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Filtration and assimilation efficiency of *Ruditapes philippinarum*; why do they not keep growing?

Bastien Debeuf

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Mémoire de Fin d'Etudes

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Filtration and assimilation efficiency of *Ruditapes philippinarum* ; why do they not keep growing?

Par : Bastien DEBEUF

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Abbreviations list

[algae]: algal concentration.

AE: Assimilation efficiency, efficiency of individual to assimilate food ingested in the guts.

AFDW: ash-free dry weight.

CR: Clearance rate, volume of water filtered by the individual per unit of time.

DEB model: Dynamic Energy Budget model.

DW: Dry weight.

IR: Ingestion rate, weight of food ingested by the individual per unit of time.

PIM: Particulate Inorganic Matter.

POM: Particulate Organic Matter

SPM: Solid Particulate Matter.

Introduction

The growing world population and the rising living level in third world countries lead to an increasing necessity for protein, especially from marine sources. But the fisheries captures are not sufficient to subsidize this demand (Neori et al. 2004). According to the FAO statistics, 50% of the fish protein is furnished by the aquaculture, that increases by 6.9% per year (Troell et al. 2009). At the same time, the fish food price reaches its maximum level, increasing production costs. Moreover consumers ask for more sustainable and ecological-friendly practices and fish farmers have to invest a lot of money to install nutrients extracting facilities.

This situation has revived the interest of the aquaculture community for the historical concept of integrated multi-trophic aquaculture (IMTA, Troell et al. 2009). IMTA is an aquaculture concept that integrates predator - prey interactions in the culture of species. The goal is to reduce nutrient discharge while increasing production rate compared to traditional aquaculture. Asian countries have developed associated cultures of rice or mulberry trees and fish or shrimps, to recycle aquaculture wastes into soil nutrients, for centuries (Li 1987; Chopin et al. 2001). Western countries rediscover such a concept to prevent water enrichment, nitrification and to reduce the cost of a production kilogramme. Moreover, it is a source of revenues diversification, which could secure the durability of finfish mono-rearing farms. By increasing the number of product types you sell, you reduce the effect of one product price crash. IMTA is the only nutrients removing method which provides additional money incomes by adding crops (Troell et al. 2009).

To attain the goal of IMTA one has to know the optimal circumstances for the complete system, which depends on growth and population dynamics of all species concerned as well as the interactions between species taking place. Many of these circumstances are not entirely known, leading to a lack of knowledge on how to adjust the system to attain its goal. Moreover, it is needed to have a deep understanding of the biological cycle of every species that could be used in such systems, in order to allow a good production and sustainable farms.

Last year, growth has been monitored in a Japanese clams (*Ruditapes philippinarum*) farm in Yerseke, the Netherlands. Monitoring revealed it took long to grow the clams to the commercial size (around 40mm) and that this size was barely reached within a year. Clams stopped growing too soon for the farm to sell their products within a year. There are several hypothesises that could explain this slow growth. One hypothesis is that vital rates as standardized CR and AE are not constant, but decline over size, because of physical limitations (Kooijman 2010). Consequently, given constant supply of food, larger individuals have trouble to meet living requirements, especially if we assume living requirements also increase over size. A second hypothesis is that the quantity and/or the nutritional quality of the algal diet limit growth (Gouletquer et al. 1989; Coutteau et al. 1994; Sobral 1995; Han et al. 2008). Additionally, both growth and filtration rate have been proven to be temperature-dependent for *R. philippinarum* (Gouletquer and Bacher 1988; Gouletquer et al. 1989; Bensch et al. 1992; Fan et al. 2007; Han et al. 2008), so temperature-limitation is another hypothesis for the slow-down of growth. . According to Han et al. (2008) assimilation efficiency is temperature independent but we checked the effect of water temperature on this particular rate.

In order to cover these potential limitations, this report mainly focuses on the influence of food concentration and physical limitations over size, while another internship centred on nutrient cycle in the pond. To test hypotheses, we monitored a batch of clams and measured filtration rate, algal densities, temperature and size over time. We used a statistical model to assess the effects of the different parameters (size, temperature and algal density) on

standardized ingestion rate to allow a better understanding of what is actually limiting the growth and what are the main parameters to act on to improve production in the farm.

Materials and methods and Flow-through system testing

Temperature

Temperature was measured three times a day, approximately every hour and a half, in one of the individual chambers, using a thermometer.

Length / Weight

Length of every individual sampled was measured each experimental day. Clams were measured with micrometer calipers (anterior/posterior length). Flesh DW was then calculated with an allometric relation based on another project data. We chose this method because a non-destructive method was needed in order to keep the same batch of clams during the experimental period. Size is given as mm and DW as g.

Algae charge / Clearance rate (CR) / Ingestion rate (IR)

Clearance rate (CR, ml.h⁻¹) was calculated according to Petersen et al. (2004) equation:

$$CR = [(C_{in} - C_{out})/C_s] \times Q$$

where C_{in} and C_{out} are respectively the inflow and outflow algae concentrations (particles.ml⁻¹), and Q the flow rate (ml.min⁻¹). C_{in} is considered equal to C_s that is to say C_{out} in the control chamber.

Approximately every 90 min outflow water was sampled from each chamber during 1 minute, using a 1l plastic bottle. Flow rates were measured during these samplings, with a sized beaker.

Algae concentrations were determined using a Multisizer™ 3 COULTER COUNTER® (Beckman Coulter, Inc) with a the size range chosen for counting of [4;20]µm.

Ingestion rate (IR, gDW.h⁻¹) was calculated using the following equation :

$$IR = CR \times [food] \times DW_{coeff}$$

With [food] = number of particles of [4;20]µm per ml
and DW_{coeff} = linear regression coefficient between number of particles between 4 and 20 µm and DW (gDW.particles⁻¹).

To get a better view of possible changes over size, CR and IR have been standardized to 1g flesh DW individual by the following allometric relation:

$$Rate_{std} = \left(\frac{DW_{std}}{fleshDW}\right)^b \times Rate$$

Where $Rate_{std}$ and $Rate$ are respectively standardized rate and rate, DW_{std} and $fleshDW$ respectively DW which rates are standardized on and DW of clam flesh measured, and b the allometric coefficient for standardization found in literature (Moschino et al. 2011).

Assimilation efficiency (AE)

The Conover ratio method (Conover 1966) was used to measure the assimilation efficiency (AE, %). It requires measurements of the ash-free dry weight and dry weight of both food (F) and faeces (E). The following equation is used:

$$AE = \left[\frac{(F' - E')}{(1 - E') \times F'} \right] \times 100$$

Where $F' = \frac{F - Af}{F}$; $E' = \frac{E - Ae}{E}$

And F = total particulate matter ingested DW (gDW), Af = total particulate matter ingested AFDW (gAFDW)

E = total particulate matter excreted DW (gDW), Ae = Af = total particulate matter excreted AFDW (gAFDW)

Faeces from 4 groups of 4 individuals were gently pipetted and then filtered with washed, ashed and pre-weighed GF/C filters. Salts were then washed out with 0.5 M ammonium formate (10 ml). Blank GF/C filters, also washed, ashed and pre-weighed were used to correct weight changes due to humidity variations. Filters were dried at 70 °C for at least 48 hours, weighed and ashed at 450 °C for 3 hours before being weighed again.

The Conover method is based on static method of CR determination. In order to adapt this method to a flow-through system, the DW_{coeff} was used to transform an estimation of the quantity of food ingested into a DW.

This estimation is based on the following calculation:

$$F = CR_{average} \times [food]_{average} \times time\ spend\ in\ the\ chamber \times DW_{coeff}$$

Modelling

R software was used to perform statistical modelling and analysis (R core development, 2011). 4 linear models have been tested.

- $IR_{standardized} \sim Temp + Size + [algae]$
- $\ln (IR_{standardized}) \sim Temp + Size + [algae]$
- $IR_{standardized} \sim Temp + Size + \ln([algae]) + Temp \times Size$
- $\ln (IR_{standardized}) \sim Temp + Size + \ln ([algae])$

Attention has been given to the p-value of every variable (including Temp x Size), the R^2 value of the model, Shapiro-test value of the model and to the graphic analysis of residuals normality of every model tested. Models have been tested against the Akaike criteria. Interactions of second order have been studied and kept when relevant in the model. The best modelling we had was with a formula based on the following variables :

$$\ln (IR_{standardized}) \sim Temp + Size + \ln ([algae])$$

With the following figure (figure 1), we can state that the residuals distribution obtained with the model chosen was normal and allowed us to perform the linear modelling. The Shapiro test done in addition assured also the normality of residuals.

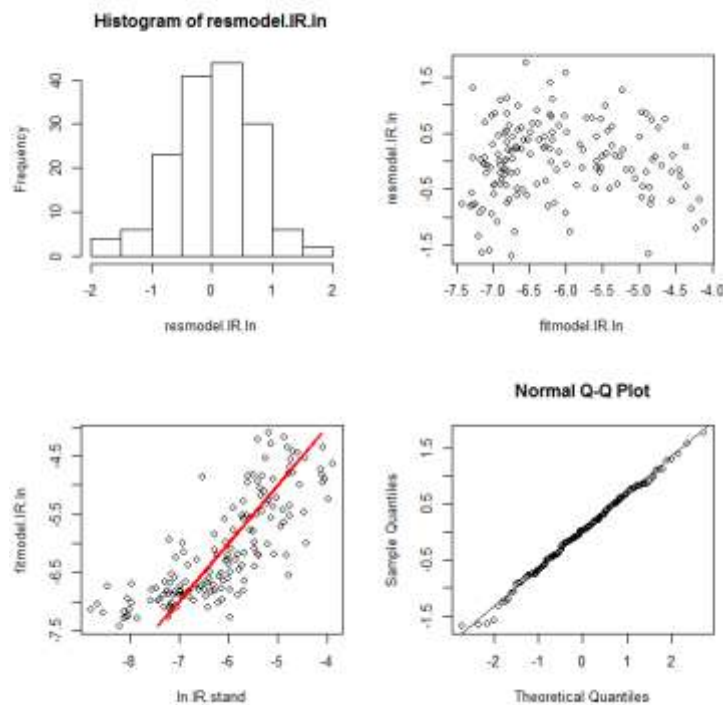


Figure 1: Graphic tests for residuals normal distribution

Flow speed choice and stability

Several studies have been done to propose a validation method for flow-through systems (Filgueira et al. 2006; Larsen and Riisgård 2012), but they deal with mussels and larger size ranges than used in this study. In order to validate our set-up, different tests have been done prior to the experiments.

Flow speed has been measured during two days, four times per day. Number of hours and flow speed were not correlated ($R^2 = 0.02479$, $p=0.374$). So the flow speed in chambers was significantly stable over time and the variation in filtration rates was not due to variations in flow speed.

Different flow speeds have been tested from 210 ml/min to 70 ml/min (figures 2 to 4), to find the one that allows enough algae clearance to calculate a CR. For the first test, the Standard deviation exclusion method, (explained further), wasn't chosen yet. When the flow speed has been decreased, the number of filtering events had increased. As it was difficult to reduce the flow speed further, we maintained it at 70 ml/min to cover a larger clam size range for filtration rate analysis.

