

MASTER THESIS

**Gill and labial palp areas in blue
mussels (*Mytilus edulis*) at sites
with different food quantity**



Master of Science in Aquatic Ecology



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Picture on front page:

The gill and labial palp with the surrounding mantle in the blue mussel (*Mytilus edulis*) (Photo: Birgitte Kathrine Sunde)

Takk til

Fem lærerike og utruleg utfordrande år ved Universitetet i Bergen går mot slutten. Det har vore mange fantastiske personar som har støtta, motivert og «pusha» meg gjennom alle desse åra. Eg hadde ikkje klart dette utan dykk.

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Birgitte Kathrine Sunde

Abstract

Suspension feeding bivalves captures and process particles with their gills and labial palps. These foraging apparatus are known to be flexible in size related to seston quantity and quality. It is important to understand morphological and physiological adaptations in bivalves to understand the mechanisms of the feeding processes. Gill and labial palp areas were measured in the blue mussel, *Mytilus edulis*, from two sites in Lysefjorden (Norway), one upwelling site that was under influence of forced upwelling to enhance chlorophyll *a* concentrations and one control station outside the influenced area of upwelling. Measurements of gill and labial palp areas were conducted in March, June and October 2011. Annual mean concentrations of estimated chlorophyll *a* were significantly different between the two sites and were 1.38 mg/m³ and 1.60 mg/m³ at the control and upwelling site respectively. The annual suspended particulate matter (SPM) was 2.5 g/m³ (control) and 3.3 g/m³ (upwelling), and was not significantly different between sites.

Gill and labial palp areas (mm²) were closely and positively related to shell length (mm) and dry flesh weight (g), but there were no clear difference in these areas between the sites. There was a significant difference in gill-to-palp (GA: PA) ratio between the two sites in October, where GA: PA increased with shell length at the upwelling site, and decreased at the control site. Changes in GA: PA ratio was probably related to labial palp area variations which may have been influenced by the significant difference in chlorophyll *a* concentration during the year. Further it was found that measures of gill areas was significantly higher for frozen opposed to live tissue, and mussels sampled in March and June (frozen) could not be compared to mussels sampled in October (live). The measuring of gill area was more accurate compared to labial palp area, but both areas were measured with a standard deviation less than 10 % the reference value. A regression of gill area (GA) against dry flesh weight (W) in the form $GA = a \cdot W^b$ provided smaller *b*-value at the control site compared to other studies, while the *a*-value was more similar. The results indicate differences in GA: PA ratio within the same fjord at small differences in chlorophyll *a*, while differences in gill and labial palp area probably need larger differences in seston concentration to see significant difference similar to what have been found in other studies.

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1 Introduction

Suspension feeding bivalves are important for the flow of energy and matter in coastal and estuarine systems, and to the coupling between benthic and pelagic systems. Bivalves can be part of the human food source and the aquaculture production has a great commercial value worldwide. There are several mechanisms that regulate the feeding rate in these organisms, which are key to understanding growth and the effect bivalves have on trophic interactions (energy- and matter flow) in natural systems. There are studies (Barillé et al. 2000; Drent et al. 2004; Dutertre et al. 2007; Dutertre et al. 2009; Essink et al. 1989; Honkoop et al. 2003; Kiorboe and Mohlenberg 1981; Payne et al. 1995; Piersma and Lindstrom 1997; Piersma and Drent 2003; Theisen 1982) indicating that suspension feeding bivalves adjust their foraging apparatus according to local food regimes. The objective of this thesis is to investigate adaptations in the gill and labial palp area in the blue mussel (*Mytilus edulis*) at different seston quantities.

Low seston environments

Seston applies to all particles suspended in water, including plankton, organic and inorganic material. Most studies of bivalves are conducted where seston quantity and quality vary from 3 to 100 g suspended particulate matter (SPM) m^{-3} which 5-80 % may be organic (Bayne and Hawkins 1990). The fjords and coastal water in Norway are characterised as low seston environments (Strohmeier et al. 2008).

There is about 21,000 km coastline in Norway, including fjords and bays (Erga et al. 2012). Some of the factors that influence fjord circulation are wind, tides, freshwater runoff, topography and the rotation of the earth. Stratification of water masses in the fjords is primarily caused by freshwater runoff, which peaks in May-June in the southern and western Norwegian fjords (Erga et al. 2012). Stratification restricts the vertical mixing of nutrients into the euphotic layer (Aure et al. 1996) and represent a limitation on primary production.

Low seston environments have suspended particulate matter (SPM) and chlorophyll less than 1.0 g/m^3 and 1.5 mg/m^3 respectively (Erga 1989; Strohmeier et al. 2007), except during phytoplankton blooms mainly in the spring. Compared to most bivalve aquaculture sites, the Norwegian coastal system has a significantly lower seston concentration, and these

environments have an increased risk of food depletion that can reduce bivalve production (Strohmeier et al. 2007). Filtration activity of bivalves may cause large spatial variation in food supply and local depletion of food that can set constraints on bivalve growth (Prins et al. 1998).

Mytilus edulis

Rocky shore communities in cooler waters of the northern and southern hemispheres have a dominant component of mussels in the genus *Mytilus*, where the blue mussels (*M. edulis*, Fig. 1) have the widest distribution (Gosling 2003). *Mytilus sp.* are located from subtidal to high intertidal (Gosling 2003; Strohmeier et al. 2007), and due to this tidal cycle they have a high tolerance for extreme environmental conditions (Hovgaard et al. 2001) where they have adapted to different temperature and salinity levels during the day (Dame 2012; Hovgaard et al. 2001). They are attached to a wide variety of substrates by byssus threads. Mussels are euryhaline, which means that they can survive in salinities ranging from 4-5 PSU to fully marine conditions (Gosling 2003). Temperature is an important factor in regulation feeding, growth, respiration and reproduction in bivalves (Dame 2012; Gosling 2003). The mussels are growing until they reach a size of 5-6 cm shell length in their second or third year, and the spring and summer season is when the major spawning activity occurs (Duinker et al. 2008).



Figure 1: The study species blue mussel (*M. edulis*), photo IMR.

Mytilus sp. has the hormorhabdic filibranch gill-type, which is the simplest gill structure in bivalves (Gosling 2003). The inner surface of the labial palp is folded into numerous ridges and is facing the gill, while the outer surface is smooth (Gosling 2003). They are active suspension feeders, which imply that they use their own energy to transport seawater across their feeding apparatus.

Suspension feeding

Suspension feeding bivalves capture and process particles on their pallial organs, i.e. gills and labial palps, before ingestion (Ward and Shumway 2004). The gills have a large surface area, which allows suspension feeders to filter a large volume of water (Gosling 2003). On each side of the mouth the bivalves have a paired, leaf-shaped structure called the labial palps (Gosling 2003). In contrast to deposit feeders, suspension feeders have relatively larger gills than palps for pumping (Compton et al. 2008). The labial palps and their complex ciliated tracts have long been considered as the main organs of pre-ingestive particle selection (Kiorboe and Mohlenberg 1981). Particles that are captured on the gills are moved in mucus strings (ventral tract) or less cohesive mucus slurry (dorsal) (Beninger et al. 1993; Ward and Shumway 2004) along the grooves toward the labial palps where material suitable for food is removed from the food tracts on the gills (Gosling 2003). The food is sorted by the labial palps and transported to the mouth, or rejected as pseudofeces (Dame 2012). All particles cleared out of suspension are ingested at low seston quantities (Hawkins et al. 1999).

By actively adjusting various physiological components of their feeding and digestion, the suspension feeding bivalves adapt to a natural diet that is changing in terms of quantity and quality (Strohmeier et al. in prep.). The ability to control the clearance rate is what primarily determined the food acquisition (Strohmeier et al. 2009). The structure, ciliation and mucocyte distribution of the gills determine the retention efficiency (RE) of particles and the clearance rate (CR). Retention efficiency is the fraction of particles of a given size retained during one single passage on the gills (Bayne and Newell 1983; Pouvreau et al. 1999), and the clearance rate is defined as the volume of water completely cleared of particles per unit of time (Bayne et al. 1976; Pouvreau et al. 1999).

The retention efficiency varies with the size of the particles, and has recently been shown to vary seasonally (Strohmeier et al. 2011). Mussels can retain bacteria (0.3-1.0 μm) and

flagellates (1.0-2.0 μm) with low efficiency (Gosling 2003). The RE for mussels decrease to 35-90 % with smaller particle ca. 2 μm (Gosling 2003; Møhlenberg and Riisgard 1978) while mussels have a 100 % RE of particles above 3-4 μm (Møhlenberg and Riisgard 1978; Strohmeier et al. 2007). Pouvreau et al. (1999) found that in the pearl oyster (*Pinctada margaritifera*) particles larger than 5 μm were 100 % retained. The clearance rate is directly related to gill area (Jones et al. 1992; Meyhofer 1985; Pouvreau et al. 1999), as larger gills collect more particles per unit time than smaller gills. Growth of suspension feeding bivalves is mainly controlled by food availability (Berg and Newell 1986; Winter 1978).

Suspension feeding bivalves couple the benthic and pelagic systems by consuming large quantities of primary producers and being a prey for both benthic and semi-pelagic predators (Dame 2012). Dense populations of bivalves remove large quantities of suspended particulate organic materials from coastal ecosystems, and transform them into forms that can be utilized by phytoplankton (Dame 2012).

Adaption to different seston regimes and turbidity

An organism's ability to adjust to variations in food availability has been related to the morphological plasticity of their foraging apparatus (Drent et al. 2004; Piersma and Lindstrom 1997; Piersma and Drent 2003). Several studies on suspension feeding bivalves have established a relationship between the natural turbidity and the size of the gills and labial palps, showing a morphological flexibility of these pallial organs (Barillé et al. 2000; Dutertre et al. 2007; Dutertre et al. 2009; Essink et al. 1989; Honkoop et al. 2003; Kiorboe and Møhlenberg 1981; Payne et al. 1995; Theisen 1982). This relationship is characterized by decreasing gill size and increasing palp size at increasing seston concentration, and by relatively smaller palps and larger gills at less turbid sites (Dutertre et al. 2009; Essink et al. 1989; Theisen 1982).

A good representation of the feeding process is very important in growth models, since it provides the link between the environment and growth of an organism. However, due to incomplete understanding and/or lack of data with sufficient precision level, these processes are often represented by simple functions that overlook potentially important feeding mechanisms. The Dynamic Energy Budget (DEB) model (Kooijman et al. 2004) has been used to simulate growth and energy budgets of mussels. The ingestion rate is expressed by the

half-saturation coefficient X_k ($\mu\text{g Chlorophyll } a \text{ L}^{-1}$), which specifies where the ingestion rate is half of the maximum (Rosland et al. 2009). The X_k value expresses several properties about food uptake, such as the quality of the food and the efficiency of filtration- and clearance rate and it also depends on the maximum ingestion rate per unit surface area (Rosland et al. 2009). The half saturation coefficient X_k is known to vary according to food quality and quantity and thus between different ecosystems and/or food proxies. In many applications of the DEB model in bivalves, it is the only free-fitted (Pouvreau et al. 2006; Rosland et al. 2009).

In the latest applications of the DEB model on bivalves (*e.g. Crassostrea gigas, M. edulis*), differences in some DEB parameters related to food uptake could partly be explained by the plasticity in ingestion capacity (Pouvreau et al. 2006; Rosland et al. 2009), and in particular, the half saturation coefficient X_k (Pouvreau et al. 2006). Ingestion capacities in the Pacific oyster (*C. gigas*) depend on the size of the gills and the palps (Barillé et al. 2000). Ward et al. (1998) found that ctenidia play a minor role in particle selection in mussels but transport particulate matter to the palps.

Relationship between different variables and environment

Pouvreau et al. (1999) and reference therein show that the relationship between gill areas (GA, mm^2) and dry flesh weight (W, g), *i.e.* $GA = a \cdot W^b$ is comparable between several bivalve species. The a - and b -value vary between species and different food quantity. The b -coefficient value ranging between 0.38 and 0.94, had a mean value of 0.67 (Hawkins et al. 1990; Jones et al. 1992; Pouvreau et al. 1999), while the gill surface area related to dry tissue weight and/or clearance rate, *i.e.* a -value, have a wide range between bivalve species (Pouvreau et al. 1999). The highest a -value when comparing bivalves from only low turbidity waters is recorded to be $3502 \text{ mm}^2/\text{g}$ for the pearl oyster (*P. margaritifera*) in French Polynesia (Pouvreau et al. 1999), while the mussels *M. edulis* and *M. californianus* also showed relatively high a -values (respectively 2458 and $2740 \text{ mm}^2/\text{g}$) (Meyhofer 1985; Mohlenberg and Riisgard 1979; Pouvreau et al. 1999). It seems that the gill area varies both between species and in different types of environments.

In *C. gigas* the gill-to-palp (GA:PA) ratio changed with different turbidity conditions (Dutertre et al. 2009). Barillé et al. (2000) found that variations in gills and labial palps in *C. gigas* occurred on small geographic scale. Honkoop et al. (2003) also noticed a flexibility in the main feeding organs in the Sydney rock oyster (*Saccostrea glomerata*) and in *C. gigas* that was not a constant proportion of total body mass or related to size of shells. Morphological adjustments of gill and labial palp areas in response to different food regimes are processes that can be important to understand the mechanisms involved in filtration and particle selection in blue mussel. The aim to quantify filtration processes by means of mechanistic modeling approaches requires information that can explain adaptation and flexibility in mussel feeding.

1.1 Research objectives

The main objective of this study was to test if blue mussels (*M. edulis*), grown at sites with different seston concentrations exhibited differences in their gill and labial palp areas. A second objective was to test if the freezing process influences gill and labial palp areas, and to quantify any differences between frozen and fresh gill and labial palp tissue. A third objective was to test the accuracy of the method based on visual comparisons of live and frozen gills and labial palps based on picture analysis.

2 Materials and methods

2.1 Sampling sites

2.1.1 Lysefjorden

Lysefjorden (Fig. 2) is a long and narrow fjord on southwest coast of Norway. It has a maximum depth of 460 m, is approximately 40 km long and 0.5-2 km wide with a 14 m deep sill at the entrance. The mean tidal range is 0.4 m and it has a surface area of 44 km². Lysefjorden has been used to perform a large scale upwelling experiment to increase nutrient and phytoplankton availability (Aure et al. 2007).

Data were collected from two sites in the fjord; one within (upwelling site) and one outside (control site) the influence area of the forced upwelling. The upwelling site (N59° 03.249' E6° 37.866') is near the head of the fjord (Lysebotn). The control site (N59° 00.800' E6° 17.514') is located 20 km away from the upwelling site in the outer part of the fjord at Bakken.

