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Adaptation of gill-palp ratio by mussels after transplantation to culture plots with different seston conditions

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ABSTRACT

Transplantation of bivalves between culture areas or systems that vary in environmental conditions is an important tool for growers to increase aquaculture productivity, but it sometimes leads to adverse effects on growth and survival. Bivalves filter ambient water including seston. Particles are retained on the gills and transported to the palps, where edible particles are selected for further digestion and where the rest is excreted as pseudofaeces. Both quantity and quality of suspended particles in the water affect efficiency of this process. As a consequence of transplantations, shellfish are forced to spend energy on adapting the gills and palps. This has implications for the energy available for growth and reproduction and might ultimately reduce yields. Here, we investigate, using gill-to-palp ratio as proxy, if adaptations in the feeding apparatus after transplantation of mussels to a culture area with higher seston quantity but lower quality, can explain an observed reduction in yield. We hypothesize that when mussels are transplanted to an environment with higher seston concentrations, (1) the gill-to-palp ratio becomes smaller, because mussels will grow larger palps to process the filtered material, while growth of gills will be reduced to reduce the amount of seston filtered and (2) condition of mussels will remain lower than reference levels during adaptation period. Three different mussel cohorts that were transported from the Oosterschelde (OS, NL) to the Wadden Sea (WS, NL) were monitored. Wadden Sea is more turbid (~2.4 × Total Particulate Matter OS), and is higher in chlorophyll-*a* concentration (~1.6 × Chl-a OS), but lower in food quality (~0.65 × ratio Chl-a:TPM OS). Gill-to-palp ratios and condition indices were measured from transplanted mussel cohorts and from reference populations over a period of three months. Results reveal that the gill-to-palp ratio between OS and WS is indeed significantly different (on average respectively 3.4 and 2.3), and that transplanted mussels show a remarkable physiological plasticity by adapting the gill-to-palp ratio within 1 month after transplant to match reference levels. They achieve this by a relative increase in the growth rate of the palps, while the growth rate of the gills remain constant. Condition index of transplanted mussels were not lower than reference levels with an equivalent increase. It is more likely that observed lower yields of transplanted mussels are related to factors that affect survival, because mussel adjustment to feeding conditions seems to occur quickly and mussel condition swiftly follows the reference population trajectory.

1. Introduction

Both wild and cultivated bivalves rely on the food availability in the surrounding water. Filter feeding bivalves pump the ambient water and its seston (i.e. all particles in the water, including organisms and non-living matter (Hutchinson, 1967)) through their gills, which act as filters that retain the seston, irrespective of the quality of the particles (Jørgensen, 1990). The filtered particles are captured in mucus and transported by cilia to the food grooves and subsequently to the four labial palps where major sorting takes place (Ward, 2003; Ward et al., 1998). The palps select the edible particles (generally high food quality) and transport them toward the mouth for further ingestion. The rejected particles (generally low food quality) are excreted as pseudofaeces (Payne et al., 1995; Ward and Shumway, 2004). The clearance rate (i.e.

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volume of water cleared of particles per unit time) is proportional to the size of the gills (Riisgård, 2001), while pre-ingestive particle selection efficiency can be related to palp size (Dutertre et al., 2007; Kiørboe and Møhlenberg, 1981). Compared to smaller gills, larger gills result in higher clearance rates and consequently collect more particles per unit time (Honkoop et al., 2003). In environments with low food concentrations, having large gills is an advantage. If, however, particles collected by the gills are present in large amounts and/or of low nutritional quality, there is an advantage of having large palps and smaller gills, that allows the mussel to better select and control the quality of the food it ingests (Honkoop et al., 2003).

Bivalves show reversible phenotypic plasticity in response to food quantity and quality, because they adapt to specific environmental conditions by changing the size of their gills and palps (Compton et al., 2008; Dutertre et al., 2017; Honkoop et al., 2003; Payne et al., 1995). Gill-to-palp ratio in bivalves can, therefore, be related to the quality and concentration of the seston in the water (Barillé et al., 2000; Essink et al., 1989; Foster-Smith, 1978; Honkoop et al., 2003; Payne et al., 1995; Theisen, 1977, 1982). For example, in a transplant experiment, Essink and Bos (1985) demonstrated that transplanted blue mussels (*Mytilus edulis*) changed the size of their gills and palps within months to resemble the sizes in the local population (Essink et al., 1989). More flexible adaptation processes are described for pacific oysters (*Crassostrea gigas*), where seasonal variation in gill and palp sizes is an efficient foraging strategy when food is abundant (Dutertre et al., 2017; Honkoop et al., 2003).

Sudden changes in food conditions often occur when bivalves are transplanted. In aquaculture, transplantations of bivalves during their life cycle has always been an important tool to increase productivity, for example to alter density and reduce competition, or to areas with higher growth or survival rates (Andrews, 1980; Dumbauld et al., 2009; Groesbeck et al., 2014; Kamermans and Capelle, 2019; Powell et al., 1998; South et al., 2017; Wu and Shin, 1998). As a consequence of such transplantations, bivalves are forced to spend energy in adaption of the

