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Interactions between the introduced Pacific oyster *Crassostrea gigas* and the indigenous blue mussel *Mytilus edulis*. Local-scale food competition.

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Index

Frontpage: *The picture shows the oysterbed near Sint-Annaland during low-tide, which was used in this research. Also three maps of the Oosterschelde estuary and its population of Pacific oysters are included (shown as red areas), indicating the rapid expansion of the population in this area, during the last two decades.*

Abstract

The aim of this study was to determine if food competition between mussels and oysters occurs, and how mussel and oyster growth is affected by this interaction. This was done by (1) relating mussel growth to oyster density (2) relating oyster growth to oyster biomass and (3) perform a field control, by inventory the natural situation of wild mussels living in an oyster bed on a tidal flat located in the Dutch Oosterschelde estuary. Mussel growth and condition were found to be negatively affected with increasing oyster biomass, while oyster growth was not affected. Growth was not affected by confounding factors in both bivalve species. Oysters appeared to form a suitable substratum for mussels to settle. Considering (1) the rapid expansion of the Pacific oyster population, (2) the observed overgrowth of wild mussel beds by Pacific oysters in the Wadden Sea, (3) the relatively high filtration rate of Pacific oysters and (4) the fact that Pacific oysters and mussels use the same food source, food competition between these species is likely to be the process underlying these findings.

1. Introduction

1.1 *Crassostrea gigas* in the Netherlands

Since 1870, the cultivation of European oysters (*Ostrea edulis*) in the Netherlands (in the Oosterschelde estuary, figure 1.1) was of very important economical value. The strong winter of '62/'63, however, caused an enormous reduction in oyster stocks.

Figure 1.1. Location of the Oosterschelde estuary. In the left picture, the red area is the Oosterschelde estuary; a magnification of this area is depicted in the right picture. Red lines represent tidal lines.

Before that winter the stock consisted of 120 million oysters, but afterwards only 4 million oysters were left. In order to enlarge the broodstock to keep the market production about 30 million oysters per year, *O. edulis* was imported from Norway and France (Brittany). Due to unfavourable environmental conditions for oyster growth in the Netherlands, this import of oysters from other countries continued, until in 1977 nearly all European strains (England, Ireland, Italy and Greece) of *O. edulis* were imported in the Oosterschelde estuary. During this period various attempts to search for alternative oyster species that could replenish the exploited European oyster, such as the American oyster (*Crassostrea virginica*) and the Portugese oyster (*Crassostrea angulata*), largely failed (Drinkwaard, 1999). European oyster

cultivation in the Oosterschelde estuary ended abruptly in 1980, when a parasite, *Bonamia ostrea*, was introduced which caused a devastating impact on the flat oyster population (Drinkwaard, 1999; Haenen, 2001).
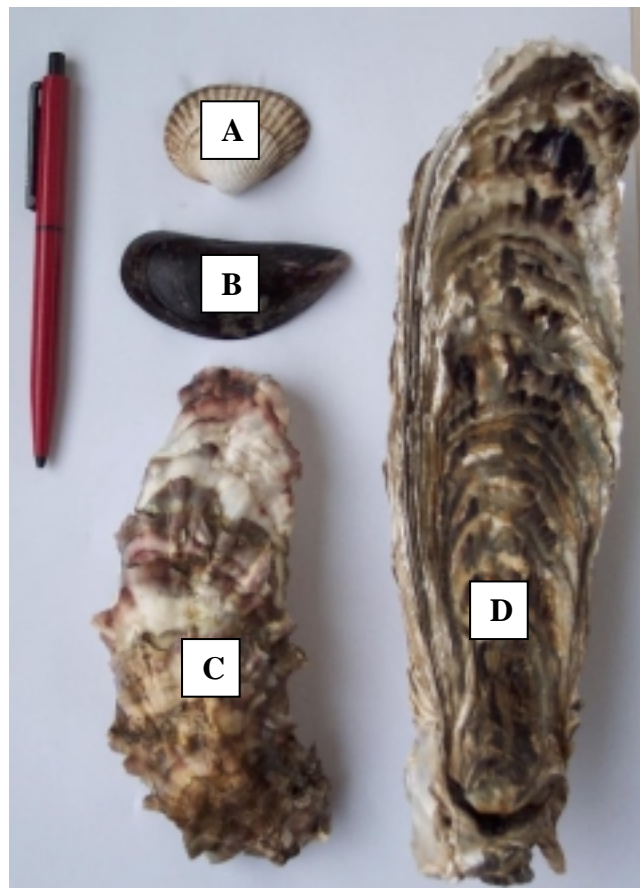

Figure 1.2. Comparison between the three major filter feeding bivalves living in the Oosterschelde estuary. **A**: cockle (*Cerastoderma edule*), **B***: Mussel (Mytilus edulis),* **C***:* Pacific oyster (*Crassostrea gigas),* **D***:* Pacific oyster (*Crassostrea gigas).* Two examples of *C. gigas* are depicted, illustrating the high morphological plasticity in these bivalves.

However, in 1964, spat of the Pacific oyster (*Crassostrea gigas,* 'Japanese oyster') was imported from British Columbia, Canada. After an experimental phase to test this oyster's performance in Dutch waters, it was concluded that *Crassostrea gigas* was a

suitable replacement for *O. edulis*, and from then on the Pacific oyster could be commercially cultivated in the Oosterschelde estuary. This conclusion was based on the experimental results which suggested that the Pacific oyster reached market size (100 g) in two growth seasons and the summer temperatures would be too low for successful recruitment (Drinkwaard, 1999). *C. gigas* has been imported to Holland regularly from France since 1964, yet not untill the unusually hot summer of 1976 did natural spat recruitment occur (Shatkin et al, 1997). In this summer, water temperature reached values of over 20 °C for more than 50 days, which caused a major spatfall of *C. gigas* in the Oosterschelde (Drinkwaard, 1999). The definitive introduction of Pacific oyster became a matter of fact by a new larval outburst in 1982. From 1982, *C. gigas* was also observed in the Wadden Sea and in 1987 also in Lake Grevelingen. Sustained summer water temperatures of >20 °C resulted in an extensive expansion of the Pacific oyster population in the Oosterschelde estuary (Drinkwaard, 1999). Figure 1.3 shows the harvest of *C. gigas* in tons per year, and shows a large increase in harvest over the past two decades, up to 2400 tons in 1994. These numbers illustrate the fast development of the Pacific oyster population.
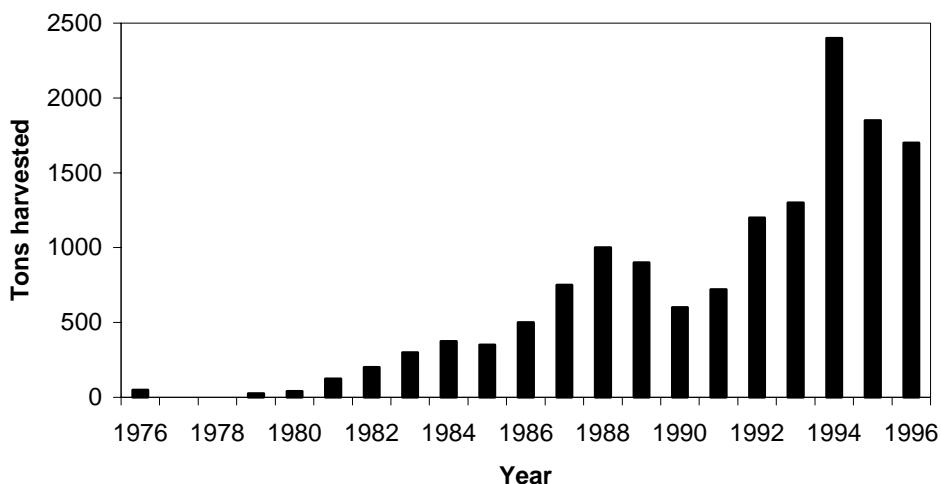

Figure 1.3. Harvest of *C. gigas* in the Netherlands in tons per year. One ton corresponds roughly to 9000 oysters (*adapted from Drinkwaard, 1999*).

