Aleksander Handå

Cultivation of Mussels *(Mytilus edulis)*

Feed requirements, Storage and Integration with Salmon *(Salmo salar)* farming

Thesis for the degree of Philosophiae Doctor

Trondheim, April 2012

Norwegian University of Science and Technology
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Aleksander Handå
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ABSTRACT

Norwegian salmon production doubled from 0.43 million tons in 1999 to 0.86 million tons in 2009, with further growth expected. A considerable amount of the feed used is released into the surrounding waters as respiratory products, faeces and uneaten feed, and there is an increasing concern regarding the potentially negative impacts that this nutrient load may have. One of the major challenges for the sustainable development of salmon aquaculture is therefore to minimize waste discharges that may lead to degradation of the local marine environment. For this purpose, it has been suggested to cultivate extractive and filter feeding species, e.g. seaweed and mussels, close to fish farms in integrated multi-trophic aquaculture (IMTA), thereby contributing to a more ecologically balanced ecosystem approach in marine aquaculture.

The primary objectives of this thesis were to investigate whether blue mussels (*Mytilus edulis*) can incorporate and utilize components of salmon fish feed and faeces particles for growth. The secondary objectives were to assess the ambient conditions for mussel cultivation in the coastal areas of Central Norway, and to test for the possibility of using land-based storage or creating non-toxic areas for storage of mussels at sea to meet a possible increase in mussel production from a development of IMTA in Norway.

Mussels cleared salmon feed and faeces particles out of suspension with a high efficiency, suggesting that mussels can remove particulate wastes from salmon farming. In combination with a better growth for mussels fed salmon feed than faeces, a more pronounced incorporation of salmon feed compared to salmon faeces components in mussel tissues indicated that mussels will utilize salmon fish feed more efficiently than faeces particles in an integrated production with salmon.

A one-year case study further revealed the incorporation of salmon fish feed in mussel tissues and five months with a higher soft tissue weight of mussels co-produced with salmon compared to control mussels, particularly during autumn and winter when phytoplankton concentrations were low, while control mussels demonstrated a higher soft tissue weight after peak phytoplankton levels in early summer. Mussels at the salmon farm showed a faster growth in length during the spring, while control mussels grew faster during the summer, thus resulting in equal growth rates for the fastest growing mussels co-produced with salmon and control mussels for the entire year. The results suggest that the combined production of mussels and salmon can be seen as a strategy to mitigate environmental effects of particulate nutrient wastes from salmon farming, and to maintain a higher soft tissue content of mussels during autumn and winter.

Ambient Chl *a* concentrations in the coastal areas of Central Norway ranged bellow 2 μg L^{-1} after the spring bloom and were considered low. Food availability measured as suspended particulate matter (SPM) was, however, consistently above the threshold level of 4 mg L^{-1} for pseudo-faeces production in mussels of 1 g soft tissue dry matter, with an organic content of 32-44%, and did not appear to restrict mussel growth. SPM may therefore be an important food source to sustain mussel growth when phytoplankton concentrations are low.

Temperature-dependent feed requirements were evident from significantly higher oxygen consumption and ammonia-N excretion rates at 14°C compared to 7°C at land-based storage conditions. Minimum feed requirements for the weight maintenance of mussels with 500 mg soft tissue dry matter is estimated at 240 and 570 μg C ind^{-1} h^{-1} at 7°C and 14°C, respectively. Mussels kept at land-based storage conditions maintained their soft tissue content and thus a high quality in early summer (May-June) while a significant decrease in soft tissue matter was evident among farmed mussels at sea in the same period. The results suggest that land-based storage can be used for obtaining a continuous mussel production in Norway independent of harvesting problems related to toxic algae blooms and extreme weather.

Artificial upwelling in a stratified fjord resulted in an increased nutrient supply to euphotic waters and a correspondingly increase in phytoplankton biomass with a relative reduction of toxic algae. The increase in phytoplankton biomass was mainly represented by non-toxic dinoflagellates, and not diatoms, which was expected from an increased input of silicate from deep water. Nevertheless, the result is promising when it comes to creating controlled geographical areas with non-toxic food for storage of mussels and a continuous mussel production.

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II. Handå, A., Alver, M., Edvardsen, C.V., Halstensen, S., Olsen, A.J., Øie, G., Reitan, K.I., Olsen, Y. & Reinertsen, H. 2011. Growth of farmed blue mussels (*Mytilus edulis* L.) in a Norwegian coastal area; comparison of food proxies by DEB modeling. *Journal of Sea Research* 66, 297-307.

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ABBREVATIONS

IMTA	Integrated multi-trophic aquaculture	
Mussels	**Description**	**Unit**
SMR	Standard metabolic rate	
AMR	Active metabolic rate	
RMR	Routine metabolic rate	
CR	Clearance rate	L h^{-1} ind^{-1}
RE	Retention efficiency	%
AE	Absorption efficiency	%
L	Length	mm
DW	Soft tissue dry weight	mg
DW'	Standardized DW	mg
AGR_L	Average growth rate in length	µm day^{-1}
$SGR_{DW'}$	Specific growth rate in DW'	% day^{-1}
DG	Digestive gland	
M	Mantle	
G	Gills	
Feed rations		
RB	*Rhodomonas baltica*	µg C h^{-1} ind^{-1}
FD	Salmon feed	µg C h^{-1} ind^{-1}
FC	Salmon faeces	µg C h^{-1} ind^{-1}
ST	Starvation	
Seston parameters		
SPM	Suspended particulate matter	mg L^{-1}
POM	Particulate organic matter	mg L^{-1}
PIM	Particulate inorganic matter	mg L^{-1}
OC	Organic content	%
Chl *a*	Chlorophyll *a*	µg L^{-1}
POC	Particulate organic carbon	µg L^{-1}
PON	Particulate organic nitrogen	µg L^{-1}
POP	Particulate organic phosphorus	µg L^{-1}

1 INTRODUCTION

1.1 Marine aquaculture and sustainability

Aquaculture is the fastest growing animal food production sector worldwide (6.6% per annum), and accounted for 46% of the world's food fish production for human consumption in 2008 (FAO, 2010). Freshwater species accounted for 43% (29 million tons) out of a total aquaculture production of 68 million tons, while the remaining 57% (39 million tons) was produced in the marine environment, to which seaweeds and molluscs contributed 40% and 34%, respectively, while crustaceans and carnivore finfish contributed 13% each, respectively (FAO, 2010). Aquaculture is expected to continue to grow to support the steadily increasing food requirements of the growing human population (Tacon and Metian, 2008; Duarte et al., 2009; Péron et al., 2010), and since freshwater is already a limited resource, further growth will likely take place in the marine environment (Cohen, 1995; Marra, 2005). In the meantime, there is an increasing public concern about marine aquaculture, which may limit this growth (Amberg and Hall, 2008; FAO, 2009).

Concerns are particularly directed at the monoculture of species using feed containing fish meal and fish oil (Naylor et al., 2000; Neori et al., 2007), as this form of aquaculture puts pressure on wild fish stocks (Naylor et al., 2000; Pauly et al., 2002; Deutsch et al., 2007). While aquaculture production using feed containing fish meal and oil increased fourfold from 1995 to 2007 (from 4 to 16 million tons), global production of fish meal and oil has remained between 5-7 and 0.8-1.1 million tons, respectively (Tacon and Metian, 2008). Stagnation in the commercial fishery landings questions the sustainability of using fish meal and fish oil as a resource in fed aquaculture (Cho and Bureau, 1997; Mente et al., 2006; Péron et al., 2010), and restricted availability may limit further growth (Péron et al., 2010).

Moreover, there is an increasing concern regarding the potentially negative environmental impacts that nutrient emissions from marine aquaculture may possess (Braaten, 2007; Tett, 2008; Amberg and Hall, 2008; FAO, 2009), with one of the major challenges for the sustainable development of salmonid cage mariculture therefore being to minimize waste discharge that potentially may cause degradation of the marine environment (Chesuk et al., 2003). For example, the sedimentation of particulate matter may cause the organic enrichment of sediments (Carroll et al., 2003; Jusup et al., 2007; Kutti et al., 2008), which may have a negative effect on the benthic community if sedimentation rates exceed the turnover rate of the community (Holmer et al., 2005; Kalantzi and Karakassis, 2006), while dissolved nutrients may cause eutrophication (Folke et al., 1994; Nixon, 1995; Cloern, 2001; Skogen et al., 2009). Accordingly, there

is a need for a more balanced ecosystem approach in aquaculture (Neori et al., 2007; Chopin et al., 2007), particularly in fed, e.g. salmon cage aquaculture (Dalsgaard et al., 1995; Ritter, 1997).

1.2 Salmonid aquaculture

Global salmonid production increased by ~60% from 1999-2009 (1.26 to 2.17 million tons), and further growth is expected. Atlantic salmon (*Salmo salar*) aquaculture accounts for the majority of the production (1.44 million tons), and Norway, which doubled its production from 1999 to 2009 (0.43 to 0.86 million tons), is the leading producer (FAO, 2011).

Waste products

Salmonid aquaculture is based on the use of high-quality fish feed, and by assuming theoretical assimilation efficiencies of the major feed components, it is estimated that 67-84% of the nutrients (carbon, nitrogen and phosphorous) from the feed input are released into the surrounding waters as respiratory products, faeces and uneaten feed particles (Gowen and Bradbury, 1987; Hall, 1990; Hall et al., 1992; Holby and Hall, 1991; Troell et al., 2003 and references therein, Norði et al., 2011). Waste nutrients are dispersed in dissolved inorganic or particulate organic form. Dissolved inorganic nutrients, e.g. dissolved inorganic nitrogen (DIN) (ammonium-NH_4) and phosphorous (DIP) (PO_4) are immediately taken up by phytoplankton (Olsen et al., 2008) and macroalgae (Foy and Rosell, 1991ab; Kelly et al., 1994; Krom et al., 1995; Ahn et al., 1998; Schneider et al., 2005; Sara, 2007). Dissolved organic nutrients such as dissolved organic nitrogen (DON) and phosphorous (DOP) consist of molecular nutrient components that form complex chemical compounds from faeces and feed which are made slowly available to phytoplankton for a longer time. DON may also be consumed by bacteria and enter microbial food webs, as well as aggregate and sink as marine snow in slow processes. Particulate nutrients, e.g. particulate organic nitrogen (PON), phosphorous (POP) and carbon (POC), typically originate from feed and faeces (Cheshuk et al., 2003; Hall et al., 1992; Holby and Hall, 1991; Norði et al., 2011) and other particles from fouling on equipment. Davies (2000) estimated a 5% direct feed loss from cage aquaculture and a total particulate load (feed and faeces) constituting 15% of feed use, while Gowen and Bradbury (1987) found that 26% of the eaten food is released as faeces. Larger particles are consumed by fish, or sink rapidly to the seafloor where they accumulate in sediments, whereas smaller particles are suspended in the water column where they are consumed by filter feeders and bacteria within days. Dispersal patterns depend on local current conditions, with the transport distance

affecting the loading rate on the benthic marine environment (Weston, 1990; Beveridge, 1996; Kutti et al., 2007).

The mean nutrient release from Norwegian salmon aquaculture has been estimated at 61% of feed-N and 69% of feed-P. Out of this, 41% N and 19% P are released in dissolved form, while 20% N and 50% P are released in particulate form (Olsen et al., 2008). The theoretically mean nutrient dispersal from Norwegian salmon aquaculture (FCR=1.15, 6% N and 0.9% P content in feed) is accordingly: 24,250 tons DIN, 1,710 tons DIP, 11,950 tons PON and 4430 tons POP. The dissolved part constitutes a potential nutrient source for seaweed growth, while the particle wastes can potentially be utilized for the increased growth of filter feeders in IMTA. Fish feed contains ~50% of marine sources (Tacon and Metian, 2008; Olsen, 2011) with high proportions of e.g. 20:1 (n-9) and 22:1 (n-11), and there has been an increase in the use of terrestrial sources in recent years (Dahlsgaard et al., 2003; Skog et al., 2003; Narváez et al., 2008) that has high proportions of e.g. 18:1 (n-9) and 18:2 (n-6) which can be used as tracers of the incorporation of fish feed and faeces particulate wastes into mussel tissues (Gao et al., 2006; Redmond et al., 2010).

1.3 Mussel cultivation

Mussel aquaculture contributed 1.59 million tons (12.1%) to the global production of 13.1 million tons of molluscs in 2008. Other main contributors were oysters (31.8%), carpet shells and clams (24.6%) and scallops (10.7%) (FAO, 2010). From a global perspective, the volume of mussel aquaculture is comparable to that of salmonids. In Norway, however, a peak production of a modest 4,885 tons of blue mussels (*Mytilus edulis*) was reached in 2005 followed by a steady decrease (19-28% per year) to 1,650 tons in 2009 (FAO, 2011), thereby reflecting the poor situation for the mussel industry compared to the salmon industry.

Having Europe's longest coastline with potentially suitable areas for mussel cultivation is an advantage to the Norwegian mussel industry, although the development of a significant production has been more difficult to achieve than first anticipated. Several factors may account for this such as a low meat ratio in relation to overcrowded stocks and a lack of husbandry knowledge (Aure et al., 2007a), fouling and predation (Strand and Vølstad, 1997), low resuspension of organic material at deep farming sites (Strohmeier et al., 2008) and varying ambient seston concentrations in general. Moreover, the mussel industry is severely hampered by the widespread presence of toxic algae and mussels containing diarrhetic shellfish poisoning (DSP) toxins as a

result of the occurrence of toxic dinoflagellates, which is the most common reason for a ban on mussel harvesting in Norway (Torgersen et al., 2005).

On the one hand, the many challenges listed above may restrict the rapid expansion of the Norwegian mussel industry. On the other hand, the production potential has not yet been realized, and Norway is seen as one of the few countries in Europe where an increase in mussel production could take place as the production capacity apparently reached its limit in the traditional areas along the European Atlantic coast a decade ago (Smaal, 2002). At present, the possibilities for using blue mussels to remove particulate nutrient wastes from salmon farming is being assessed as a strategy to reduce the potentially negative environmental impact that salmon cage aquaculture may exert on the marine environment.

Particle selection, food parameters and nutrient utilization

Phytoplankton is a natural part of seston that is selected for by *M. edulis* prior to ingestion (Kiørboe and Møhlenberg, 1981), with selection further made between different phytoplankton species and other organic and inorganic particles (Kiørboe et al., 1980; Newell and Jordan, 1983; Newell et al., 1989; Bougrier et al., 1997; Prins et al., 1991; 1994; Defossez and Hawkins, 1997; Rouillon and Navarro, 2003). The criteria for selection are not known, but chemical composition, shape and size have been suggested to play a role (Newell and Jordan, 1983; Ward and Targett, 1989; Jørgensen, 1996). The ingestion rate has been found to peak at 12.7 mg dry weight (DW) matter per h for a 1 g DW mussel (Bayne et al., 1989) and Riisgård (1998) measured a 100% retention efficiency (RE) for particle sizes between 4 and 90 µm, while others have measured a 90% RE for particles larger than 3 µm (Møhlenberg and Riisgård, 1979; Vahl, 1972), an 82% RE for 2 µm particles and a 57% RE for particles smaller than 1.6 µm (Lucas et al., 1987).

Most Norwegian fjords are regarded as oligotrophic, low-seston environments in terms of chlorophyll *a* (Chl *a*) (Aure et al., 2007b), and Chl *a* concentrations are typically low (<1-2 µg L^{-1}) after the spring bloom due to nutrient limitation (Frette et al., 2004; Paasche and Erga, 1988). Seston concentrations and their organic content (OC), defined as fraction particulate organic material (POM) of total suspended particulate material (SPM), is a feed variable that affects the excess energy for growth (Widdows et al., 1979; Bayne et al., 1987; Navarro et al., 2003; Hawkins et al., 1997). High concentrations of particulate inorganic material (PIM) may dilute the OC, leading to a reduction in food quality, filtration rate, absorption efficiency (AE) and growth (Widdows et al., 1979; Bayne et al., 1987; Navarro et al., 2003; Iglesias et al., 1996). The OC, particularly the carbon content, is a feed parameter that largely determines the

amount of surplus energy available for growth (Bayne et al., 1987; Navarro et al., 1991; Hawkins et al., 1997), and since mussels have shown the same AE for particulate organic phosphorous (POP), nitrogen (PON) and carbon (POC), their growth rates will depend on the nutrient composition of absorbed POM and how this meets mussels requirements (Hawkins et al., 1997). Mussels can alternate between two different strategies to take maximum advantage of the available POM (Bayne et al., 1993; Arifin and Bendell-Young, 1997). When the suspended particulate matter (SPM) is high, particles with a high organic content are chosen prior to those with less organic content and inorganic ones, resulting in an increased organic portion in the feed. Inorganic particles are packed in mucus and transported forward as pseudo-faeces in increasing amounts, with a reduced concentration of POM (Iglesias et al., 1996). When the particle concentration is low, however, there is no selection even with poor OC, leaving mussels feeding on both organic and inorganic materials. PIM is assumed to pass the digestion system without becoming absorbed, while POM only passes if the organic content is very high (Prins et al., 1991).

Biometric growth

Growth in shell and growth in soft tissue are uncoupled processes in mussels (Kautsky, 1982; Rodhouse, 1984a; Hilbish, 1986; Mallet et al., 1987). Growth in length is observed to be high in spring and summer and low or insignificant in winter, while changes in soft tissue weight seem to be associated with the reproduction cycle (Bayne and Worrall, 1980; Rodhouse et al., 1984b; Page and Hubbard, 1987; Garen et al., 2004). Young mussels spend most of their energy on somatic and shell growth, whereas older individuals progressively spend more of their energy on the production and development of gonads (>90% of their available energy) (Thomson, 1984). Maximum growth takes place with seawater temperatures between 10 and 20°C (Widdows et al., 1979), and temperature changes have been associated with gonad development (Bayne, 1975; Gray, 1997) and spawning in *Mytilus* species (Chipperfield, 1953; Wilson and Seed, 1975; Kautsky, 1982; Sprung 1983). Following spawning a refractory period takes place, during which most of the energy is metabolized for gamete production (Lowe et al., 1982; Rodhouse et al., 1984b). Spawning has been related to an increase in temperature (Starr et al., 1990), while other studies have shown no such relation, instead suggesting that the reproductive cycle is related to the seasonal cycle in the food supply (Newell et al., 1982; Lowe et al., 1982; Seed and Suchanek, 1992). Two spawning patterns that relate gonad development to the seasonal cycle in the food supply are described in the literature: The first patterns involves gonad development in autumn and winter based on energy reserves accumulated in the mantle tissue during the summer period with a high food availability. A peak spawning is then observed in spring and/or early summer, sometimes with several spawnings. The opposite pattern is evident when

mussels are low in carbohydrates as the stores are used for gonad development in winter, though not sufficiently for a complete maturation, leaving the main growth of gonads to occur in spring in conjunction with the spring bloom, and spawning occurs in late summer.

Toxic algae

DSP toxins are produced by certain dinoflagellates of the genus *Dinophysis* (Yasumoto et al., 1980) and *Prorocentrum* (Murakami et al., 1982). Many dinoflagellates are considered mixotrophic, and can adopt alternative nutritional strategies (Graneli and Carlsson, 1998), move vertically and adapt well to stratified water masses (Lassus et al., 1990) in contrast to non-motile diatoms, which cannot move vertically and tend to dominate in homogeneous and turbulent water masses (Margalef, 1978; Estrada and Berdalet, 1998). Most diatoms are considered non-toxic, except for members of the genus *Pseudo-nitzschia* spp., which are known to contaminate mussels with amnesic shellfish poisoning (ASP) toxin. It has been demonstrated that an abundance of *Dinophysis* spp. correlates strongly with the stratification of water masses (Delmas et al., 1992; Lassus et al., 1993; Reguera et al., 1995) and low salinity (Perperzak et al., 1996; Soudant et al., 1997; Godhe et al., 2002; Penna et al., 2006). Most fjords in Norway are stratified during the summer with a surface layer of brackish water due to freshwater runoff from rivers and weak wind-driven vertical mixing (Aure et al., 1996; Asplin et al., 1999). In the summer, this layer may be depleted of nutrients due to earlier algal blooms in the spring and summer, leaving mussels with low food availability as the primary production is reduced (Erga et al., 2005). Artificial upwelling is suggested as a method to increase the primary production and create areas dominated by non-toxic phytoplankton for use in continuous mussel production and for avoiding harvesting problems due to harmful algal blooms (Aksnes et al., 1985; Berntsen et al., 2002; Olsen, 2002; Aure et al., 2007b).

1.4 Integrated multi-trophic aquaculture

The utilization of waste nutrients from fed species at lower trophic levels in an integrated multi-trophic aquaculture (IMTA) have been suggested as a strategy to mitigate the potentially negative environmental impacts of the nutrient release from fish cage aquaculture. The principle of IMTA is letting one species feed on the waste of another, thereby recycling lost nutrients or energy similar to naturally based ecosystems (Rawson et al., 2002). IMTA has two non-conflicting overall objectives; it is a means to obtain increased biomass production, thus adding to the value of feed investments that in the meantime may mitigate the potentially negative environmental impacts of nutrients and in that way contribute to a more sustainable aquaculture production

(Chopin et al., 2001, 2008; Neori et al., 2004; Neori, 2008; Troell et al., 2003, 2009). In a properly designed IMTA system, the dissolved inorganic nutrient wastes can be taken up by inorganic extractive species such as seaweeds (Buschmann et al., 2001; Chopin et al., 2001, 2004), while waste particulate organic nutrients can be consumed by filter feeding species such as mussels. Several studies have indicated that bivalve filter feeders can provide bio-remediative services when co-cultivated with a fed fish cage aquaculture (Folke and Kautsky, 1989; Folke et al., 1994; Troell and Nordberg, 1998; Soto and Mena, 1999; Mazzola and Sarà, 2001; Whitmarsh et al., 2006; Peharda et al., 2007; Gao et al., 2008, Redmond et al., 2010), hence helping to support that filter feeding activity may reduce the negative environmental impact associated with the great release of particulate organic matter from marine cage aquaculture (Cheshuk et al., 2003 and references therein). Meanwhile, little is known about the impact of salmon farm particulate wastes on shellfish growth (MacDonald et al., 2011).

While many studies indicate a better growth for mussels grown adjacent to cage fish farms (Wallace, 1980; Stirling and Okomus, 1995; Lander et al., 2004; Peharda et al., 2007; Sarà et al., 2009), others have failed to demonstrate such an effect (Taylor et al., 1992; Chesuk et al., 2003; Navarrete-Mier et al., 2010), which rather suggests that the distance from the farms does not substantially influence food availability and growth. Previous research has suggested several possible explanations for the lack of a distinct growth response in mussels co-cultivated with fish cage aquaculture such as: a) fish farm particulate wastes do not increase seston concentrations significantly above ambient levels, b) ambient seston concentrations remain consistently above the pseudo-faeces threshold level, thus limiting the potential for mussels to increase their growth by feeding on fish farm waste (Chesuk et al., 2003), c) the mussels' filtering response is to slow to adapt to pulsed feeding regimes accompanied by d) non-uniform effluents from salmon farms, leaving mussels to only ingest farm particulate wastes when natural seston concentrations are scarce, and e) that spatial and temporal differences in hydrodynamic conditions between sites, as well as experimental designs, differ in ways that make it difficult to obtain univocal conclusions for the IMTA concept (Troell and Nordberg, 1998; Troell et al., 2009, 2011). Conflicting results bring some uncertainty as to whether the combined cultivation of fish and blue mussels can reduce the organic load from fish cage aquaculture; there is therefore a need to further elaborate the potential of mussels to incorporate components and grow when feeding on salmon fish feed and faeces particles.

2 AIMS OF THE THESIS

The primary objectives of this thesis were to investigate whether blue mussels can incorporate and utilize components of salmon fish feed and salmon faeces particles for growth.

The secondary objectives were to assess the ambient conditions for mussel cultivation in the coastal areas of Central Norway, and to test for the possibility of using land-based storage or creating non-toxic areas for storage of mussels at sea to meet a possible increase in mussel production from a development of IMTA in Norway. To accomplish this, the specific research questions listed in Table 1 were formulated:

Table 1: Major research questions in the present work and how the papers relate to them.

	Paper*					
Research question (RQ)	**I**	**II**	**III**	**IV**	**V**	**VI**
1) What are the feed requirements for weight maintenance and growth in farmed blue mussels?	•					
2) How do the ambient food concentrations in the coastal areas of Central Norway meet the mussels' feed requirements?		•				
3) Can land- and sea-based storage be developed for continuous mussel production?	•		•	•		
4) Can mussels filter out, incorporate and utilize components of salmon fish feed and faeces particles for growth?					•	•
5) Will mussels grow faster in an integrated production with salmon compared to monoculture cultivation?		•				•

*To answer RQ 1, an initial laboratory experiment was carried out to estimate the feed requirements of farmed mussels from a study area located along the coast, north of the Trondheimsfjord in Central Norway (**Paper I**), while ambient food concentrations and corresponding growth rates of mussels within the same area were measured to answer RQ 2 (**Paper II**). This work resulted in new knowledge about the ambient conditions for mussel farming in Central Norway, which was used to design the experiments and interpret the results in order to answer RQs 3-5. The possibility for land-based storage is considered in **Paper I**, while **Papers III** and **IV** deals with the large-scale testing of upwelling technology, which aims at the establishment of storage areas with an increased production of non-toxic algae in stratified fjords (RQ 3). Finally, the incorporation of salmon fish feed and faeces in mussels was measured in two laboratory experiments (**Paper V**), followed by a one-year study of the incorporation of fish feed, as well as the growth of mussels in close proximity to a salmon farm (**Paper VI**), to help answer RQs 4 and 5.

3 MAIN RESULTS AND DISCUSSION

3.1 Feed requirements (Paper I)

The aim of this study was to estimate temperature-dependent feed requirements in farmed blue mussels from the coastal area of Central Norway. To accomplish this, specific growth rates in standardized dry matter of the soft tissue ($SGR_{DW'}$), oxygen consumption and ammonia excretion rates (O:N ratios) were measured in single mussels (40-48 mm, 536±13 mg) from the Åfjord (63° 56′ N, 10° 11′ E) kept in flowing seawater at 7°C and 14°C in the laboratory, respectively. For each temperature, the mussels were fed seven different feed rations of microalgae (5-735 µg C ind^{-1} h^{-1}).

$SGR_{DW'}$ ranged between -0.3% and 1.0% day^{-1} at 7°C and -1.5% and 0.9% day^{-1} at 14°C, and was exponentially related to feed ration according to the following equations: $y=-0.25+0.11e^{0.0034x}$ ($R^2=0.88$, $p<0.05$) at 7°C and $y=-0.75+0.05e^{0.0048x}$ ($R^2=0.53$, $p<0.05$) at 14°C. Temperature-dependent feed requirements were evident from significantly higher mean oxygen consumption and ammonia-N excretion rates at 14°C (290 µg O^2 and 27.3 µg N ind^{-1} h^1) compared to 7°C (160 µg O^2 and 11.4 µg N ind^{-1} h^{-1}) ($p<0.05$), suggesting that the contribution of energy from the diet used for metabolism and growth was the highest at 7°C. Mean ammonia-N excretion rate for mussels fed ≥105 µg C h^{-1} increased by a factor of 3.5 from 7°C to 14°C, while the mean oxygen consumption rate increased by a factor of 2.0. The mean O:N ratio accordingly declined with an increasing temperature, which indicates that protein rather than carbohydrates and lipids were used to meet the increasing demand for energy when activity increased at 14°C.

Based on the established relationships between feed ration and $SGR_{DW'}$, it has been estimated that minimum feed requirements for the weight maintenance of 500 mg DW mussels is ~240 and ~570 µg C ind^{-1} h^{-1} at 7°C and 14°C, respectively, while a specific growth rate of 0.5% day^{-1} will require a feed ration of 565 µg C ind^{-1} h^{-1} at 7°C and 680 µg C ind^{-1} h^{-1} at 14°C. Finally, 716 and 749 µg C ind^{-1} h^{-1} could support a $SGR_{DW'}$ of 1% day^{-1}. Correspondingly, O:N ratios measured 24 and 16 for weight maintenance, 29 and 23 for a specific growth rate of 0.5% day^{-1} and 43 and 31 for a $SGR_{DW'}$ of 1% day^{-1} at 7°C and 14°C, respectively. Low O:N ratios indicate protein catabolism and an unfavourable condition, while high ratios indicate that carbohydrate is the primary energy source. Combining the $SGR_{DW'}$ with the measured O:N ratios, the results suggest that O:N ratios ≥25 correspond to a positive $SGR_{DW'}$ at 7°C, while O:N ratios ≥17 support a positive $SGR_{DW'}$ at 14°C. This is comparable to the suggested levels of O:N<10 for the relatively higher utilization of dietary protein compared to carbohydrates and O:N>20 for the higher catabolism of carbohydrates (Kreeger and

Langdon, 1993), suggesting that the contribution of energy from the diet used for metabolism and growth was highest at 7°C. This was supported by significantly higher oxygen consumption and ammonia-N excretion rates at 14°C compared to 7°C. Reduced metabolic rates and a positive SGR_{DW}, for feed rations <5 µg C ind^{-1} h^{-1} at 7°C also suggests that mussels under starvation conditions can reduce their metabolic rates and increase storage life at low temperatures if they do not feed.

3.2 Ambient food availability (Paper II)

In order to assess the ambient conditions for mussel cultivation along the coastal areas of Central Norway, seston variables and the growth of mussels were measured during the growth season from March to October in three suspended longline farms: one in the inner part of the Åfjord (63° 56′ N, 10° 11′ E) and two in Inner and Outer Koet, respectively (63° 49′ N, 9° 42′ and 47′ E). Four seston variables were used as alternative input values in a Dynamic Energy Budget (DEB) model to compare their suitability as food proxies for predicting mussel growth: 1; SPM, 2; POM, 3; OC and 4; Chl *a*.

The mean SPM and POM was 6.1 and 1.9 mg L^{-1} in the Åfjord, 10.3 and 4.2 mg L^{-1} in Inner Koet and 10.5 and 4.6 mg L^{-1} in Outer Koet, respectively, resulting in a mean OC of 32, 41 and 44% in the Åfjord and Inner and Outer Koet, respectively. The mean Chl *a* measured 1.6 µg L^{-1} in the Åfjord, 3.1 µg L^{-1} in Inner Koet and 1.6 µg L^{-1} in Outer Koet, and remained <2 µg L^{-1} after the spring bloom. SPM concentrations were consistently above the threshold level of 4 mg L^{-1} for pseudo-faeces production in mussels of 1 g DW soft tissue (Widdows et al., 1979). Indeed, POM concentrations in the Åfjord were roughly similar to measurements at mussel farms in Holland, Scotland and Spain (Smaal and van Stralen, 1990; Stirling and Okumus, 1995; Garen et al., 2004), while by comparison the POM values in Koet were even higher.

The DEB model showed the best match for a single criterion for growth in both length and soft tissue dry weight for different food proxies depending on location. SPM yielded the best match in the Åfjord, while Chl *a* and POM gave the best match in Inner and Outer Koet, respectively. The results indicated that different food sources had a different impact on growth at different locations.

Summer temperatures peaked at 12°C in the Åfjord and at 17 °C in Koet. The maximum growth of mussels has been found to take place with seawater temperatures in the range between 10°C and 20°C (Widdows et al., 1979). In this study, temperatures were within this range from July to October, whereas temperatures at many mussel sites in Southern

Europe are within or close to this range for most of the year (Camacho et al., 1995; Navarro et al., 1996; Sara et al., 1998; Fuentes et al., 2000).

The results suggested that temperature is an important factor, whereas food availability measured as SPM does not appear to restrict mussel growth in the coastal areas of Central Norway. Meanwhile, Chl *a* concentrations of <2 μg L^{-1} after the spring bloom are consistent with measurements in most Norwegian fjords, which are regarded as oligotrophic, low-seston environments in terms of Chl *a* (Aure et al., 2007b). Relatively high SPM concentrations may therefore be an important food source to sustain mussel growth when phytoplankton concentrations are low.

3.3 Continuous production (Papers I, III and IV)

Highly developed storage systems can be used for obtaining a continuous mussel production in Norway independent of harvesting problems related to toxic algae blooms and extreme weather. Mussels can either be stored in land-based systems or in artificially created non-toxic areas at sea. The two strategies can be combined to meet a possible increase in mussel production from a development of IMTA in Norway, thereby enabling a continuous production and stable supply of mussels to the market.

Land-based storage

The second aim of the experiments presented in **Paper I** was to investigate the possibility of maintaining quality measured as standardized dry matter of the soft tissue (DW') during land-based storage. This was done by comparing the DW' of mussels kept at different feed rations in the laboratory with the DW' of mussels in a longline farm in the Åfjord at the same time (**Paper II**).

The DW' of mussels kept at storage conditions was maintained with both the highest and lowest feed ration at 7°C, and it even increased with the highest feed ration at 14°C despite significantly higher temperature-dependent energy requirements related to oxygen consumption, while a significant decrease in DW' was evident among farmed mussels at sea. The maintenance of weight may be commercially important, especially at times when spawning occurs at sea.

The results also suggest that mussels under starving conditions can reduce their metabolic rates and consequently increase their life span during storage if they do not feed. No feeding will save operation and management costs for mussel production, and reduce the requirements for water exchange during storage. At the same time, starvation in combination with a low water exchange rate may lead to elevated

ammonia-N concentrations, and although mussels are tolerant to elevated ammonia-N concentrations over time, low oxygen concentrations in combination with elevated ammonia-N concentrations may create a toxic environments for the mussels (Sadok et al., 1995)

Sea-based storage

Two different approaches were tested to investigate the possibilities for creating an artificial upwelling that could bring nutrient-rich deep water up to the photic zone and stimulate the growth of non-toxic phytoplankton to provide a local region for sea-based storage and a continuous production of mussels: a) A 100-m-long bubble curtain consisting of three perforated pipes was submerged to a depth of 40 m in the Arnafjord (61° 0' N, 6° 22' E), which is a side arm of the Sognefjord in Western Norway, and b) a diffuser plate was submerged above a 40-m-deep, 26-m^3s^{-1} discharge of freshwater from the Jostedal hydropower plant in the Gaupnefjord (61° 23' N, 7° 18' E), which is another side arm of the Sognefjord.

In the Arnafjord, an air supply of 44 Nm^3 each minute lifted 60 m^3s^{-1} of deeper seawater to the upper mixed layer during a period of three weeks. The mixed water flowed from the mixing region at depths from 4 to 17 m, and covered most of the inner portion of the Arnafjord within a few days. In the Gaupnefjord, the increased entrainment of seawater to the buoyant plume led to an intrusion of the discharge into the compensation current at 5–10 m depth, with a longer residence time in the local fjord arm. The field experiment showed an entrainment of 117 m^3s^{-1} of nutrient-rich seawater to the rising plume, thus being more energy-efficient than the bubble curtain. The technical analysis for both experiments is presented in **Paper III**, while the biological survey of the experiment in the Arnafjord is presented in **Paper IV**.