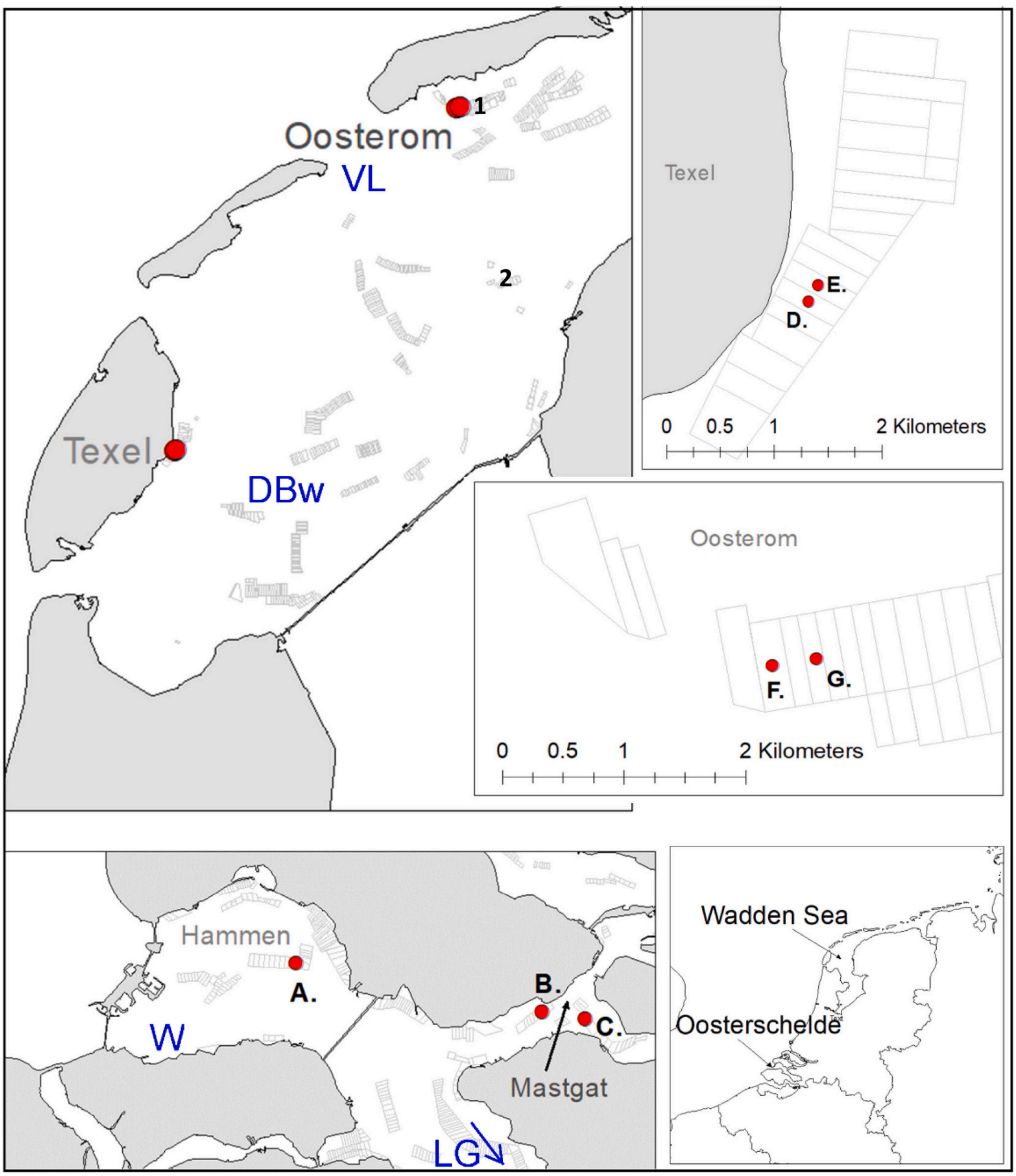

Fig. 1. Sampling locations on mussel culture plots in Oosterschelde: original & reference site (A, B, C) and Wadden Sea, transplant site: (E & F), reference site (D & G) and locations from where water quality was collected (https://waterinfo.rws.nl/), VL = Vliestroom, DBw = Doove Balg west, W = Wissenkerke, LG = Lodijkse Gat, number 1 and 2 in Wadden Sea refer to locations were extra samples were taken to estimate the correlation between gill and palp area and their weight.

gills and palps, that has implications for the energy available for growth and reproduction (Bayne et al., 1993; Hawkins et al., 1999; Hawkins et al., 1998). For the management of cultured bivalves, the adaptation of the feeding organs can be considered as a trade-off between adaptation costs and the aim to maximize biological performance, especially when transplantation occurs between areas with very different seston conditions.

In the Netherlands, mussel (*Mytilus edulis*) seed are cultured on-bottom at culture plots. For resource provisioning, mussel seeds are collected in the water column with Seed Mussel Collectors, or fished from natural mussel seed beds in the Wadden Sea (Kamermans and Capelle, 2019). During the on-growing process, mussels are transplanted approximately twice between culture plots with different characteristics, within the cultivation area or between cultivation areas. In the Netherlands, regular transplantations occur between the Wadden Sea in the North, which is the major source of mussel seed, and the Oosterschelde in the South (Fig. 1). The Wadden Sea is a dynamic area with high suspended particle concentrations in the water and open access to the North Sea, while the Oosterschelde is a more sheltered bay with lower suspended particle concentrations. To mitigate storm losses, most transplants to the Oosterschelde occur before winter. However, since food quantity in the Wadden Sea is better, mussels grow faster in the Wadden Sea (on average it takes 2 years to get from seed to marked size compared to 3 years in the Oosterschelde), which makes the Wadden Sea the preferred area for cultivation outside storm season (winter). Transplant activities is in general not allowed to reduce the risk of spreading non-indigenous species from the Oosterschelde to the Wadden Sea. However, Oosterschelde – Wadden Sea transplantations were temporally permitted in 2014 and 2015 after a screening procedure and a fresh water treatment to kill non-indigenous species. Contrary to expectation, mussel growers reported low yields of those transplanted cohorts. We therefore investigated if transplantation from Oosterschelde (lower seston concentration) to the Wadden Sea (high seston concentration) caused adaptations in the feeding apparatus, using gill-to-palp ratio as proxy, and whether this adaptation co-occurred with a reduction in mussel condition. We hypothesized that when mussels are transplanted to an environment with higher seston concentrations, (1) the gill-to-palp ratio becomes smaller, because mussels will grow larger palps to process the filtered material, while growth of gills will be lower to reduce the amount of seston filtered and (2) condition of mussels will remain lower than reference levels at the new site during the adaptation period.

