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Response of Mytilus edulis to enhanced phytoplankton availability by controlled upwelling in an oligotrophic fjord

Strohmeier Tore [1, *], Strand Øivind [1], Alunno-Bruscia Marianne [1, 2], Duinker Arne [3], Rosland Rune [4], Aure Jan [1], Erga Svein Rune [4], Naustvoll Lars [5], Jansen Henrice [1, 6], Cranford Peter J. [7]

[1] Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway
[2] Ifremer, UMR 6539, 11 Presqu'île du Vivier, 29840 Argenton-en-Landunvez, France
[3] National Institute of Nutrition and Seafood Research, PO Box 2029 Nordnes, 5817 Bergen, Norway
[4] University of Bergen, Dept of Biology, PO Box 7803, 5020, Norway
[5] Institute of Marine Research, Nye Flødevig veien 20, 4817 His, Norway
[6] Institute for Marine Resources and Ecosystem Studies (IMARES), PO Box 77, 4400 AB Yerseke, The Netherlands.
[7] Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

* Corresponding author : Tore Strohmeier, email address : tore.strohmeier@imr.no

Abstract :

The controlled upwelling of nutrient-rich deep water in oligotrophic coastal regions has been proposed as a means of increasing phytoplankton and, subsequently, bivalve aquaculture production. This was tested as part of a large-scale upwelling experiment in an oligotrophic environment (Lysefjord, Norway). The mean chlorophyll a concentration in the upwelling area was consistently higher than at the control site (mean ± SD: 3.3 ± 1.9 and 1.5 ± 0.6 mg Chl a m-3, respectively) during the 4 mo of controlled upwelling. After 2 mo with upwelling, the dry flesh weight of 1 yr-old and 2 yr-old mussels was 95% and 24% higher, respectively, than that of the mussels at the control site. The 1 yr-old mussels at the upwelling site achieved up to 2.4-fold higher dry flesh weight compared to the control. Reproductive output was also higher at the upwelling site and only there, spawning of 1 yr-old mussels was detected. Standardized clearance and respiration rates showed maximum values during the most intense period of tissue growth. Average ingestion rates were 40% higher at the upwelling than the control site. Tissue growth and clearance rates were not correlated with the measured seston parameters, suggesting that food acquisition was responsive to other exogenous parameters and/or to increased endogenous energy demands. It was concluded that the sustained upwelling of nutrient-rich deep water in an oligotrophic fjord can increase phytoplankton biomass, resulting in improved mussel growth performance and increased aquaculture production carrying capacity. Thus, controlled upwelling represents a simple but effective ecosystem engineering approach for enhancing human food production.

Keywords : Bivalve aquaculture, production carrying capacity, physiology, fjord ecosystems, shell growth, tissue growth

1. Introduction

Bivalve aquaculture is typically most productive in regions where the seawater is rich in nutrients, such as at natural upwelling sites (Pitcher & Calder 1998, Figueiras et al. 2002, Alvarez-Salgado et al. 2008) and where anthropogenic nutrient runoff causes eutrophic conditions (Saxby 2002). These nutrient-rich sites sustain the high phytoplankton concentrations needed to support high growth rates in dense populations of suspension feeding bivalves, and are valuable places to aquaculture and production of human food. Access to productive coastal areas is, however, limited due to conflicts on use of space. The demand for more marine human food resources has stimulated initiatives for aquaculture development even within oligotrophic environments. Despite chronic low food availability, these environments supports many economically-important bivalve species (Pouvreau et al. 1999, Yukihira et al. 1999, Sara & Pusceddu 2008, Strohmeier et al. 2009).

The Norwegian coast comprise an enormous physical carrying capacity for aquaculture, yet the bivalve production carrying capacity (i.e. the cultured biomass and/or growth rate that can be sustained by available food) in most fjords is expected to be low(Aure et al. 2001, Andersen et al. 2014). Most Norwegian fjords are oligotrophic as a result of nutrient limitation in the euphotic zone during summer (Paasche & Erga 1988). Stratification between the upper brackish layer and the nutrient-rich intermediate layer

segregates the euphotic zone from the deeper nutrient-rich water for extended periods of the year(Erga et al. 2005, Erga et al. 2012) and plays an important role in regulating pelagic primary production and the vertical distribution of phytoplankton (Erga & Heimdal 1984, Erga 1989a, b, Erga & Skjoldal 1990, Erga et al. 2005). In most fjords the chlorophyll *a* (Chl *a*) concentration is low (0.5 to 2 mg m^{-3}) during most of the growth season of blue mussels (*Mytilus edulis*). Depletion of seston by farmed mussels has been shown to influence their growth performance, physiology and the production carrying capacity (Strohmeier et al. 2005, Aure et al. 2007b, Strohmeier et al. 2008, Rosland et al. 2009, Strohmeier et al. 2009, Rosland et al. 2011). The development of a bivalve farming industry in Norway, currently at a level of 2000 metric tons of mussels, involves knowledge on production carrying capacity in an oligotrophic environment. The use of controlled upwelling of nutrient-rich deep water in fjords (Aure et al 2007a) represents a measure to enhance such capacity and is considered to be one of the most promising ways to increase seafood production in a sustainable manner (Andersen et al. 2014).

To enhance primary production in Lysefjord, an oligotrophic mussel cultivation area in Norway, a large-scale upwelling experiment was initially conducted during the summers in 2004 and 2005 (Aure et al. 2007a). Forcing brackish surface water (at a rate of 2 m^3 s^{-1}) to a depth of 30 m created an upwelling of nutrient-rich deep water into the euphotic zone. This upwelling approximately tripled the mean Chl *a* concentration within an area of 10 km^2. The increased phytoplankton concentration due to controlled upwelling was within the natural variability of the fjord ecosystem and confined to the area of interest. A multiple box ecosystem model showed carrying capacity scenarios of mussel farming in the inner influenced regions of Lysefjord taking into account stocking densities, upwelling alternatives, and the cultivation areas(Filgueira et al. 2010). A higher and stable concentration of phytoplankton, dominated by non-toxic species is likely to increase the fjords carrying capacity of suspension feeders and could form the basis of more predictable mussel cultivation in oligotrophic environments. The objective of the present study was to test the hypothesis that controlled upwelling could significantly improve dietary conditions and blue mussel growth performance within an upwelling area in the Lysefjord. A secondary objective was to determine the feeding response of

mussels to the changes in dietary conditions resulting from upwelling to further improve our understanding of mussel feeding strategies and the physiological control of growth.

Suspension feeding bivalves are often exposed to a natural diet that is highly variable in terms of availability and composition. The functional feeding response of bivalves is known to be responsive to dietary conditions and food acquisition is primarily determined by the ability of suspension feeding bivalves to control clearance rate (Hawkins et al. 1999, Gardner & Thompson 2001, Hawkins et al. 2001, Cranford et al. 2005, Strohmeier et al. 2009, Cranford et al. 2011). Bivalves may also increase the nutritional value of the ambient seston by altering particle retention efficiency(Strohmeier et al. 2012), by preferentially capturing particles on the gills, and/or by selectively rejecting particles as pseudofaeces (Ward & Shumway 2004). The vast literature on the capacity of bivalves to alter feeding processes in response to natural diet variability (reviewed by Cranford et al. 2011, Ward and Shumway 2004) opposes the view that feeding is a simple function of diet saturation reduction and valve closure (Riisgard et al. 2013). The latter theory is based exclusively on evidence from laboratory feeding studies with an artificial diet designed to stimulate maximal clearance rate (Riisgard 2001, Riisgard et al. 2013). Consequently, this viewpoint and the related methodology are not widely accepted (Bayne 1998, 2001, Cranford 2001, Widdows 2001, Cranford et al. 2011). Elucidating the feeding strategies of bivalves under natural systems remains as an active field of research partly because no clear relationships have been found between the seasonal variations in feeding activity and many potential environmental forcing functions (Cranford & Hill 1999, Strohmeier et al. 2009). Functional feeding responses are also needed to improve the accuracy of model-based assessments of the carrying capacity of different sites for bivalve aquaculture (e.g. Filgueira et al. 2010).