In the Arnafjord, an increased nutrient input to euphotic waters resulted in an increased growth of phytoplankton with a relative reduction of toxic algae. However, despite a significant increase in silicate supply during the experiment, the increase in phytoplankton biomass was mainly represented by non-toxic dinoflagellates, and not diatoms, which was expected as diatoms depend on silicate to grow. The results suggest that the created turbulence and the breakdown of stratification were not sufficient to hamper the growth of dinoflagellates and support a significant growth of diatoms, which was expected. Nevertheless, a significantly better growth of non-toxic dinoflagellates, mainly *Ceratium furca* and *C. tripos,* compared to toxic species was a promising result when it comes to creating controlled geographical areas with non-toxic food for continuous mussel production. A mean phytoplankton biomass of 58 µg C L^{-1} was obtained, which corresponded to 0.72 µg Chl *a* L^{-1}. One the one hand, this was

sufficient to support active feeding and the weight maintenance of mussels with a 1 g DW (50 mm L) based on a zero net energy balance with Chl *a* values between 0.67 and 1.02 µg L^{-1} (Hawkins et al., 1999). One the other hand, the POC concentration of 58 µg C L^{-1} would leave mussels of 40 mm length with a feed intake of 151 µg C ind^{-1} h^{-1}, given a clearance rate of 2.6 L ind^{-1} h^{-1}, which has been found for mussels of this size (**Paper V**). This is lower than the temperature-dependent requirement of 240 to 570 µg C ind^{-1} h^{-1} for 500 mg DW mussels estimated in **Paper I**, but comprises only phytoplankton-POC. Other SPM may also be an important food source.

3.4 Filtration and incorporation of salmon farm wastes (Paper V and VI)

Filter feeding activity may reduce the negative environmental impact associated with a great release of particulate organic matter from marine fish aquaculture. The possibility for blue mussels to filter out and incorporate components of salmon fish feed and faeces, and their corresponding growth, was investigated in a 28-day feeding experiment (**Paper V**). Mussels (38-42 mm) were fed mixed rations of either salmon feed and *Rhodomonas baltica* (FD+RB) or salmon faeces and *R. baltica* (FC+RB), with a mono ration of *R. baltica* (RB) acting as the control.

Mussels cleared salmon feed (2.42 L h^{-1} ind^{-1}) faeces (2.85 L h^{-1} ind^{-1}) and *R. baltica* (2.44 L h^{-1} ind^{-1}) with a high efficiency. Salmon fish feed and faeces contains a high amount of 18:1 (n-9) (>25%) and 20:1 (n-9), respectively, while 18:2 (n-6) is found in high amounts in *R. baltica*. A principle component analysis (PCA) of fatty acid profiles demonstrated a clear incorporation of fatty acids from salmon fish feed and *R. baltica* in digestive gland and gill tissue, whereas no systematic pattern was seen for mantle tissue. For digestive gland data, a PCA particularly identified the contribution of 18:1 (n-9) and 18:3 (n-3) as being the single fatty acids most responsible for the difference between mussels fed FD+RB and RB, while 20:1 (n-9) and 18:2 (n-6) also separated Day 28 samples of mussels fed FD+RB from mussels fed FC+RB, and FD+RB and FC+RB samples from Day 0 samples, respectively.

Based on the experiments conducted in **Paper V**, we concluded that mussels will incorporate and utilize components of salmon fish feed more efficiently than salmon faeces for growth. In order to further investigate the potential for mussels to perform bio-remediative services in an integrated production with salmon, we conducted a one-year case study (June 2010-June 2011) of the incorporation of fish feed components and the growth of *M. edulis* in close proximity to a salmon (*Salmo salar*) farm at Tristein (63° 52’ N, 9° 37’ E) in a coastal area of Central Norway. Mussels (30.5-32.5 mm) were cultivated at three experimental stations; one on the west side (FW), one on the east side

(FE), one 100 m east of the farm (FE100) and a reference station (RS) 4 km south of the farm. The total salmon production was 4,705 tons, with a corresponding use of feed at 5,216 tons during the sampling period.

Similar to the results from the feeding experiment presented in **Paper V**, a PCA of fatty acid profiles also demonstrated the incorporation of 18:1 (n-9) in the digestive gland and mantle tissue of mussels at sea. The incorporation was more pronounced in mussels close to the fish farm compared to that in mussels at the RS station in February compared to August, whereas no differences were found in June, thus suggesting a seasonal-dependent incorporation of components of fish feed particles in *M. edulis*.

3.5 Utilization of salmon farm wastes for growth (Paper V and VI)

Average growth rate in shell length (AGR_L), standardized dry matter of the soft tissue (DW') and a specific growth rate based on the mussels' DW' ($SGR_{DW'}$) were measured in the 28-day feeding experiment and each month during the one-year case study. In the feeding experiment (**Paper V**), the AGR_L was 33, 25 and 12 μm day^{-1}, respectively, while the $SGR_{DW'}$ measured 0.24%, 0.0% and -0.8% day^{-1} for RB, FD+RB and FC+RB. More pronounced changes in the mussels' fatty acid composition in the direction of the salmon fish feed, in comparison to the salmon faeces profile accompanied by better growth in length and soft tissue of mussels fed mixed rations of salmon feed and *R. baltica* compared to salmon faeces and *R. baltica*, suggests that mussels are more capable of incorporating and utilizing components of salmon fish feed than salmon faeces for growth. Nevertheless, a high clearance rate of fish feed and faeces, as well as indications that mussels incorporated some of the salmon faeces fraction, suggested that mussels can also clear out salmon faeces from suspension. The results are important considering the potential for blue mussels to mitigate the potentially negative environmental impacts of the particulate nutrient release from salmon farming.

In the one-year case study (**Paper VI**), the mussels' standardised soft tissue weight (DW') was significantly correlated to the use of feed at the fish farm ($r=0.53$) ($p<0.05$), and the DW' of mussels at stations at the fish farm was higher compared to that of mussels at the RS station in August (at FW), September (FW, FE and F100), October (FE), December (FW, FE and F100) and February (FE), while the DW' of the mussels at the RS station was significantly higher compared to that of mussels at the stations at the fish farm in June ($p<0.05$). The results therefore suggest that the mussels at the fish farm used less of their energy storage in the autumn-winter period compared to the mussels at the reference station.

The AGR_L ranged between 0.1 and 125 µm day^{-1} within single months and the growth was generally high during summer (June-September) and low in autumn and winter (October-February). The AGR_L correlated significantly to the feed use at the fish farm ($r=0.89$) and to the SPM concentration ($r=0.53$) in the autumn-winter period ($p<0.05$). The mussels at the RS station displayed a faster AGR_L (106 µm day^{-1}) compared to the mussels at all stations at the fish farm (67-84 µm day^{-1}) during the summer, while mussels at the FW station grew faster than the mussels at the RS station during the spring (31 vs. 20 µm day^{-1}, respectively) ($p<0.05$). The AGR_L was faster for mussels at the RS station (41 µm day^{-1}) than for mussels at the FW (34 µm day^{-1}) and FE100 stations (31 µm day^{-1}) ($p<0.05$), while no significant differences were found between the mussels at the RS station and those at the FE station (36 µm day^{-1}) for the entire year. The results suggest that the growth in length appeared to be closely related to season while the localization of mussels at the fish farm versus at the reference station was of minor importance to the result. However, a significantly slower AGR_L for mussels at the FW and the FE100 stations than for mussels at the RS station, while mussels at the FE station and control mussels showed equal growth rates emphasizes the importance of the placement of mussels within an IMTA system.

The average growth rates of mussels at the stations at the fish farm in spring (26 µm day^{-1}) and summer (75 µm day^{-1}) (**Paper VI**) were comparable to that of farmed mussels (38-65 µm day^{-1}) of similar length in monoculture during this period of the year in the landlocked Koet Bay close to the study area (**Paper II**). The results further support that mussels may not grow faster in length in IMTA under such conditions as the ones studied in this work. However, the results did indicate that mussels will clear out and incorporate a part of the particulate wastes from salmon farming, thereby mitigating the environmental impact of particulate nutrient wastes from salmon farming, and also that mussels maintained a higher soft tissue content during autumn and winter in integrated production with salmon. Mussel cultivation may also contribute to balancing the nutrient concentrations on a regional scale, e.g. a fjord system, by filtering out phytoplankton that has accumulated anthropogenic N from fish farming (see part 4.2 Perspectives). Furthermore, the average growth of mussels at sea in spring was comparable to that of mussels fed a mono diet of *R. baltica* (33 µm day^{-1}) or a mixed diet of salmon fish feed and *R. baltica* in the feeding experiment in June (25 µm day^{-1}) (**Paper V**). In comparison, the growth of mussels fed salmon feed and *R. baltica* was twice as high compared to that of mussels fed a mixed diet of salmon faeces and *R. baltica* (12 µm day^{-1}), which suggested that mussels were able to utilize components of salmon fish feed particles more efficiently for growth than salmon faeces.

4 CONCLUSIONS AND PERSPECTIVES

4.1 Conclusions

The results of this thesis suggest that mussels will incorporate components of salmon fish feed and faeces, and that the integrated production of mussels and salmon can be seen as a strategy for mitigating the environmental impacts of particulate nutrient wastes from salmon farming. The main conclusions of the research questions (RQ) raised in this thesis are summarized in Table 2.

Table 2: Main conclusions from the present work.

RQ 1	Minimum feed requirements for the weight maintenance of 500 mg DW mussels in June-July is 240 and 570 µg C ind^{-1} h^{-1} at 7°C and 14°C, respectively, while 0.5% $SGR_{DW'}$ day^{-1} requires a feed ration of 565 µg C ind^{-1} h^{-1} at 7°C and 680 µg C ind^{-1} h^{-1} at 14°C.
RQ 2	Different food variables (SPM, POM and Chl *a*) have a different impact on growth at different locations in the coastal areas of Central Norway. While ambient Chl *a* concentrations were considered low, food availability measured as SPM and POC did not appear to restrict mussel growth. SPM may therefore be an important food source to sustain mussel growth when phytoplankton concentrations are low.
RQ 3	The mussels' soft tissue content can be maintained if mussels are kept at storage on land during spawning periods at sea (peak soft tissue content was found in May and September). Storage at sea can be a way to handle a significant increase in mussel production from a development of IMTA in Norway. Artificial upwelling may stimulate the growth of non-toxic algae in suitable areas, hence supporting that this can be a strategy for storage at sea and thereby for the maintenance of a continuous mussel production.
RQ 4	Mussels cleared salmon fish feed and faeces particles with a similar high efficiency as *R. baltica*. More pronounced changes in the mussels' fatty acid composition in the direction of the salmon fish feed, compared to the salmon faeces profile accompanied by better growth in L and DW' of mussels fed mixed rations of salmon fish feed and *R. baltica* compared to salmon faeces and *R. baltica,* suggests that mussels are more capable of incorporating and utilizing components of salmon fish feed than salmon faeces for growth.
RQ 5	Mussels in integrated production with salmon exhibited a higher soft tissue weight compared to control mussels during autumn and winter, whereas control mussels demonstrated a higher soft tissue weight in early summer. Mussels at the salmon farm showed a faster growth in length during the spring, while control mussels grew faster during the summer, thus resulting in equal growth rates for the fastest growing mussels in combined production with salmon and control mussels for the entire year. Consequently, mussels may not grow faster in IMTA under such conditions as the ones studied in this work, although the results suggest that they will clear out and incorporate a part of the particulate wastes from the salmon farming.

4.2 Perspectives

The results from the present work indicate that mussels are able to utilize components of salmon fish feed particles more efficiently than salmon faeces for growth. On a single-farm scale, the bio-remediative capacities of blue mussels must be considered when taking this into account. On a regional scale, mussels can still contribute to balancing the nutrient concentrations in, e.g. a fjord system, by filtering out phytoplankton that has accumulated anthropogenic N from fish farming. Based on the results, two different approaches are suggested for the potential growth of mussels in IMTA with salmon depending on whether the location is sheltered or exposed. Sheltered sites, e.g. fjords with a low current velocity, uniform currents and a long water retention time, have the potential for increased phytoplankton growth within the IMTA system. However, a low current speed is a disadvantage regarding feed wastes in that it will sink rapidly below the fish cages, thus constituting a negligible contribution to mussel growth at such sites. On the other hand, the feed particles at exposed sites will form a larger part of the food availability for mussels, whereas the currents will dilute and transport waste nutrients away so quickly that phytoplankton growth will take place outside the IMTA system. The careful monitoring of Chl *a* levels, in combination with modelling of the local current conditions and the corresponding nutrient dispersal patterns downstream from salmon farms, can be a useful tool to localize possibly high productive areas with increased phytoplankton growth at a distance from the fish farm. Mussel production in such areas has the potential to contribute in equal terms to traditional IMTA, taking into consideration the indirect removal of anthropogenic nutrients from salmon farming, although in indirect terms.

The waste particulate food source for mussels to feed on in IMTA with salmon has been seen as the particulate part of all nutrient wastes. Given that mussels will utilize feed particles more efficiently than faeces, and that feed wastes probably account for less than 5% of the feed use in modern cage aquaculture of salmon (Mente et al., 2006), the possibility of using mussels for nutrient regeneration and bio-remediating services in IMTA has to be reconsidered. In contrast, the largest salmon farms are currently producing 12,000 tons of fish, with a corresponding feed use of 13,800 tons (FCR=1.15) and a theoretical 5% feed loss constituting 690 tons of particles or 345 tons POC from a single farm. Moreover, a 5% feed loss from the Norwegain salmon production of 0.84 million tons in 2009 (FAO, 2011) comprises 49,500 tons of particles, which have the possibility to be utilized by filter- and deposit feeders in IMTA. In addition, although salmon faeces seems to be a poor food source for mussels, there is still a chance that the faeces can be filtered out and removed together with other food particles.

Nonetheless, given that mussels will preferentially utilize salmon fish feed and not faeces for growth, another aspect well worth investigating is the potential of mussels to feed on particulate organic matter (eroded frond tissue) from seaweed (Duggins and Eckman, 1997; Duggins et al., 1989), which together with salmon fish feed, can make up a major food source for mussels to feed on in IMTA.

"The Norwegian salmon industry is not optimizing its production, it's maximizing it"
Professor Thierry Chopin
University of New Brunswick, Canada

5 FURTHER RESEARCH

Recommendations for further research based on the results in this thesis are summarized in Table 3.

Table 3: Recommendations for further research

1) Seasonally-dependent feed requirements should be identified, and feeding versus non-feeding as a strategy during storage should be further assessed, taking into account the seasonality of mussel activity.

2) The seasonal variation in the food quality of SPM should be further assessed to reveal whether the high SPM levels found in the coastal waters of Central Norway can sustain mussel growth when phytoplankton concentrations are low.

3) The mussels' requirements for essential nutrients (N and P) and how these are met by salmon fish feed and faeces should be identified.

4) The selection coefficients and assimilation capacities should be identified for salmon fish feed and faeces components under ambient SPM concentrations to assist in identifying threshold levels above which mussels will filter out and incorporate a part of the particulate wastes from salmon farming.

5) The incorporation of salmon fish feed and faeces components and the growth of mussels should be assessed under exposed and sheltered cultivation conditions to further investigate the possibility for integrated salmon-mussel production along the Norwegian coast.

6) The upscaling of mussel and seaweed cultures in IMTA with salmon is essential to further assess the potential for mitigating the environmental effects of nutrient wastes from salmon farming, in addition to obtaining increased growth in IMTA under Norwegian coastal conditions. For example, the upscaling of pilot experiments can take place at existing salmon farms: Anchoring frames for fish cages are typically 100x100 m, and provide a 1 ha submerged frame that can easily be modified to provide anchoring at desired depths from which a floating structure can be installed to produce mussels and/or seaweed on vertical ropes, or seaweed lines can be attached horizontally.

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Paper I

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Paper II

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Growth of farmed blue mussels (*Mytilus edulis* L.) in a Norwegian coastal area; comparison of food proxies by DEB modeling

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ABSTRACT

Seston variables and growth of the blue mussel (*Mytilus edulis* L.) were measured during the growth season from March to October in three suspended longline farms in Central Norway; one in the inner part of Åfjorden (63° 56′ N, 10° 11′ E) and two in Inner and Outer Koet, respectively (63° 49′ N, 9° 42′ and 47′ E). Four seston variables were used as alternative input values in a Dynamic Energy Budget (DEB) model to compare their suitability as food proxies for predicting mussel growth: 1; total particulate matter (TPM), 2; particulate organic matter (POM), 3; organic content (OC) and 4; chlorophyll a (chl a).

Mean TPM and POM measured 6.1 and 1.9 mg L^{-1} in Åfjorden, 10.3 and 4.2 mg L^{-1} in Inner Koet, and 10.5 and 4.6 mg L^{-1} in Outer Koet, respectively, resulting in a mean OC of 32, 41 and 44% in Åfjorden and Inner and Outer Koet, respectively. Mean chl a measured 1.6 μg L^{-1} in Åfjorden, 3.1 μg L^{-1} in Inner Koet, and 1.6 μg L^{-1} in Outer Koet.

Average length growth was 0.20% day^{-1} in medium sized mussels (24–36 mm) in Åfjorden and 0.08% day^{-1} in large mussels (40–55 mm) in Inner and Outer Koet. Mean standardized soft tissue dry weight ranged between 250 and 390 mg in Åfjorden, 600 and 1175 in Inner Koet, and 600 and 960 mg in Outer Koet, and showed a seasonal pattern independent of growth in length with scattered spawnings.

The model showed the best match for a single criterion for growth in both length and soft tissue dry weight for different food proxies depending on location. TPM gave the best match in Åfjorden, while chl a and POM gave the best match in Inner and Outer Koet, respectively. For Åfjorden, growth in length decreased markedly at the end of the sampling period, and this decrease was not reproduced by the model for any of the food proxies. For Inner and Outer Koet, agreement between measured and modeled length was quite good for the optimal choices of food proxy, with clear variations between the proxies for both farms. The model fit the observed soft tissue dry weight well in Åfjorden and Outer Koet, while underestimating it in Inner Koet. The differences in fit between proxies were minor for Åfjorden and Outer Koet, while OC gave the best fit and chl a the poorest fit for Inner Koet.

The results indicate that different food sources have different impact on growth at different locations. DEB modeling is a useful tool in comparing which proxies give the most relevant information.

1. Introduction

When studying the growth conditions for blue mussels (*Mytilus edulis* L.), and for modeling mussel growth, one of the important choices is how to measure food availability. Many field studies of mussel growth focus on chlorophyll a as a proxy for food, based on the assumption that phytoplankton is the main component of the mussels' diet (e.g. Smaal and van Stralen, 1990; Wildish and Miyares, 1990; Fernández-Reiriz et al., 1996; Garen et al., 2004; Strohmeier et al., 2005, 2008). However, other organic matters may also be an important part of the diet, especially when phytoplankton concentrations are low (Bayne et al., 1993; Arifin and Bendell-Young, 1997; Grant and Bacher, 1998). E.g. in the modeling study by Rosland et al. (2009) the carbon concentration estimated from chlorophyll a levels needed to be multiplied by a factor of 4 for one specific location in order to match the measured growth. For the other locations, however, the model matched well. These findings suggest that chlorophyll a may not always be an absolute proxy for food concentration.

Growth in shell length and growth in tissue are uncoupled processes in mussels (Kautsky, 1982a; Rodhouse et al., 1984; Hilbish, 1986). Growth in length is generally high in spring and summer and low or insignificant in winter, while changes in soft tissue dry weight

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are mainly associated with the reproduction cycle (Bayne and Worrall, 1980; Rodhouse et al., 1984; Page and Hubbard, 1987; Garen et al., 2004). Spawning has been related to temperatures reaching 8 °C to 10 °C coincidently with the spring bloom of phytoplankton (Starr et al., 1990). Other studies contradict such a relation, rather suggesting that the reproductive cycle is related to the seasonal cycle in food availability (Newell et al., 1982; Seed and Suchanek, 1992; Thorarinsdóttir and Gunnarsson, 2003).

The hypotheses for effect of food availability on mussel growth can be evaluated by field studies in combination with model simulations. The prerequisite for such a method is a sufficiently accurate model of the growth process of the mussels. Dynamic Energy Budget (DEB) theory (Kooijman, 2000; van der Veer et al., 2006) outlines a model at a suitable detailed level, that has shown to be applicable to mussels (Ross and Nisbet, 1990; van Haren and Kooijman, 1993; Ren and Ross, 2001; Kooijman, 2006; Rosland et al., 2009) with readily available parameter estimates (van der Veer et al., 2006).

The primary objective of this study was to compare the suitability of different seston variables as proxies for predicting mussel growth by DEB modeling. For this purpose, total particulate matter (TPM), particulate organic matter (POM), organic content (OC) and chlorophyll a (chl a) were in turn applied as food input for a DEB model. Growth data on mussels from three aquaculture sites in Central Norway were compared to the model output, and the level of agreement between model and field observations was quantified. The hypothesis is that given an accurate and representative food input, the model should show similar growth rates as was observed. Secondary objectives were to obtain data on food availability, length growth rates and spawning pattern in order to evaluate the conditions for mussel farming in Central Norway.

2. Materials and methods

2.1. Locations

Mussel growth and seston variables were measured in three longline farms in a coastal area north of Trondheimsfjorden in Central Norway; one in the inner part of Åfjorden (63° 56′ N, 10° 11′ E) and two in the inner and the outer parts of Koet, respectively (63° 49′ N, 9° 42′ and 47′ E) (Fig. 1a). Åfjorden is a shallow fjord with maximum depth of 120 m in sheltered environments while Koet is a landlocked bay with maximum depth of 100 m.

2.2. Sampling stations and sampling program

Sampling was performed every second week from March to October in 2001 and 2003 in Åfjorden and in Inner and Outer Koet, respectively. Mussels (n = 40) were kept in circular perforated plastic baskets (Ø 0.5 × 0.2 m) at 2 m depth at Stations A1–A6 in Åfjorden and at Stations B1–B3 in Inner Koet and C1–C3 in Outer Koet (Fig. 1b). Length was measured every second week at Stations A1–A3, B1–B3 and C1–C3 and every fourth week at Stations A4–A6. Mussels (n = 50) of homogenous size were sampled from mussel socks every second week at Stations A1, B1 and C1 to measure length and soft tissue dry weight.

Samples for environmental variables were taken at 2 m depth. Temperature was measured every hour at Stations A1–A6, B3 and C3 while salinity was measured at all stations every second week. Water samples for seston analysis of TPM, POM, and chl a were taken at 2 m depth at Stations A1 and A6 in Åfjorden and at Stations B1–B3 and C1–C3 in Koet at the same time as for mussel growth.

2.3. Environmental and seston variables

Temperature was measured by Tinytag (−10/40 °C) loggers while salinity was measured with an Atago refractometer (~0–100‰). Water samples for analysis of seston variables were taken in parallels of ~9 L by mixing consecutive samples from a Ruthner water collector (3 L). The samples were pre-filtered in duplicates with a 200 μm net prior to a second filtration of 2–8 L, depending on the particle density, with pre-combusted and weighed Whatman GF/C filters. 1/16 of the filters were punched out and stored at −81 °C for analysis of chl a before the filters were dried for 48 h at 70 °C to measure TPM followed by burning at 600 °C for 12 h to measure particulate inorganic matter (PIM) and calculate POM by subtracting PIM from TPM. Chl a was extracted with methanol and placed in a fridge for 2 h prior to

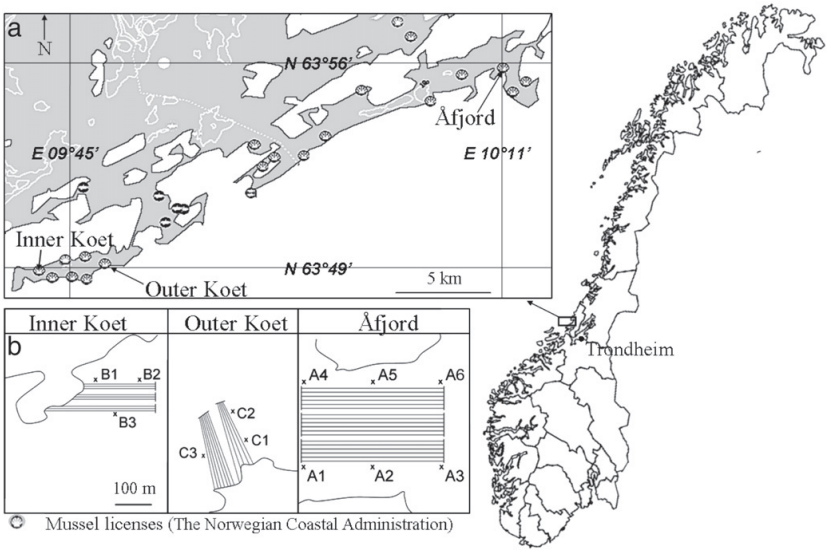

Fig. 1. Geographic location of longline mussel farms (a) and sampling stations (b) in Koet and Åfjorden in Central Norway (The Norwegian Coastal Administration).

measurement of in vitro fluorescence on a Turner Design fluorometer to measure chl a content according to Strickland and Parsons (1965).

2.4. Mussel growth

Shell length (L) was measured to the nearest 0.01 mm on individually marked mussels with a digital caliper. Mean initial shell length was 24–34 mm (mean 29.6 mm, n = 240) in Åfjorden and 40–55 mm (mean 47.2 mm, n = 120) and 40–55 mm (mean 47.9 mm, n = 120) in Inner and Outer Koet, respectively, reflecting the difference in age among the sites. Mussels in Inner Koet originated from Outer Koet. Settling occurred in August 1999 in Åfjorden and in June 2001 in Koet.

Variation in soft tissue dry weight (DW) within groups and between sampling dates was presented using a condition index standardized to a certain length L′ according to Bayne and Worrall (1980) and Bonardelli and Himmelman (1995): DW was measured after drying of tissue at 70 °C for 48 h and was then calculated as standardized soft tissue dry weight DW′ by the following equation:

$$DW' = DW\frac{L'^{b}}{L^{b}} \quad (1)$$

where DW is weight in g, L length in mm and b the slope of $\log_{10}$ DW plotted as a function of $\log_{10}$ L. DW′ corresponds to the condition index, scaled so it equals DW when L equals L′. L′ was set to 40 mm in Åfjorden and 50 mm in Koet based on an average shell length of 42.0 ± 4.5 mm (n = 600) during the sample period in Åfjorden and 49.0 ± 6.5 mm (n = 1400) in Koet. Initial standardized condition index was then 250 ± 40 mg in Åfjorden and 630 ± 130 mg in Koet. Daily specific growth rate (μ, d^{-1}) in length (SGR-L) and condition index (SGR-DW′) was calculated by the equation:

$$\mu = \frac{\ln(Y_t) - \ln(Y_0)}{t} \times 100 \quad (2)$$

where Y_0 and Y_t are the mean length and condition indices on Day 0 and Day t, respectively.

2.5. Statistics

Homogeneity of variance was tested with Levene statistics. Equality of means between specific growth rates and condition indexes was tested with one-way ANOVA followed by post hoc comparisons at each sampling date by Tamhane's T2, not assuming equal variances. Nonparametric equality of means between food variables at the two sides of Åfjorden and between Inner and Outer Koet was tested with the Mann–Whitney *U* Test (SPSS for Windows and Rel. 17.0, 2009). The significance limit was set to 0.05. Means are given with standard deviation.

2.6. DEB model

The basic DEB model has three state values; the structural volume (denoted V) represents the organism's body size, and has the unit cm^3, the energy reserve (E) represents the amount of energy in Joule (J) available in reversible storage and the reproductive buffer (R) represents the energy in J set aside for reproduction. The model parameters and the values used in our simulations are summarized in Table 1. The model Eqs. ((A.1)–(A.10)) are given in Appendix A.

Ingestion rate in the model depends on the food concentration X, and is tuned through the parameter X_K. X and X_K relate to one of the five food proxies to be investigated, and are given in the same units depending on the natural choice for each proxy. The maximum filtration rate is dependent on $V^{2/3}$, which relates to mussel length and surface area, but independent of E, so there is no direct correspondence between body weight and filtration rate. This is in consistency with Filgueira et al. (2008), who found that the relationship between gill area and clearance rate and between length and clearance rate was independent of condition index.

Table 1
Parameter values.

Symbol	Description	Value	Unit
$[E_G]$	Volume-specific cost of growth	1900	J cm^{-3}
κ	Energy partitioning parameter	0.7	–
k_{as}	Assimilated fraction of ingested feed	0.75	–
K_Y	Parameter for effect of seston on X_K	8	mg L^{-1}
$\{p_{Am}\}$	Maximum surface-area specific assimilation rate	147.6	J cm^{-2} day^{-1}
$[p_M]$	Volume-specific maintenance costs	24	J cm^{-3}
ρ	Shape coefficient	0.258	–
T_A	Arrhenius temperature	5800	K
T_{AH}	Arr. temp. upper boundary	31376	K
T_{AL}	Arr. temp lower boundary	45430	K
T_H	Temp. range upper boundary	296	K
T_L	Temp. range lower boundary	275	K
v	Energy conductance	0.067	cm d^{-1}
V_P	Size at maturity	0.06	cm^3
W_E	Energy-specific weight of reserves	$0.9 \cdot 10^{-4}$	g J^{-1}
W_R	Energy-specific weight of reproductive tissue	$0.9 \cdot 10^{-4}$	g J^{-1}
$[W_V]$	Volume-specific weight of structure	0.2	g cm^{-3}
X'_K	Feed intake half-saturation constant	0.28	mg L^{-1}

The total weight of a mussel is calculated as sum of the structural weight, the weight of reserves and the weight of the gonads and gametes—i.e. the reproductive buffer:

$$W_d = [W_V]V + W_E E + W_R R. \quad (3)$$

In order to compare variations in soft tissue dry weight with the field data, the values are transformed according to Bonardelli and Himmelman (1995) (Eq. (1)). For the model values we have no basis for calculating b for each measurement point, but as the soft tissue dry weight of structure is proportional to L^3, the value b = 3 will be used. With this choice, the structure compartment's contribution to the transformed soft tissue dry weight is constant, which is consistent with representing the condition index of the mussels.

Reproduction is a complex process to model, due to the difficulty to define when the gametes are released. It is hard to find comprehensive quantitative data on triggers and gamete release rates, most likely due to methodological challenges. Ross and Nisbet (1990) chose a rule stating that gametes are released at the point where the soft tissue dry weight of eggs reach a certain level compared to soft tissue dry weight, rather than depending on environmental triggers. In the current simulations we have chosen to simply set spawning to occur at those times where the field data indicate spawning events.

2.7. DEB model parameters

The model parameters used in this work are based on DEB model parameters described for several bivalve species by Van der Veer et al.

Table 2
Initial values for single-season simulations.

Parameter	Åfjorden	Koet
Start date	March 20	March 15
Length	2.9 cm	4.75 cm
V	0.45 cm^3	1.87 cm^3
E	380 J	1309 J
$[E_0]$	700 J cm^{-3}	700 J cm^{-3}
R	200	400

(2006). The food intake half-saturation constant X_K requires tuning for each food proxy at either location. This is done by seeking out the values that minimize the deviation between observed and modeled lengths and standardized soft tissue dry weights in each case. A metric for the overall deviation is obtained by computing the mean of the squared deviation at each field measurement point for length and DW separately, and combining these values into a single criterion:

$$y = \log\left(\overline{\Delta length^2}\right) + \log\left(\overline{\Delta DW'2}\right) \quad (4)$$

where $\overline{\Delta length^2}$ and $\overline{\Delta DW'2}$ stand for the mean square deviations of length and DW′, respectively. By using as optimization criterion the

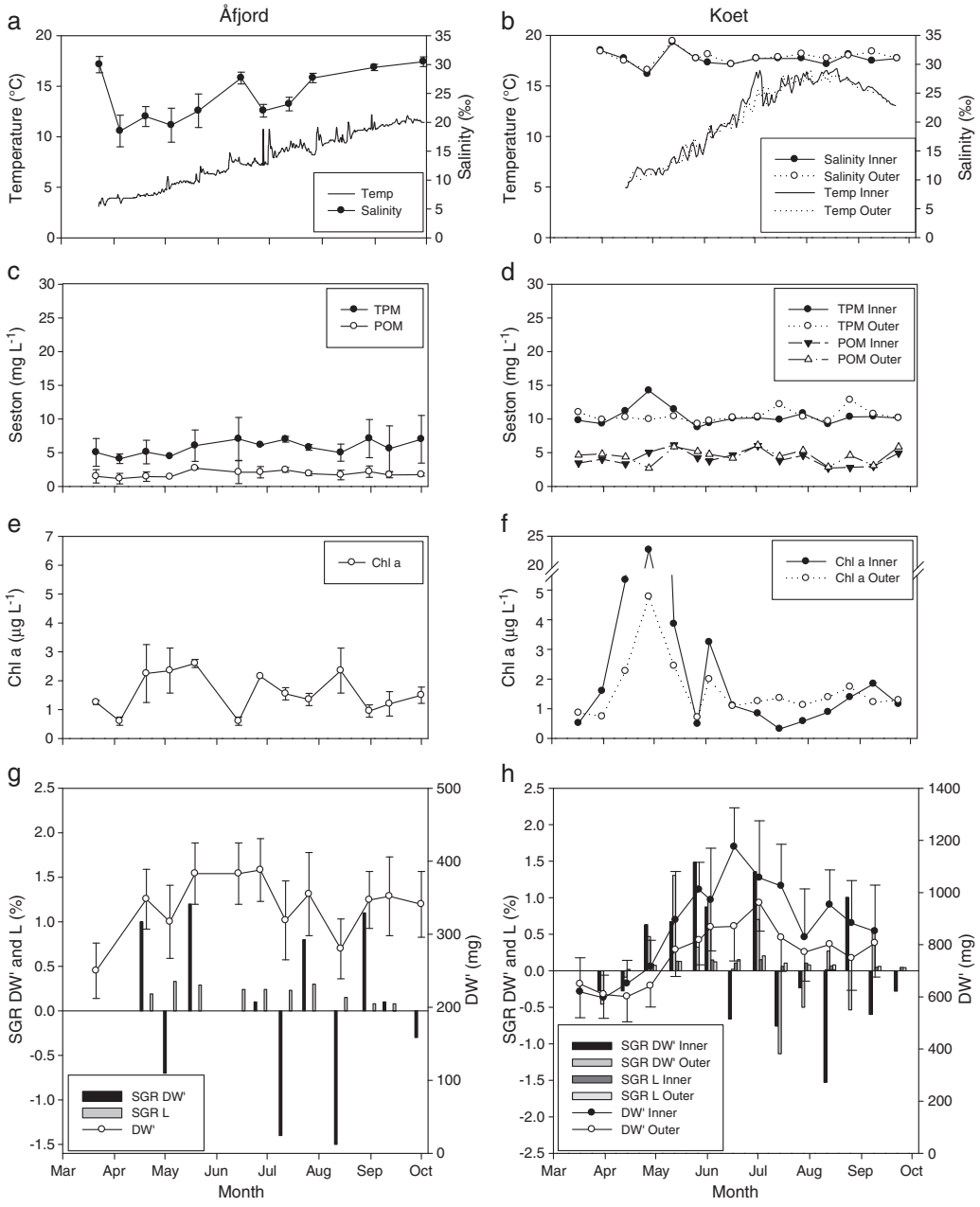

Fig. 2. Environmental and seston variables and mussel growth at 2 m depth in Åfjorden and Koet; a) and b) temperature (left axis) and salinity (right axis), c) and d) total particulate matter (TPM) and particulate organic matter (POM), e) and f) chlorophyll a, g) and h) standardized dry weight (DW', right axis) and daily specific growth rate in dry weight and length (SGR-DW' and L, left axis).

sum of the natural logarithms of each mean squared deviation we obtain a criterion that disregards differences in magnitude between lengths and weights, and weighs relative changes similarly between the two variables. The optimal value for each proxy at each location was found by comparing this criterion at a gradient of X_K values and choosing the best value.