2. Material and methods

2.1. Areas and sampling locations

The Wadden Sea is described as a shallow system, strongly influenced by the tide. The tide transports sediment and nutrients between the Wadden Sea and the North Sea. The Wadden Sea is a system with

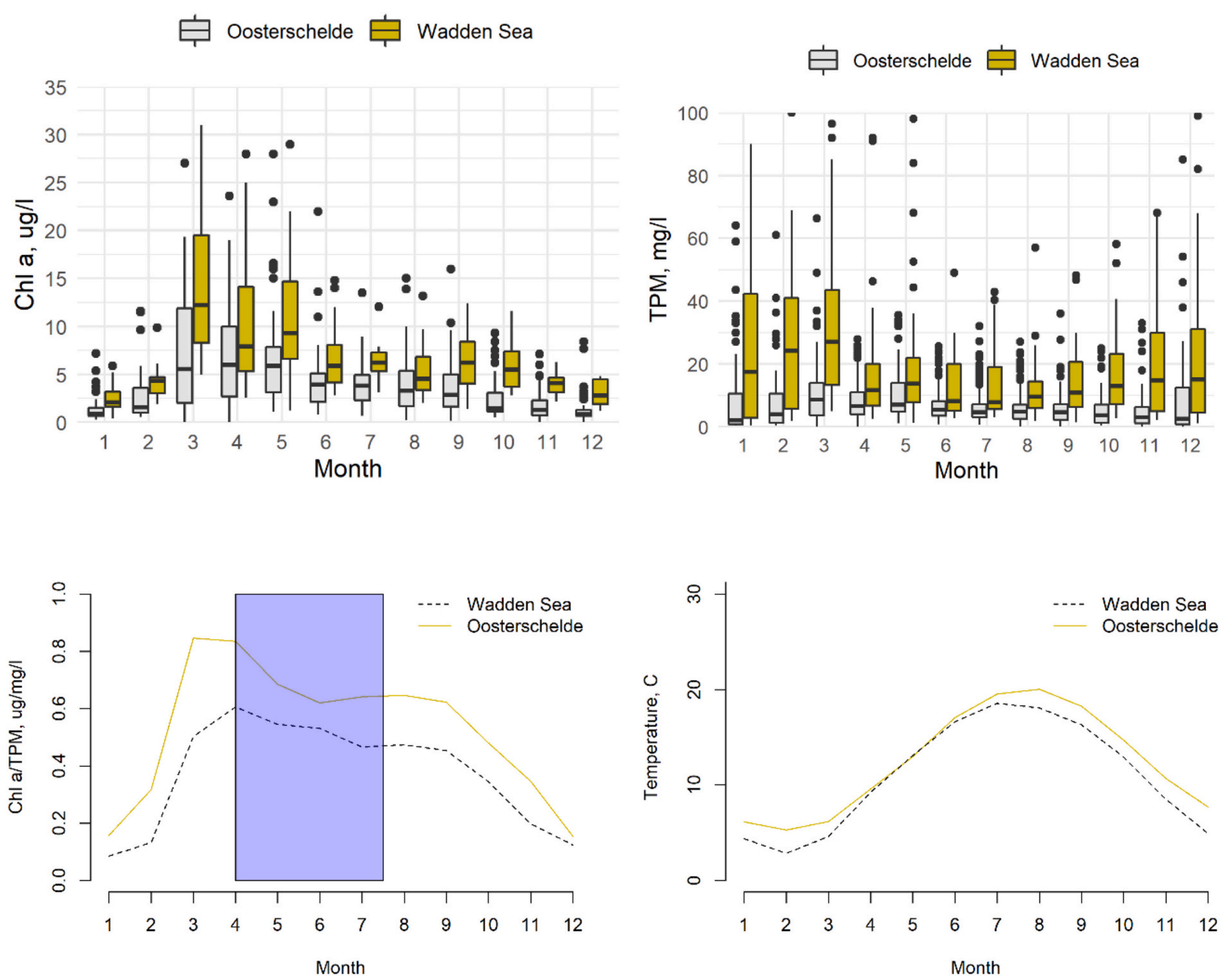

Fig. 2. a) boxplot of chlorophyll-a (Chl a) b) boxplot of Total Particulate Matter (TPM) c) average Chl a as fraction of TPM and d) average temperature for the Oosterschelde and for the Wadden Sea. Data taken from https://waterinfo.rws.nl/ and aggregated per month over the period 2005–2017. The blue quadrant in panel c elucidates the timing when samples were taken. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

both high food quantity as well as a high concentration of suspended sediment. The Oosterschelde on the other hand, is partially closed off from the North Sea by a storm barrier and the river input by dams, which has led to decreased concentrations of suspended solids and nutrients (Wetsteyn and Kromkamp, 1994). The ratio between chlorophyll-*a* to Total Particulate Matter (TPM) is regarded as an indication of food quality for bivalves (Prins et al., 1991; Van Stralen, 1995), Oosterschelde, has a high chlorophyll-a to TPM compared to the Wadden Sea (Fig. 2).

Three mussel transplant activities by mussel growers between distinct grow-out sites from Oosterschelde (South) to the Wadden Sea (North) occurred relatively simultaneously in spring of 2015. The transplant activities were monitored to assess gill-to-palp ratios and mussel condition. Samples were collected from the transplanted cohort in the Oosterschelde prior to transportation and twice after relay in the Wadden Sea. In addition, samples were collected from a reference location in the Oosterschelde (mussels at the same plot from the same origin that were not transplanted) and from a reference location in the Wadden Sea (mussels from a neighboring plot), see Fig. 1. All samples were collected by mussel growers during their regular work activities. Samples were collected with a monthly interval. Mussel growers were not always in the vicinity when sampling was due, therefore samples were not always aligned in time.