Pacific oyster surveys, conducted yearly (started in 1998) by the Netherlands Institute for Fisheries Research, also indicate a strong increase in population area in the

Oosterschelde estuary; from 25 ha in 1980 to 766 ha in 2003 (*Gelderman, 2003: intern RIVO report; Kater et al, 2002*).

1.2 Competition

Considering the high economical and ecological importance of mussel and cockle culture in the Oosterschelde estuary, the expansion of the Pacific oyster population in this area is accompanied with questions concerning negative effects on these cultures. Van Stee (2000) concluded that oysters had replaced mussels on almost all former littoral mussel culture sites in the Oosterschelde estuary. Pacific oysters tend to settle on mussels and replace wild mussel beds in the Dutch Wadden Sea also (Dankers, 2004).

Pacific oysters can filter particles from the POM-pool with a minimum size of 2 µm. Efficiency is increasing with increasing particle size, with a maximum between 6 and 8 µm (Ropert & Goulletquer, 2000). Mussels and cockles also can retain particles from 2 microns (Vahl, 1972; Møhlenberg & Riisgård, 1978). Additionally, *C. gigas* can filter considerable amounts of sea water per time unit, as compared to other important bivalves, such as mussels and cockles, (table 1.1) and in the Oosterschelde estuary, oysters experience very low predation pressure (Kater, 2002).

Table 1.1. Average densities and filtration rates of the three most abundant filter feeding bivalves in the Oosterschelde estuary.

Species	density (N/m^2) (RIVO-CSO)	Filtration (l/h/ind)	Water filtered (l/h/m2)
cockle	2000	1.0 – 3.4*	2,000 – 7,000
mussel	6000	0.4 – 9.1**	2,000 – 55,000
oyster	10000	3.0 – 25.0***	30,000 – 250,000

      *   Foster-Smith (1975); Mølenberg, Riisgard (1979)

      **   Foster-Smith (1975); Mølenberg, Riisgard (1979); Walne (1975); Smaal (1997)

      ***   Dupuy et al. (1999); Walne (1975)

Although filtration rate estimates from other studies vary greatly, values for *C. Gigas* are found to be higher as compared to *M. edulis* and *C. edule.* Consequently, on population scale, the presence of Pacific oysters may reduce the food availability for other important filter feeders (Drinkwaard, 1999; Habraken, 1999; Kater, 2003; Shatkin, 1997).

This interspecific competition for food is an important factor in bivalve growth and is found to occur globally. For example, one likely cause for a decline in Rock oysters at Port Stephens (Australia) is the increased cultivation of the Pacific oyster, due to faster rates of feeding and greater metabolic efficiencies of both feeding and growth (Bayne, 2002). Another example is given by Talman & Keough (2001). They suggest that a possible mechanism underlying the impact of an exotic clam (*Corbula gibba*) on the commercial scallop *Pecten fumatus* in Port Phillip, Australia, is competition for food. Engle and Chapman (1951) showed that Eastern oyster (*Crassostrea virginica)* condition was negatively affected by attached mussels, probably caused by food competition.

Effects of food competition between Pacific oysters and mussels can be directly investigated on a local scale: mussels living in an oyster bed may provide information on these effects of food competition, in terms of differences in mussel growth and condition at sites with different local oyster biomasses. Bayne (1976) points out that, in comparative investigations, mussel growth measurements should not solely depend on one linear parameter, such as shell length increment or condition, but rather a combination of different parameters.

Apart from local oyster biomass, growth and condition of mussels living in an intertidal oyster bed are influenced by many other factors. Buschbaum (2001) states that on tidal coasts, duration of air exposure is one of the most important factors for growth in mussels and may lead to considerable variations in size and shape between intertidal and subtidal mussels. A longer immersion time is accompanied by more filtration time, and therefore potentially more growth. Thus, tidal height appears to be a key factor in mussel growth and is therefore also expected to occur on an intertidal oyster bed.

Intraspecific competition is also an important factor in oysterbeds and musselbeds. The growth of mussels is reported to be density-dependent and a reduced growth rate in the seabed could be explained by this intraspecific competition (Dolmer, 1997). Honkoop and Bayne (2002) investigated the optimal stocking density of Pacific oysters. They found that high density decreases growth of these bivalves, possibly due to food limitation.

The aim of this study was to determine if food competition between mussels and oysters occurs, and how mussel and oyster growth is affected by this interaction. This was done by (1) relating mussel growth to oyster density (2) relating oyster growth to oyster biomass and (3) perform a field control, by inventory the natural situation of wild mussels living in an oyster bed. Considering the rapid expansion of the Pacific oyster population, the observed overgrowth of wild mussel beds by Pacific oysters in the Wadden Sea, the relatively high filtration rate of Pacific oysters and the fact that Pacific oysters and mussels use the same food source, we expect mussel growth to be negatively affected. No significant density dependent oyster growth is expected. As written above, apart from the potential effects of oyster density, mussel and oyster growth also depends on important confounding factors.

2. Materials and methods

2.1 Location

The Oosterschelde is a 351-km² estuary in the south-western part of The Netherlands (Fig. 1). Water temperatures reach from –3 to 24 °C and salinities vary between 28 – 30 ppt (Shatkin et al. 1997). Some hydrodynamic characteristics of the Oosterschelde estuary, dated from 1994 and earlier, are listed in table 2.1.

Table 2.1. Mean hydrodynamic characteristics of the Oosterschelde Estuary (Nienhuis & Smaal, 1994)

Total surface, km²	351
Water surface, (MWL) km²	304
Tidal flats, km²	118
Salt Marshes, km²	6.4
Mean tidal range, Yerseke, m	3.25
Max. flow velocity, m s^{-1}	1.0
Residence time, d	10-150
Average depth, m	8
Maximum depth, m	55
Average conc. Suspended matter, mg l^{-1}	15
Mean tidal volume, m³·10^6	880
Total volume, m³·10^6	2750
Mean freshwater load, m³·s^{-1}	25

2.2 Experimental set-up

In this research, a growth experiment and a field control were performed at 20 different sample points. For each sample point the local oyster biomass was determined, in order to relate the results of the growth experiment and the field control to the local oyster biomass. The growth experiment consisted of two parts: (1) relating mussel growth to oyster biomass, and (2) relating oyster growth to oyster biomass. In this experiment, two size classes of mussels and oysters were used, because contrary to older mussels, young mussels convert most of their energy into somatic growth (Maquire, 2003).

Secondly, a field control experiment was performed by means of an inventory on wild mussels living in an oyster bed. Since these mussels naturally live in the oyster bed there are no duration effects which are present in the relatively short growth experiment.

Sample locations for the growth experiment and field control were chosen visually. The criteria were: different oyster densities and different distances to the edge of the oyster bed. Sample points and oyster bed borders were marked using GPS (Global Positioning Satellite system) and with GIS-software (Geographic Information System) a map of the oyster bed and the sample points was created and depicted as figure 2.2.