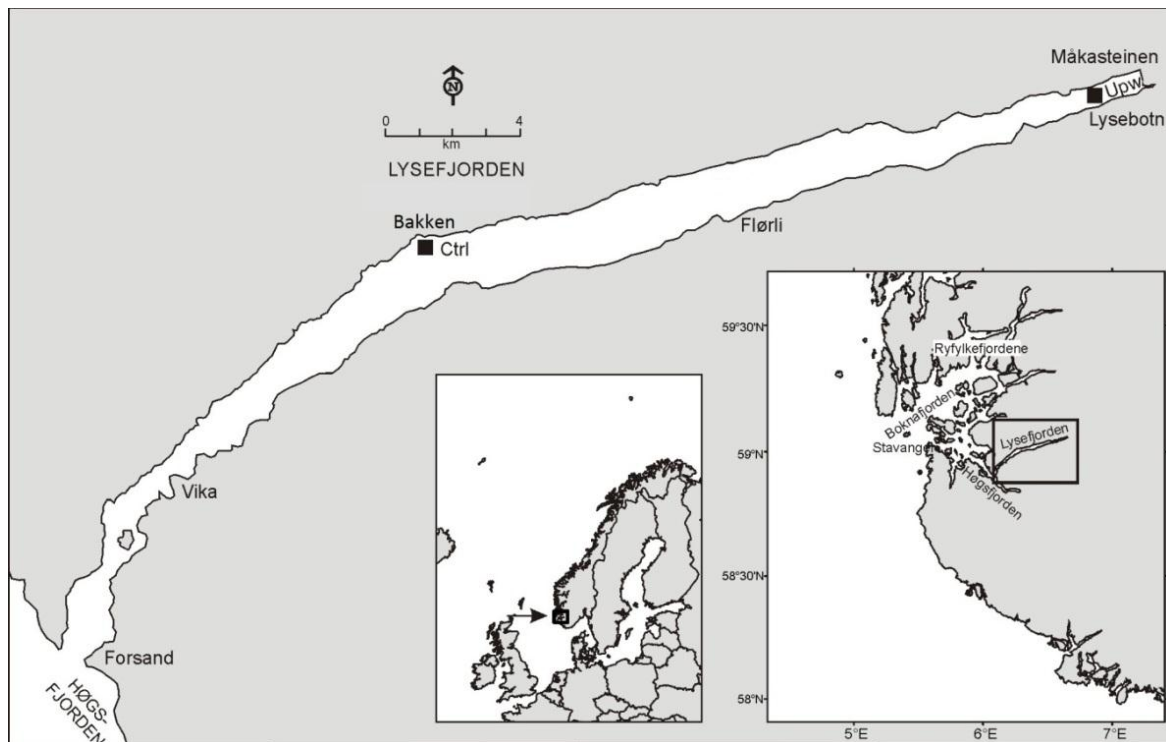


Figure 2: Map of Lysefjorden, the upwelling site is near the head of the fjord (close to Lysebotn) and the control site is in the outer part of the fjord (at Bakken).

Mussels

The mussels used in the experiments were sampled from a cohort that had been stocked as juveniles in 2009 and transferred, on 2nd March 2011, to the control and upwelling sites. The mussels were suspended from long-line lantern nets at 7 m depth at the two sites. Stocking density was approximately 40 individuals per dish (80 individuals per m²). Mussels collected in March and June were put in the freezer immediately after collection and transported to the research station of the Institute of Marine Research (IMR) at Austevoll (Fig. 5) and stored in the freezer until dissection. The mussels collected the 7th of October were brought back live from Lysefjorden to Austevoll and held in filtrated (< 1µm) seawater until dissection (overview in Table 1).

Table 1: Sampling site, sampling and dissection dates, number of mussels sampled, number of individuals analyzed and treatment of samples. Some of the mussels were dead or they were destroyed during dissections and therefore they could not be used further in the analysis. The number of mussels dissected and used in the analyses differs from the number of mussels that were sampled. Some of the samples were frozen when dissected and some were live.

| Site | Sampling date | Dissection date | Nr. of individuals sampled | Nr. of individuals in analysis | Treatment |
|-------------|----------------------|------------------------|-----------------------------------|---------------------------------------|------------------|
| Upwelling | 28.03.11 | 10.01.12 | 20 | 19 | Frozen |
| Control | 29.03.11 | 11.01.12 | 20 | 20 | Frozen |
| Upwelling | 15.06.11 | 09.01.12 | 23 | 19 | Frozen |
| Control | 16.06.11 | 10.01.12 | 19 | 19 | Frozen |
| Control | 07.10.11 | 10-11.10.11 | 40 | 32 | Live |
| Upwelling | 07.10.11 | 11-12.10.11 | 40 | 35 | Live |

Temperature and seston

The temperature and seston data that are described below are part of the GATE project (Strohmeier et al. 2011). They are used in this section of the Material and Methods to provide an overview/description of the environmental conditions that the mussels encountered during the study. The data was collected by two STD/CTD (SAIV AS, SD 204), and measurements were recorded each 30 min.

Water temperatures range from 4°C to 16°C during 2011, with an annual mean temperature of 8.5°C at the control site and 7.8°C at the upwelling site (Fig. 3) which was significant different from each other (t-test, $t= 17.02$, $df=19107.93$, $p< 2.20\cdot 10^{-16}$). From February to

April the upwelling site had the highest temperature (Fig. 3). After April there appears to be a change and the control site had the highest temperature the rest of the year. The trend line in Figure 3 of temperature and chlorophyll *a* is generated by a Generalized Additive Model.

The largest difference in chlorophyll *a* concentration between the two sites occurs from April to June. In late April the chlorophyll *a* concentration was the highest, with approximately 4 mg/m³ at the upwelling site and 1.5 mg/m³ at the control site (Fig. 3). The annual mean concentration of estimated chlorophyll *a* was significantly higher at the upwelling site compared to the control site (t-test, $t=-20.3155$, $df= 22695.93$, $p< 2.20\cdot 10^{-16}$) with a mean \pm SE at the control site of 1.38 mg/m³ (± 0.0050) and at the upwelling site 1.60 mg/m³ (± 0.0096).

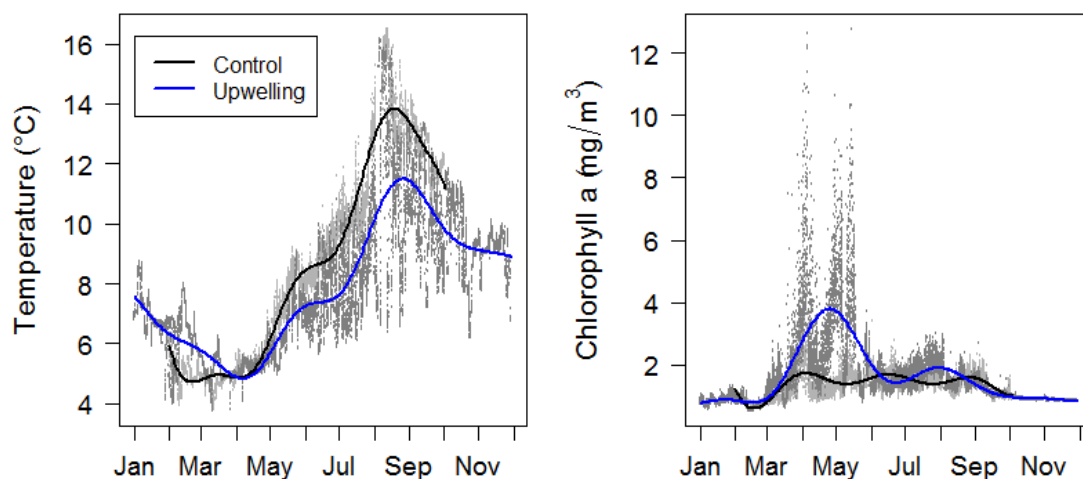


Figure 3: Time series of temperature (°C, left panel) and estimated chlorophyll *a* (mg/m³, right panel) during 2011 at the Upwelling site and the Control site. Measurements are from the holding depth of the mussels (7 m depth), and presented as a running mean (per=12=6h).

Measurements of chlorophyll *a*, particle volume, particle organic carbon and suspended particulate matter taken during 2011 are shown in Figure 4. Students t-tests were used to test for significant difference in seston concentration between the two sites, and concluded with no difference (Table 2). The highest measured level of chlorophyll *a* was during April (control site 6.5 mg/m³) and May 2011 (upwelling site 3.5-4.5 mg/m³). At the end of July and in August the concentrations was slightly higher at the upwelling site and similar to the estimated chlorophyll *a* (Fig. 3).

The particle volume at the control site reached the highest value in April. In early May and in July the upwelling site had exhibits particles with a higher volume compared to the control site. It was approximately the same the rest of the year. Suspended particulate matter was almost the same throughout the year. Annual mean suspended particulate matter (SPM) in 2011 was 2.5 g/m^3 and 3.3 mg/m^3 at the control upwelling site respectively. Particle organic carbon differs at the end of March (control highest) and in May-July (upwelling highest).

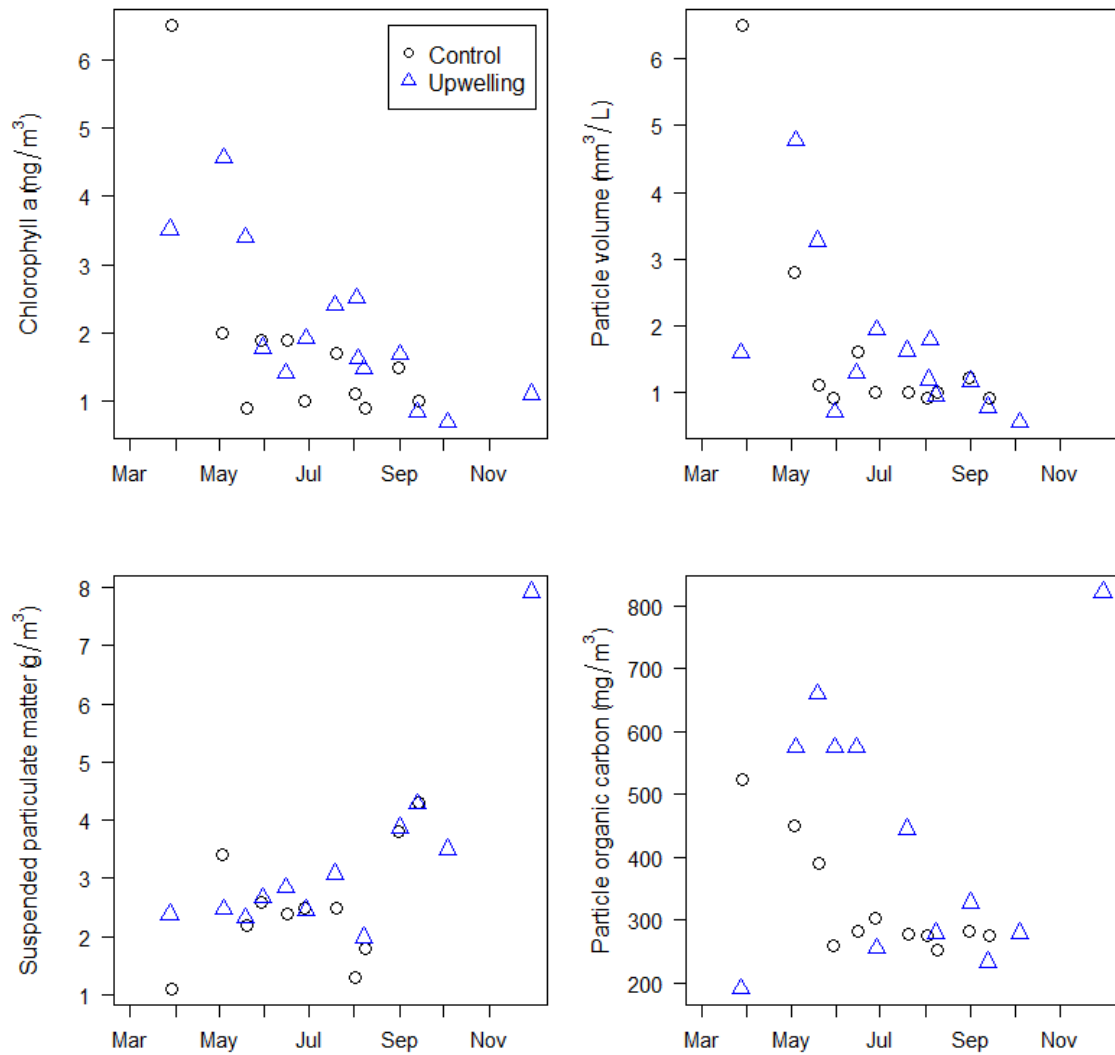


Figure 4: Time series of; top left: Chlorophyll *a* (mg/m^3) (upwelling $n=14$ and control $n=11$). Top right: particle volume (mm^3/L) (upwelling $n=13$ and control $n=11$). Bottom left: suspended particulate matter (g/m^3) (upwelling $n=13$ and control $n=11$). Bottom right: particulate organic carbon (mg/m^3) (upwelling $n=13$ and control $n=11$). All measurements are taken from water samples at the holding depth of mussels (7 meter) during 2011.

Table 2: Students t-tests were used to test for significant differences in seston between the two sampling sites. There were no significant differences.

| | t-value | Df | p-value |
|---|----------------|-----------|----------------|
| Chlorophyll α | -0.37 | 17.11 | 0.714 |
| Suspended particulate matter (SPM) | -1.93 | 18.50 | 0.173 |
| Particle volume (PV) | 0.10 | 17.48 | 0.918 |
| Particle organic carbon (POC) | -1.71 | 15.39 | 0.107 |

2.1.2 Austevoll

The second objective of this study was to test if there were any effects of the freezing process on the tissue and whether the freezing process was effecting the estimation of the gill and labial palp areas. Blue mussels collected at Austevoll (N60° 05', E5° 15', Fig. 5) in January 2012 were used to test this. The third objective was to test the accuracy of the measuring method. All groups of mussels collected at Austevoll were used in this test (Table 3).

The mussels were collected from a natural population which was attached to the pier close to the IMR experiment facilities. A uniform size distribution was assumed for the two groups. The 15 mussels collected on the 17th of August were dissected and photographed, then frozen again until the 30th of August until new pictures were taken.

Table 3: Sampling site, sampling and dissection dates, number of mussels sampled, number of individuals analyzed and treatment of samples. Some of the mussels were dead or they were destroyed during dissections and therefore they could not be used further in the analysis. The number of mussels dissected and used in the analyses differs from the number of mussels that were sampled. Some of the samples were frozen when dissected and some were live.

| Sampling date | Dissection date | Location | Nr. of individuals sampled | Nr. of individuals used in analysis | Treatment |
|----------------------|------------------------|-----------------|-----------------------------------|--|------------------|
| 17.08.11 | 17.08.11 | Austevoll | 15 | 14 | Live |
| 17.08.11 | 05.09.11 | Austevoll | 15 | 14 | Frozen |
| 25.01.12 | 25.01.12 | Austevoll | 25 | 22 | Live |
| 25.01.12 | 14.02.12 | Austevoll | 25 | 23 | Frozen |

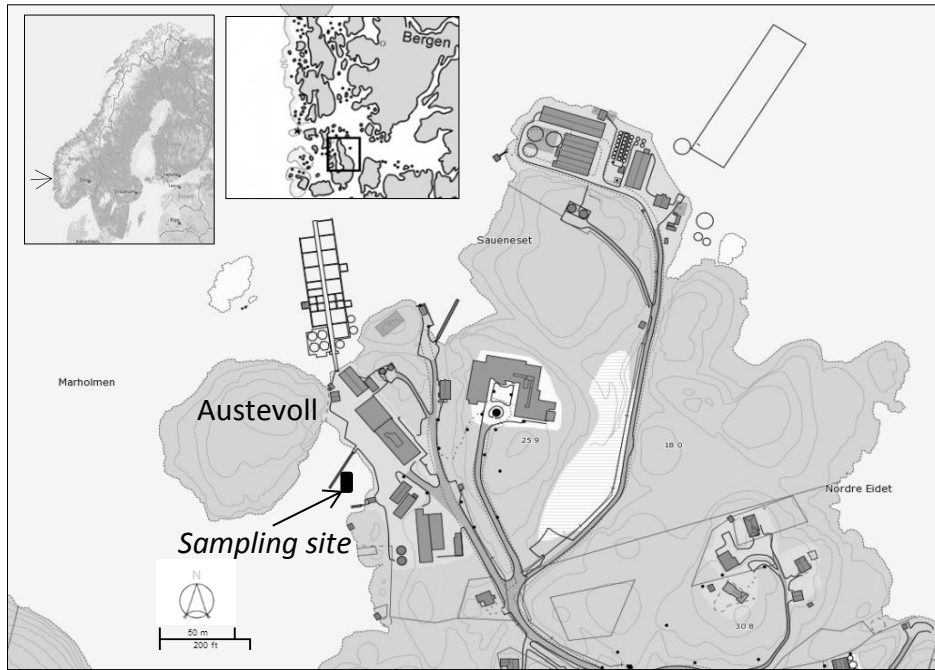


Figure 5: Map of the sampling site at Austevoll, Hordaland, Norway made from Norgeskart.no (Kartverket 2012). The arrow indicates the sampling site.