For calculation of the dry flesh weight of mussels from the state variables, $[W_V]$ was set to 0.2 g DW cm^{-3}, the value that was chosen by Rosland et al. (2009). W_E, and W_R were both set to $0.9 \cdot 10^{-4}$ g J^{-1}.

2.8. DEB simulation runs

Simulations of the entire experimental period are made for each of the farms (Åfjorden, Outer Koet and Inner Koet) with the optimal tuning of X_K for each food proxy. The model output is compared to the field data in order to see how well the model agrees with the data, and the food proxies are evaluated quantitatively. In all simulations a single individual is used as a representative of the whole farmed population. This approach implies the assumption that all individuals are presented with identical environmental conditions, and that the model represents an average individual.

The initial value of V was in each case chosen to give initial shell length matching the average measured value. The initial value of E was set to $[E_0]V$, where $[E_0]$ was set to 700 J cm^{-3} for all locations. The initial values are summarized in Table 2.

The value for each food proxy at each point in time was estimated by linear interpolation between the two closest measurement points.

3. Results

3.1. Environmental and seston variables

Environmental and seston variables are presented in Fig. 2. Summer temperatures peaked at 12 °C in Åfjorden and 17 °C in Koet, while salinity ranged between 18 and 30‰ in Åfjorden due to freshwater runoff from the rivers Nordal and Stordal and between 28 and 34‰ in Koet (Fig. 2a and b).

TPM and POM concentrations were relatively stable in both experiments (Fig. 2c and d). Mean TPM never exceeded 7.1 mg L^{-1} in Åfjorden, while it ranged between 8.8 and 14.2 mg L^{-1} in Koet. Mean TPM and POM measured 6.1 ± 1.9 and 1.9 ± 0.8 in Åfjorden and 10.3 ± 1.3 and 4.2 ± 1.1 in Inner and 10.5 ± 0.9 and 4.6 ± 1.1 mg L^{-1} in Outer Koet, respectively, resulting in an OC of $32 \pm 11\%$, $41 \pm 10\%$ and $44 \pm 11\%$ in Åfjorden and Inner and Outer Koet, respectively.

Chl a peaked occasionally in periods with increased mixing (i.e. increased salinity) after periods of persistent stratification. Mean chl a

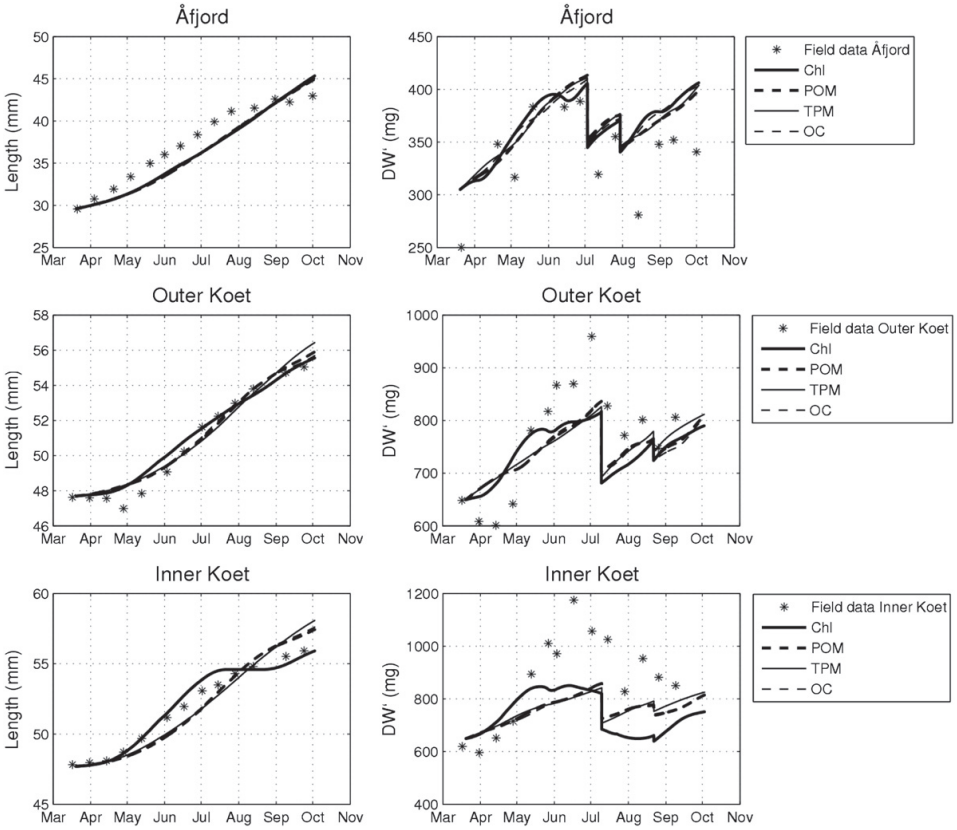

Fig. 3. Comparison of simulated and measured length and standardized dryweight (DW′) for Åfjorden, Outer Koet and Inner Koet using different feed proxies. The left panels show modeled length for the four proxies chl a, POM, TPM and OC compared to the field measurements at the three locations. The right panels show modeled DW′ compared to field data for the same proxies and locations.

measured $1.6 \pm 0.4\ \mu g\ L^{-1}$ in Åfjorden and $3.1 \pm 5.6\ \mu g\ L^{-1}$ in Inner and $1.6 \pm 1.0\ \mu g\ L^{-1}$ in Outer Koet (Fig. 2e and f). Meanwhile, due to an extreme peak in Inner Koet in late April, chl a was significantly higher in the inner ($4.8 \pm 7.4\ \mu g\ L^{-1}$) compared to the outer part ($1.9 \pm 1.4\ \mu g\ L^{-1}$) from March to July ($p<0.05$), while nearly similar values were evident from July to October ($1.0 \pm 0.5\ \mu g\ L^{-1}$ and $1.3 \pm 0.2\ \mu g\ L^{-1}$).

3.2. Overall comparison between food proxies

Looking at the single criterion describing the overall fit for both length and soft tissue dry weight, the model showed the best match for different food proxies depending on location. TPM gave the best match in Åfjorden, while chl a and POM gave the best match in Inner and Outer Koet, respectively.

Fig. 3 shows the length and DW′ predicted by the model for all four feed proxies for each of the three farms, while Fig. 4 summarizes the optimal fit found between the model and field data for each of the food proxies, with lower values (further from 0) indicating better fit. For Åfjorden, the best fit was found using TPM as food proxy, although the difference between the proxies was fairly small both in length and DW′, as can be seen from Fig. 3. For Outer Koet, POM gave the best fit. Here there is a clear difference in the fit of the length, while less difference is found for DW′. For Inner Koet, chl a gave the best overall fit, and there are clear differences between proxies both for length and DW′.

3.3. Length–growth relationship

Shell length increased from March to the end of August in Åfjorden and from April to the end of September in Koet (Fig. 2g and h). Daily length growth rate was $0.20 \pm 0.04\%$ in Åfjorden and $0.083 \pm 0.019\%$ in Inner and $0.084 \pm 0.023\%$ in Outer Koet. Mussels on a single collector in Inner Koet had grown to 49.0 ± 7.0 mm ($n = 146$) in late May 2003, indicating that mussels will reach an average length of 50 mm within their second full growth season in Koet, as opposed to the Åfjorden location, where mussels had grown to 44 ± 3.3 mm ($n = 50$) in August 2001, indicating that a third growth season is required. 50 mm is a typical marketable size which may be used for comparison with mussel growth other places (see Table 3 in discussion).

Mussel length measured throughout the season for both Åfjorden and Koet is shown in Fig. 3, compared to model simulations for each of the food proxies. Comparing the model simulations using the best food proxies (TPM for Åfjorden, chl a for Inner and POM for Outer Koet) to the length measurements (Fig. 5), we find that the model correctly predicts lengths within the standard deviation of the field measurements. Total growth in the period is the same in the model as in the field data for the Koet farms, while the model slightly overestimates growth in Åfjorden.

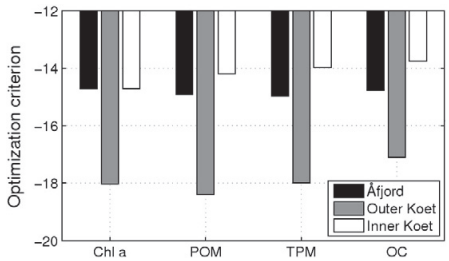

Fig. 4. Comparison of the best values obtained for the optimization criterion for the four feed proxies at Åfjorden, Outer Koet and Inner Koet. Lower values (further from 0) imply better fit. Each value is calculated as the sum of the natural logarithms of the mean squared deviation between model and field values for length and standardized dry weight, respectively.

The observed growth rate for Åfjorden decreased rapidly from August, and the model does not reproduce this decrease for any of the food proxies.

Comparing between and within results from Åfjorden and Koet, the field data shows a negative relationship between initial length and the growth rate throughout the season. In order to see how the model agrees with the field data on this relationship, we run a series of simulations with initial lengths from 2 cm to 6 cm. All simulations were run once with the Åfjorden environmental data using TPM as food proxy, once with the Outer Koet data using POM and once with the Inner Koet data using chl a. In all cases the simulation period was from March 21 until September 24. The model's initial value of V was calculated based on Eq. (A.10) for each desired initial length, and each initial value of E by multiplying V by an energy reserve density of $[E_0]$ for each location similar to the values used in the single-season simulations. The initial value of R was set to 0 J. For each simulation, the specific growth rate in length was recorded in the 187 day period from March 21 until September 24. The initial date coincides with one of the Åfjorden measurements, and comparable length values for Koet were calculated by linear interpolation between the measurements at March 31 and April 14. The final date coincides with one of the Koet measurements, and linear interpolation was done for Åfjorden between the closest measurements before and after this date.

Fig. 6 shows how the growth rate varies with initial size in the model, compared to the field data for individual mussels. The specific growth rate is calculated according to Eq. (2). Using the environmental data from either location, the model predicts a similar relationship between initial size and growth rate as that observed. In the Åfjorden field data, the decrease in growth rate with initial size appears a little steeper than

Table 3
Growth time of mussels to 50 mm length at different places.

Cultivation method	Country	Growth time	References
Longline	Norway[1], Northern–north	6 summers	Wallace (1980)
	Northern–south	3–4 summers	Wallace (1983)
	Central	3–4 summers	Lande (1973)
	Central	2–3 summers	Handå et al. (2011), this study
	Western	2 years	Duinker et al. (2008)
	Eastern	2 summers	Bøhle (1974)
	Sweeden[1]	15–16 months	Loo and Rosenberg (1983)
	Iceland[1]	24 months	Thorarinsdóttir (1996)
	Canada[1]	18–24 months	Drapeau et al. (2006)
	Italy[2]	24 months	Sara et al. (1998)
	New Zealand[3]	12 months	Hickman et al. (1991)
	Chile[4]	14–16 months	Winter et al. (1984)
	USA[1]	2–6 summers	Lutz (1980)
Raft	Scotland[1]	24 months	Stirling and Okumus (1995)
	Scotland[1]	10–12 months[5]	Mason (1969)
	Spain[1]	8–9 months	Gosling (2003)
	Spain[2]	<12 months	Camacho et al. (1995)
Bottom	Denmark[1]	>30 months[6]	Dolmer (1998)
	Holland[1]	2 summers	Korringa (1976)
	England[1]	5 summers	Bayne and Worrall (1980)
	Canada[1]	4 years	Thompson (1984)
	South Africa[2]	6 months	Heasman et al. (1998)

[1] *Mytilus edulis*.
[2] *Mytilus galloprovincialis*.
[3] *Perna canaliculus*.
[4] *Mytilus chilencis*.
[5] 67 mm in 14 months.
[6] 45 mm in 30 months.

that predicted by the model. For larger sizes, the model predicts better growth under the Åfjorden environmental conditions than under the Koet conditions. As we would expect after seeing the deviations in the final part of the growth period in Fig. 5, all sets of simulations somewhat overestimate the growth rate in Åfjorden. In Koet, both sets of simulations based on Koet environmental data match the measured growth quite well, while the simulations based on Åfjorden data predict a slightly higher growth rate.

3.4. Soft tissue dry weight

In Åfjorden, DW′ ranged between 250 ± 40 and 390 ± 40 mg (Fig. 2g), with an average of 340 ± 50 mg (L′ = 40 mm, n = 600). Maximum increase between two sampling dates was 53% when DW′ peaked from mid May to June, while overall increase from March to October was 36%. Mean daily specific growth in DW′ ranged between −1.5% and 1.2% (Fig. 2g). DW′ increased significantly from March to April and early and late May and August, respectively ($p<0.05$), while significant decreases were observed in July and August ($p<0.05$).

Growth in DW′ was significantly better in Inner compared to Outer Koet ($p<0.05$). Except for the extreme chl a peak in Inner Koet in late April, no differences were registered in the environmental variables at the two sites. DW′ ranged between 600 ± 90 and 1175 ± 150 mg in Inner and 600 ± 90 and 960 ± 110 mg in Outer Koet (Fig. 2h), with an average of 870 ± 175 mg in Inner and 770 ± 100 mg in Outer Koet (L′ = 50 mm, n = 700). Maximum increase between two sampling dates was 90% and 60% when DW′ peaked in Inner and Outer Koet in June and July, respectively, while overall increase from March to October was 36% in Inner and 24% in Outer Koet. Mean daily specific growth in DW′ ranged between −1.1% and 1.3% in Inner and −1.5% and 1.5% in Outer Koet, respectively (Fig. 2h), and showed a similar pattern at both sites from March to August, after which an opposite growth pattern was evident among the sites. Growth in soft tissue dry weight took place from early April to mid and late June in Inner and

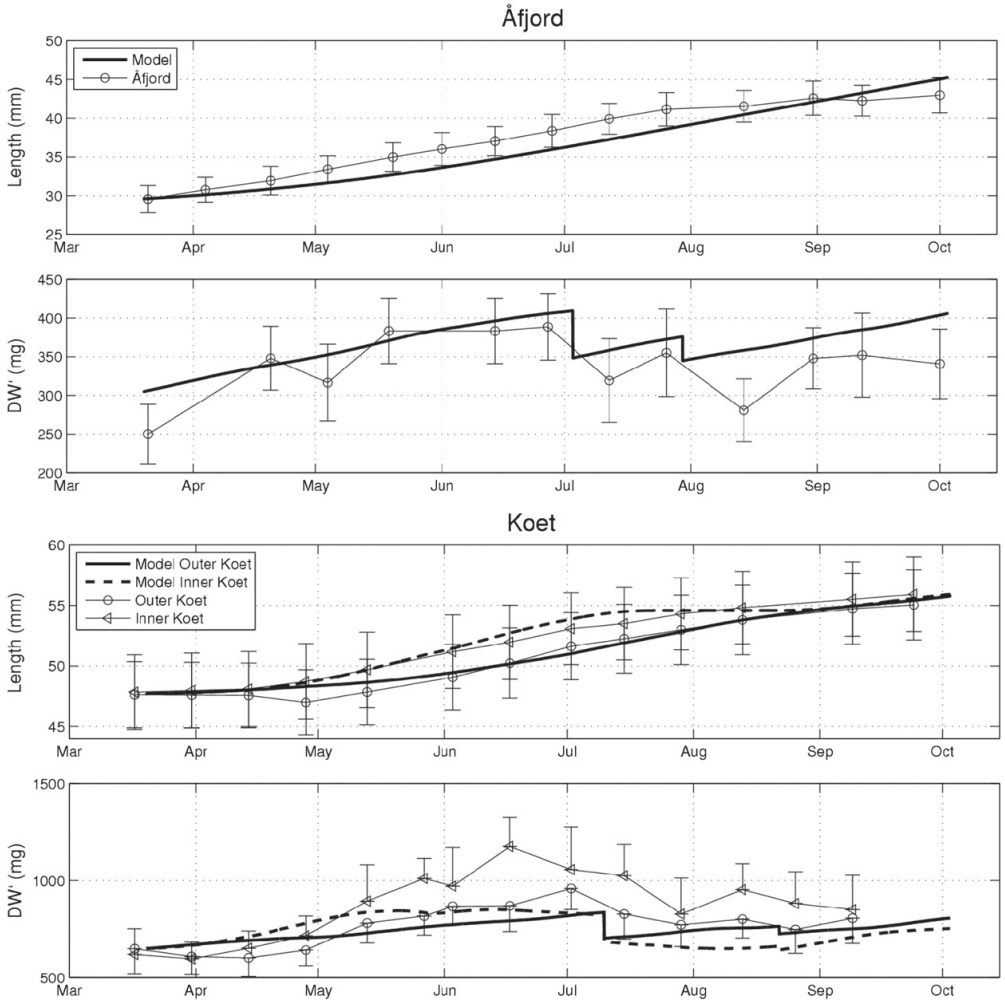

Fig. 5. Length and standardized dry weight (DW′) in model simulations compared to field data for Åfjorden and Koet in the period March to October in 2001 and 2003, respectively. Standard deviations among mussels (*M. edulis* L.) in the field data are shown. The simulations are run using the feed proxy that was found to give the smallest root mean square deviation from field measurements (TPM for Åfjorden, POM for Outer Koet and chl a for Inner Koet).

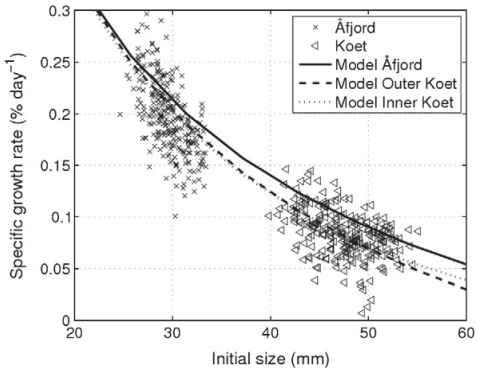

Fig. 6. Average specific growth rates in the period from March 21 until September 24. Measured growth rates of individual mussels (*M. edulis*) plotted against their shell length at March 21 for both Åfjorden and Koet. The solid line shows modeled growth rates against initial length using the Åfjorden field data with TPM as feed proxy, the hatched line shows the same using the Outer Koet data with POM as proxy, and the dotted line shows the same using Inner Koet data with chl a as proxy.

Outer Koet, respectively, with significant increases at both sites the first half of May ($p<0.05$) and in Inner Koet the first half of June ($p<0.05$). Significant decreases were observed the first half of July in Outer and the second half of July in Inner Koet, respectively ($p<0.05$).

Soft tissue dry weight was standardized by assuming isometric growth. The mean relation between weight and length varied from 2.1 to 3.9, with an average of 3.0 ± 0.5 ($n=42$ samplings of 50 mussels), and was consistent with similar measurements in other studies of mussel growth (Bayne and Worrall, 1980; Kautsky, 1982b; Loo and Rosenberg, 1983; Rodhouse et al., 1984; Reiss, 1989). The average of 3.0 supports the choice of $b=3$ in the model.

The simulated DW′ depends on the assumptions that have been made for spawning times. When following the soft tissue dry weight of mussels through a growth season, one can try to pinpoint the spawning times by looking for measurements where the mussels' condition index decreases. Fig. 5 compares modeled DW′ using the best food proxies with the field data with spawning times preset based on the field data. In general, the modeled DW′ is somewhat high compared to the Åfjorden data, although within a standard deviation for 9 out of 12 measurement points. For Koet, the simulation shows a fairly good fit for the outer location (within a standard deviation for 13 out of 14 measurement points), but a poor fit for the inner one, with the modeled DW′ being too low during the second half of the simulation.

4. Discussion

4.1. Environmental and seston variables

Temperature and seston variables did not appear to restrict growth during summer. Temperatures ranged between 8 °C and 17 °C and exceeded the suggested lower limit of 8 °C for mussel growth (Widdows and Bayne, 1971) from early June. TPM concentrations ranged consistently above the threshold level of 4 mg L^{-1} for pseudofeces production in mussels of 1 g soft tissue dry weight (Widdows et al., 1979). POM concentrations in Åfjorden (1.9 ± 0.4 mg L^{-1}) were roughly similar to measurements at mussel farms in Holland, Scotland and Spain (1.3–3.2 mg L^{-1}) (Smaal and van Stralen, 1990; Stirling and Okumus, 1995; Garen et al., 2004), while by comparison the POM values in Koet were slightly higher (4.4 ± 1.1 mg L^{-1}).

Furthermore, chl a values ranged predominantly above the range at which pumping traditionally has been observed to cease in *M. edulis* (0.3–0.6 μg L^{-1}) (Norén et al., 1999; Dolmer, 2000; Riisgard, 2001; Strohmeier et al., 2005). Chl a concentrations (1.6 ± 0.4 μg L^{-1}) were roughly similar to registrations at aquaculture sites in Western Norway (0.6–2.4 μg L^{-1}) (Strohmeier et al., 2005, 2008), and Iceland, Scotland and Spain (0.1–4.7 μg L^{-1}) (Stirling and Okumus, 1995; Thorarinsdóttir and Gunnarsson, 2003; Garen et al., 2004; Maar et al., 2008), while being lower than registrations at mussel producing areas in e. g. Denmark, France and Holland (4–12 μg L^{-1}) (Smaal and van Stralen, 1990; Dame and Prins, 1997; Dolmer, 1998). Most Norwegian fjords are regarded as oligotrophic low-seston environments in terms of chl a (Aure et al., 2007) and chl a concentrations are typically <1–2 μg L^{-1} after the spring bloom, due to nutrient limitation (Frette et al., 2004; Paasche and Erga, 1988). Other organic material may thus be an important food source to sustain mussel growth when phytoplankton concentrations are low.

Chlorophyll a as well as temperature and salinity measurements from Inner and Outer Koet suggests that spatial variability was of less importance than temporal variability in the experimental period. Therefore, and since no differences were found for seston variables among stations within each site on each sampling date, measurements were averaged within sites to filter out spatial heterogeneity. In general, interpretation and comparison of seston variables should be made with care as both spatial and temporal variability may cause seston variables to change tenfold within minutes and season in coastal environments (Smaal et al., 1986; Fréchette et al., 1989; Fegley et al., 1991).

4.2. Comparison of food proxies

The model showed the best match for a single criterion for growth in both length and soft tissue dry weight for different food proxies depending on location. Comparison of different seston variables revealed that TPM gave the best match in Åfjorden, while chl a and POM gave the best match in Inner and Outer Koet, respectively. The results indicate that the chlorophyll a level may not always represent the absolute food availability for mussels, and supports that other organic matter may also be an important part of the diet. This is in consistency with other studies where mussel growth has been related to the organic content of total particulate matter rather than phytoplankton abundance or chl a (Hickman et al., 1991; Bayne et al., 1993; Fernández-Reiriz et al., 1996; Hawkins et al., 1997; Sara and Mazzola, 1997). Since phytoplankton is selected for by *M. edulis* prior to ingestion (Kiørboe and Møhlenberg, 1981; Newell et al., 1989), the relevance of other seston variables than chl a is likely to increase along with decreasing phytoplankton densities, particularly if ambient concentrations are approaching a threshold level to sustain normal metabolism and growth.

4.3. Length

Medium sized mussels in Åfjorden showed more than twice the daily specific growth rate in length than the average for larger mussels in Koet. This is in agreement with other studies showing higher size-specific growth rates and scope for growth in small compared to larger mussels (Thompson and Bayne, 1974; Bayne, 1976; Navarro and Winter, 1982; Widdows and Johnson, 1988; Dolmer, 1998; Duinker et al., 2007). In general, no direct comparison should be made between growth in Åfjorden and Inner and Outer Koet as measurements were done in different seasons on mussels with different origin, but as seen from Fig. 6 the relationship between the growth rates in the three locations agrees reasonably well with model predictions. In the Åfjorden field data, the decrease in growth rate with initial size appears a little steeper than that predicted by the model. This could be related to the stagnation in growth seen from August, which was not reproduced by the model.

Growth time to 50 mm in length in a number of areas is presented in Table 3. The field measurements from this study indicate that it takes two growth seasons to reach this length in Koet (49.0 ± 7.0 mm in 24 months) and three growth seasons in Åfjorden (44 ± 3.3 mm in

24 months). According to Table 3, growth to 50 mm in length is somewhat faster in Central compared with Northern Norway, while being slower than in South-Eastern and Western Norway. Furthermore, growth to 50 mm in length takes more than twice the time in North-Western Europe compared to Southern Europe.

4.4. Soft tissue dry weight

Standardized soft tissue dry weight showed a seasonal pattern independent of growth in length. While no differences were found between growth in length in Inner and Outer Koet, growth in soft tissue dry weight was significantly better in Inner Koet. This is in consistency with other studies showing no relation between growth in length and growth in somatic tissue in the Mytilus genus (Kautsky, 1982a; Hilbish, 1986; Cartier et al., 2004). The distinctly better growth in soft tissue dry weight in Inner Koet from March to June was most likely due to twice as high chl a levels in Inner compared to Outer Koet, suggesting that phytoplankton was the principal food source in this period.

Several spawning periods and a major spawning period in late summer were evident in Åfjorden and Inner Koet, whereas only one spawning period was evident in late summer in Outer Koet. Peak spawning periods in late summer are in agreement with a spawning pattern resulting from low carbohydrate stores after gonad development in winter and main growth of gonads in spring in conjunction with the spring bloom. Scattered spawnings and a major spawning period in late summer have also been described for mussel populations in Eastern and Western Norway (Bøhle, 1974; Duinker et al., 2008), on Iceland (Thorarinsdóttir and Gunnarsson, 2003) and in Newfoundland (Thompson, 1984) and UK (Newell et al., 1982). A different reproductive cycle, which involves gonad development in autumn and winter based on energy reserves accumulated in the mantle tissue during the summer period with high food availability, has been observed in Western Norway (Barkati and Ahmed, 1990) and in many other European populations (see Thorarinsdóttir and Gunnarsson, 2003 and references therein). Peak spawning is then observed in spring or/and early summer, sometimes with several spawnings.

4.5. DEB model limitations

The use of a single model individual to represent an entire blue mussel farm is an obvious simplification. In a real farm there can be differences in what current speeds and food concentrations are experienced by individuals in different locations (Strohmeier et al., 2005; Aure et al., 2007). If resources are limited, the stocking density and the size of the farm will have an effect on growth (Strohmeier et al., 2008). If mortality is differentiated by size, e.g. with higher mortality among smaller individuals, the average growth rate will be skewed. A relatively simple box model attempting to describe some of these interactions has been published by Dowd (1997). In order to obtain a more flexible model, the representation of the farm's geometry and the distributed population model needs to be coupled to a model representing the dynamics of the environment and how they depend on geographical features and tidal movements. This is being addressed through a coupling of the present DEB model with the ocean circulation model SINMOD (Slagstad and McClimans, 2005; Wassmann et al., 2006), which allows the interactions between the environment and the mussel farm, and possibly other aquaculture facilities, to be modeled.

4.6. Deviations between model and field studies

The comparison of feed proxies depends on the DEB model representing the growth dynamics of the average mussel in each farm reasonably well. Although there are some deviations between the field data and the optimized model runs, these are for the most within a standard deviation of the field data. Comparing chl a levels and temperatures between the Åfjorden and Koet field data, it is surprising that the Koet mussels exhibit equally rapid growth in the final part of the period while growth in the Åfjorden farm stagnates, despite the Åfjorden mussels being smaller and experiencing higher chl a levels. In the Åfjorden simulation, we see a clear deviation in growth rate in the last two months of the period of the field studies. The measurements show a marked decrease in growth, which is not seen in the model simulations. The deviation in this period varies little between the four food proxies tested, and none of them show a decrease in food concentration significant enough to explain the stagnation of the growth. High seston concentrations could negatively affect ingestion rate (Kooijman, 2006), which is taken into account by the model. However, for Åfjorden, the seston concentration is actually lower in the last half of the field study than in the first part, while for Koet it is more variable but only about 10% higher on average in the last half of the study. The data therefore do not indicate that seston concentration could explain the deviation in growth rate. Fluctuating salinity could, on the other hand, be one possible explanation. Variation in salinity has been shown to have negative impact on mussel growth (Seed and Suchanek, 1992). Furthermore, according to Widdows (1985), mussels will reduce their filtering activity at low or fluctuating salinities if they are adapted to salinities above 30 ppm, as was the case for mussels in Åfjorden at the beginning of the sampling period. The farm in Åfjorden was located adjacent to the mouths of the rivers Nordal and Stordal and as a consequence mussels were exposed to fluctuating salinity in the range 20–30 ppm during the sampling period. These fluctuations may have affected growth in length negatively at the end of the sampling period.

5. Conclusions

Temperature and food availability did not appear to restrict mussel growth during summer. Comparison of different seston variables as food proxies for growth in length and soft tissue dry weight revealed that total particulate matter, particulate organic matter and chlorophyll a resulted in best fit in three studied mussel farms, respectively. The results indicate that the chlorophyll a level is an overall good indicator of food availability for mussels, but not the best in all cases, implying that other organic matter may also play an important part in the mussels' diet. Since mussels select for phytoplankton prior to ingestion, the relevance of other seston variables than chlorophyll a is likely to be of particular importance when ambient phytoplankton concentrations are too low to sustain normal metabolism and growth.

Appendix A

This appendix outlines the equations of the DEB model used in this study. The model's states are V (structural volume, cm^3), E (energy reserve, J) and R (reproductive buffer, J). The equations, based on DEB theory as given by Kooijman (2000), are as follows:

$$\frac{dV}{dt} = \frac{\kappa \dot{p}_c - [\dot{p}_M] C_T V}{[E_G]} \tag{A.1}$$

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C \tag{A.2}$$

$$\frac{dR}{dt} = (1-\kappa)\dot{p}_C - \dot{p}_J \tag{A.3}$$

where

$$\dot{p}_C = \frac{[E]\left([E_G]\dot{v}V^{2/3} + [\dot{p}_M] C_T V\right)}{E_G + [E]\kappa} \tag{A.4}$$

$$\dot{p}_J = mV, V_P n[\dot{p}_M] C_T \frac{1-\kappa}{\kappa} \quad (A.5)$$

$$\dot{p}_A = \{\dot{p}_A\}_m C_T V^{2/3} f \quad (A.6)$$

where f represents the functional response of feed ingestion as a function of feed concentration. The ingestion rate is modeled as a Holling (1965) type II functional response:

$$f = \frac{X}{X + X_K} \quad (A.7)$$

where X is the feed concentration, and X_K is the half-saturation constant for ingestion rate. Since the mussels filter out seston from the water, which also consists of particles with low organic content and non-digestible matter, excess particles are extracted as pseudofeces. High seston concentrations will thus potentially reduce food ingestion rate by saturating the filtration process. The effect of pseudofeces production caused by non-edible seston is modeled according to Kooijman (2006) as effectively increasing the value of the half-saturation constant:

$$X_K = X'_K(1 + Y / K_Y) \quad (A.8)$$

where Y is the seston concentration and K_Y is a parameter modulating the effect of seston concentrations.

As can be seen from Eqs. (A.1) and (A.3), structural growth and investment in reproduction are driven by the catabolic flux pc, which is split between these by the parameter κ. Somatic maintenance is subtracted before energy is used for structural growth, and maturity maintenance is subtracted before energy is invested in reproduction. The catabolic flux pc is dependent on V and E, but not directly on the feed assimilation rate pA, since assimilated energy can only be utilized after having been deposited in the energy reserve. If the growth rate according to Eq. (A.1) is negative, it means that pC is insufficient to cover somatic maintenance. The mussel is considered to be in starvation. In this case dV/dt is set to 0, and the equation for dR/dt is changed according to Rosland et al. (2009) so energy is withdrawn from the reproductive buffer to cover the maintenance deficit:

$$\frac{dR}{dt} = \kappa \dot{p}_C - \dot{p}_M. \quad (A.9)$$

Assuming that the mussels grow isometrically, the shell length is proportional to the cubic root of the structural volume V:

$$L = \frac{V^{1/3}}{\dot{p}}. \quad (A.10)$$

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Paper III

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Controlled artificial upwelling in a fjord to stimulate non-toxic algae

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ABSTRACT

During the summer, primary production in the surface layers of some fjords depletes the nutrients to the degree that some species of toxic algae can dominate. We describe field experiments employing a bubble curtain and a submerged freshwater outlet to lift significant amounts of nutrient-rich seawater to the light zone to provide an environment in which non-toxic algae can bloom. The motivation for the experiment is to provide a local region with stimulated growth of non-toxic phytoplankton and thereby creating a possibility for mussels to be cleansed from the effects of toxic algae.

In the first experiment, a 100-m long bubble curtain, using three perforated pipes submerged to 40 m depth, was operated in the Arnafjord, a side arm of Sognefjorden in western Norway. An air supply of 44 Nm^3 each minute lifted 65 m^3/s of deeper seawater to the upper layer with intense mixing during a period of 3 weeks. The mixed water flowed from the mixing region at depths from 5 to 15 m. Within a few days, the mixture of nutrient-rich water covered most of the inner portion of Arnafjord.

In the second experiment, the 40 m deep, 26 m^3/s discharge of freshwater from the Jostedal hydropower plant to Gaupnefjord, another side arm of Sognefjorden, was manipulated to enhance the upwelling of seawater by using a diffuser plate. The increased entrainment of seawater to the buoyant plume led to an intrusion of the discharge into the compensation current at 5–10 m depth and a longer residence time in the local fjord arm. The field experiment showed an entrainment of 117 m^3/s of nutrient-rich seawater to the rising plume compared with 140 m^3/s obtained in a small-scale laboratory simulation, implying a sub-optimal placement of the plate over the outlet plume. This, however, was still more energy-efficient than the bubble curtain. In both experiments (bubbles and freshwater discharge) the increased nutrient inputs to the light zone resulted in increased growth of phytoplankton with a relative reduction of toxic algae.

1. Introduction

There is a large potential for growing blue mussels in the fjords of western Norway. The estuarine circulation brings nutrients to the region and there is a controlled growth of algae throughout the summer months. Normally, diatoms, which are seldom harmful, have a much faster growth rate than flagellates. In time, however, the surface waters become depleted of the nutrients and potentially harmful dinoflagellates have a strategic advantage since they can migrate vertically to reach the nutrients at depth and increase their growth. This is especially true for the inner reaches of fjords where the density stratification due to river runoff is greatest.

It has been demonstrated that the abundance of *Dinophysis* spp. correlates strongly with the stratification of water masses (Delmas et al., 1992; Lassus et al., 1993; Reguera et al., 1995) and low salinity (Peperzak et al., 1996; Soudant et al., 1997; Godhe et al., 2002; Penna et al., 2006). In western Norway, the abundance of toxic dinoflagellates increases in the upper brackish layer from June to September (Erga et al., 2005). Harmful dinoflagellates, such as *Dinophysis* spp. are considered mixotrophic and can adopt alternative nutritional strategies (Graneli and Carlsson, 1998), move vertically and adapt well to stratification in water masses (Lassus et al., 1990) in contrast to non-toxic diatoms that cannot move vertically. Diatoms normally dominate in homogeneous and turbulent water masses (Margalef, 1978; Estrada and Berdalet, 1997).