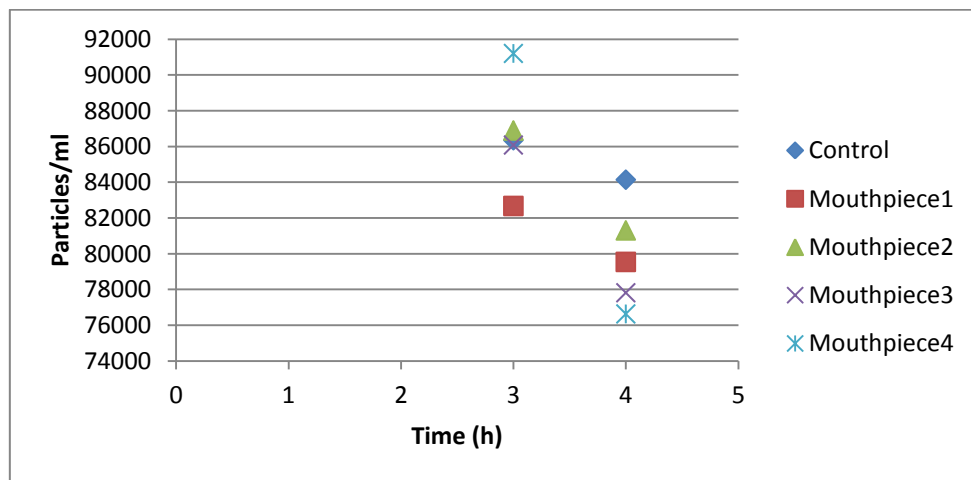


Figure 2: Particles counting Flow speed = 210 ml/min

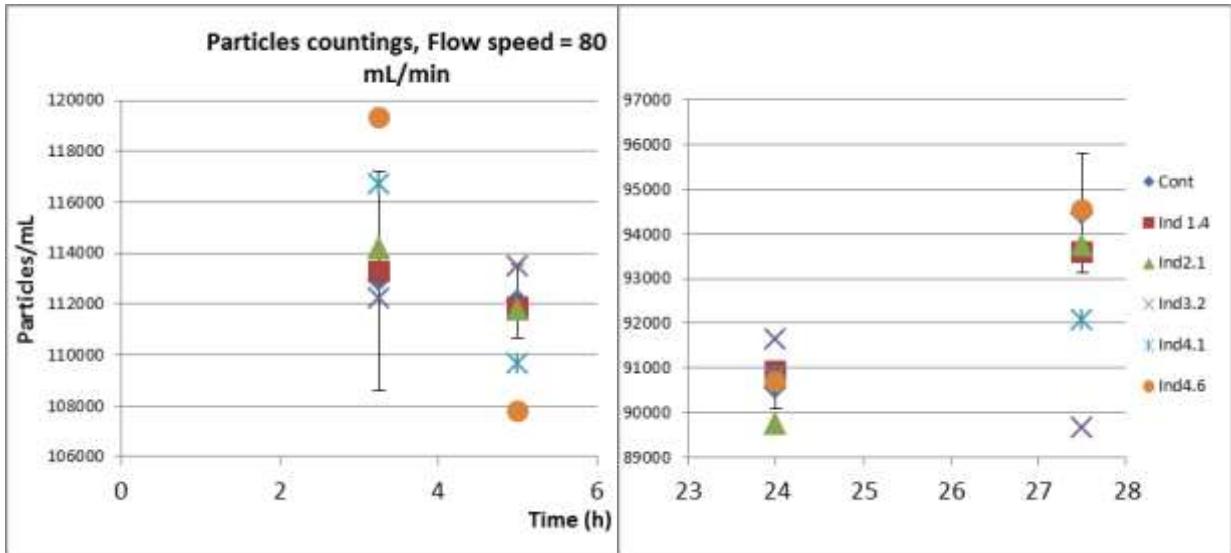


Figure 3: Particles counting Flow speed = 80 ml/min

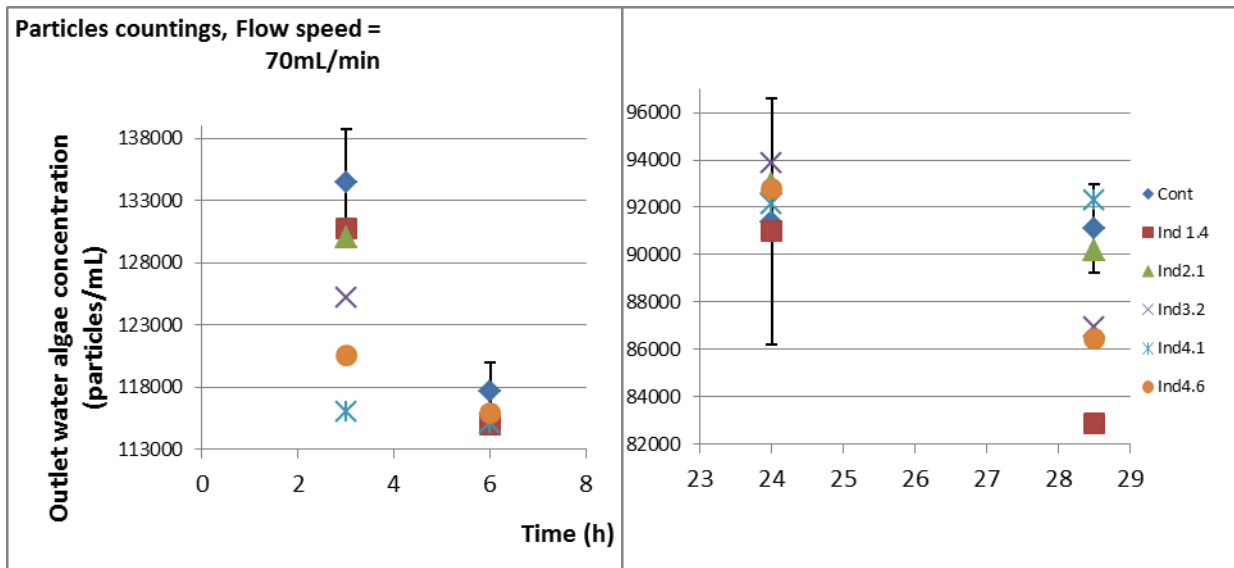


Figure 4: Particles counting Flow speed = 70 ml/min

Algae settlement

Outflow water samples from 4 different chambers have been compared with water sample from the pond three times a day, at 70ml/min, to see any significant difference in algae concentrations. At the same time, flow speed was measured with a sized beaker.

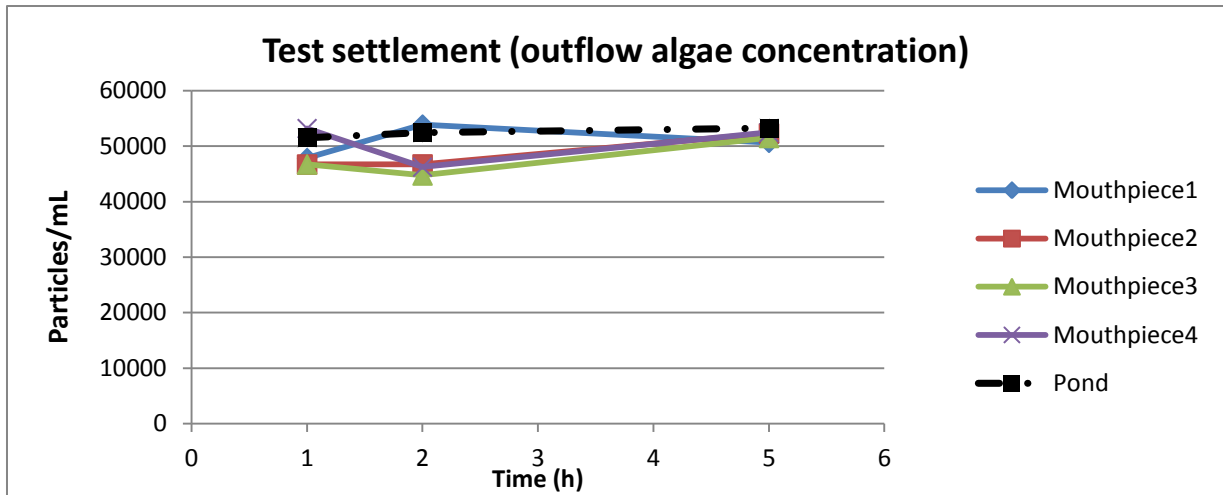


Figure 5: Test settlement (outflow algae concentration) in the 4 mouthpiece of the flow-through system

There is no correlation between the source of water and the outflow algae concentration (figure5), $R^2 = 0.002582$ ($p=0.875$) over time. So settlement has been considered as negligible and the comparison between control and individual chambers considered to be not biased by a loss of algae caused by other reasons than uptake by clams.

CR measurement method

To avoid any effects of coulter counter accuracy, four controls were used and an average outflow algae concentration with standard deviation was considered against every outflow algae concentration of tested individuals. Only individuals with an outflow algae concentration lower than the average control outflow algae concentration minus its SD were considered as filtering. The rest was considered as non-filtering and not taken in consideration for the calculation of an average individual clearance rate:

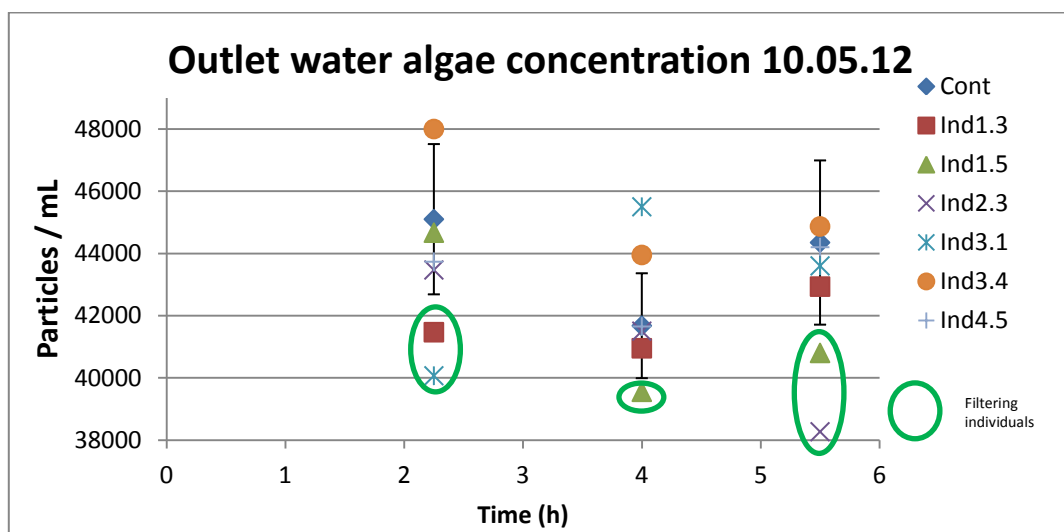


Figure 6: Method to exclude non-filtering individuals

The main issue of this method is that the number of individual values decreases. In the literature, there are different points of view about taking or not in consideration the non-filtering individuals. On the other hand the number of filtering versus non-filtering individuals can be used as a measure of activity.