2.2 Measuring gills and labial palps

2.2.1 Dissections

The frozen mussels were thawed for half an hour before dissection. For live mussels, gill contraction was avoided by using a magnesium chloride (MgCl_2) solution, which contained $50 \text{ mg MgCl}_2 \text{ L}^{-1}$; 1/3 filtered seawater and 2/3 freshwater. The mussels were placed in this solution for about 3 hours before the dissection could start (Kiorboe and Mohlenberg 1981; Suquet et al. 2009).

The shell length was measured from umbo to the posterior end with vernier calipers to the nearest 0.1 mm. The anterior adductor muscle was cut with a scalpel in the left valve and gently removed the mantle from the shell. At last, the posterior adductor muscle was released from the left shell valve. This procedure was repeated on the right shell valve. The mantle surrounds the inner organs (tissues). The flesh was put in a black box filled with filtered seawater until it covered the whole tissue. This allowed avoiding reflections in the pictures, to make the gills and palps floating so that it was easier to work with without damaging these tissues. The mantle on the left side was removed with a small scissor, and

the gills turned around to float in the water. After being photographed, the tissue of each individual mussel was freeze-dried for at least 44°C hours to measure dry flesh mass (M, g) to the nearest 10^{-3} g.

The pictures were taken by a Canon 600D, attached to a stand (Fig. 6) with light on each side of the camera and an angle of 45 degrees to the object. The manual settings on the camera was ISO100, picture style are neutral, shutter time $\frac{1}{4}$ and aperture 8.0. Only the light on the side of the camera was turned on in the room in order to reduce reflections in the pictures.

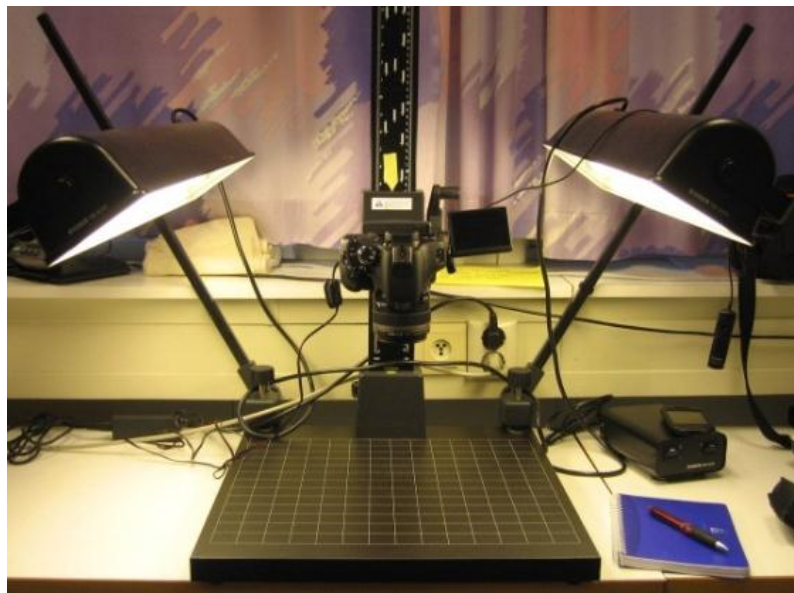


Figure 6: The stand with the camera attached to it.

2.2.2 Picture analysis

The pictures were analyzed with the image analysis software IMAQ Vision Builder (National Instrument) to delineate organ outlines and calculate their areas (mm^2). This program measures the area in pixels. The function used in the software was image-measure-area-polygon tool. Some of the pictures were analyzed using the function color-extract color planes-RGB-Blue plane in the software. This function helped to improve the details in the picture. For example in pictures where outline of gill and labial palps were hard to detect this function showed the line more clearly (Fig. 7, left panel).

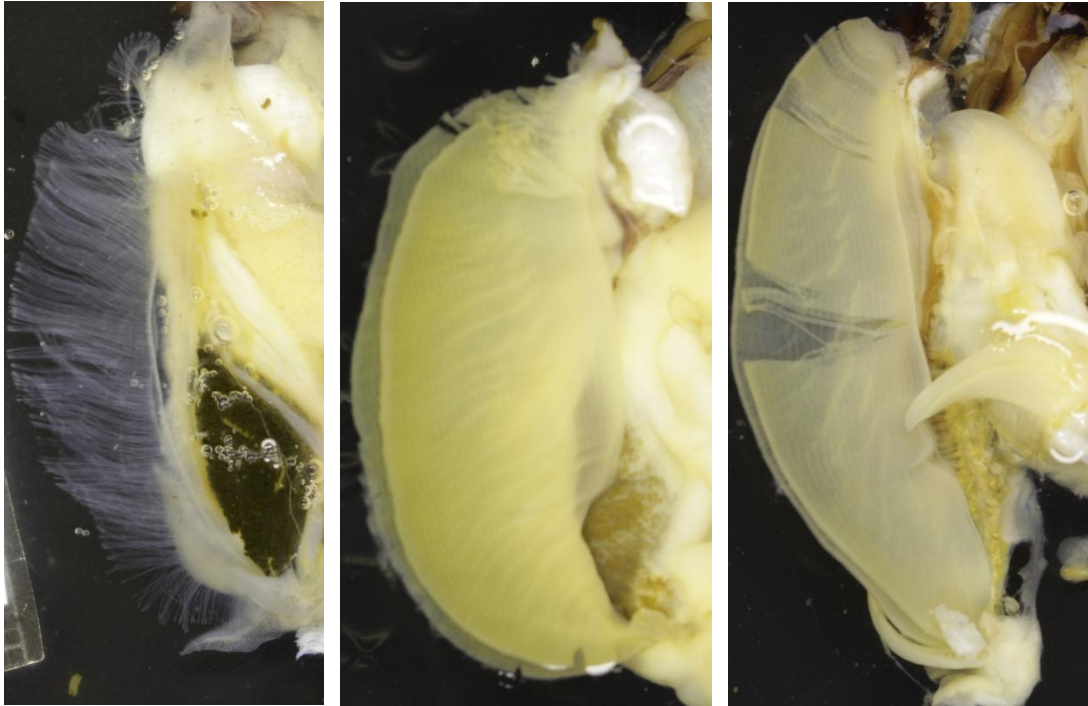


Figure 7: Left panel: an example of a frozen gill and labial palp where it was not easy to determine the outer boundary of parts of the gill. Mid panel: A gill from a live mussel where parts of the gill are hidden and where it is a bit curled. Right panel: live gill that has rifts.

There are four gills and four labial palps in the mussel. It was assumed that the gills and palps within the same individual have the same size. The gills and palps from the left valve were used in the measurements, but in cases where they were destroyed, the gills and palps from the right valve were used. If the gill and labial palp area were hidden, curled (Fig. 7, mid panel), or had rifts (Fig. 7, right panel) the line to determine the gill or labial palp area was drawn where the outer line was expected to go.

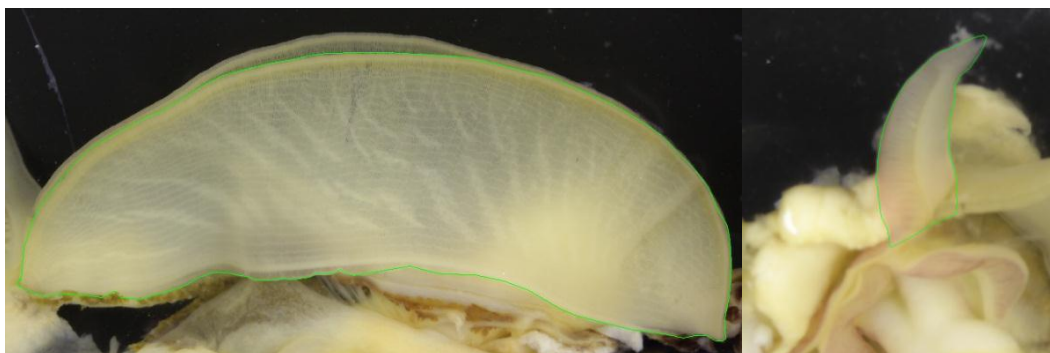


Figure 8: The green contour line is an example of the drawn area around the labial palp and the gill.

A function on the copy machine converted mm paper from orange with red strips to black with white stripes on a wet paper that was cut to a known area (30x10 mm). This known area was used in the image analysis software. The lines were drawn manually around the known area, the palps and the gills, with the polygon tool (Fig. 8). A pen tablet (WACOM Bamboo, model: CTL-661) was used during this process to simplify the job. Since the area was later provided in pixels it needed to be converted into mm². This was done with formula 1 and 2.

$$k = \frac{\text{known area}(mm^2)}{\text{known area (pixels)}} \quad (1)$$

$$\text{Area (mm}^2\text{)} = \text{Area (pixels)} \times k\left(\frac{mm^2}{\text{pixel}}\right) \quad (2)$$

2.3 Testing the accuracy of the method

To test the accuracy of the method, the drawing process was repeated three times for the same picture. If there were several pictures from the same gill and labial palps, but from different angles, there was a comparison between the areas measured in the different pictures. Standard deviation (SD) was used to statistically test the accuracy of the method. SD shows how much variation exists from the average, and a low SD indicates that the data points tend to be very close to the mean.

2.4 Statistical analysis

The statistics were conducted with the free statistical software R (3.0.0; 2013-04-03) and Microsoft Excel® (version 2010) for Windows. Estimates of the relationship between GA and dry tissue mass (M) were done on all the dissected mussels from Lysefjorden. The functional association of gills and palps in mussels were expressed as the gill-to-palp (GA: PA) ratio. The significance level was set to 0.05 throughout this project.

Linear models (lm) were used to reveal differences in continuous response variables (gill area, labial palp area, GA: PA ratio, shell length, and dry flesh weight) according to different categorical and continuous response variables (shell length; continuous, site; categorical, month; categorical, dry flesh weight; continuous, labial palp area; continuous). The model assumes constant variance and normally distributed residuals.

Two models were used to describe the results from mussels from Lysefjorden. One linear model tested the difference in the mussels from March and June, since both of the groups were frozen mussels. The main focus was on the October mussels, and therefore a second linear model was used for these mussels. The reason was that October had live flesh, the largest n (sample size), and the longest time to adapt to the conditions since these mussels had been at the two sites since March.

To compare the data from this thesis with other studies, the gill area and dry flesh weight was log transformed and the gill area was multiplied with 8 to allow for 8 filtering surface (4 per ctenidium). Then a - and b -values in the regression equation $GA=a \cdot W^b$ was estimated.

A tukey HSD test is a multi comparisons test for unplanned comparisons and was used in cases of significant results in the linear models. Model-checking plots were used to test the linear models. The student t-test was used to test if there was an effect from the freezing process on the Austevoll shells. Standard error (SE) of the sample mean was calculated as a function of variance and the sample size to illustrate the margin of errors in the measurements.

3 Results

3.1 Effect of the freezing process on gill- and labial palp areas

To determine if there were any differences in gill and labial palp tissue size between frozen and live mussels, 22 live mussels (LV) and 23 frozen mussels (FZ) were used. Students t-test showed that the mussels had a similar mean shell length (t-test, $t=1.50$, $df= 149.39$, $p = 0.137$). The mean shell length (\pm SE) of frozen mussels was 55.6 mm (\pm 0.6) and 54.2 mm (\pm 0.7) for the live mussels.

Gill and labial palp area from frozen and live mussels

The frozen mussels had a larger gill area than live mussels (t-test, $t=12.57$, $df= 141.22$, $p < 2.20 \cdot 10^{-16}$, Fig. 9). The mean \pm SE gill area for the frozen mussels was 473.8 mm² (\pm 10.5) and 296.6 mm² (\pm 9.4) for the live specimens. Frozen mussels had a gill area that was 37 % larger than the live mussels. There was no significant difference in the labial palp area between the two treatments ($t=-0.65$, $df= 156.62$, $p= 0.517$, Fig. 9). The mean (\pm SE) labial palp area was 22.8 mm² (\pm 0.8) for the frozen mussels and 23.5 mm² (\pm 0.8) for the live mussels.

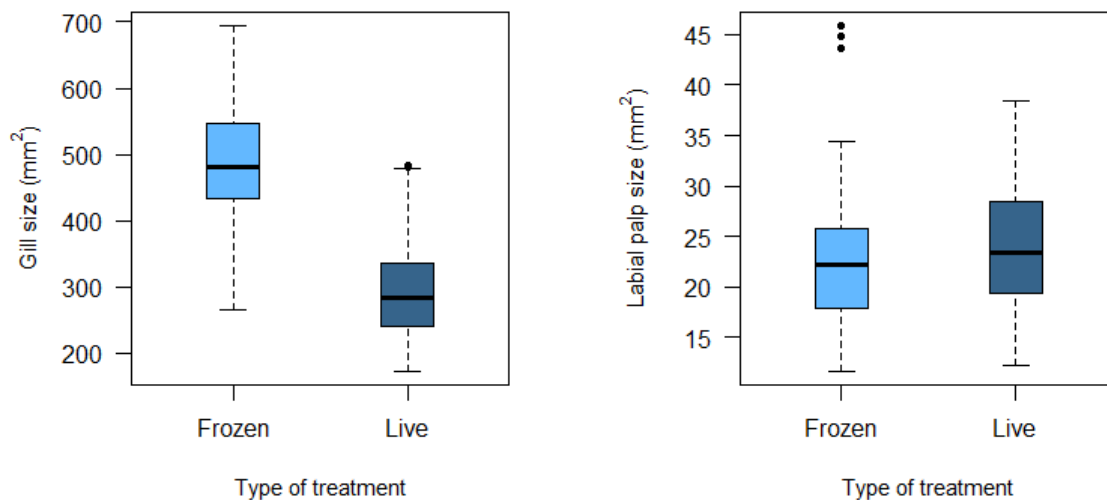


Figure 9: The left panel shows the gill size (mm²) and the right panel shows the labial palp size (mm²) from frozen and live mussel. The box comprises median, first and third quartiles, while the whiskers display the max and min values, except when outliers are present. Outliers are defined as data-points located more than 1.5 box lengths away from the median. There are three outliers in the plot of labial palp area and one in the plot of gill size.

