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

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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 (*Mytilus edulis*) 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 at 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.

KEY WORDS: Bivalve aquaculture · Production carrying capacity · Physiology · Fjord ecosystems · Shell growth · Tissue growth

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

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populations of suspension-feeding bivalves, and are valuable places for 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 support many economically important bivalve species (Pouvreau et al. 1999, Yukihira et al. 1999, Sara & Pusceddu 2008, Strohmeier et al. 2009).

The Norwegian coast comprises 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, 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 (0.5–2 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 and physiology and the production carrying capacity (Strohmeier et al. 2005, 2008, 2009, Aure et al. 2007b, Rosland et al. 2009, 2011). The development of a bivalve farming industry in Norway, currently at a level of 2000 metric tons of mussels per year, involves knowledge of 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 of 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 fjord's 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 the clearance rate (Hawkins et al. 1999, 2001, Gardner & Thompson 2001, Cranford et al. 2005, 2011, Strohmeier et al. 2009). 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 and Ward & 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 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).

MATERIALS AND METHODS

Blue mussel (*Mytilus 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 0.5–2 km wide, with a maximum depth of 460 m, 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; 59° 03′ 22″ N, 6° 37′ 75″ E), a pump was used to force brackish water through a pipe, at a rate of approximately 0.7–0.9 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 27 April and shut down on 20 August 2010. The ascending plume of nutrient-rich water has been estimated to rise at a rate of ~10–15 m^3 s^{-1} to an intrusion depth of 6–10 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 14 km 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 (2 yr old mussels, mean ± SD shell length: 47 ± 1.3 mm) and 2009 (1 yr old mussels, mean ± SD shell length: 18 ± 0.9 mm) cohorts were divided into groups of 40 individuals, which were individually marked for later identification and transferred, on 3 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 2 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 1 m long lantern nets at 7 m depth, at the experimental sites. Stocking density was approximately 40 individuals per dish (80 ind. m^{-2}). The shell length and DFW of mussels was monitored on a bi-weekly or monthly basis, from March to December 2010. The lantern nets were cleaned of fouling on each sampling date.

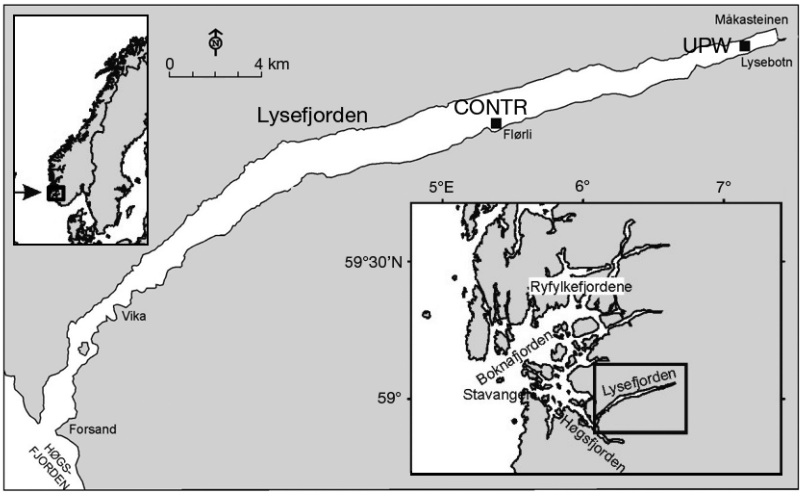

Fig. 1. Lysefjord, with the experimental sites indicated (UPW: upwelling site, CONTR: control site). Insets: NW Europe (left), SW Norway (right)

Environmental parameters

Temperature, salinity, and fluorescence were simultaneously measured at both sites, at 30 min intervals and at a depth of 7 m, using STD/CTD 204 instruments (SAIV A/S). The optical surface of the fluorometer was cleaned every second week.

The STD/CTD instrument located at the UPW site was also used to profile the water column at both sites down to 30 m depth on 8 occasions between April and August. For profiling, the instrument was set to log at 1 Hz and lowered at approximately 0.2–0.4 m s^{-1}. Data from both down- and up-cast has been used.

