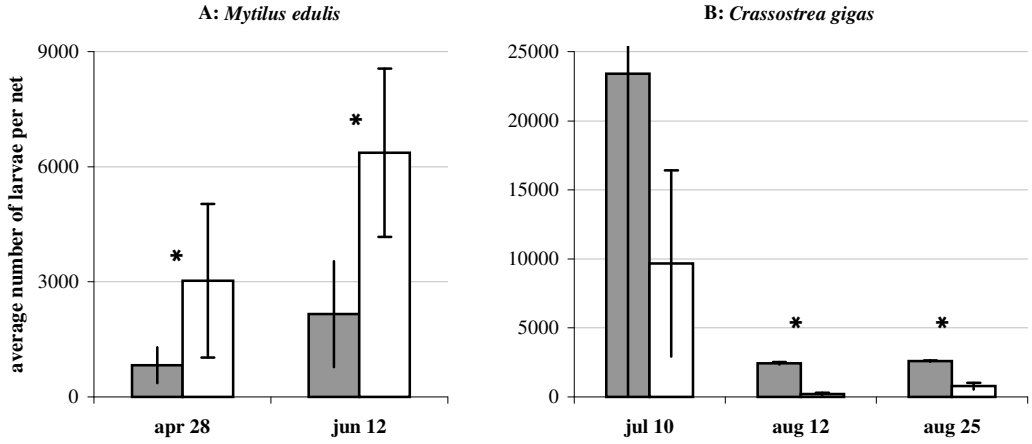



Figure 7: Fluid deformation rate plotted for a mussel (A) and an oyster (B). The mussel is lying horizontally, its valves oriented vertically. The oysters is lying horizontally, its valves also oriented horizontally. For both, the valves are drawn schematically in grey. Maximum fluid deformation rates are depicted with either red or blue. Red denotes a change in direction to the right, whereas blue shows a change in direction to the left. Lowest fluid deformation rates are shown in bright green.

### *Field observations*

In April and June, mainly mussel larvae were found in the plankton samples. Above oyster beds, significantly less mussel larvae were found than above the bare reference sites (figure 8). In July and August, mainly oyster larvae were found. These numbers show the opposite pattern: significantly more larvae were counted above the oyster bed, on two out of three comparisons.




Figures 8: average number of mussel (A) and veliger larvae caught per plankton net (n=4) with standard deviation. Numbers counted above oyster beds are shown in grey, numbers counted above bare flats nearby are shown in white bars. Significant differences between oyster beds and bare flats are depicted with a star (ANOVA, $p<0.05$).

## Discussion and conclusion

### *Inhalant feeding current velocities*

Higher current velocities were found in oysters (5.6 mm/s) than in mussels (4.0 mm/s). Green *et al.* (2003) analysed the flow field of mussels (*Mytilus edulis*) and found maximum inhalant feeding current velocities of about 5.0 to 6.0 mm/s. These values are in the same range as the values found for both species in the present study. Green *et al.* studied their mussels in September at a water temperature of 17°C whereas we studied our animals in November with a water temperature of 15°C. The slightly higher values found by Green *et al.* might be due to differences in temperature, season or the type of food offered between the two studies. The number of animals studied was

comparable but low. Green *et al.* used one mussel to map the flow field whereas we used two individuals. In a follow-up study, more mussels will be added to the present observations, as well as cockles (*Cerastoderma edule*).
The velocity of inhalant feeding currents increased significantly with the body weight of oysters. In order to make a more reliable comparison between oysters and mussels, this relationship should also be established for mussels.