3.2 Effect of seston quantity on mussel growth, gills and labial palps

3.2.1 Shell length

There was a significant increase in shell length over time (lm, $F_{2,138} = 3.39$, $p = 0.037$). A comparison of shell length between sampling dates by a Tukey HAD test demonstrated that the shell length in October was significantly different from March (Tukey, $t = 2.60$, $p = 0.028$), while June – March (Tukey, $t = 1.47$, $p = 0.310$), and October – June (Tukey, $t = 0.93$, $p = 0.619$) were not significantly different. There was no significant difference in shell length between the two sites (lm, $F_{1,138} = 0.44$, $p = 0.508$).

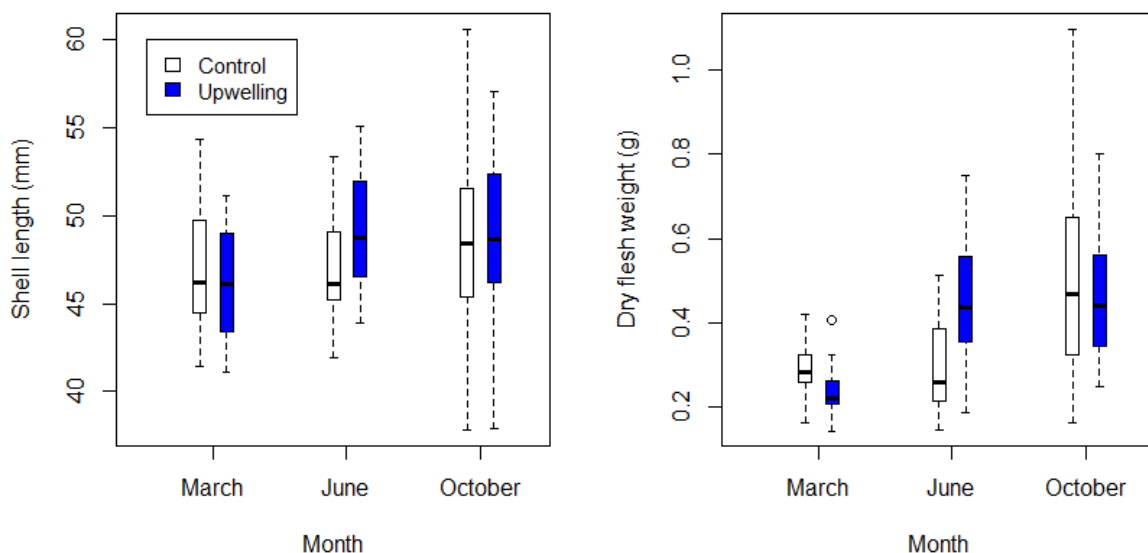


Figure 10: Boxplot (explanation in Fig. 9) of shell length (mm) (left panel) and dry flesh weight (g) (right panel) at the control (white box) and upwelling (blue box) site at three different months in 2011.

3.2.2 Dry flesh weight

There was a clear trend that dry flesh weight increased during the year, and the spread in dry flesh weight was much higher in October compared to March (Fig. 10, right panel). The range in dry flesh weight at the control site in March was 0.165 -0.420 g ($n=20$) while it was 0.164 -1.084 g ($n=35$) in October. There was a significant relationship between the dry flesh weight and the month which means that dry flesh weight differs between the sampling dates (lm, $R^2 = 0.71$, $F_{2, 132} = 33.38$, $p = 1.85 \cdot 10^{-12}$). Dry flesh weight seemed to increase with

shell length in June and October, while in March it seemed to have a smaller increase with size (Fig. 11), which can be seen with a steeper slope of the line June and October compared to March. The lack of difference between shell length and dry flesh weight may indicate high spawning activity. The statistics also confirm a strong significant relationship between the shell length and the dry flesh weight (lm, $F_{1, 132} = 216.40$, $p < 2.20 \cdot 10^{-16}$). There was no significant difference in dry flesh weight between the two sites, but the statistics demonstrated a significant interaction between month and site (lm, $F_{2, 132} = 5.52$, $p = 0.005$). This interaction indicates that the change in dry flesh weight at the control and upwelling site was not the same between the different months. There was also a significant interaction between shell length and month (lm, $F_{2, 132} = 7.47$, $p = 8.44 \cdot 10^{-04}$) which suggests that the relationship between shell length and dry flesh weight differs between months.

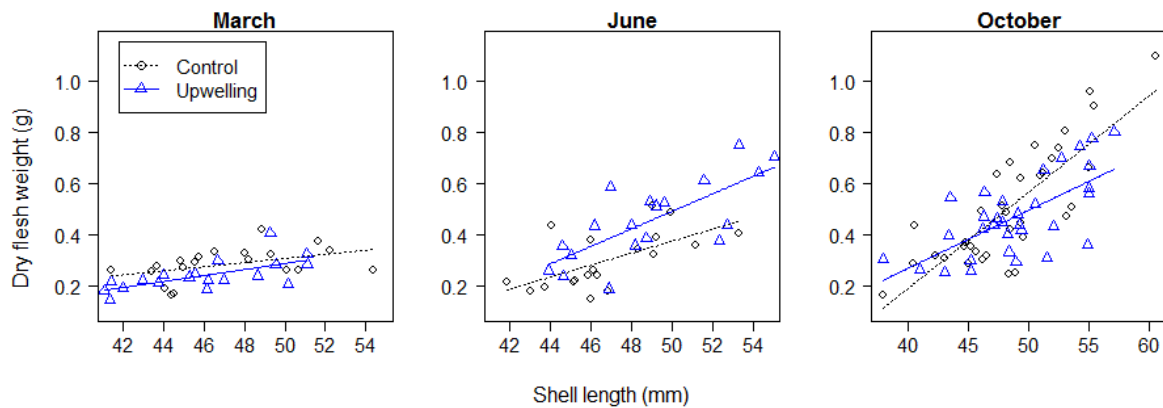


Figure 11: The relationship between dry flesh weight (g) and the shell length (mm) with a regression line for each of the sites (control and upwelling) in March, June and October. October has a longer range in size along the x-axis compared to March and June.

3.2.3 Gill area and labial palp area

March and June analysis

Figure 12 shows that gill area increases with increasing shell length. The statistical analysis confirms a strong relationship between gill area and shell length in March and June (lm, $R^2 = 0.61$, $F_{1, 69} = 84.72$, $p = 1.27 \cdot 10^{-13}$). The analysis indicates a significant difference in gill size between the two sampling dates (lm, $F_{1, 69} = 20.75$, $p = 2.19 \cdot 10^{-05}$), which are not explained from changes in shell length. There were no significant differences in gill size between the two sites.

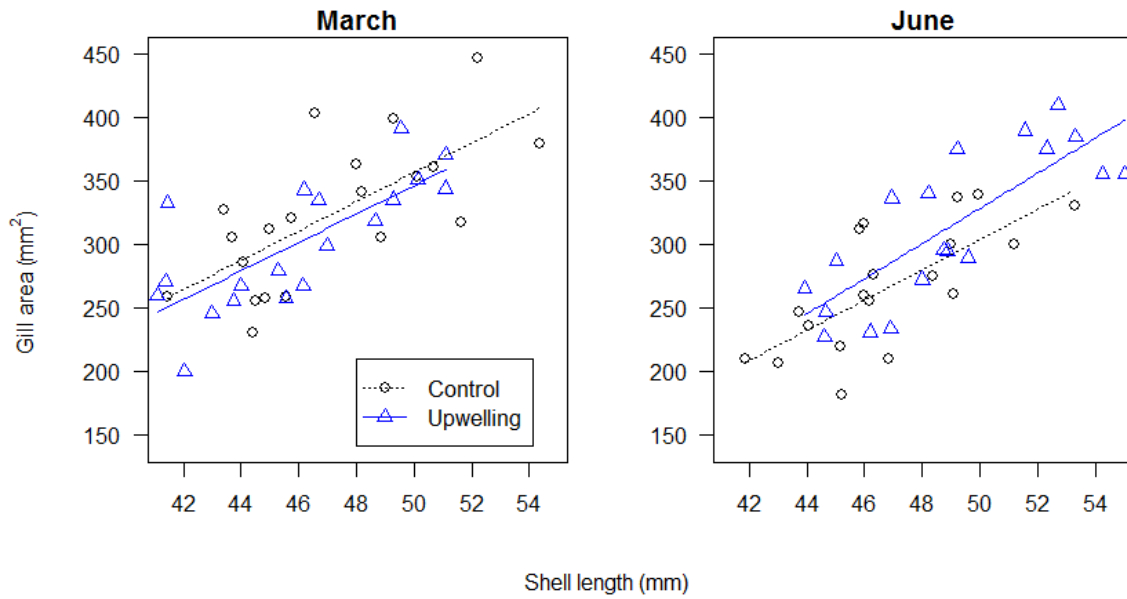


Figure 12: The relationship between gill area (mm^2) and the shell length (mm) with a regression line for each of the sites (control and upwelling). There is one figure for each month (March and June).

There is a significant relationship between shell length and labial palp area (lm , $R^2 = 0.25$, $F_{1,69} = 12.10$, $p = 8.80 \cdot 10^{-04}$) in March and June at both sites. Figure 13 indicates that the labial palp area increased with increasing shell length at the upwelling site in March and June, while the labial palp area at the control site was almost the same at different shell lengths. The statistics confirmed that it was an interaction between the shell length and sites (lm , $F_{1,69} = 7.31$, $p = 0.009$), meaning that the change in labial palp area according to shell length was not the same for the control and upwelling sites. The mean labial palp area at the control site was different from the upwelling site in March (lm , $t = -2.07$, $p = 0.042$). While the control site had a small negative correlation with shell length, the upwelling site had a small positive correlation that was significantly different from the control site in March (lm , $t = 2.13$, $p = 0.037$). The individual variation in the labial palp area in the upwelling area in March ranged from 10 to 25 mm^2 for mussels of 46 mm in shell length.

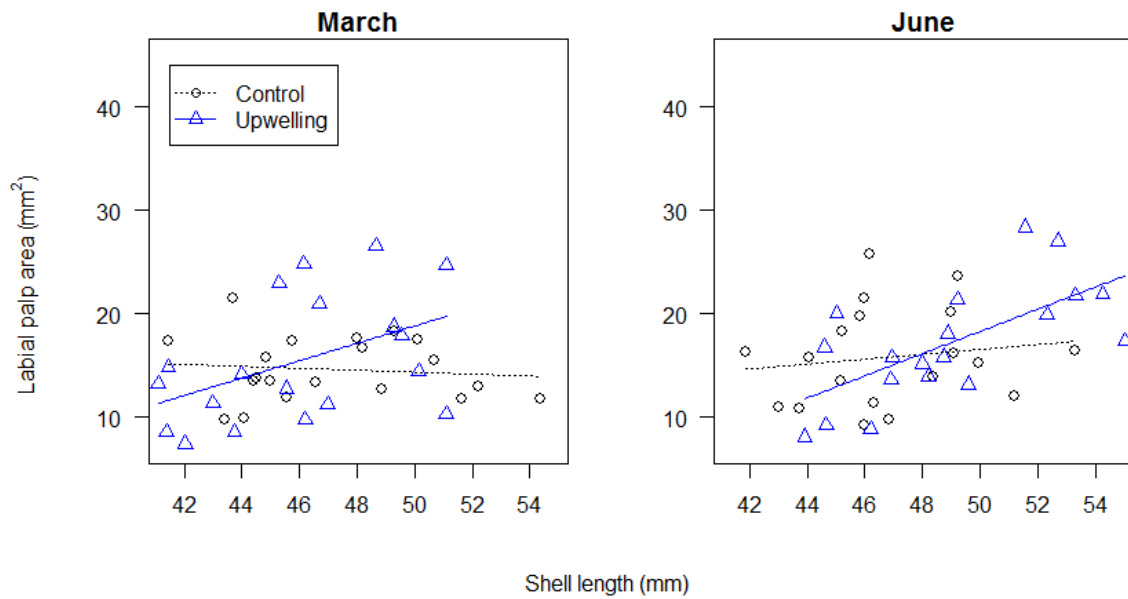


Figure 13: Relationship between labial palp area (mm²) and the shell length (mm) with a regression line for each of the sites (control and upwelling). There is one figure for each month (March and June).

Both Figure 14 and the statistics demonstrates that there was a positive relationship between gill area and dry flesh weight (lm , $R^2 = 0.43$, $F_{1, 69} = 25.59$, $p = 3.34 \cdot 10^{-06}$). There was no difference between the sampling sites, but there was a difference between the two sampling dates (lm , $F_{1, 69} = 24.55$, $p = 4.95 \cdot 10^{-06}$) which was not explained by the dry flesh weight.

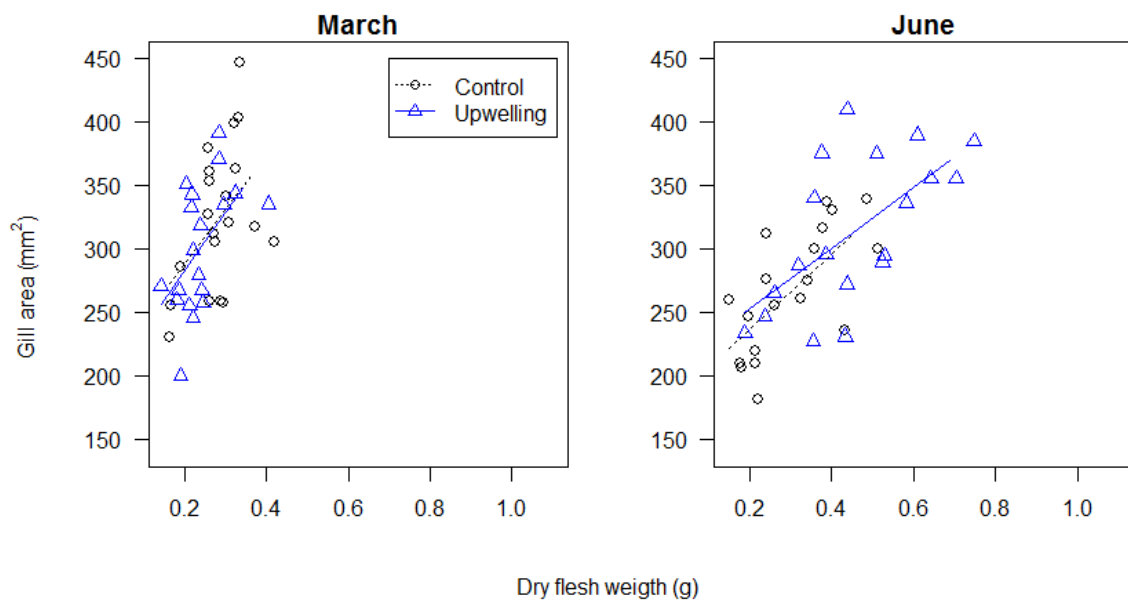


Figure 14: The relationship between gill area (mm²) and dry flesh weight (g) with a regression line for each of the sites (control and upwelling). There is one figure for each month (March and June).

The labial palp area in March and June increased with increasing dry flesh weight (Fig. 15, lm, $R^2 = 0.19$, $F_{1, 69} = 13.64$, $p = 4.40 \cdot 10^{-04}$). There were no statistical differences between the two sites, but note that the data were very scattered.