In Table 1 an overview is provided for the three distinct transplants, with reference to the labels (A:G) in Fig. 1 and is summarized as follows:

Transplant activity 1: Site A in Oosterschelde was a collection site, mussels from Site A were transplanted to Site F in the Wadden Sea and mussels remaining at Site A throughout the course of the experiment or on a nearby plot in the Wadden Sea (Site G) were used as references for the palp-to-gill ratios and condition at the source and transplant sites respectively.

Transplant activity 2: Site B in Oosterschelde was a collection site, mussels from Site B were also transplanted to Site F in the Wadden Sea and mussels remaining at Site B throughout the course of the experiment or on a nearby plot in the Wadden Sea (Site G) were used as references for the palp-to-gill ratios and condition at the source and transplant sites respectively.

Transplant activity 3: Site C in Oosterschelde was a collection site, mussels from Site C were transplanted to Site E in the Wadden Sea and mussels remaining at Site C throughout the course of the experiment or on a nearby plot in the Wadden Sea (Site D) were used as references for the palp-to-gill ratios and condition at the source and transplant sites respectively.

2.2. Environmental data

Data on chlorophyll-*a* and Total Suspended Matter were retrieved from https://waterinfo.rws.nl/. Data were available on bi-weekly to monthly intervals and mean values per month were aggregated over the period 2005–2017. Per area two spatially distinct sampling locations were selected from the database: Wissenkerke (W in Fig. 1) and Lodijkse Gat (LG in Fig. 1) in the Oosterschelde and Vliestroom (VL in Fig. 1) and Doove Balg west (DBw in Fig. 1) in the Wadden Sea.

2.3. Sampling and sample processing

Mussel samples were collected by mussel growers during their regular work activities. At least 30 mussels per location were directly placed in plastic jars and preserved in ethanol (90%). Because of tissue deformity after preservation in ethanol we used a gill-to-palp weight ratio, following a similar methodology as in Drent et al. (2004) and Compton et al. (2007). Gills and palps were dissected completely from the mussels in the lab and weight was determined for each organ (gills, palps and remaining flesh tissue) separately. In addition length (L, mm) was recorded for each mussel. Samples were dried at 80 °C to obtain dry weight (DW) and ashed at 540 °C (ash weight AW) until change in weight was less than 1% and 0.1% respectively. Ash-free dry-weight (AFDW) was calculated by subtracting ash-weight from dry-weight.

Some studies that deal with changes in gill palp ratio's, use the ratio between the areas of the pallial organs, instead of the weight ratio. We investigated the relation between AFDW and area of mussel gill and palp *a postiori*, from mussels from the Wadden Sea, with the only purpose to be able to make valid comparisons between ratios based on weight and ratios based on area. In other words can the results we have obtained using a weight ratio be compared with other studies where an area ratio was used? Therefore, sixty fresh mussels were collected from the Wadden Sea (on 28 and 29 Sep 2020, at location 1 and 2 in Fig. 1), gill and palp area was measured from the fresh mussels to the nearest 0.1 mm^2 for each individual using the same methodology as Sunde (2013). After size measurements the AFDW of individual gills and palps were obtained using a prepASH 229 that performs fully automatic thermo-gravimetric analysis (https://www.precisa.co.uk).

Gill-to-palp ratio was calculated by $AFDW_{palp}/AFDW_{gill}$. Condition index (mg/cm^3) was calculated as: $(AFDW_{gill} + AFDW_{palp} + AFDW_{flesh})/L^3$.

2.4. Data analysis

Differences in gill-to-palp ratio and condition index were compared

Table 1
Overview of samples taken from mussel transplantations between Oosterschelde and Wadden Sea in 2015, from each sample gill-to-palp ratio and condition index of the mussels was determined.

Transplant activity	Sample	Mussel origin (mussel size)	Sample	Sampling location	Day	Label (Fig. 1)
1	1	Oosterschelde (49.9 ± 0.4 mm)	Prior transplant	Hammen, Oosterschelde	30-Mar	A
	2		After transplant	Oosterom, Wadden Sea	20-May	F
	3				15-Jul	
	4		Reference Oosterschelde	Hammen, Oosterschelde	16-Jun	A
	5	Wadden Sea (61.0 ± 0.5 mm)	Reference Wadden Sea	Oosterom, Wadden Sea	22-May	G
	6				13-Jun	
2	7	Oosterschelde (49.7 ± 0.6 mm)	Prior transplant	Mastgat, Oosterschelde	20-Apr	B
	8		After transplant	Oosterom, Wadden Sea	20-May	F
	9				16-Jun	
	10				15-Jul	
	11		Reference Oosterschelde	Mastgat, Oosterschelde	18-May	B
	12	Wadden Sea (61.0 ± 0.5 mm)	Reference Wadden Sea	Oosterom, Wadden Sea	22-May	G
	13				13-Jun	
3	14	Oosterschelde (41.1 ± 0.5 mm)	Prior transplant	Mastgat, Oosterschelde	20-Apr	C
	15		After transplant	Texel, Wadden Sea	12-May	E
	16				8-Jul	
	17		Reference Oosterschelde	Mastgat, Oosterschelde	15-Jun	C
	18	Wadden Sea (40.8 ± 1.1 mm)	Reference Wadden Sea	Texel, Wadden Sea	8-Jul	D

between samples per transplant activity with its references with a general linear model. In the gill-to-palp ratio we applied no correction for mussel size; although gill size and palp size are related to mussel size, the ratio between palp and gill are more related to particle concentration than to mussel size (Brett Suzanne and Wassenaar, 1990; Sunde, 2013). A *post-hoc* Tukey's pairwise comparison was carried out to find differences between gill-to-palp ratios within a series.