Figure 2.1. Location of Oosterschelde estuary and sampling area. The red square indicates the location of the oyster bed near Sint Annaland (Fig. 2.2) where the experiments were performed.
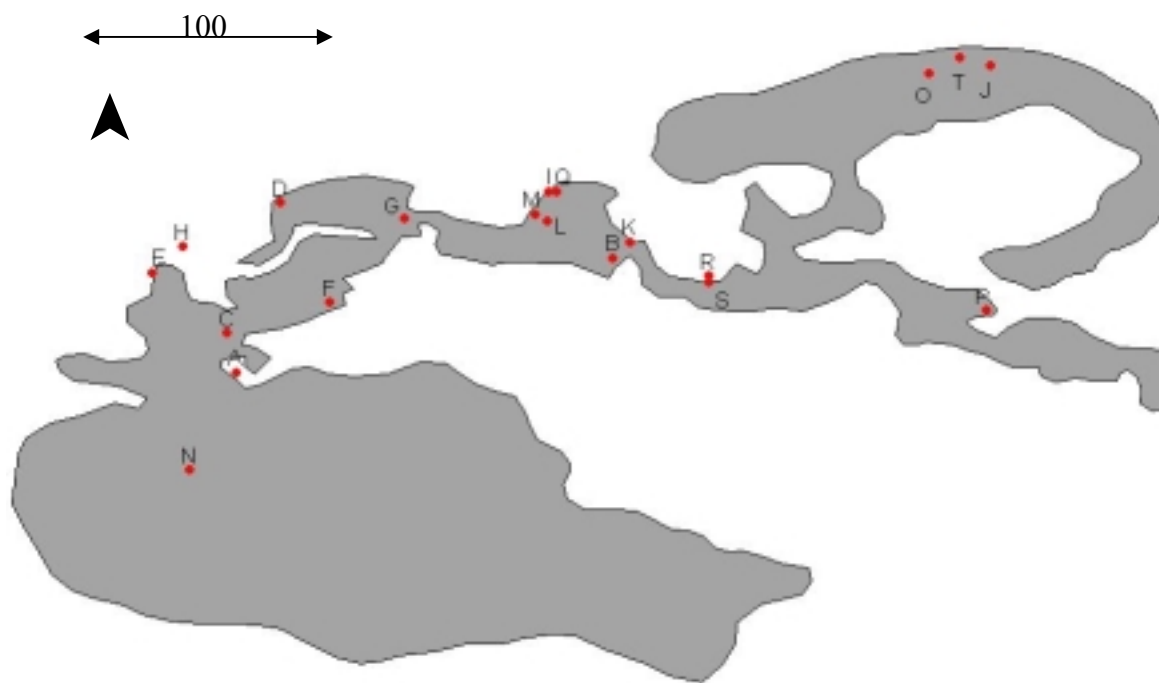
Figure 2.2. Sample locations, shown as red dots, on a part of the oysterbed near Sint-Annaland (figure 2.1). The grey area represents the oyster bed; differences in oyster biomass are not shown.

2.3 Oyster biomass

Using a 0.25 m^2 square, from each sample point all oysters within the square were taken to the lab where the local oyster biomass was determined. Biomass is expressed as the ash free dry weight per standardised measure of weight

To determine the ash free dry weight, first, the dry weight was measured by drying mussel meat at 70 °C untill weight constancy was achieved. Subsequently, the dry meat was placed at 520 °C for at least 3 hours, depending on the amount of flesh to be ashed. The weight loss at this temperature is considered to represent the biomass of the sample.

2.4 – a Mussel growth

To determine mussel growth in relation to oyster biomass, tidal height and different distances to the edge of the bed, a cage experiment was performed. Obviously, the main purpose of the cages was to protect the mussels from predation by crabs, starfish and birds and to prevent the animals from migrating. The potential influence of mussel caging on their growth is not considered here, because with regard to the research question, the relative differences in mussel growth are sufficient, assuming every cage exhibits the same influence on mussel growth.

Each cage contained mussels from two different size-classes; 7 small (28-30 mm) mussels and 6 large (40-43 mm) mussels (fig 2.3), derived from a suspended rope culture and a bottom-culture plot site, respectively, collected by the H.M.S. Schollevaer. After having spent four days in a tank with running seawater outside the RIVO building, the mussels were caged and installed in the field. In order to measure both local and individual growth, all mussels were individually marked with a scalpel. At the 3rd of August 2003, 20 cages were installed on the oyster bank near Sint Annaland (figure 2.2) for two months. October 14th, the cages were taken to the lab for sample analysis. Before (t=0) and after (t=1) the experiment, shell lengths were measured using a digital calliper (to the nearest 0.01 mm). Before the experiment an average condition index for t=0 was estimated by determining the condition indices of 7 large mussels and 17 small mussels (no more were available) and after the experiment (t=1) individual mussel condition indices were determined. Mussel condition is determined using a general expression for length-weight relations:

$$a = W (L^{b})^{-1}$$

a = measure for condition; the condition index (g / mm)
W = ashfree dryweight of the mussel ($\approx$biomass) (g)
L = length (mm)
b = 2.8 for mussels (personal comments Bert Brinkman, Alterra)

Mussel ashfree dry weight was determined equivalent to the oyster biomass (section 2.3). The condition index of a bivalve is described as the proportion of internal cavity occupied by body tissue and should indicate the status of the oyster's metabolic reserves (Brown & Hartwick, 1988).

Figure 2.3. Example of a cage construction. The square cage contains 10 oysters, the round cage contains 13 mussels. In total 20 of these sets were involved in the growth experiment.

2.4 – b Oyster growth

To determine oyster growth in relation to oyster density, thus in fact testing for intraspecific competition, oysters were also included in the cage-experiment. Again, two size classes were used: 5 small (29.52<l<48.12 mm) individuals and 5 large (55.73<l<93.33 mm) oysters in each cage (figure 2.3), individually marked with nail polish. The small oysters were taken from an intertidal oyster bed near the Yerseke Harbour, and the large oysters were collected from a culture site (Perceel HK19) by the H.M.S. Schollevaer and after spending three days in a tank with running seawater outside the RIVO building, the oysters were caged and installed in the field. Before

(t=0) and after (t=1) the growth experiment, shell-length and -width were measured with a digital calliper (to the nearest 0.01 mm). Since oyster growth is highly variable, measuring solely oyster length is not sufficient. Therefore, in this research also oyster width is measured. Consequently, oyster condition on t=0 and t=1 was determined as follows:

CI = afdw / icv (Baird, 1958; Brown & Hartwick, 1987; Lawrence & Scott, 1982; Neudecker, 1979)

CI = condition index (g / ml)

Afdw = ashfree dry weight (g)

Icv = internal cavity volume (ml)

The ash free dry weight was obtained similar to the oyster ashfree dry weight as explained in section *2.3 Oyster biomass*. Internal cavity volume (icv) was measured by submerging the empty shell in water, then pushing the two valves together tightly, resulting in a closed, water-retaining oyster shell. The water in the closed shell then is poured in a cup placed on a balance. The weight of the added water in grams corresponds with the internal cavity volume of the oyster in millilitres.

2.5 Field control

Using a 0.25 m² square, four parameters were determined for each sample point. (1) the oyster biomass (g afdw m² $^{-1}$), (2) mussel biomass (g afdw m² $^{-1}$), (3) length frequency distribution for mussels and (4) condition indices for same size class (28 – 32 mm) mussels. All mussels and oysters found within the square, from each sample point, were taken to the lab (fig. 2.4). Mussel shell length was measured using a digital calliper (to the nearest 0.01 mm) and mussels with a length between 28 and 32 millimeter were separated for condition analysis in order to compare the condition

indices from mussels from different oyster density with the same shell length. Mussel condition and biomass was determined as described in section 2.4 - a: *mussel growth.*

Figure 2.4. All oysters and mussels within a 0.25 m2 square were taken to the lab for analysis.