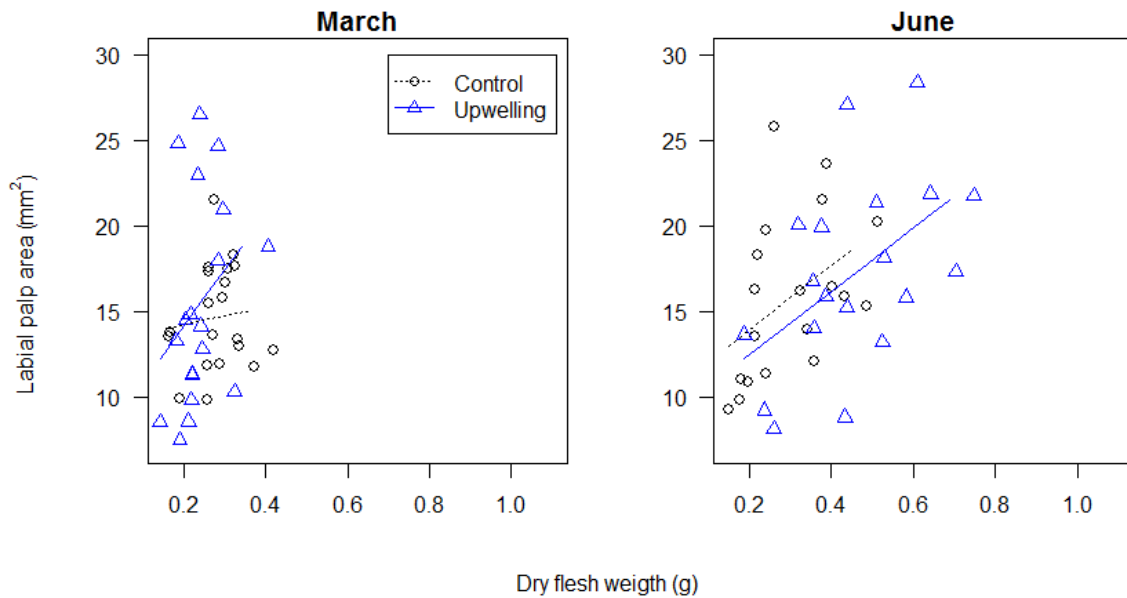


Figure 15: The relationship between labial palp area (mm²) and dry flesh weight (g) with a regression line for each of the sites (control and upwelling). There is one figure for each month (March and June).

October analysis

Figure 16 indicates similar gill area between the two sites, and an increase in gill area with increasing shell length. The statistics supported this with a highly significant relationship between the gill area and the shell length (lm, $R^2 = 0.71$, $F_{1, 63} = 151.52$, $p < 2.20 \cdot 10^{-16}$), but a lack of a significant difference in gill area between the two sites.

There was a positive relationship between the shell length and the labial palp area (lm, $R^2 = 0.41$, $F_{1, 63} = 38.535$, $p < 4.69 \cdot 10^{-08}$). The statistics confirmed an interaction between shell length and sites (lm, $F_{1,63} = 4.21$, $p = 0.044$), meaning that the effect of shell length on labial palp area depends on site. There was a difference in mean labial palp area between the two sites (lm, $t = 2.10$, $p = 0.040$). The lines have different slopes (lm, $t = -2.05$, $p = 0.044$), but both are positively correlated with shell length.

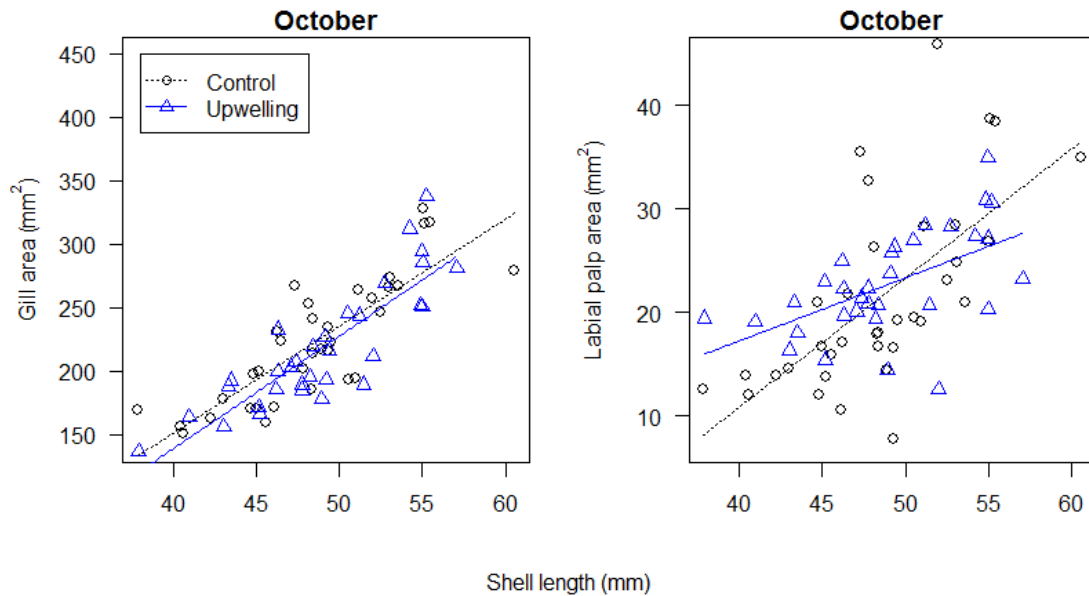


Figure 16: The relationship between labial palp area (mm^2) and the shell length (mm) with a regression line for each of the sites (control and upwelling) for October.

Figure 17 shows a positive relationship between dry flesh weight and gill area (lm , $R^2= 0.62$, $F_{1, 63}= 94.70$, $p= 3.59 \cdot 10^{-14}$). There was also an interaction between dry flesh weight and site (lm , $F_{1, 63}= 6.50$, $p= 0.013$). This means that the effect of dry flesh weight on gill area is site dependent. The upwelling site had a steeper line than the control site, indicating that gill area increased faster with increasing dry flesh weight compared to the control site. The statistics showed a difference in slope of the line (lm , $t= 2.55$, $p= 0.013$) and the two sites had different mean gill area (lm , $t= -2.28$, $p= 0.026$).

The dry flesh weight had a positive relationship with the labial palp area (lm , $R^2= 0.46$, $F_{1, 63}=49.76$, $p= 1.61 \cdot 10^{-09}$). There was no significant difference between sites (lm , $F_{1, 63}=2.69$, $p= 0.106$). Figure 17 shows a steeper incline at the control station, but there was no significant difference in the slope of line between the two sites.

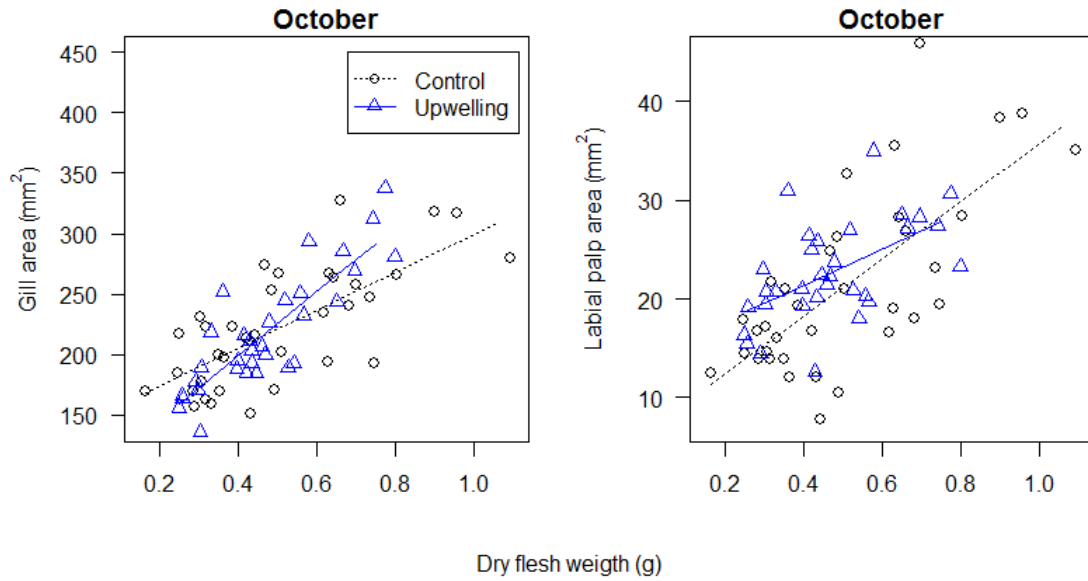


Figure 17: The relationship between gill area (mm^2) and dry flesh mass (g) in the left panel and the labial palp area (mm^2) and dry flesh weight (g) in the right panel, with a regression line for each of the sites (control and upwelling).

3.2.4 The relationship between gill area and labial palp area and the GA: PA ratio

March and June analysis

There was a positive correlation between the gill and labial palp areas (Fig. 18, lm , $R^2 = 0.35$, $F_{1, 69} = 16.29$, $p = 1.39 \cdot 10^{-4}$). The data also showed a difference between the two sampling dates (lm , $F_{1, 69} = 7.13$, $p = 0.009$). Figure 18 shows that the two lines in June had a steeper slope compared to those in March. This tells us that gill area increased quicker than the labial palp area in June. There was a significant interaction between the labial palp area and month (lm , $F_{1, 69} = 5.01$, $p = 0.028$), which means that the relationship between gills and labial palps were depended on the month. There was also a significant interaction between site and month (lm , $F_{1, 69} = 6.59$, $p = 0.012$), indicating an effect of site on gill area depended on the month. The difference in gill area between the two sites was not the same in March and June. There was a switch between the regression lines at the different site between March and June.

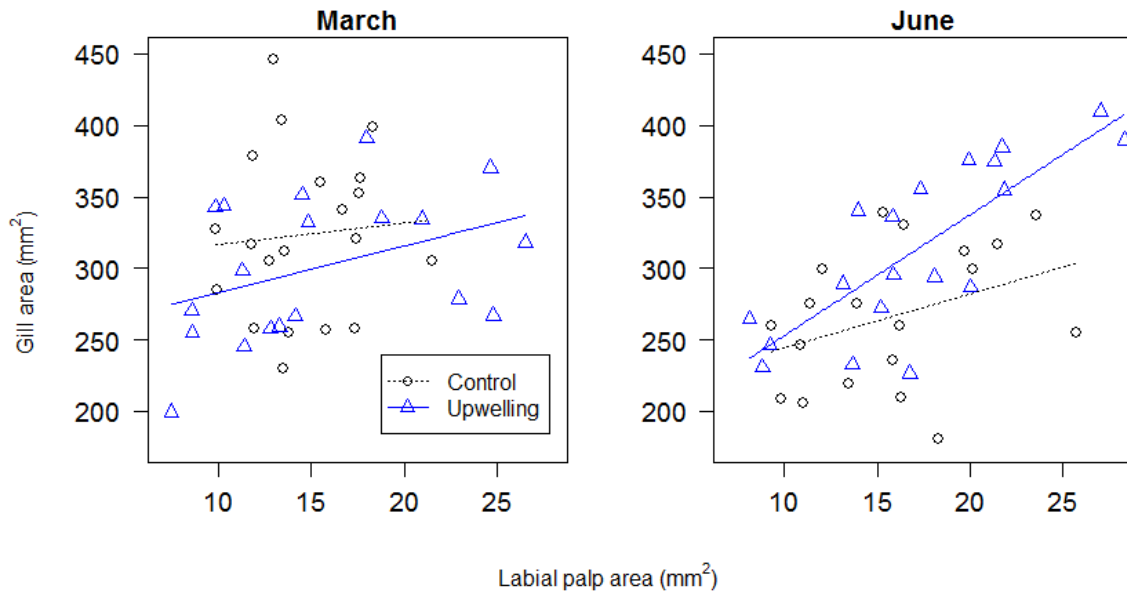


Figure 18: The relationship between the gill area and labial palp area with a regression line for each of the sites. There is one figure for each month (March, June).

The gill-to palp (GA: PA) ratio is the functional association of gills and palps in mussels. Shell length had no significant effect on the GA: PA ratio, but the ratio changed differently between March and June (lm , $R^2 = 0.21$, $F_{1, 69} = 8.56$, $p = 0.005$). Figure 19 shows that this ratio has a positive correlation with shell length both in March and June at the control site, and a negative correlation at the upwelling site. The statistics confirms an interaction between shell length and site (lm , $F_{1, 69} = 6.73$, $p = 0.012$). The upwelling site had a different mean compared to the control site in March (lm , $t = 2.09$, $p = 0.040$), but not in June. There was also a significant difference in slope of the lines between the control and upwelling site in March (lm , $t = -2.13$, $p = 0.037$). Note that the data in Figure 18 and 19 from March were scattered, and thus difficult to observe any clear pattern.

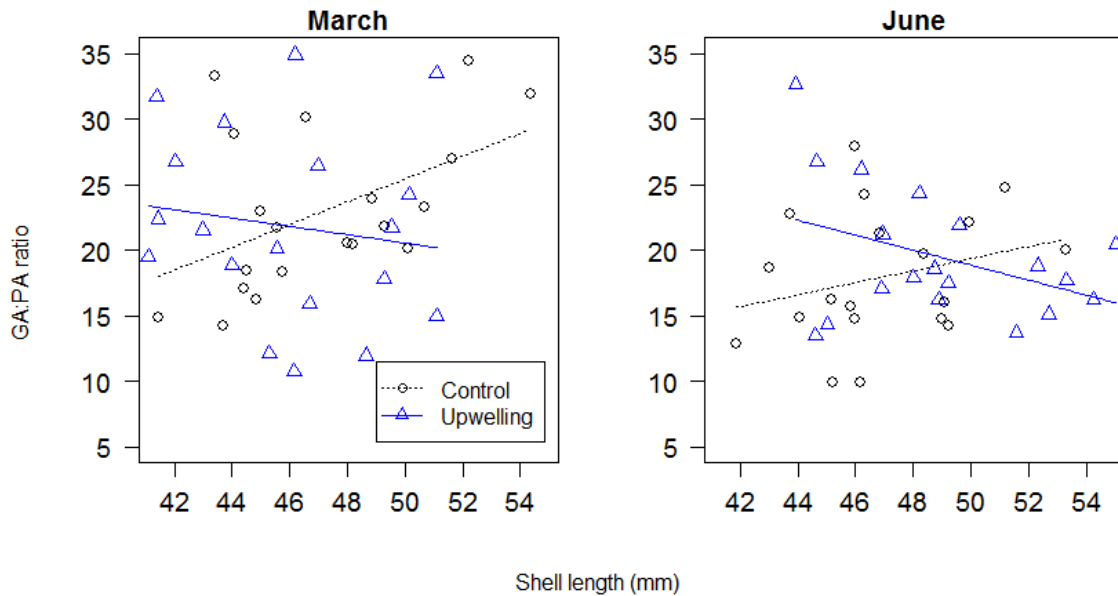


Figure 19: The relationship between GA: PA ratio and the shell length (mm) with a regression line for each of the sites. There is one figure for each month (March, June).

October analysis

There was a strong positive relationship between the gill area and labial palp area (Fig. 20, lm , $R^2 = 0.51$, $F_{1, 63} = 60.61$, $p = 8.47 \cdot 10^{-11}$). The labial palp area was not significantly related to the site (lm , $F_{1, 63} = 3.92$, $p = 0.052$). The gill area increased quicker than labial palp area at the upwelling site compared to the control site (Fig. 20). There was a significant difference between mean gill area at the control site compared to the upwelling site (lm , $t = -2.23$, $p = 0.029$).

