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Food competition between *Crassostrea gigas* and *Mytilus edulis* in the Oosterschelde estuary

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Summary

The Pacific oyster (*Crassostrea gigas*) is an invasive species in the Oosterschelde estuary. It was originally brought there to replace the native flat oyster *Ostrea edulis* which had been greatly reduced in numbers due to diseases and parasites. Because of some hot summers the pacific oyster could spawn, spreading throughout the Oosterschelde estuary. The pacific oyster now spawns in most years and continues to increase in number. This might cause competition with other filterfeeding bivalves that have commercial and ecological importance. That is why it is important to know how the oyster and these bivalves respond to competition for food. The blue mussel *Mytilus edulis* was chosen for this research because it is easy to use in the set-up. The goal is to find out how the mussels and the oysters respond to low food availability and how they fare in competition. Food availability was influenced by three factors; the biomass of the oysters around the experiment location, the tidal height of the location and the distance from the edge of the oyster bed of the location. For oysters the oyster biomass around the location had a significant negative effect on growth. A high biomass around the location caused lower growth. The distance from the edge of the oyster bed also had a significant negative effect on growth. Locations that were further into the oyster bed had lower growth. For the mussels no significant effects were found. The mussel data was a bit odd, with only condition decreases and very high standard deviations. Due to this no comparison could be made between the two species, thus no conclusions could be drawn about the competition between the two species.

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1. Introduction

The Oosterschelde estuary is an important area for the cultivation of oysters in the Netherlands. Traditionally the European flat oyster (*Ostrea edulis*) was used for this, but after the severe winter of 1962 – 1963 their numbers were reduced from 120 to 4 million. Because of this oyster growers started looking for alternatives. In 1964 the Pacific oyster (*Crassostrea gigas,* figure 1) was imported, both by a Dutch oyster farmer and the Molluscan Shellfish Department of the Netherlands Institute for Fishery (Drinkwaard 1999). It seemed a good alternative since it grew well in the Oosterschelde estuary, and it was unable to reproduce itself because the water temperatures were assumed to be too low. In the original plan for the Delta Project the Oosterschelde estuary would be closed off completely from the sea in the year 1978. It would then become a stagnant lake in which the water would slowly lose its salinity, an environment in which the oysters cannot survive. In 1974 this plan was changed because of pressure from conservationists and

Figure 1. *Crassostrea gigas*

the shellfish industry. The Oosterschelde estuary would remain open to the sea (Nienhuis & Smaal 1994). From 1964 onward the Pacific oyster was imported every year, but most oyster farmers still used the flat oyster, which they imported from Brittany, Ireland and the Adriatic sea. This became more and more difficult, as "Abers disease" was spreading through all the flat oyster populations. By 1975 this disease was present in all major oyster regions in France. Then, in 1976 there was a very hot summer which resulted in the Pacific oysters spawning. The larvae settled throughout the Oosterschelde estuary. This caused much objections by oyster farmers and nature conservationists (Drinkwaard 1999). By the end of 1976 importing Pacific oysters was prohibited. For several years the oyster industry ran on imported flat oysters. In 1980 there was another setback for cultivation of the European flat oyster. The *Bonamia ostrea* parasite was discovered in the French populations of flat oysters (Pichot et al. 1979). The parasite causes mortality among the flat oysters. The parasite also appeared in the Oosterschelde estuary and remains there still. The continued presence of this parasite is one of the reasons flat oysters have never recovered their numbers. In july 1982 there was a new natural spawning of the Pacific oysters it became so widespread, and flat oysters were so rare that most oyster growers now switched to growing Pacific oysters. It was then also accepted that the Pacific oyster was an established part of the ecosystem in the Oosterschelde estuary (Drinkwaard 1999). After this the Pacific oysters spawned almost every year and quickly covered large areas of the intertidal area of the Oosterschelde estuary. In 1990 oyster beds covered 2.9 square kilometres of the intertidal area of the Oosterschelde estuary, in 2002 this was 6.4 square kilometre (Kater et al. 2002).

The rapid spread of the Pacific oyster will be a problem when their numbers are so high that their numbers will put a constraint on food availability. At the current rate of growth this may soon happen. The Pacific oyster is a filter feeder, its food competition is mostly with other bivalve filter feeders. Examples of these are the cockle (*Cerastoderma edule*) and the blue mussel (*Mytilus edulis,* figure 2). These other bivalves are of both economic and ecological significance to the Oosterschelde estuary area. For this research the blue

Figure 2. *Mytilus edulis*

mussel was chosen, because of all the native bivalve species it is the one that is easiest to use in this type of experiments.

This leads to the research questions: what is the influence of food availability on growth in Pacific oysters and blue mussels? How do these two species respond to low food availability? Is there competition between these two species at low food availability?

It is expected that the Pacific oyster will be less affected by low food availability than the blue mussel. This is because the Pacific oyster has a much higher filtration rate than the blue mussel. The blue mussel has a filtration rate of 0.4 – 9.1 litre per hour per individual (Foster-Smith 1975, Walne 1975, Smaal 1997), while the oyster has a filtration rate of 3.0 – 25.0 litre per hour per individual (Walne 1975, Dupuy et al. 2000). This means that on average the Pacific oysters filter a lot more water than the blue mussels. Under food limitation that means oysters get a bigger share of the available food.

In order to have locations with different food availability, it was decided to set the experiment up in an oyster bed. Three factors were identified that influenced food availability within an oyster bed. The first is local oyster biomass. This is the biomass of oysters and any other filterfeeders found at a location. The higher the biomass, the higher the competition and the less growth is expected for all species (Peterson & Beal 1989, Rheault & Rice 1996, Honkoop & Bayne 2002). The second factor is tidal height. Tidal height determines for how long a location will be covered with water each day. Thus it determines the time available for filtration. High tidal height means relatively less time for filtration, low tidal height means relatively more time for filtration. So higher growth is expected with lower tidal height (Peterson & Black 1988, McQuaid et al. 2000). The last factor is distance from the edge of the oyster bed. The further a location is from the edge of the oyster bed, the further the water has to travel across the oysters. Since all the oysters are feeding, the amount of food in the water is expected to be reduced as it passes over more oysters.