Size range of food choice

R. philippinarum has been shown to be efficient in filtrating particles from 2 to 200 μm (Nakamura 2001). In order to know what is the best size range to measure for CR, different size ranges of particles have been tested to see on which one clams feed.

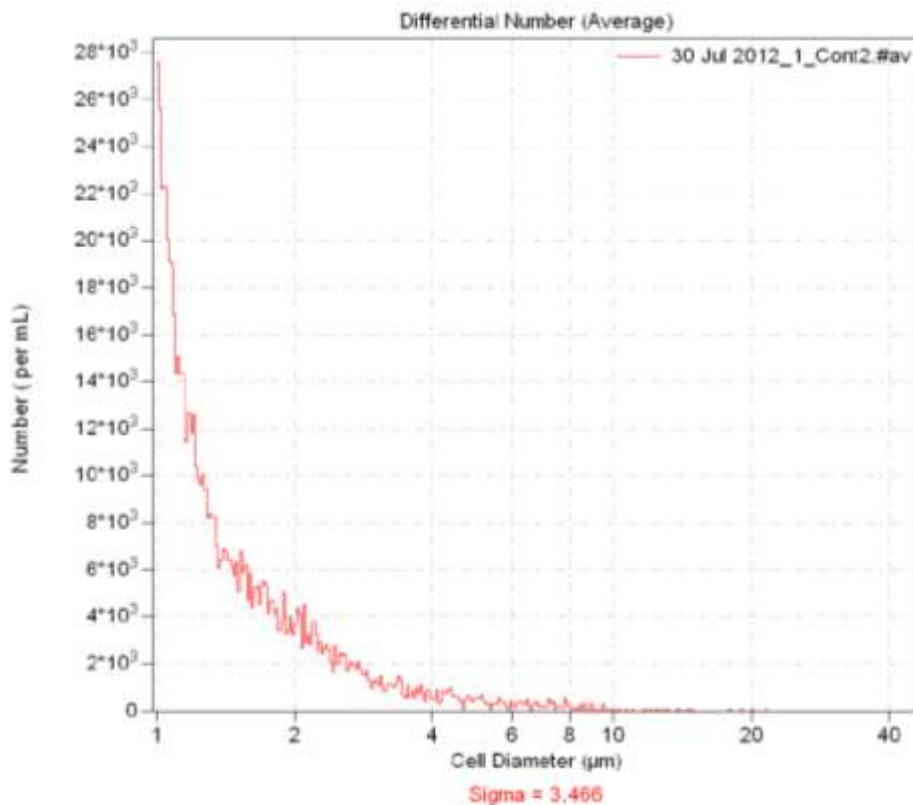


Figure 7: Size distribution of particles in a pond water sample

Regarding the size distribution of particles in the pond water, several categories have been chosen. Considering the big peak from 1 to 4 μm diameter-long particles quite homogeneously decreasing, we chose to divide it only per two (1-2 μm and 2-4 μm). And as over 4 μm of diameter particles become significantly less numerous, we didn't separate particles over a diameter of 4 μm .

Table 1: number of filtering individuals for 83 different particles counting

Nb of countings	Nb of filtering events (1-2μm)	Nb of filtering events (2-4μm)	Nb of filtering events (4< μm)
83	19	26	41

According to our results, clams feed on every size range but are more efficient on particles over 4 μ m. Nakamura (2001) showed that *Ruditapes p.* can feed with the same efficiency on prey from 2 to 200 μ m, and is less efficient but can feed also on picocyanobacteria and bacteria. A previous study (Sauriau and Baud 1991) recommended to measure particles from 4.65 to 14.76 μ m of diameter to target *Skeletonema costatum* colonies. Our results agree also with the same measurement on 13 other species (Møhlenberg and Riisgård 1978). Therefore we chose to count particles over 4 μ m to determine the CR. We never encountered particles larger than 25 μ m.

Experimental set-up

Approximately 5 weeks prior to the start of experiments, 20 carpet shells of 7mm, on average, were placed in a culture pond. The experiments were carried out from the beginning of May to the end of August. All measurements were done every 3 weeks, 4 days per week, to consider both long term and short term variations. A flow-through system used to mimic the culture pond conditions was built with 24 grazing chambers of 250 ml capacity. 20 chambers were used for individual clams and 4 for control. The same phytoplankton enriched water, from the culture pond, supplied every chamber at a 70ml.min⁻¹ flow speed, in average.

First, clams were acclimated for three hours in their chambers prior to the beginning of the experiments. Experiments lasted between 2.5 and 3 hours. After the experiment, they were removed from the flow-through system every end of day to spend the rest of time in a common bucket placed in the culture pond.

Results

Environmental conditions evolution

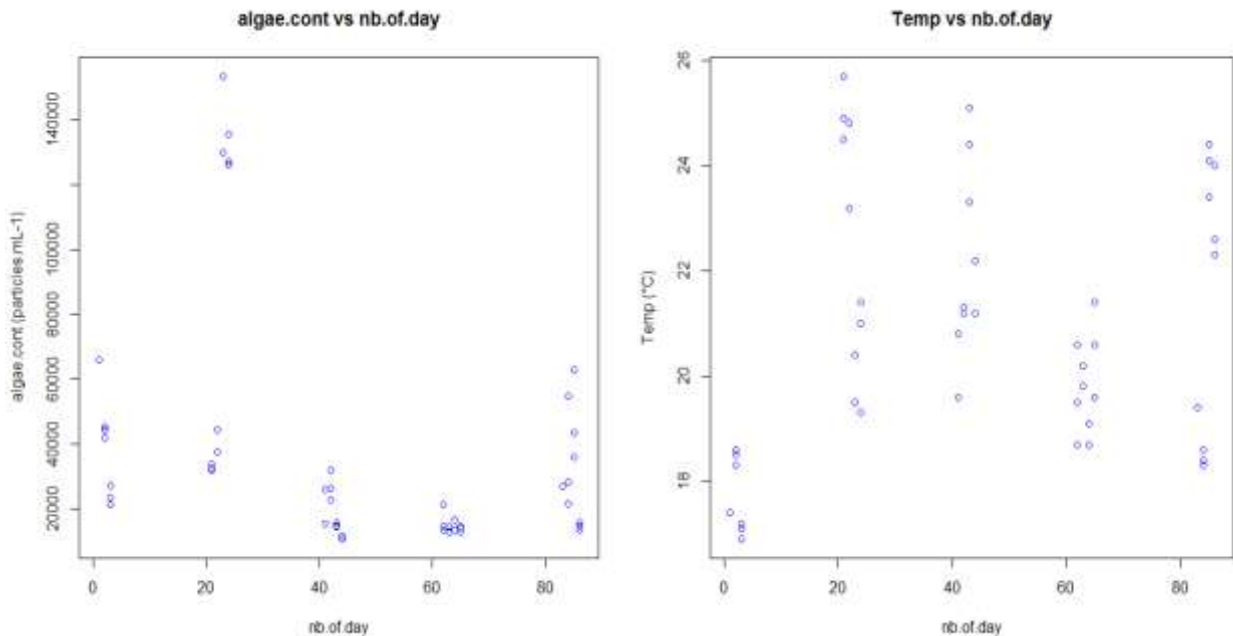


Figure 8: Environmental conditions variance over time

Algae concentration in the pond and water temperature (figure 8) varied a lot during the three months of experiments. Temperature (figure 8) increased after three weeks, at the end of April, from 18°C to 22°C on average. It also varied widely on a short term, from one day to another during the same week (differences could reach 4°C), but also during a day (up to 2°C). Algae concentration (particles.mL⁻¹, particles counted were mainly chains of three to six cells of *Skeletonema costatum*, optical microscope observations) decreased (figure 8) from 70 000 to 10 000 particles per ml, with peaks at the end of April (up to 130 000 particles.mL⁻¹ on days 23 and 24) and during the last week of experiments (up to 30 000 and 40 000 particles.mL⁻¹ on respectively days 84 and 85). The first peak was due to farm managers' choice whereas we asked for the second one to see clams behaviour with a higher algae concentration at this time.

Growth

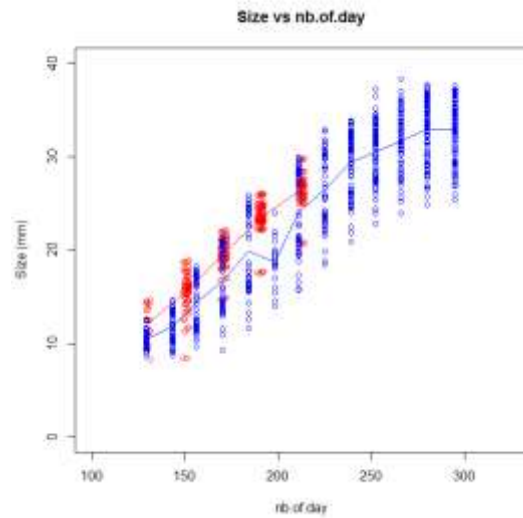


Figure 9: Comparison of 2012 (blue) and 2011 (red) clams size monitoring

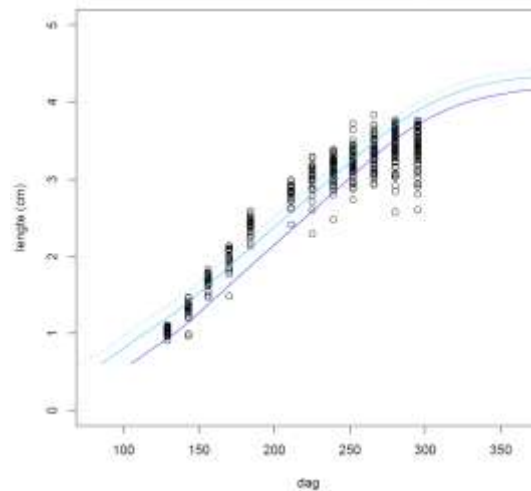


Figure 10: 2011 growth data against DEB model predictions adjusted on 2011 temperature, algae concentration and weight recording

By plotting size data from this study with size data from last year (figure 9), it is possible to observe that size increased as the same rate at least until 220 days, with longer individuals in 2012. We actually didn't see a slow-down in growth in 2012 but given data from last year we assumed that in the future, we would be able to see a slow-down in growth rate in the 2012 batch. We also noticed that the clams barely reach the commercial size (35mm, (Baud et al. 1992), from 32 to 63.5mm according to sellers offer). Comparison with a DEB model adjusted on 2011 data (figure 10) shows that clams stop growing when reaching 35mm, whereas the model forecasts a better growth if it is only based on temperature and food concentration. So there are other parameters involved here.