The statistics show a significant difference between the two sites (lm , $R^2 = 0.14$, $F_{1, 63} = 5.39$, $p = 0.024$), which was not explained by changes in shell length. The GA: PA ratio in Figure 20 shows a negative correlation with shell length at the control site, while this relationship was slightly positive at the upwelling site, and the statistics confirms an significant difference in slope of the line between the two sites (lm , $t = 2.15$, $p = 0.036$). There was also a significant interaction between the two variables shell length and site (lm , $F_{1, 63} = 4.62$, $p = 0.036$), which means that the change in GA: PA ratio in relation to shell length is not the same between the two sites. The effect of shell length depended on the site. There was also a difference in mean GA: PA ratio between the upwelling and control site (lm , $t = -2.36$, $p = 0.021$).

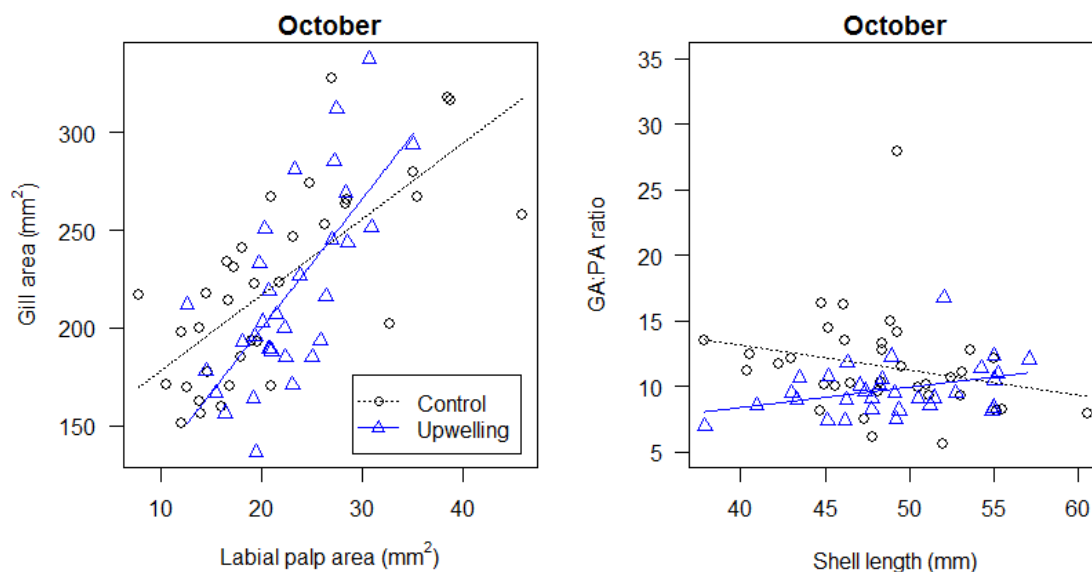


Figure 20: The left panel show the relationship between the gill area and labial palp area while the right panel illustrates the relationship between GA: PA ratio and the shell length (mm). There is a regression line for each of the sites (control and upwelling).

3.3 Testing the accuracy of the method

Except for two values all the measurement of the gill area had a standard deviation less than two percent of the reference value, (the other two values were 2.36 % and 6.40 %). The measurements of the labial palps showed a standard deviation less than ten percent of the reference value, except one that showed a value of 12.17 % (See Appendix I).

3.4 Regression of gill area and dry flesh weight in *Mytilus edulis*

Several studies have used a regression equation of gill area (GA , mm^2) against dry flesh weight (W , g) in the form $GA = a \cdot W^b$. Table 4 shows the regression of gill area and dry flesh weight with the a - and b -values from the October data. There is an interaction between dry flesh weigh and site, which means that the change in gill area against dry flesh weight is not the same between the control and upwelling site (Im , $F_{1, 63} = 4.40$, $p = 0.040$).

Table 4: Regressions of gill area (mm^2) and dry tissue weight (g) in the blue mussel (*M. edulis*) from mussels collected in October in Lysefjorden.

| Location | n | Gill area: dry flesh weight | Turbidity | Reference |
|---------------|----|-----------------------------|-----------|------------|
| Control | 32 | $2239W^{0.34}$ | Low | This study |
| Upwelling | 35 | $2630W^{0.54}$ | Low | This study |
| Combined data | 67 | $2344W^{0.41}$ | Low | This study |

4 Discussion

The comparison of gill- and labial palp areas demonstrated a difference in GA: PA ratio between the upwelling and the control sites in October. There was also an interaction between site and shell length in some of the analyses, which suggests that the response variable (labial palp area, GA: PA ratio) changed differently according to shell length between the two sites. A significant difference between gill area from live and frozen tissue samples were also detected, which made it difficult to compare the mussels sampled in March and June with the mussels collected in October. The measurements of gill area proved to be more accurate than the measurements of labial palp area.

4.1 Methodical issues

Differences in gill and labial palp area from frozen and live tissue samples

Since measurements of gill areas were significantly higher for frozen as opposed to live tissue, mussels sampled in March and June (frozen) could not be compared to the mussels sampled in October (live). If the live vs. frozen experiments (Austevoll cohort) had been conducted on the same group of mussels (the Lysefjorden cohort) it could be possible to correct for this difference with a scaling factor.

Most studies (Barillé et al. 2000; Dutertre et al. 2007; Dutertre et al. 2009; Honkoop et al. 2003; Jones et al. 1992; Kiorboe and Mohlenberg 1981) used live mussels while Theisen (1982) preserved the mussels in 4 % formalin and Essink et al. (1989) used 5 % formaldehyde to fixate the shells. To my knowledge no experiments have used frozen mussels.

There were advantages and disadvantages associated with both treatments. Frozen mussels were easier to transport from Lysefjorden to the research station at Austevoll. Live mussels, on the other hand, had to be stored in an environment that was different from Lysefjorden, which in combination with the transport is stressful for the mussels. Ideally the mussels should have been collected and processed at the same location, i.e. Lysefjorden.

Live mussels were kept in large holding tanks and transferred to a bucket that contained 10 L water and 0.5 g MgCl₂ solution. It was observed that many of the mussels were closed for a long time, leading to different exposure times of the sedative MgCl₂ solution. This may have

influenced the muscle tension, and thus the measured area of gills and labial palps. Most bivalves respond quickly to environmental changes (i.e. temperature and salinity) by closing the shell (Dame 2012). A small difference in temperature and salinity between the holding tanks and the bucket could have induced shell closure, thereby reducing effect of the $MgCl_2$ solution. An increase in temperature could also induce spawning in mussels (Dame 2012), which could lead to a reduction in dry flesh weight in the live mussels in October. A reduction in dry flesh weights possibly occurred in mussels from March and June due to the freezing process. However, based on visual observations these quantities most likely represent minor fractions of the dry flesh weight.

The frozen tissue was more fragile and the color of the labial palp was more transparent (Fig. 7, left panel) compared to live mussels. The outer boundary of the gill and labial palp was harder to delineate in the mussels that had been frozen, and this could have led to errors in the measurements.

Parts of the labial palp were hidden behind the gills and parts of it were often twisted. Consequently, the labial palp area was then slightly underestimated (Fig. 8). Parts of the gill are also sometimes hidden or curled up (Fig. 7, mid panel), which lead to underestimation of the gill area. Occasionally, both live and frozen gills had rifts (Fig. 7, right panel). If so, the gill underneath was used to define the area. This approach was based on the assumption that gills and labial palps were equally sized within individuals. This assumption has not been verified within the literature.

In order to improve the experimental design, ideally, the three groups of mussels should have undergone the same treatment, i.e. frozen or live. Overall there were more disadvantages using frozen mussels compared live mussels. Therefore using live mussels is recommended in future studies.

Seston quantity at the upwelling and control station

The results presented in this thesis are based on large scale *in situ* experiments where environmental settings cannot be controlled in the same way as in a laboratory. Factors such as wind, tides and freshwater runoff influence the environmental conditions at the upwelling and the control sites. The mean annual concentration of estimated chlorophyll *a* was

significantly higher at the upwelling site in 2011, but differed less compared to 2010 (Strohmeier et al. in prep.). The absence of significant difference in PV, POC and SPM may affect the results.

4.2 Effect of seston quantity on gills and labial palps

Most studies that have established a relationship between changes in gill and labial palp areas were performed in areas with higher seston quantities compared to those in this study. In the study of variation in pallial organs in *C. gigas*, the site Bourgneuf Bay showed an annual range in mean SPM of 24.1-630.4 g/m³ (Dutertre et al. 2007; Dutertre et al. 2009). The closest study area in relation to SPM concentration was Essink et al. (1989), which looked at variations in relative gill and labial palp size in the Dutch Wadden sea (mean SPM larger than 25 g/m³) and in the North Sea (mean SPM 4 g/m³) and Theisen (1982) that used the same study area. Barillé et al. (2000) studied variation in gill and labial palp area between two sites located 15 km apart in the same bay. The annual mean SPM concentration between the sites in this bay was 154 g/m³ and 34 g/m³. In contrast the annual mean seston concentrations in Lysefjorden were 2.5 g/m³ at the control site and 3.3 g/m³ at the upwelling site, yet no significant difference in SPM concentration was detected between the two sites in 2011.

Several studies have found that gill area is proportional to filtration rate (clearance rate) (Jones et al. 1992; Meyhofer 1985; Pouvreau et al. 1999). Strohmeier et al. (2009) found that the blue mussel had higher clearance rate in low seston environments, which could possibly correspond to large gills. Previous findings demonstrated flexibility in the size of gills and palps to natural turbidity and indicate smaller gills and larger labial palps at turbid sites (Barillé et al. 2000; Essink et al. 1989; Theisen 1982). The high nutritional quality of the seston diet appears to be a critical factor explaining the high feeding rates observed at low seston concentrations (Strohmeier et al. 2009).

Gill area was positively correlated with shell length in March, June and October, but the gill area in June was smaller relative to shell length, compared to March (Fig. 12), and a significant effect of month on gill area supports these findings ($p < 2.19 \cdot 10^{-05}$). The small increase in chlorophyll *a* level from March to June may have possibly influenced the change in gill area between these two dates. Essink et al. (1989) showed that mussels relocated

between the North Sea (low turbidity) and Wadden Sea (high turbidity) effected the size of the feeding apparatus within four months when exposed to different SPM concentrations. However, since there was no difference between the two sites the influence must have occurred at both the sites from March to June. The increase in food concentration may have led to a decreased gill area, according to previous findings in the flexibility in the gill size (Barillé et al. 2000; Dutertre et al. 2007; Dutertre et al. 2009; Essink et al. 1989; Honkoop et al. 2003; Kiorboe and Mohlenberg 1981; Payne et al. 1995; Theisen 1982). No evidence was found for different gill areas between the two sites in October. As mentioned before, this group of mussels could not be compared to mussels from March and June, because two samples were frozen and the other was live.

Jones et al. (1992) found that gill area varied closely with shell length and dry flesh weight. In this study there were also positive relationships between these variables, both in the March/June analysis and in the October analysis. Gill area increased faster with dry flesh weight at the upwelling site compared to the control site in October. This may be the development of a stronger difference in gill area related to dry flesh weight between the two sites. There was also a positive relationship between labial palp area and dry flesh weight; however, it appears that shell length is a better indicator for gill area than dry flesh mass. This seems reasonable because dry flesh mass shows large short term fluctuations during the reproductive cycle and negative growth during winter starvation (Rosland et al. 2009; Strohmeier et al. in prep.).

The labial palp area changed differently with shell length between the two sites on all sampling dates. The mean labial palp area and the slope of the line were significantly different between the two sampling sites in March and October, but the site alone could not explain any differences in labial palp area in this experiment. The result from October shows a positive relationship between labial palp areas and shell length within sites (Fig. 12), where the lines for upwelling and control cross each other at a shell length of ca. 50 mm. The palps were larger for small sized mussels at the upwelling site, but smaller in larger sized mussels, compared to the control station. Thus, palp size increased faster with shell length at the control site in October as opposed to March and June when palps increased faster with length at the upwelling site. In the Pacific oyster *C. gigas* the labial palp area was closely and positively correlated to the turbidity gradient, while there was no clear pattern between the

gill area and the gradient of suspended particulate matter (Dutertre et al. 2007). The palp area was significantly smaller and larger at low and high turbid sites, respectively (Dutertre et al. 2009).

Kiorboe and Mohlenberg (1981) investigated the functional consequence of variable palp size in different turbid environments. They observed higher selection efficiency in *M. edulis* with larger palps. There were no clear differences in seston levels between the two sampling sites in Lysefjorden. This may be one of the reasons for not having observed any significant differences in labial palp area that was only explained by site. However, there is a difference in labial palp area when shell length was included, and in October it appeared that the labial palp area increased faster and were larger according to shell length at the control site compared to the upwelling site. Equally to the gill area, the shell length seemed to be a better indicator for labial palp area than the dry flesh mass. In general, the labial palps plots are more scattered than gill area plots. This is probably due to the accuracy of the method, as it was easier to measure the gill area compared to the labial palp area. On the other hand, the labial palps were much smaller compared to the gills, which make any measurement error relatively larger.

In the relationship between gill area and labial palp area in March and June (Fig. 18) there appeared to be a switch in the lines between the two sites. The gill area changed differently related to labial palp area between the two sites in March and June. It is uncertain why this switch occurred, but there was no significant difference between sites in the analysis. However, this difference was much clearer in this plot compared to the switch in gill area and length (Fig. 12). Different chlorophyll *a* concentrations may have influenced the mussels differently in March and June between the two sites. This is probably why there was a significant difference between the two months, as well as an interaction between site and month. The gill area increased more with the labial palp area at the upwelling site compared to the control site in October (Fig. 20), and there was a tendency of different slopes of the line. This may indicate the beginning of a difference in gill and labial palp area development between the two sites.

Adaption over the full growth season of gill and labial palp area to the ambient seston quantity was hard to detect due to the fact that mussels sampled in March and June could

not be compared to those collected in October. The similarity in seston quantities between the two sites is the likely explanation for the lack of a clear difference in gill and labial palp area between the two sites.

4.3 Compare gill area vs. dry flesh weight in *M. edulis* with other studies

There are several studies with data on relationship between gill area (GA , mm^2) and dry flesh weight (W , g), which are given in the form $GA=aW^b$, (Jones et al. 1992; Meyhofer 1985; Mohlenberg and Riisgard 1979; Pouvreau et al. 1999), where a and b are constants. A comparison of gill area and dry flesh weight for *M. edulis* from different studies are presented in Table 5. The table shows a regression equation of gill area against dry flesh weight. This was a comparison of the data from October together with two other studies on *M. edulis*.