Material and Methods

Blue mussel (*M. edulis*) shell and tissue growth and physiological responses were investigated between March and December 2010 in Lysefjord, Norway (Fig. 1).

Lysefjord is approximately 40 km long and 0.5 to 2 km wide, with a maximum depth of 460 meters, a mean tidal range of 0.4 m, and a surface area of 44 km^2. The fjord has a 14 m deep sill at the entrance. At the forced upwelling site, situated near the head of the fjord (Fig. 1; N 59° 03'22'', E 6° 37' 75''),a pump was used to force brackish water through a pipe, at a rate of approximate0.7 to 0.9 m^3 s^{-1}, down to a depth of 30 m, where it dispersed into the surrounding nutrient-rich deep water. We used the same upwelling platform as Aure et al. (2007a). The pump was started on the 27th of April and shut down on the 20th of August, 2010. The ascending plume of nutrient-rich water has been estimated to rise at a rate of ~10 to 15 m^3 s^{-1} to an intrusion depth of 6 to 10 m, based on Aure et al. (2007a). At present the upwelling is forced by gravity, and there are low operational costs linked to the upwelling.

Mussel growth performance and environmental factors were measured within the upwelling area near the head of the fjord (UPW site) and at a control (CONTR) site located 14km outside the UPW site.

Experimental bivalves

The cohorts of *M. edulis* used in experiments were collected in March 2010 from suspended ropes in the Lysefjord. To ensure that the mussels were from known cohorts, they were collected from separate ropes that had been stocked as juveniles in 2008 and 2009. On each collection occasion, each cohort was graded to a narrow range of shell length. The 2008 (two-year-old mussels, mean shell length 47 mm, SD 1.3) and 2009 (one-year-old mussels, mean shell length 18 mm, SD 0.9) cohorts were divided into groups of 40 individuals, which were individually marked for later identification and transferred, on the 3rdof March 2010, to the UPW and CONTR sites. The marked mussels were used to follow individual increases in shell length (measured, by a digital calliper, from umbo to posterior edge, ±0.01 mm). An additional 800-900 graded mussels from each of the above cohorts were divided between the two sites and used to follow temporal changes in dry flesh weight (DFW). On each sampling occasion, DFW was determined (± 0.01 g) for approximately 20 mussels by freeze-drying the tissue. The mussels were suspended from a single long-line, perpendicular to the current direction, in one meter

159 long lantern netsat 7 m depth, at the experimental sites. Stocking density was
160 approximately40 individuals per dish (80 individuals per m^2). The shell length and DFW
161 of mussels was monitored on a bi-weekly or monthly basis, from March to December
162 2010.The lantern nets were cleaned of fouling on each sampling date.
163

164 **Environmental parameters**

165 Temperature, salinity and fluorescence were simultaneously measured at both sites, at 30
166 min intervals and at a depth of 7 m, using STD/CTD 204 instruments (SAIV A/S,
167 Norway). The optical surface of the fluorometer was cleaned every second week.
168 The STD/CTD instrument located at the UPW site was also used to profile the water
169 column at both stations down to 30 meter depth on eight occasions between April and
170 August. For profiling, the instrument was set to log at 1 Hz and lowered at approximately
171 0.2-0.4 m s^{-1}. Data from both down and up-cast has been used.
172

173 Fluorescence units were converted to chlorophyll *a* (Chl *a*) concentrations, based on the
174 results of discrete water sample analysis at the study sites. Water samples (1.5 L) for
175 seston concentration and organic content analysis were collected from seven meters
176 depth, usually on a fortnightly basis. Suspended particulate matter, particulate organic
177 matter, and particulate inorganic matter (SPM, POM, and PIM respectively; mg L^{-1}) were
178 determined in triplicate for seston filtered onto pre-ashed and tared 1.2 µm nominal pore-
179 size filters (Whatman GF/C). Salt was expelled from SPM samples by rinsing each filter
180 under vacuum with isotonic ammonium formate. Filters were then dried at 60°C
181 overnight and weighed, to determine SPM. The SPM samples were then heated to 450°C
182 and reweighed, to determine POM and PIM.
183

184 Samples for the determination of Chl *a*, particulate organic carbon (POC) and particulate
185 organic nitrogen (PON) were collected simultaneously(for all parameters N=1),as SPM
186 samples, by filtering seston (0.50 L) onto a 1.2 µm filter (Whatman GF/C). Chl *a* was
187 analysed after extraction with 90% acetone using the fluorescence method, corrected for
188 acidified measurements (Strickland & Parson 1968). The fluorometer (Turner Designs
189 Model 10-AU) was calibrated with known concentrations of Chl *a* (Sigma Chemicals, St.

Louis, Mo., USA) and measured, using a spectrophotometer. Fluorescent measurements(x) obtained by the two fluorometers were converted to Chl *a* concentration using the following equations:

2010 UPW site; mg Chl *a* m^{-3} = 1.31x – 0.11; (r^2 = 0.96, n = 8)

2010 CONTR site; mg Chl *a* m^{-3} = 0.32x + 0.46; (r^2 = 0.42, n = 8)

The latter correlation was relatively low due to the limited range of Chl concentrations measured at the control site.

POC and PON were determined using a Thermo Finnigan FlashEA 1112 NC Analyzer after drying and fuming the filters over concentrated HCl for 0.5 h in a closed container to remove inorganic carbon.On each sampling occasion, the number and volume concentration of suspended particles, within 30 size-intervals between 1 and 60 µm diameter, were determined by a laser particle counter (PAMAS GmbH, Model S4031GO, Germany). In calculating particle volume (PV) we assumed that particles were spherical.

Determination of clearance rate

A time-series of average shell length standardized clearance rate (*C*, L h^{-1}) measurements was determined at the UPW and CONTR sites, from the 2008 cohort using natural seawater pumped from a depth of 7m. All *C* measurements were obtained using the same flow-through method, feeding chambers and protocols as previously reported in Strohmeier et al. (2009, 2012). The internal dimensions of the mussel chambers were 3.8 cm wide x 19.5 cm long x 8.1 cm height. This chamber design restrains recirculation and therefore helps to prevent re-filtration of water by the bivalves. Flow rates into each chamber were carefully controlled to exceed values known to allow water recirculation and re-filtration (Strohmeier et al. 2009).

On each biweekly or monthly sampling date, 20 marked mussels were temporarily transferred from the lantern nets to individual feeding chambers that were then left undisturbed in flowing seawater for at least 0.5 h, so that feeding was resumedprior to water sampling from the outlet of the chambers. Two additional chambers were left

empty, to serve as controls. The water samples were analysed for particle concentration using the laser particle counter described above. *C* was calculated as

$$C = RE * F,$$

where *F* is the flow rate (L h^{-1}) measured at the outlet of each chamber, and *RE* is the particle retention efficiency, calculated as

$$RE = (PV_C - PV_B) / PV_C,$$

where PV_C is the mean particle volume (mm^3L^{-1}) exiting the control chambers, and PV_B is the particle volume exiting the bivalve chamber. *F* was typically 11-14 L h^{-1}, giving estimated current speeds in chambers of between 0.2 and 0.3 cm s^{-1}. These flow rates were selected on the basis of initial observations to prevent *C* results from being underestimated by water refiltration at insufficient flow. For the calculation of *C*it was assumed that the maximum particle retention efficiency occurs across the 4 to 30 µm particle size range. Each chamber was carefully examined for pseudofaeces production, which was absent at both stations throughout the study period.