***Swimming speeds veliger larvae***
For *M. edulis*, an average swimming speed of 1.1 millimetres per second was found, which is too slow to be able to swim against the inhalant feeding currents of adult oysters and mussels. Although maximum swimming speeds of mussels will be higher than the mean value of 1.1 given by Konstantinova (1966), they are not likely to exceed the maximum feeding current velocities found in this study. Swimming speeds of *C. gigas* are yet unknown, but might resemble swimming speeds of their relatives, *C. virginica* oyster larvae, with average swimming speeds of up to 10.0 millimetres per second (found by Wood and Hargis, 1971). Velocities of about 10.0 millimetres per second would allow oyster larvae to escape feeding currents of mussels and oysters. In a follow-up study, swimming speeds of *C. gigas*, *M. edulis* and *C. edule* will be determined using Particle Tracking Velocimetry (see Stamhuis and Videler, 1995).

***Fluid deformation rate***
Differences in the situation of highest fluid deformation rates near the shell opening suggest that feeding currents of oysters (outside the shell) are more diffuse than feeding currents of mussels. Thus, it is very well possible that veliger larvae detect mussel feeding currents earlier than oyster feeding currents, maybe allowing them to swim away in time or to induce an escape response. It has been shown in many studies that escape responses of copepod nauplii are triggered by critical fluid deformation rates in the flow field of artificial (suction pipette) and natural predators (summarized by Green *et al.*, 2003). Critical fluid deformation rates vary per copepod species (Green *et al.*, 2003). The same may be true for different species of bivalve veligers. Therefore, escape responses of veliger larvae of *Mytilus edulis*, *Cerastoderma edule* and *Crassostrea gigas* to inhalant feeding current velocities will be studied in future experiments.

***Filtration activity***
Estimated oyster filtration rates ranged from 1 to 5 litres per hour per gram ash-free dry tissue weight, while literature values ranged from 0 to 17 litres per hour (Bougrier *et al.*, 1995; Dupuy *et al.*, 2000; Gerdes, 1983; Walne, 1972). Estimated mussel filtration rates were 4.5 and 4.6 litres per hour per gram ash-free dry weight while literature values ranged from 0 to 11 litres per hour (Foster-Smith, 1975; Møhlenberg and Riisgård, 1979; Petersen *et al.*, 2004; Riisgård. and Møhlenberg, 1979; Walne, 1972; Winter, 1973). Although the estimated filtration rates fit within ranges found in literature, particularly those of oysters are rather low. Due to experimental conditions and minor disturbances, filtration activity of oysters might have been inhibited, yielding lower maximum feeding current velocities. We observed that oysters are more sensitive to small disturbances than mussels. When disturbed, they temporarily reduce their valve gape width or close their shell entirely. Estimated filtration rates were however significantly and positively related to oyster body mass according to the allometric equation (eq. 2). This means that all oysters performed relative to their body mass, indicating they performed without being hampered.

***Field observations***
Counts of mussel larvae support the hypothesis that adult oysters filter significant amounts of mussel larvae. Recruitment of mussels might be reduced because by the filtration activity of oysters. However, there is still a possibility that the observed difference in larval numbers between the oyster bed and the reference location was caused by differences in local hydrodynamics. In the oyster bed, mussel larvae may have sunk passively to the bottom or settled actively on the hard substrate provided by oyster shells. This explanation, on the other hand, is contradicted by the observation that oyster larvae showed the opposite pattern. If local hydrodynamics facilitate sinking or settlement of mussel larvae, then sinking or settlement of oyster larvae should be facilitated in

the same way, at the same locations. It is not yet clear why we found significantly more oyster larvae above the oyster bed than above the bare flat. Maybe the larvae were produced in the same oyster bed as they were sampled. Another possibility is that they congregate above the oyster bed, attracted by chemical cues, in order to settle there.

### *Conclusions*

Concluding, adult oysters as well as oyster larvae have an advantage over their mussel counterparts. Inhalant feeding currents of oysters are more difficult to detect for bivalve veliger larvae than inhalant feeding currents of mussels. If an escape response is triggered by a critical fluid deformation rate, veliger larvae will be more vulnerable to oyster predation than to mussel predation. If *Crassostrea gigas* larvae swim approximately as fast as their relative *C. virginica*, oyster larvae will be less vulnerable to predation by mussels and oysters than mussel larvae.