2. Materials and Methods

2.1 Location choice

The oyster bed at the Zandkreek (figure 3) was selected because it was easily accessible from land and had clearly defined zones of oyster density. Oyster density is an indication of local oyster biomass, so different zones of oyster density means different local oyster biomass values. Tidal height and distance from the edge of the oyster bed could also be incorporated into the experimental set-up at this location.
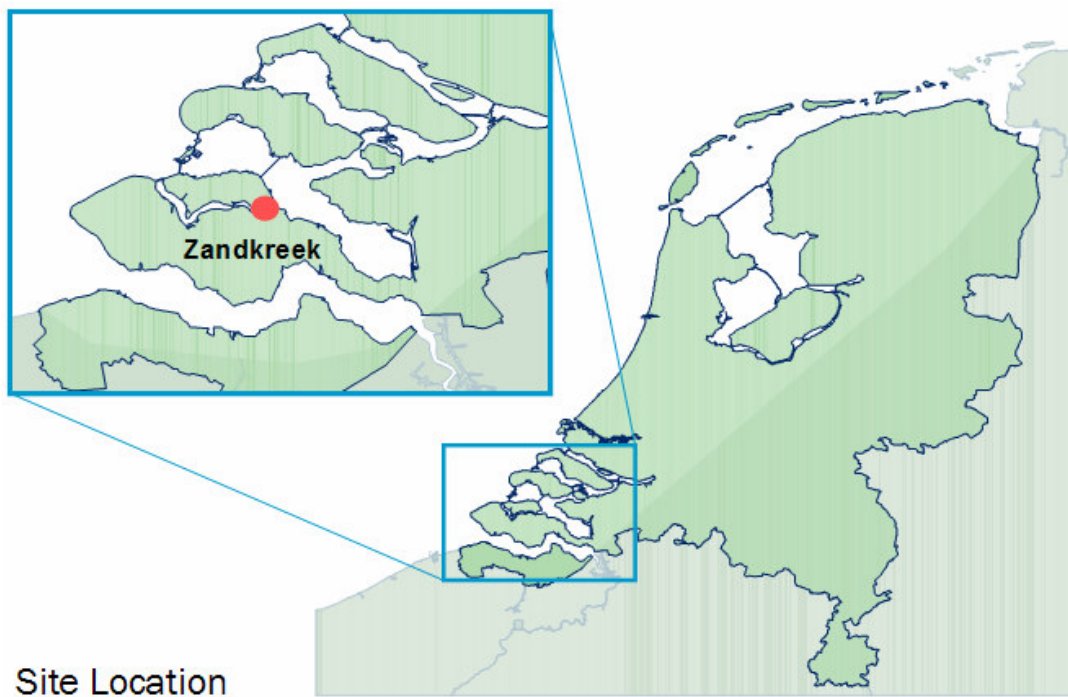

Figure 3. Location of the Zandkreek within the Netherlands.

2.2 Set-up

Selection of the experiment locations within the oyster bed

The oyster bed was mapped with GPS (Global Positioning System). These GPS coordinates were then loaded into the Arcview software, which created a map based on these coordinates. Using this map of the oyster bed and the different densities within it the locations for the experiment were selected (figure 4). The selection of the locations was based on the three factors; tidal height, distance from the edge of the oyster bed and local oyster biomass. All four series were placed in such a way that every locations in the series was at a different oyster density (as explained before, oyster density is expected to be indicative of the oyster biomass). Series 2, 3 and 4 were all set up so that even though the locations in each series were at different densities all the locations in a series were at the same distance from the edge of the oyster bed. This resulted in a connection between biomass and tidal height. With this set up the lowest density was always at the greatest height. In order to distinguish between biomass and tidal height series 1 was set up differently. Distance from the edge of the oyster bed was ignored for this series, it was set up so that all locations in the series were at roughly the same height (figure 4). The coordinates of these location were then loaded into the GPS and the GPS was used to find these locations in the field.
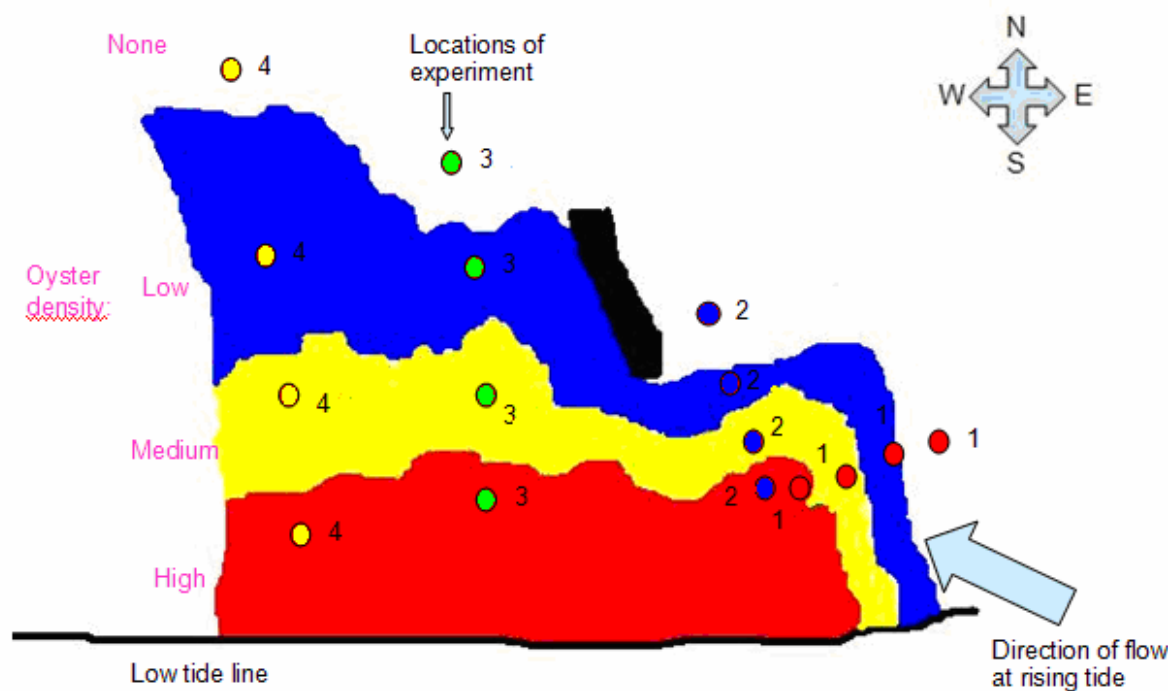
Figure 4. The Gis map of the oyster bed. The red area is the area of high density. The yellow area is the area of medium density. The blue area is the area of low density. The white area is the area of no density. The black shape is a pier that extended right up to the oyster bed. The black line at the bottom indicates the low tide line. The dots represent the locations for the experiment. The red dots are series 1, the blue dots are series 2, the green dots are series 3 and the yellow dots are series 4. The arrow at the bottom right indicates the direction of the tidal flow at rising tide. This direction was determined using flow maps obtained from Cees van de Male at the National Institute for Coastal and Marine Management (see appendix 1).