Individual clearance rates were standardized to an equivalent individual of 50 mm shell length,using the following equation:

$$Ys = \left(\frac{Ws}{We}\right)^b * Ye$$

where Y_s is the standardised parameter (*C* of a 50 mm mussel), W_s is the standardised shell length, W_e is the shell length of the mussel, Y_e is the mean measured *C* and *b* is the mean allometric exponent. A *b* value of 2.092 was chosen for mussels (Jones et al. 1992, Filgueira et al. 2008).*C* was standardized to shell length instead of dry flesh weight owing to the potential confounding effects of any differences in mussel condition index at the two study sites (reviewed by Cranford et al. 2011).

Respiration rate

A time-series of average standardised (dry flesh weight) respiration rate (*R*, mg O_2 g^{-1} h^{-1})measurements was determined at the UPW and CONTR sites for the 2008 cohort using individual incubation chambers (0.4 L) supplied with natural seawater pumped from a depth of 7 m. These measurements were conducted on 10 of the 20 individually-marked

M. edulis used for the *C* measurements. To maintain ambient temperature during the experiment, the incubation chambers were placed in a water bath supplied by flowing sea water from a seven meter depth. The mussels were held in the chambers with flowing water for at least 30 minutes, at which time all flow into the chambers was terminated and the incubation started. Oxygen concentration and temperature in the experimental chambers was measured, at the beginning and end of each experiment, with an oxygen optode (Aanderaa Data Instruments, Mod. 3835, Norway). We varied the incubation period (which ranged from 0.5 to 1.5 h) according to the ambient water temperature, so as to limit the oxygen decrease, to levels not higher than approximately 20% of the initial concentration. One chamber remained empty, as a control for any non-bivalve effects on the oxygen concentration, over the incubation period.

The respiration rate was calculated as:

$$R = \frac{(A - B) * V}{t}$$

where *R* is the respiration rate (mg O_2 h^{-1}), A and B are oxygen concentrations (mg O_2L^{-1}) at the start and at the end of the experiment, respectively, V is the volume of the chamber (excluding the bivalve volume, in litres),and t is the elapsed time expressed in hours. *R* was corrected to account for differences between initial and end values of oxygen concentration in the control chamber.

All respiration rates were standardized to an equivalent individual of 1 g DFW as follows:

$$Ys = \left(\frac{Ws}{We}\right)^{b} * Ye$$

where Y_s is the standardised parameter, W_s is the standardised DFW, W_e is the DFW of the experimental animals, Y_e is the mean measured R, and *b* is the allometric exponent, which was set to 0.7,according to(Smaal et al. 1997).

Calculations and statistics

Any significant differences in the mean annual seston quantity (Chl *a*, PV, SPM and POC)and quality(POM% and C:N)at the UPW and CONTR sites were tested using *t*-tests. Repeated-measures ANOVA were used to test for sampling site and date

differences in mean shell length, *C* and *R*. Prior to each statistical test, homogeneity of variance was evaluated using Greenhouse-Geisser's and Huynh-Feldt epsilon indices for repeated measures (Latour & Miniard 1983). Two way ANOVA was used to test for differences in DFW in the group of mussels from each site,at different sampling dates and between the two sites. Cases of a significant ANOVA result were followed by a Tukey HSD *post hoc* test, when relevant(Zar 1996).Environmental and seston variables relating to mussel growth, *C* and *R* were identified from a Pearson correlation matrix. Statistical tests were performed at $\alpha = 0.05$ with Statistica Version 11.1 (StatSoft, Inc 2012).

Results

Environmental parameters

Brackish water (psu < 25) was typically found in the upper 5 meter at both sites (Fig. 2). The surface layer at the upwelling site showed relatively low saline water in May, corresponding to the melting of snow in the highland and increased freshwater runoff mixing with the underlying water outward the fjord. The mean salinity and temperature at the holding depth of the mussels (7 m) was 27.8and 29.7 psu and 11.7 and 12.3 °Cat the UPW and CONTR sites, respectively. The temperature at the CONTR station tends to increase about about14 days earlier than at UPW (Fig. 2). The Chl *a* concentration at the UPW site showed typically higher values at the intrusion layer (6 to 10 m depth) compared to the CONTR station (Fig. 2).

The mean concentrations of Chl *a* (Table 1), at the holding depth of the mussels at the UPW site, was significantly higher than those at the CONTR site for both the water samples (*t*-tests, df = 14, $p = 0.017$, F-ratio =10.4, $p = 0.006$) and for the continuous measurements (*t*-tests, df = 10373, $p = 0.001$, F-ratio = 9.3, $p = 0.001$). The temporal variation in Chl *a* concentration at the depth of the mussels (7 m) shows the largest differences between the UPW and CONTR sites from mid-May to mid-July, with the concentration at the UPW site being two-three times higher than at the CONTR site (Fig. 3). Mean annual seston concentrations of PV, SPM and POC indicated that the highest

values were recorded at the upwelling site (Table 1, Fig 4) but the differences between sites were not significant (*t* –tests; $p > 0.05$).

The nutritional quality of the seston, as indicated by the mean annual organic fraction (POM%)ranged between 54 and 59% (Table 1) and there was no significant difference between the two stations (*t*-test; $p > 0.05$). The C:N molar ratio, another measure of diet quality, indicated mean values ranging between 5.9 and 7.0 (Table 1)with minimum and maximum values of 2.0 to 13.9, respectively(Fig. 4).The highest C:N (lowest food quality) was detected in late summer (Fig. 4). In summary, mussel food quantity, as indicated by the Chl *a* concentration, was significantly enhanced at the upwelling site compared to the control, and this enhancement was most prominent throughout mid-May to mid-July. The physical properties of the water column (temperature and salinity) and indicators of the nutritional quality (for consumers) of the seston were, however, similar between stations. Temporal variations in food quality indicators indicate relatively stable levels throughout much of the year.

Mussel shell growth

The effect of location (UPW vs CONTR) on mean shell length was significant for both cohorts and this effect was dependent on the sampling date for both cohorts (Table 2). At the end of the upwelling period and at the end of the experiment the shell length was significant higher at the UPW site for the 2008 cohort, but not for the 2009 cohort (Table 2 and Fig. 5). The differences in shell length comprised only a few mm. The estimated daily shell growth rate was highest for the 2009 cohorts(Fig. 6). The highest daily shell growth in the 2008 cohorts was obtained in July at the UPW site at 60 $\mu m\ d^{-1}$. High daily shell growth (> 80$\mu m\ d^{-1}$) was detected from May to September in the 2009 cohorts from both sites. Shell growth rate was not positively correlated with any of the seston parameters measured ($p > 0.05$).