### Acknowledgements

We thank Jos de Wiljes for his assistance in the laboratory at the Biological Centre in Haren. We are also grateful to Daniël Blok for his help in the field, and to Jaap Poelman, Ad van Gool and Iris Hendriks for their help in identifying the different species of bivalve veligers. This project was funded by the Netherlands Organisation for Scientific Research (NWO).


### References


André, C., P. R. Jonsson and M. Lindegarth, 1993: "Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour." *Marine Ecology Progress Series 97: 183-192.*

Anonymous, 1999: "Resultaten monitoring." *Jaarboek Monitoring Rijkswateren 1999 Kroniek. R. RIKZ: 47.*

Armonies, W., 1994: "Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review." *Helgoländer Meeresuntersuchungen 48: 299-320.*

Bayne, B. L., 1969: "The gregarious behaviour of the larvae of *Ostrea edulis* L. at settlement." *Journal of the Marine Biological Association of the United Kingdom 49: 327-356.*

Bougrier, S., P. Geairon, J. M. Deslous-Paoli, C. Bacher and G. Jonquières, 1995: "Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg)." *Aquaculture 134: 143-154.*

Bult, T. P., B. J. Ens, R. L. P. Lanters, A. C. Smaal and L. Zwarts, 2000: "Korte termijn advies voedselreservering Oosterschelde. Samenvattende rapportage in het kader van EVAII." RIKZ, Alterra, RIVO, RIZA, *RIKZ/2000.042.*

Bult, T. P. and J. J. Kesteloo, 2001: "Het kokkelbestand in de Nederlandse kustwateren in 2001." *RIVO rapport C041/01.*

Craeymeersch, J. A., J. J. Kesteloo and P. Kamermans, 2000: "Het kokkelbestand in de Oosterschelde, de Westerschelde, de Waddenzee en de Voordelta in het voorjaar van 2000." *RIVO rapport C022/00.*

Cragg, S. M., 1980: "Swimming behaviour of the larvae of *Pecten maximus* (L.) (Bivalvia)." *Journal of the Marine Biological Association of the United Kingdom 60: 551-564.*

Dankers, N. M. J. A., E. M. Dijkman, M. L. de Jong, G. de Kort and A. Meijboom, 2004: "De verspreiding en uitbreiding van de Japanse Oester in de Nederlandse Waddenzee." *Alterra rapport 909.*

Drinkwaard, A. C., 1999: "Introductions and developments of oysters in the North Sea area: a review." *Helgoländer Meeresuntersuchungen 52: 301-308.*

Dupuy, C., A. Vaquer, T. Lam-Höai, C. Rougier, N. Mazouni, J. Lautier, Y. Collos and S. Le Gall, 2000: "Feeding rate of the oyster *Crassostrea gigas* in a natural planktonic community of the Mediterranean Thau Lagoon." *Marine Ecology Progress Series 205: 171-184.*

Foster-Smith, R. L., 1975: "The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupsis pullastra* (Montagu)." *Journal of Experimental Marine Biology and Ecology 17: 1-22.*

Gerdes, D., 1983: "The Pacific oyster *Crassostrea gigas*. Part I. Feeding behaviour of larvae and adults." *Aquaculture 31: 195-219.*

Green, S., A. W. Visser, J. Titelman and T. Kiørboe, 2003: "Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*." *Marine Biology 142:727-733.*

Hiddink, J. G., 2002: "The adaptive value of migrations for the bivalve *Macoma balthica*." Institution, *PhD Thesis.*

Hidu, H. and H. H. Haskins, 1978: "Swimming speeds of oyster larvae of *Crassostrea virginica* in different salinities and temperatures." *Estuaries 1: 252-255.*

Jones, H. D., O. G. Richards and T. A. Southern, 1992: "Gill dimensions, water pumping rate and body size in the mussel *Mytilus edulis* L." *Journal of Experimental Marine Biology and Ecology 155: 213-237.*