Table 5: Comparisons between regressions of gill area (mm^2) and dry tissue weight (g) in the blue mussel (*M. edulis*).

| Location | n | Gill area: dry flesh weight | Turbidity | Reference |
|----------------------|-----|-----------------------------|-----------|------------------------------|
| Laboratory, Denmark | 28 | $2458W^{0.66}$ | Low | Møhlenberg and Riisgård 1979 |
| Lytham, England | 101 | $1862W^{0.69}$ | - | Jones et al. 1992 |
| Millport, Scotland | 47 | $2692W^{0.69}$ | - | Jones et al. 1992 |
| Conwy, England | 21 | $2188W^{0.49}$ | - | Jones et al. 1992 |
| Combined data | 169 | $1820W^{0.61}$ | - | Jones et al. 1992 |
| Control | 32 | $2239W^{0.34}$ | Low | This study |
| Upwelling | 35 | $2630W^{0.54}$ | Low | This study |
| Combined data | 67 | $2344W^{0.41}$ | Low | This study |

When comparing the result from this thesis with two other studies performed on blue mussels (Jones et al. 1992; Mohlenberg and Riisgard 1979) the b -value from the control site was lower than the other measurements (Table 5). Earlier studies show that the b -value ranged from 0.38 to 0.94 between different species of bivalves (Hawkins et al. 1990; Jones et al. 1992; Pouvreau et al. 1999). The b -value at the control site was 0.34 and was close to the lowest value reported earlier. At higher seston concentrations we would expect a smaller b -value, according to findings about smaller gills and larger labial palps (Essink et al. 1989), and the opposite in low seston environments.

In the combined data from Lysefjorden, the a -value was higher than the combined data in Jones et al. (1992), and lower than the Mohlenberg and Riisgard (1979) study (Table 5). Compared to the two other studies, the b value was much smaller in this study. This relationship between the different regression equations is shown in Figure 21 (left panel).

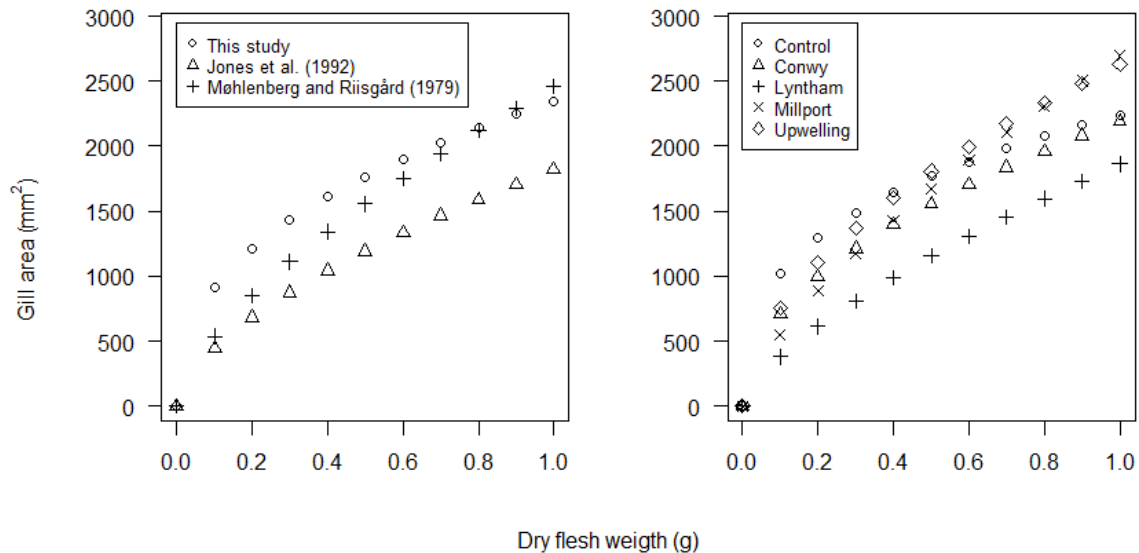


Figure 21: The left panel compare the results from this study with the combined data in the study of Jones et al. (1992) and the study performed by Møhlenberg and Riisgård in 1979. In the right panel the results from the two sites in this study are compared to the findings in Jones et al. (1992).

When comparing data from different sites (Fig. 21, right panel) it appears that the upwelling site in this study was more similar to Millport, while the control site was more similar to the mussels collected at Conwy. Mussels collected in Millport and at the upwelling site had a similar a -value. The control site had a larger a -value compared to both Lyntham and Conwy. At low dry flesh weight, mussels from the control site had the largest gill area, while at high dry flesh weight; mussels from Millport and the upwelling site had the largest gill area. Lyntham and Millport had the same b -value, but the largest difference in a -value. Lyntham have smallest gills according to dry flesh weight.

When comparing all the studies the a -value at the control site was lower than the value from the laboratory experiment performed by Mohlenberg and Riisgard (1979), the upwelling site also had a higher a -value. The a -value from the upwelling site is very similar to that of Millport, Scotland (Jones et al. 1992). In comparison, the control site was more similar to the two sites in England. There was no information about the turbidity level in Jones et al.

(1992), while the laboratory experiment in Mohlenberg and Riisgard (1979) and this study were conducted in environments with low turbidity.

The differences in a - and b -values between the upwelling and control site, and in the other studies, could be due to seasonal differences in weight and/or different turbidities. Only data from October was used in this comparison. If mussels from March, June and October had the same treatment (live/frozen), there could have been a comparison between the sampling dates to see if the a - and b -values changed over time.

4.4 Gill-to-palp ratio

Figure 19 shows that the gill-to-palp (GA: PA) ratio was positively correlated with shell length at the control site, while it was negatively correlated at the upwelling site in March and June. In October this switched; the upwelling site was positively correlated, and control was negatively correlated. The development in GA: PA ratio in March and June was as expected according to previous studies (Dutertre et al. 2009), where the GA: PA ratio decreases with increasing turbidity. In April to June there was an increasing amount of estimated chlorophyll a at the upwelling site, which may have influenced the GA: PA ratio in this direction in March and June. In October the opposite occurred, but this could probably not be explained by the estimated chlorophyll a levels since these were more similar between the sites from July to October. The data from March and June were more scattered and without any clear pattern compared to those in October. In October there was a significant difference in GA: PA ratio between the two sites while the difference between sites was related to shell length in March and June. In contrast to the difference in GA: PA ratio between sites there was no difference in gill or palp areas in October. The GA: PA ratio enhances possible differences that were not significant when gill and labial palp areas were evaluated separately. Perhaps this indicates that differences were in development, but also that the difference in seston quantity was not detectable in gill and labial palp areas separately. There was an interaction between shell length and site, which means that the labial palp area changes differently with shell length between the two sites in October. This suggests that the labial palp area is more important than gill area in the explanation of difference in the ratio in October.

Dutertre et al. (2009) found that in the Pacific oyster, *C. gigas*, the gill-to-palp ratio decreased with increasing turbidity. In this study the October-mussels from the control site had a higher mean GA: PA ratio compared to the mean ratio at the upwelling site. Payne et al. (1995) investigated several freshwater bivalve species, and they found that the palp to gill area ratio (PA: GA) was higher in populations from sites with high versus low suspended solids concentrations.

The SPM concentration was relatively similar between the two sites during 2011, while the mean temperature was higher at the control site. Since the SPM concentrations were similar during the year, there were probably other factors that had influenced the mussels to develop different GA: PA ratio between the two sites in October. There could also be individual differences in mussels between the two sites, even if they were taken from the same cohort. This difference in GA: PA ratio could have been a result of collecting food with optimal efficiency, even if the seston concentration did not show any significant differences.

4.5 Concluding remarks

Gill and labial palp areas were closely and positively related to shell length and dry flesh weight, but no significant differences between sites in these areas were detected. However, there were tendencies in the data supporting that differences in gill and labial palp areas may have been significant if there were slightly larger differences in food concentration. Based on a comparison between data from this study and the literature, it may have been the small difference in food concentration that causes the lack of significant difference in gill and labial palp areas between sites in this study.

The regression of gill area (GA) against dry flesh weight (W) in the form $GA=a \cdot W^b$ provided smaller b -value at the control site compared to other studies, while the a -value was more similar. A significant difference in the regression lines between the two sites was found. This combined with the labial palp area, which changed differently with shell length between sites, and differences in gill area between March and June suggests flexibility in the foraging apparatus. It is important to keep in mind that it was not the same individuals that were measured each sampling date and that individual differences probably have affected the result.

Gill areas measured from samples that were frozen were significantly higher compared to live tissue, which influenced the possibility to conduct a time-series study. Furthermore, a study to clarify whether all four labial palps and the gills in a mussel have the same size or not is needed.

The significant difference in gill-to-palp ratio between the sites in October was probably related to variations in labial palp area. This variation may have been influenced by the significant difference in estimated chlorophyll *a* concentration during the year.

In further studies I suggest to determine gill and labial palp areas at increasing food quantities to determine the quantity needed to induce morphological changes in the foraging apparatus. Analyses to determine how fast changes in gill and labial palp areas could occur will also be valuable.

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Appendices

Appendix I – Testing the accuracy in the method with standard deviation

To test the accuracy of the measuring of gill and labial palp areas, the drawing process was repeated three times for the same picture. If there were several pictures from the same gill and labial palps, but from different angles, the same procedure was performed. Same individual are therefore listed several times. Standard deviation (SD) was used to statistically test the accuracy of the method. Standard deviation (SD) is represented as percentage difference from the mean.

The gill area

| Live mussels 17.08.11 | | | | | |
|-----------------------|--|-----------------|-----------------|---------------|------|
| Individual | Measured gill area (GA) (mm ²) | | | Mean GA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 280.54 | 278.75 | 281.97 | 280.42 ± 1.32 | 0.47 |
| 2 | 470.15 | 478.92 | 481.29 | 476.79 ± 4.79 | 1.01 |
| 3 | 275.74 | 273.64 | 276.73 | 275.37 ± 1.29 | 0.47 |
| 3 | 270.65 | 273.86 | 272.90 | 272.47 ± 1.35 | 0.49 |
| 4 | 402.80 | 418.56 | 409.17 | 410.18 ± 6.48 | 1.58 |
| 5 | 243.79 | 246.03 | 247.49 | 245.77 ± 1.52 | 0.62 |
| 6 | 358.74 | 358.72 | 357.62 | 358.36 ± 0.52 | 0.15 |
| 7 | 364.13 | 365.18 | 370.73 | 366.68 ± 2.90 | 0.79 |
| 8 | 467.70 | 480.86 | 466.85 | 471.80 ± 6.42 | 1.36 |
| 9 | 276.61 | 275.79 | 275.23 | 275.88 ± 0.57 | 0.21 |
| 10 | 340.06 | 333.65 | 337.68 | 337.13 ± 2.65 | 0.78 |
| 11 | 298.58 | 304.61 | 301.89 | 301.69 ± 2.46 | 0.82 |
| 13 | 353.57 | 339.05 | 346.14 | 346.25 ± 5.93 | 1.71 |
| 14 | 349.72 | 349.04 | 346.11 | 348.29 ± 1.57 | 0.45 |
| 15 | 467.59 | 475.81 | 477.16 | 473.52 ± 4.23 | 0.89 |

| Live mussels that have been frozen after dissection and taken new pictures of 30.08.11 | | | | | |
|--|--|-----------------|-----------------|---------------|------|
| Individual | Measured gill area (GA) (mm ²) | | | Mean GA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 289.93 | 292.02 | 289.70 | 290.55 ± 1.04 | 0.36 |
| 2 | 533.24 | 537.54 | 535.55 | 535.44 ± 1.76 | 0.33 |
| 3 | 357.80 | 362.51 | 356.00 | 358.77 ± 2.75 | 0.77 |
| 5 | 248.75 | 251.67 | 254.40 | 251.61 ± 2.31 | 0.92 |
| 6 | 323.65 | 323.44 | 316.21 | 321.10 ± 3.46 | 1.08 |
| 7 | 419.08 | 419.47 | 422.58 | 420.38 ± 1.57 | 0.37 |
| 8 | 524.31 | 507.68 | 515.11 | 515.70 ± 6.80 | 1.32 |
| 9 | 268.16 | 274.86 | 277.84 | 273.62 ± 4.05 | 1.48 |
| 10 | 356.35 | 359.02 | 355.74 | 357.04 ± 1.42 | 0.40 |

| | | | | | |
|----|--------|--------|--------|---------------|------|
| 11 | 363.59 | 369.23 | 369.23 | 367.35 ± 2.66 | 0.72 |
| 12 | 372.93 | 367.96 | 374.59 | 371.82 ± 2.82 | 0.76 |
| 13 | 321.55 | 334.62 | 340.22 | 332.13 ± 7.82 | 2.36 |
| 14 | 355.31 | 344.51 | 351.67 | 350.49 ± 4.49 | 1.28 |
| 15 | 425.27 | 429.51 | 433.52 | 429.43 ± 3.37 | 0.78 |

| Frozen mussels 05.09.11 | | | | | |
|--------------------------------|--|-----------------|-----------------|---------------|------|
| Individual | Measured gill area (GA) (mm ²) | | | Mean GA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 539.34 | 541.99 | 552.81 | 544.71 ± 5.82 | 1.07 |
| 2 | 585.56 | 582.35 | 580.85 | 582.92 ± 1.96 | 0.34 |
| 3 | 641.33 | 631.71 | 640.05 | 637.70 ± 4.27 | 0.67 |
| 4 | 674.18 | 677.90 | 656.76 | 669.61 ± 9.22 | 1.38 |
| 5 | 570.65 | 573.91 | 572.43 | 572.33 ± 1.33 | 0.23 |
| 6 | 482.26 | 496.22 | 492.39 | 490.29 ± 5.89 | 1.20 |
| 7 | 508.20 | 518.03 | 509.84 | 512.02 ± 4.30 | 0.84 |
| 8 | 538.38 | 539.04 | 540.00 | 539.14 ± 0.67 | 0.12 |
| 9 | 349.76 | 362.45 | 355.98 | 356.07 ± 5.18 | 1.45 |
| 10 | 447.89 | 461.69 | 469.86 | 459.82 ± 9.07 | 1.97 |
| 11 | 472.97 | 470.41 | 482.21 | 475.20 ± 5.07 | 1.07 |
| 12 | 456.45 | 458.92 | 469.57 | 461.65 ± 5.69 | 1.23 |
| 13 | 372.19 | 365.78 | 366.85 | 368.27 ± 2.81 | 0.76 |
| 14 | 420.97 | 434.59 | 436.22 | 430.59 ± 6.84 | 1.59 |

| Live mussels 25.01.12 | | | | | |
|------------------------------|--|-----------------|-----------------|---------------|------|
| Individual | Measured gill area (GA) (mm ²) | | | Mean GA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 275.14 | 275.00 | 275.14 | 275.09 ± 0.07 | 0.02 |
| 2 | 263.54 | 260.44 | 260.66 | 261.54 ± 1.41 | 0.54 |
| 2 | 262.09 | 266.67 | 263.74 | 264.16 ± 1.89 | 0.72 |
| 3 | 432.28 | 428.63 | 436.52 | 432.47 ± 3.22 | 0.75 |
| 4 | 235.36 | 240.00 | 240.00 | 238.45 ± 2.19 | 0.92 |
| 5 | 304.97 | 303.31 | 305.00 | 304.43 ± 0.79 | 0.26 |
| 6 | 232.42 | 234.07 | 237.02 | 234.50 ± 1.90 | 0.81 |
| 7 | 304.97 | 296.70 | 304.97 | 302.22 ± 3.90 | 1.29 |
| 8 | 256.22 | 260.87 | 260.87 | 259.32 ± 2.19 | 0.85 |
| 9 | 278.57 | 275.27 | 284.75 | 279.53 ± 3.93 | 1.40 |
| 11 | 365.73 | 369.10 | 367.42 | 367.42 ± 1.38 | 0.37 |
| 12 | 418.03 | 417.03 | 413.51 | 416.19 ± 1.94 | 0.47 |
| 13 | 337.30 | 340.98 | 335.68 | 337.99 ± 2.22 | 0.66 |
| 14 | 363.35 | 357.98 | 360.48 | 360.60 ± 2.19 | 0.61 |
| 15 | 313.33 | 321.91 | 320.22 | 318.49 ± 3.71 | 1.16 |
| 16 | 280.11 | 279.89 | 283.33 | 281.11 ± 1.57 | 0.56 |
| 17 | 178.69 | 181.67 | 180.33 | 180.23 ± 1.22 | 0.68 |
| 18 | 207.09 | 206.85 | 209.67 | 207.87 ± 1.27 | 0.61 |
| 20 | 334.43 | 336.07 | 330.81 | 333.77 ± 2.20 | 0.66 |