Mussel dry flesh growth

The effect of location (UPW vs CONTR) on mean dry flesh weight was significant for both cohorts (ANOVA both cohorts, $p< 0.001$), and this overall effect was dependent on the sampling date (ANOVA both cohorts, $p< 0.001$). The temporal changes in DFW were distinct in both cohorts (Figs. 7 and 8). The main site-specific differences in DFW occurred in the last two weeks in June, when the mass of the 2009 cohort at the UPW site increased by almost three times, while the CONTR mussels showed only minor changes (Fig. 7). The mean daily growth rate in this period was 15 mg DFW d^{-1}, and is by far the highest growth rate detected for the 2009 cohort during the experiment (Fig. 8). The 46% drop in DFW mass from late July to August indicated that these mussels spawned. Spawning was not indicated for the 2009 cohort at the CONTR site. The highest DFW growth rates by the 2008 cohorts(UPW =32 and CONTR= 15 mg d^{-1}) corresponded in time with the rapid DFW growth of the 2009 cohort in mid-June, and occurred after a spawning period in both the 2008 cohorts. The DFW lost during spawning (i.e. reproductive output) was larger at the UPW site (0.31 and 0.19 mg) compared to that in the CONTR site (0.22 and 0 mg) for the 2008 and 2009 cohorts, respectively. Weight recovery after spawning was fastest at the UPW site (Fig. 7). The mean difference in DFW after two months with upwelling was 24 and 95% higher at the UPW site for the 2008 and 2009 cohorts, respectively (calculated from data shown in Fig. 7).The cumulative DFW growth enhancement at the UPW site, relative to the CONTR, was actually larger, as the above calculation does not account for the greater reproductive output and subsequent tissue mass recovery (Fig. 7).

Temporal variations in mean daily dry tissue growth rate for 2008 cohorts show two distinct periods of rapid growth (Fig. 8); negative growth (spawning) in late May followed by positive growth in June. The magnitude of both growth patterns was largest at the UPW site. Rapid daily growth rates in the 2009 cohorts were only detected at the UPW site. The timing of positive growth corresponded with the 2008 cohorts, and was similar in magnitude to the 2008 cohort at the CONTR site (15 mg DFW d^{-1}).The DFW growth rate did not positively correlate with any of the seston parameters measured ($p> 0.05$).

Clearance rate

The length-standardized clearance rate (*C*)of mussels at the UPW site averaged 2.8 L h^{-1}, and this value was significantly lower than the 3.5 L h^{-1}average determined for mussels at the CONTR site (Table 2). *C* ranged from 1.2 to 5.0 and 2.2 to 5.2 L h^{-1}, respectively, at the UPW and CONTR sites and the sampling date factor had a significant effect on differences in mean *C* between the two sites (Table 2 and Fig. 9). The highest *C* values were obtained in late June corresponding to the period of highest DFW growth (Fig. 7). The mean ingestion rate of Chl *a*(*C* x Chl *a*) was 7.8 and 4.7µg Chl *a* h^{-1} at the UPW and CONTR site, respectively. Average *C* values measured on each sampling date were not significant correlated with temperature, salinity or any of the measured seston parameters. Negative relationships (possibly non-linear) may, however, exist for some of the food quantity variables. For example, the mean *C*at Chl *a* concentration > 3 mg $m^{-3}$was 30 to 40% less than the average value at lower food concentrations.

Respiration rate

There was no significant difference in the mean weight standardized respiration rate (*R*) measured at the UPW and the CONTR sites (Table 2). Mean *R*was0.95 and 0.96 mg O_2 h^{-1} g^{-1}at the UPWsite and at the CONTR site, respectively. Although temporal patterns in *R* between the sites were found to be significantly different (Table 2), respiration levels at both sites peaked in mid-June (Fig. 9). The peak respiration rate in June corresponded to a late phase of spawning or the initiation of rapid DFW growth (Figs. 7 and 8) and increased *C* (Fig. 9).*R*was linearly correlated with particle volume (r = 0.71, $p < 0.004$), phaeopigment concentration (r = 0.64, $p < 0.014$), suspended particulate matter concentration (r = 0.60, $p < 0.029$) and particulate organic matter concentration (r = 0.57, $p < 0.047$), but notto temperatureor salinity.

Discussion

The results of this study show that controlled upwelling in a stratified oligotrophic environment can significantly increase phytoplankton biomass. Although upwelling was

399 limited to a four month period in the present study, it resulted in a significant
400 enhancement of blue mussel growth performance over the mussel growth period. This
401 demonstrates that anthropogenic enhancement of bivalve dietary conditions may facilitate
402 cultivation of bivalves in oligotrophic environments that have previously been considered
403 to be of limited use for human food production. Phytoplankton biomass at the upwelling
404 station in Lysefjord approximately doubled as a result of the upwelling of nutrient-rich
405 water. This is in accordance with previous studies in Lysefjord that showedapproximately
406 tripled phytoplankton concentration(Aure et al. 2007a). The lower response to the
407 upwelling of nutrient rich deep water in the present study is likely due to a lower
408 pumping rate of brackish water to force the upwelling, estimated at 0.7 to 0.9 m^3 s^{-1}
409 compared to the 2 m^3 s^{-1} used in the study by Aure et al. (2007a). The differences in
410 chlorophyll *a* concentration between stations disappeared as the pump was shut down in
411 August.
412
413 The enhanced tissue growth at the upwelling site compared to the control site resulted in
414 24(2008 cohort)to 95%(2009 cohort) higher tissue mass after two months of upwelling.
415 Since these values do not include weight loss through spawning and, since reproductive
416 output was greater at the upwelling site, the cumulative growth enhancement at the
417 upwelling site was underestimated. As an example of maximal differences; harvesting
418 one year old mussels from the upwelling site in mid-July (before spawning) would result
419 in 2.4 times more DFW compared to the control site(Fig. 7). The present study is the first
420 to demonstrate how enhanced phytoplankton biomass, driven by controlled upwelling of
421 naturally abundant and composition of nutrients, can improve mussel growth
422 performance.Enhanced phytoplankton concentrations by forced upwelling may also
423 affect other grazers and higher trophic levels in coastal ecosystem (Yanagi & Nakajima
424 1991, Jeong et al. 2013).
425
426 The observed changes in tissue mass between sampling dates provides information on
427 both somatic and reproductive tissue growth. We assume that rapid(< 2 weeks) and large
428 decreases (exceeding the DFW loss during winter starvation,> 1-4 mg d^{-1}, (Strohmeier
429 2009)in mean dry flesh weight represents spawning. Temporal variations in tissue growth

were typically positive through most the year, except during spawning periods. Tissue growth rate was highest in the pre-spawning period for the 2009 cohort at the upwelling site and in the post-spawning period for both the 2008 cohorts, and probably coincided with gametogenesis. The rapid building of tissue mass during post-spawning periods occurred at both sites for the 2008 cohorts, yet the magnitude of tissue increase before spawning, the reproductive output (weight loss as gametes), and the recovery rate, was larger in mussels at the upwelling site. It is also notable that the one-year-old mussels at the upwelling site went through gametogenesis and spawned while the mussels at the control site showed no signs of gametogenesis and did not spawn.The greater availability of phytoplankton at the upwelling site, particularly from mid-May to mid-July, is the apparent cause ofenhanced tissue growth, reproductive output, and meat yield in thetwo mussel cohorts situated inside the upwelling region of Lysefjord.