Kater, B. J., J. M. D. D. Baars and M. v. Riet, 2002: "Japanse oesters in de Oosterschelde: Reconstructie van oppervlakten in het verleden en schatting van het huidige oppervlak." *RIVO rapport C017/03*

Konstantinova, M. I., 1966: "Characteristics of movement of pelagic larvae of marine invertebrates." *Doklady Akademii Nauk SSSR 170: 726-729.*

Kristensen, I., 1957: "Differences in density and growth in a cockle population in the Dutch Wadden Sea." *PhD Thesis, University of Leiden, the Netherlands.*

Mann, R., 1988: "Distribution of larvae at a frontal system in the James River, Virginia." *Marine Ecology Progress Series 50: 29-44.*

Mann, R., B. M. Campos and M. W. Luckenbach, 1991: "Swimming rate and responses of larvae of three Mactrid bivalves to salinity discontinuities." *Marine Ecology Progress Series 68(3): 257-269.*

Mann, R. and C. C. Wolf, 1983: "Swimming behaviour of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature." *Marine Ecology Progress Series 13: 211-218.*

Møhlenberg, F. and H. U. Riisgård, 1979: "Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves." *Marine Biology 54: 143-147.*

Petersen, J. K., S. Bougrier, A. C. Smaal, P. Garen, S. Robert, J. E. N. Larsen and E. B. M. Brummelhuis, 2004: "Intercalibration of mussel *Mytilus edulis* clearance rate measurements." *Marine Ecology Progress Series 267: 187-194.*

Quayle, D. B., 1964: "Distribution of introduced marine mollusca in British Columbia waters." *Journal of the Fisheries Research Board of Canada 21: 1155-1181.*

Reise, K., 1998: "Pacific oysters invade mussel beds in the European Wadden Sea." *Senckenbergiana Maritima 28: 167-175.*

Riisgård, H. U., 1988: "Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves." *Marine Ecology Progress Series 45: 217-223.*

Riisgård., H. U. and F. Møhlenberg., 1979: "An improved automatic recording apparatus for determining the filtration rate of mytilus edulis as a function of size and algal concentration." *Marine Biology 52: 61-67.*

Schaub, B., D. v. Oevelen, W. Sistermans, M. Rietveld, P. M. J. Herman and H. Hummel, 2002: "Veranderingen in de samenstelling van het macrobenthos van het Grevelingenmeer (periode 1990-2002) en mogelijke oorzaken." *NIOO-CEMO rapport, 2002-01.*

Smies, M. and A. H. L. Huiskes, 1981: "Holland' s Eastern Scheldt estuary barrier scheme: some ecological considerations." *Ambio 10: 158-165.*

Stamhuis, E. J. and J. J. Videler, 1995: "Quantitative flow analysis around aquatic animals using laser sheet particle image velocimetry." *Journal of Experimental Marine Biology and Ecology 198: 283-294.*

Stamhuis, E.J., J.J. Videler, L.A.van Duren and U.K. Müller, 2002: "Applying digital particle image velocimetry to animal-generated flows: Traps, hurdles and cures in mapping steady and unsteady flows in *Re* regimes between $10^{-2}$ and $10^{5}$." *Experiments in Fluids 33: 801-813.*

Tamburri, M. N. and R. K. Zimmer-Faust, 1996: "Suspension feeding: basic mechanisms controlling recognition and ingestion of larvae." *Limnology and Oceanography 41: 1188-1197.*

Walne, P. R., 1972: "The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves." *Journal of the Marine Biological Association of the United Kingdom 52: 345-374.*

Winter, J. E., 1973: "The filtration rate of *Mytilus edulis* and its dependence on algal concentration, measured by a continuous automatic recording apparatus." *Marine Biology 22: 137-328.*

Winter, J. E., 1978: "A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems." *Aquaculture 13: 1-33.*

Wood, L. and W. J. Hargis, 1971: "Transport of bivalve larvae in a tidal estuary." *Proceedings of the fourth European Marine Biology Symposium, Bangor,1969 (ed. D. J. Crisp), 29-44. Cambridge University Press.*