The question is how to exploit the production potential for growing mussels in the fjords. Mussels harvested from these regions risk having too high values of the toxins DSP and YTX to be marketed. The problem: detoxifying the mussels. Although it has been proposed that these toxins can be purged with high feed concentrations (Svensson, 2003), the purging may be difficult to accelerate. Artificial upwelling to increase phytoplankton production near the mussel farms has been proposed as a method to produce toxin-free, high-quality mussels by creating conditions that favor non-toxic algae, primarily by enriching the upper, brackish waters with nutrients (Aksnes et al., 1985; Berntsen et al., 2002; Olsen, 2002; Aure et al., 2007).

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Fig. 1. The sites of experiments with artificial upwelling in Sognefjorden.

Two alternatives to detoxifying mussels using natural algae include moving the mussels to regions of high production of non-toxic algae or creating such regions locally to avoid large transport costs. The present project "DETOX", considered both, but focused on the latter. Rehabilitation stations require an artificial upwelling of nutrient-rich seawater from below the photic zone. Two technical solutions were studied in side arms of Sognefjorden on the west coast of Norway (Fig. 1). The locations were chosen from the following criteria:

- Protected from rapid exchange with the outer basin and winds.
- Limited area to get measurable results.
- No sill to restrict the inflow of seawater.
- The possibility of lifting the nutrients to the photic zone.

These criteria are essentially the same as those that favored Samnangerfjord, to the east of Bergen, in the earlier FJORDCULT study (McClimans et al., 2002). With the above criteria, we chose Arnafjord and Gaupnefjord (Fig. 1). Gaupnefjord is only marginally qualified, but here, there is a significant submerged source of fresh water available at no cost. Preliminary studies of the hydrography showed that exchange due to internal tides was insignificant in both fjords.

2. Bubble curtain

A bubble curtain was used in the inner part of Arnafjord (Figs. 1–3) to lift deeper, nutrient-rich seawater to the upper layer. The design was based on the results of laboratory tests (see McClimans, 2008 for references), field tests (see McClimans et al.,

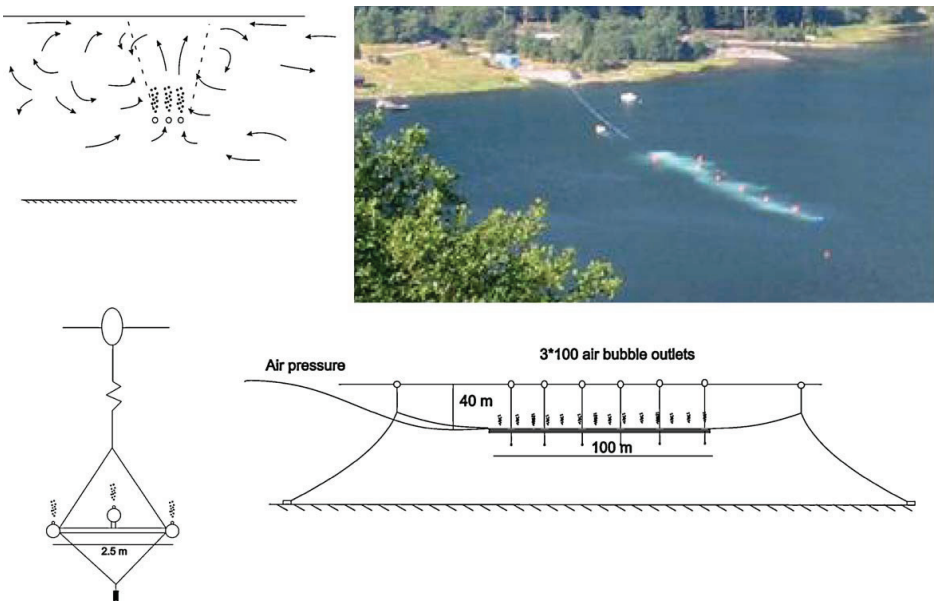

Fig. 2. The bubble curtain in Arnefjord. Upper left: cross-section of the induced circulation. Upper right: view from the mountain side. Lower left: cross-section of the construction. Lower right: suspension scheme.

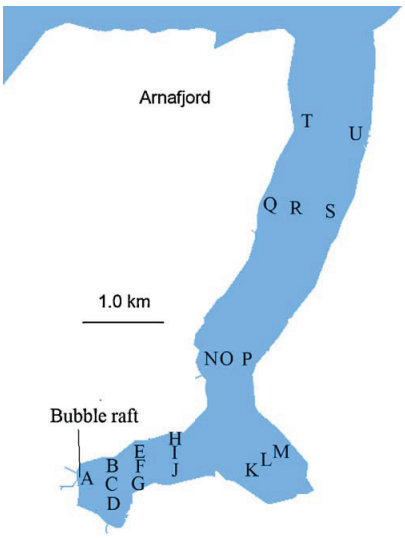

Fig. 3. Locations of the diffuser (A) and the hydrography stations in Arnafjord.

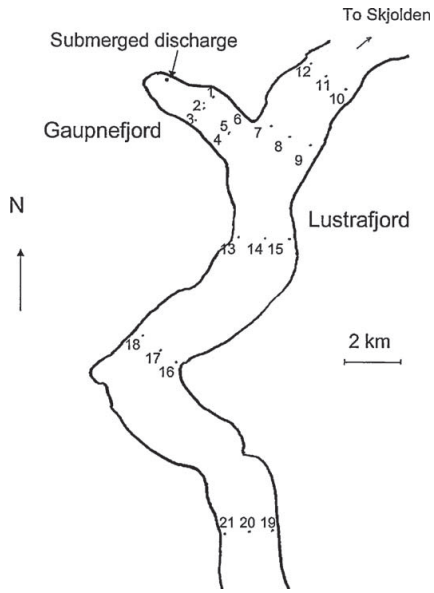

Fig. 4. Location map for the discharge of fresh water in the Gaupnefjord and measurement stations.

2002 for references) and experience with manifolds (Miller, 1990). The design is shown in Fig. 2. Three parallel, perforated pipes, 100 m long, were suspended at 40 m depth. A horizontal separation of the pipes (Fig. 2, lower left) distributed the buoyancy flux to the extent that the virtual source of the plume was a few meters deeper. An Ingersoll-Rand through-flow compressor operated by Aggreco, pressed 44 m^3 of air at normal pressure through 300, 2½ mm diameter holes each minute to produce the buoyancy flux. The compressor used 390 kW.

Violent mixing with the upper water in the bubble curtain gave a density of the mixed water close to that of the ambient water at 10 m depth. This was the nominal intrusion depth of the spreading, nutrient-enhanced water. The bubble curtain was in near-continuous operation during 4–25 September 2002. The mixing region was less than 0.2% of the surface area of the inner arm of Arnafjord. All elements were fabricated and assembled on land and the assembly was deployed using a small motor boat in calm weather. The lines between the floats and the raft were adjusted to secure a constant 40 m depth along the entire curtain (Fig. 2, lower right). The central upper pipe was used for flotation and ballast. An air hose was attached to one end, while on the far end there was an opening for water inlet/outlet. The system was deployed and retrieved by air pressure manipulation.

3. Submerged freshwater discharge

During Fjordcult (McClimans et al., 2002), laboratory tests were performed to study, among other things, the proper way to inject freshwater at depth to optimize the lift of nutrient-rich seawater to the surface layer. The results showed that the depth, diameter, volume flux and angle of the outlet all affected the mixing and the intrusion depth. The laboratory set up was intended to simulate the conditions found in Samnangerfjord, near Bergen, to the south of Sognefjorden. The discharge pipe of fresh water was directed downwards, parallel to the 45° sloping bottom. The finite laboratory basin required a finite time of discharge to establish quasi-stationary conditions of the near and far fields of the buoyant jets. Scaling of these results to natural basins follows Froude similitude as long as the volume and buoyancy fluxes of the outflow are the main driving agents for the currents and turbulence in the basin. The fluorescent tracer Rhodamine was used to simulate nutrients in the deeper seawater and to trace the intrusion of the mixed water into the basin. Details of the laboratory study and a numerical parametric study were presented in McClimans et al. (2002). For a given discharge and chosen depth (to lift deeper seawater), there is an optimal diameter for a desired intrusion between 5 and 10 m depth.

The Jostedal power station is an existing outlet of freshwater at 40 m depth in Gaupnefjord (Fig. 4). The reason for submerging the discharge was to avoid the freezing of a fresh water outflow from hydroelectric production during the cold winter months and the associated problems with ice on navigation in the fjord, among other things. The 7 m diameter outlet, however, is too large to produce an optimal mixing and intrusion depth for the present purposes. It was therefore decided to place a diffuser plate over the outlet to distribute the outflow over a larger number of smaller plumes. A sketch of the scheme is shown in Fig. 5. Here, too, the source of buoyancy is at a depth of 40 m.

Before the diffuser plate was designed, the concept was tested at small scale in SINTEF's hydraulics laboratory, using the same technique as for the Samnangerfjord study. The local bottom topography at the outlet was copied at a scale of 1:100. The width of the receiving basin (Gaupnefjord) was equivalent to 100 m in nature,

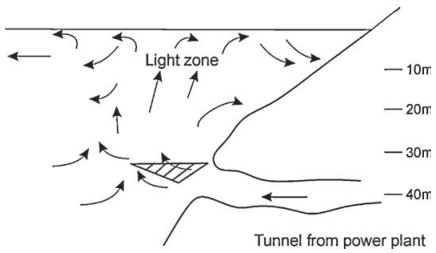

Fig. 5. A sketch of the diffuser plate over the submerged outlet from the Jostedal hydro power station.

Fig. 6. Side views of the simulated fresh water plumes (dyed black) in the stratified recipient with (right) and without (left) a diffuser plate over the outlet.

Fig. 7. The diffuser plate designed to increase mixing with the seawater.

far enough away from the near field of the discharge to allow a realistic intrusion of the mixed water to the stratified fjord. The recipient was stratified according to field measurements of density. Hydrographic measurements and video recordings of the scheme were made for two discharges (25 and 55 m^3/s) with and without the diffuser plate over the outlet.

Since the horizontal area of the laboratory test basin was finite (8 m^2) it is possible to measure the amount of deepwater moved to the upper layer by measuring the descent of the halocline during the 4–6 min discharge. To compute the entrainment, salinity profiles ($S(z)$) are measured before and after each test. The convergence of the isohals represent the water removed at different depths. The entrainment to the light zone is computed by measuring the volume loss below 20 m depth from the adjustment in the salinity field and computing the gain to 15 m, the assumed depth of the photic zone, using the formula for plumes in Fischer et al. (1969; p. 330). Salinity is measured to an accuracy of ±0.05 ppt with a 1 cm resolution in z and the changes are on the order of 1 ppt, giving a measurement error up to 5%. The positions of the measurements are relatively exact.

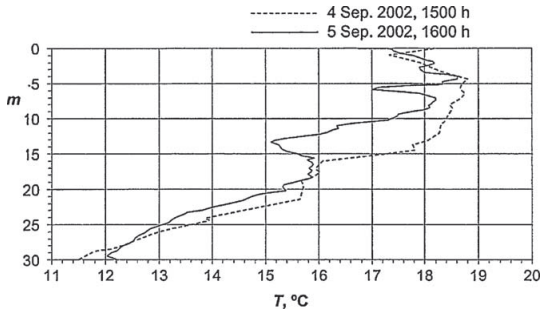

Fig. 8. Temperature profiles at St. C near the bubble curtain before (dashed line) and 18 h after (solid line) the onset of bubbling.

The fluorescent tracer Rhodamine is used to measure the depth of intrusion of the deeper water in the upper layer. Pictures from the video recordings for a simulated discharge $Q_o = 55\ m^3/s$, dyed with black ink, with and without the diffuser plate are shown in Fig. 6. Note the wider plume and the deeper intrusion with the plate over the outlet. For these conditions, the initial entrainment of $1.9Q_o$ (without the plate) was increased to $2.8Q_o$. For $Q_o = 25\ m^3/s$, it went from $2.3Q_o$ to $5.4Q_o$. From the video, it was apparent that the diffuser plate more than doubled the effective diameter of the rising plume. Furthermore, turbulence at the surface was greatly reduced, implying a more efficient conversion of the energy to mixing and production of potential energy.

Based on these small-scale experiments, a diffuser plate (Fig. 7) was constructed to meet the hydrodynamic and operational requirements. To avoid too much buoyancy of fresh water under the plate, it was formed as a boat hull. The picture on the left of Fig. 7 shows the size of the plate (16 m long) and the right pic-

ture shows it in its submerged orientation before lowering it to its operating depth of 36 m. The plate was suspended from a large number of surface floats and held in place by bolts along the slope and anchor lines at two outer points. The plate was designed to allow it to be rotated to a vertical position during the winter season when additional mixing is not needed.

4. Measurements of the spreading of nutrient-rich water

4.1. Arnafjord

Measurements of salt and temperature were used to calculate the effect of the bubble curtain on the redistribution of the water masses in Arnafjord. Measurement stations and the location of the bubble diffuser are shown in Fig. 3. During the experiment, the temperature profile was quite unusual, with a large amount of warm water throughout the upper 15 m of the water column. Fig. 8 shows the temperature distributions prior to and 1 day after the onset of bubbling.

The colder water on the fifth of September represents the adjustment at this station due to the buoyancy flux of the bubble curtain. The spreading layer of mixed water is seen between 5 and 15 m depth. To calculate the *amount* of water mixed by the bubble curtain, we consider the initial phase as the volume of mixed water increases. The spreading of this water was measured at many locations after 18 h to compute the entire volume of mixed water in the fjord. Fig. 9 shows the distribution of the thickness of the intruding, mixed water. From this volume and the temperature changes, it is estimated that the bubble curtain lifted about 65 m^3/s of deeper water to the photic zone the first 18 h, and presumably during the following weeks of operation. This result is in reasonable agreement with experience from other well-dimensioned bubble curtains (McClimans, 2008). The time history of the spreading of the nutrient-enriched water is given in Table 1 and station locations are shown in Fig. 3. Reference stations are noted for Day 11 and Day 21. One conclusion from this experiment is that the intrusion depth was a bit deep in the photic zone for optimal local primary production. A method to increase the buoyancy (i.e., reduce density) of the mixed water should be sought to raise the intrusion depth toward 5 m.

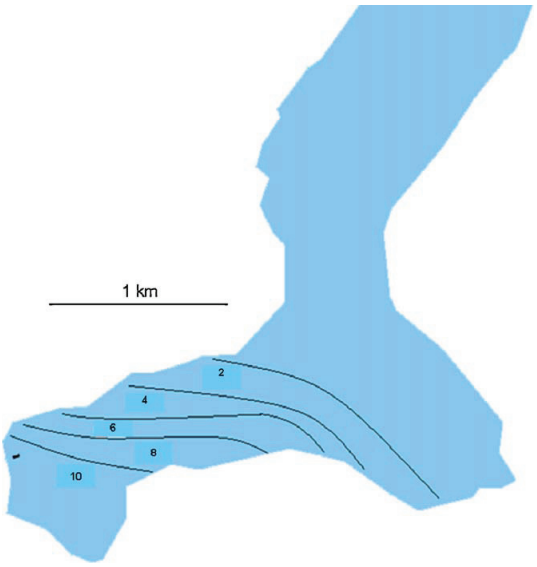

Fig. 9. Distribution of the thickness (m) of the spreading, mixed water 18 h after the onset of bubbling.

Table 1
Estimated thickness of the surface layer (D1) and intruding water (D2) in Arnafjord based on hydrographic stations A–U (Fig. 3). Bubbling lasted from 22 h, 4 September (Day 0) to 14 h, 25 September 2002.

St	Day 1			Day 11			Day 21		
	Hour	D_1 (m)	D_2 (m)	Hour	D_1 (m)	D_2 (m)	Hour	D_1 (m)	D_2 (m)
A	–	–	–	–	–	–	18	7	3
B	9	5	10	13	5	10	18	7	2
	16	4	11						
C	9	11	4	13	5	10	18	7	2
	16	5	10						
D	9	10	5	14	6	9	18	6	5
	16	7	8						
E	9	6	5	14	6	9	–	–	–
	16	5	10						
F	9	12	3	14	5	10	–	–	–
	16	9	6						
G	9	9	6	14	5	10	–	–	–
	16	7	8						
H	16	5	8	–	–	–	18	6	3
I	16	8	7	–	–	–	18	8	2
J	16	8	7	–	–	–	18	8	2
K	15	11	3	14	6	7	18	6	1
L	15	11	3	14	7	6	19	5	3
M	15	11	3	14	6	7	19	5	3
N	12	x	x	14	4	6	17	7	2
	15	x	x						
O	11	x	x	15	6	9	17	6	2
	15	x	x						
P	11	x	x	15	6	9	17	6	1
	15	x	x						
Q	–	–	–	Ref	Ref	Ref	17	6	5
R	–	–	–	15	6	9	–	–	–
S	–	–	–	15	6	9	16	7	2
T	–	–	–	–	–	–	Ref	Ref	Ref
U	–	–	–	–	–	–	16	6	3

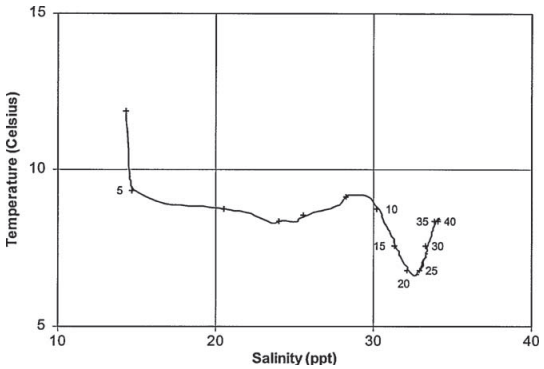

Fig. 10. Temperature salinity diagram from Gaupnefjord 23 h after the onset of the discharge with a diffuser plate. Numbers refer to observation depth in m.

4.2. Gaupnefjord

The results of the spreading of mixed water resulting from the diffuser plate were computed from measurements of salt and temperature during the initial phase of spreading, as in Arnafjord. To this end, the cold water from the power plant discharge, entrained the cold water below 10 m depth and allowed for the use of a temperature-salinity diagram to demark the intruding water mass, as was the case in Arnafjord. An example of this, from St. 3 in Gaupnefjord, 23 h after the flow was initiated, is shown in Fig. 10. The "trough" of cooler, less saline water between 15 and 27 ppt salinity intrudes between 5 and 9 m depth. The salinity in this outflow is a measure of the entrainment to the fresh water plume.

The additional buoyancy of the fresh water has indeed led to a shallower intrusion of mixed water than in Arnafjord. From earlier field data, the intrusion of mixed water without the diffuser plate is between 2 and 5 m depth. At this depth, the water is quickly transported seaward with the brackish outflow from the local rivers. The deeper intrusion leads to a much longer residence time in the fjord arm and the mixture is embedded in the compensation current of the fjord's estuarine circulation. Ellingsen et al. (2006) have simulated this process and have revealed a deep compensation inflow to the plume entrainment at 15–25 m depth. These results are in reasonable agreement with the laboratory simulations. The mixing region near the plume is much less than 100 m in diameter and is less than 0.1% of the horizontal area of Gaupnefjord.

The estimates of the thickness of the intrusion at all locations in Fig. 4 are given in Table 2 for six cruises to the fjord during the summer of 2003. From the laboratory results, and Froude similitude, the diffuser plate should lift $5.4 \times 26\,m^3/s = 140\,m^3/s$ of seawater from below 15 m depth to the upper layer. From the change in volume between Day 1 and Day 4, it is estimated that $117\,m^3/s$ of nutrient-rich seawater is raised to the photic zone. This is less than that obtained in the laboratory and implies that the plate is not exactly in the location that was intended. The visibility in the fjord is not good and there was not time to make fine adjustments while the power station was shut down for the installation. Alternatively, the reduced volume in the intruding layer could be the result of wind erosion, which is a far-field process that was not simulated in the laboratory. However, the winds were very weak during the first 4 days of the experiment.

The results in Table 2 are shown graphically in Fig. 11. Here, it is seen that the mixed water flows toward the head of Lusterfjord, to the northeast. This almost stationary flux of nutrient-rich water to the system implies that such a scheme can be valuable for the growth of high-quality mussels in this fjord system. Within a month's time, the entrained water was measured from 5 to 11 m depth throughout the entire area of measurement. The flow of the mixed water toward Skjolden, to the northeast, supplemented the normal estuarine circulation toward the river at the innermost end of Lustrafjord. As this region filled, the mixed water spread more to the south. It is estimated that the residence time of the mixed

Table 2
Estimates of thickness Δh (m), core temperature T_c (°C) and depth of the core of the intruding water D_i (m) in Gaupnefjord and Lustrafjord during the summer of 2003. (Station locations in Fig. 4.) The plate was installed on 6 July (Day 0), when the discharge was restored [– means no data and x refers to no observed core].

Day Sta[a]	−2	4.5 kg/m^4		1	4.0 kg/m^4		4	3.6 kg/m^4		22	3.5 kg/m^4		57	3.7 kg/m^4		88	2.0 kg/m^4	
Q_f[b]	26 m^3/s			26 m^3/s			27 m^3/s			25 m^3/s			26 m^3/s			26 m^3/s		
St	Δh	T_c	D_i	Δh	T_c	D_i	Δh	T_c	D_i	Δh	T_c	D_i	Δh	T_c	D_i	Δh	T_c	D_i
1	>1.5	8.9	6.0	3.0	8.6	8.0	3.0	8.6	8.0	6.5	8.7	8.0	6.0	12.2	5.0	6.0	10.1	5.0
2	>2.5	8.7	5.5	3.0	8.5	7.5	3.0	8.6	8.0	7.0	8.6	8.0	5.5[c]	11.5	4.0	6.0	9.8	5.0
3	>3.0	7.8	2.0	4.0	8.3	7.0	3.0	8.6	8.5	>7.0	8.4	8.5	6.0	10.0	5.0	7.0	9.8	5.0
4	4.0	8.3	6.0	3.0	8.5	7.5	3.0	8.4	8.5	8.0	8.6	8.0	6.0	11.0	4.0	7.0	9.6	5.0
5	4.0	8.3	5.0	3.5	8.6	7.5	3.0	8.6	8.5	7.0	8.7	8.0	6.0	10.6	5.0	6.0	9.8	5.0
6	1.5	x	x	0.0	x	x	3.0	8.8	8.0	6.5	8.7	8.0	5.5	10.8	5.0	7.0	9.9	4.0
7	0.0	x	x	0.0	x	x	0.0	x	x	5.5	9.0	8.0	5.0	12.0	5.0	–	10.3	5.0
8	2.5	9.3	6.0	0.0	x	x	3.0	8.8	8.0	6.5	9.1	8.0	5.0	11.5	5.5	6.0	10.3	6.0
9	2.5	9.5	5.5	0.0	x	x	2.0	9.3	8.0	6.5	9.4	8.5	5.0	11.5	6.0	6.0	10.4	6.0
10	0.0	x	x	0.0	x	x	2.5	9.5	7.5	6.5	9.1	8.0	5.0	11.2	5.0	6.0	10.5	6.0
11	0.0	x	x	0.0	x	x	2.0	9.3	8.0	7.5	8.9	8.0	6.0	11.6	5.0	5.5	10.5	6.0
12	–	–	–	0.0	x	x	0.0	x	x	4.5[d]	9.6	8.0	5.0	11.8	6.5	6.0	10.6	5.0
13	2.5	8.9	5.0	2.5	8.9	8.5	2.5	9.3	8.0	8.0	8.9	8.5	6.5	12.3	5.0	5.5	10.2	6.0
14	2.5	9.0	5.5	0.0	x	x	0.0	x	x	6.5	9.3	8.0	6.5	11.6	5.5	6.0	10.0	5.0
15	2.5	9.0	5.5	0.0	x	x	0.0	x	x	6.5	9.8	7.5	5.5	11.7	5.5	6.0	9.7	5.0
16	0.0	x	x	0.0	x	x	0.0	x	x	5.5	11.7	7.0	4.0	12.1	5.0	6.0	10.0	5.0
17	1.5	9.5	5.0	0.0	x	x	0.0	x	x	3.5	11.9	6.0	5.0	12.2	5.0	5.5	10.0	5.0
18	2.5	9.4	5.0	3.5	9.2	8.5	0.0	x	x	5.5	9.7	6.0	4.0	12.4	5.0	6.0	10.0	4.0
19	0.0	x	x	–	–	–	–	–	–	–	–	–	–	–	–	6.5	10.3	5.0
20	0.0	x	x	–	–	–	–	–	–	–	–	–	–	–	–	6.0	10.2	5.0
21	1.5	9.7	5.0	–	–	–	–	–	–	–	–	–	–	–	–	6.5	10.3	5.0

[a] Stability = density gradient in Lustrafjord through a 4 m thick pycnocline.
[b] Q_f = fresh water discharge from Jostedal kraftverk prior to field measurements ($Q = 0$ for Days −1 and 0).
[c] Due to surface cooling, an upper limit of 15 ppt is used for the salinity.
[d] Double layer = 6 m.

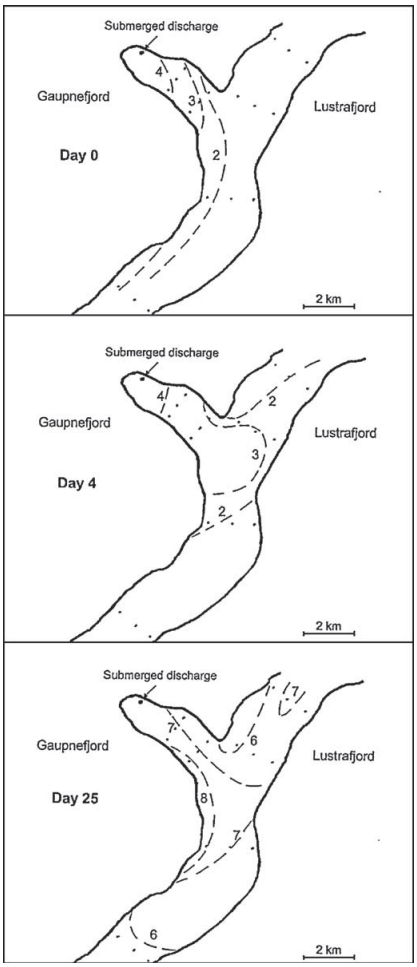

Fig. 11. The geographical distribution of the thickness (m) of the intruding layer of enhanced nutrients (see Table 2).

water forward to locations H16–H18 is 6 days. The random currents in the fjord causes a significant lateral spreading of the nutrients to create a more uniform primary production and a flux of algae to the filter feeders in the basin. The nutrients are consumed by the primary production as the water spreads from the source.

5. Discussion

5.1. A comparison of techniques

The two schemes tested in the Sognefjorden system show promise for a technical solution of the toxic algae problem of farming mussels in these productive stretches of the fjord. The scheme in Gaupnefjord produces a more reasonable intrusion depth at a more reasonable cost. In this particular case, the outlet from the power station was already deep enough to solve another problem—avoiding freezing due to the winter discharge of fresh water. This has cost the power company between a quarter (corresponding to the discharge during these experiments) and a half (corresponding to full discharge) MW of energy that has gone to turbulence and mixing. By using the diffuser plate, the quarter MW loss has produced a transport of 117 m^3/s of nutrient-rich seawater to the photic zone. In spite of the inferior result compared with the mixing in the small-scale laboratory simulations, it compares quite favorably with the 65 m^3/s for 390 kW of bubbling. The comparison with the laboratory simulations implies that a proper adjustment of the plate could increase the mixing by 20%.

An additional advantage of having a large discharge of fresh water in a tunnel or pipeline is that it can be used as an effective spreader for nutrients, artificially introduced into the system at the power station. Here, a well-controlled composition of nutrients may be administered to the fjord to achieve a desired biological result.

These and other field results have been used to validate a numerical hydro-bio model of the fjord system (Ellingsen et al., 2006).

5.2. Some other considerations

5.2.1. Alternatives for lifting the deeper water

During the initial phases of our work, we studied the effects of submerged thrusters to lift the seawater toward the surface. This turned out to be difficult because the larger part of the thrust went to overcoming gravity in the stratified water mass, and the lifting distance was quite limited. Since the fjords are stratified, with a large amount of brackish water near the surface, it is possible to use pumps to push the lighter water to a desired depth, through a well, and let the buoyancy of this water lift the seawater to a proper intrusion depth. Here, too, the pump must work against gravity to produce a pressure head to drive the buoyant water through the well of desired diameter and length (McClimans et al., 2002). This method has been pursued by Aure et al. (2007).

5.2.2. Supersaturation of nitrogen

There have been raised concerns that the use of bubble curtains at depth may lead to a supersaturation of nitrogen that could poison fish in nearby fish farms as well as wild fish, although the latter will swim to depths where nitrogen supersaturation cannot be sensed. We *hypothesize* that the level of turbulence in the bubble curtain is extremely high, and that the surface area of the bubbles allows for a rapid equilibrium as the water approaches the surface boil and flows away toward calmer waters, in near equilibrium with atmospheric pressure. We have not seen any measurements that show this to be a problem. In fact, data from a bubble curtain in a northern Norwegian fjord (Molvær and Braaten, 2003) indicate the opposite. There, a bubble curtain is used to enhance mixing of seawater to the outflow from a hydroelectric power plant to eliminate ice in the winter. The bubbler, at 15 m depth, has actually reduced supersaturation of water from the power plant. The water from the power plant becomes supersaturated both by compression of air in the high pressure tunnels and by solar heating on its seaward journey. A literature survey conducted by the authors did not reveal any relevant work on the subject (Jarle Molvær, private communications). Also, in Rissabotn, a land-locked fjord near Trondheim, a bubble curtain at 30 m depth, to improve water quality, has been in operation for several years without reports of negative biological effects (Kjersti Moltubakk, private communications). O_2 measurements from three locations in the basin suggest changes similar to those observed by Molvær and Braathen.

5.3. Future prospects for artificial upwelling

The future possibilities for using artificial upwelling techniques in aquaculture are many. The present techniques were developed for the specific conditions (and problems) in stratified fjords. In each case, the potential depends on the ambient density profiles (McClimans et al., 2002). In many ways, the entrainment in Gaupne-

fjord is ideal, as a larger entrainment would cause a denser mixture that would flow out in a deeper layer. Thus, there are many considerations to tailor technical solutions to the natural variability with each new application.

The alternative to a pure fresh water discharge at depth is to pump brackish surface water to large depth to lift the nutrient-rich, deeper water to the near-surface halocline as mentioned above (Aure et al., 2007). They pumped brackish surface water to a depth of 30 m and produced an upwelling of 28 m^3/s using a 60 kW pump. This is close to the efficiency obtained in Gaupnefjord with a less-than-optimal diffuser and superior to the bubble curtain. This is a more portable scheme and may be of use in other regions around the world where toxic algae are a problem and the conditions are favorable to solve the problem with artificial upwelling. This scheme can also be used as a spreader to add nutrients that favor non-toxic algae.

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Paper IV

Artificial upwelling to create areas for continuous mussel cultivation in stratified fjords

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Abstract

Large-scale artificial upwelling was tested as a method to enhance the environmental conditions for the growth of non-toxic algae in a Norwegian fjord (61° 0' N, 6° 22' E). The experiment was designed to evaluate if nutrient-rich seawater, brought up from below the mixed zone of a stratified fjord to the euphotic zone by air bubbling, would stimulate the growth of non-toxic relative to toxic algae. Pumping 44 m^3 min^{-1} of air at 1 atm through a pipe diffuser submerged at 40 m depth formed a buoyancy flux that lifted 60 m^3 s^{-1} of deep sea water over a period of 21 days. The upwelling generated a local breakdown of the stratification close to the upwelling zone with intrusions of mixed water from 4 m to 17 m. The pumping lifted about 4½ m^3 s^{-1} of deep water and 6½ m^3 s^{-1} of intermediate water to the upper 10 m of the euphotic zone.

The supply of silicate, inorganic nitrogen and phosphate to the upper water masses in the fjord increased, and a significant increase in the biomass of non-toxic algae was observed. The upwelling gave an increased growth of the non-toxic dinoflagellates *Ceratium furca* and *C. tripos*. After termination of the experiment, the phytoplankton biomass decreased significantly whereas a distinct increase occurred in the relative biomass of the potentially toxic *Dinophysis* spp. The result is considered promising when it comes to creating controlled geographical areas with non-toxic food for mussel production.

1. Introduction

Artificial upwelling is suggested as a method to create areas dominated by non-toxic phytoplankton for use in continuous mussel production and avoiding harvesting problems due to harmful algal blooms (Aksnes et al. 1985, Olsen 2002, Aure et al. 2007). Simulation models have shown that it is possible to enhance primary production up to three times by use of artificial upwelling (Aure et al. 2000, Berntsen et al. 2002, McClimans et al. 2002). These model results need to be evaluated in large-scale experiments to test whether increased upwelling is likely to enhance the environmental conditions for primary production and the growth of non-toxic relative to toxic algae.

Blue mussels (*Mytilus edulis*) containing diarrhetic shellfish poisoning (DSP) toxins, as a result of the occurrence of toxic dinoflagellates are the most common reason for a ban on mussel harvesting in Norway (Torgersen et al. 2005). DSP toxins are produced by certain dinoflagellates of the genus *Dinophysis* (Yasumoto et al. 1980) and *Prorocentrum* (Murakami et al. 1982). Many dinoflagellates are considered mixotrophic and can adopt alternative nutritional strategies (Graneli & Carlsson 1998), move vertically and adapt well to stratified water masses (Lassus et al. 1990) in contrast to non-motile diatoms, which cannot move vertically and tend to dominate in homogeneous and turbulent water masses (Margalef 1978, Estrada & Berdalet 1997). Most diatoms are considered non-toxic, except for members of the genus *Pseudo-nitzschia* spp. that are known to contaminate mussels with amnesic shellfish poisoning (ASP) toxin. In the fjords of western Norway, the abundance of potentially toxic dinoflagellates increases in the upper brackish layer from June to September (Erga et al. 2005). The problem with toxic algae increases with increasing distance from the coast (Ramstad et al. 2001) and is particularly profound in the inner areas of the fjords (Lee et al. 1988) where high concentrations of DSP toxins in mussels may persist for the whole year (Séchet et al. 1990). In the Sognefjord, *D. acuta* and *D. acuminata* have been shown to cause high toxicity of DSP toxins in mussels during the autumn, while *D. norvegica* has been associated with toxicity in the spring bloom (Séchet et al. 1990). It has been demonstrated that the abundance of *Dinophysis* spp. correlates strongly with the stratification of water masses (Delmas et al. 1992, Lassus et al. 1993, Reguera et al. 1995) and low salinity (Perperzak et al. 1996, Soudant et al. 1997, Godhe et al. 2002,

Penna et al. 2006). Most fjords in Norway are stratified during the summer, with a surface layer of brackish water due to freshwater runoff from rivers and weak wind-driven vertical mixing (Aure et al. 1996, Asplin et al. 1999). In the summer, this layer may be depleted of nutrients due to earlier algal blooms in the spring and summer, leaving mussels with low food availability as the primary production is reduced (Erga et al. 2005).

The present work was designed to test the hypothesis that increased nutrient supply and enhanced mixing of water masses in the euphotic zone would improve the growth conditions for non-toxic relative to toxic algae. A submerged air pipe diffuser was used to create artificial upwelling which could bring nutrient-rich deep water up to the euphotic zone. The experiment was carried out in the inner part of a fjord to test the possibility of creating a controlled geographical area with non-toxic algae for mussel cultivation. This paper presents the biological survey of the experimental study, while the technical analysis is presented in McClimans et al. (2010).