The relation between the area and weight of the pallial organs that were sampled *a postiori*, was fitted with a linear function and on a log-log scale to assess allometry (Pélabon et al., 2018). An F-test was used to select the best fit. The relationship between weight of gills and palps and L^2 (as a proxy for shell area) was assessed from transplant activity 1 and was fitted with a linear function and on a log-log scale to assess allometry, an F-test was used to select the best fit. Change in gill and palp AFDW (mg) were standardized by length squared (as proxy for shell area) and compared with a general linear model and a p*ost-hoc* Tukey's pairwise comparison. Shell area was used to for standardization instead of AFDW, because AFDW is strongly affected by condition. Shapiro-Wilk test was used to check normality of the residuals, an evaluation of residual plots showed no indication of heteroscedasticity for the models that were applied.

3. Results

3.1. Environment

Fig. 2 shows the yearly distribution in Chlorophyll-a, TPM and their ratio aggregated per month over an extended period (2005–2017) for Oosterschelde and Wadden Sea. The blue quadrant indicates the period of the year (April and mid-July) this study was performed. The average values for the period in 2015 when samples were taken were: for chlorophyll-*a* and Total Particulate Matter respectively 7.6 (Interquartile range [IQR]: 3.6–9.2) μg/l Chl-a and 21.1 (IQR: 11.4–26.8) mg/l TPM for the Wadden Sea and 4.8 (IQR: 2.3–6.7) μg/l Chl-a and 8.8 (IQR: 4.4–12.2)mg/l TPM for the Oosterschelde. Underlying time series for all stations are provided in supplementary files.

3.2. From location A in Oosterschelde to location F in Wadden Sea (Fig. 3)

Gill-to-palp ratio was lower for all samples collected at location G (reference location) and F in the Wadden Sea, compared to the samples collected at location A in the Oosterschelde ($F_{1,100} = 41.1$, $p < 0.001$). The gill-to-palp ratio of the transplanted mussels decreased from 3.1 to 2.3 after 51 days ($p < 0.001$) when they had similar gill-to-palp ratios to reference location G in the Wadden Sea ($p > 0.05$). After that, from mid-May to mid-July, neither gill-to-palp ratios of the mussels at locations G and F in the Wadden Sea changed over time ($p > 0.05$), while the difference between Oosterschelde and Wadden Sea remained (Tukey all-pair comparison, $p < 0.05$). Condition index of transplanted mussels increased from the beginning of June when were found to have a similar condition as mussels from reference locations in Oosterschelde and Wadden Sea. Condition at the Wadden Sea site F was similar in condition to the Oosterschelde site in mid-June.

3.3. From location B in Oosterschelde to location F in Wadden Sea (Fig. 4)

The average Gill-to-palp ratio of all samples collected at locations G (reference location) and F in the Wadden Sea was lower than the average gill-to-palp ratio of the mussels collected at location B in the Oosterschelde ($F_{1,111} = 39.0$, $p < 0.001$). The average gill-to-palp ratio of the transplanted cohort decreased after transplantation from location B in the Oosterschelde to location F in the Wadden Sea from 3.1 to 2.4 after 30 days ($p < 0.05$) when they had similar gill-to-palp ratios to reference location G in the Wadden Sea ($p > 0.05$). Transplanted mussels at location F in the Wadden Sea followed a similar trajectory as the reference mussels at location G. Condition index of transplanted mussels increased from the beginning of June and were found to have a similar condition as mussels from reference locations in Oosterschelde and Wadden Sea.

3.4. From location C in Oosterschelde to location E in Wadden Sea (Fig. 5)

Location C is situated in the northern part of the Oosterschelde, where TPM concentrations are generally lower than at the other locations. This reflects on the gill-to-palp ratio, which is higher (mean 4.0) than those at the other Oosterschelde locations (both with a mean of 3.1). Thirty days after transplantation of the mussels to location E in the Wadden Sea (mid-May), the average gill-to-palp ratio of the mussels (mean 3.5) was not yet distinctive from the reference location C in the

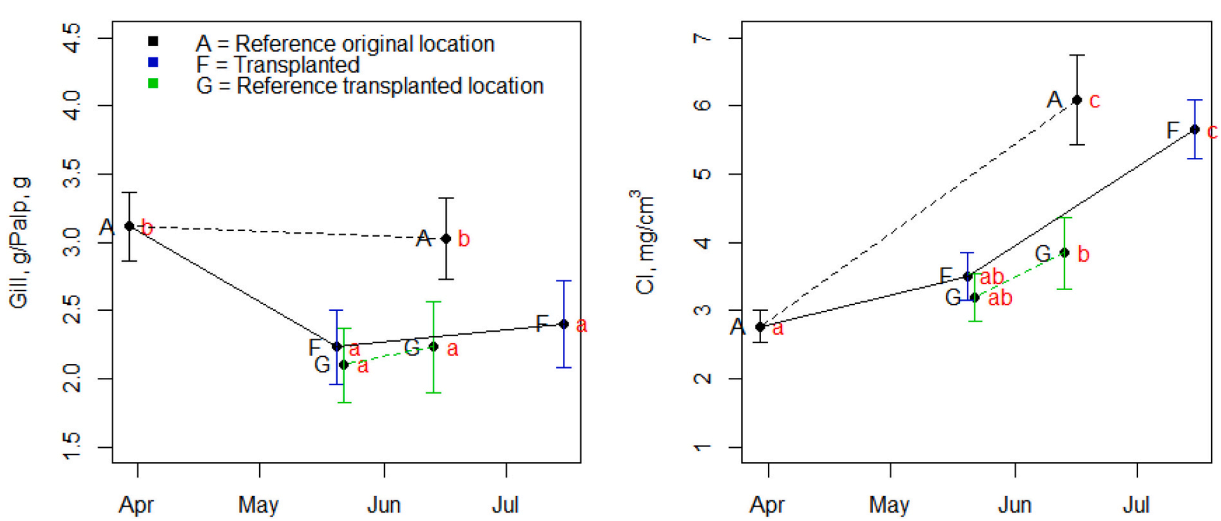

Fig. 3. Changes in gill-to-palp AFDW ratio (left panel) and Condition Index (right panel) of a transplanted mussel cohort from Oosterschelde (Location A) to Wadden Sea (Location F) the dotted black line (A) shows the development of gill-to-palp ratio and condition index at reference location in the Oosterschelde, the solid black line (A- > F) the development of gill-to-palp ratio and condition index after transplant to the Wadden Sea and the dotted green line shows the development of palp-to gill ratio and condition index at a reference location (Oosterom 4) in the Wadden Sea, letters indicate significance with an α-level of 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