Evolution of CR/IR and AE

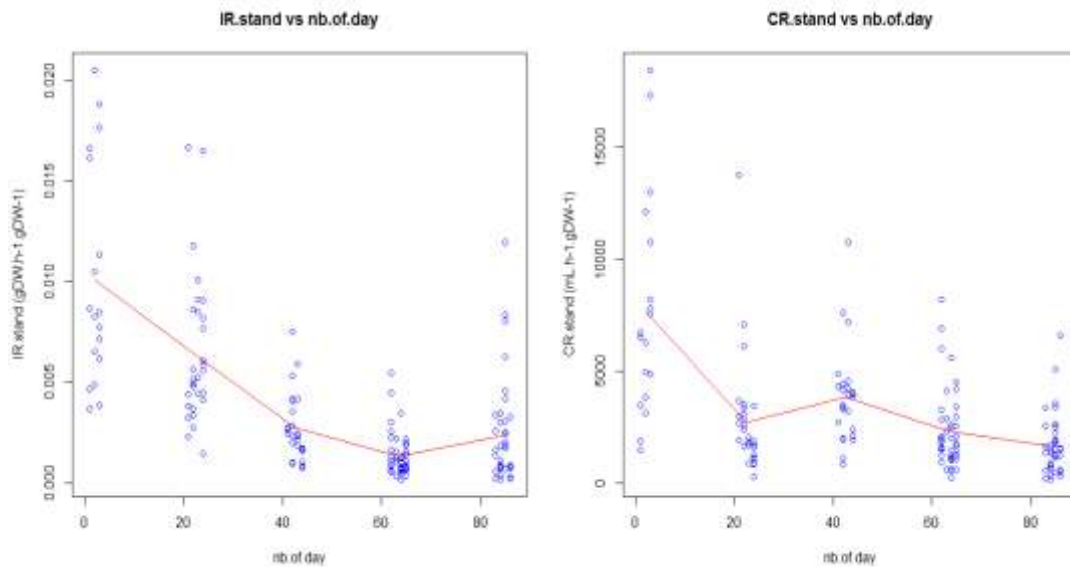


Figure 11: Variation of standardized clearance rate and ingestion rate over time, in red average rates per week

Monitoring of both standardized CR and IR shows a decrease over time in the average of these two rates among individuals. The average standardized CR declined sharply from $\sim 7500 \text{ ml.h}^{-1}.\text{gDW}^{-1}$ to $\sim 3000 \text{ ml.h}^{-1}.\text{gDW}^{-1}$ during the first weeks, and declined more slowly from the second week to the beginning of August (3000 to $1500 \text{ ml.h}^{-1}.\text{gDW}^{-1}$). The average standardized IR decreased homogeneously during the first 40 days (from 0.010 to $0.0025 \text{ gDW of food.h}^{-1}.\text{gDW}^{-1}$) and then decreased slower from 0.0025 to $0.001 \text{ gDW of food.h}^{-1}.\text{gDW}^{-1}$ until the end of the experiments. The standardized IR of last week was a little bit higher than during the previous week, but we asked for algae pulses during two days what has falsed “normal” results.

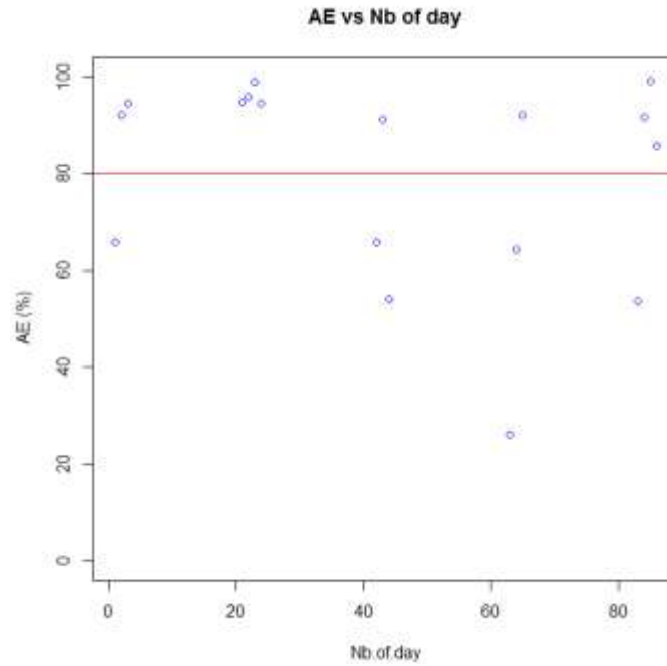


Figure 12: Variation of assimilation efficiency over time (blue), average assimilation efficiency over the experiences (red)

It is hard to define any pattern of AE over time (figure12). We can mention that most of the time, AE is over 85% but after 40 days the AE varied more and could be much lower (around 60% of even lower) half of the time. The average AE was 79.96%.

Influence of the parameters

- Size

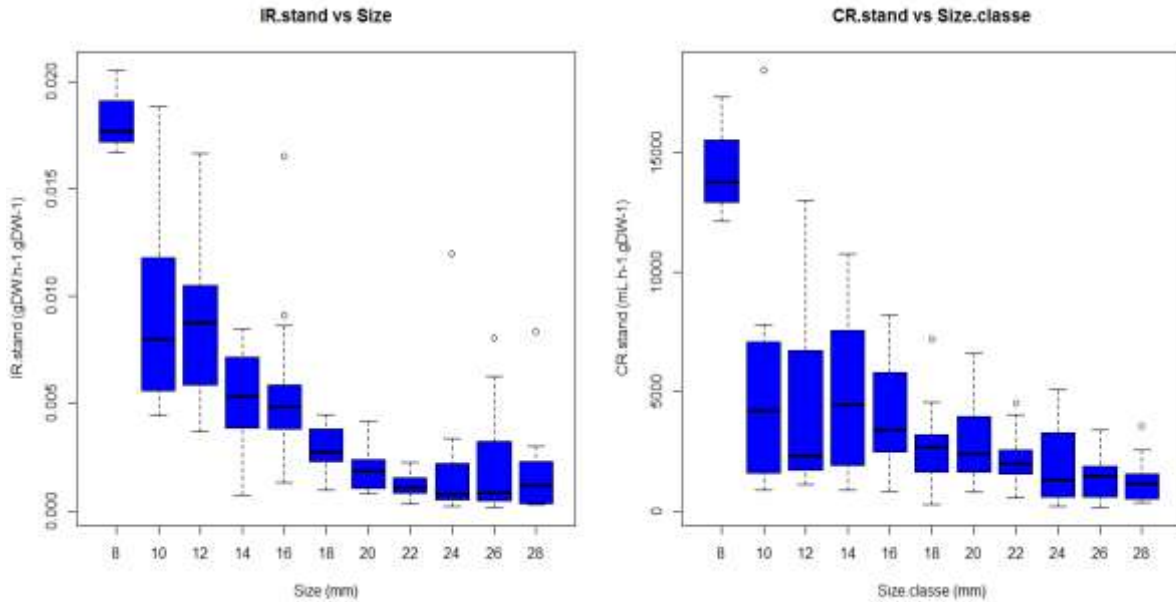


Figure 13: Distribution of standardized clearance rate and ingestion rate over size

Standardized CR drops from $\sim 13\,500$ to $\sim 4\,000$ $\text{mL.h}^{-1}.\text{gDW}^{-1}$ (figure 13) when clams grow over 8 mm. Then the standardized CR slowly declines until $\sim 1\,000$ $\text{mL.h}^{-1}.\text{gDW}^{-1}$ when clams grow up to 28 mm. Standardized IR decreases from 0.017 to 0.002 gDW of $\text{food.h}^{-1}.\text{gDW}^{-1}$ (figure 13) when clams grow from 8 to 20 mm. Over 20 mm, the standardized IR becomes stable around 0.002 gDW of $\text{food.h}^{-1}.\text{gDW}$. Variance over the average decreases over 18mm. This indicates size largely determined IR and CR at sizes over 18mm and that other factors also influenced IR and CR at sizes smaller than 18 mm.

There is no point to show AE over size because it is calculated per day with a plot of faeces from 4 times 4 individuals and link to an average size per day. So it is completely correlated to the variability over time.

- Temp

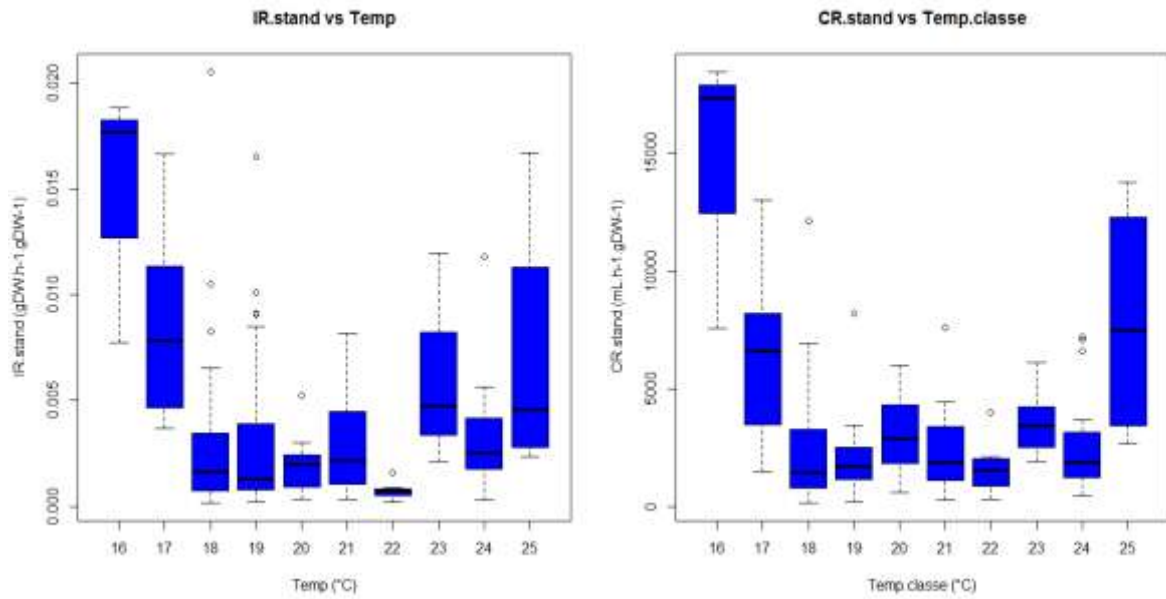


Figure 14: Distribution of standardized clearance rate and ingestion rate over temperature

First it has to be mentioned that the first 3 temperatures have only be reported for small individuals (figure 8, around 12.5mm), during the first week of experiments. After that the temperature was more homogeneously distributed over size. So we had to analyse separately 16 to 18°C range and the rest. From 16 to 18°C both standardized CR and IR decrease respectively from 17 000 to 2 000 mL.h⁻¹.gDW⁻¹ and from 0.018 to 0.002 gDW of food.h⁻¹.gDW⁻¹ (figure 14). Over 18°C standardized CR stabilizes around 2 000 mL.h⁻¹.gDW⁻¹ and standardized IR increased from 0.002 to 0,004 gDW of food.h⁻¹.gDW⁻¹ but not because of CR. It is difficult to give any meaning to the increase at 25°C of both standardized CR and IR.