2.6 Tidal height & distance to the edge of the bed

Data considering duration of air exposure (= tidal height) is provided by the RIKZ. The 'duration of exposure-maps' are gridfiles, consisting of 20 x 20 m grids (Fig: 2.5). Colours represent the percentage of time a grid is exposed to air (for detailed methodology: B.J. Kater & J.M.D.D. Baars, 2002).
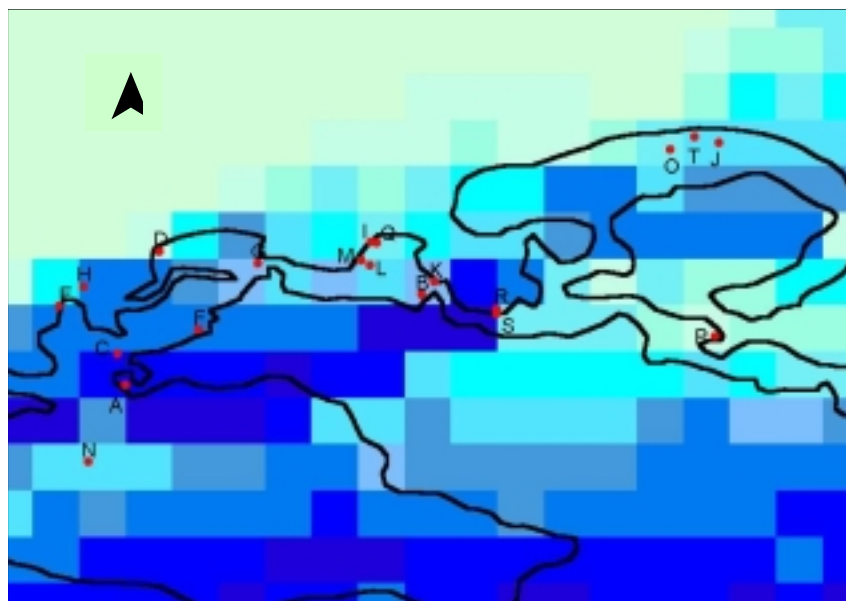
Figure 2.5. Duration of air exposure increases with more intense blue colors.
Duration of air exposure is a measure for tidal height.

In order to obtain data on distances to the edge of the bed, the current direction is essential. Kamermans (1993) stated that in the Balgzand, floodwaters contain more chlorophyll a than ebb waters. We assume that this is the same for the Oosterschelde estuary, also since there is no large fresh water input, which can increase [chl a] in ebb waters. Figure 2.6 shows maximum flood current velocity and direction on an average tidal cycle. This data is from RIKZ, provided by C. van de Male. The current direction on the maximum current velocity moment was used to determine the distance from each sample point to the edge of the bed, where the flood current comes in (Fig. 2.7). This distance was measured with a ruler and represents the relative distance from each point. In biological terms this distance gives an indication of the number of oysters the water encounters before arriving at a particular sample point. A longer distance represents more oysters upstream, resulting in a potentially decreased food availability for mussels and oysters.
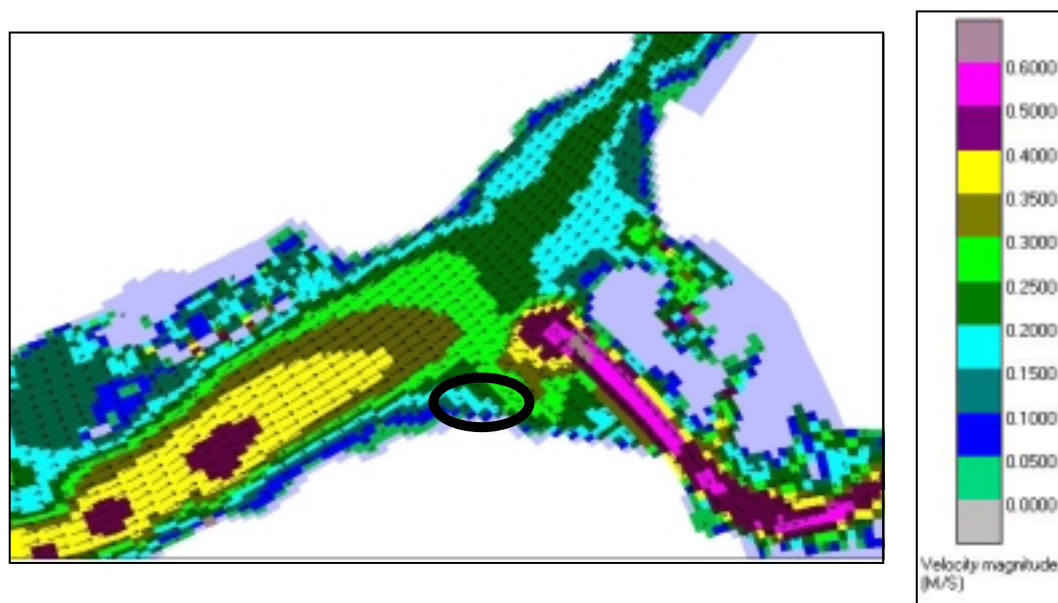
Figure 2.6. Current velocity and direction at maximum current velocity. The circle indicates the location of the oyster bed used in this research.
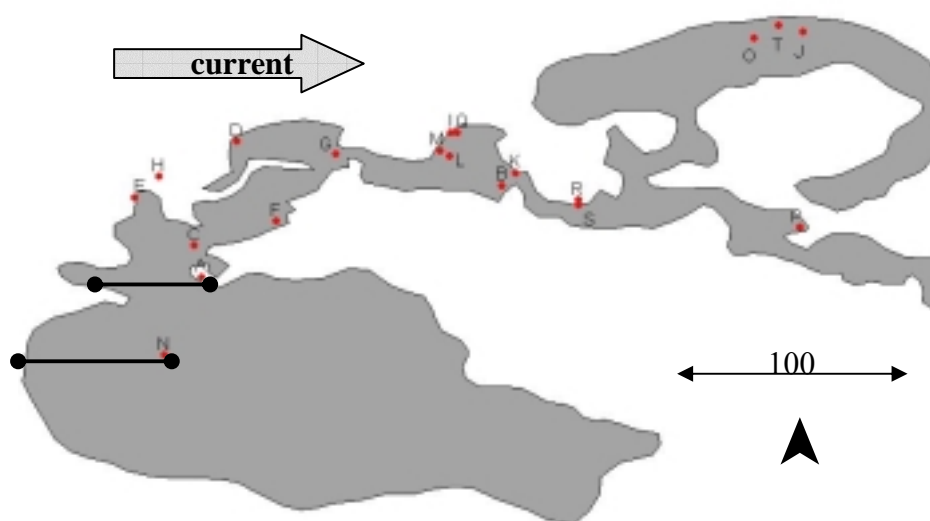

Figure 2.7. Distance to the edge of the bed. The distance is exactly the opposite of the current direction and actually gives an indication on the amount of oysters upstream. A longer distance represents more oysters upstream, resulting in a potentially decreased food availabilty for mussels and oysters. Two examples of the disance determination are shown in the figure (black bars).

2.7 Data analysis

First, oyster biomass for each sample point was determined. These data were used to plot oyster biomass against the results of the mussel growth experiment and the oyster growth experiment and the wild mussel situation inventory. Secondly, Stepwise Multiple Regression, performed in SPPS 11.0 for windows, was used to analyse the results in which oyster density, duration of air exposure and distance to the edge are all included as three factors.

3 Results

3.1 Oyster biomass

Oyster biomass ranges from zero to just over 1200 g afdw/m^2 (Figure 3.1). Sample point I, M and O have no oyster biomass. The results of the growth experiments and the field control are related to these biomass data.
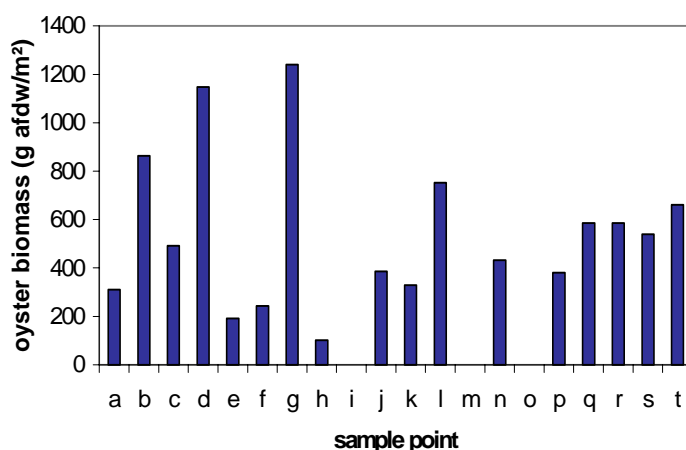

Figure 3.1. Oyster biomass (g afdw/m²) per sample point.