The findings of this study add to the results of several studies, from meso- to eutrophic environments, showing that bivalve growth is dependent on food availability, albeit in a manner that is often poorly understood(Coe 1945, Winter 1978, Widdows et al. 1979, Bayne & Newell 1983, Frechette & Bourget 1985, Macdonald & Thompson 1985, Soniat & Ray 1985, Berg & Newell 1986, Page & Hubbard 1987, Gibbs et al. 1991, Hickman et al. 1991, Grant 1996, Hawkins et al. 1999, Karayucel et al. 2003). Apparently the cumulative tissue growth over the sampling period was more affected by phytoplankton concentration compared to shell growth, as only minor- or non-differences in mussel shell length were detected between the upwelling and control site(Figs. 5 and 7). The lack of correlation between the seston parameters and shell growth also indicates that growth in shell length is largely independent of the range of food concentration studied. These findings support the previous conclusion that the seasonal growth in shell and tissue is uncoupled (Hilbish 1986), that the internal shell volume does not restrain tissue growth (Palmer 1981), and that a lesser fraction of the surplus energy (20-30%) is allocated to shell growth (Hawkins & Bayne 1992, Duarte et al. 2010). However, following Dynamic Energy Budget theory (Kooijman 2010), tissue weight is divided into structural tissue and reproductive tissue. Of these only the structural weight should be compared to shell length. We did not dissect the mussel in these components. Yet, assuming that all

reproductive tissue is lost during spawning, then Fig. 7 indicate that the structural weight is rather similar at both locations and the differences in weight were related to the changes in reproductive tissue. This opens for the structural weight to be closer related to food availability than detected for the DFW in this study.

Regulation of tissue growth by suspension feeding bivalves is mainly achieved through the control of food acquisition, by modifying clearance rate(Hawkins et al. 1999, Gardner & Thompson 2001, Hawkins et al. 2001, Cranford et al. 2005, Strohmeier et al. 2009). An increase in both clearance-and respiration rates of the two-year-old mussels corresponded with the pre- and post-spawning periods in June, when growth rates were highest.Clearance rates, averaged across the study period, were significantly lower in mussels held under the enhanced dietary conditions at the upwelling site. The clearance rates reported herein were similar to values previously reported for *M. edulis* under low-seston conditions (Strohmeier et al. 2009), but higher food concentrations were also encountered in the present study and the clearance rates of mussels tended to decrease at these levels. Seston concentration typically has a strong influence on bivalve clearance rate,with many species having been observed to decrease clearance rate with increasing food quantity (reviewed by Cranford et al. 2011). This allows food intake to be maximized during periods of low availability (Bayne et al. 1987). Our results indicate that increased reproductive growth was achieved by increasing clearance rate, which apparently more than compensated for the increased energy demand of reproduction that was indicated by the increased respiration rate. The longer-term increase in tissue growth at the upwelling site was achieved despite a decrease in clearance rate, simply due to greater food concentration. This is demonstrated by the 40% higher ingestion rate at the upwelling site(data not shown). Although mussel growth is highly sensitive to changes in food absorption efficiency, the similar seston quality observed at both study sites (Table 1)would result in a similar absorption efficiency (Vahl 1980, Bayne et al. 1987, Cranford 1995, Cranford et al. 1998, MacDonald et al. 1998).

This study shows that increased phytoplankton concentrations in oligotrophic fjords may be achieved by controlled upwelling of nutrient-rich deep water and that this results in

492 increased mussel tissue growth. Although mussels held in the upwelling region lose more
493 tissue mass during spawning, they also rebuild reproductive tissue faster, compared to
494 mussels kept at naturally-low seston concentrations. The main consequence of enhanced
495 food conditions for mussel cultivation is the potential for higher meat yields from a given
496 area of fjord during the production season. The increased primary production and bivalve
497 production carrying capacity of controlled upwelling systems in oligotrophic
498 environments will allow increased stocking density and thereby reduce the area required
499 for human food production.
500

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504 The experiments comply with the current laws of the country in which the experiments
505 have been conducted.
506

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Table 1. Mean values (± SD) of seston quantity and quality indicators at7 m depth at the upwelling (UPW) and control (CONTR) stations during May 6th to August 11th2010. Mean chlorophyll *a* values are calculated from *in situ* fluorometer (fChl *a*) and discrete water sample (wChl *a*) data. PV is the particle volume concentration, SPM is suspended particulate matter, POC is particulate organic carbon, POM% is the organic content of SPM and C:N is the molar carbon to nitrogen ratio.

Site	fChl *a* (mg m^{-3})	wChl *a* (mg m^{-3})	PV (ml m^{-3})	SPM (mg m^{-3})	POC (mg m^{-3})	POM% (%)	C:N
UPW	2.9 (1.8)	3.3 (1.9)	4.0 (3.1)	3.1 (1.2)	302 (198)	54	5.9
CONTR	1.4 (0.4)	1.5 (0.6)	2.5 (1.4)	2.5 (1.2)	239 (128)	59	7.0

Table 2. Summary of results from repeated measures ANOVA comparisons of site (upwelling vs. control Lysefjord locations) effects on the mean shell length (SL), and standardized clearance (*C*) and respiration rates (*R*) of two mussel cohorts. Separate test results are shown for the indicated mussel cohort and significant mean effects (* = $p \leq 0.05$; ** = $p \leq 0.01$; and *** = $p \leq 0.001$) and adequate statistical power at $\alpha = 0.05$ (*; $1\text{-}\beta \geq 0.8$) are indicated.

Parameter (Cohort)	SS	Degr. Of Freedom	MS	F	*P*	1-β
Shell Length (2008)						
Intercept	1485174	1	1485174	419475	<0.001***	1.000*
Samp. Date	1082	11	98	28	<0.001***	1.000*
SL * site	303	1	303	104	<0.001***	1.000*
SL * S. Date	171	11	16	5.4	<0.001***	1.000*
Shell Length (2009)						
Intercept	485303	1	485303	33255	<0.001***	1.000*
Samp. Date	14064	11	1279	88	<0.001***	1.000*
SL	20	1	20	1.8	0.179	0.269*
SL * S. Date	15	11	1.4	0.1	0.999	0.092*
***C*(2008)**						
Intercept	2727	1	2727	855	<0.001***	1.000*
Sample Date	145	6	24	8	<0.001***	0.999*
C	38	1	38	21	<0.001***	0.996*
*C**Date	173	6	29	21	<0.001***	1.000*
***R*(2008)**						
Intercept	124	1	124	2657	<0.001***	1.000*
Sample Date	6.2	6	1.03	22	<0.001***	1.000*
R	0.00	1	0.00	0.04	0.84	0.055
*R**Date	0.88	6	0.15	2.60	<0.026*	0.815*