Experimental animals

To measure the effects of food availability oysters and mussels were put in the field and their growth measured. To be able to protect them from predation and to be able to find them again in the field they were put in the field in plastic cages. These were round cages with mesh sizes of about 1 cm, a diameter of 50 cm and four compartments (figure 5). One cage was placed at each location, leading to 16 cages in total (figure 6). Oysters were already available at the RIVO, from a batch that had been ordered from a hatchery in England. They had been in a basin at the RIVO for six weeks. Oysters between 2.5 and 4.0 cm were selected for the experiment. Mussels were collected in the Wadden Sea and transported dry and cooled to the RIVO. Mussels between 3.5 and 4.0 cm were selected. To determine how many oysters and mussels were needed for the experiment power calculations were performed, using data on length and weight of both oysters and mussels supplied by Willemijn Noordoven from the NIOO and Jobine Glerum from the RIVO. For oysters a larger number was needed to get sufficient statistical power than for mussels. Because of that more the experimental set-up contains more oysters than mussels. Furthermore it was decided to mark part of the oysters so that individual growth could be measured. By measuring individual growth it is possible to get higher power in the statistical analysis. Oysters were marked by gluing small glass beads to the shells using superglue (cyanoacrylate). The number of animals in each cage was 20 mussels and 40 oysters. Of these oysters 20 were marked. 100 mussels and 100 oysters were kept in the lab to determine the starting condition (shell length, weight and ashfree dryweight).
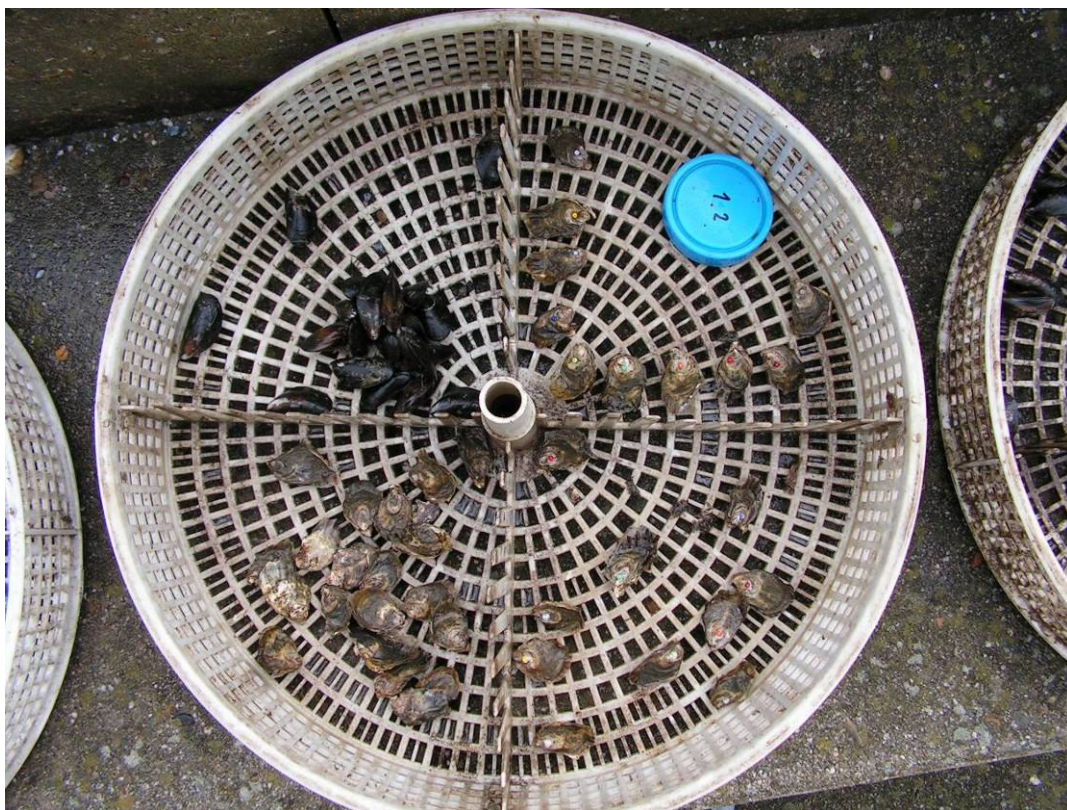
Figure 5. Experiment cage containing 20 mussels, 20 oysters and two sets of 10 marked oysters.

Figure 6. Experiment cage in the field.

2.3 Measuring factors that determine food-availability

Biomass around the cages

The local oyster biomass was determined by removing all animals from a ¼ m² quadrant. This quadrant was placed on a concentration of oysters that filled up the quadrant as much as possible. The percentage of the quadrant that had oysters in it was estimated so that the biomass of a full ¼ m² quadrant could later be calculated. All the oysters in the quadrant were then collected. These quadrants were taken at about 4 meters from the cages so the biomass near the cages remained undisturbed.
The samples were taken back to the lab and the living oysters and mussels were then selected from the sample. The dead material was discarded. The living oysters and mussels were taken from their shells and dried for three days at 70 ˚C. After this their dryweight was determined. They were then put in an oven at 560 ˚C, turning their remains to ash. After this their ashweight was determined. From dryweight minus ashweight the ashfree dryweight (afdw) was calculated. The afdw is a measure of the biologically active portion of the weight. That is why it is a suitable indicator of the biomass around the cages. This biomass in grams of afdw was then used to calculate the biomass per m². This was done by using the percentage coverage in the quadrant to calculate what the biomass would be at full coverage, and then multiplying by four to get one square metre. This did not give the biomass around the cages yet, for that the percentage coverage around the cages was needed. That was estimated by using a 1 m² framework with a number of lines crossing it. These lines had 36 intersections. The coverage was estimated by putting the framework down at each of the four corners of the cage and counting underneath how many of the intersections oysters were located. Combining this percentage coverage with the biomass per m² gave the oyster coverage immediately around the cages. But since it was unknown if the oyster coverage immediately around the cage had the most influence, the coverage estimate was also repeated by taking estimates at four randomly selected locations at a five meter distance from the cage. This was to allow for a comparison between the importance of local scale food limitation and larger scale food limitation. From this a biomass value for immediately around the cages was calculated, as well as a biomass value for five meters from the cages and an average biomass value from these two. The value derived from the oyster surface coverage directly around the locations is called biomass 1. The value derived from the oyster surface coverage at five meters distance is called biomass 3. The average of these two is called biomass 2. In the calculation of the average biomass 1 and biomass 3 did not have an equal weight. Since all four coverage measurements at the location were essentially taken on the same spot, it was decided to treat them as one single measurement. The four measurements taken at five meters distance were all taken at different locations, not immediately next to each other. So biomass 2 was calculated according to this formula: biomass 2 = (biomass 1 + (biomass 3 * 4))/5.
Infauna was also sampled by taking three soil samples per location with a core sampler that had a diameter of 10 cm. But at only one of the locations infauna was found, and that was only one individual. So the infauna was present at such low levels that it was not taken into account for the calculations of bivalve filter-feeder biomass.