3.2 – a Mussel growth

With an increasing oyster biomass, a significant decrease in mussel length increment is observed for both mussel size classes (Figure 3.2). However, the effect on small mussels is much stronger and more significant ($p < 0.001$) than the effect of oyster biomass on large mussel length increment ($p < 0.05$). Mussel length increment at the absence of oysters is nearly twice as high as mussel length increment at high oyster biomass. On the average, mussels from the small size class grew about 2.07 times faster as compared to the large mussels. Stepwise multiple regression revealed that tidal height and distance to the edge of the bed show a significant effect on small mussel growth, but not on large mussel growth (Table 3.1).
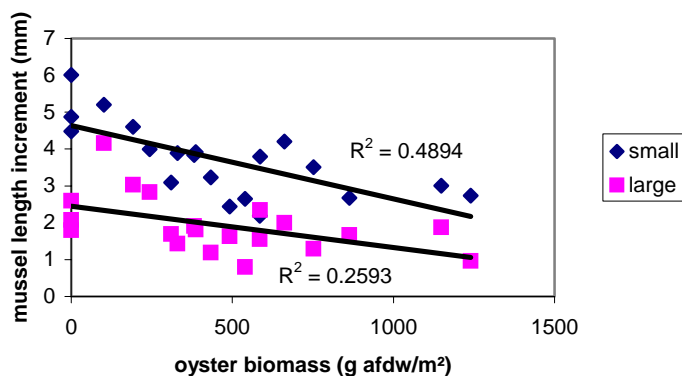
Figure 3.2. Small and large mussel length increment (growth) in millimeters related to oyster biomass. Lineair regression, $p_{small}<0.001$ and $p_{large}<0.05$.

Table 3.1. Stepwise multiple regression results. Small mussel growth is significantly correlated to in order of highest significance: oyster biomass, tidal height and distance to the edge. Large mussel growth only shows a significant correlation with oyster biomass. Mussel condition is not influenced by one of the three factors (n.s = not significant).

	Oyster biomass	Tidal height	Distance to edge
mussel length small	0.001	0.004	0.013
mussel length large	0.022	n.s.	n.s.
ci mussel small	n.s.	n.s.	n.s.
ci mussel large	n.s.	n.s.	n.s.

No significant decrease in condition of small and large mussels is found with increasing oyster biomass (figure 3.3). Condition of large mussels has not changed with respect to the condition on t=0 (average difference = 0.01 g/mm). However, the condition of the small mussels is on the average 1.12 (g/mm) lower at t=1 as compared to the initial condition of these mussels (figure 3.3). Multiple regression showed there was no significant influence of either oyster biomass, tidal height and distance to the edge of the oyster bed, on the condition of both small and large mussels (Table 3.1).
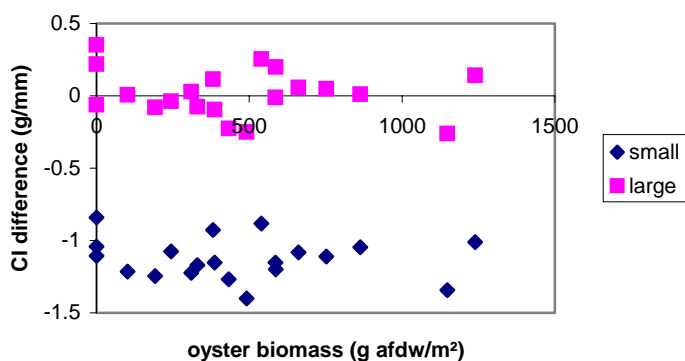
Figure 3.3. Difference in mussel condition index t=0 and t=1. Mussel condition was not influenced by oyster biomass. Small mussel condition at t=1 was lower than at t=0. Large mussel condition at t=1 was the same than at t=0. Linear regression, p_{small}>>0.05 and p_{large}>>0.05.

Tidal height and distance to the edge appear to be significantly correlated with the length increment of small mussels (Table 3.1). A longer duration of air exposure results in a lower length increment of small mussels (Fig. 3.4). A longer distance to the edge of the oyster bed also results in a lower length increment of small mussels (Fig. 3.5).
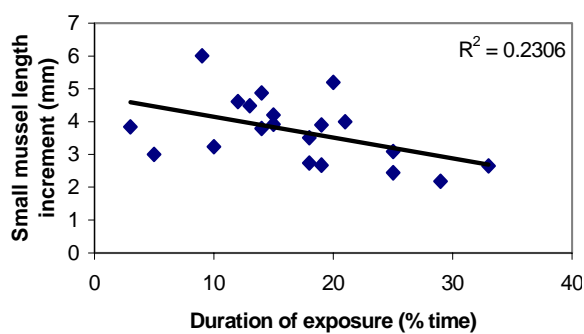

Figure 3.4. Small mussel growth decreases with increasing duration of exposure (≈tidal height). Linear regression, p<0.05.
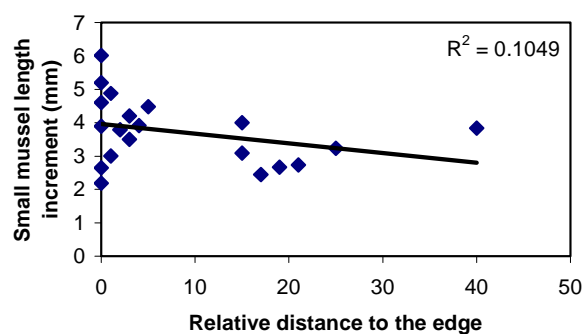
Figure 3.5. Small mussel growth decreases with an increasing distance to the edge of the oyster bed. Linear regression, p<0.05.

3.2 – b Oyster growth

No significant relations were found between oyster biomass and oyster growth, in terms of length increment (figure 3.6) and width increment (figure 3.7) for both size classes. Also oyster condition for both size classes was not influenced by oyster biomass (figure 3.8).

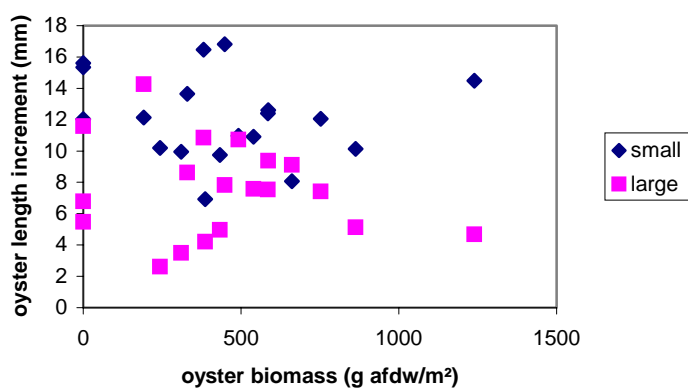Figure 3.6. No significant correlations are found between oyster biomass and oyster length increment for both size classes. Linear regression, $p_{small}>>0.05$ and $p_{large}>>0.05$
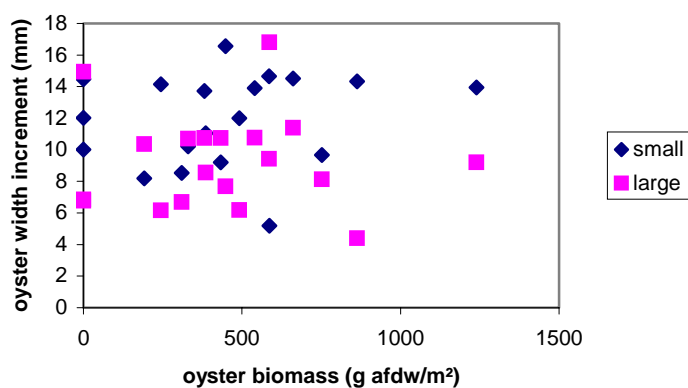