2. Materials and methods

2.1 Location

The study site was located in the inner part of the Arnafjord, an arm of the Sognefjord in southwestern Norway (61° 0’ N, 6° 22’ E) (Fig. 1A). The fjord is approximately 8.5 km long and 0.7 to 1.3 km wide with a surface area of 10 km^2 and maximum depths of 88 m in the inner part and 200 m in the outer part. The fjord was chosen for its shape and topography, low freshwater supply from rivers (less than 2 m^3 s^{-1} in the inner part of the Arnafjord), steep mountains reducing wind mixing and an infrastructure for transport of equipment and access to electrical power. The weather was relatively calm during the experiment, with average wind speed measuring 2.6 m s^{-1} in September (The Norwegian Meteorological Institute: www.met.no). Thus, wind-generated mixing did not affect the water masses substantially during this late summer experiment. A reference station that was not affected by the artificial upwelling was chosen from the National mussel monitoring program (Norwegian Food Safety Authority) in the outer part of a branch of the main fjord (61° 15’ N, 6° 33’ E) (Fig. 1A) .

2.2 Sampling stations

Temperatures and salinities were measured in 5 cross-sections (Stations B-P) at stations in the middle of the fjord and on each side (Fig. 1B). Measurements of nutrients were made at stations S1, S2, S4 and S6 and measurements of phytoplankton were made at stations S1-S6 (Fig. 1B) and at the reference station (Fig. 1A). Station S1 was located on the west side of the inner part, close to the upwelling zone, Station S2 in the middle of the inner part, Station S3 on the east side of the inner part, stations S4 and S5 on the west and east side of the passage between the inner and the outer part of the fjord, respectively, and Station S6 in the middle of the outermost part of the fjord. The distance from the upwelling zone to each station was, 0.5 km, 1.7 km, 2.9 km, 2.9 km, 3.1 km, 6.5 km and 30 km for stations S1-S6 and the reference station, respectively.

2.3 Air pipe diffuser

Three 100 m long air pipes with individual horizontal separations of 1.25 m (Fig. 2) were placed at 40 m depth in the inner part of the Arnafjord. The 50.8 mm diameter pipes were perforated with one 2.5 mm hole per meter and the total air supply was 44 $m^3\ min^{-1}$ of air at normal pressure of 1 atm ($Nm^3\ min^{-1}$). The dimension and distribution of the holes were based on Miller (1990) and the air was supplied by an Ingersoll-Rand screw compressor using 390 kW. The diffuser created an upwelling zone that constituted less than 0.2% of the surface area of the inner fjord, and was run for an experimental period of 21 days.

2.4 Hydrography

Profiles of temperature and salinity were recorded at depths of 0 to 50 m (or bottom) with a CTD (SD 204, SAIV LTD, Norway). Profiles were taken the day before the artificial upwelling started and after 1, 11, 21, 22 and 23 days of bubbling.

2.5 Nutrients

Samples for nutrient measurements were taken three times a week at stations S1, S2, S4 and S6 over a period of 41 days, starting on 4. September 2002 (Day 0 of the sampling period). The bubble curtain was turned on at 22:00 h on Day 0. The water samples were taken with a 10 m tube sampler of 10 mm inner diameter, which integrates the water

column from 0 to 10 m depth. The samples were mixed and subsamples of 250 ml were frozen and stored for the analysis of the sum of nitrite (NO_2^-) and nitrate (NO_3^-) nitrogen, orthophosphate (PO_4^{3-}) and silicate (SiO_4^{4-}) in parallels according to Norwegian Standard, NS4745 (1991), NS4724 (1984) and Strickland and Parsons (1968), respectively.

2.6 Estimation of nutrient supply to the upper layer

The estimation of the nutrient supply to the upper water masses (0-10 m) was undertaken by two independent methods, 1) the Si-mass balance method and 2) the dose-response method. The Si-mass balance method is based on the mass balance of Si, allowing for the estimation of the gross supply of silicate to the upper water masses from Day 0 to Day 25. Si is necessary for cell wall formation of diatoms. The increase of Si concentration in the water was measured while the increase of Si in diatoms was estimated from the increase in diatom biomass. The method relies on the following assumptions:

1. Si is present either in water or in diatoms ($Si_{total} = Si_{dissolved} + Si_{diatoms}$, i.e $\Delta Si_{diatoms} = - \Delta Si_{dissolved}$).
2. Inorganic N, P and Si are transported with deep water in Redfield molar ratio (Redfield 1958, Sakshaug & Olsen 1986).
3. Inorganic N and P are taken up relatively fast by all phytoplankton ($\Delta P_{dissolved}$ and $\Delta N_{dissolved} \sim 0$).
4. The specific growth rate (μ) of the diatoms was set to 1.0 day^{-1}.

Growth rates in diatoms have been measured in the range 1.22 - 1.40 day^{-1} in *Skeletonema costatum* (Nielsen & Sakshaug 1993) and 1.29 and 1.06 day^{-1} in *Chaetoceros* sp. and *Phaeodactylum tricornutum*, respectively (Reitan et al. 1994). A specific growth rate of 1.0 day^{-1} is accordingly a conservative assumption to avoid overestimation of diatom growth.

The second method involved the use of an established inorganic empirical relation describing nitrogen dose (dose-response) versus phytoplankton biomass in the summer season period (June-September) in Norwegian coastal waters. The empirical relationship was established in a 5-year fertilization experiment of the coastal lagoon

system of Hopavågen in Central Norway as part of the MARICULT programme (Olsen 2002). They found a linear relationship between N-fertilization rate (N-load) and average seasonal phytoplankton biomass (Phyto-POC, µg C L^{-1}) described by the equation,

$$\text{Phyto-POC} = 6.61x \text{ N-load} + 13.8,\ R^2 = 0.86, \text{ equivalent to} \quad (1)$$

$$\text{N-load} = 0.15 \text{ x Phyto-POC} + 2.1, \quad (2)$$

where Phyto-POC is phytoplankton biomass (µg C L^{-1}) and N-load is the input of inorganic N (µg N L^{-1} d^{-1}) to euphotic waters. This method was applied. The average phytoplankton biomass (µg C L^{-1}) in the Arnafjord on Day 0 was used as initial data. This allowed extrapolation of the supply rate of inorganic N.

2.7 Phytoplankton

Sampling of phytoplankton was performed three times a week starting on Day 0 of the sampling period. The water samples were taken with the tube sampler used for sampling of nutrients. Subsamples of 300 ml were preserved with a Lugols iodine solution. In addition, vertical samples were taken with a 20 µm plankton net from 0 to 10 m depth. Subsamples of 50 ml taken from this sample were preserved with formaldehyde. The samples were analyzed according to Norwegian Standard NS9429 (2007). Cell numbers were converted to biomass (µg C L^{-1}) according to Table 1, Panel 3 (Smayda 1978). Quantitative analyses of dinoflagellates were made from Lugol-preserved water samples on cellulose nitrate filters after filtration of 50 ml, whereas the other phytoplankton groups were analysed in 0.1 ml volumes without concentration.

2.8 Statistics

Homogeneity of variances was tested with the Levene's test. Equality of means for nutrient and phytoplankton concentrations in the fjord on each sampling day were tested with one-way ANOVA followed by *post hoc* comparisons by Tamhane's T2, not assuming equal variances (SPSS rel. 17.0). The significance limit was set to 0.05. Means are given with standard error.

3. Results

3.1 Hydrography

During the 21-day bubbling period, there was a forced transport of nutrient-rich deep water to the upper layer (McClimans et al. 2010). Upwelling and intense mixing with entrained surface water took place near the bubble curtain and the intrusion of the nutrient-enhanced water flowed out mainly on the right-hand side of the Arnafjord, but covering the entire width of the fjord. Fig. 3 shows the distributions of density anomaly (σ_t = density – 1000 kg m^{-3}) (A) and temperature (B) at Station C 400 m to the east of the bubble curtain prior to and 18 h after the onset of bubbling. The observations were recorded at the same tidal phase to avoid changes due to internal tides. At this location, the mixing produces a slightly increased (5 %) stratification above 5 m depth and a reduced stability below. The density gradient in the intruding mixture is reduced by 20%. The stability of this layer is 1/8 that of the upper pycnocline. The colder water after the onset of bubbling (Fig. 3B) represents the adjustment of water properties at this location due to the bubble curtain. The intrusion depth of cooler, mixed water was from 4 m to 17 m. Due to the unique distribution of warm water in the fjord (4 Sep.), the spreading of this water was traced by temperatures (thermoclines) at all locations (Fig. 1B) to obtain the horizontal distribution of the thickness of the intruding, mixed water after 18 h. From this volume and the temperature changes, McClimans et al. (2010) estimated that the bubble curtain lifted about 65 m^3 s^{-1} of deeper water to the euphotic zone the first 18 hours and presumably during the following weeks of operation. The stratification in the inner fjord on Day 11 was essentially the same as on day 1, but the temperatures were from 1 to 2 ºC colder throughout the water column. This is partly due to the upwelling of colder water and a colder water mass in the outer fjord which flows to the bubbler.

McClimans et al. (2010) considered the total supply of deep water in the spreading flow. The temperature profiles in Fig. 3B show, however, that there are *two* cold cores, both of which contain larger amounts of the upwelled deeper water. The deeper cold core at about 14 m depth is a mixture of the deeper water with the water below the brackish surface water, characteristic of bubble plumes in stratified ambients, since the bubbles do not impart buoyancy to the fluid (*e.g.* Asaeda & Imberger 1993). The upper layer between 5 and 10 m depth is of most concern for the present analysis. This is a layer

that contains entrained water and algae from the brackish surface layer. The characteristics of this water are seen in the temperature-salinity diagram in Fig. 3C. A dashed line showing the assumed mixing in the bubble plume is shown. The dips in the T-S trace shows 3-point mixing of the spreading fluid in the ambient. The locations of the intrusions suggest that the *upper* intruding layer contains approximately two parts of the lower mixture, containing about 40% deeper water, and one part surface water. The temperature distributions at the hydrographic stations after 18 h of bubbling are used to estimate the equivalent thickness of deep water in each intrusion. These results are given in Table 1.

The volume of these masses is obtained from the geographical distribution of the layer thicknesses after 18 h of bubbling. The results from Table 1 suggest that 56 $m^3 s^{-1}$ of upwelled water flows out in the lower core (11 – 17 m) while about 4½ $m^3 s^{-1}$ of deep water and 6½ $m^3 s^{-1}$ of intermediate water flows out above 10 m depth. This upper cold core contains about 5½ $m^3 s^{-1}$ of entrained surface water. Salinity data suggest that more than half of the local fresh water supply is contained in this water. These outflows are consistent with the results of Aseda & Imberger (1993) for the observed density gradient and bubbling of this experiment. The distributions of the layer thicknesses show that the deeper intrusion flows out to the right (southern side of the fjord) while the upper intrusion flows out along the northern shore. In time, these layers span the entire width of the fjord.

3.2 Nutrients

The mean concentration of dissolved silicate-Si increased three-fold in the upper water masses of the fjord (0-10 m) during the first part of the experiment, from Day 4 to Day 15 ($p < 0.05$), and remained at a significantly higher level compared to Day 0 throughout the sampling period ($p < 0.05$) (Fig. 4). The concentrations of phosphate-P were generally very low (<0.15 mmol m^{-3}). The concentrations of nitrate-N showed the same tendency as phosphate-P, with low and almost constant values during the upwelling. The mean total silicate supply rate was estimated to be 2.1 mmol m^{-2} day^{-1} for the upper 10 m (10 m^3), with the dose-response method and 1.3 mmol m^{-2} day^{-1} with the Si-mass balance method in the period with upwelling (Day 3-24) (Fig. 5). The

respective average supply of nitrogen was estimated to be 1.1 and 0.6 mmol m^{-2} day^{-1}, whereas the average supply of phosphate was estimated to be 0.15 and 0.09 mmol m^{-2} day^{-1} with the dose-response method and the Si-mass balance method, respectively.

3.3 Phytoplankton

A decrease was seen in phytoplankton biomass at initiation of the bubbling period followed by a significant increase from Day 9 to Day 20 ($p < 0.05$), and the biomass was significantly higher when it peaked at Day 25 compared to Day 6 ($p < 0.05$) and Day 9 ($p < 0.05$) (Fig. 6A). Furthermore, a significant decrease was evident after termination of the upwelling, from Day 25 to Day 28 ($p < 0.05$). The relative biomass of *Dinophysis* sp. (*i.e.* the fraction of the total phytoplankton biomass) increased significantly from Day 9 to Day 15 ($p < 0.05$), but levelled off from Day 15 to Day 25 and increased further after termination of the bubbling, from Day 25 to Day 30 ($p < 0.05$) (Fig. 6A).

The increase in phytoplankton growth was mainly represented by non-toxic dinoflagellates and not diatoms (Fig. 6B). There was a significant increase in biomass of the genus *Ceratium* sp. during the period of artificial upwelling, from Day 13 to Day 25 ($p < 0.05$), while the growth decreased significantly after the end of the experiment, from Day 25 to Day 41 ($p < 0.05$). *Ceratium furca* and *C. tripos* were the dominant *Ceratium* species, showing a significant increase in biomass from Day 9 to Day 20 ($p < 0.05$) peaking on Day 25 followed by a decrease after termination of the bubling.

During the period of artificial upwelling the mean concentration of *Dinophysis acuta* was below the threshold level of 200 cells L^{-1}, above which there is a ban on mussel harvesting in Norway, whereas after termination it increased and peaked at 480 cells L^{-1} on average on Day 30 (Fig. 7A). The concentration at the reference station in the main fjord exceeded 1000 cells L^{-1} on Day 6 and 2000 cells L^{-1} on Day 30. *Dinophysis acuminata* and *D. norvegica* were subdominant *Dinophysis* sp. recorded in concentrations below 120 cells L^{-1} in the Arnafjord and at the reference station, showing no clear trend with time.

A bloom of the diatom *Pseudo-nitzschia calliantha*, which is a potential neurotoxin producer, was terminating at the beginning of the experiment. A similar pattern was also found for *P. calliantha* at the reference station in the main fjord (Fig. 7B). The non-toxic diatom *Skeletonema costatum* was present in relatively high concentrations in the Arnafjord during the upwelling. *Chaetoceros* spp and *Thalassionema nitzschioides* were subdominant diatoms. The concentration and biomass of the phytoplankton species in the Arnafjord are presented in the Appendix.

4. Discussion

The physical, chemical and biological results support the hypothesis that increased nutrient supply rate and mixing of euphotic water masses can improve the growth conditions for non-toxic relative to toxic algae. However, the hypothesis was more specific, diatoms that had a fast growth rate, but less mobility, would be favoured in the mixed water masses created by the bubble curtain. The mixing reduced the stability (stratification) of the intruding water by only 20% and increased it above 5 m depth. The growth of diatoms was insignificant compared to the growth of non-toxic dinoflagellates in the upper 10 m. The modest upwelling of nutrient-rich deep water to this layer, however, was correlated with a significant increase in biomass of algae from the non-toxic genus *Ceratium* sp., whereas no significant increase was revealed in diatom biomass. The mixing energy gave a significant reduction of the stratification close to the bubble curtain, but most of the fjord was less affected with respect to stratification of water masses. This prolonged the retention time for diatoms. In Arnafjord, vertical diffusion in the less stratified outflowing layer may have contributed to a flux of nutrients to the upper 10 m layer. The observed increase in non-toxic dinoflagellate biomass supports the idea that artificial upwelling of nutrients in fjords has the potential for creating controlled geographical areas with non-toxic algae for mussel production.

4.1 Hydrography

The experimental system changed the stratification in the vicinity of the upwelling zone and led to an effective intrusion of nutrient-rich water between 4 and 17 m depth. The

intrusion depth for most of the deeper water was too deep in the euphotic zone (>10 m) for optimal local primary production. Above 10 depth the bubble plume lifted a mixture of deep and intermediate water to mix with the brackish surface water and form a shallow (4-9 m depth) intrusion in the euphotic zone.

For more effective lifting of the nutrient-rich deep water, more buoyancy is needed, as with the fresh water discharge in Gaupnefjord (McClimans et al. 2010). An alternative method to lift deep water is to pump brackish water to the deeper nutrient source (Aure et al. 2007). This can be done in fjords with sufficient fresh water supply and weak stratification, but in Arnafjord, the limited fresh water supply could lead to a deep intrusion. The intrusion above 10 m depth appears to consume most of the available local fresh water supply.

4.2 Nutrients

Due to the geographical circumstances that shield the water from winds, the *enhanced* nutrient supply to the upper water layers of the fjord was due mostly to the artificial upwelling of deep water. The concentration of dissolved nutrients in the upper 10 m did not quantitatively reflect the rate of nutrient supply to the upper water masses, as the concentrations of nitrogen and phosphate remained low while the biomass of non-toxic algae increased significantly. Nutrient concentrations are rather an expression of the balance of input and consumption of nutrients in the water. Phytoplankton, which is often growth-limited by N and/or P, quickly removes nitrogen and phosphate once they are supplied in higher rates than normal (Sakshaug & Olsen 1986). As a consequence, only dissolved silicate increased significantly in the water masses during the experiment. This is the basis of the Si-mass balance method. The Si-mass balance and the dose-response methods showed similar patterns but the dose-response method yielded twice as high nitrogen supply compared to the Si-mass balance method.

As the N:Si:P ratios are fairly constant in deep water (Redfield 1958, Sakshaug & Olsen 1986, Stigebrandt & Aure 1988), it follows that the nutrients must be transported to photic waters in the same element-ratios. This was supported by the elemental N:Si:P ratios in the upper water masses at Day 30 (N:Si:P = 9:8:1) and 41 (N:Si:P = 15:11:1),

which were in the same range as ratios observed in deep water in Norwegian fjords (N:Si:P = 11:14:1) (Stigebrandt & Aure 1988).

4.3 Phytoplankton

The average phytoplankton biomass increased by ~40% from Day 0 to Day 25, but the increase was not significant due to a bloom of *Pseudo-nitzschia* calliantha that was terminating at the onset of the experiment. A similar pattern was also evident for *Pseudo-nitzschia calliantha* at the reference station in the main fjord, suggesting that the termination occurred naturally and was not caused by the upwelling. By ignoring the biomass of *Pseudo-nitzschia calliantha*, the increase in total biomass becomes significant from the start of the experiment ($p < 0.05$). However, despite the significant increase in silicate supply during the experiment, the increase in biomass was mainly represented by non-toxic dinoflagellates and not diatoms. The results suggest that the artificially created turbulence and the break-down of stratification were local and not sufficient to reduce the growth of dinoflagellates and favour significant growth of diatoms over the fjord. However, non-toxic dinoflagellates responded to the increased nutrient supply better than the diatoms.

The slight increase of stability in the near-surface layer does not allow us to test the hypothesis that turbulent water masses improve the growth conditions for diatoms relative to dinoflagellates (Margalef, 1978, Thomas & Gibson 1990). The biomass of non-toxic dinoflagellates, mainly *Ceratium furca* and *C. tripos*, increased significantly in the period of artificial upwelling and decreased immediately after termination of the experiment. Non-toxic *Ceratium* sp. became also the dominant phytoplankton in another full-scale experiment with artificial upwelling in a western Norwegian fjord (Aure et al. 2007).

The significant increase in biomass of the potentially toxic *D. acuta* in the first half of the experiment ceased in the second part when it appeared to be overwelmed by non-toxic *Ceratium* sp. A possible explanation is that the upwelling created favourable physical conditions for the growh of *Ceratium* sp. but not *D. acuta*. Turbulence and strong mixing have been shown to hamper cell division and affect swimming activity of

dinoflagellates (Estrada & Berdalet 1997, Karp-Boss et al. 2000). However, these were limited to the innermost part of the experimental area, close to the bubble curtain, and can thus explain neither the overall better growth in *Ceratium* sp. compared to *D. acuta* during the upwelling nor the significant rise in *D. acuta* after termination of the upwelling at the same time that *Ceratium* sp. ceased**.**

The observed decrease in phytoplankton biomass from Day 0 to Day 9 suggests that the phytoplankton growth was terminated and brought to a zero-state during the initial phase of the artificial upwelling, before all main groups of phytoplankton responded to increased nutrient supply and the average phytoplankton biomass increased threefold. Nutrient limitation and low initial phytoplankton concentrations were most likely the two main factors controlling the response-time in biomass. The time it took to establish a stationary replenishment of nutrients over the entire Arnafjord (days) may also have contributed to the observed response-time. Nutrients are normally assimilated within minutes to hours while the response in phytoplankton growth may occur after 2-5 days, and an increase in biomass may not be expected until 3-7 days later (Olsen et al. 2007). The nutrient input must thus be considered as an integrated signal over several days.

4.4 Mussel perspective

By applying a ratio of 81 for carbon biomass to chlorophyll *a* (a typical value for Western Norwegian fjords during summer, n = 288, Erga et al. 2005), the obtained phytoplankton biomass (58 µg C L^{-1}) corresponded to 0.72 µg chlorophyll *a* L^{-1}. Pumping has previously been observed to cease at chlorophyll *a* values between 0.3 and 0.6 µg L^{-1} (Noren et al. 1999, Dolmer, 2000, Riisgård, 2001, Strohmeier et al. 2005), whereas in a recent study by Strohmeier et al. (2009) it was demonstrated that *M. edulis* is capable of clearing particles out of suspension at chl *a* concentrations down to 0.01 µg L^{-1}. Furthermore, a zero net energy balance is sustained in *M. edulis* with 1 g soft tissue dry weight (~50 mm shell length) by chl *a* values between 0.67 and 1.02 µg L^{-1} (Hawkins et al. 1999). The obtained phytoplankton biomass in the Arnafjord was presumably sufficient to support active feeding and weight maintenance of blue mussels with market size.

The power consumption of the compressor was 390 KW. Sea-based storage of *e.g.* 300 tons of mussels for clensing over a period of 30 days before harvest would yield an energy cost of 0.1 € kg^{-1} mussels, with an electricity cost of 0.1 € KWh^{-1} (30 days x 24 hours x 390 KW = 224,640 KWh). 300 tons of mussels (5 cm length, 1 g dry weight soft tissue per mussel) with a clearance rate of 2.2 L per mussel per hour (Widdows, 1978), can filter about 1 million m^3 water each day. This is approximately the amount of deep and intermediate water that is lifted above 10 m depth. The response of the biotope suggests also a vertical transport of nutrients in the weaker pycnocline. Thus, rapid water replacement would most likely generate a sufficient nutrient supply to maintain phytoplankton concentrations above the limit for active pumping if long-lines are arranged to maximize the water exchange rate in the mussel farm. Storage of 300 tons of mussels will cover an area of 6 ha with a low density design (< 0.2 mussels L^{-1}) using 30 long-lines measuring 200 m in length with 10 m spacing, covering less than 10 % of the inner area of the fjord (~75 ha).

4.5 Pilot experiment and technology limitations

Temperature profiles from Station C (Fig. 1B), close to the upwelling zone, were used as input data to estimate the mixed layer in the fjord. This approach can introduce some inaccuracy due to the time it takes to visit all stations and phase differences of internal tides. Comparisons are therefore made with data sets close to the same tidal phase. The effective thickness of the spreading, upwelled water (Table 1) showed a systematic decrease to zero about 2.5 km from the mixing after 18 h of bubbling.

The input data in the Si-mass balance method included dissolved silicate-Si in water and organic Si assimilated by diatoms derived from the Redfield C:Si ratio ($Si_{dissolved} = Si_{total} - Si_{diatoms}$). Si in diatoms is the most uncertain part of the accounting as the concentration of Si dissolved in water was only 7 % of Si assimilated by diatoms. Furthermore, a part of the diatom biomass will become consumed by zooplankton causing Si assimilated by diatoms to be slightly underestimated. The Si-mass balance method assumes a conservative specific growth rate of diatoms of 1.0 day^{-1}. A higher growth rate of, say, 1.2 day^{-1} would increase the N-load by 39 %, whereas a lower

growth rate of 0.8 day^{-1} would reduce the N-load by 32 %, showing that this parameter is quite sensitive to this assumption.

The temporal response to the mixing of water masses and spreading of nutrient upwelling was quite evident. Although a seasonal effect is not very likely to occur exactly when the upwelling was initiated and when the biomass increased within the time-span of 21 days in the present experiment, parallel data from a control fjord could have provided a basis to evaluate the role of possible other changes that could shed light on the experimental conditions.

Conclusions

The experiment demonstrated that a submerged bubble curtain can transport nutrient-rich deep water up to 4 - 17 m depth and generate a local reduction of stratification close to the upwelling zone. Due to ambient stratification, there are two intrusions of deep water in this depth range. The upper intrusion between 4 and 10 m depth is of most interest in the present study. The hydrography suggest that 4½ $m^3 s^{-1}$ of deep water and 6½ $m^3 s^{-1}$ of intermediate water mixes with surface water to create this outflow. In addition to this, vertical diffusion of nutrients from the deeper intruding core can reach the upper 10 m of the euphotic layer. The observed rise in phytoplankton biomass is considered to be a result of the total increased nutrient supply to this layer created by the artificial upwelling.

Growth of diatoms was insignificant compared to the dinoflagellate growth. The stability of the upper layer only a short distance from the bubble curtain, and our sampling of the upper 10 m depth did not allow a test of the hypothesis that immobile diatoms with fast growth rates would be favoured over dinoflagellates in the mixed water masses created by the bubble curtain. Nevertheless, significantly better growth of non-toxic species compared to toxic species is a promising result for artificial upwelling when it comes to creating controlled geographical areas with non-toxic food for mussel production.

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Tables

Table 1. Equivalent thickness (m) of deep water in the intrusions after 18 h of bubbling.

Station	Upper intrusion	Lower intrusion
B	0.5	3.0
C	0.3	3.4
D	0	3.2
E	0.5	1.0
F	0.1	1.4
G	0	1.5
H		0.4
I		1.3
J		1.9
K		0.1

Figure captions

Fig. 1. A) The experimental area in Arnafjord (61° 0' N, 6° 22' E), a fjord arm of the Sognefjord in western Norway, and reference station in the outer part of a branch of the main fjord, ~30 km from the experimental area (61° 15' N, 6° 33' E). B) Local hydrography stations (B-P) and stations for sampling of nutrients (S1, S2, S4, S6) and phytoplankton (S1-S6).

Fig. 2. The air bubble diffuser. Upper panel: View from the mountain side. Middle panel: Sketch of the induced circulation. Lower panel: Suspension scheme (McClimans et al. 2010).

Fig. 3. Distributions of density anomaly, σ_t (density – 1000 kg m^{-3}), (A) and temperature, T, (B) at Station C, 400 m to the east of the bubble curtain, prior to (grey line) and 18 h after (black line) the onset of bubbling. C) Temperature-salinity properties at Station C, 18 h after the onset of bubbling. The curved lines are σ_t and the dashed line shows the assumed mixing in the bubble plume.

Fig. 4. Dissolved nutrients in the upper water masses (mmol m^{-3}, 0-10 m) of the Arnafjord before, during and after artificial upwelling (mean value for station S1, S2, S4 and S6±se).

Fig. 5. Estimated nutrient supply to the upper water masses (mg m^{-2}, 0-10 m=10 m^3) in the Arnafjord during artificial upwelling (Day 3-24) (mean value for station S1-S6±se).

Fig. 6. A) Total phytoplankton biomass (µg C L^{-1}, 0-10 m, left axis) and relative biomass of Dinophysis sp. (i.e. the fraction of the total phytoplankton biomass, right axis). B) Biomass of diatoms and non-toxic dinoflagellates (µg C L^{-1}, 0-10 m) in the Arnafjord before, during and after artificial upwelling. Mean value for station S1-S6±se. Data are missing for S5 and S6 on Day 28.

Fig. 7. A) Concentration of Dinophysis acuta and B) Pseudo-nitzschia calliantha (cells L^{-1}, 0-10 m) in the Arnafjord (mean value for station S1-S6±se) and at the reference station in the Sognefjord (n=1) before, during and after artificial upwelling.

Fig 1

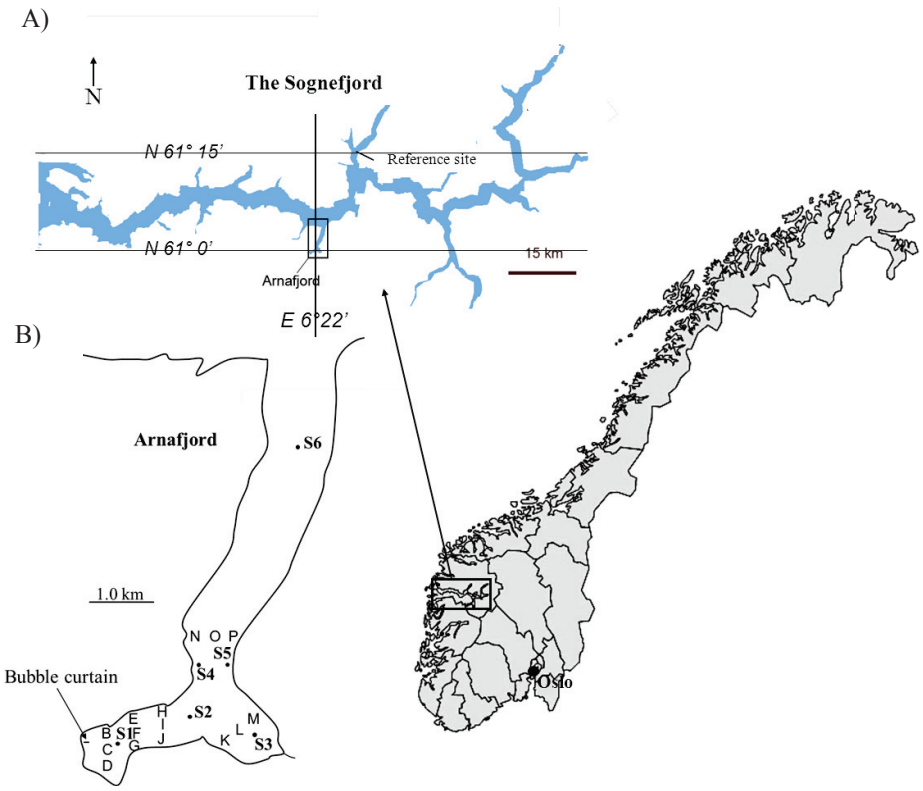

A)
N
The Sognefjord
N 61° 15'
Reference site
N 61° 0'
15 km
Arnafjord
E 6°22'
B)
Arnafjord
S6
1.0 km
N O P
S5
S4
Bubble curtain
S2
S1
S3
Oslo

Fig 2

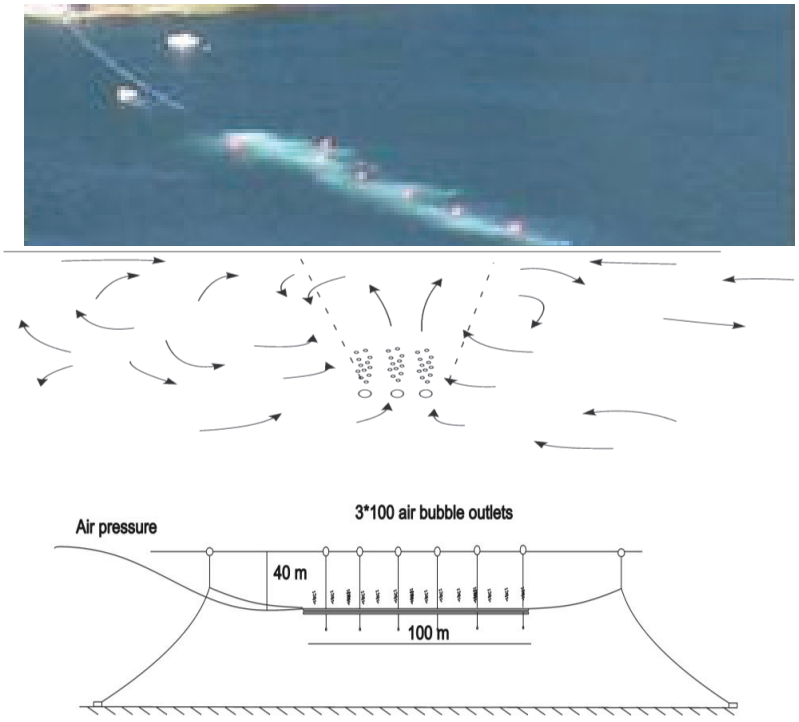
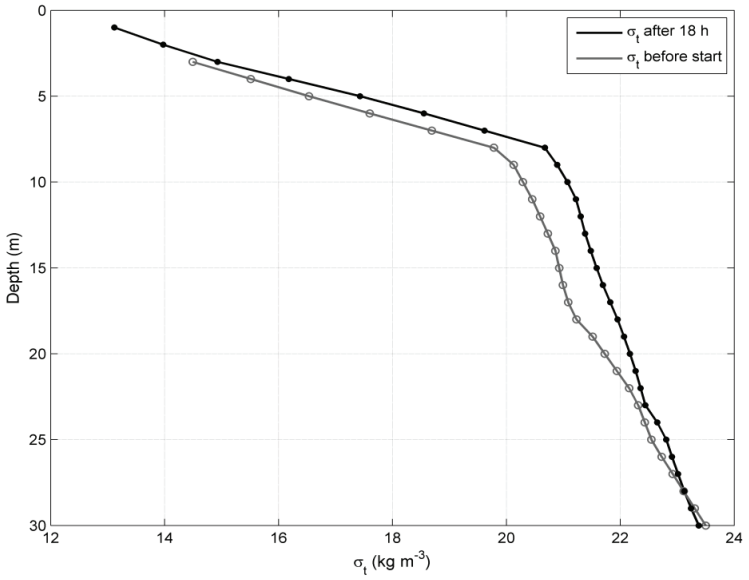
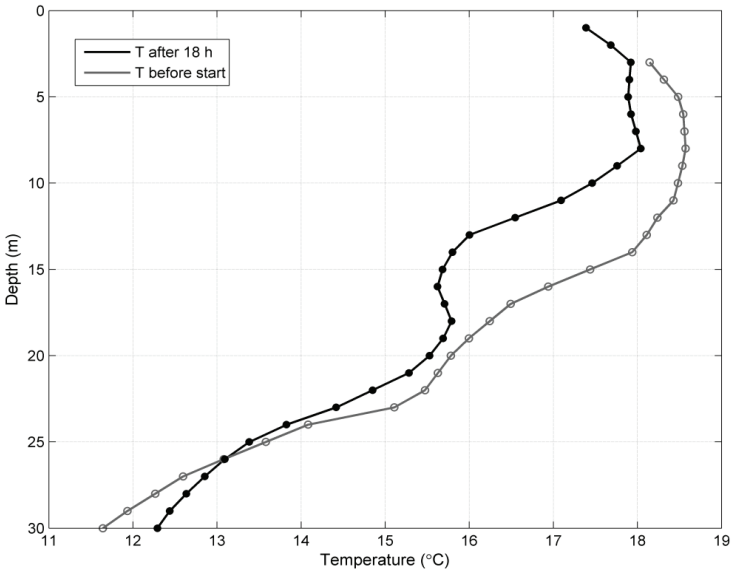


Fig 3

A)