Fluorescence units were converted to chl *a* concentrations, based on the results of discrete water sample analysis at the study sites. Water samples (1.5 l) for seston concentration and organic content analysis were collected from 7 m depth, usually on a fortnightly basis. Suspended particulate matter, particulate organic matter, and particulate inorganic matter (SPM, POM, and PIM respectively; mg l^{-1}) were determined in triplicate for seston filtered onto pre-ashed and tared 1.2 µm nominal pore-size filters (Whatman GF/C). Salt was expelled from SPM samples by rinsing each filter under vacuum with isotonic ammonium formate. Filters were then dried at 60°C overnight and weighed, to determine SPM. The SPM samples were then heated to 450°C and reweighed, to determine POM and PIM.

Samples for the determination of chl *a*, particulate organic carbon (POC), and particulate organic nitrogen (PON) were collected simultaneously (for all parameters, n = 1), as SPM samples, by filtering seston (0.50 l) onto a 1.2 µm filter (Whatman GF/C). Chl *a* was analysed after extraction with 90% acetone using the fluorescence method, corrected for acidified measurements (Strickland & Parson 1968). The fluorometer (Turner Designs Model 10-AU) was calibrated with known concentrations of chl *a* (Sigma Chemicals) and measured, using a spectrophotometer. Fluorescent measurements (x) obtained by the 2 fluorometers were converted to chl *a* concentration using the following equations:

2010 UPW site:

$$\text{mg chl } a\ \text{m}^{-3} = 1.31x - 0.11\ (r^2 = 0.96,\ n = 8) \quad (1)$$

2010 CONTR site:

$$\text{mg chl } a\ \text{m}^{-3} = 0.32x + 0.46\ (r^2 = 0.42,\ n = 8) \quad (2)$$

The latter correlation was relatively low due to the limited range of chl *a* 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). In calculating particle volume (PV), we assumed that particles were spherical.

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 7 m. 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 × 19.5 cm long × 8.1 cm high. 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 resumed prior 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 in the previous subsection. C was calculated as:

$$C = RE \times F \quad (3)$$

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:

$$RE = (PV_C - PV_B)/PV_C \quad (4)$$

where PV_C is the mean particle volume (mm^3 l^{-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 4–30 µm particle size range. Each chamber was carefully examined for pseudofaeces production, which was absent at both sites throughout the study period.

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

$$Y_s = (L_s/L_e)^b \times Y_e \quad (5)$$

where Y_s is the standardized parameter (C of a 50 mm mussel), L_s is the standardized shell length, L_e is the

shell length of the mussel, Y_e is the mean measured parameter (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 DFW owing to the potential confounding effects of any differences in mussel condition index at the 2 study sites (reviewed by Cranford et al. 2011).

Respiration rate

A time series of average standardized (DFW) 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 seawater from a 7 m depth. The mussels were held in the chambers with flowing water for at least 30 min, 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, Model 3835). 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:

$$R = [(A - B) \times V]/t \quad (6)$$

where R is the respiration rate (mg O_2 g^{-1} h^{-1}), A and B are oxygen concentrations (mg O_2 l^{-1}) at the start and at the end of the experiment, respectively, V is the volume of the chamber (excluding the bivalve volume; l), and t is the elapsed time (h). 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:

$$Y_s = (W_s/W_e)^b \times Y_e \quad (7)$$

where Y_s is the standardized parameter, W_s is the standardized DFW, W_e is the DFW of the experimental animals, Y_e is the mean measured parameter (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 ratio) 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 2 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).

RESULTS

Environmental parameters

Brackish water (psu < 25) was typically found in the upper 5 m 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 27.8 and 29.7 psu and 11.7 and 12.3°C at the UPW and CONTR sites, respectively. The temperature at the CONTR site tends to increase about 14 d earlier than at UPW (Fig. 2). The chl *a* concentration at the UPW site showed typically higher values at the intrusion layer (6–10 m depth) compared to the CONTR site (Fig. 2).

The mean concentrations of chl *a* (Table 1) at the holding depth of the mussels at the UPW site were significantly higher than those at the CONTR site for both the water samples (*t*-tests: df = 14, p = 0.017; ANOVA: $F = 10.4$, p = 0.006) and for the continuous measurements (*t*-tests: df = 10373, p = 0.001; ANOVA:

$F = 9.3$, $p = 0.001$). 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 2–3 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