Figure 3.7. No significant correlations are found between oyster biomass and oyster width increment for both size classes. Linear regression, $p_{small}>>0.05$ and $p_{large}>>0.05$
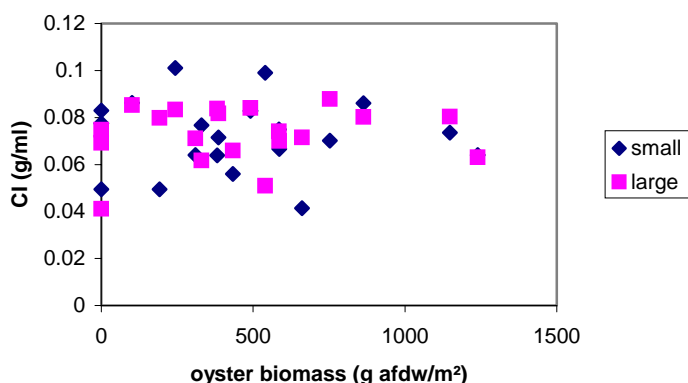
Figure 3.8. No significant correlations are found between oyster biomass and oyster condition for both size classes. Linear regression, $p_{small}>>0.05$ and $p_{large}>>0.05$

Table 3.2. Stepwise multiple regression results. No significant correlations were found within the results of the density dependent oyster growth, except for the condition of small oysters in relation to the tidal height. Significant values are given, n.s = not significant ($p>0.005$)

	Oyster biomass	Tidal height	Distance to edge
oyster length small	n.s.	n.s.	n.s.
oyster length large	n.s.	n.s.	n.s.
oyster width small	n.s.	n.s.	n.s.
oyster width large	n.s.	n.s.	n.s.
ci oyster small	n.s.	0.017	n.s.
ci oyster large	n.s.	n.s.	n.s.

Using multiple regression, it appeared that besides oyster biomass, also distance to the edge of the oyster bed had no significant influence on oyster condition and oyster growth, in terms of length increment and width increment for both size classes (table 3.2). However, the condition of small oysters is significantly correlated with tidal height (table 3.2). A scatter plot of these data shows this relation to be positive (Figure 3.9): when the duration of air exposure (tidal height) increases, the condition of small oysters also increases.
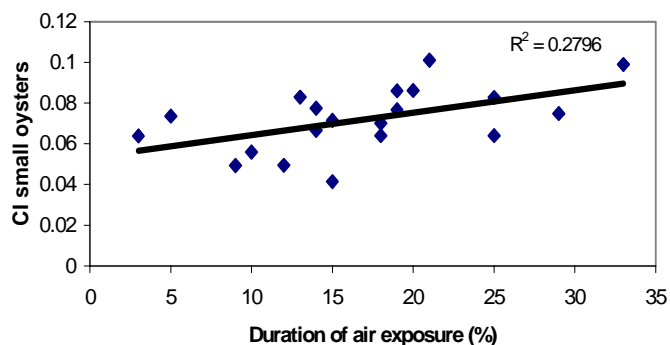
Figure 3.9. Condition of small oysters increases with an increasing duration of air exposure, which corresponds with an increasing tidal height. Linear regression, $p<0.05$.

3.3 Field control

Mussels naturally living on oyster beds showed high differences in abundance, length, condition and biomass, at sites with different local oyster biomasses. Figure 3.10 is an

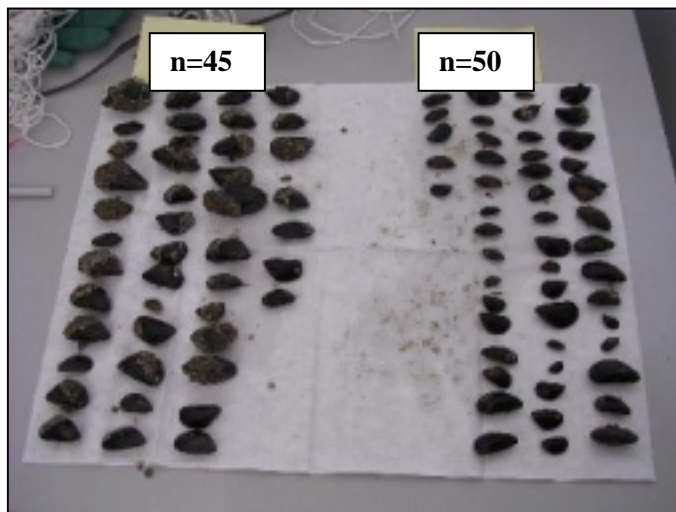Figure 3.10. Illustration of difference in mussel length per sample point. On the left side, mussels were derived from sample point A (n=45), with a local oyster biomass of 310 (g afdw/m^2). Mussels on the right side (n=50) came from sample point M, where the oyster biomass was 432 (g afdw/m^2). See figure 3.@@ for a graphical comparison of these mussel lengths

example of two out of the, in total, 20 sample points. It depicts mussels from two different sample points, with different oyster biomasses, illustrating the high variability in size between sample points potentially caused by different oyster biomasses. A graphical comparison of these mussels is given in figure 3.11. However, the average mussel length per sample point was not correlated with oyster biomass (figure 3.12)
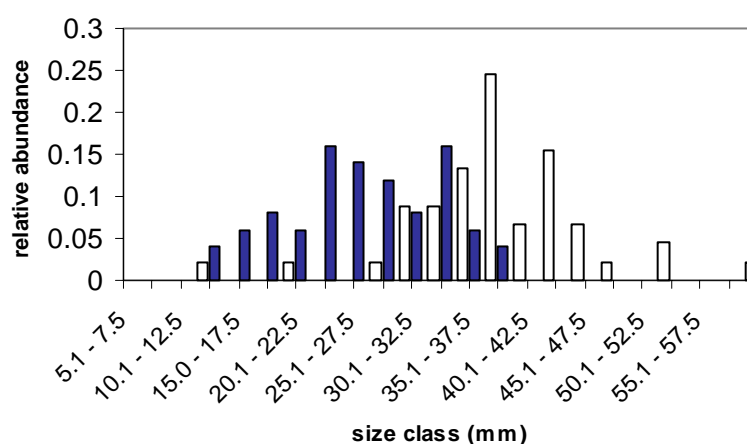

Figure 3.11. Graphical comparison of mussel length distributions from 2 different sample points. The blue bars represent mussels from sample point M: n=50, oyster biomass=432 (g afdw/m^2) and the white bars represent mussels from sample point A: n=45, oyster biomass=310 (g afdw/m^2). See figure 3.10 for a visual comparison of these mussels.