σt after 18 h
σt before start
Depth (m)
σt (kg m-3)
0
5
10
15
20
25
30
12
14
16
18
20
22
24

B)


T after 18 h
T before start
Depth (m)
Temperature (°C)
0
5
10
15
20
25
30
11
12
13
14
15
16
17
18
19

C)

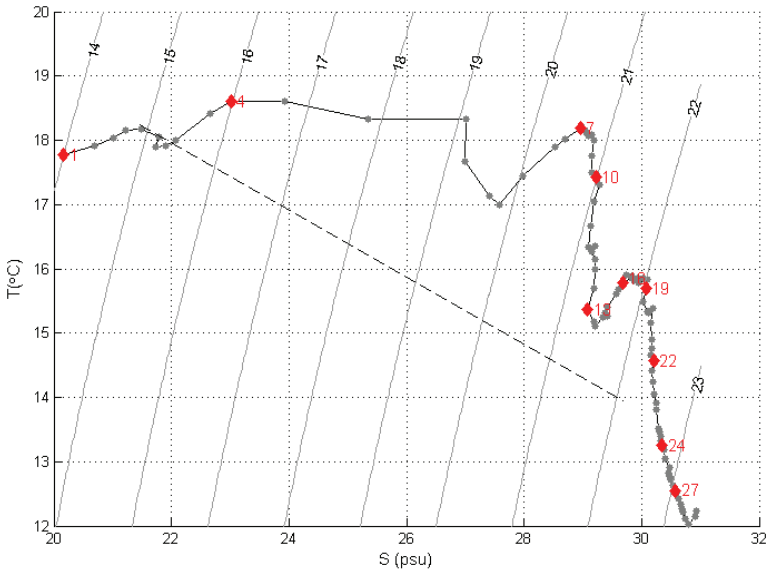


Fig 4

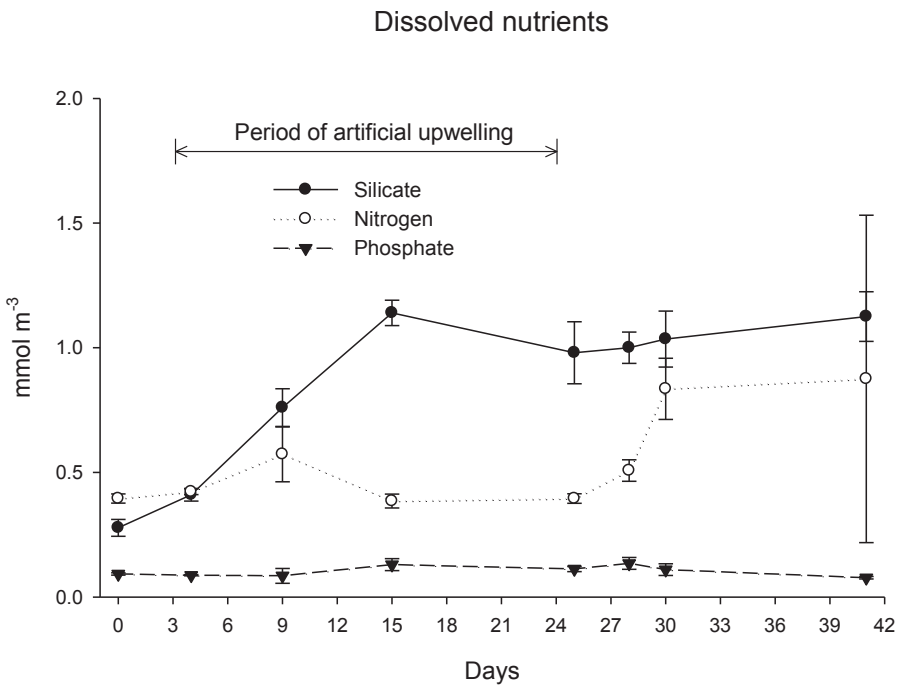

Dissolved nutrients
Period of artificial upwelling
Silicate
Nitrogen
Phosphate
mmol m-3
2.0
1.5
1.0
0.5
0.0
0
3
6
9
12
15
18
21
24
27
30
33
36
39
42
Days

Fig 5

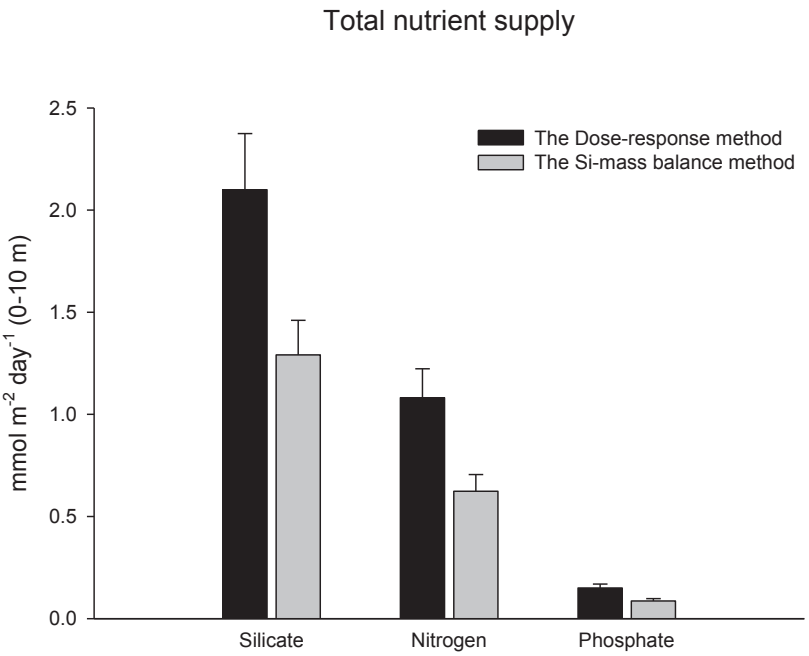
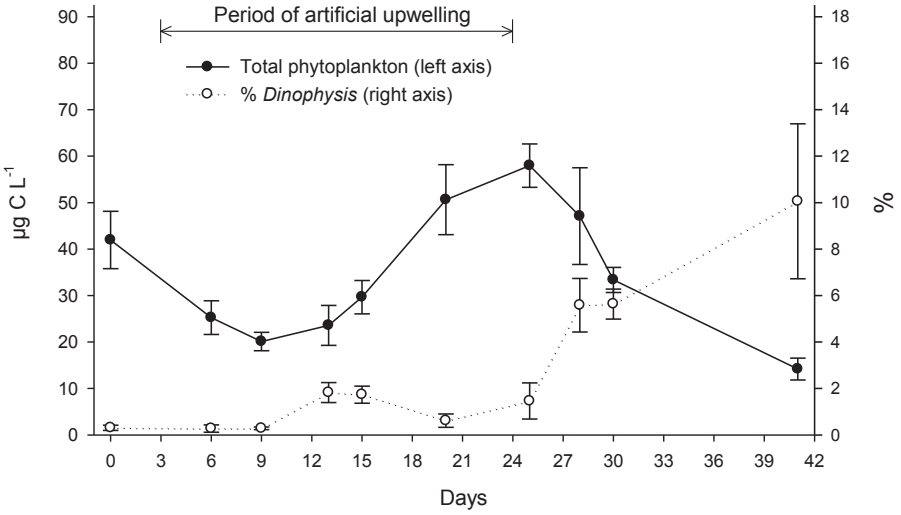

Total nutrient supply
The Dose-response method
The Si-mass balance method
mmol m-2 day-1 (0-10 m)
2.5
2.0
1.5
1.0
0.5
0.0
Silicate
Nitrogen
Phosphate

Fig 6

A)


Period of artificial upwelling
Total phytoplankton (left axis)
% Dinophysis (right axis)
µg C L-1
%
Days

B)

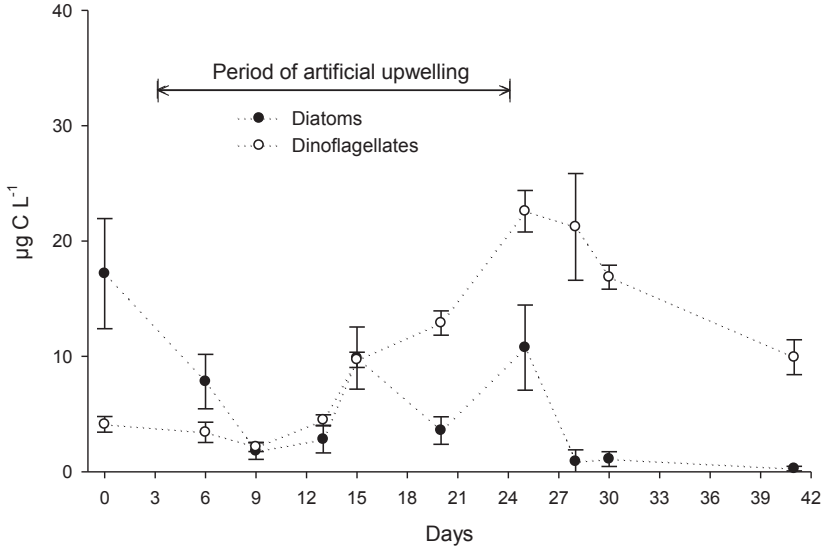
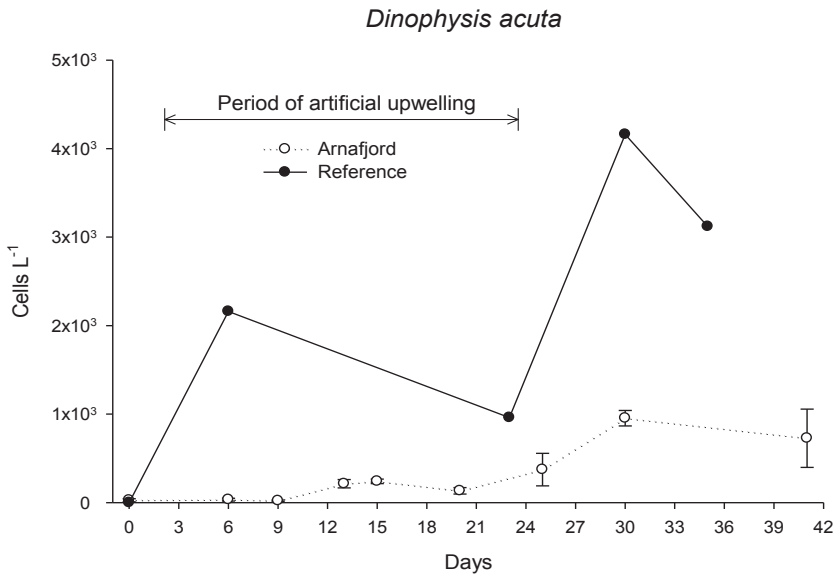
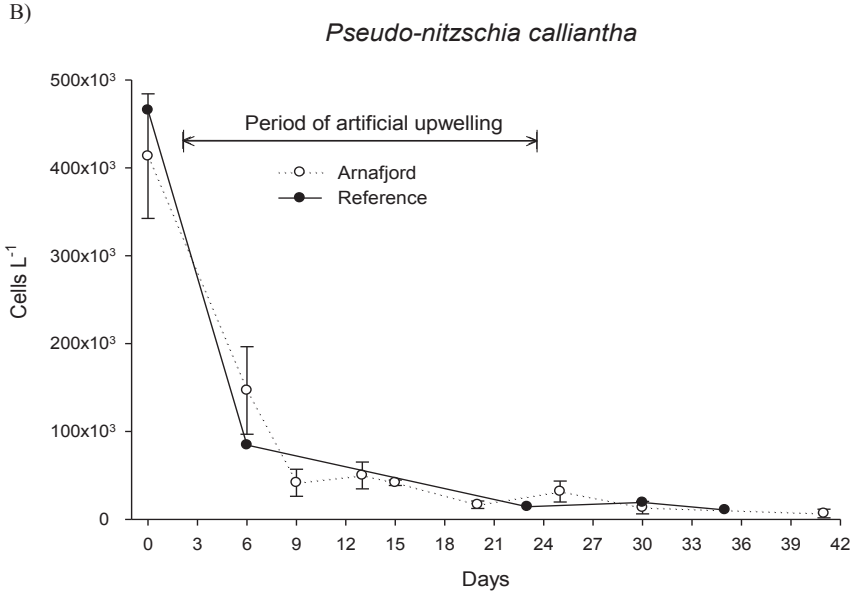

Period of artificial upwelling
Diatoms
Dinoflagellates
µg C L-1
Days

Fig 7

A)


Dinophysis acuta
5x10³
4x10³
3x10³
2x10³
1x10³
0
Cells L⁻¹
Period of artificial upwelling
Arnafjord
Reference
0 3 6 9 12 15 18 21 24 27 30 33 36 39 42
Days

B)


Pseudo-nitzschia calliantha
500x10³
400x10³
300x10³
200x10³
100x10³
0
Cells L⁻¹
Period of artificial upwelling
Arnafjord
Reference
0 3 6 9 12 15 18 21 24 27 30 33 36 39 42
Days

Paper V

Growth and incorporation of food components in tissues of mussels (*Mytilus edulis*) fed salmon fish feed and faeces: implications for integrated multi-trophic aquaculture

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Key words: *Mytilus edulis*; salmon fish feed; salmon faeces; fatty acids; bivalve growth; integrated multi-trophic aquaculture.

Abstract

The incorporation of salmon fish feed and faeces components in the digestive gland, mantle, and gill tissue of blue mussels (*Mytilus edulis*), as well as the corresponding growth in shell length and soft tissue dry weight, were studied in two laboratory experiments run for 21 days in March (Experiment 1) and 28 days in June 2009 (Experiment 2), respectively. In Experiment 1 mussels fed mono rations of *Rhodomonas baltica* (RB) or salmon fish feed (FD) were compared to starved mussels (ST) (control). In Experiment 2 mussels were given mixed rations of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or mono rations of either a full (RB) or half ration (1/2RB) of *R. baltica*. Feeding trials were designed to supply a particulate organic carbon ration equal to ~5% of soft tissue carbon content ind^{-1} day^{-1}.

The length growth rate for RB, FD and ST in Experiment 1 measured 0.8, 0.26 and 0.15 μm day^{-1}, respectively, while negative growth rates were evident for tissue dry weight; -1.1%, -1.9% and -2.1% day^{-1}, respectively. A similar length growth was seen for RB in Experiment 2 (0.82 μm day^{-1}), while the growth rate for FD+RB, ½RB and FC+RB measured 0.6, 0.3 and 0.4 μm day^{-1}, respectively. The dry weight growth in Experiment 2 was 0.24%, 0.0%, 0.0% and -0.8% day^{-1} for RB, FD+RB, ½RB and FC+RB, respectively.

Significant changes in the fatty acid composition, which appointed that of the food profiles, were evident in the digestive gland and gill tissue ($p<0.05$), whereas no changes were found in mantle tissue. 18:1 (n-9), 20:1 (n-9) and 18:3 (n-3) were identified as the single fatty acids contributing most to the changes, which were more pronounced in mussels feeding on salmon fish feed than faeces.

The results indicated that blue mussels incorporated and utilized salmon fish feed more efficiently for growth than salmon faeces.

Abbrevations

RB	*Rhodomonas baltica*
FD	Fish feed
FC	Fish faeces
ST	Starvation
AGR_L	Average growth rate in length
$SGR_{DW'}$	Specific growth rate in soft tissue dry weight
DG	Digestive gland
M	Mantle
G	Gills

1. Introduction

Global salmonid production increased by ~60% from 1999-2009 (1.26 to 2.17 million tons) (FAO, 2011), and further growth is expected. Atlantic salmon (*Salmo salar*) cage aquaculture accounts for the majority of the production (1.44 million tons in 2009, FAO, 2011), and it is estimated that 67-84% of the nutrients (carbon, nitrogen and phosphorous) from the feed input are released into the surrounding waters as respiratory products, faeces and uneaten feed particles (Gowen and Bradbury, 1987; Hall, 1990; Hall et al., 1992; Holby and Hall, 1991; Troell et al., 2003 and references therein, Norði et al., 2011). There is an increasing concern with regard to the negative environmental impacts associated with this nutrient load (Braaten, 2007; Amberg and Hall, 2008; Tett 2008), with one of the major challenges for the sustainable development of salmonid mariculture therefore being to minimize waste discharges that can potentially lead to deterioration of the local marine environment (Chesuk et al., 2003).

As a measure to reduce this menace it has been suggested to cultivate extractive and filter feeding species at lower trophic levels in close vicinity to the fish farms in an integrated multi-trophic aquaculture (IMTA) system. IMTA has two non-conflicting overall objectives: 1) Increased biomass production and added value based on the feed investments, and 2) mitigating potentially negative environmental impacts of waste nutrients. In this way, IMTA may contribute to a more sustainable aquaculture production (Chopin et al., 2001, 2008; Neori et al., 2004, 2008; Troell et al., 2003, 2009). In a properly designed IMTA system, the dissolved nutrient wastes can be taken up by inorganic extractive species such as seaweed (Buschmann et al., 2001; Chopin et al., 2001; 2004), while wastes of particulate organic nutrients can be consumed by filter feeding species such as mussels. Particulate wastes from fish cage farms mainly consist of uneaten feed and faeces (Cheshuk et al., 2003; Hall et al., 1992; Holby and Hall, 1991), and the loading rate and level of impact on the benthic marine environment depends on the transport distance (Weston, 1990; Beveridge, 1996; Kutti et al., 2007). Several studies have indicated that bivalve filter feeders can provide bioremediative services when co-cultivated with fed fish produced in cage aquaculture (Folke and Kautsky, 1989; Folke et al., 1994; Troell and Nordberg, 1998; Soto and Mena, 1999; Mazzola and Sarà, 2001; Whitmarsh et al., 2006; Peharda et al., 2007; Gao et al., 2008),

thus supporting the idea that filter feeding activity may reduce the negative environmental impact associated with a great release of particulate organic matter from marine cage aquaculture (Cheshuk et al., 2003 and references therein). For example, Davies (2000) estimated a 5% direct feed loss from cage aquaculture and a total particulate load (feed and faeces) constituting 15% of the feed use, while Gowen and Bradbury (1987) found that 26% of the eaten food was released into the surrounding water as faeces.

Blue mussels have been shown to filter small particles of salmon fish feed (MacDonald et al., 2011; Reid et al., 2010) and faeces (Reid et al., 2010), while changes in fatty acid composition have been used to demonstrate an incorporation of salmon fish feed components in bivalves (Gao et al., 2006; Redmond et al., 2010). Fish feed contains a high percentage of lipids from marine sources with high proportions of, *e.g.* 20:1 (n-9) and 22:1 (n-11), but there has been an increase in recent years in the use of terrestrial lipid sources (Dahlsgaard et al., 2003; Skog et al., 2003; Narváez et al., 2008 with high proportions of, *e.g.* 18:1 (n-9) and 18:2 (n-6). Significant changes in the proportions of these fatty acids in the digestive gland of mussels take place within 28 days after a change in diet (Redmond et al., 2010). However, although efforts have been made to investigate the potential of bivalve filter feeders to perform bioremediative services in IMTA, little is known about the ability of particulate wastes originating from salmon farming to promote shellfish growth (MacDonald et al., 2011).

Several studies have indicated better growth for mussels grown adjacent to cage fish farms (Wallace, 1980; Stirling and Okomus, 1995; Lander et al., 2004; Peharda et al., 2007; Sarà et al., 2009), while others have failed to demonstrate this (Taylor et al., 1992; Chesuk et al., 2003; Navarrete-Mier et al., 2010), suggesting that the distance from the farms does not substantially influence food availability and growth. The explanations given are that: a) the particulate wastes of the fish farms do not increase the seston concentrations significantly above ambient levels, b) that the ambient seston concentrations remain consistently above the pseudofaeces threshold level, thereby limiting the potential of mussels to increase their growth by feeding upon fish farm wastes (Chesuk et al., 2003), c) that the mussels' filtering response is to slow to adapt to

pulsed feeding regimes accompanied by d) non-uniform effluents from salmon farms leaving mussels to only ingest farm particulate wastes when natural seston concentrations are scarce, and e) that spatial and temporal differences in hydrodynamic conditions between sites, in addition to the experimental design, differ in ways which make it difficult to obtain univocal conclusions for the IMTA concept (Troell and Nordberg, 1998; Troell et al., 2009, 2011). In any case, conflicting results bring some uncertainty to whether the combined cultivation of fish and blue mussels can reduce the organic load from fish cage aquaculture. There is therefore a need to further explore the incorporation of salmon fish feed and faeces and the corresponding mussel growth.

This study aimed to examine food incorporation and the growth of blue mussels fed salmon fish feed and faeces particles. For that purpose, two experiments were carried out with continuous feeding under controlled laboratory conditions in order to eliminate temporal and spatial variations in feed and faeces fluxes and to enable high particulate waste concentrations relative to microalgae densities, thereby forcing mussels to feed upon salmon fish feed and faeces. The hypothesis was that mussels would incorporate salmon fish feed and faeces particles and exhibit the same growth performance in shell length and soft tissue dry weight as mussels fed the microalgae *Rhodomonas baltica*.

2. Material and methods

2.1. Experimental design

Blue mussels (*Mytilus edulis*) were fed salmon fish feed, faeces and the microalgae *Rhodomonas baltica* in two laboratory experiments reviewed in Table 1, one in March 2009 in which mussels were fed mono rations of *R. baltica* (RB) or salmon fish feed (FD), with starved mussels (ST) acting as a control (Experiment 1; M-mussels), and one in June 2009 in which mussels were offered two mixed rations consisting of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or a full (RB) diet or half ration (1/2RB) of *R. baltica* (Experiment 2; J-mussels). The particulate organic carbon (POC) content of experimental diets corresponded to ~5% day^{-1} of the carbon content of soft tissue dry weight (DWC) of the individual mussels (DWC was ~40%, n=10).

Feed pellets were of the Optiline 2500 type (Skretting Ltd). Faeces were collected at a salmon cage farm at Sistranda (Frøya) in Central Norway. Salmon (3-6 kg) were anaesthetized with benzoak prior to squeezing for faeces, which were then frozen in thin plates at -80°C. *R. baltica* (Clone NIVA 5/91, d=6-10 µm, ~41.4 pg C $cell^{-1}$, ~7.4 pg N $cell^{-1}$) was cultivated semi-continuously at 20±2 °C and maintained at 50% of their maximum growth rate by daily dilution. The cultures were enclosed in 160 and 200 l polycarbonate tubes (40 cm in diameter) with natural seawater at ambient salinity (33-34 psu) and enriched with a Conwy medium (Walne, 1974). The cultures were continuously illuminated by six GE Polylux XL 830 F58W fluorescent tubes from three sides, producing an irradiance level of 400 µEinstein m^{-2} s^{-1} measured in the centre of an empty and clean culture tube. The algae were kept in suspension by aeration from the bottom by compressed air-added CO_2 to keep the pH in the cultures in the range of 7.5-8.5. Prior to use, 1 µm-filtered sea water was collected in a 700l reservoir for temperature acclimation, and sterilized with sodium hypochlorite (25 ml industrial grade (10-15%) NaOCl / 100 l of seawater for at least six hours) before neutralization with sodium thiosulphate pentahydrate (3.0 gr/25ml NaOCl for at least six hours) under aeration. All diets were homogenized and freeze-dried for 24 h prior to analyses of the carbon content on a Carlo Erba CHN model 1106 elemental analyser. The carbon and nitrogen content of salmon fish feed and faeces were 50% and 6.5% and 30% and 2.6%, respectively, of dry weight (n=3).

Each day during the experiments, feed pellets and frozen faeces were weighed (Mettler Toledo UMX2) and crushed for 10 sec in 500 ml 1 µm-filtered seawater using a kitchen blender (Electrolux ASB 2600) before the pastes and *R. baltica* were transferred to cleaned feeding tanks with a cone bottom filled with filtered, aerated seawater (2 µm) to maintain a uniform feed distribution. The volume of feed suspension in the feeding tanks (30 L in Experiment 1 and 90 L in Experiment 2) was adjusted to exceed the daily supply to the experimental trays by 20% to help maintain a sufficient water level to keep the feed in suspension. After the new feed was added, water samples (20 ml, n=3) were taken from the feed tanks to determine the particle density with a Beckman Coulter-Counter Multisizer 3 (BCCM3) (mean of three counts) before the feed

concentrations were firmly adjusted by adding more food or diluting with seawater if needed. One feed tank was applied for each type of food.

2.2. Mussels

Mussels (38-42 mm) were collected from a suspended longline farm at Møriholmen in Åfjorden in Central Norway (63° 56' N, 10° 11' E), and transferred to laboratory facilities at the No☺rwegian University of Science and Technology (NTNU) for acclimatization in flow-through raceways (40x20x400 cm, 320 L volume, 6.0 L min^{-1} exchange rate) at 10°C for 14 days prior to each experiment. Sand-filtered and UV-treated seawater (35 ppt) from 70 m depth in the Trondheimsfjord was temperature-regulated in aerated reservoirs before impurities were successively removed by two serially coupled CUNO AquaPure filters with nominal retention of particles >50 µm and >2 µm, respectively. *R. baltica* was continuously added in the front of the raceway with peristaltic pumps (Watson-Marlow 505U), keeping the inflow concentration at ~1000-2000 cells ml^{-1}. The temperature was increased to 16ºC for 2 h prior to Experiment 2 in order to induce spawning in mature mussels, although only minor spawning incidents were observed.

After acclimatization, the mussels were placed on horizontal grid plates (25x0.4x50 cm) 2 cm above the bottom in rectangular plastic trays (40x15x70 cm, 30 L) with flowing seawater (Table 1). A perforated plastic plate (2 mm holes) was installed vertically in the water stream in front of the horizontal plate to avoid strong turbulence and to create a uniform feed distribution. Food was continuously added to the mixing zone in front of the perforated plate with peristaltic pumps (Watson-Marlow 505U). The water level was regulated by an overflow device made by a vertical circular discharge pipe (height over tray bottom 14 cm) at the "distal" end of the tray. The water exchange was 6 L h^{-1} (20% of the volume), which should theoretically be sufficient to maintain the oxygen saturation above 70% based on a maximum oxygen consumption rate of 0.5 ml O_2 ind^{-1} h^{-1} (Handå et al., *in press*). To minimize sedimentation and maintain a uniform distribution of food particles in the trays, the water was constantly pumped from the distal end of the tray to the mixing zone in front of the perforated plate at a rate of 3 L min^{-1} by an external aquarium pump (New-Jet 1), leaving the water volume in the trays

to be circulated 6 times h^{-1}. During the experiment, water samples (20 ml, n=3) were taken in front of the perforated plate and the recirculation inlet five times between day 7 and the termination of each experiment to measure particle concentrations in the experimental trays with a BCCM3.

2.3. Clearance rates

Clearance rates (CR) were measured for salmon fish feed, faeces and *R. baltica* by placing single mussels (n=7 for each food type) in circular glass containers filled with 2 L of 1 µm-filtered and aerated seawater-added salmon fish feed, faeces or *R. baltica* particles. Water samples (20 ml) were taken every 30 min for two hours to calculate the CR based on particle counts with a BCCM3 as follows:

$$CR\ (L\ h^{-1}) = V \times (\log C_1 - \log C_2)/t, \quad (1)$$

where V is the water volume, C_1 and C_2 are particle concentrations at the start and end of each sampling period and t is the time in hours (Widdows and Staff, 1997). The measurements were corrected for particle density reduction due to sedimentation using data from control containers with the food source dispersion only.

2.4. Growth measurements

The shell length and dry weight (DW) of soft tissue were measured both prior to-, and at the end of each experiment. The length was measured with a digital caliper (Vernier 150 mm), while changes in the soft tissue dry weight (DW) were expressed as a condition index standardized to a certain shell length L' according to Bayne and Worrall (1980) and Bonardelli and Himmelman (1995). The DW was measured with an electronic weight (Mettler Toledo Precisa 180A) after drying the tissue at 60ºC in a Termaks heat cabinet for 48 hours, and the index was then calculated as a standardized dry weight (DW') by the following equation:

$$DW' = DW\ (L'^{b}/L^{b}) \quad (2)$$

where DW is the weight in mg, L the length in mm and b the slope of $\log_{10}$ DW plotted as a function of $\log_{10}$ L. DW' corresponds to the condition index, and was scaled so it equals the DW when L equals L'. L' was set to 40 mm based on an average shell length of 40.2±1.0 mm (n=580) in March and 40.2±1.2 mm (n=450) in June. The mean initial

DW' before the feeding experiments was 312±4 mg (n=150) in March and 325±4 mg (n=60) in June. The specific growth rate (μ, d^{-1}) in DW' ($SGR_{DW'}$) was calculated by the equation:

$$\mu = (\ln DW'_t - \ln DW'_0)/t \quad (3)$$

The percentage growth per day (*P*) was calculated by the equation:

$$P = 100 \times (\exp(\mu) - 1) \quad (4)$$

The average rate of length increase (μm, d^{-1}) (AGR_L) was calculated by the equation:

$$\mu m = (L_t - L_0)/t \quad (5)$$

where L_0 and L_t are L at the start and end of each experiment, respectively, and t is the time in days.

2.5. Fatty acid analysis

Fatty acid composition in each food source and in the mussels' digestive gland, mantle and gill tissue was analysed in Experiment 2. The *R. baltica* was centrifuged (Hettich Zentrifugen Universa 32R) in 50 ml tubes at 2500 rpm (15°C) for 2.5 minutes. The precipitated material (0.5-1 ml) was transferred to 15 ml pre-cooled tubes prior to a second centrifugation at 2500 rpm (15°C) for 2.5 min before the supernatant was removed and the *R. baltica* transferred to 1.5 ml Eppendorf tubes that were centrifuged at 3000 rpm (15°C) for three more min followed by a final removal of the supernatant. The samples of *R. baltica*, salmon fish feed, faeces (n=6) and mussel digestive gland, mantle and gill tissue (n=5) were flushed with nitrogen to avoid oxidation and maintain the original polyunsaturated fatty acids, and stored at -80°C until analysis.

The total lipids were extracted according to Bligh and Dyer (1959), followed by analysis of fatty acids after treating the samples according to Metcalfe et al. (1966). 0.8 ml of distilled water, 2 ml of methanol and 1 ml of chloroform with C19:0 as an internal standard (Nu-Chek Prep, Japan) were added to the freeze-dried and weighed samples before being vortexed (1 min) and added 1 ml of chloroform. The tubes (kimax) were then vortexed (20 s), added 1 ml of distilled water and re-vortexed (20 s), followed by centrifugation (4000 rpm, 10 min, 4°C) (Hettich universal 32R). 0.5-1 ml of the chloroform phase was then transferred to kimax tubes from which the chloroform was

steamed off. 1 ml of 0.5N NaOH-methanol was then added and the tubes were vortexed and heated (100°C, 15 min) to release the fatty acids (hydrolysis). The tubes were then cooled on ice, after which 2 ml of 12 BF_3 in methanol was added for esterification. The samples were then again vortexed, heated (5 min, 100°C) and cooled again. Finally, 1 ml of isooctane was added to the samples, which were vortexed, heated (1 min, 100°C) and then cooled again before 3 ml of saturated NaCl solution was added. The methyl esters were then extracted with isooctane (3x0.5 ml) and centrifuged (4000 rpm, 3 min) before the upper isooctane phase was transferred to vials and analysed for fatty acids using a gas chromatograph (Perkin Elmer AutoSystem XL) with TotalChrom Version 6.3.1 software. The system was equipped with an auto injector (injection volume of 1 µl, on-column injection, inlet temperature 250 °C) and a flame ionization detector (FID, 280 °C). A fused silica capillary column (Varian, 25 m, 0.25 mm i.d.) coated with a chemically bonded polyethylene glycol (CP-wax 52CB) was used. The temperature programme for the oven was 90 °C for 1 min, which was then raised to 150 °C at 30 °C min^{-1} and finally to 225 °C at 3 °C min^{-1} and held for 7 min. Helium was used as the carrier gas. The retention times of the fatty acid methyl esters were compared to commercial standards (Nu-Chek Prep, Japan) and quantified by the use of C19:0 as an internal standard in combination with external standard curves.

2.6. Gender determination

Gametes from the mantle tissue were activated by placing a small tissue sample dissected with a scalpel in filtered (1 µm) seawater. A glass pipette was used to transfer the activated gametes to a microscope (Leitz Wetzlar Dialux), where the sperm or eggs were visually identified. Mussel sperm is activated in contact with salt water, while the spherical eggs (68-70 µm diam.) remained passive. Gender was determined in order to reveal any differences between the fatty acid composition in male and female mantle tissue.

2.7. Data analysis

The growth rate data for Experiment 1 are presented as mean±standard error represented by four experimental trays (n=4) with 50 mussels in each, while the growth data for Experiment 2 were pooled to obtain mean values as there were different

numbers of experimental trays for each treatment (See Table 1) (n=50, 100, 150 and 150 mussels for the 1/2RB, RB, FD+RB and FC+RB diets, respectively). Average growth rates are therefore represented with error bars for the mean of four experimental trays for each treatment in Experiment 1 and for mussels from all trays representing each treatment (without error bars) for Experiment 2.

The data for shell length and DW' were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variance using a Levene's test. The Mann Whitney U test for non-parametric data was used to analyse the equality of mean particle densities in both experiments and equality of means for growth in length and DW' in Experiment 1. For Experiment 2, the equality of means for shell length, DW' and relative content of identified fatty acids (% per g wet tissue of digestive gland, mantle and gills) between Day 0 and Day 28 samples, and between the different treatments on Day 28, were tested with one-way ANOVA followed by post hoc comparisons by Tamhane's T2, not assuming equal variances. The sum of monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) was analysed using a Mann Whitney U test. The means for fatty acid data are given with standard error. The significance limit was set to 0.05.

Statistical analyses were performed using SPSS (rel. 17.0, Chicago, SPSS Inc.), while a principal component analysis (PCA) for fatty acid composition was performed with an Unscrambler version 9.8 2008 (Camo Software LTD). The data was analysed without weighing, therefore leaving open the chance for the PCA of each tissue to be dominated by the fatty acids that dominated the fatty acid composition.

3. Results

3.1. Particle sizes

After mixing salmon fish feed pellets and frozed faeces with filtered seawater, more than 99% of the salmon fish feed and faeces particles were distributed within the size range equivalent to a sphare diameter between 2 and 30 µm. Within this size range, 85% of the fish feed particles were 2-5 µm, 11% were 5-10 µm and 4% were 10-30 µm (Fig. 1A). Salmon faeces particles in the range of 2-5 µm comprised 72% of the 2-30 µm size distribution, while 24% were 5-10 µm and 3.6% were 10-30 µm (Fig. 1B). The cell size of *R. baltica* was 6-10 µm.

3.2. Clearence rate

Mussels cleared salmon fish feed, faeces and *R. baltica* with high efficiency and exhibited a similar pattern of variation for the various food sources. Among the particle concentrations that were obtained within the sample intervals, the highest CR measured 2.42, 2.85 and 2.44 L h^{-1} at ~1680, ~2450 and ~1080 particles ml^{-1}, respectively, while a significant lower CR was found for higher and lower particle concentrations ($p<0.05$) (Fig. 1C). The CR was significantly higher for *R. baltica* compared to feed and faeces at the highest particle concentrations, while being low for all types of food with particle densities <500 ml^{-1}. The clearance of feed, faeces and *R. baltica* was ceased at 354, 433 and 235 particles ml^{-1}, respectively.