Distance from the edge of the oyster bed

The Gis map of the oyster bed that was made earlier was used to determine the distances of each location to the edge of the oyster bed. For this the average direction of flow at rising tide was needed. This direction was determined using flow maps obtained from the National Insitute for Coastal and Marine Management. These maps showed the direction of flow at rising tide for every half hour (see appendix 1 for an example). By taking the average of all these directions the average direction of flow at rising tide was obtained. The distance of each point to the edge of the oyster bed along the lines of the direction of flow at rising tide was then measured on the Gis map. The scale of the Gis map was then used to calculate the distance in meters of each location to the edge of the oyster bed.

Tidal Height

The height was determined relative to the NAP (National Amsterdam Level). To do this the measurements were started at a beacon near the experiment site. This particular beacon was a metal bolt set in the wall of a nearby farm by the Dutch Kadaster. The Kadaster also has the height compared to NAP of each of their beacons on file. By transferring this fixed point using a levelling instrument the height of all the locations relative to NAP was determined.

2.4 Total particulate matter and chlorofyl a

These samples had to be taken with water high over the oyster bed, so it was necessary to take them by boat. Water samples were taken with a pump at a number of locations that were determined in advance using the Gis map of the oyster bed. These locations were then loaded into the GPS to find them more easily. The locations were chosen along a transect of the oyster bed (figure 7). Two samples were taken at each location, one for suspended matter analysis and one for chlorofyl a analysis. Some locations were sampled twice. The samples consisted of 1 litre bottles of water taken between 10 and 20 centimetres above the sediment. The total particulate matter (TPM) analysis was done by filtering the water across a Whatman GF/C filter which was weighed in advance. This filter was then dried for three days at 70 ˚C and weighed again. The weight of the filter with the suspended matter minus the weight of the filter gave the dryweight of the suspended matter. The chlorofyl a samples were processed by the analysis facilities of the Centre for Estuarine and Marine Ecology of the NIOO-KNAW, but those data were lost.
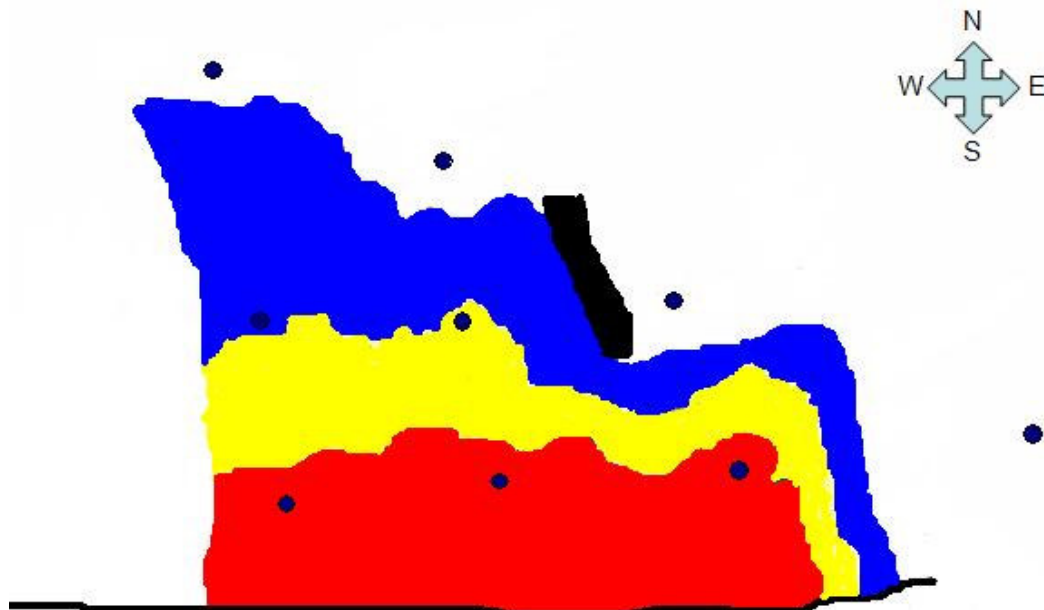

Figure 7. Sampling points for total particulate matter and chlorofyl a samples. The black line is the low water line. The red outline is the high density part of the oyster bank. The yellow outline is the medium density part and the blue outline is the low density part. The dark blue dots are the sampling points.

2.5 Growth experiment

The ashfree dry-weight of the 100 mussels and 100 oysters for the starting conditions was determined using the same method as was described for the local oyster biomass. Ashfree dry-weight was used here because it is possible that some of the animals will decrease in condition over the course of the experiment. The ashfree dryweight will actually also show such decreases, while other weight measures might not show such effects.

The cages were left in the field for two months (from July 25 to Oktober 10,2005). After that they were collected from the field and taken back for analysis. All the animals were weighed and measured. After that their ashfree dry-weight was also determined. Their growth was calculated as the difference in ashfree dry-weight between the start and the end of the experiment.

2.6 Statistical analysis

All data was tested in Systat. Relations between factors were tested using linear regression. The effects of the factors on growth was tested using ANOVA and General Linear Model, with the results of the General Linear Model being used. All tests had a significance level of 0.05.

3 Results

3.1 Factors

For each location the values of the factors were determined, the factors being: the tidal height, distance from the edge of the oyster bed and average local oyster biomass. As expected from the set-up, the tidal height was almost constant for the first series, but differed for series 2, 3 and 4 (figure 8). The distance from the edge was almost constant in series 2, 3 and 4, but differed for series 1 (figure 9). Average local oyster biomass also showed the predicted pattern. The high density locations have high average oyster biomass, the medium density locations have medium average oyster biomass, the low density locations have low average oyster biomass and the none density locations have little to no average oyster biomass (figure 10). Also, series 1, the one closest to the edge of the oyster bed, seems to have higher average oyster biomass values than series 3 and 4, which are farther from the edge.