Mussel abundance also varied highly per sample point: from 0 (at sites with no oysters) to 273 individuals/0.25m^2. These numbers were positively correlated (p<0.01) with oyster biomass (figure 3.12). The condition of mussels living in an oyster bed seem to decrease significantly (p<0.05) with increasing oyster biomass (figure 3.12). While the average mussel length also shows a negative trend with increasing oyster biomass, this trend is not a significant correlated (p>0.05) with oyster biomass (figure 3.12). The fourth graph of figure 3.12 shows the positive relation (p<0.01) between oyster biomass and mussel biomass.
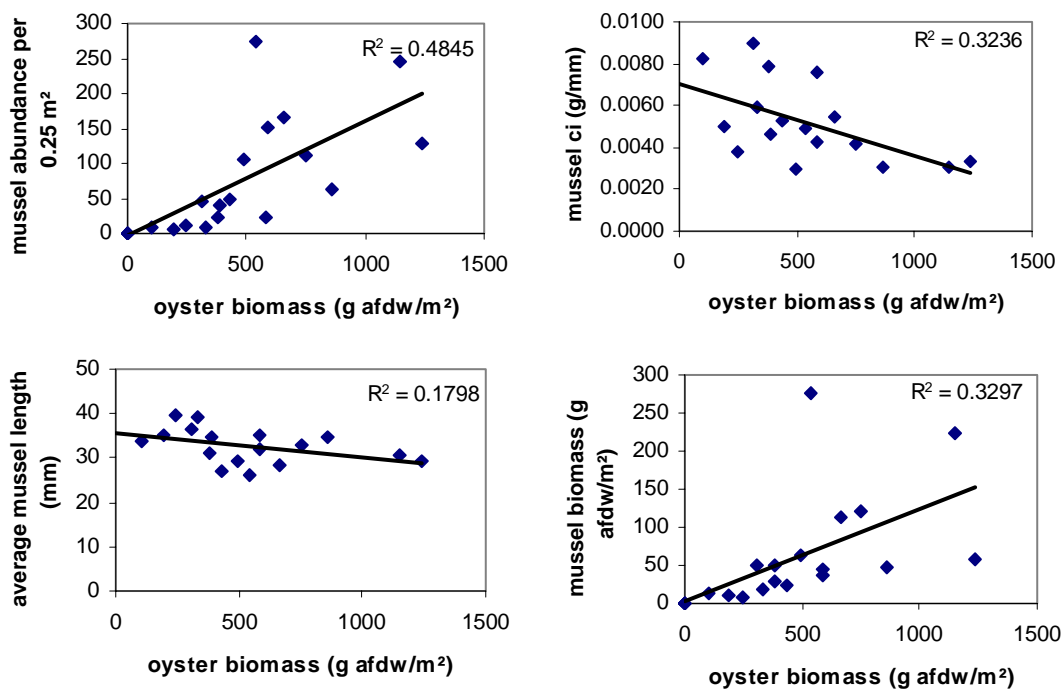
Figure 3.12. Oyster biomass related to the four measured mussel parameters: mussel abundance, condition, average length and biomass. Linear regression resulted in a positive relation between oyster biomass and mussel abundance ($p<0.01$), mussel condition ($p<0.05$), and biomass ($p<0.01$). Average mussel length was not correlated to oyster biomass ($p>0.05$).

Multiple regression showed that oyster biomass was the only factor affecting the four measured parameters: tidal height and distance to edge were found not to be correlated significantly with mussel abundance, mussel condition, average mussel length and mussel biomass (table 3.3).

Table 3.1. Stepwise multiple regression results. Tidal height and distance to the edge of the bed had no significant effect on the measured mussel parameters. Oyster biomass had a significant on mussel biomass, -abundance and –condition from the same size class.

	Oyster biomass	Tidal height	Distance to edge
mussel biomass	0.009	n.s.	n.s.
mussel abundance	0.001	n.s.	n.s.
average mussel length	n.s.	n.s.	n.s.
ci same size class	0.017	n.s.	n.s.

4. Discussion & Conclusion

4.1 Sample locations

Initially, the experimental set-up was to compare mussel performance at three different oyster densities: low, medium and high. Therefore, sample locations were chosen visually, depending on oyster density, tidal height and distance to the edge of the oyster bed. GIS software was used afterwards, when became clear that the visually chosen sample points could have chosen better to improve the statistical reliability of the results, in terms of more significant results: a wider range of tidal heights and distances to the edge of the bed are essential for more reliable results.

Local oyster biomass ranged from 0 to over 1200 g afdw/m^2, but these numbers may be underestimated. At sites with high oyster biomass, up to 50% of the oyster shells were found to be empty, and these oyster were deceased not long ago (shell interior was clean of barnacles and meat remains were sometimes present). This high oyster mortality was probably due to the extreme warm and long summer of 2003. Another cause can be intraspecific competition, because mussels were present in vast numbers attached to the dead oyster shells (no indication for intraspecific competition was found in this research). Therefore, wild mussels may have lived at much higher oyster biomasses than the oyster biomasses determined in this research.

4.2 Mussel growth

During the experiment, mussel growth, in terms of length increment, ranged from 2.5 to 6 mm. Local oyster density seems to be very important here; at sites with a local oyster biomass of zero, mussel length increment of small mussels was twice as high as compared to sites with highest oyster biomass values. The large mussels showed less length increment, but also a factor 2 difference in low and high local oyster biomass sites. Thus, small mussels grew faster but the effects of oyster biomass were

present in both size classes. This coincides with findings of Maquire (2003) that young mussels convert most of their energy into somatic growth, instead of gonad production. Data on mussel growth was analysed with linear regression, but mussel growth and oyster biomass may be exponentially related (fig. 4.1). Although the relations are significant (p<0.01 for small mussels and p<0.05 for large mussels), R^2 changes are minimal; -0.0291 (small mussels) and +0.0128 (large mussels). More data is required in order to test this relation to be exponential or linear.
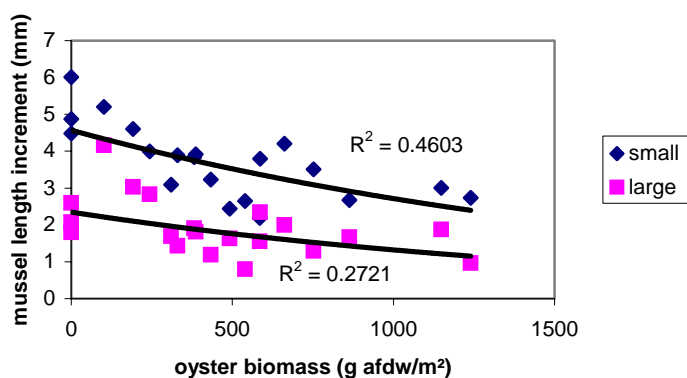

Figure 4.1. Mussel growth as an exponentional function of oyster biomass. p_{small}<0.001 and p_{large}<0.05.

No effects of local oyster biomass on mussel condition were observed. However, the small mussels showed a decrease in condition as compared to the t=0 situation. These mussels were derived from a so-called 'suspended rope culture' where high food availability and little predation cause relatively good growth conditions. Consequently, a decrease in condition for all mussels can be expected when these mussels are exposed to food limiting conditions, present in regions of an oyster bed and in the benthic environment. Another explanation is that the observed decrease in small mussel condition is the result of an annual growth pattern in mussel condition. However, effects of local oyster biomass on mussel condition may be expected on a longer temporal scale. When limited in food, mussels can use fat reserves (and thus decreasing condition) or decreasing the growth rate, resulting in less growth but a stable condition. The condition of wild mussels from the field control showed a significant correlation with local oyster density and mussel, which emphasises that a condition decrease can not be observed in a two months experiment.

Multiple regression on these results indicated that local oyster biomass was not the only factor significantly influencing mussel growth. Also, in order of significance, tidal height followed by distance to the edge of the oyster bed were significantly related to small mussel growth. Again, on a longer temporal scale, these effects can also be expected on mussels from the large size class. Small mussel decreased at increasing tidal heights. Thus, a longer duration of air exposure means a decrease of filtering time, decreasing the growth. An increase in distance to the edge of the bed corresponds with a longer travel time for the chl a rich waters. This is in fact a biotic factor, considering the decrease in nutrient concentrations caused by filter feeders as this distance increases. The observed decrease in small mussel growth at increasing distances is therefore logically explained. However, the range of distances can be questioned; the majority of distances (Fig. 3.5) are within the first 20% of the distance-axis, resulting in a very low R^2 value (0.1049). So, despite this correlation to be significant, it remains questionable.

Mortality among caged mussels was extremely low; after the growth experiment only 0.77% of the mussels was dead.