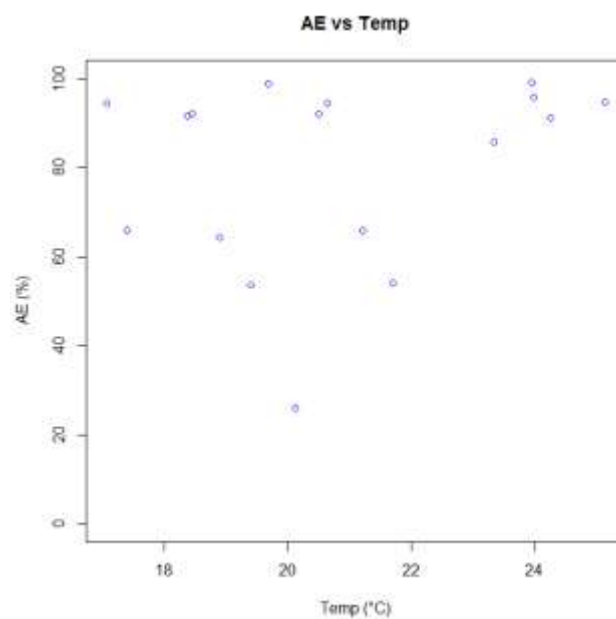


Figure 15: Variation of assimilation efficiency over temperature

From 17 to 22°C, AE varies from 25% to almost four times higher values but remains relatively stable over 22°C between 85 and 98% (figure 15).

- **Algae concentration**

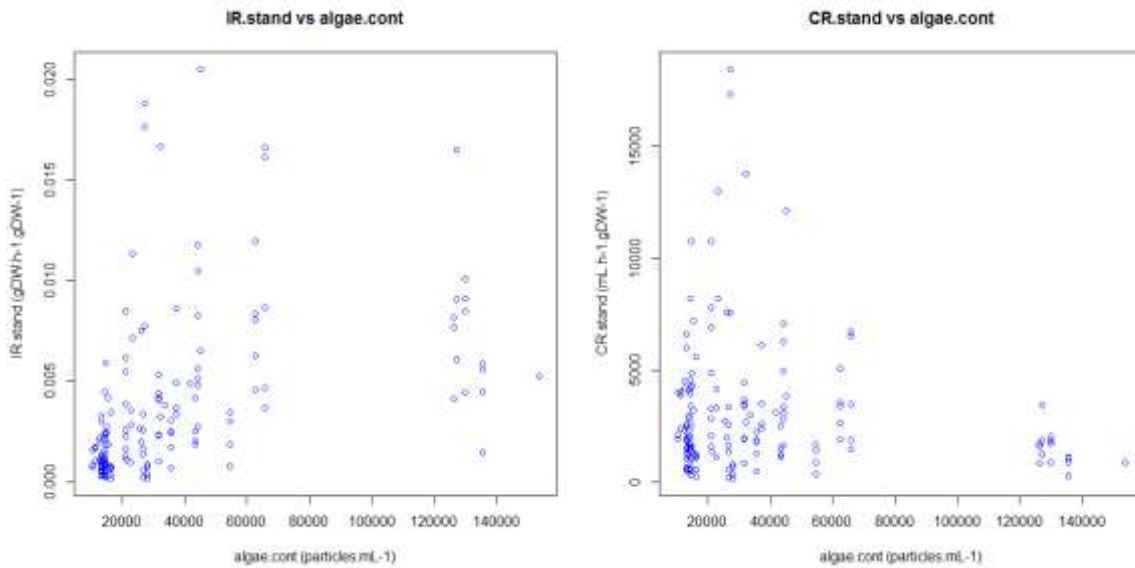


Figure 16: Variation of standardized clearance rate and ingestion rate over algal concentration

No clear pattern can be observed concerning the influence of algae concentration on standardized CR and IR (figure 16). Standardized CR and IR vary significantly over the different algae concentrations we had access to during the experiments.

Using boxplots to show the variability of standardized CR and IR over different algae concentrations (figure 17), it is possible to see something that remains hidden with plots. On days 84 and 85, we asked for higher algae concentrations and it reached respectively 50 000 particles.mL⁻¹ at the end of the day and 60 000 particles.mL⁻¹ at the beginning of the afternoon. Standardized IR increased significantly when algae concentration reached 60 000 particles.mL⁻¹. At the same time, standardized CR increased also.

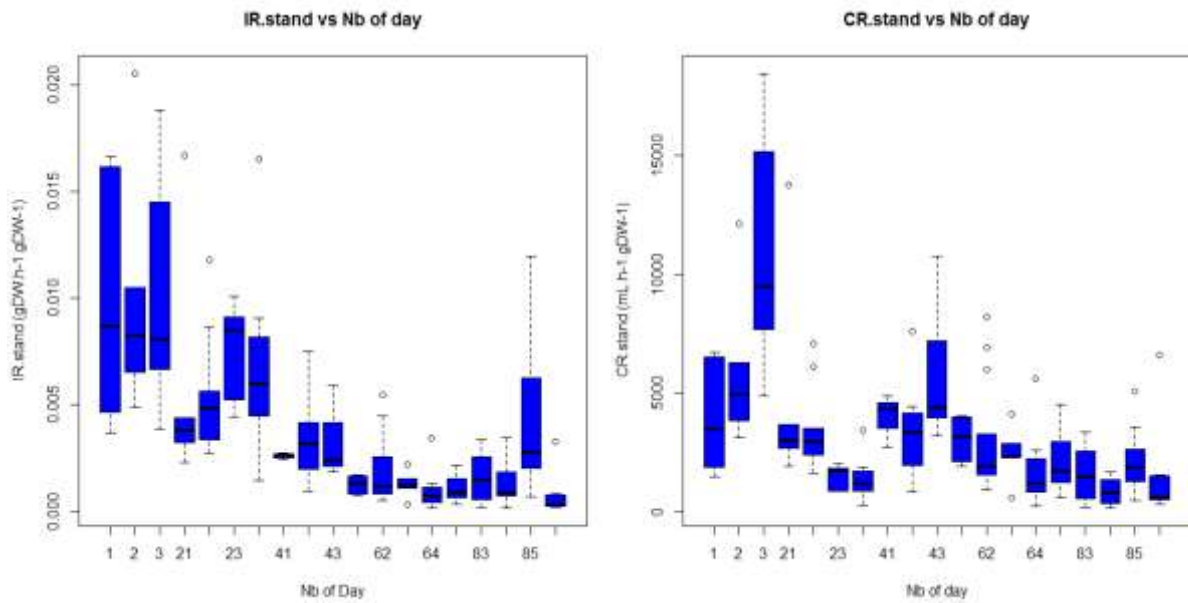


Figure 17: Distribution of standardized clearance rate and ingestion rate over time

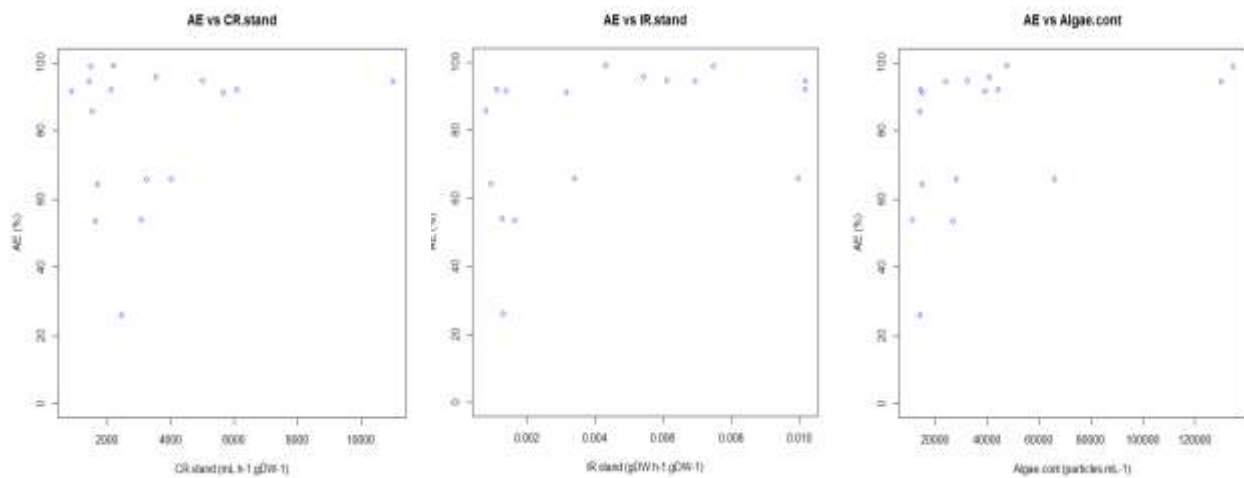


Figure 18: Variation of assimilation efficiency over standardized clearance rate, ingestion rate and algal concentration

At low algae concentrations or low standardized CR and IR, AE varies more and can be really low (figure 18, <65%). But when both algae concentration, standardized IR and CR increase, AE stabilizes over 80%.

Modelling

Given the different tests we have performed and the observations made, we chose the following model : $\ln (IR_{standardized}) \sim Temp + Size + \ln ([algae])$.

Table 2: Model output

Call:					
lm(formula)= ln.IR.stand ~ Size + Temp + ln.algae.cont , data=data)					
Residuals:					
Min	1Q	Median	3Q	Max	
-1.68952	-0.43628	0.01772	0.46614	1.76118	
Coefficients:					
	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	-10.76890	1.01514	-10.608	<2.00E-16	***
Size	-0.11600	0.01097	-10.571	<2.00E-16	***
Temp	0.05226	0.02363	2.212	0.0285	*
ln.algae.cont	0.58366	0.08176	7.139	3.62E-11	***
Residual standard error : 0.6756 on 152 degrees of freedom					
Multiple R squared : 0.6342			Adjusted R-squared : 0.627		
F-statistic: 87.84 on 3 and 152 DF				p-value: <2.20E-16	

Every parameter influences significantly the standardized IR (table2, p-value<0.05). We tested also the interactions of second order but they were not significant. Akaike criterion was the highest when considering these three parameters, without any interaction factors.

The modelling gives an idea of the influence of each parameters given the effects of the others, and it could be considering as satisfactory regarding the adjusted R^2 (table2, 0.627). We may be able to partly limit the influence if morphological limitation when studying the effects of environmental parameters. As we mentioned during the graphs analysis, there was a decrease of standardized IR over size, because Size parameter has a negative linear coefficient (table2, -11.05537). For the rest, temp and algal concentration have a positive impact on standardized IR, according to the modelling, with a much important increase of standardized IR when algae concentration is increased than for temperature (table2, 0.58366 for algal concentration against 0.05226 for temperature). Temperature effect is low but we couldn't see it on the graph, probably because of the size effect.