All graphs show the biomass 1 values for local oyster biomass and all calculations were done using the biomass 1 values as well. To test if it was really the most suitable value to use the General Linear Model (GLM) was applied to the data using all three values for local oyster biomass. For oysters it proved to have no difference, for all three of the local oyster biomass values the p value was highly significant ($p < 0.001$). For mussels it also made no difference, all three biomass values did not have significant effects.
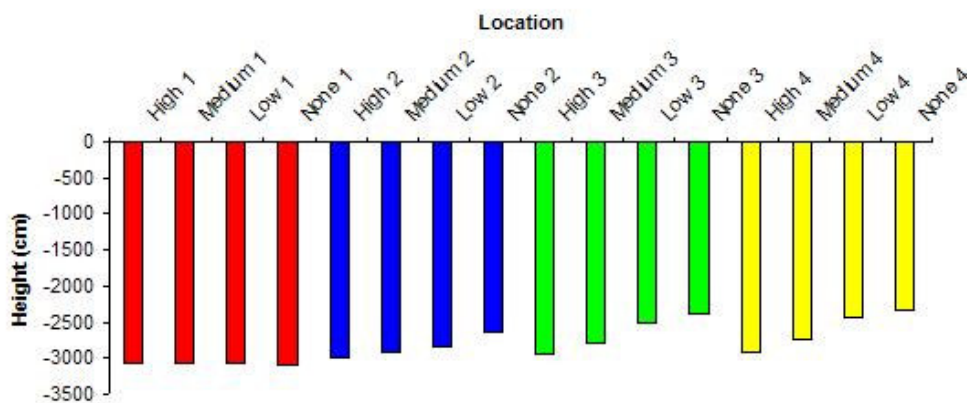

Figure 8. Tidal height per location (in) cm compared to NAP. Each series was given a different colour, red for series 1, blue for series 2, green for series 3 and yellow for series 4.
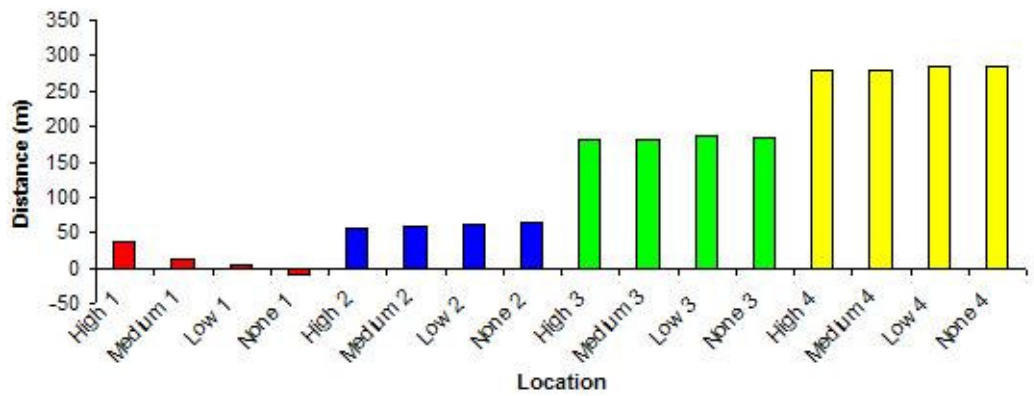
Figure 9. Distance from the edge of the oyster bed (in meters) for each location. Series 1 is indicated in red, series 2 in blue, series 3 in green and series 4 in yellow.
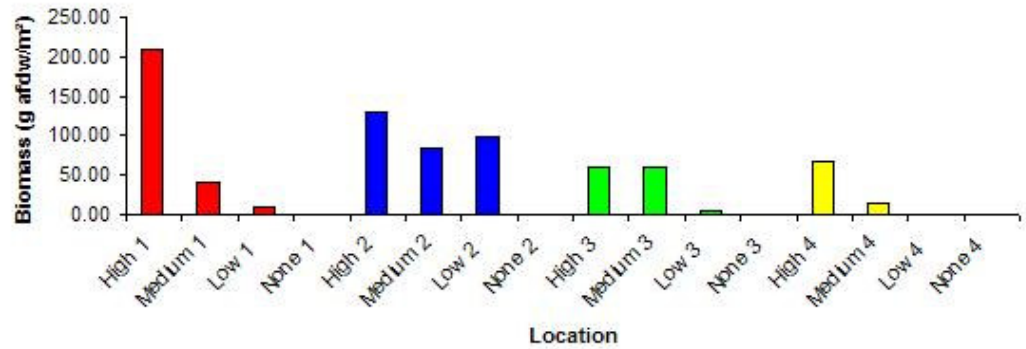

Figure 10. Average local oyster biomass per location (in grams of ashfree dryweight) per m^2. Series 1 is indicated in red, series 2 in blue, series 3 in green and series 4 in yellow.

Correlation between the factors was also tested. This showed some relations between the factors. Local oyster biomass was significantly lower at locations with greater tidal height (figure 11). Local oyster biomass was lower at locations with higher distance from the edge (figure 12), although this relation was not significant. Locations at higher tidal height were also significantly farther from the edge of the oyster bed (figure 13).
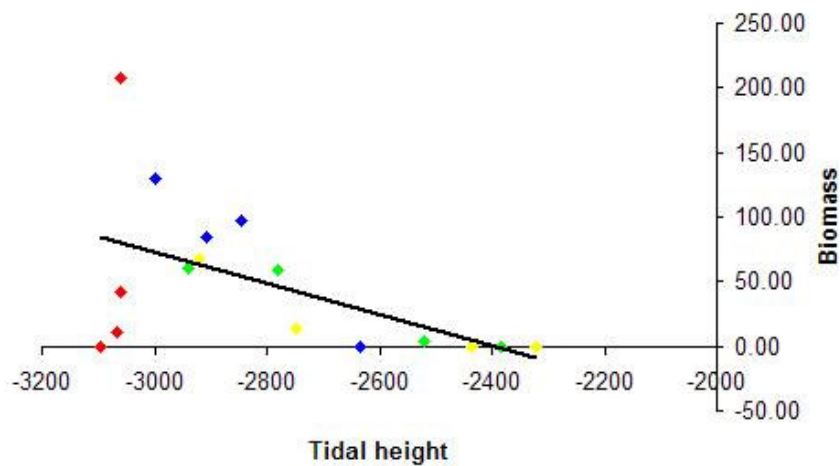

Figure 11. Local oyster biomass (in grams of ashfree dryweight per m^2) against tidal height (in m compared to NAP). Series 1 is indicated in red, series 2 in blue, series 3 in green and series 4 in yellow. $R^2 = 0.2867$, $P = 0.033$

Figure 12. Local oyster biomass (in grams of ashfree dryweight per m^2) against distance from the edge of the oyster bed (in m). Series 1 is indicated in red, series 2 in blue, series 3 in green and series 4 in yellow. R^2 = 0.1098, P = 0.210