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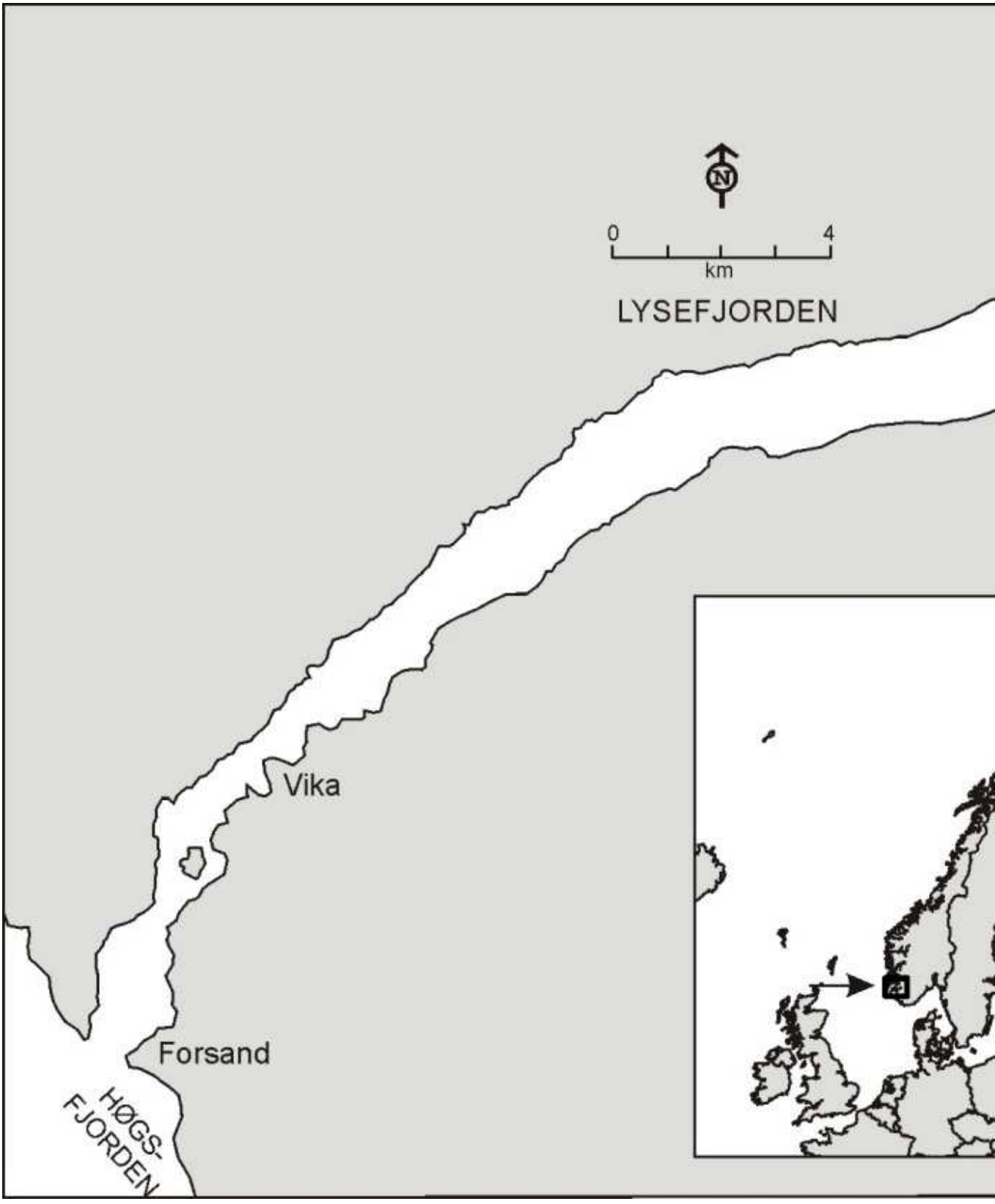

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Figure 1. Map of North-Western Europe (insert), South-Western Norway (insert) and Lysefjord indicating the experimental sites, where Upw represents the upwelling station and Ctrl represents the control station.

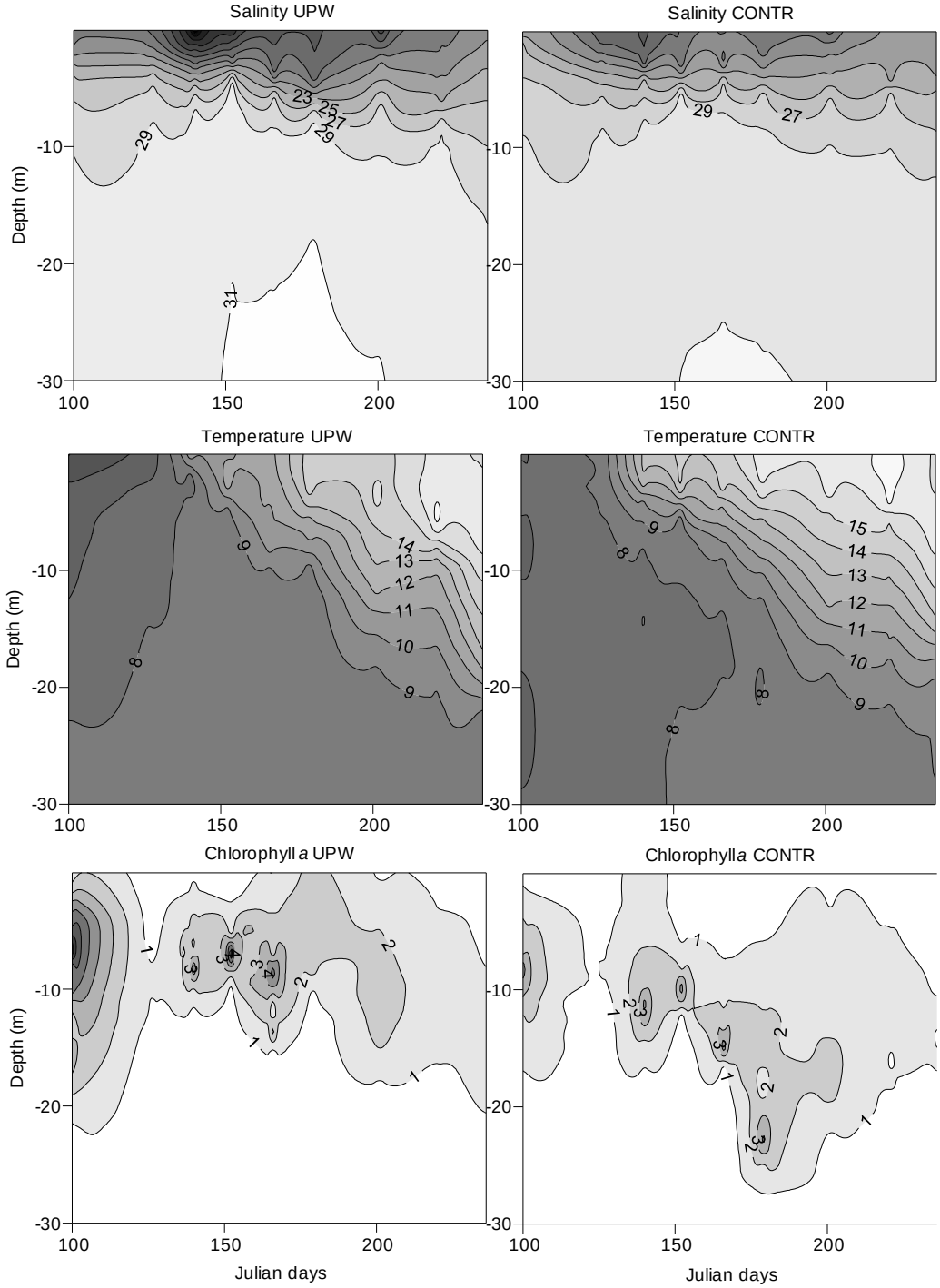

Figure 2. Time series of salinity, temperature and estimated chlorophyll *a* at the upwelling station (UPW) and control station from the 10th of April to the 24th of August in the upper 30 m of the Lysefjord.