To have an idea of the efficiency of each parameter to increase standardized IR we performed an analysis of the effect over size of one parameter when the other one is fixed. The formula we obtained adjusting the model on our data is :

$$\ln(\text{standardized IR}) = -10.76890 - 0.11600 \times \text{Size} + 0.05226 \times \text{Temperature} + 0.58366 \ln([\text{algae}])$$

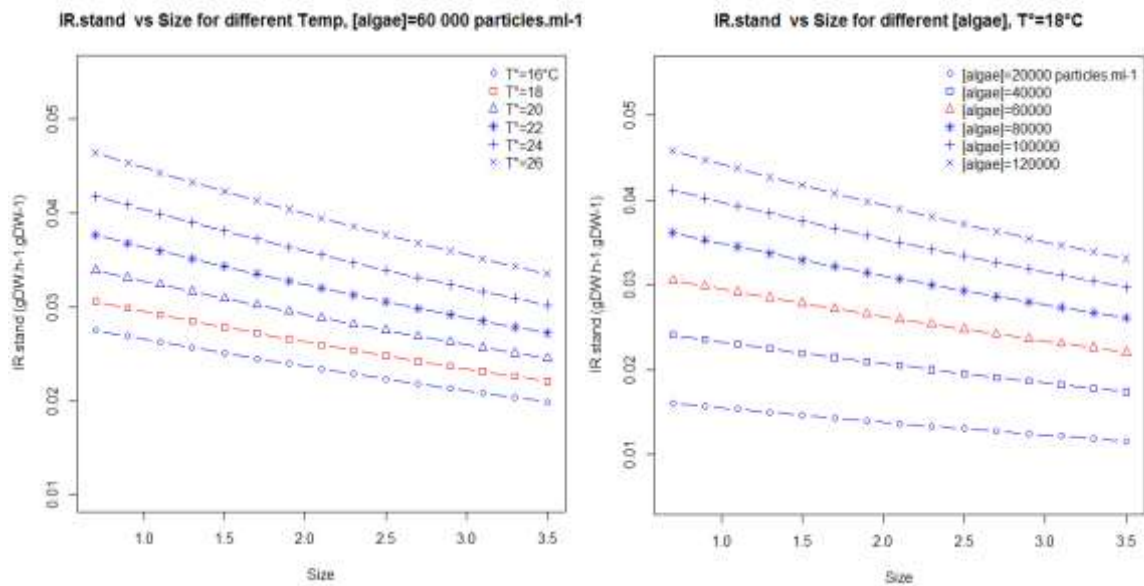


Figure 19: Predictions of standardized ingestion rate over size for different values of one environmental parameter given the other one fixed

According to the model prediction (figure 19), increasing algal concentration from 20 000 to 80 000 particles.ml⁻¹ is more efficient than increasing the temperature from 16 to 22°C. The effect of increasing algal concentration decrease over algal concentration.

Temperature increase positive effect on standardized IR is more and more important when temperature increases (figure 19), but stays lower than the increase of standardized IR when increasing low algae concentration.

Discussion

CR morphological limitation

Standardized CR decreases exponentially over size, what has been documented in another study (Nakamura 2004). Possibly physical limitations cause larger individuals to have trouble to meet living requirements, especially if we assume living requirements also increase over size (Kooijman 2010). There are mechanisms that could cause this limitation. The first one is the difference of increase of inhalant syphon diameter and body-weight. Basically when size increases, the clam will gain more weight than syphon diameter. Wong and Levinton (2005) showed that siphon diameter (SD, mm) and tissue dry weight (TDW, g) of the zebra mussel are linked to shell size (SHS, mm) by the following equations:

- $SD = 0.17 \times SHS + 0.39$
- $TDW = 1.22 \times SHS - 1.33$

So over 1.64 mm, when individuals grow of 1 mm their weight will increase seven times more than their inhalant siphon diameter. It is probably the same for *R. philippinarum*. That means that filtration is morphologically limited over size (figure 13), and this is a pattern that is not solvable but should be taken in consideration. Another mechanism for such a decreasing standardized CR over size could be a change in gills performance. When clams grow the gill apparatus expands also, which could affect the lower particle diameter it can retain. This phenomenon would imply that smaller individuals could filter a bigger range of “prey” sizes and could have access to a higher amount of food at the same algae concentration. It has already been shown that *R. philippinarum* juveniles can filtrate, with a relatively lower efficiency, bacteria and picobacteria (diameter < 2µm) and prey from 2 to 200µm (Nakamura 2001). It is conceivable that larger individuals would lose that ability to filter particles smaller than 2µm, depriving themselves of a part of food. SPM concentration in the water could play a role in the decrease of standardized CR over the experiment time. CR values have been reported to be depleted by 20 and 70% at respectively 100 and 300 ppm of SPM, compared to CR at 10ppm for *R. decussatus* (Sobral and Widdows 2000). Lei et al. (1996) have shown that when SPM concentration increases, CR decreases in several bivalves species. We also know that farm managers decided to introduce new algae species (a diatom and a chlorophycea). Shape, motility, density and chemical cues of an algae species can influence retention efficiency by bivalves gills (Hawkins and Bayne 1992). This shift in algae diet could have affected clams CR.

Effects of environmental parameters on standardized CR and IR

The first observation that can be made is that the culture conditions can vary very sharply (figure 8). The algae concentration in pond varied from ~40 000 to ~130 000 particles.ml⁻¹ within two days and temperature decreased from 24 to 19.5°C at the same scale. (Robert et al. 1993) stated that sharp variation in environmental parameters could slow-down growth. It could create a stress that forces clams to close, causing more interruptions in filtering.

Looking at the distribution of temperature over time during our experiments (figure 8), it is clear that temperatures under 18°C occurred only at the beginning of the experiments. After the 21st day of experiment, the temperature varied more from one day to another, between 18 to 25°C. That led to separate the analysis of temperature effects into two periods: the first week on one hand, the rest of the experimental time on the other. So we can state that for small individuals (<15 mm shell-long), both standardized CR and IR decrease when the temperature increases, at least from 16 to 18°C (figure 14). For bigger individuals, from 18 to 25°C, both standardized CR and IR are not correlated to temperature (figure 14). Temperature effects on CR and IR have been studied a lot. Gouletquer et al. (1989) and Bernard (1983) showed that CR presents a maximum for 16°C (1.25 l.h⁻¹) and decreases when temperature rises until 25°C (0.75 l.h⁻¹), in a batch of clams of 28mm in average, grown on the intertidal zone of Marennes-Oléron. Nakamura (2004) reported the same thing shifted up by 5°C on clams from Tokyo Bay. Deslous-Paoli et al. (1987), in the same area than Gouletquer et al., didn't notice any variations due to environmental conditions, with a CR of 3.19±1.00 l.h⁻¹

$l.gDW^{-1}$ over the year. Han et al. (2008), stated that standardized CR and IR increase with temperature from 5 to 25°C. Our modelling gave the same interpretation of temperature effect on standardized IR, with a positive linear relation between these two variables. Han et al. (2008) also reported higher standardized CR in 26 mm shell-length individuals (from 1.22 to 5.06 $l.h^{-1}.gDW^{-1}$) than in 36 mm shell-length individuals (from 0.85 to 3.58 $l.h^{-1}.gDW^{-1}$), with an increasing difference when the temperature rises. The same phenomenon has been noticed for standardized IR during these experiments. Our graphic results are quite different from the literature but all the papers done so far were focused on individuals grown in the sea. We worked on clams from a hatchery, raised in fully controlled conditions, and grown in a farm behind the dikes. Their reactions to the parameters could have been completely different, but it should be mentioned that standardized CR and IR were on the same scale as in the other studies. That could explain the difference of temperature effects on standardized CR and IR on small and large individuals, with an acclimation to higher and variable temperatures after several weeks spent in the pond.

It is possible to compare our results to Gouletquer et al. (1989)'s, in a sense that the optimum culture temperature would be close to 16°C. The range of temperatures we measured and the poor distribution over size (figure 8) have not allowed us to see this theoretical optimum when considering size and algae concentration effects, even if we may have observed this phenomenon on small individuals (<15mm).

The effects of particle concentration on CR and IR have been well documented in several bivalves species since the 70's. Riisgård et al. (2003) stated the existence of a limit algal concentration below which shellfish close and filtrate less, in three bivalves species. They mentioned also two papers that suggest the hypothesis of a threshold in algal concentration below which *M. edulis* (Thompson and Bayne 1972), or other bivalves species (Bernard 1983), don't filter at all. In our data standardized CR was much lower below 15 000 particles. ml^{-1} , than at other concentrations (figure 16). Possibly this concentration is close to the limiting algal concentration. There are two different views on the influence of algae concentration on CR. The first one is that there is no correlation between algal density and CR (Bernard 1983; Nakamura 2001), what would imply that IR increases linearly with increasing algae concentration. The second one is that bivalves are able to regulate their IR by decreasing CR when algae density rises (Bricelj and Malouf 1984; Berg et al. 1996; Bacon et al. 1998), with still a slow increase in IR (Bacon et al. 1998). We observed the same in our batch of clams. Higher standardized CR was observed at 20 000 to 45 000 particles. ml^{-1} and over these concentrations standardized CR was much lower (figure 16), whereas standardized IR was stable (figure 16). However, it is difficult to enlight an optimal algal concentration for CR in our results because of the influence of the morphological limitation over size, and the lack of food input after day 40. The only thing that can be clearly established here is that at really high concentrations (>120 000 particles. ml^{-1}) standardized CR of small individuals was at the same level as for low algae concentrations (~15 000 particles. ml^{-1}) with big individuals (figure 16). That means that even without a morphological limitation, small individuals reduced their CR to regulate the IR, which is in accordance with previous results from the literature. Our model gave the same interpretation of the results. We could see that the relative increase of standardized IR when algal concentration is increase slow-down when really high food concentration are reached (figure 16). Pseudofaeces production occurs at high SPM concentration or more precisely at saturated IR (Gouletquer et al. 1989; Bacon et al. 1998). We even may have overestimated the increase of standardized IR with algae concentration, at high level, by not taking in account the pseudofaeces production in our model. Pseudofaeces production was really low during our experiments and sometimes it was difficult to separate

faeces from pseudofaeces, which could have led to over estimation of IR at very high algal concentration.

When we asked for an algae pulse in the pond, at the end of the experiments, the standardized IR increased only when the concentration reached 60 000 particles.ml⁻¹. It stayed low at 50 000 particles.ml⁻¹ (figure 17). A hypothesis that could explain this phenomenon would be that the algal concentration threshold provoking a drop in CR is higher for larger individuals. It would be interesting to check the evolution of this threshold over size, in order to see if it increases when the clams get bigger.

Influence of environmental parameters on AE

In addition to CR variations, AE was not constant over experimentation time (figure 12) but higher (between 26,03 and 98.96%, with an average of 79.96%) than what has been reported (between 36.5 and 80%) in previous studies on *R. philippinarum* (Gouletquer et al. 1989; Nakamura 2004; Han et al. 2008). Bayne et al. (1983) reported higher AE when bivalves are in an algal culture than in natural medium, which was the case in our study. Moreover, as we used clams grown in a hatchery, it would be possible that they were more efficient in processing organic matter, when the right conditions of assimilation have been encountered in the pond. Higher AE values we obtained, compare to the literature (figure 12), are probably the results of strong hypothesis we made when we designed the experiments. The Conover ratio method is adapted to static system for measurement of CR (Conover 1966). We used a flow-through system, and change the calculation for food terms in the equations. Basically, we considered the individuals filtering all day long, at the average CR of the day, and the food ingested was the results of multiplication of CR and food density. But as we noticed, clams don't filter homogeneously along the day so we probably overestimated the food input. This would mean that we underestimated the AE. On the other hand, we could have overestimated AE because we assumed all faeces produced during measurements originated from the food given during the experiments. This is probably not the case because the time it takes to digest might exceed three hours (acclimation period). Most often clams were hardly fed at night because enriched water flow was closed before staff left the farm.