| | | | | | |
|----|--------|--------|--------|---------------|------|
| 21 | 311.29 | 311.29 | 311.29 | 311.29 ± 0.00 | - |
| 22 | 482.20 | 480.63 | 479.69 | 480.84 ± 1.04 | 0.22 |
| 23 | 173.08 | 177.05 | 180.33 | 176.82 ± 2.96 | 1.68 |
| 24 | 193.44 | 201.12 | 197.24 | 197.27 ± 3.13 | 1.59 |

| Frozen mussels 14.02.12 | | | | | |
|-------------------------|--|-----------------|-----------------|---------------|------|
| Individual | Measured gill area (GA) (mm ²) | | | Mean GA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 562.11 | 556.02 | 551.56 | 556.56 ± 4.32 | 0.78 |
| 2 | 485.71 | 498.39 | 480.00 | 488.03 ± 7.68 | 1.57 |
| 3 | 436.07 | 433.52 | 434.43 | 434.67 ± 1.05 | 0.24 |
| 4 | 484.24 | 477.05 | 487.29 | 482.86 ± 4.29 | 0.89 |
| 4 | 458.82 | 450.00 | 448.44 | 452.42 ± 4.57 | 1.01 |
| 5 | 396.07 | 394.38 | 400.00 | 396.82 ± 2.35 | 0.59 |
| 6 | 436.81 | 443.33 | 447.49 | 442.54 ± 4.39 | 0.99 |
| 7 | 331.67 | 333.33 | 335.20 | 333.40 ± 1.44 | 0.43 |
| 8 | 403.23 | 398.94 | 402.67 | 401.61 ± 1.91 | 0.47 |
| 9 | 354.24 | 361.02 | 357.30 | 357.52 ± 2.77 | 0.78 |
| 10 | 265.00 | 271.19 | 272.73 | 269.64 ± 3.34 | 1.24 |
| 11 | 531.67 | 530.77 | 532.42 | 531.62 ± 0.67 | 0.13 |
| 12 | 498.95 | 504.19 | 503.68 | 502.27 ± 2.36 | 0.47 |
| 13 | 555.25 | 555.00 | 550.28 | 553.51 ± 2.29 | 0.41 |
| 14 | 439.23 | 433.52 | 437.57 | 436.77 ± 2.40 | 0.55 |
| 15 | 444.32 | 451.61 | 454.05 | 450.00 ± 4.13 | 0.92 |
| 16 | 689.53 | 693.55 | 687.30 | 690.13 ± 2.59 | 0.37 |
| 17 | 488.52 | 490.76 | 488.52 | 489.27 ± 1.05 | 0.22 |
| 18 | 583.24 | 576.80 | 570.33 | 576.79 ± 5.27 | 0.91 |
| 19 | 434.25 | 444.94 | 442.37 | 440.52 ± 4.56 | 1.03 |
| 20 | 552.46 | 547.54 | 546.20 | 548.73 ± 2.69 | 0.49 |
| 21 | 356.15 | 360.33 | 358.06 | 358.18 ± 1.71 | 0.48 |
| 22 | 543.96 | 551.93 | 551.93 | 549.27 ± 3.76 | 0.68 |
| 23 | 531.67 | 533.33 | 530.00 | 531.67 ± 1.36 | 0.26 |
| 24 | 572.87 | 568.25 | 573.02 | 571.38 ± 2.21 | 0.39 |
| 25 | 741.76 | 745.90 | 733.70 | 740.45 ± 5.07 | 0.68 |

The labial palp area

| Live mussels 17.08.11 | | | | | |
|------------------------------|---|-----------------|-----------------|--------------|------|
| Individual | Measured labial palp area (PA) (mm ²) | | | Mean PA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 17.37 | 17.38 | 17.89 | 17.55 ± 0.24 | 1.38 |
| 2 | 23.57 | 22.99 | 22.59 | 23.05 ± 0.40 | 1.75 |
| 3 | 17.83 | 17.37 | 18.05 | 17.75 ± 0.28 | 1.59 |
| 3 | 18.45 | 17.69 | 18.99 | 18.38 ± 0.53 | 2.91 |
| 4 | 27.38 | 30.59 | 31.97 | 29.98 ± 1.92 | 6.41 |
| 5 | 15.29 | 14.36 | 15.60 | 15.09 ± 0.53 | 3.50 |
| 6 | 18.75 | 21.03 | 22.09 | 20.62 ± 1.39 | 6.75 |
| 7 | 26.49 | 27.15 | 27.10 | 26.91 ± 0.30 | 1.12 |
| 7 | 24.55 | 24.23 | 24.78 | 24.52 ± 0.22 | 0.91 |
| 8 | 47.77 | 43.61 | 42.08 | 44.49 ± 2.40 | 5.40 |
| 10 | 24.41 | 23.83 | 24.55 | 24.26 ± 0.31 | 1.28 |
| 11 | 21.07 | 21.00 | 21.30 | 21.12 ± 0.13 | 0.61 |
| 13 | 12.36 | 12.71 | 13.22 | 12.76 ± 0.36 | 2.79 |
| 14 | 22.84 | 22.10 | 21.13 | 22.02 ± 0.70 | 3.18 |
| 15 | 34.35 | 35.29 | 35.97 | 35.20 ± 0.67 | 1.89 |

| Live mussels that have been frozen after dissection and taken new pictures of 30.08.11 | | | | | |
|---|---|-----------------|-----------------|--------------|------|
| Individual | Measured labial palp area (PA) (mm ²) | | | Mean PA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 16.66 | 16.57 | 15.77 | 16.33 ± 0.40 | 2.45 |
| 1 | 19.42 | 18.42 | 18.21 | 18.68 ± 0.53 | 2.81 |
| 2 | 30.31 | 27.72 | 26.89 | 28.31 ± 1.46 | 5.16 |
| 3 | 19.10 | 20.46 | 20.76 | 20.11 ± 0.72 | 3.58 |
| 5 | 15.70 | 13.03 | 13.68 | 14.14 ± 1.14 | 8.03 |
| 6 | 25.11 | 23.84 | 24.31 | 24.42 ± 0.53 | 2.16 |
| 7 | 25.22 | 23.59 | 25.42 | 24.74 ± 0.82 | 3.31 |
| 8 | 36.63 | 36.29 | 38.29 | 37.07 ± 0.88 | 2.36 |
| 9 | 22.17 | 22.32 | 25.14 | 23.21 ± 1.37 | 5.89 |
| 10 | 24.94 | 26.38 | 25.32 | 25.55 ± 0.61 | 2.40 |
| 11 | 18.81 | 18.45 | 21.74 | 19.67 ± 1.47 | 7.48 |
| 12 | 29.47 | 29.44 | 30.04 | 29.65 ± 0.28 | 0.93 |
| 13 | 13.93 | 12.11 | 11.43 | 12.49 ± 1.06 | 8.46 |
| 14 | 23.14 | 22.22 | 22.13 | 22.50 ± 0.46 | 2.03 |
| 15 | 31.11 | 31.51 | 31.64 | 31.42 ± 0.23 | 0.72 |

| Frozen mussels 05.09.11 | | | | | |
|-------------------------|---|-----------------|-----------------|--------------|-------|
| Individual | Measured labial palp area (PA) (mm ²) | | | Mean PA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 47.82 | 41.84 | 37.56 | 42.41 ± 4.21 | 9.92 |
| 2 | 23.16 | 22.49 | 21.20 | 22.28 ± 0.82 | 3.66 |
| 3 | 31.12 | 28.22 | 33.06 | 30.80 ± 1.99 | 6.45 |
| 4 | 60.25 | 60.01 | 50.62 | 56.96 ± 4.49 | 7.87 |
| 4 | 64.26 | 64.16 | 60.59 | 63.00 ± 1.71 | 2.71 |
| 5 | 37.00 | 31.92 | 36.74 | 35.22 ± 2.34 | 6.64 |
| 6 | 30.19 | 30.65 | 30.87 | 30.57 ± 0.29 | 0.93 |
| 7 | 40.37 | 38.65 | 37.60 | 38.87 ± 1.14 | 2.94 |
| 8 | 21.53 | 20.76 | 21.94 | 21.41 ± 0.49 | 2.28 |
| 9 | 14.81 | 13.81 | 13.61 | 14.07 ± 0.52 | 3.73 |
| 10 | 20.56 | 22.73 | 21.43 | 21.57 ± 0.89 | 4.13 |
| 11 | 17.69 | 15.77 | 13.09 | 15.52 ± 1.89 | 12.17 |
| 12 | 16.83 | 18.17 | 17.29 | 17.43 ± 0.56 | 3.19 |
| 13 | 20.66 | 21.97 | 23.48 | 22.03 ± 1.15 | 5.23 |
| 14 | 20.34 | 18.95 | 19.03 | 19.44 ± 0.63 | 3.26 |

| Live mussels 25.01.12 | | | | | |
|-----------------------|---|-----------------|-----------------|--------------|------|
| Individual | Measured labial palp area (PA) (mm ²) | | | Mean PA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 13.20 | 14.15 | 13.38 | 13.57 ± 0.41 | 3.03 |
| 2 | 30.24 | 30.51 | 29.68 | 30.14 ± 0.35 | 1.15 |
| 2 | 30.78 | 29.51 | 31.83 | 30.71 ± 0.95 | 3.09 |
| 3 | 38.36 | 37.88 | 37.81 | 38.02 ± 0.24 | 0.64 |
| 4 | 17.31 | 16.98 | 16.32 | 16.87 ± 0.41 | 2.44 |
| 4 | 17.38 | 17.92 | 17.73 | 17.68 ± 0.22 | 1.26 |
| 5 | 22.76 | 21.27 | 21.18 | 21.73 ± 0.72 | 3.33 |
| 6 | 24.34 | 23.36 | 23.82 | 23.84 ± 0.40 | 1.68 |
| 7 | 23.37 | 24.61 | 24.77 | 24.25 ± 0.63 | 2.59 |
| 8 | 20.24 | 19.66 | 19.48 | 19.79 ± 0.33 | 1.65 |
| 8 | 19.94 | 19.53 | 19.68 | 19.71 ± 0.17 | 0.87 |
| 9 | 24.60 | 23.79 | 24.80 | 24.39 ± 0.44 | 1.79 |
| 11 | 30.88 | 30.05 | 30.21 | 30.38 ± 0.36 | 1.18 |
| 12 | 34.53 | 35.72 | 35.96 | 35.40 ± 0.62 | 1.76 |
| 13 | 19.37 | 20.86 | 19.22 | 19.82 ± 0.74 | 3.73 |
| 14 | 22.61 | 22.20 | 24.18 | 23.00 ± 0.85 | 3.71 |
| 15 | 25.30 | 26.59 | 25.90 | 25.93 ± 0.53 | 2.03 |
| 16 | 23.35 | 23.40 | 23.41 | 23.38 ± 0.02 | 0.11 |
| 17 | 16.52 | 16.04 | 15.72 | 16.09 ± 0.33 | 2.03 |
| 18 | 14.56 | 15.80 | 14.07 | 14.81 ± 0.73 | 4.90 |
| 20 | 25.35 | 25.22 | 24.58 | 25.05 ± 0.34 | 1.35 |
| 21 | 28.46 | 28.47 | 28.07 | 28.33 ± 0.19 | 0.66 |
| 22 | 29.72 | 29.94 | 31.80 | 30.49 ± 0.93 | 3.07 |
| 23 | 21.84 | 22.19 | 21.19 | 21.74 ± 0.42 | 1.92 |
| 24 | 12.14 | 12.28 | 12.62 | 12.35 ± 0.20 | 1.61 |

| Frozen mussels 14.02.12 | | | | | |
|-------------------------|---|-----------------|-----------------|--------------|------|
| Individual | Measured labial palp area (PA) (mm ²) | | | Mean PA±SD | % SD |
| | 1 st | 2 nd | 3 rd | | |
| 1 | 29.65 | 31.89 | 29.63 | 30.39 ± 1.06 | 3.49 |
| 2 | 19.26 | 18.11 | 18.25 | 18.54 ± 0.51 | 2.76 |
| 3 | 21.97 | 22.27 | 21.19 | 21.81 ± 0.46 | 2.09 |
| 4 | 45.84 | 43.59 | 44.91 | 44.78 ± 0.92 | 2.06 |
| 5 | 23.42 | 20.94 | 19.59 | 21.32 ± 1.59 | 7.44 |
| 5 | 18.14 | 16.77 | 17.37 | 17.42 ± 0.56 | 3.22 |
| 6 | 26.05 | 24.46 | 24.96 | 25.16 ± 0.66 | 2.64 |
| 7 | 19.86 | 20.86 | 18.89 | 19.87 ± 0.81 | 4.05 |
| 7 | 18.83 | 16.73 | 16.89 | 17.49 ± 0.95 | 5.46 |
| 8 | 26.38 | 23.72 | 25.15 | 25.08 ± 1.08 | 4.32 |
| 9 | 13.04 | 11.84 | 11.65 | 12.18 ± 0.61 | 5.04 |
| 9 | 13.53 | 14.92 | 13.58 | 14.01 ± 0.64 | 4.58 |
| 10 | 13.79 | 12.99 | 13.20 | 13.33 ± 0.34 | 2.55 |
| 11 | 25.12 | 24.55 | 24.45 | 24.71 ± 0.30 | 1.20 |
| 12 | 15.32 | 16.27 | 17.32 | 16.30 ± 0.82 | 5.01 |
| 13 | 27.21 | 26.57 | 26.39 | 26.72 ± 0.35 | 1.32 |
| 14 | 25.14 | 23.74 | 22.30 | 23.72 ± 1.16 | 4.87 |
| 14 | 22.30 | 20.73 | 18.55 | 20.53 ± 1.53 | 7.48 |
| 15 | 21.94 | 22.18 | 23.22 | 22.45 ± 0.55 | 2.47 |
| 16 | 34.30 | 34.42 | 34.38 | 34.37 ± 0.05 | 0.14 |
| 17 | 17.69 | 16.67 | 18.03 | 17.46 ± 0.58 | 3.32 |
| 18 | 20.53 | 22.10 | 23.98 | 22.20 ± 1.41 | 6.36 |
| 19 | 27.34 | 29.99 | 29.57 | 28.97 ± 1.16 | 4.02 |
| 20 | 16.08 | 16.57 | 16.49 | 16.38 ± 0.22 | 1.32 |
| 21 | 27.97 | 25.42 | 24.80 | 26.07 ± 1.37 | 5.27 |
| 22 | 19.79 | 20.42 | 21.59 | 20.60 ± 0.75 | 3.63 |
| 23 | 24.00 | 25.22 | 23.40 | 24.21 ± 0.76 | 3.13 |
| 24 | 33.70 | 32.28 | 31.11 | 32.36 ± 1.06 | 3.27 |
| 25 | 52.56 | 48.61 | 50.13 | 50.43 ± 1.63 | 3.23 |