Figure 13. Distance from the edge of the oyster bed (in m)against tidal height (in m compared to NAP). Series 1 is indicated in red, series 2 in blue, series 3 in green and series 4 in yellow. R^2 = 0.475, P = 0.003
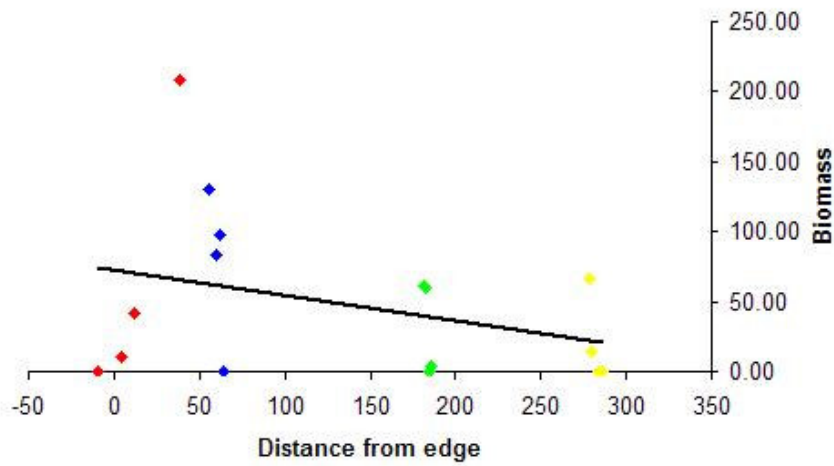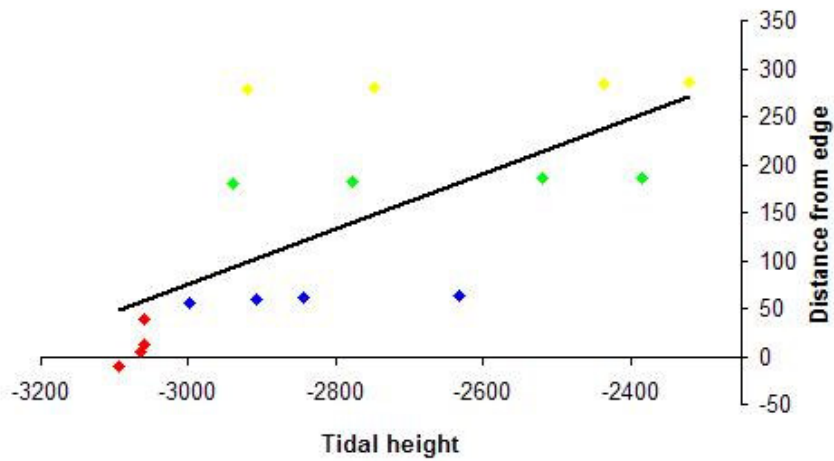
3.2 Total particulate matter

Total particulate matter stayed constant across the oyster bed (figure 14).

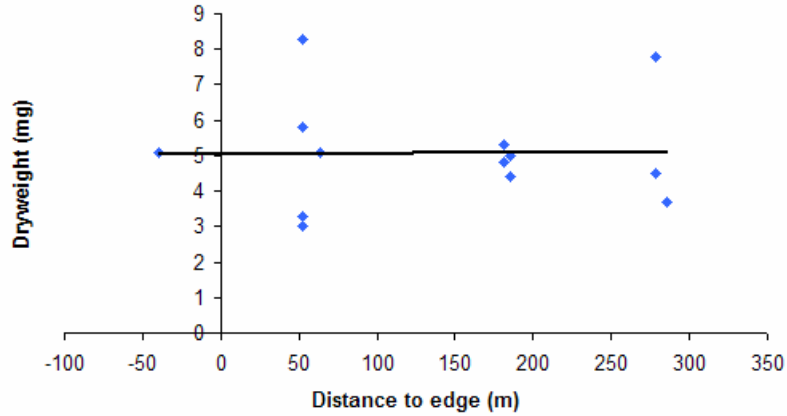
Figure 14. Total particulate matter (in mg dryweight) against distance to the edge of the oyster bed ($R^2 = 0.0005$).

3.3 Growth Experiment

Oyster growth was lower in the high density locations than in the lower density locations (figure 15). This pattern can be seen in all four series, with exceptions in series 3 and 4 where the no density locations show lower growth than the low density. Also growth was higher in the series that were closer to the edge.
There were quite a lot of significant differences in oyster growth between the locations. High density locations are usually significantly lower than the low and no density locations (Table 1).
Growth for mussels does not show such a clear pattern (figure 16). To begin with the mussels do not show growth, they only decreased in weight. Series 3 and 4 show a pattern, with the least decrease in the locations of lowest density. But series 1 and 2 show absolutely no pattern. Also, the variation in the data for the mussels was very high, resulting in a very high standard error. This makes it very difficult to detect significant differences.
Mussel growth showed no significant differences in growth between the locations.
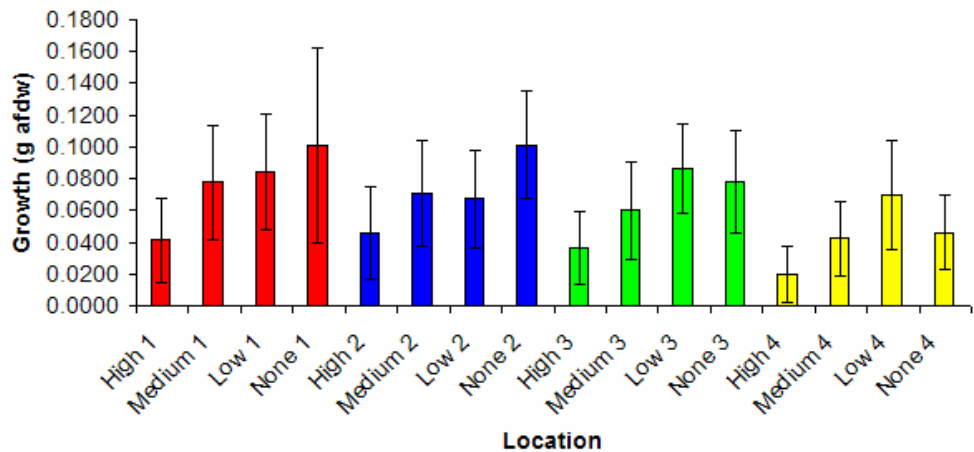