4.3 Oyster growth

Growth rate and -direction appeared to be highly variable in Pacific oysters, independent of the environmental factors measured in this experiment (local oyster biomass, distance to the edge and tidal height). Possibly, the absence of any correlation is caused by this high variability. Due to this extreme variable growth, it was virtually impossible to get comparable oysters with the same length, width and thickness that could be used for the growth experiment. Considering the low numbers of oysters available for condition analysis at t=0, variation between these oysters was too high to determine a reliable condition estimate at t=0, which was determined as the average condition of 6 large en 2 small oysters. A much larger number of comparable oysters is required to obtain a proper estimation of oyster condition at t=0. For large oysters, average condition on t=0 was 0.097 g afdw ml^{-1} (n=6), but the

standard deviation of 0.038 causes this average value to be highly unreliable. More importantly, these values were obtained with a different method (the so-called 'water displacement method', described by Baird, 1958) than the method explained earlier. This method did not work properly, especially for small oysters, where no volume change could be observed when the small oyster shell was submerged, caused by the surface tension of water. Additionally, there were only 2 small oysters available, resulting in a very unreliable condition index for small and large oysters at t=0. Ergo, results considering oyster condition indices, only consist of condition values at t=1. Contrary to local oyster biomass and distance to the edge of the oyster bed, the measured condition indices of small oysters at t=1 appeared to be significantly related with tidal height. When the tidal height increases it appears that the condition of small oysters also increases. Our expectations provide no suitable explanation for these findings.

Mortality among caged oysters (11%) was larger than mortality among caged mussels (0.77%). This correlates with the high mortality among oysters on the oyster bed near Sint-Annaland.

4.4 Field control

Tidal height and distance to the edge of the oyster bed had no influence on the results. This may be caused by the fact that the estimates of these factors are very inaccurate and not the only confounding factors determining the natural situation of mussels living in an oyster bed. Possibly, on a larger geographical scale, meaning a wider range of tidal heights and distances to the edge of the bed, these inaccurate estimates could result in significant relations. Contrary to these factors, the local oyster biomass did play an important role: with increasing oyster biomass the number of mussels (abundance) and mussel biomass increased, but the condition of mussels decreased. These results may suggest a trade-off situation for mussels living in an oyster bed, between food availability and substratum for settlement, which also may provide protection from predation by, for example, birds. On low tide, the presence of many

mussel predating birds, predominantly oyster catchers, caused very much mortality among the mussels living between the oysters, but mussels were still present in the crevices of the oyster congregations (personal observation). Contrary to what was expected, average mussel length did not significantly decrease with increasing oyster density. Considering the high variation in mussel numbers and lengths per sample location, working with these average lengths is not reliable. With regard to the possible trade-off situation, mentioned before, mussels were therefore divided in three size classes: small (0 – 20 mm), medium (20 – 40 mm) and large (40 – 60 mm) to see if there are any trends to support the trade-off hypothesis. This situation is also described by Honkoop and Bayne (1998) in terms of optimal oyster density for cultivation, and seems to be a common characteristic in bivalve growth.
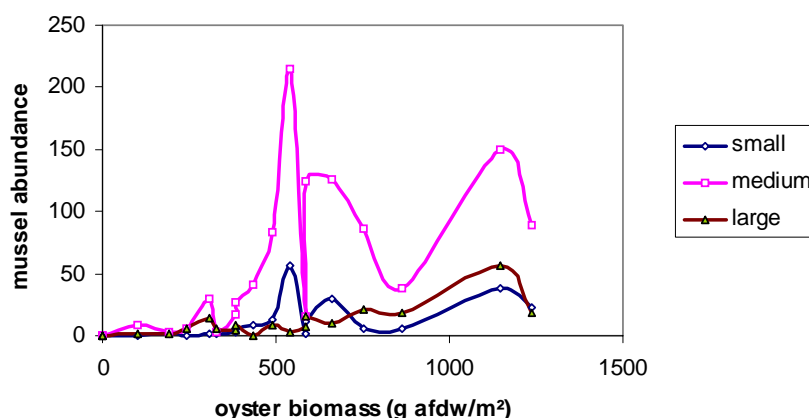

Figure 4.2. Trends in mussel size classes: small (0 – 20 mm), medium (20 – 40 mm) and large (40 – 60 mm). Points are connected by a smooth line. Linear regression showed that mussel abundance in all three size classes significantly increased with increasing oyster biomass (p<0.01).

Medium sized mussels are most abundant at all oyster densities. There is an increasing trend in mussel abundance with increasing oyster biomass for all three size classes. Despite the clear peak at an oyster biomass of 500 – 700 g afdw/m^2, mussel abundance increases again with increasing oyster biomass. These results do not support the trade-off hypothesis.

Samples for the field control were taken in a range of one month, in which considerable growth takes place. Growth in mussels occurs from April to October,

with a maximum in June (Walne & Mann, 1975). The mussel growth experiment showed a maximum length increment of about 6 mm in a period just over two months at a local oyster density of zero. In one month the maximum length increment of mussels then would be 3 mm. Considering the high variation in mussel lengths sampled at different oyster biomasses (Figure 3.10), it is not very likely that the mentioned period in which the sampling took place had any significant effects on the results.

It appeared that very few small (<10 mm) mussels could be found. This is probably due to the fact that sampling took place in August and September, so the new spat had already grown for several months. Reise (1998) reports that most Pacific oysters in the Northern Hemisphere spawn in July and August, but also in June and September spawning may occur. Spawning is believed to be triggered by genetic factors, instead of environmental factors (Baghurst & Mitchell, 2002).

In this research, no information on mussel age is obtained. The age of *M. edulis* seems difficult to determine in relation to mussel size (Dolmer, 1997). Effects of food limitation may result in smaller mussel shells as compared to 'free-living' mussels and differences in mussel length therefore can be misleading. Also shell thickening as a defence mechanism for mussels (Leonard, 1999) living in an intertidal oyster bed, where predation by crabs and birds can be very high, may cause misleading effects on result interpretation. Data on mussel age combined with length-data would be more reliable, but this data appeared to be too labour intensive to obtain in the available time.

4.5 Conclusions

The aim of this study was to determine if food competition between mussels and oysters occurs, and how mussel and oyster growth is affected by this interaction.

Considering (1) the rapid expansion of the Pacific oyster population, (2) the observed overgrowth of wild mussel beds by Pacific oysters in the Wadden Sea, (3) the relatively high filtration rate of Pacific oysters and (4) the fact that Pacific oysters and

mussels use the same food source, food competition between these species is very likely to occur. Mussel growth and condition were found to be negatively affected with increasing oyster biomass, while oyster growth was not affected. Tidal height and distance to the edge only played a very small role in this local orientated experiment. Oysters appeared to form a suitable substratum for mussels to settle.

4.6 Future research

In recent history, as at many other locations in the Oosterschelde estuary, there was no oyster bed at Sint Annaland, while nowadays a huge intertidal oyster bed provides habitat and shelter to hundreds of thousands of other animals from many species. Future research is essential in order to test the potential benefits for animals to live in an oyster bed. Here, biodiversity is a key factor.

Since we observed very high oyster mortality, it would be interesting to know what triggers oyster mortality in terms of, for example, temperature tolerance levels or food availability.

Comparing mussel growth of mussels growing at different locations, e.g. oyster beds, mussel bed and suspended rope cultures in the Oosterschelde estuary and the Wadden Sea, should provide valuable information on how the mussels are affected by the presence of Pacific oysters. If mussels are negatively affected by Pacific oysters, one can wonder why mussels settle and survive on oyster beds. Although in this research no indications for a trade-off were found, such a mechanism could be the answer. Also a study on food availability on population scale should provide useful information. It is likely that the whole Oosterschelde population of Pacific oyster can significantly reduce food availability for other important filter feeders, but not much is known about this. With the help of remote sensing, fluctuations and potential decreasing trends in chlorophyll a concentrations can be investigated.

Mussel culture is and remains a very important economical source, which has required and will require a lot of research.

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