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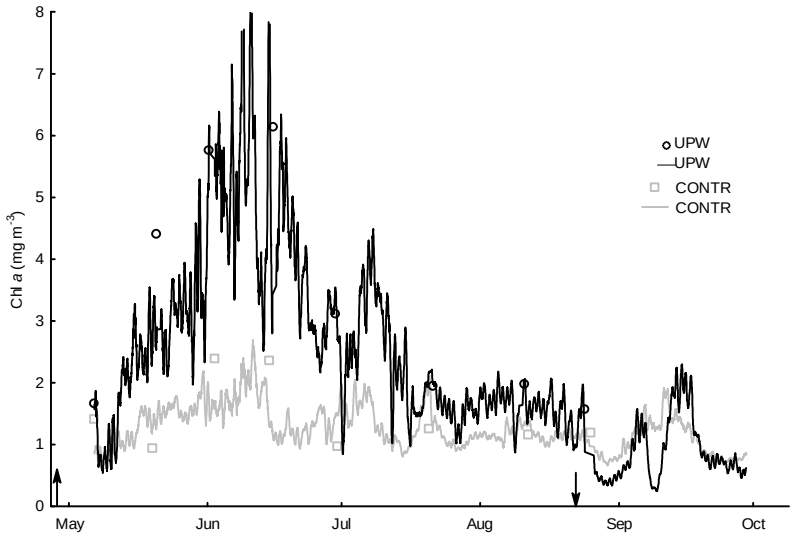

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735 **Figure 3**. Time series of estimated chlorophyll *a* (Chl *a*) from *in situ* flurometers (lines)
736 and from water samples (o and □) at 7 m depth within the upwelling area (UPW) and at
737 the control station (CONTR). *In situ* instrument measurements are presented on a daily
738 basis (running mean of 24 hourly samples). Arrows on x-axis indicate when the pump
739 was started and shut down.

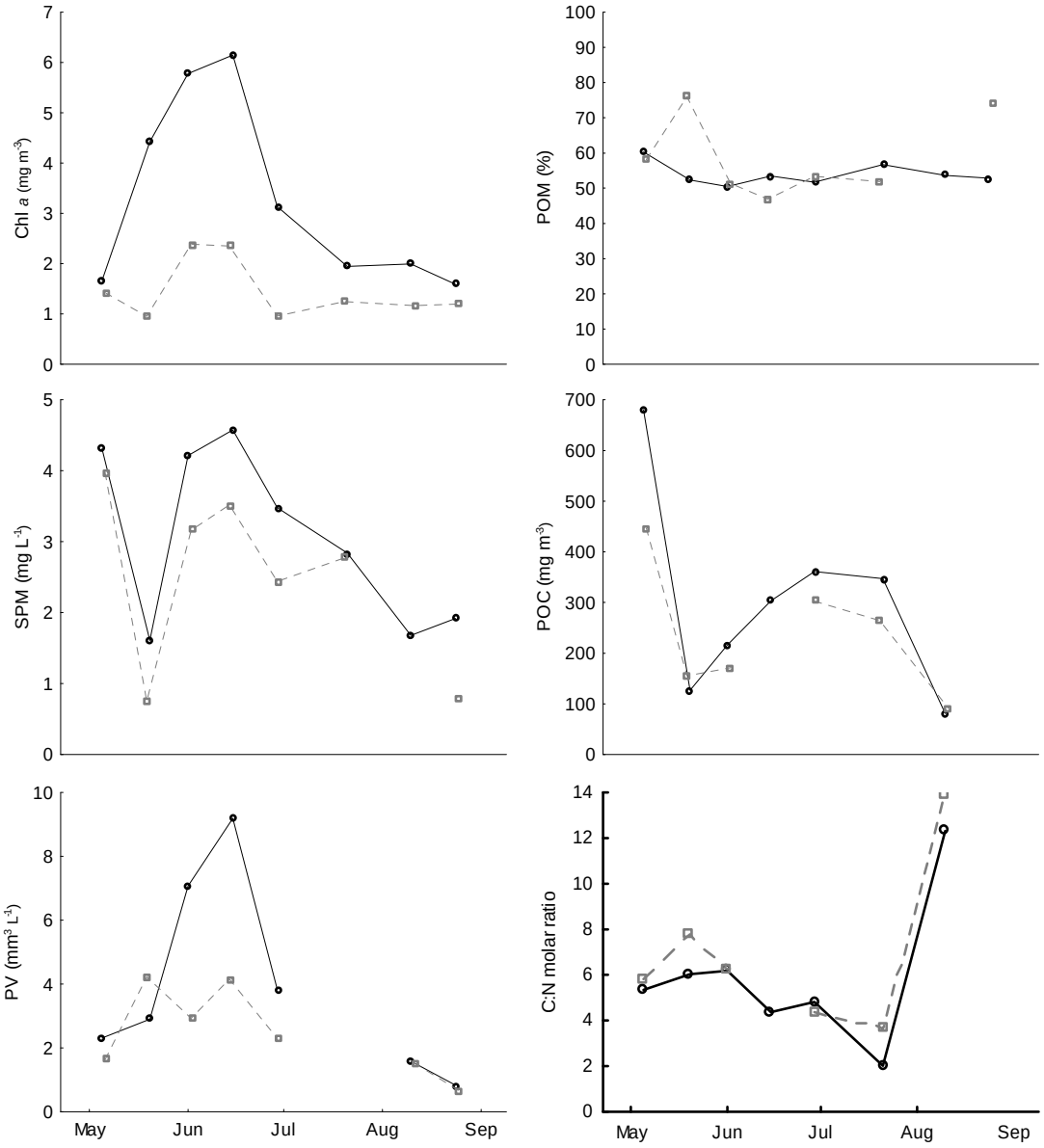

Figure 4. Time series of chlorophyll *a* (Chl *a*, from water samples), mean particle volume concentration (PV;total for 1-60 µm particles), particulate organic carbon (POC), suspended particulate matter (SPM), organic matterfraction (POM%) and the ratio of carbon to nitrogen (C:N) at 7 m depth at upwelling (UPW, line) and control (CONTR dotted line) stations.Missing data points due to lack of sampling (PV) and disrupted filters (SPM and CN)

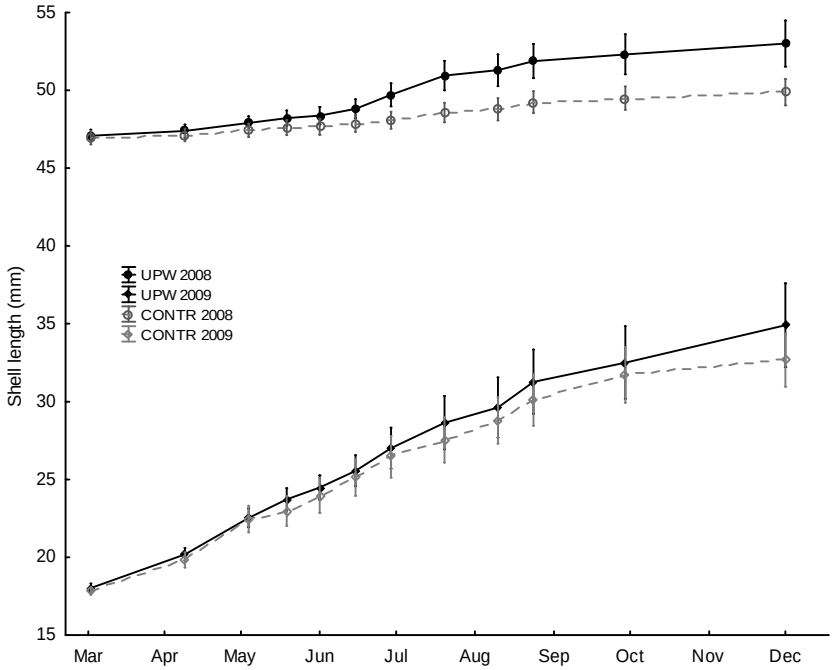

Figure 5. Temporal changes in mean shell length (mm) for individually marked *M. edulis* from two mussel cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) stations. Vertical lines indicate ±95% confidence limits.