3.3. Food availability

In Experiment 1, the mean particle concentration was significantly higher in FD trays (2035±130 ml^{-1}) than in RB trays (1160±80 ml^{-1}), and significantly higher in RB trays than in ST trays (630±90 ml^{-1}) ($p<0.05$) (Fig. 2A). The concentration in the one control tray without mussels (C) was 520±108 particles ml^{-1}, thereby reflecting the concentration of particles in the inlet water. In Experiment 2, the mean particle concentration was significantly higher in FD+RB (2010±180 ml^{-1}) and FC+RB trays (2100±160 ml^{-1}) than in 1/2RB (975±190 ml^{-1}) and RB trays (1460±150 ml^{-1}) ($p<0.05$) (Fig. 2B). The concentration in the C-tray without mussels was significantly lower (524±85 particles ml^{-1}). The particle densities were accordingly in the range in which the mussels showed the highest CR.

3.4. Growth in shell length

Both the growth in length and the average length growth rate were significantly higher for M-mussels fed RB (AGR_L=33.3 µm day^{-1}) than for mussels fed FD (10.3 µm day^{-1}) and ST (5.9 µm day^{-1}) ($p<0.05$), whereas no differences were found between mussels fed FD and ST (Fig. 3 AC). A significant length growth was also evident for J-mussels fed RB as well as RB+FD ($p<0.05$), whereas no significant growth in length was found for mussels fed the 1/2RB or FC+RB (Fig. 3 BD).

3.5. Growth in soft tissue

All treatments resulted in weight loss for M-mussels ($p<0.05$) (Fig. 4A) and the $SGR_{DW'}$ was significantly less negative for mussels fed RB (-1.1% day^{-1}) compared to mussels fed FD (-1.9% day^{-1}) or ST (-2.1% day^{-1}) ($p<0.05$) (Fig. 4C). The DW' of J-mussels was significantly higher for mussels fed RB compared to FD+RB, FC+RB and ½ RB at the end of the experiment ($p<0.05$), (Fig. 4B). This resulted in an $SGR_{DW'}$ of 0.24% day^{-1} for the RB treatment and weight maintenance of mussels fed the 1/2RB and FD+RB ($SGR_{DW'}$=0.0% day^{-1}), whereas mussels fed FC+RB demonstrated a significantly lower and negative $SGR_{DW'}$ (-0.8% day^{-1}) ($p<0.05$) (Fig. 4D).

3.6. Fatty acid content

The fatty acid content (% of total FA in DW tissue) was significantly higher in the digestive gland of the mussel (6.1±0.5%) than in the mantle tissue (3.9±0.6%), and significantly higher in mantle tissue than in gill tissue (1.6±0.2%) at the start of the experimental period ($p<0.05$) (Fig. 5A). The fatty acid content increased significantly in the digestive gland tissue of mussels fed FD+RB during the experimental period, from 6.1 to 9.5% of DW ($p<0.05$), whereas no significant changes were seen in mantle and gill tissues for this treatment or in any tissues in the mussels that were fed FC+RB or RB. The fatty acid content was highest in salmon fish feed (25.4±0.5%) and lower and not significantly different in faeces (5.3±0.1%) and *R. baltica* (5.6±0.3) (Fig 5B).

3.7. Fatty acid composition

The fatty acid composition of the digestive gland, mantle and gill tissue of mussels at Day 0 (control, fed *R. baltica* for 12 days), and for mussels fed RB, FD+RB and FC+RB, is shown in Table 2 A-C. Significant changes in the fatty acid composition of tissues in the direction of the composition of salmon fish feed and faeces were evident in the digestive gland and gill tissue ($p<0.05$), whereas no changes were identified in the mantle tissue (Fig. 6 A-C). The fatty acid composition (% of identified FAs in dried material of salmon fish feed, salmon faeces and *R. baltica* is shown in Table 3. A lower total fatty acid content and mono- and polyunsaturated FAs, and a higher content of saturated fatty acids in faeces than in fish feed, indicated a poorer nutrient quality for faeces.

3.7.1 Digestive gland

Out of 22 identified fatty acids in the digestive gland samples at Day 28, the 18:1 (n-9) was the only one that had increased more in mussels fed FD+RB and FC+RB than in mussels fed RB (from 1.6% at Day 0 to 7.1, 2.2 and 1.5% at Day 28, respectively) ($p<0.05$) (Table 2A). The more pronounced increase of this acid in mussels fed FD+RB compared to FC+RB ($p<0.05$) reflected the higher content of 18:1 (n-9) in salmon fish feed (26%) than in salmon faeces (11%), while *R. baltica* contained only 2% (Fig. 6 D).

There was also a significant increase in 20:1 (n-9) in mussels fed FD+RB (2.2 to 3.3% of total FA), ($p<0.05$), while no changes were obtained for mussels fed FC+RB, despite this FA making a larger contribution to the profile in the faeces (3.2%) than in the feed (2.5%). 20:1 (n-9) was not present in *R. baltica*. There were no significant contributions of other fatty acids in mussels fed FC+RB that could reflect changes in the direction of the faeces profile, *e.g.* 16:0, 18:3 (n-6) and 22:1 (n-11).

At Day 28, the four fatty acids 16:0, 18:3 (n-3), 20:5 (n-3) (eicosapentaenoic acid, EPA) and 22:6 (n-3) (docosahexaenoic acid, DHA) contributed to 58.3, 56.8 and 62.2% of the digestive gland tissue FAs for mussels fed RB, FD+RB and FC+RB, respectively. The relative concentration of 18:3 (n-3) increased significantly for all treatments from Day 0 (3.3% of total FA) to Day 28, though more in mussels fed RB (11.1% of total FA) and

FD+RB (7.3%) than in mussels fed FC+RB (6.2%). The *R. baltica* contained 24.4% 18:3 (n-3). The same tendency was indicated for 18:2 (n-6), which increased more in the digestive gland samples of mussels fed FD+RB compared to mussels fed FC+RB ($p<0.05$). The increases, however, were not significantly higher than in samples of mussels fed RB, reflecting the high contribution of 18:2 (n-6) to the profile in both *R. baltica* (15.7%) and salmon fish feed (7.9%). The salmon faeces did not contain 18:2 (n-6).

A significant increase was also evident for 18:4 (n-3) from Day 0 to Day 28 in the digestive gland samples of mussels fed RB ($p<0.05$), thus reflecting the high value in *R. baltica* (15.6%). The fraction of EPA decreased significantly from Day 0 to Day 28 for all treatments ($p<0.05$), while no significant differences were identified for DHA despite a decrease from 20.2 to 14.4% of total FA for mussels fed the mono ration of *R. baltica*, which was probably due to large variation among samples.

Through the exposure period there was a significant increase in the total amount of monounsaturated fatty acids (MUFAs) in the digestive gland (14.3 to 20.3% of total FA) and gill (5.5 to 13.3% of total FA) samples, in addition to a significant decrease in polyunsaturated fatty acids (PUFAs) in both the digestive gland (62.9 to 58.9% of total FA) and gill (65.2 to 56.7% of total FA) tissues, which reflected the salmon fish feed signature.

3.7.2 Gills

The same pattern of variation in fatty acid composition as for digestive gland tissue was seen for gill tissue (Fig. 6C), in which 18:1 (n-9) and 20:1 (n-9) increased from 0.1 to 4.0% and 4.5 to 5.3% in tissue from mussels fed FD+RB and RB, respectively ($p<0.05$). The increase in 18:1 (n-9) was also significant for mussels fed FC+RB, but not different from that of the mussels fed RB. There was also a significant increase in 18:1 (n-7) in the gill tissue of mussels fed FC+RB at Day 28, although the contribution to the total profile was not significantly higher than in mussels fed RB ($p<0.05$).

3.7.3 Mantle

Although no significant differences in fatty acid composition were identified in mantle tissue, the general trend of change, e.g. for 18:1 (n-9), 20:1 (n-9), 18:2 (n-6) and 18:3 (n-3), was the same as in the digestive gland and gill tissue. In contrast to the digestive gland and gill tissue, the average fraction of DHA, EPA and PUFA (% of total FA tended to increase, and this increase was more pronounced for DHA in males than in females.

3.8. Incorporation of food components in mussel tissues demonstrated by PCA

The principle component analysis of fatty acid profiles clearly demonstrated incorporation of nutritional components from salmon fish feed and *R. baltica* in the digestive gland and gill tissue of the mussels, whereas no systematic pattern was revealed for mantle tissue (Fig. 7 A-C). For the digestive gland, mantle and gill tissue, the score plots (upper panels) showed that 81, 96 and 83% of the variance in the data was explained by the two first principal components. The fatty acid profile in the digestive gland and gill tissue changed from Day 0 to Day 28, and the changes were more pronouced in the direction of the food signatures for mussels fed FD+RB and RB in comparison to those fed FC+RB. One RB outlier was removed from the PCA analysis.

In the digestive gland samples, the loading plots (lower panels) confirmed the incorporation of 18:1 (n-9) from salmon fish feed and faeces, 20:1 (n-9) from salmon fish feed, 18:2 (n-6) from salmon fish feed and *R. baltica* and 18:3 (n-3) and 18:4 (n-3) from *R. baltica*, while 20:5 (n-3) and 22:6 (n-3) contributed more to the total fatty acid profile in the control mussels at Day 0. The same pattern of variation was found for these fatty acids in the gill tissue, except for the lack of 18:4 (n-3) and the presence of 18:1 (n-7), and there was a large contribution of 16:0 to the variance in samples of mussels fed salmon fish feed and faeces. In the mantle tissue, the loading plot indicated that there was a larger contribution of DHA in males than in females, and that 16:1 (n-7) appeared to be higher in females. As was also found for the gill tissue, the low fraction of 16:0 in mussels fed RB contributed strongly to the variance.

4. Discussion

4.1. Clearence rate and food availability

Mussels cleared salmon fish feed, faeces particles and *R. baltica* with a high efficiency, and demonstrated a typical Holling type III functional response (Holling 1956) with a rapid increase in CR when particle concentrations exceeded the minimum level for active filtration, above which the CR decreased for higher particle concentrations as the particle densities approached the mussels' saturation level for particle intake. A maximum CR could not be identified, as only one measurement point was obtained in the range where peak CR could be expected. A high CR for both salmon fish feed and faeces is consistent with recent studies by MacDonald et al. (2011) and Reid et al. (2010). However, the CR was significantly higher for *R. baltica* compared to salmon fish feed and faeces at the highest particle concentrations. In previous reports, mussels have shown ~100% RE for particles ≥ 4 µm (Møhlenberg and Riisgard, 1978), >80% RE for particle sizes of 2-5µm (Vahl, 1972) and ~50% RE for particle sizes of 1.6-2 µm (Newell and Shumway, 1993; Lucas et al., 1987). Accordingly, the higher CR for *R. baltica* was most likely a result of different particle sizes and also possibly the particle's shape. However, the fact that the clearance of salmon fish feed and faeces ceased at almost the same level (<500 particles ml^{-1}) as for *R. baltica* reveals support for the mussels being able to filter out salmon fish feed and faeces particles with high efficiency. Salmon fish feed and faeces concentrations were lowered down to mean particle concentrations of ~350 and ~430 ml^{-1}, indicating that this is close to the threshold level for the active filtration of these particles in *M. edulis*, while *R. baltica* was depleted to a minimum concentration of ~235 cells ml^{-1} (equivalent to 0.18 µg Chl a L^{-1}, Clausen and Riisgård, 1996). The obtained minimum concentration of *R. baltica* to sustain filtration activity in *M. edulis* was lower than previously reported for this microalgae (~630 cells ml^{-1}) (Riisgaard et al., 2003), although the result is consistent with Strohmeier et al. (2009), who demonstrated that *M. edulis* is capable of clearing particles out of suspension at such and even lower Chl *a* concentrations (down to 0.01 µg Chl a L^{-1}).

A mussel diet consisting of 50% of *R. baltica* and 50% POC from either salmon fish feed or faeces has a relatively high non-algal organic content. It has been hypothesized

that mussels will only ingest salmon farm effluents when phytoplankton concentrations are low (Troell and Norberg, 1998). It is therefore important to study feed incorporation and growth at relatively low concentrations of natural seston combined with a high content of salmon farm wastes in order to force mussels to feed upon and incorporate these particles. Particle densities in the experimental trays were adjusted to the lower range of that which supported the highest CR, leaving mussels with just high enough particle densities to maintain a high CR. A high CR without reaching peak CR levels can involve weak starvation, thereby forcing mussels to feed upon the fish feed and faeces from the mono diets and the feed and faeces fraction of the mixed diets. However, although particle concentrations appeared to be high enough to sustain active feeding, this was only reflected in the growth of mussels fed *R. baltica* and salmon fish feed, while in contrast, no response was seen for mussels fed salmon faeces.

4.2. Growth in length

In M-mussels, the RB ration resulted in a significantly better length growth compared with the FD ration. Indeed, no significant differences were found between mussels fed FD and those which starved (ST), suggesting that salmon fish feed alone was not an optimal diet. However, we hypothesize that salmon fish feed particles will not account for the majority of the seston composition in IMTA systems, at least not for longer periods. In any case too little is known about size distribution and how the fraction of particulate wastes from salmon farms in ambient seston varies with, *e.g.* season, salmon biomass and production cycle, to make any valid speculations.

A significant growth in length was also evident for J-mussels fed RB and in J-mussels fed FD+RB, which stands in contrast to the poor growth response seen for FD in Experiment 1, whereas no significant growth were found for mussels fed FC+RB or for the 1/2RB. The results suggest a poorer food quality and inferior growth condition for mussels fed salmon faeces compared to salmon fish feed particles.

The RB diet resulted in an average length increase of ~33 µm day^{-1} in both M- and J-mussels. By comparison, this is somewhat lower than previously reported growth for farmed mussels of similar length (~38-65 µm day^{-1}) under natural conditions in the

coastal areas of Central Norway (Handå et al., 2011), hence supporting that mussels experienced weak starvation conditions during the experiments. The average growth in length for J-mussels fed FD+RB (25 µm day^{-1}) was twice as high compared to J-mussels fed FC+RB (12 µm day^{-1}), supporting that mussels were able to utilize salmon fish feed particles more efficiently for growth than salmon faeces.

4.3. Growth in soft tissue

Standardized soft tissue dry weight (DW') decreased and daily relative growth rates were negative for all treatments in M-mussels, though significantly less negative in mussels fed RB compared to mussels fed FD and ST, suggesting that mussels fed RB covered a larger part of their energy need from the diet than mussels fed FD. As for a growth in length, the DW' tended to decrease less for mussels fed FD compared to ST, but, surprisingly, no significant differences were found. The contrasting growth in shell length and soft tissue dry weight agrees with other studies which show that there is no clear relationship between a growth in length and a growth of somatic tissue in the *Mytilus* family (Kautsky, 1982; Rodhouse et al., 1984; Hilbish, 1986; Cartier et al., 2004). In contrast to the measured decrease in DW' for all treatments in M-mussels, an increase was found for J-mussels fed RB, while DW' was maintained in mussels fed FD+RB and in mussels fed the 1/2RB, thereby suggesting that the ration given was sufficient to sustain the DW' in J-mussels.

The daily food supply rate set at ~5% of the carbon content of soft tissues was chosen based on an estimated temperature-dependent POC requirement between ~2.9% and ~8.2% of soft tissue carbon content for a 0-0.5% daily growth at 7°C and 14°C, respectively, found in mussels from the same population during early summer (June-July) (Handå et al., *in press*). Interestingly, M-mussels fed the mono diet of *R. baltica* exhibited a decrease in DW' of 2.9 mg ind^{-1} day^{-1}, suggesting that the energy need for weight maintenance was ~20% higher than 6 mg POC supplied daily (40% carbon content of 2.9 mg DW loss is 1.2 mg POC). In contrast, J-mussels demonstrated an increase in DW' of 0.8 mg (0.33 mg POC) day^{-1}, accounting for 10% of the ration POC (6.6 mg ind^{-1} day^{-1}). The observed differences in growth response could perhaps be related to a higher energy demand in M-mussels, which is possibly associated with the

main growth of gonads in spring in conjunction with the spring bloom for this population (Handå et al., 2011).

Weight maintenance, though no net growth in J-mussels fed FD+RB, did not indicate any significant utilization of salmon fish feed. Nonetheless, weight maintenance in combination with a significant growth in length suggested that mussels were more capable of utilizing salmon fish feed than salmon faeces particulates for growth. A growth in L and DW' was significantly higher for mussels fed RB and FD+RB than in those fed FC+RB despite the high CR for all food types. By comparison, a lower C, N and lipid content in faeces compared to salmon fish feed can presumably explain the poor growth responses to faeces. Moreover, though feed rations were prepared to supply the same amount of POC for all types of food, it is speculated that the poor growth could be attributed to a lower nutrient value of salmon faeces compared to salmon fish feed, as well as possible nutritional limitations in mussels fed FC+RB.

4.4. Fatty acid content and composition

The significant time-related increase in total fatty acid content reflecting the total lipids in the digestive gland tissue of mussels fed FD+RB (6.1 to 9.5 %) indicates that salmon fish feed was filtered and assimilated, while in contrast, no significant increases were found for the fatty acid content in mantle or gill tissue. Incorporation time is related to the metabolic activity (Paulet et al., 2006), and tissues with high turnover rates are likely to accomplish a short-term ration change, whereas tissues with a low turnover rate will better reflect the long-term feeding history in bivalves (Lorrain et al., 2002; Piola et al., 2006). For example, mantle tissue has previously been shown to significantly alter fatty acid content and composition in the direction of the feed source first after more than 90 days of exposure (Post, 2002; Fukumori et al., 2008). The present results support the idea that digestive gland tissue has a faster turnover rate than mantle tissue in blue mussels, which is in agreement with Narváez et al. (2008) and Redmond et al. (2010) and similar studies of scallops (*Pecten maximus*) (Malet et al., 2007), while the missing response in mantle tissue is in agreement with recently reported results for blue mussels (Redmond et al., 2010) and green mussels (*Perna viridis*) (Shin et al., 2008). In mussels fed FC+RB or RB, no changes were found in the

fatty acid content of any of the three tissues. This was as expected, considering that the fatty acids content in faeces (5.7%) and *R. baltica* (5.8%) was significantly lower than in salmon fish feed (26%).

The more pronounced changes in the mussels' fatty acid composition in the direction of the salmon fish feed, as compared to the salmon faeces profile, suggest that mussels were more capable of accumulating salmon fish feed than salmon faeces. However, the fact that 18:1 (n-9) increased in the digestive gland tissue of mussels fed both FD+RB and FC+RB (from 1.6 to 7.1% and 2.2%, respectively) nevertheless suggests that the mussels also incorporated some of the salmon faeces fraction. The more pronounced increase of 18:1 (n-9) in mussels fed FD+RB compared to FC+RB was most likely caused by a combination of a higher content in salmon fish feed (25.8%) than in salmon faeces (11%), in addition to a more efficient incorporation and utilization of salmon fish feed, which was in agreement with the length and DW' results.

By contrast, an increase in 20:1 (n-9) was only evident for mussels fed FD+RB, while no changes were found in the direction of the food source for mussels fed FD+RB despite a higher contribution of this fatty acid in faeces than in the feed, further indicating that mussels were not able to utilize faeces as efficiently as salmon fish feed. Furthermore, no increase was found for 18:3 (n-6) in the direction of the content in faeces, although this fatty acid was only found in faeces and could therefore be a possible tracer of this food source, or in 22:1 (n-11), which accounted for a larger share of the fatty acid composition in faeces than in salmon fish feed.

18:3 (n-3) increased significantly in digestive gland tissue for all treatments from Day 0 to Day 28. This increase was more pronounced in mussels fed RB and FD+RB than in mussels fed FC+RB, again suggesting a higher feeding activity for mussels fed salmon fish feed than in mussels fed faeces. *R. baltica* contained a high percentage of 18:3 (n-3) (24.4% of total FA), while salmon fish feed and faeces contained 4% and 1.2%, respectively, meaning that the change in this fatty acid will reflect the feeding activity upon *R. baltica*. The same tendency was seen for 18:2 (n-6), which increased more in the digestive gland samples of mussels fed FD+RB than in mussels fed FC+RB.

However, as found for 18:1 (n-9), there was also a significant increase in 18:2 (n-6) in the digestive gland tissue of mussels fed FC+RB, indicating some feeding upon *R. baltica* since the faeces did not contain 18:2 (n-6).

The same pattern of variation that was seen for digestive gland tissue was, surprisingly, since the gill tissue was expected to be more conservative than the mantle tissue, also seen for 18:1 (n-9) and 20:1 (n-9) in the gill tissue from mussels fed FD+RB, as well as for 18:1 (n-9) in mussels fed FC+RB.

Plant oils are typically depleted in n-3 highly unsaturated fatty acids (HUFA) when compared to marine sources (Menoyo et al., 2007), therefore leaving salmon fish feed pellets with a high inclusion of terrestrial oils to accordingly contain high concentrations of MUFA. For example, the content of MUFA and PUFA in the salmon fish feed used in these experiments was 41% and 34% of total FA compared to 5% and 73% in *R. baltica*. Salmon faeces contained 25% MUFA and as little as 10% PUFA, indicating a poor nutrient quality for faeces that was reflected in the restricted or absent growth response obtained for this treatment. Mussels fed salmon fish feed and *R. baltica* increased their total amount of MUFA in the digestive gland (14.3 to 20.3% of total FA) and gill tissue (5.5 to 13.3% of total FA), and a significant decrease was found in PUFA, reflecting the salmon fish feed composition.

The principle component analysis supported the observed changes in fatty acid composition of the different tissues. For the digestive gland and gill tissue samples, there was a clear pattern separating Day 28 from Day 0 samples according to a decrease in the fraction of EPA and DHA in combination with the incorporation of single fatty acids recognizable from the various food sources. For the digestive gland tissue in particular, the loading plot identified the fraction of 18:1 (n-9) and 18:3 (n-3) as being the fatty acids most responsible for the difference between mussels fed FD+RB and RB. 20:1 (n-9) and 18:2 (n-6) separated Day 28 samples of mussels fed FD+RB from mussels fed FC+RB and FD+RB and FC+RB samples from Day 0 samples, respectively, indicating some incorporation of *R. baltica* (18:2 n-6) and salmon faeces (20:1 n-9) after 28 days of exposure. The same pattern was found for gill tissue, except

that 16:0 was identified as being the primary fatty acid responsible for the difference between mussels fed FD+RB and FC+RB compared to mussels fed RB and to Day 0 samples.

5. Conclusions

The results indicate that mussels are more capable of incorporating and utilizing salmon fish feed than salmon faeces particulates for growth. This can be concluded based on the more pronounced changes in mussels' fatty acid composition in the direction of the salmon fish feed compared to the salmon faeces profile, which is also accompanied by a better length growth and soft tissue dry weight response in mussels fed mixed rations of salmon fish feed and *R. baltica* compared to salmon faeces and *R. baltica*. A high clearance rate of feed and faeces, as well as indications that mussels incorporated some of the salmon faeces fraction, suggested that mussels can also clear salmon faeces from suspension. These results are important considering the potential of blue mussels to perform bioremediative services on particulate nutrient wastes from salmon cage aquaculture.

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Tables

Table 1. Experimental treatments showing food supply corresponding to 5% of soft tissue carbon content per mussel and day based on the food carbon content of salmon feed, salmon faeces and the microalgae *Rhodomonas baltica* in Experiment 1 in March (M-mussels) and Experiment 2 in June (J-mussels).

			Feed ration (mg carbon)				
Experiment 1	Treatment	Abb.	Feed	Faeces	*R. baltica*	mg C ind^{-1} day^{-1}	Trays (ind $tray^{-1}$)
M-mussels	Salmon feed	FD	6	-	-	~6	4 (40)
Mono rations	*R. baltica*	RB	-	-	6	~6	4 (40)
	Starvation	ST	-	-	-	~0	4 (40)
Experiment 2							
J-mussels	Feed and *R. baltica*	FD+RB	3.3	-	3.3	~6.6	3 (50)
Mixed	Faeces and *R. baltica*	FC+RB	-	3.3	3.3	~6.6	3 (50)
rations	*R. baltica*	RB	-	-	6.6	~6.6	2 (50)
	R. baltica	1/2RB	-	-	3.3	~3.3	1 (50)

Table 2. Total fatty acid content (mg FA g DW^{-1}) and fatty acid composition (% of total FA) of: A) digestive gland, B) mantle and C) gill tissue of mussels at Day 0 and in mussels fed a mono ration of *Rhodomonas baltica* (RB), mixed rations of either salmon fish feed and *R.baltica* (FD+RB) or salmon faeces and *R.baltica* (FC+RB) for 28 days in Experiment 2 (mean±se, n=5). Letters denote significant differences among treatments. The food supply corresponded to 5% of soft tissue carbon content per mussel and day based on food carbon content.

A) *Digestive gland*		Day 28		
	Day 0	RB	FD+RB	FC+RB
Total FA (mg g DW^{-1})	60.9±4.8	90.6±17.1	94.5±7.9	71±9.4
% of total FA				
14:0	2.9±0.2	3.5±0.6	2.9±0.1	2.6±0.1
16:0	15.6±0.4	16.1±1.9	14.7±0.6	16.5±0.6
18:0*	4.2±0.2^{b}	3.7±0.4^{ab}	3.2±0.2^{a}	4.0±0.2^{ab}
*ΣSFA**	*22.6±0.4^{b}*	*23.4±2.8^{ab}*	*20.8±0.6^{a}*	*23.1±0.3^{ab}*
16:1 (n-7)	8.2±0.7	6±1.1	6.2±0.4	5.9±0.4
18:1 (n-9)*	1.6±0.1^{a}	1.5±0.2^{a}	7.1±0.1^{c}	2.2±0.1^{b}
18:1 (n-7)*	2.5±0.1^{a}	3.7±0.4^{ab}	3.4±0.1^{b}	3±0.1^{ab}
20:1 (n-9)*	2.1±0.1^{a}	1.9±0.2^{a}	3.3±0.1^{b}	2.4±0.1^{a}
22:1 (n-11)	0±0	0±0	0.2±0	0±0
22:1 (n-9)*	0±0^{a}	0.7±0.1^{c}	0.3±0.1^{b}	0.1±0.1^{a}
*Σ MUFA**	*14.5±0.8^{a}*	*13.8±1.9^{a}*	*20.3±0.4^{b}*	*13.6±0.4^{a}*
18:3 (n-3)*	3.3±0.3^{a}	11.1±2.2^{c}	7.3±0.5^{c}	6.2±0.5^{b}
18:4 (n-3)*	6.3±0.4^{a}	9.2±2.0^{b}	6.2±0.5^{a}	6.7±0.5^{ab}
20:3 (n-3)	0.2±0.1	0.3±0.1	0.1±0.1	0.2±0.1
20:4 (n-3)	0.6±0.1	0.5±0.2	0.5±0.1	0.5±0.1
20:5 (n-3)*	23.8±0.3^{a}	16.7±3.1^{b}	17.1±0.6^{b}	19.8±0.6^{b}
22:5 (n-3)	1.1±0	0.7±0.2	1.1±0.1	1.1±0.1
22:6 (n-3)	20.2±1.2	14.4±3.3	17.6±0.9	19.7±0.9
18:2 (n-6)*	1.6±0.1^{a}	3.7±0.9^{abc}	4.4±0.2^{c}	2.9±0.2^{b}
18:3 (n-6)	0±0	0.8±0.7	0.2±0	0±0
20:2 (n-6)*	1.5±0.1^{b}	1.9±0.3^{ab}	1±0.1^{a}	1.4±0.1^{ab}
20:3 (n-6)	0±0	0.2±0.12	0±0	0±0
20:4 (n-6)*	3.5±0.2^{ab}	2.9±0.4^{ab}	2.7±0.2^{a}	3.8±0.2^{b}
22:5 (n-6)	0.9±0.1	0.5±0.2	0.6±0.1	0.9±0.1
*ΣPUFA**	*62.9±0.6^{b}*	*62.8±11.9^{ab}*	*58.9±0.8^{a}*	*63.3±0.8^{b}*

*Indicates significant changes in relative content (%) among treatments (α=0.05). SFA=saturated fatty acids (FA), MUFA=monounsaturated FA and PUFA=polyunsaturated FA.

B) Mantle		Day 28		
	Day 0	RB	FD+RB	FC+RB
Total FA (mg g DW^{-1})	38.8±5.7	35±4	47.2±10.5	32.1±8.5
% of total FA				
14:0	2±0.5	1.8±0.4	2.1±0.4	1.7±0.3
16:0	23.8±1.4	19.5±0.8	22.2±0.7	22.2±0.8
18:0	5.3±1	4.9±0.6	4.6±0.9	5.5±0.8
Σ SFA	*31.3±1.8*	*26.3±0.6*	*28.8±1.0*	*29.3±0.7*
16:1 (n-7)	6±2.1	3.7±1.3	4.7±1.5	3.8±1.2
18:1 (n-9)	1.4±0.6	1.1±0.4	2.6±0.2	1.8±0.4
18:1 (n-7)	2.6±0.2	2.6±0.1	2.6±0.1	2.5±0.3
20:1 (n-)9	2.8±0.2	2.5±0.1	3±0.3	3.2±0.4
22:1 (n-11)	0±0	0±0	0±0	0±0
22:1 (n-9)	0±0	0.1±0	0±0	0±0
Σ MUFA	*12.9±2.5*	*10.1±1.6*	*12.9±1.5*	*11.3±1.5*
18:3 (n-3)	1.7±0.6	3.2±0.3	2.4±0.6	1.9±0.5
18:4 (n-3)	2.2±0.9	3.2±0.6	2.8±0.9	1.9±0.8
20:3 (n-3)	0.2±0.1	0.1±0	0.1±0.1	0.1±0.1
20:4 (n-3)	0.2±0.1	0.1±0	0.1±0.1	0±0
20:5 (n-3)	23±1.3	22.3±0.2	21.7±1.3	22.1±0.6
22:5 (n-3)	1.2±0.2	1.5±0.1	1.4±0.1	1±0.3
22:6 (n-3)	21.3±3.5	24.9±2.2	22.7±2.1	24.7±2.6
18:2 (n-6)	0.6±0.3	1.8±0.2	1.5±0.4	0.9±0.3
18:3 (n-6)	0±0	0±0	0±0	0±0
20:2 (n-6)	0.9±0.3	1.4±0.1	0.7±0.3	0.7±0.3
20:3 (n-6)	0±0	0±0	0±0	0±0
20:4 (n-6)	4.2±0.4	4.4±0.3	4.5±0.6	5.9±0.6
22:5 (n-6)	0.4±0.2	0.6±0.2	0.4±0.2	0.3±0.2
Σ PUFA	*56±3.4*	*63.6±2.0*	*58.3±0.8*	*59.4±1.6*

SFA=saturated fatty acids (FA), MUFA=monounsaturated FA and PUFA=polyunsaturated FA.

C) Gills		Day 28		
	Day 0	RB	FD+RB	FC+RB
Total FA (mg g DW^{-1})	16.3±1.6	16.5±0.7	18.1±0.5	18.1±0.4
% of total FA				
14:0	1.2±0.2	1.7±0.1	1.4±0	1.7±0.1
16:0	21.3±1.4	20.2±1.5	23.7±0.4	25.4±0.2
18:0*	6.8±0.3^{a}	6.8±0.7^{ab}	4.9±0.1^{b}	5.2±0.2^{b}
*ΣSFA**	*29.3±1.7^{ab}*	*28.7±1.9^{ab}*	*30±0.5^{a}*	*32.2±0.3^{b}*
16:1 (n-7)	0.5±0.2	0.6±0.2	0.1±0.1	0±0
18:1 (n-9) *	0.1±0.1^{a}	0.7±0.3^{ab}	4.0±0.1^{c}	2.1±0.4^{b}
18:1 (n-7) *	0.4±0.2^{a}	2±0.5^{ab}	2.6±0^{b}	2.4±0.2^{b}
20:1 (n-)9*	4.5±0.3^{ab}	4.2±0.1^{a}	6.8±0.1^{c}	5.4±0.2^{b}
22:1 (n-11)	0±0	0±0	0±0	0±0
22:1 (n-9)	0±0	0.1±0.1	0±0	0±0
*Σ MUFA**	*5.5±0.5^{a}*	*7.5±1.0^{ab}*	*13.3±0.1^{c}*	*9.8±0.5^{b}*
18:3 (n-3)	0±0	2.0±0.6	0.9±0.3	1.5±0.4
18:4 (n-3)	0±0	0.8±0.4	0±0	0±0
20:3 (n-3)	0±0	0±0	0±0	0±0
20:4 (n-3)	0±0	0±0	0±0	0±0
20:5 (n-3) *	19.9±0.7^{b}	14.6±0.7^{a}	13.5±0.3^{a}	14.7±0.3^{a}
22:5 (n-3)	0±0	1.1±0.4	1.1±0.3	0±0
22:6 (n-3) *	35.1±1.8^{b}	30.9±0.9^{ab}	28.8±0.3^{a}	29.4±0.7^{a}
18:2 (n-6) *	0±0^{a}	2.1±0.3^{b}	2.6±0.1^{b}	1.5±0.4^{ab}
18:3 (n-6)	0±0	0±0	0±0	0±0
20:2 (n-6)	0±0	0.8±0.3	0±0	0±0
20:3 (n-6)	0±0	0±0	0±0	0±0
20:4 (n-6)	10.2±0.4	10.8±0.3	9.8±0.3	10.9±0.2
22:5 (n-6)	0±0	0.8±0.4	0±0	0±0
*ΣPUFA**	*65.2±1.9^{c}*	*63.8±1.0^{c}*	*56.7±0.5^{a}*	*58±0.5^{b}*

*Indicates significant changes in relative content (%) among treatments (α=0.05). SFA=saturated fatty acids (FA), MUFA=monounsaturated FA and PUFA=polyunsaturated FA.

Table 3. Fatty acid content (mg FA g DW^{-1}) and fatty acid composition (% of total FA) of salmon fish feed (FD) and faeces (FC) and the microalgae *Rhodomonas baltica* (RB) (mean±se, n=5).

	Feeds		
FA	FD	FC	RB
Total FA (mg g DW')	254.2±4.9	52.9±1.1	56.4±2.8
% of total FA			
14:0	5.9±0	5.6±0	10.4±0.1
16:0	15.7±0	37.6±0.4	10.5±0.8
18:0	2.7±0	20.3±0.4	0.5±0.1
20:0	0.3±0	0.9±0	0±0
22:0	0.1±0	0.4±0.1	0±0
ΣSFA	*24.7±0*	*64.8±0.8*	*21.3±0.7*
16:1 (n-7)	6.3±0	1.5±0.1	0.7±0
18:1 (n-9)	25.8±0	11±0.3	1.9±0.4
18:1 (n-7)	3±0	1.5±0	2.6±0.1
20:1 (n-9)	2.5±0	3.2±0	0±0
22:1 (n-11)	2.7±0	5.5±0.1	0±0
22:1 (n-9)	0.3±0	0.8±0	0±0
24:1	0.5±0	1.4±0	0±0
ΣMUFA	*40.9±0*	*24.9±0.4*	*5.1±0.3*
18:3 (n-3)	3.4±0	1.2±0	24.4±0.3
18:4 (n-3)	1.9±0	0.3±0.1	15.6±0.9
20:4 (n-3)	0.5±0	0±0	0.4±0
20:5 (n-3)	9.9±0	1.6±0.1	7.4±0.3
22:5 (n-3)	1.3±0	0±0	0.2±0
22:6 (n-3)	7.8±0	2.5±0.1	7.6±0.2
18:2 (n-6)	7.9±0	0±0	15.7±0.6
18:3 (n-6)	0±0	4.8±0	0±0
20:2 (n-6)	0.2±0	0±0	0.1±0
20:3 (n-6)	0±0	0±0	0.1±0
20:4 (n-6)	0.6±0	0±0	1.6±0
22:5 (n-6)	0.2±0	0±0	0.3±0
ΣPUFA	*34.3±0*	*10.3±0.5*	*73.3±1*

SFA=saturated fatty acids (FA), MUFA=monounsaturated FA and PUFA=polyunsaturated FA.