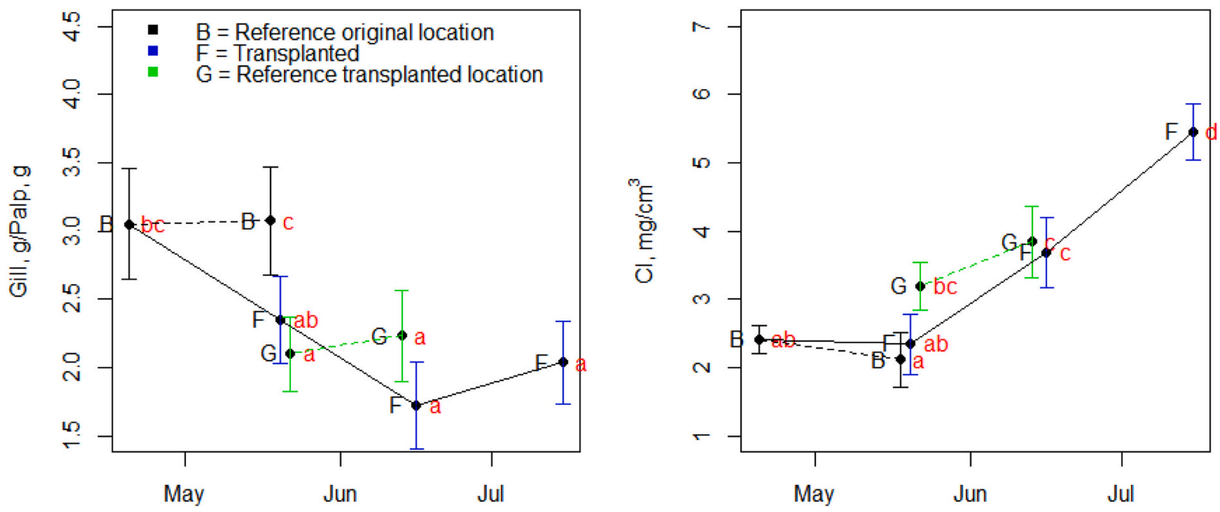

Fig. 4. Changes in gill-to-palp AFDW ratio (left panel) and Condition Index (right panel) of a transplanted mussel cohort from Oosterschelde (Location B) to Wadden Sea (Location F) the dotted black line (A) shows the development of gill-to-palp ratio and condition index at a reference location in the Oosterschelde, the solid black line (A- > F) the development of gill-to-palp ratio and condition index after transplant to the Wadden Sea and the dotted green line shows the development of palp-to gill ratio and condition index at a reference location (Location G) in the Wadden Sea, letters indicate significance with an α-level of 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

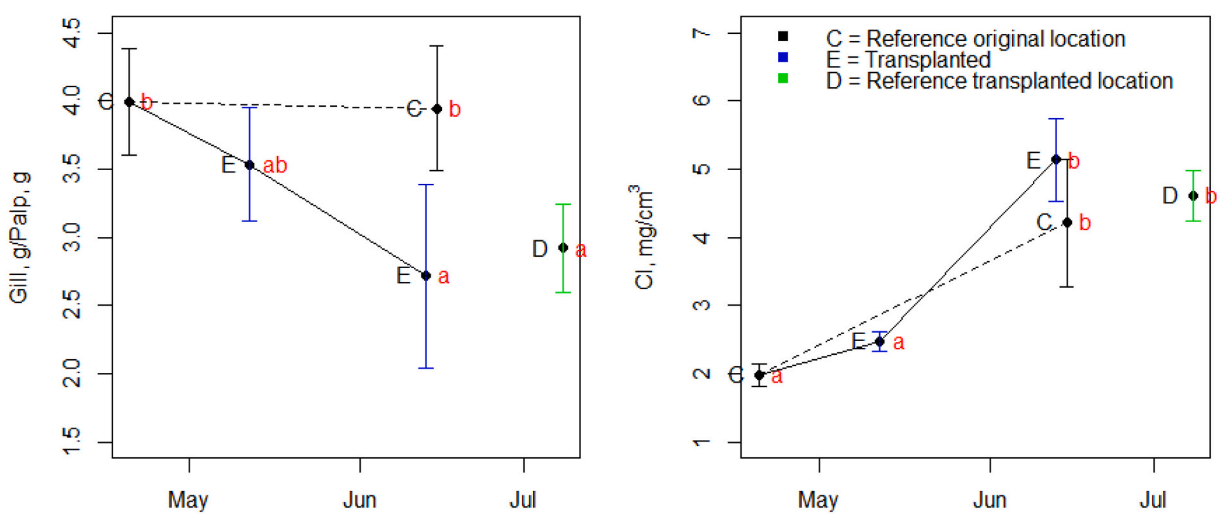

Fig. 5. Changes in gill-to-palp AFDW ratio(left panel) and Condition Index (right panel) of a transplanted mussel cohort from Oosterschelde (Location C) to Wadden Sea (Location E), the dotted black line (A) shows the development of gill-to-palp ratio and condition index at a reference location in the Oosterschelde, the solid black line (A- > F) the development of gill-to-palp ratio and condition index after transplant to the Wadden Sea and the dotted green line shows the development of palp-to gill ratio and condition index at a reference location (Location D) in the Wadden Sea, letters indicate significance with an α-level of 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Oosterschelde, but also not from the reference location D in the Wadden Sea (mean 2.9). After two months (56 days – mid June) the transplanted mussels at location E had developed a distinct and lower average gill-to-palp ratio (mean 2.7) than from the reference location C in the Oosterschelde (mean 3.9). Condition index trajectory was comparable between Oosterschelde and Wadden Sea and the transplanted mussels followed the same line.