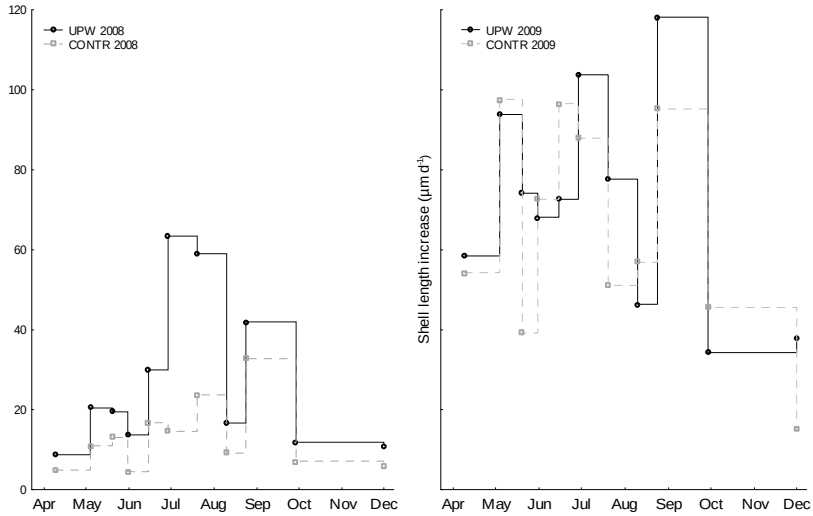

Figure 6. Temporal changes in the mean daily growth of *M. edulis* shell (µm d^{-1}), from two cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) stations in Lysefjord.

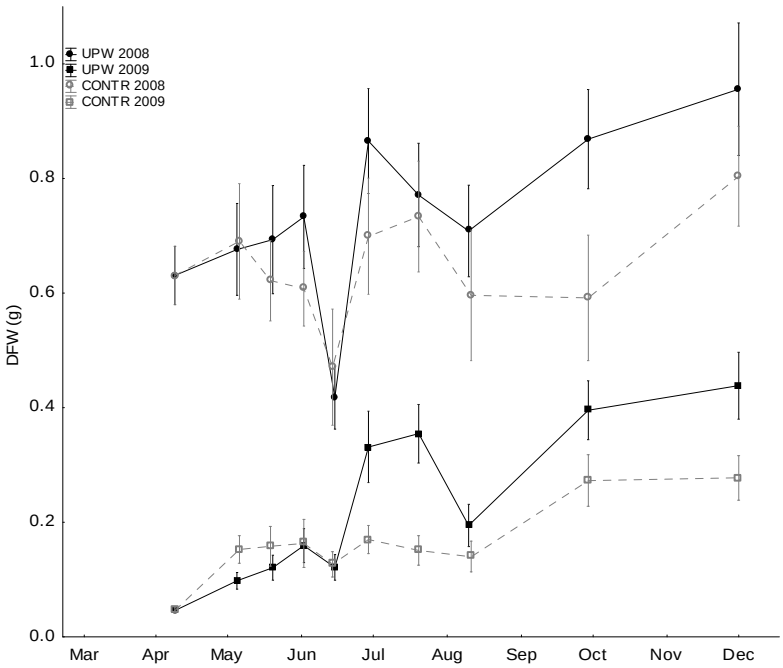

Figure 7. Temporal changes in mean dry flesh weight (DFW, g) oftwo*M. edulis*cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) stations in Lysefjord from March 2010 to December 2010. Vertical lines indicate ±95% confidence limits.

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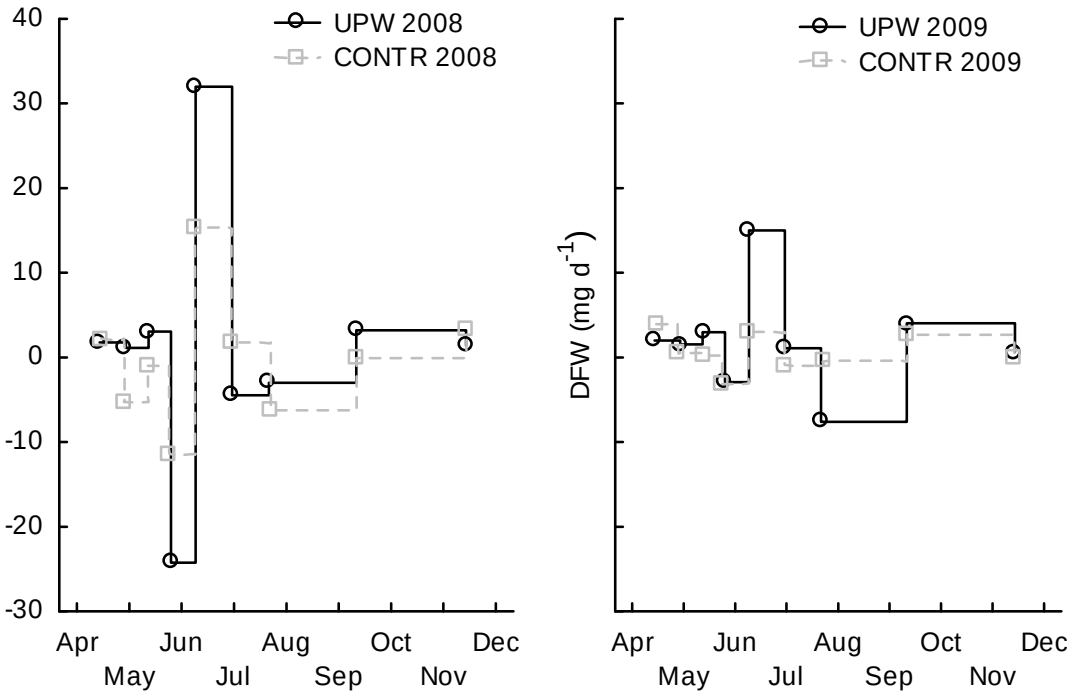

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764 **Figure 8**. Temporal changes in estimated mean daily dry flesh growth rate (DFW; mg d-
765 1) of two *M. edulis*cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and
766 control (CONTR) stations in Lysefjord**.**

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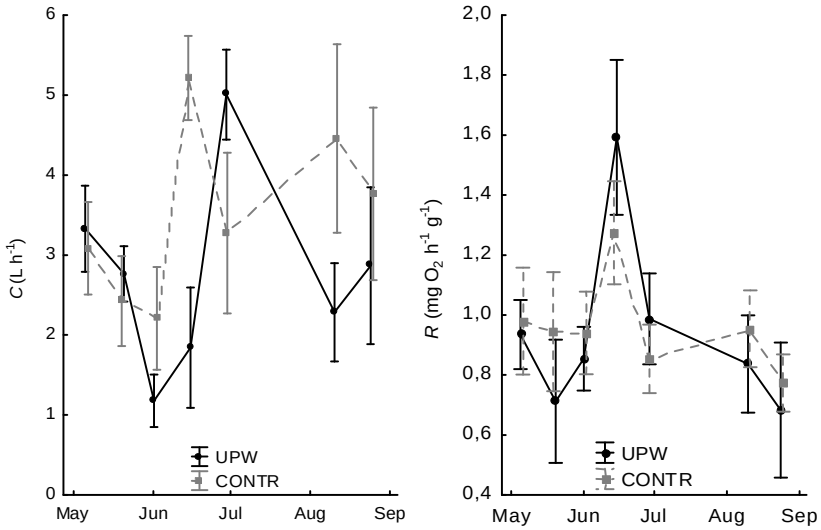

770 **Figure 9.**Temporal
771 changes in mean clearance rate standardized to a 50 mm shell length individual (*C*; L h^{-1})
772 and dry flesh weight standardized respiration rate (*R*; mg O_2 h^{-1} g^{-1}) for the 2008 cohorts
773 held at the upwelling (UPW) and control sites (CONTR) in Lysefjord.