Figure 15. Average oyster growth (in grams of ashfree dryweight) per location with bars showing the standard deviation.
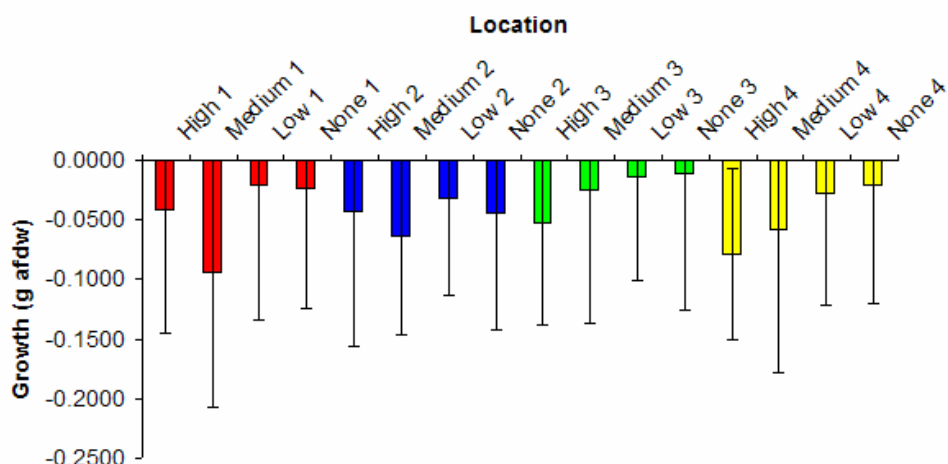
Figure 16. Average mussel growth (in grams of ashfree dryweight) per location with bars showing the standard deviation.

Table 1. Differences between the locations. Significant differences are indicated with an **s**. H = high, M = medium, L = low and N = none.

Oesters	H1	M1	L1	N1	H2	M2	L2	N2	H3	M3	L3	N3	H4	M4	L4	N4
H1	-	s	s	s	X	s	X	s	X	X	s	s	X	X	s	X
M1	s	-	X	X	s	X	X	X	s	X	X	X	s	s	X	s
L1	s	X	-	X	s	X	X	X	s	X	X	X	s	s	X	s
N1	s	X	X	-	s	s	s	X	s	s	X	X	s	s	s	s
H2	X	s	s	s	-	X	X	s	X	X	s	s	X	X	X	X
M2	s	X	X	s	X	-	X	s	s	X	X	X	s	s	X	X
L2	X	X	X	s	X	X	-	s	s	X	X	X	s	X	X	X
N2	s	X	X	X	s	s	s	-	s	s	X	X	s	s	s	s
H3	X	s	s	s	X	s	s	s	-	X	s	s	X	X	s	X
M3	X	X	X	s	X	X	X	s	X	-	s	X	s	X	X	X
L3	s	X	X	X	s	X	X	X	s	s	-	X	s	s	X	s
N3	s	X	X	X	s	X	X	X	s	X	X	-	s	s	X	s
H4	X	s	s	s	X	s	s	s	X	s	s	s	-	X	s	s
M4	X	s	s	s	X	s	X	s	X	X	s	s	X	-	s	X
L4	s	X	X	s	X	X	X	s	s	X	X	X	s	s	-	X
N4	X	s	s	s	X	X	X	s	X	X	s	s	s	X	X	-

3.4 Effects of factors on growth

To test if the factors had a significant effect on growth the General Linear Model (GLM) was chosen. The GLM was chosen because this model compares the means to see if there is a difference between groups, just like the Analysis of Variance (ANOVA). But the GLM is able to estimate missing values, resulting in higher power than the ANOVA, which discards other values to compensate for the missing values.

Before the GLM was applied to the data, the data was first tested with a Multiway Factorial Analysis of Variance. This because the Multiway Factorial Analysis of Variance also tests the effect that the interaction between factors has on the variable. This test showed that for oysters local oyster biomass, tidal height and distance from edge all had very significant effect ($p<0.001$) on growth. But all the interactions between factors (local oyster biomass X tidal height, local oyster biomass X distance from edge, tidal height X distance from edge and local oyster biomass X tidal height X distance from edge) also had very significant effects ($p<0.001$). For mussels none of the factors or interactions between factors had a significant effect.

After this the GLM was applied to the data. This provided quite different p values. For oysters local oyster biomass and distance from edge still had a very significant effect ($p<0.01$) on growth, but tidal height no longer was significant ($p=0.222$). For mussels the factors still did not have significant effects.

4 Conclusion and discussion

4.1 Conclusions

Food availability affects growth in Pacific oysters. High food availability results in relatively high growth, low food availability results in lower growth. The data for the mussels did not provide any significant results, thus nothing can be said about the influence of food availability on mussels. Because it is not know what effect food availability has on mussels, no comparison could be made between oysters and mussels. No proof of competition between these two species could be found in this research.

4.2 Oyster growth

Oyster growth was affected by both local oyster biomass and distance from the edge of the oyster bed. As expected the higher the local biomass, the lower the growth and the further into the bed the lower the growth. Tidal height was not found to have an effect, but this might have to do with tidal height and local oyster biomass showing correlation.
This research was also done in a previous year (Hans 2004), and oddly enough it had very different results. Oyster growth showed no significant effects and mussel growth and condition was negatively affected by increasing oyster biomass. Tidal height and distance to the edge of the bed were found to have no effect. There may be a number of reasons for these differences. For oyster growth very few oysters were used per location and to determine starting conditions. This gives very weak statistics and makes it difficult to get significant results. The differences in the factors may have to do with the difference in shape of the oyster beds. The Zandkreek oyster bed is fairly continuous, but the oyster bed at St. Annaland has large gaps.

4.3 Mussel growth

Another odd thing is that while the oysters showed different measures of growth, the mussels only showed a decline in condition. This is unexpected and might have several reasons. The first reason is that the mussels were gathered in the Wadden Sea. The waters of the Wadden Sea are much richer in food than the waters of the Oosterschelde estuary (average 7,4 µg chlorofyl a/l for the Wadden Sea and average 4.8 µg chlorofyl a/l for the Oosterschelde estuary. Both values are the averages of four randomly chosen locations in the area. Data taken from www.waterbase.nl). Because of this drop in available food the mussels possibly had trouble adapting and did not do well. The second reason is that the mussels were gathered in the Wadden Sea from the subtidal. In the research are they were placed in a tidal zone. This meant that they had less time to gather food than they were used to, since they now spent part of the day outside the water. These first two reasons both would result in a decline in condition because of a great drop in the levels of available food. The theory behind this is that the huge difference caused by the transfer from the Wadden Sea to the Oosterschelde estuary made it impossible to pick up the smaller differences caused by the conditions at the experiment site. The last reason the mussels might have done bad is that they might have spawned. Spawning also causes the mussels to have a decline in their condition. Spawning occurs in April and May, sometimes in June or July (Bayne 1967, Sastry 1979). This means the mussels most likely did not spawn within the research period. This is not one of the reasons for their decline in condition.