3.5. Relation between mass and area of pallial organs and relative change in gill and palp sizes

From the samples that were collected *a postiori* (see section 2.3), AFDW of gills (GW, g) and palps (PW, g) were related to their respective area (GA and PA, in mm^2). An allometric fit better described the relationship between variables than a linear fit. The relationships were: (F-test, $p < 0.05$). Relations were: $Log_{10}[GA] = 0.43*log_{10}[GW] + 6.9$, ($F_{1,40} = 12.93$, $p < 0.01$, $R^2 = 0.24$), and $Log_{10}[PA] = 0.41* Log_{10}[PW] + 5.5$, ($F_{1,40} = 12.17$, $p = 0.001$, $R^2 = 0.23$). This enables us to make valid comparisons between ratios based on weight and ratios based on area.

Relation between GW, PW and mussel shell area (Shell, mm^2) from transplant activity 1 was described with a linear model: GW = 0.02*Shell-0.06 ($F_{(1,161)} = 191.4$, $p < 0.001$, $R^2 = 0.54$), and: PW = 0.01*Shell-0.04 ($F_{(1,157)} = 84.3$, p < 0.01, $R^2 = 0.35$). We analyzed transplant activity 1 because it has the highest overlap between the samples. A linear relation provided a better fit (based on a lower AIC value) than an allometric relation. This enables us to express GW and PW per shell area to investigate relative changes in palp and gill size over time. Fig. 6 shows the change in gill and palp AFDW (mg) expressed per shell area (cm^2) from transplant activity 1. Mussels decrease their gill-to-palp ratio, while both gill and palp size increases. However, the increase in palp size is relatively larger than the increase in gill size.

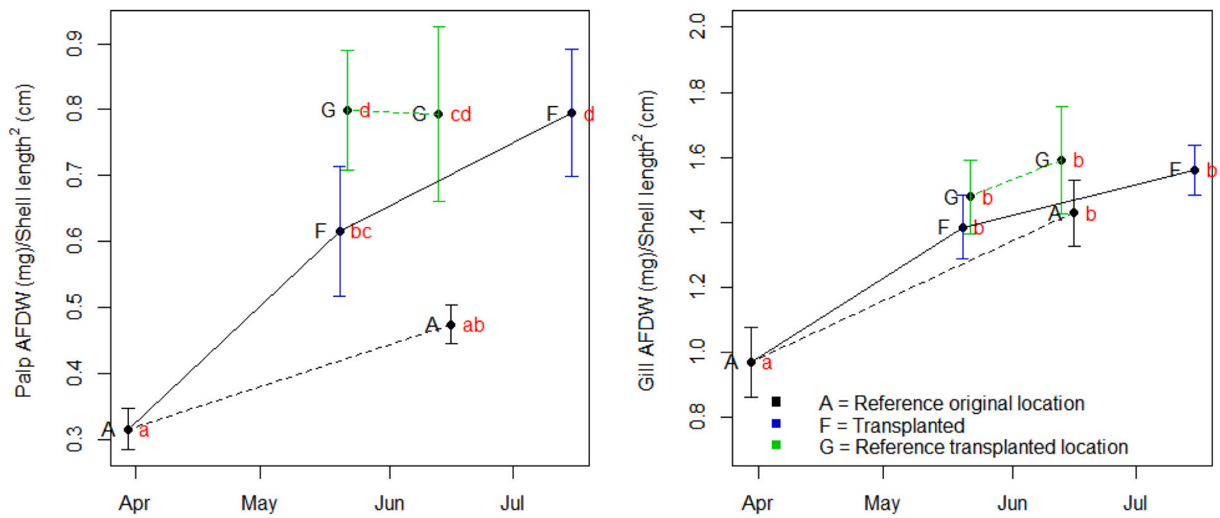

Fig. 6. Change in AFDW of the gills (left panel) and palps (right panel) standardized by length squared, of a transplanted mussel cohort from Oosterschelde (Location A) to Wadden Sea (Location F), the dotted black line (A) shows the development gill and palp weight contribution at a reference location in the Oosterschelde, the solid black line (A- > F) the development of gill and palp weight contribution after transplant to the Wadden Sea and the dotted green line shows the development of gill and palp weight contribution at a reference location (Location G) in the Wadden Sea, letters indicate significance with an α-level of 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Mussels adapted to their new environments by adjusting the gill-to-palp ratio, in a pattern that was similar for all transplantations in this study. Adaptations took place quickly, gill-to-palp ratios reached reference levels within 30–50 days, irrespective of specific locations within the cultivation areas. This was achieved by an accelerated growth rate of the palps. The decrease in gill-to-palp ratio after mussels were transplanted from Oosterschelde to the Wadden Sea was likely due to differences in seston conditions between the two areas. Average concentration of the Chlorophyll-*a* and the Total Particulate Matter is higher in the Wadden Sea, whereas the food quality (Chla:TPM) is lower than in the Oosterschelde. This requires that mussels that are transplanted from Oosterschelde to the Wadden Sea adapt to a situation with generally more, but lower quality food, which results in increased requirements for food processing and sorting.