Figure legends

Fig. 1. A and B) - Initial size ditribution of salmon fish feed and faeces (mean±se, n=10) and C) mussel clearence rates (L h^{-1}) of salmon fish feed, salmon faeces and the microalgae *Rhodomonas baltica* (mean±se, n=7). The size of *R. baltica* is 6-10 µm.

Fig. 2. A) Particle concentrations (mean±se) in experimental trays with mussels fed mono rations of *Rhodomonas baltica* (RB) or salmon fish feed (FD), with starved mussels (ST) as control in Experiment 1, and B) mixed rations consisting of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or mono rations of either full (RB) or half ration (1/2RB) of *R. baltica* in Experiment 2. One tray without mussels served as the control for the particle concentration in inlet water (C).

Fig. 3. A) Shell length (L, mean±se) of mussels at Day 0 (left bars) and fed mono rations of *Rhodomonas baltica* (RB) or salmon fish feed (FD), with starved mussels (ST) as a control for 21 days in March (Experiment 1), and B) mixed rations consisting of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or mono rations of either full (RB) or half ration (1/2RB) of *R. baltica* for 28 days in June (Experiment 2) (right bars). C) Average growth in length (AGR_L, µm day^{-1}) in March and D) June. The food supply corresponded to ~5% day^{-1} of the soft tissue carbon content of the individual mussels.

Fig. 4. A) Soft tissue dry weight of mussels (DW', mean±se) at Day 0 and fed mono rations of *Rhodomonas baltica* (RB) or salmon fish feed (FD), with starved mussels (ST) as control for 21 days in March (Experiment 1); B) mixed rations consisting of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or mono rations of either full (RB) or half ration (1/2RB) of *R. baltica* for 28 days in June (Experiment 2); C) Specific growth in soft tissue dry weight ($SGR_{DW'}$, % day^{-1}) in March, and D) June. The food

upply corresponded to ~5% day^{-1} of the soft tissue carbon content of the individual mussels.

Fig. 5. A) Fatty acid content (g^{-1} dry weight tissue, mean±se, n=5) of gills, mantle and digestive gland of mussels at Day 0 and fed mixed rations consisting of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or a mono ration of *R. baltica* (RB) for 28 days in June (Experiment 2). The food supply corresponded to ~5% day^{-1} of the soft tissue carbon content of the individual mussels; B) Fatty acid content g^{-1} wet weight tissue (mean±SE, n=5) of *R. baltica,* salmon fish feed and salmon faeces.

Fig. 6. Contribution of selected fatty acids (mean±se, n=5) to the total fatty acid content in: A) digestive gland, B) mantle and C) gill tissue of mussels at Day 0 and fed mixed rations of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or a mono ration of *R. baltica* (RB) for 28 days in June (Experiment 2). The food supply corresponded to ~5% day^{-1} of the soft tissue carbon content of the individual mussels; D) Content of selected fatty acids in *R. baltica*, salmon fish feed and faeces (mean±se, n=5).

Fig. 7. Principle component analysis of fatty acid profiles in: A) digestive gland, B) mantle and C) gill tissue of mussels at Day 0 (S) and fed mixed rations of either salmon fish feed and *R. baltica* (FD+RB), salmon faeces and *R. baltica* (FC+RB) or a mono ration of *R. baltica* (RB) for 28 days in June (Experiment 2). The upper panels show the score plot, while the lower panels show the loading plots for the corresponding fatty acids' contribution to the score plot. Numbers at the x (PC-1) - and y-axis (PC-2) are the percentages of variance in fatty acid profiles explained by principle components 1 and 2. Gender is indicated for male (M) and female (F) mantle tissues. The food supply corresponded to ~5% day^{-1} of the soft tissue carbon content of the individual mussels.

Fig 1

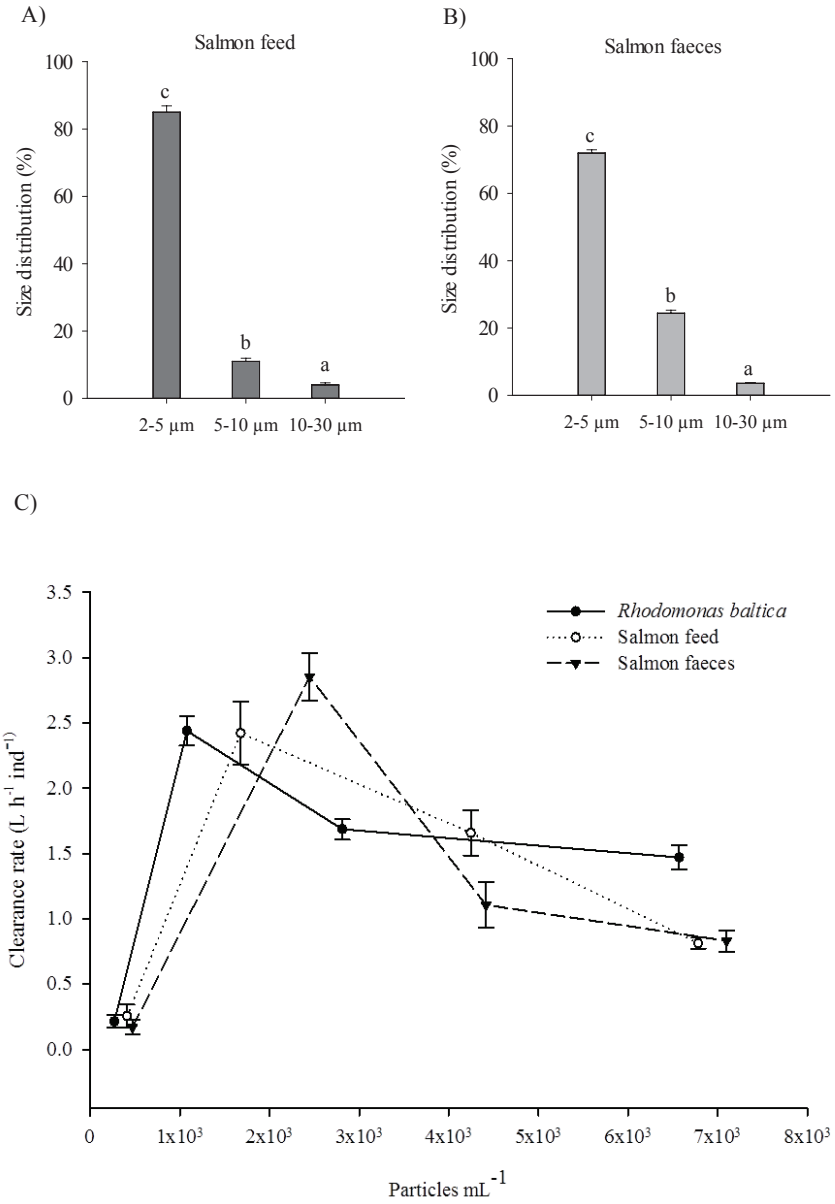

A)
Salmon feed
Size distribution (%)
100
80
60
40
20
0
c
b
a
2-5 µm
5-10 µm
10-30 µm
B)
Salmon faeces
Size distribution (%)
100
80
60
40
20
0
c
b
a
2-5 µm
5-10 µm
10-30 µm
C)
Rhodomonas baltica
Salmon feed
Salmon faeces
Clearance rate (L h-1 ind-1)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1x10³
2x10³
3x10³
4x10³
5x10³
6x10³
7x10³
8x10³
Particles mL-1

Fig 2

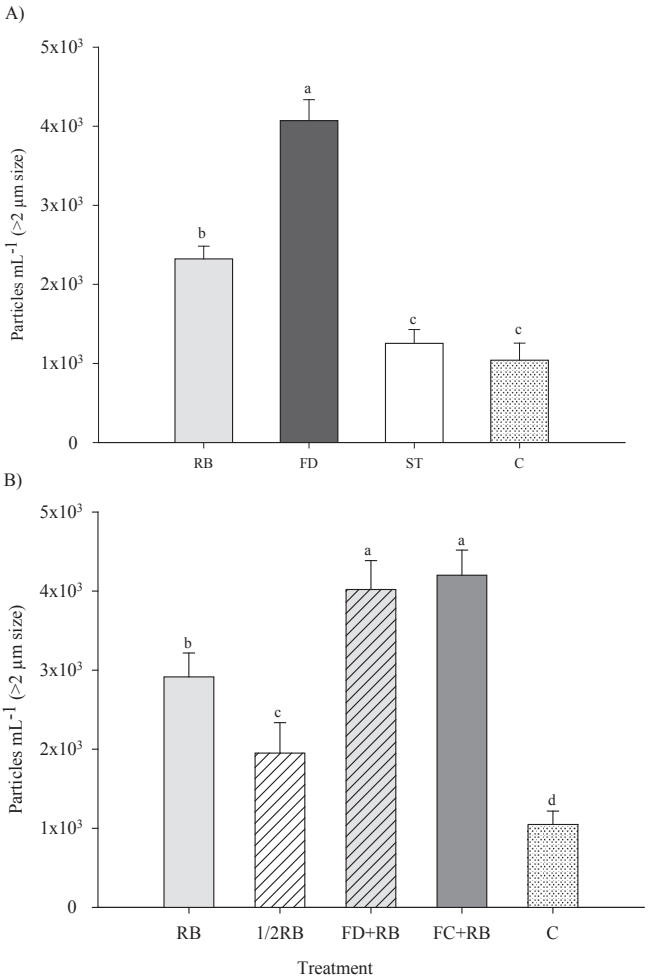

A)
5x10³
4x10³
3x10³
2x10³
1x10³
0
Particles mL-1 (>2 µm size)
a
b
c
c
RB
FD
ST
C
B)
5x10³
4x10³
3x10³
2x10³
1x10³
0
Particles mL-1 (>2 µm size)
a
a
b
c
d
RB
1/2RB
FD+RB
FC+RB
C
Treatment

Fig 3

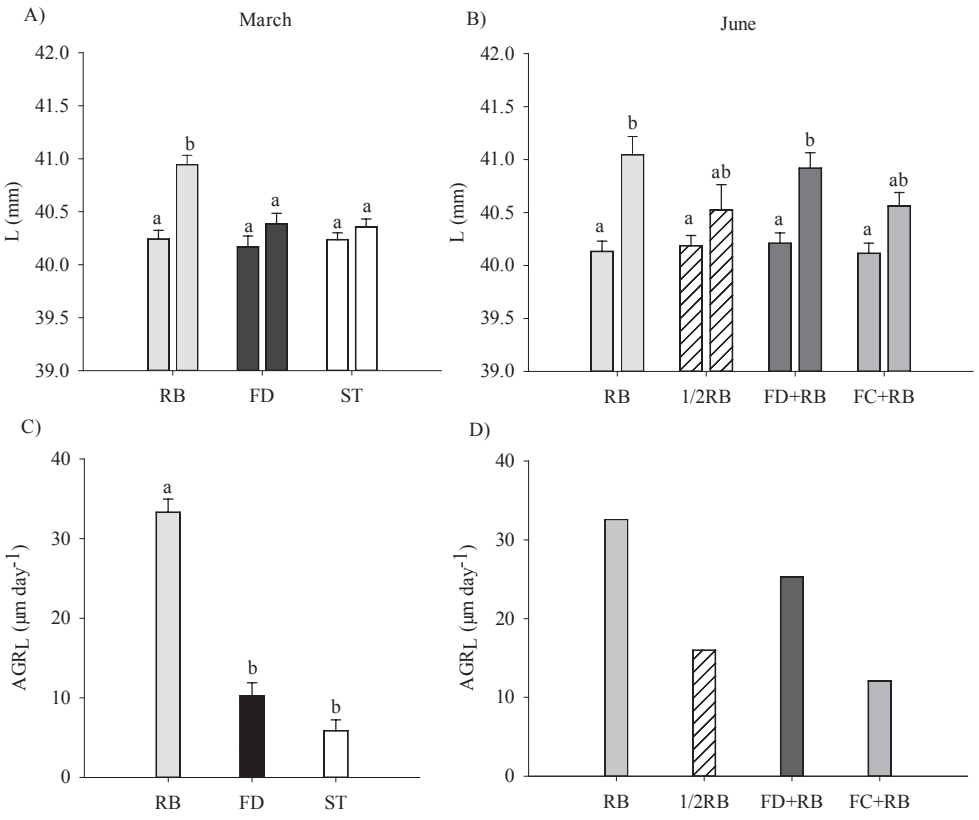

A)
March
B)
June
L (mm)
42.0
41.5
41.0
40.5
40.0
39.5
39.0
a
b
a
a
a
a
RB
FD
ST
a
b
a
ab
a
b
a
ab
RB
1/2RB
FD+RB
FC+RB
C)
D)
AGRL (µm day-1)
40
30
20
10
0
a
b
b
RB
FD
ST
RB
1/2RB
FD+RB
FC+RB

Fig 4

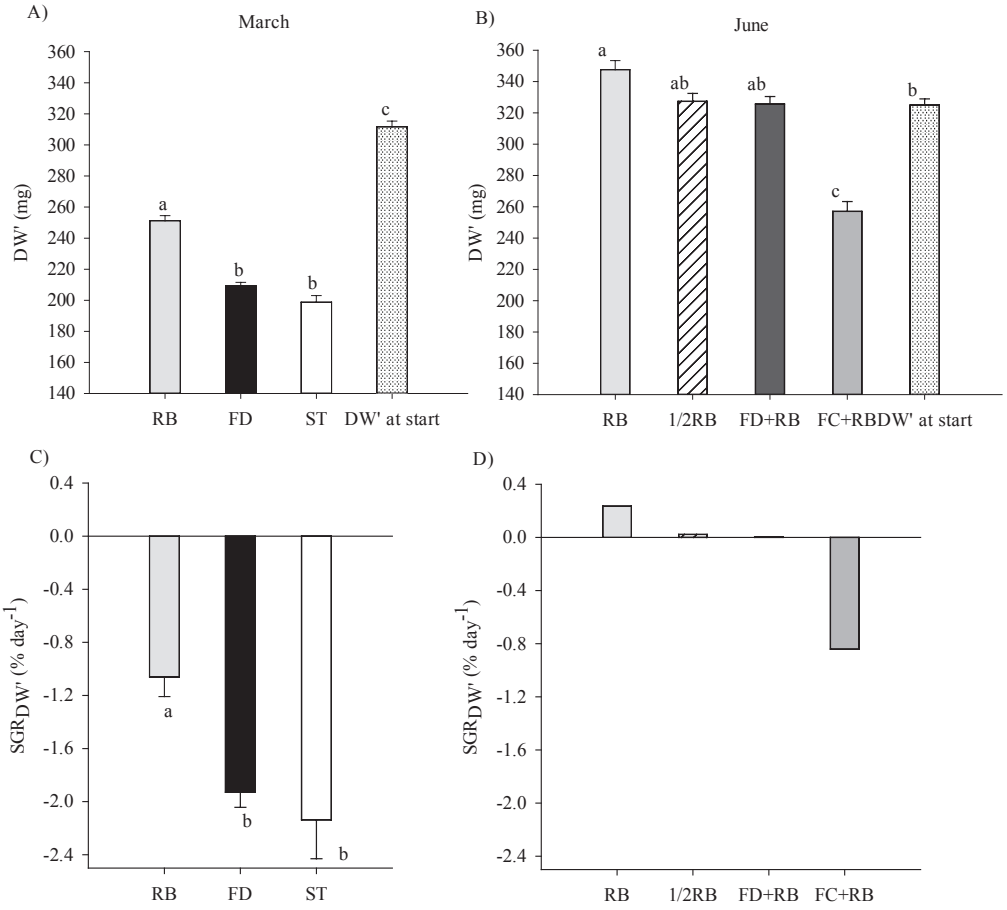

A)
March
DW' (mg)
RB
FD
ST
DW' at start
B)
June
RB
1/2RB
FD+RB
FC+RB
DW' at start
C)
SGR DW' (% day-1)
D)

Fig 5

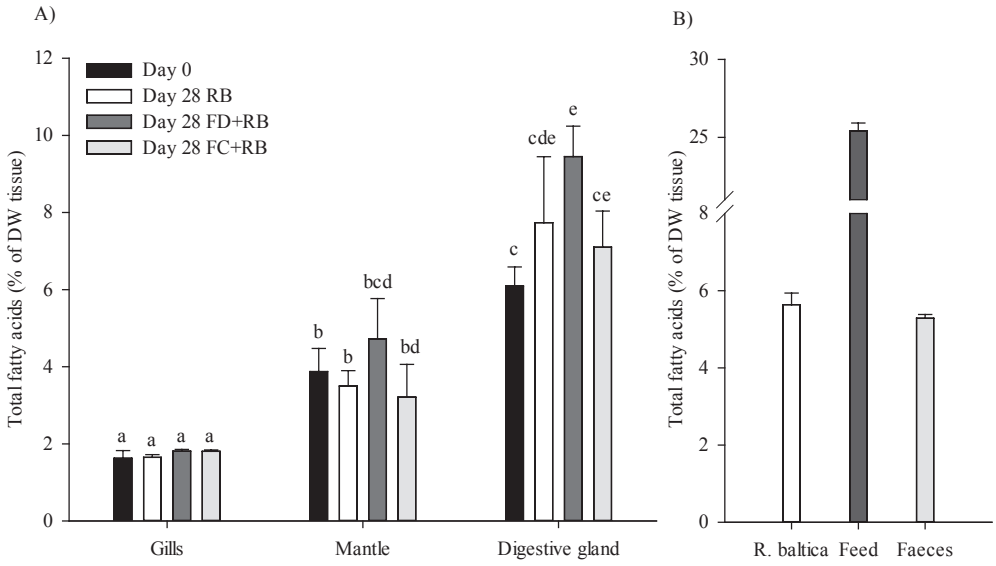

A)
B)
Day 0
Day 28 RB
Day 28 FD+RB
Day 28 FC+RB
Total fatty acids (% of DW tissue)
Gills
Mantle
Digestive gland
R. baltica
Feed
Faeces
a
a
a
a
b
b
bcd
bd
c
cde
e
ce

Fig 6

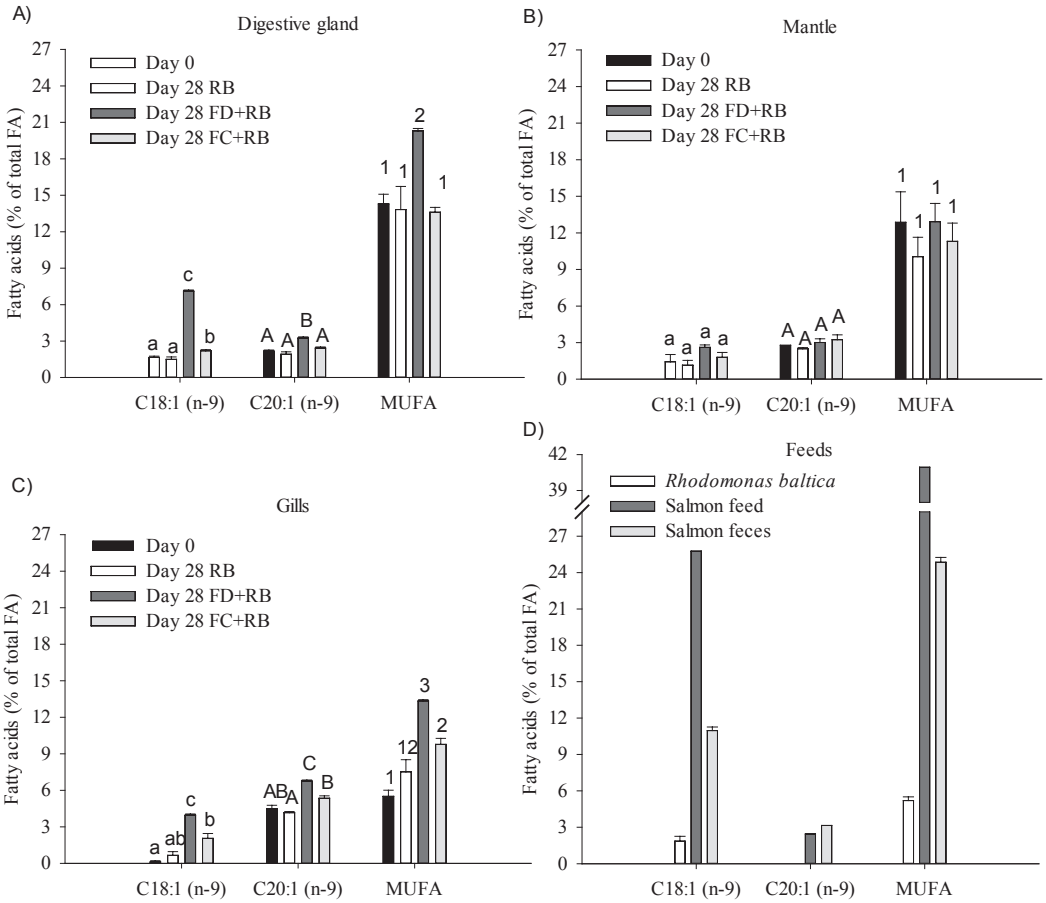
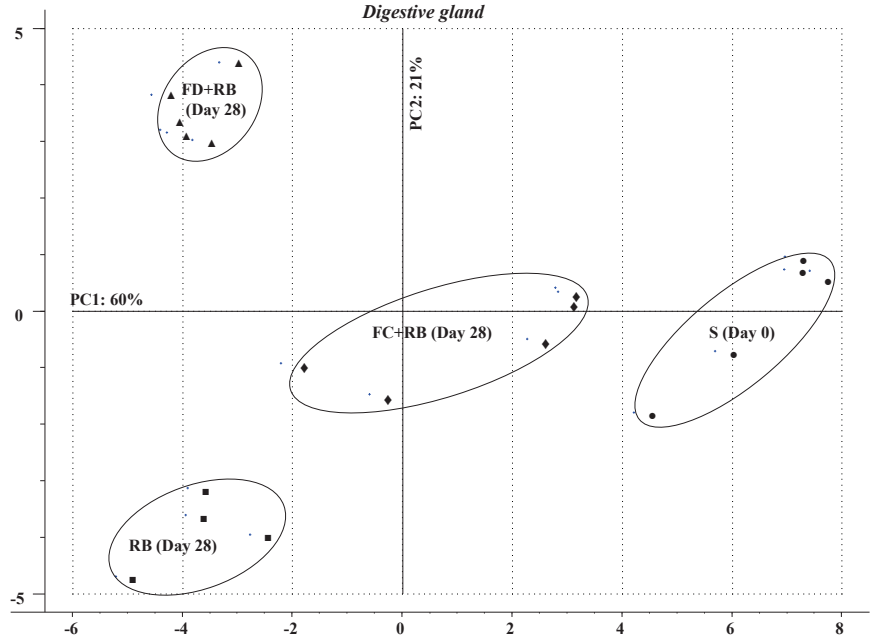
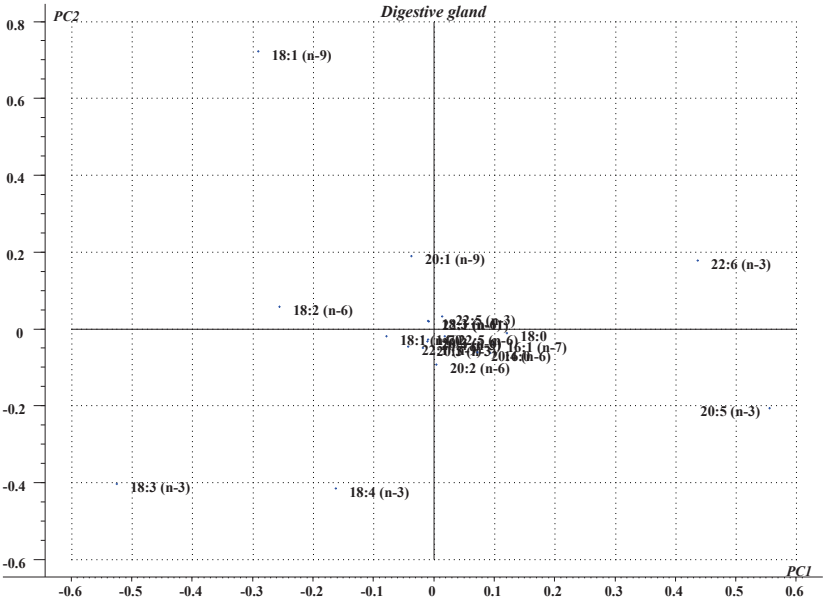

A)
Digestive gland
Day 0
Day 28 RB
Day 28 FD+RB
Day 28 FC+RB
Fatty acids (% of total FA)
C18:1 (n-9)
C20:1 (n-9)
MUFA
B)
Mantle
C)
Gills
D)
Feeds
Rhodomonas baltica
Salmon feed
Salmon feces

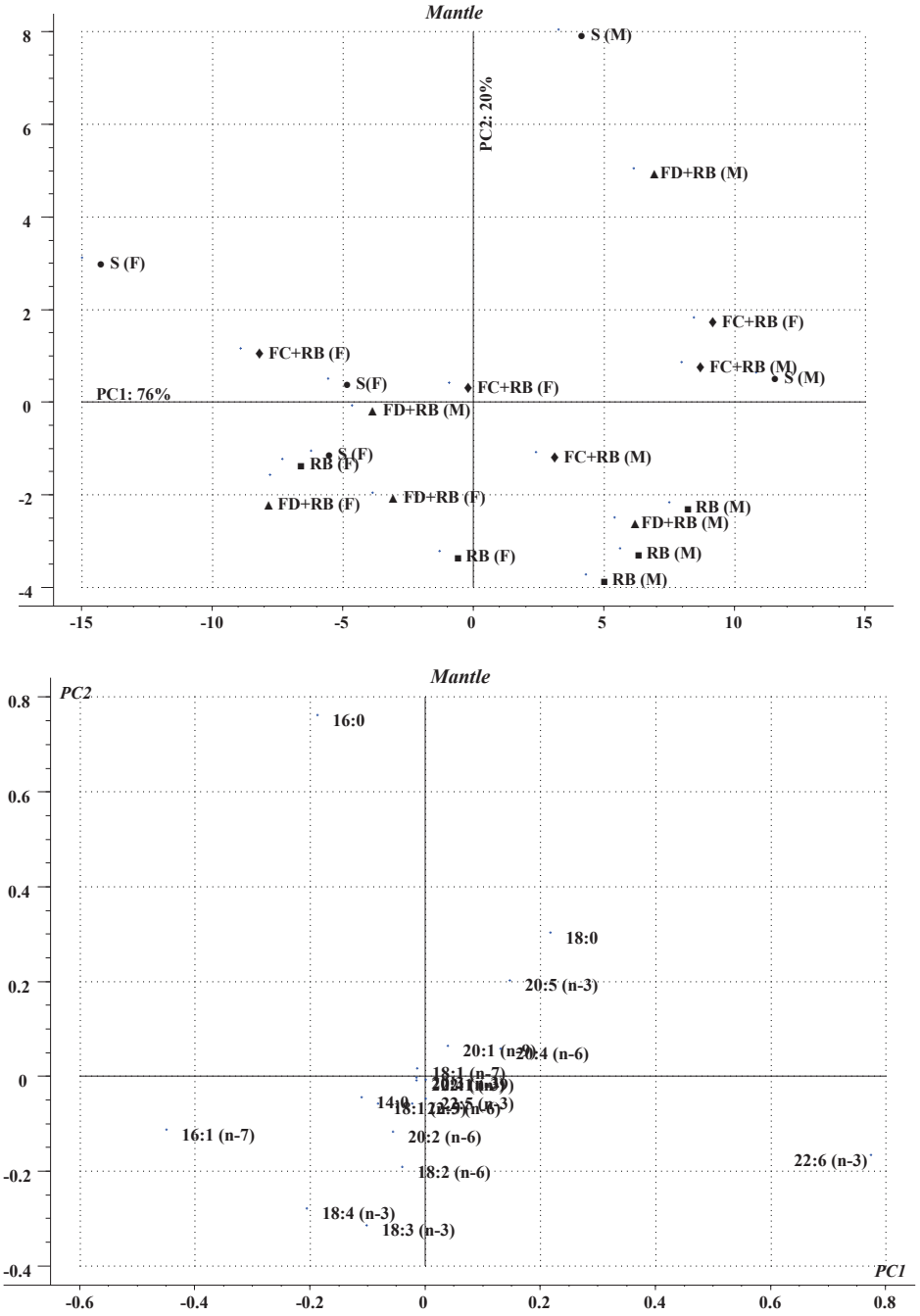
Fig 7

A)

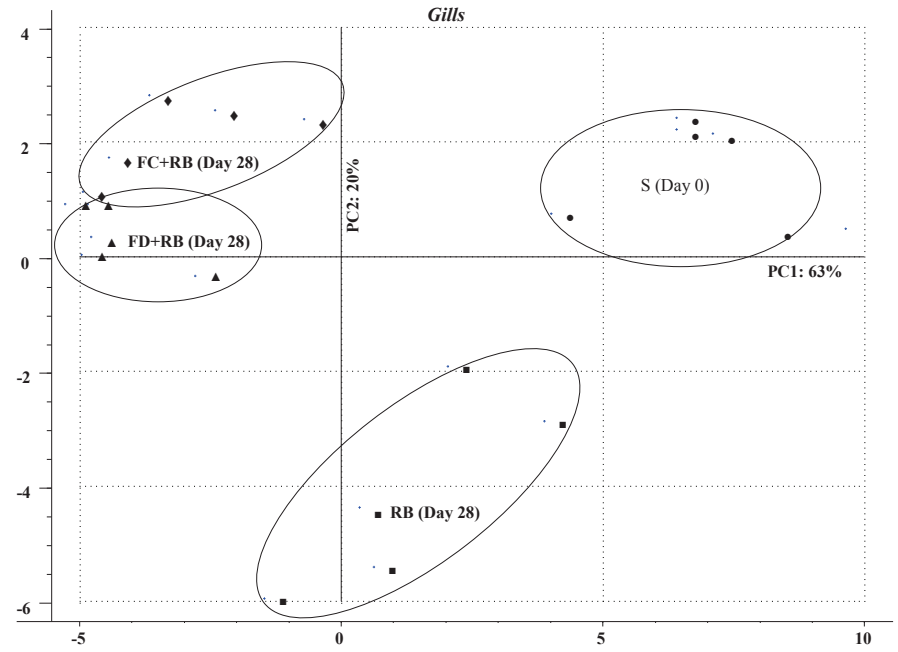

Digestive gland
PC2: 21%
PC1: 60%
FD+RB
(Day 28)
FC+RB (Day 28)
S (Day 0)
RB (Day 28)
5
0
-5
-6
-4
-2
0
2
4
6
8

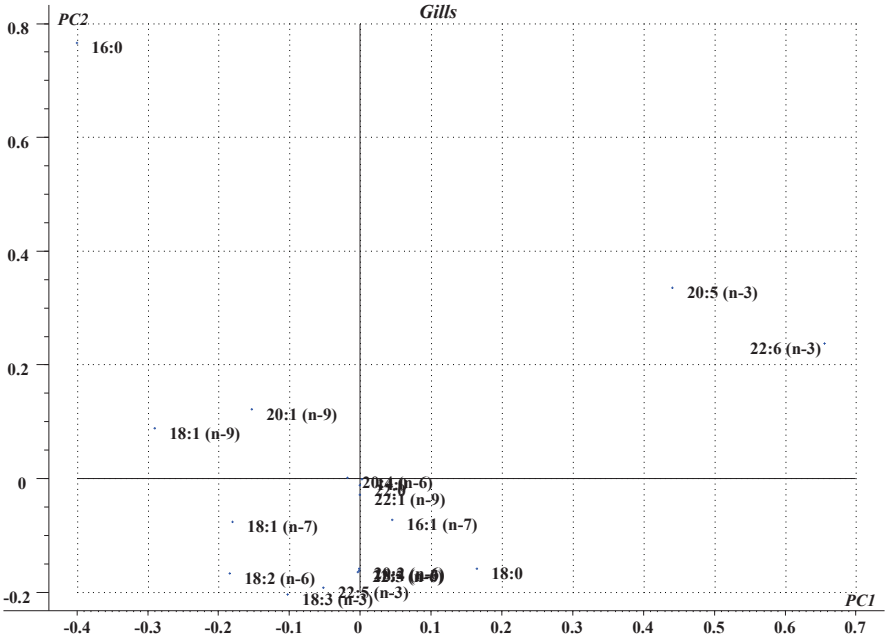

PC2
Digestive gland
PC1
18:1 (n-9)
20:1 (n-9)
22:6 (n-3)
18:2 (n-6)
18:0
20:2 (n-6)
20:5 (n-3)
18:3 (n-3)
18:4 (n-3)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5
0.6

B)


Mantle
PC2: 20%
PC1: 76%
S (M)
FD+RB (M)
S (F)
FC+RB (F)
FC+RB (F)
FC+RB (M)
S (M)
S(F)
FC+RB (F)
FD+RB (M)
S (F)
RB (F)
FC+RB (M)
FD+RB (F)
FD+RB (F)
RB (M)
FD+RB (M)
RB (F)
RB (M)
RB (M)
Mantle
PC2
PC1
16:0
18:0
20:5 (n-3)
20:1 (n-9)
20:4 (n-6)
18:1 (n-7)
14:0
16:1 (n-7)
20:2 (n-6)
22:6 (n-3)
18:2 (n-6)
18:4 (n-3)
18:3 (n-3)

C)


Gills
FC+RB (Day 28)
FD+RB (Day 28)
RB (Day 28)
S (Day 0)
PC2: 20%
PC1: 63%


Gills
PC2
PC1
16:0
20:5 (n-3)
22:6 (n-3)
20:1 (n-9)
18:1 (n-9)
22:1 (n-9)
18:1 (n-7)
16:1 (n-7)
18:2 (n-6)
18:0
18:3 (n-3)

Paper VI

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*

1987 Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988 Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988 Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988 Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988 Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989 John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989 Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989 Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989 Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990 Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990 Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990 Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990 Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990 Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990 Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991 Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991 Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991 Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991 Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991 Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991 Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991 Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism

1991 Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992 Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992 Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992 Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994 Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply

1994 Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
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1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway

1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999 Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)

1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts

2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities

2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates

2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning

2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009 Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009 Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009 Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010 Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010 Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010 Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010 Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010 Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010 Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010 Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010 Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010 Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010 Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011 Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011 Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011 Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011 Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011 Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011 Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011 Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011 Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Irja Ida Ratikainen	ph.d Biology	Foraging in a variable world: adaptions to stochasticity
2012	Aleksander Handå	ph.d Biology	Cultivation of Mussels (*Mytilus edulis*): Feed requirements, Storage and Integration with Salmon (*Salmo salar*) farming