The variation of AE may be a result of effects of environmental parameters, such as food availability, food quality and water quality. Bivalves have been shown to be able to regulate their AE. Gouletquer et al. (1989), and Sobral and Widdows (1997) for *R. decussatus*, showed the increase of AE when the ration of food decreases. To compensate a lack of food ingested, clams can restrain from selectively assimilating certain particles in the diet to increase assimilation. Temperature has been shown to not influence *R. philippinarum* AE (Nakamura 2001; Han et al. 2008). On the contrary, Sobral and Widdows (1997) have reported higher AE when temperature increases in *R. decussatus* but it has been related to the decrease of IR at the same time, in a way to maintain the scope for growth. In our experiments the lowest value of AE coincided with the lowest standardized CR and IR (figure 18), at low temperatures (figure 15). Consequently, the reason for such variability in AE should be found in other parameters.

AE has been considered a function of algae concentration and PIM concentration (Gouletquer et al. 1989; Bensch et al. 1992). AE of different bivalves species, among which *R. philippinarum*, has been shown to increase when % POM increases in seston (Bricelj and

Malouf 1984; Gouletquer et al. 1989; Hawkins et al. 1998; Cranford and Hill 1999). Bricelj and Malouf (1984) stated that the ratio PIM:sestonDW is even more linked to AE than only algae concentration. Knowing that the farm had troubles with its filter since mid-June and the low algal concentration in pond water since the same time, we can assume that %POM decreased during the last two months and made the AE drop. So even if the low AE events happened during low algal concentration, it would rather be because of a higher PIM:sestonDW ratio.

It is also known that bivalves can increase their synthesis of digestive enzymes to enhance AE (Gosling 2003). Over size, respiration costs increase with both body size and temperature. During our experiments, both algal concentration and standardized CR decreased over time while size of clams and temperature increased. It is possible that free energy for synthesis of digestive enzymes decreased, because of the higher priority for respiration needs. This would result in a degradation of AE.

Recommendations/Advices

This study gave several clues to understand the lack of growth reported last year, and which will probably be observed in the next few months, but also emphasized lacks in knowledge to improve *R. philippinarum* outdoor culture. We observed a decrease in standardized CR over size (figure 13), which could imply different changes in the energy budget of clams when they grow. We have already mentioned the possibility of a shift in the limiting algal concentration for CR over size. It would be interesting to check if larger individuals need a higher food concentration to start filtering. We can imagine such a phenomenon because of the increase of respiration costs over size, so the need to preserve energy when algal concentration is too low, by stopping the water clearance process. The effects of algal concentration on the pseudofaeces production over size should also be studied. Only one study has linked pseudofaeces production threshold to one clam size, with seston charge of 28mg.l^{-1} for 35mm shell-long individuals (Gouletquer et al. 1989). It is known that bivalves regulate their AE to maintain the energy input. So it is conceivable that larger individuals would support higher algae concentrations without rejecting organic particles through pseudofaeces, to maintain a sufficient IR. It would also be interesting to have a better overview of the effects of temperature on vital rates over size. We already know that the location of a *R. philippinarum* population has impacts on optimum growth temperature (Gouletquer et al. 1989; Nakamura 2001). We also know that temperature has a more or less strong impact on clams performances (Han et al. 2008), even if *R. philippinarum* is able to support a wide range of temperature. But temperature optimum for growth hasn't been studied on several size ranges of Japanese clam.

There are several methods possible to limit the lack of growth of clams at the end of the production cycle. The main problem is the morphological limitation of CR increasing with size, which cannot be avoided. The first way to stabilize standardized IR over size is to maintain high algae concentration over the entire production cycle, to counter the decrease of standardized CR over size. The farm has difficulties to maintain its algae production (*Skeletonema costatum*) during summer (figure 8), probably because of both a high temperature and light stress (Baud 1988), even though Baud (1988) showed that *Skeletonema*

costatum can support temperature from 5 to 30°C with an optimum temperature around 20°C. Low algal concentrations in the pond occurred before reaching 20°C (figure 8), which implies other stressful water characteristics for algal growth. The culture medium, in the ponds, may need more supply of limiting nutrients such as nitrates or phosphorous (Batista 2007) or also iron which is limiting in autumn (Brossard and Hussenot 1997) but could be also limiting during summer. Another solution to maintain the algae production is to shift to other species when environmental conditions start being limiting for *S. costatum*. For example, it would be interesting to use another algae during winter when temperature is limiting for the algae the farm uses. As summer is a critic period to grow *S. costatum*, the farm could shift to *Chaetoceros* species which are able to support higher temperatures and higher light supply, as on-going outdoor production tests performed at IMARES have shown so far. But these algae should also be in accordance to the needs of clams for growth. If it is the case, it could be a solution that doesn't imply large investments for the experimental farm.

Reducing ponds size and number of clams in it could also lead to an increase in food availability for the shellfish. The production would be lower in term of number of clams, but not necessary in term of weight, and it will certainly allow reaching the commercial size, and faster than it would be the case now.

In any case, algae concentration should never be below 20 000 particles.ml⁻¹, because it has been shown to be a limiting concentration that causes a big drop in both standardized CR and IR. Our hypothesis is that it is very close to the threshold below which clams stop filtering to save energy. It would also be useful to increase this lower limit algal concentration over size to reach 60 000 particles.ml⁻¹, when clams are 26mm shell-long, because 50 000 apticles.ml⁻¹ seems to be a limiting algal concentration for large individuals CR. That would theoretically mean an increase of 10 000 particles.ml⁻¹ every 5mm for the threshold algae concentration, from 10mm shell-long clams until the commercial size, 35mm.

When maintaining the algal concentration to a reasonable level, attention should be paid also to the filtration system of water inputs from the Schelde. AE started varying probably because of decreasing %POM in the water. It is important to limit the input of PIM during summer, especially because the algal concentration is lower during that period. Clams increase their AE when the ration of algae is too low for a good growth. They select less to maximise the food ingestion, but this process is really sensible to the water quality. It would be interesting to follow PIM:gDW ratio in ponds water during culture time, to have a better understanding of the effect of that ratio on AE.

Another solution, probably less effective regarding our model predictions, is to put clams in the best environmental conditions the farm can. We made the hypothesis, by comparing our temperature effects results with Gouletquer et al.'s (1989), that 16°C could be an optimal temperature for clams. Avoidance of limiting temperatures during summer could lead to a less pronounced decrease of CR in that period. Refreshing the water is one way to avoid these temperatures, and can be done in several different ways. One way would be to invest in a water refreshing system, another is to draw water from a salted ground water source, but both may only be considered as a second step in improving the farm production and efficiency because of the high costs. The same conclusion can be drawn for the use of a salted ground water source. It could increase temperature in winter, decrease it in summer, but costs are high and variability in Yerseke ground water composition is not well known and variable (Batista 2007), what could lead to an even worse condition of shellfish. Studies may be done prior to considering this option.

In order to avoid summertime as much as possible clams could be grown earlier in the year, which could provide them with more algae and better culture conditions until a larger size. The problem is that at winter temperatures growth is negligible, so growth in hatcheries under temperature-control is needed to be able to put larger individuals in the pond in spring. In spring, with high algae production and a water temperature of 14-18°C, it would allow culture conditions that can maintain standardized IR over size despite the decrease of standardized CR, mainly by raising the algal concentration in the pond.

Conclusion

The lack of growth observed at the end of the production cycle is due to the addition of several events occurring before summer. The first one is the decrease in standardized CR over size, consequence of a morphological limitation induced by a slower increase in inhalant siphon diameter compared to body size and maintenance costs. In addition, AE varied more in summer probably because of both higher PIM in the water and lower algal concentration. And these two events are amplified by the decrease of algal growth in summer and the impossibility to maintain the algal concentration in the pond, or even more to increase it when standardized CR decreases. So food ingestion by clams is dramatically lowered when they grow and when temperature rises. It means that increasing respiration costs are not counterbalanced by an increasing energy input, leading to a slow-down in growth which finally stops around 35mm.

Solutions can be proposed to minimize this phenomenon. The first one is to increase algal concentration when standardized CR decreases, to maintain as much as possible standardized IR. To better algal production, the farm could enrich the culture medium with limiting nutrients as nitrates, phosphorous or iron or shift from one species to another when seasons and environmental conditions change over the year. In addition, attention should be given to the filter system to limit PIM inputs during summer to maintain AE. The second solution could be to limit summer stressful conditions. A first option is to grow the clams larger in the hatchery and put them in spring at a larger size, to reach commercial size before summer. Or the farm could invest in a refreshing system for pond water, or in a salted ground water channelling, but the costs are dissuasive regarding to the weak potential effect of refreshing the water on clams vital rates and algal growth. In any case, recycled water input should be limited during summer, and the farm should prefer Schelde water input to supply ponds, because the water will be cooler then.

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Annexe 1: Flow-through system, Zeeland Aquacultuur, Yerseke



Figure 1: Overview of the flow-through system based in the Japanese clam farm



Figure 2: Main water supply to the system, after the height levelled bucket



Figure 3: 2x2x6 mouthpieces division to supply the 24 grazing chambers



Figure 4: Grazing chambers of 250 ml



Figure 5: Interior of a grazing chamber, with a 8mm clam

Annexe 2: Résumé du rapport en français

La demande croissante de protéines d'origine marine, l'augmentation du prix de la nourriture pour poissons et l'attrait du grand public pour la durabilité des secteurs de production alimentaire ont conduit à un regain d'intérêt pour le concept ancestral d'Aquaculture Intégrée Multi-Trophique (AIMT). Pour autant, les producteurs demandent de plus amples connaissances afin d'assurer leur production et leurs revenus avec de tels systèmes d'élevage.

Ce stage se propose d'enquêter sur un manque de croissance dans une ferme de *Ruditapes philippinarum* (palourdes japonaises), élevées sur eau enrichie en algues (*Skeletonema costatum*), à Yerseke, Pays-Bas. Le contrôle de la croissance du cheptel de 2011 a décelé un manque et un arrêt précoce de la croissance en fin de cycle de production. Les hypothèses pour expliquer ce phénomène sont multiples. La décroissance de taux vitaux comme les taux de filtration et d'assimilation en cours de croissance, ainsi que les effets des paramètres environnementaux sur l'ingestion et l'assimilation des ressources trophiques pourraient être à l'origine de ce frein à la production. Ce rapport présente les résultats du contrôle de la température, de la concentration algale, des taux de filtration et d'assimilation et de la taille d'un lot de palourdes sur six mois, afin d'une part de mettre en lumière les raisons de la limitation de la croissance et de proposer d'autre part des solutions pour améliorer la croissance.