Because feeding efficiency is affected by the size of the gills and palps (Kiørboe and Møhlenberg, 1981; Kiørboe et al., 1980; Ward, 2003), we further expected that a sudden change, invoked by transplant activities, would reduce feeding efficiency and would result in a substantial lower condition than the reference mussels. At first measurement after transplant from Oosterschelde, mussel condition did not significantly differ from condition of the reference populations in Wadden Sea or Oosterschelde. In fact the condition index trajectory of the transplanted batch does not show any deviation from the trajectory of the reference population in the Wadden Sea. In reference samples from Oosterschelde and Wadden Sea, gill and palp sizes increased over time, due to growth of mussels that accelerates in late spring and summer (see Fig. 2 in (Capelle et al., 2016b) and Fig. 6 in (Troost et al., 2010)). In the transplanted mussels, gill and palp weight increased to reach the same relative size (per area of shell, by proxy of quadrated shell length), as the reference samples from their destination. Here, palp size displayed a higher relative growth rate than gill size, which resulted in a decreasing gill-to-palp ratio. Essink et al. (1986) found that after mussel were transplant to areas with different sediment dynamics, relative gill and palp weight started to change faster when contrasts were larger. The average difference in food conditions between the two cultivation sites (~2.4× TPM, 1.6× Chla, 0.65× Chla:TPM for WS compared to OS) could consequently have resulted in the fast change in palp and gill size, and their ratio.

Chlorophyll-*a* and TPM show spatial differences that are likely reflected in the site-site differences in gill-to-palp ratios. Variation between locations in the systems (Oosterschelde and Wadden Sea) were not taken into account in the analysis, because environmental data on such fine scale was not available. Other sources that mention spatial variation within the systems suggest a similar trend. For example, TPM values at location C in the northern branch of the Oosterschelde are lower than at location A in the western part of the basin (see Fig. 2 in Troost et al. (2010)), TPM increases toward the western part of the basin (Jiang et al., 2019). In the Wadden Sea, location D and E have lower TPM and Chlorophyll-*a* values than location F and G (Arabi, 2019). In the transplant from Oosterschelde to Wadden Sea, food quantity increased and food quality decreased. Both an increase in quantity and a decrease in quality will hypothetically result in a decrease in the gill-to-palp ratio (Barillé et al., 2000; Compton et al., 2008; Dutertre et al., 2017; Honkoop et al., 2003). Because they occurred simultaneously, it is not possible to distinguish between food quantity or quality as contributing factor. Note that environmental data were downloaded from a national database with water-related monitoring data from samples collected in the water column (surface water). These data can be used to compare monitoring stations, but conditions on mussel culture plots (at the bottom) might be slightly different. In addition data from the water monitoring sites were amalgamated over multiple years prior to the transplant experiment, variation of conditions over this longer time span are also not captured.

According to Prosser (1991) species can either follow a regulative or a conformative strategy to deal with changes in the environment. Regulators maintain relative internal consistency, while conformers change internally to conform to changes in the environment. Species with similar morphological features may exhibit different strategies. For example, in fresh water, unionoidean mussels are regulators that are adapted to live in relative stable environments, while zebra mussels are conformers, that makes them capable to quickly colonize a range of habitats (McMahon, 2002). In marine environments marine mussels inhabit areas where large environmental fluctuations occur such as intertidal habitats. Adaptations at different levels are required to survive in habitats where conditions are variable and perturbations regularly occur (Lent, 2015). The present study shows that *Mytilus edulis* are conformers, that can adapt quickly to site characteristics within 30–50 days.

Early reproduction, large reproductive output and the semi-sedentary lifestyle of marine mussels has led them to persist over a wide range of environmental conditions. Mussels respond to small scale changes, on a (semi)diurnal timescale by altering their feeding behavior, for example in displaying tide related valve gape behavior (Bertolini et al., 2021). On longer time scales (weeks-months), plasticity of the feeding apparatus is an important trait to optimize performance under a range of environmental conditions, that are often not stable. For example, food quality fluctuates over the year and is prone to perturbations. Also, human induced perturbations are frequent in coastal zones, such as dredging (Essink, 1999), beach nourishments (Peterson and Bishop, 2005) or fisheries (Pastor et al., 2020). Advantages of such adaptations are illustrated by a study between two oyster species, that co-occur in the same estuaries by Honkoop et al. (2003): the Sydney rock oyster (*Saccostrea glomerata*) and the introduced Pacific oyster (*Magallana gigas*). In their study they found a higher plasticity in the gill-palp ratio of *M. gigas,* that translated into better growth performances than the native *S. glomerata*, through the ability to respond to changes in the environment more adequately. Our results showed that *M. edulis* is also a fast conformer: the relative size of feeding organs are growing at a different rate than flesh increase, thereby exhibit the plasticity to optimize feeding efficiency to prevailing food quality. Mussels can thereby perform rapid adaptations when food availability changes, as is demonstrated in the present study.

The capability of mussels to adapt to changing environments is an important trait for aquaculture management, where transplantations between areas and habitats are frequently carried out to optimize performance or in the transfer of seed to growing areas (Boromthanarat and Deslous-Paoli, 1988; Christensen, 2012; Dare et al., 1983; Fuentes et al., 1994; Jeffs et al., 1999). Transplantations can have several adverse effects on mussel survival, such as the occurrence of stress during transport (Calderwood et al., 2015; Calderwood et al., 2014), that may result in mortality or secondary settlement (South et al., 2021), seeding related losses due to predation or competition (Capelle et al., 2016a; Capelle et al., 2016b) and inefficient feeding can increase vulnerability for other stressors (Delorme et al., 2020). In our case, mussel farmers expected higher yields after transplantation of mussels from Oosterschelde to Wadden Sea. Yield reduction can either be caused be a reduced growth rate of by a higher mortality rate. In this case it was probably caused by the latter as reduced growth rates nor decrease in condition were observed suggesting that feeding problems did not occur after a sudden change in food conditions. Instead, a remarkable adaptive capability of the feeding apparatus was observed after transplantation to an area with challenging food conditions due to the high concentrations of resuspended sediments.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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