4.4 Experiment set-up

During the processing of the data some errors in the set-up of the experiment were discovered. The three factors all showed interaction in the ANOVA, and they also showed correlation. In the set-up series 1 was placed to avoid this. All cages of series 1 were set up at about the same tidal height but at different distances from the edge of the oyster bed, while series 2, 3 and 4 were each set up at the same distances from the edge of the oyster bed, with each location in the series on a different tidal height. But eventually the differences in distance from the edge of the oyster bed in series 1 weren't enough to avoid correlation between the factors.

For a next experiment this needs to be taken into account. In this particular oyster bed series 1 could not have been set up more spaciously, but if the location allows it it's wise to do so.

Another improvement could be in the cages that were used. While there were no problems for the mussels, who can attach themselves, the oysters were lying free in the cages. This means that if there were strong currents the oysters would be moved inside of their cages. This movement is a disturbance for the oysters and disturbs the feeding. The oysters in this experiment seemed not to suffer any ill effects from it, but especially if strong currents are expected at the location this should be taken into account.

4.5 Food selection

For oysters and mussels to be tested for competition they of course have to be using the same food source. Both mussels and oysters are filter feeders, but isotope research by Riera et al. (2002) showed that they are not necessarily competing for food sources when food is not limited. However, this research was done on just organic matter that is ingested. Both oysters and mussels filter and then select what they eat from the filtered material. Up to 60 % of the ingested organic matter can result from selective processes (Hawkins et al. 1998). The organic matter that is not selected is excreted as pseudofaeces, and thus no longer useable by other filter feeders. The difference in ingested organic matter might therefore just be due to the selective processes of the species while the filtration does provide competition.

However, a recent study shows that oysters and mussels differ in both filtration efficiency and retention of different kind of particles (May 2006). His conclusion is that niche-differentiation might be one of the options for these two species. His findings are somewhat odd, as he finds that mussels have greater filtration rates than oysters, while most studies find the reverse (Foster-Smith 1975, Walne 1975, Smaal 1997, Dupuy et al. 2000).

4.6 Future research

More research is needed to determine if there is competition between pacific oysters and blue mussels. For a next research there are some recommendations. The first is to use mussels that were gathered from the Oosterschelde estuary. If those are not available the mussels should be given time to adjust to their new conditions before putting them in the field. This will probably provide better usable data. Another advice is when you set up your experiment to make sure the factors can be separated from each other statistically. Finally it is wise to use animals that are too young to participate in spawning. The oysters used in this experiment were too young, but the mussels were a bit larger than originally intended.

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Appendix 1
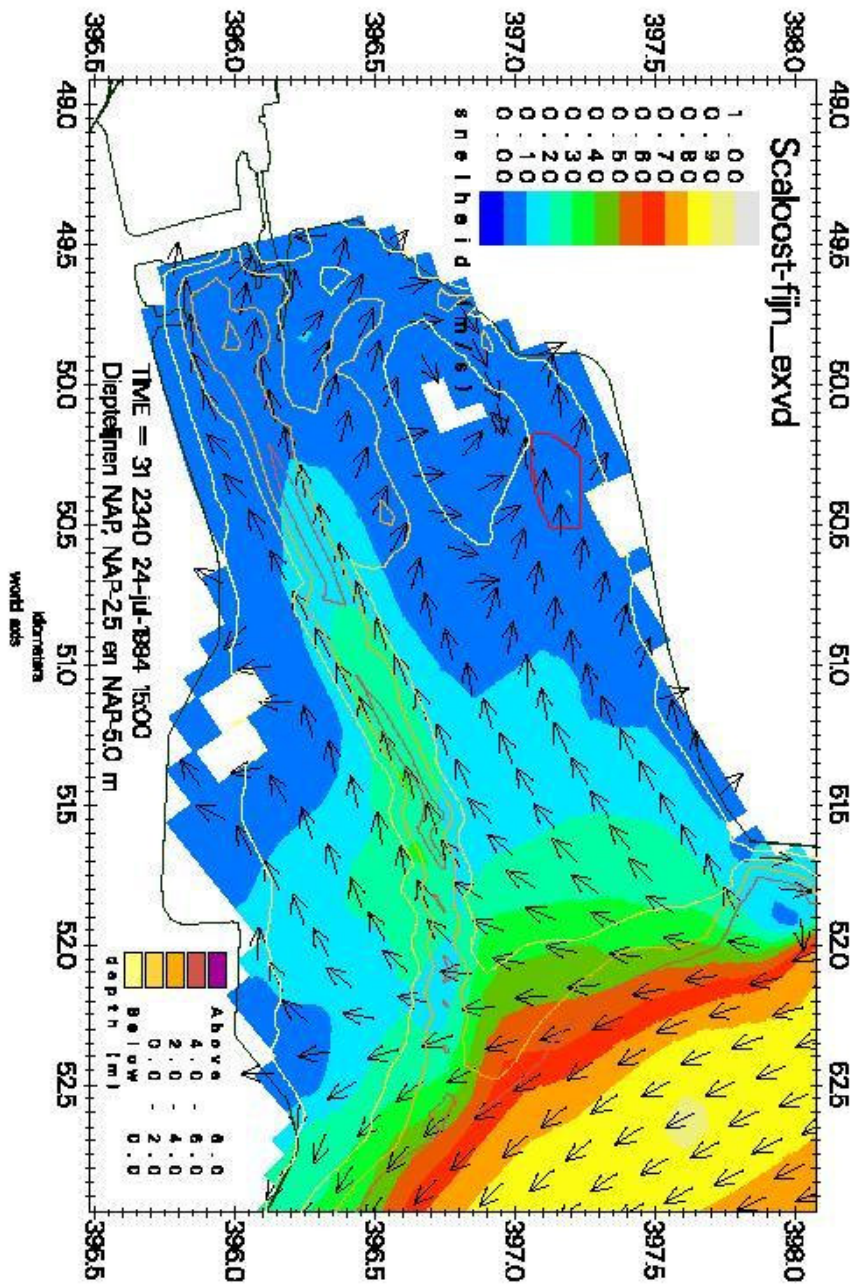
Appendix 1. Direction of flow at rising tide in the Zandkreek. The area circled in red indicates the approximate location of the oyster bed. The arrows indicate the direction of flow at that location. The colors indicate the speed of the flow at that location.