Le « flow-through system » a été développé après différents tests portant sur le volume des chambres de filtration, la vitesse de courant et sa stabilité, la sédimentation des algues et le choix de la taille des particules considérées comme nourriture. Au final, le système se compose de 24 chambres de filtration de 250ml, dont 4 contrôles, avec un courant d'environ 70 ml.min⁻¹ par chambre. Toutes les 3 semaines, pendant 4 jours, les 20 mêmes palourdes étaient mises dans les chambres pour 3 heures d'acclimatation puis toutes les 1h30, l'eau de sortie des chambres était récoltée pendant 1 minute. Afin de mesurer les taux de filtration et la concentration algale dans le bassin, les particules de 4 à 20µm (correspondantes aux colonies algales) ont été comptées dans chaque échantillon d'eau. Les individus dont l'eau de sortie de chambre était moins chargée en algue que la moyenne des contrôles moins son écart-type, étaient considérés comme filtrants et leur taux de filtration calculé selon la formule suivante:

$$CR = (([algues]_{contrôles} - [algues]_{individu}) / [algues]_{contrôles}) \times \text{Vitesse de courant}$$

En fin de journée, les fèces produites étaient récoltées, puis séchées et pesées, en vue d'obtenir le poids sec et le poids sec sans cendres. Les données ainsi obtenues permettaient de calculer le taux d'assimilation avec la méthode Conover. Une modélisation linéaire a aussi été effectuée pour mesurer les effets des variables sur le taux d'ingestion, mesuré par le produit de la concentration algale et du taux de filtration.

Les conditions environnementales ont varié de façon abrupte d'une semaine de mesure à l'autre mais aussi d'un jour à l'autre. La température a varié de 16 à 25°C, avec une décroissance de 16 à 18°C pendant la première semaine, et une distribution plus homogène

pendant le reste des expériences. La concentration algale a été enregistrée entre 10 000 et 130 000 particules.ml⁻¹, avec de très faibles concentrations pendant l'été.

Les taux de filtration et d'ingestion standardisés à 1g de poids sec de chair ont décliné tout au long des expériences de respectivement 7 500 à 3 000 ml.h-1.gPS-1 et de 0.010 à 0.0025 gPS d'algue.h⁻¹.gPS⁻¹. Le taux d'assimilation était élevé pendant l'étude (80%) avec une variation accrue, et par conséquent des valeurs plus faibles (jusqu'à 25%), pendant l'été. Avec la croissance des individus de 8 à 26mm, les taux de filtration et d'ingestion standardisés ont été divisés par respectivement 13 et 9. La température n'a pas eu d'effets sur le taux d'assimilation. Par contre, nous avons relevé des taux de filtration et d'ingestion standardisés décroissants pour les plus petits individus quand la température augmentait de 16 à 18°C. Par la suite nous avons observé une stabilisation du taux de filtration et une légère augmentation du taux d'ingestion chez les individus plus grand que 12,5mm pour des températures allant de 18 à 25°C. La baisse du taux d'ingestion n'est donc pas imputable au taux de filtration. Le taux d'ingestion standardisé semble être relativement indépendant de la concentration algale, sauf pour de très faibles concentrations. L'explication peut être trouvée dans l'évolution du taux de filtration standardisé qui décroît avec l'augmentation de la concentration algale. Pour autant, le taux d'ingestion est resté très faible à de faibles concentrations en algues. Les taux d'assimilation les plus faibles ont été mesurés pour des faibles taux d'ingestion et de filtration standardisés, ainsi que de faibles concentrations algales.

La modélisation du taux d'ingestion standardisé indique un effet positif de la température et de la concentration algale et un effet négatif de la taille des individus. L'effet positif de la concentration algale diminue avec l'augmentation de la concentration, à température constante, mais reste la source d'augmentation la plus importante du taux d'ingestion.

La diminution observée du taux de filtration au cours de la croissance des palourdes est due à l'augmentation plus faible du diamètre du siphon inhalant que celles de la taille du corps et des coûts de maintenance. Ce phénomène, déjà mentionné dans la littérature, implique une limitation morphologique du taux de filtration, et du taux d'ingestion à concentration algale constante, qui ne peut être évitée. Ajouté à cela, les concentrations algales sont extrêmement faibles en été, et semblent même être la source d'une limitation poussant les palourdes à arrêter de filtrer, ou du moins de réduire considérablement l'énergie utilisée dans ce processus. Les taux d'ingestion sont donc beaucoup plus faibles quand les palourdes croissent, et cela est d'autant plus problématique que les taux d'assimilation sont plus faibles également pendant la période estivale. La mauvaise distribution de la température et le trop faible intervalle auxquels nous avons accès pendant ces expériences ne nous ont sûrement pas permis d'observer l'effet « avec maximum » de la température sur le taux de filtration qu'avait mentionné de précédentes études. Pour autant, le fait que nous ayons observé une décroissance du taux de filtration avec l'augmentation de la température de 16 à 18°C chez les plus petits individus, pourrait nous amener à penser que la température optimum pour la filtration de *Ruditapes philippinarum* dans nos régions serait 16°C, comme l'avait rapporté une étude en France.


Les variations du taux d'assimilation observées pendant nos expériences ne sont probablement pas dues aux facteurs environnementaux que nous avons mesurés. En effet, la température n'affecte pas le taux d'assimilation. De plus, les faibles taux d'assimilation relevés à des taux d'ingestion faibles sont contraires à la théorie de régulation de l'ingestion.

Cette hypothèse explique la régulation du taux d'ingestion par une baisse du taux d'assimilation quand la capacité d'ingestion des bivalves est saturée. La littérature indique que les taux d'assimilation sont très sensibles à la variation de la teneur en matière organique particulaire de la matière solide totale. Or la ferme a eu des problèmes de filtre à la mi-juin, ce qui correspond à la baisse de la concentration algale et des taux d'assimilation. On peut donc penser que la teneur en matière organique particulaire a baissé dans l'eau entraînant une baisse du taux d'assimilation.

Nous recommandons d'étudier plus en détail l'effet de certains facteurs sur les taux vitaux des palourdes japonaises au cours de leur croissance. Nous soupçonnons une augmentation de la concentration algale induisant une limitation du taux de filtration avec la taille des individus. De même, il serait intéressant de voir quelle est l'évolution au cours de la croissance de la concentration algale induisant une production de pseudofèces, afin de fixer une limite haute de cette concentration. Enfin, nous recommandons de mieux définir l'effet de la température sur le taux de filtration afin de mettre en lumière la possibilité d'une température optimale, dont nous n'avons pas été en mesure de prouver l'existence, et de voir si elle évolue au cours de la croissance.

Nous recommandons à la ferme d'augmenter la production algale en été afin de maintenir le taux d'ingestion malgré la décroissance de taux de filtration. Ainsi, il serait préférable de changer d'espèce d'algues cultivées en été, en privilégiant peut-être une des sous-espèces de *Chaetoceros*, qui d'après des essais de culture en cours à IMARES, semblent plus aisées à cultiver à de hautes températures et de fortes luminosités. Il est également nécessaire d'enrichir le milieu de culture, qui pourrait être limité en nutriments comme les nitrates, les phosphates et le fer. Dans tous les cas, la concentration algale ne doit pas passer en dessous de 20 000 particules.ml⁻¹, qui semble induire une forte limitation du taux de filtration, et peut-être d'augmenter cette limite au cours de la croissance. Il est également nécessaire de renforcer le système de filtration pour éviter l'enrichissement de l'eau des bassins en matière inorganique, afin de maintenir de bons taux d'assimilation.

On peut également penser qu'éviter les conditions estivales stressantes pour la croissance des algues et des palourdes pourrait être une solution à ce ralentissement de la croissance des palourdes. La ferme pourrait rafraîchir l'eau en été ou utiliser un captage d'eau salée souterraine. Malheureusement les coûts engendrés et la variabilité de la composition chimique de l'eau souterraine de Yerseke, en font des solutions chères et dont les résultats ne sont pas garantis. Mais une autre solution pourrait être de cultiver plus longtemps les palourdes en écloserie, afin de les semer plus grosses au printemps et permettre d'atteindre la taille commerciale avant l'été.

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Titre anglais : Filtration and assimilation efficiency of <i>Ruditapes philippinarum</i> ; why do they not keep growing?	
<p>Résumé: Un manque de croissance a été identifié dans une ferme de <i>Ruditapes philippinarum</i> en 2011. Croissance, taux de filtration (CR), d'ingestion (IR) et d'assimilation (AE) ont été mesurés en 2012, ainsi que des paramètres environnementaux comme la température et la concentration algal, afin d'identifier les raisons de ce ralentissement de la croissance et d'y proposer des solutions.</p> <p>Les CR et IR standardisés ont chuté respectivement de 13 500 à 1 000 ml.h⁻¹.gPS⁻¹ et de 0.017 à 0.002 gPS d'algue.h⁻¹.gPS⁻¹, de 8 à 28mm. Ces de taux ont chuté quand la concentration algale est passée en dessous de 20 000 particules.ml⁻¹, qui est probablement la concentration algale limitante mentionnée auparavant dans la littérature. AE n'est pas affectée par les facteurs environnementaux, mais a été relevée plus faible pour de faibles IR et CR standardisés, ce qui élude la théorie d'un IR saturé pour expliquer les faibles AE. Un model développé a montré qu'une élévation de la concentration algale à de faibles concentrations algale est le meilleur moyen d'augmenter l'IR.</p> <p>Il y a une limitation morphologique du CR standardisé quand les palourdes croissent, due à une plus faible augmentation du siphon inhalant quand le poids et les couts de maintenance augmentent. Cette limitation, ajoutée des plus faibles concentration algale et AE en été, est la raison du ralentissement et de l'arrêt de la croissance. La meilleure solution pour maintenir et accélérer la croissance est d'augmenter la production d'algues en été en changeant l'espèce d'algues cultivée et en enrichissant le milieu de culture en nutriments limitants. Il serait également possible d'éviter les conditions stressantes estivales en cultivant plus longtemps les palourdes en éclosion, afin de les semer plus grosses dans les bassins de cultures.</p>	
<p>Abstract: A lack of growth has been reported in a <i>Ruditapes philippinarum</i> farm in 2011. Growth, clearance rate (CR), ingestion rate (IR) and assimilation efficiency (AE) have been measured in 2012, as environmental parameters, to identify the reasons of the slow-down in growth and to propose solutions.</p> <p>Standardized CR and IR decreased from 8 to 28mm, from respectively 13 500 to 1 000 ml.h⁻¹.gDW⁻¹ and from 0.017 to 0.002 gDW of food.h⁻¹.gDW⁻¹. Both standardized CR and IR dropped when algal concentration reached level under 20 000 particles.ml⁻¹ which is probably the limiting algal concentration threshold previously mentioned in the literature. AE is not affected by environmental parameters but has been found lower at low standardized IR and CR, which excludes the theory of saturated IR to explain low AE. A model performed showed that increasing algae concentration at low algal concentrations is the best way to increase IR.</p> <p>There is a morphological limitation of standardized CR over size, due to the lower increase of inhalant syphon when body size and maintenance costs increase. This limitation added to lower algal concentration and AE in summer is the reason of a slow-down and a stop in growth. The main solution to maintain and accelerate growth is to increase algal production in summer by shifting to other algae species, more adapted, and enrich the culture medium in limiting nutrients. It would also be possible to avoid summertime stressful conditions by growing clams longer in hatcheries, in order to put them larger in ponds in spring.</p>	
Mots-clés: Aquaculture, bivalves, <i>Ruditapes philippinarum</i> , croissance, taux de filtration, taux d'ingestion, taux d'assimilation, température, concentration algal, taille, limitation	
Key Words: Aquaculture, bivalves, <i>Ruditapes philippinarum</i> , growth, clearance rate, ingestion rate, assimilation efficiency, temperature, algal concentration, size, limitation	