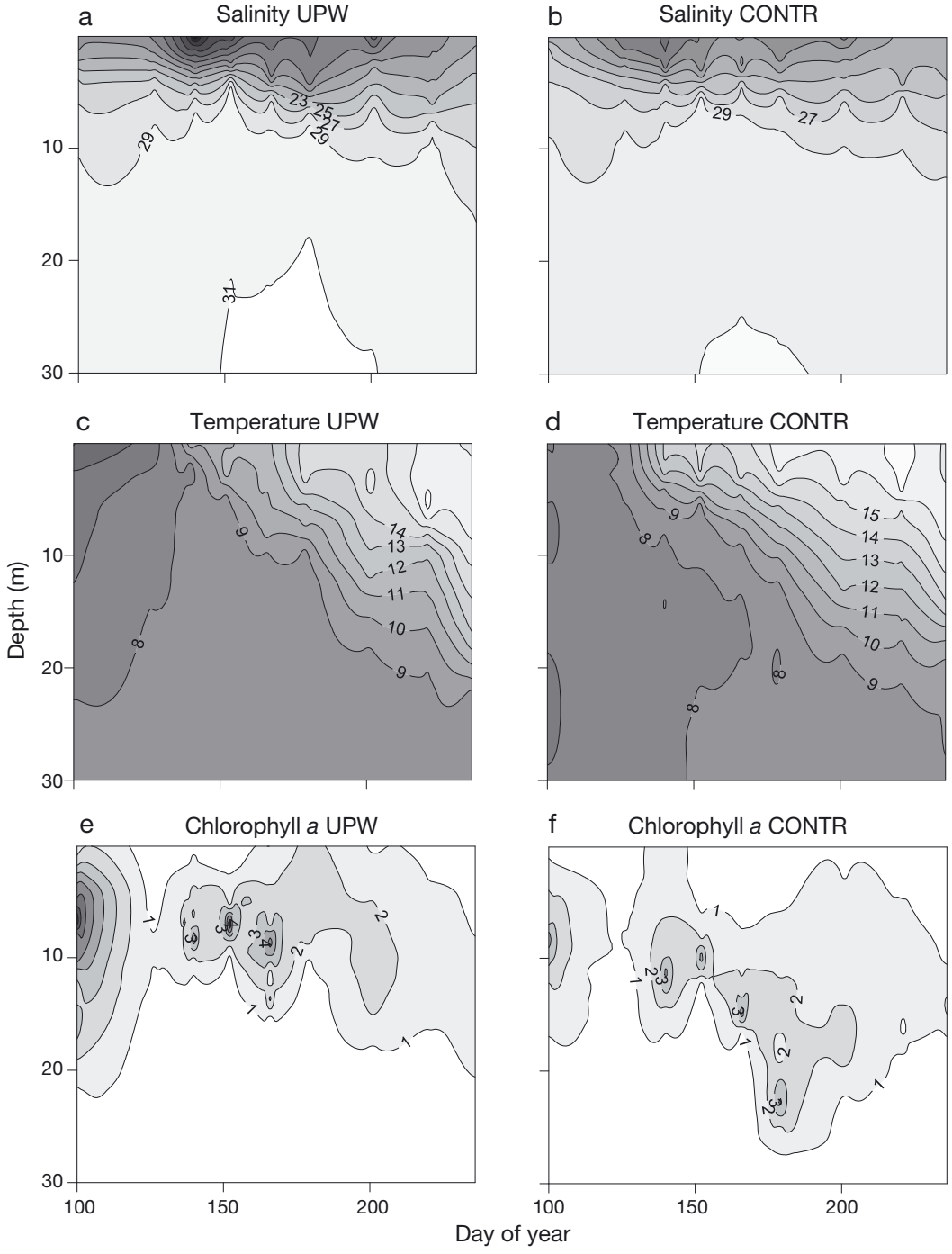

Fig. 2. Time series of (a,b) salinity (psu), (c,d) temperature (°C), and (e,f) estimated chl *a* (mg m^{-3}) at the upwelling site (UPW) and control site (CONTR) from 10 April to 24 August in the upper 30 m of the Lysefjord

Table 1. Mean values (±SD) of seston quantity and quality indicators at 7 m depth at the upwelling (UPW) and control (CONTR) sites during 6 May–11 August 2010. Mean chl *a* values are calculated from *in situ* fluorometer (fChl *a*) and discrete water sample (wChl *a*) data. PV: particle volume concentration, SPM: suspended particulate matter, POC: particulate organic carbon, POM%: organic content of SPM, C:N ratio: 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 ratio
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

between 54 and 59% (Table 1), and there was no significant difference between the 2 sites (*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 ratio (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 sites. Temporal variations in food quality indicators indicate relatively stable levels throughout much of the year.

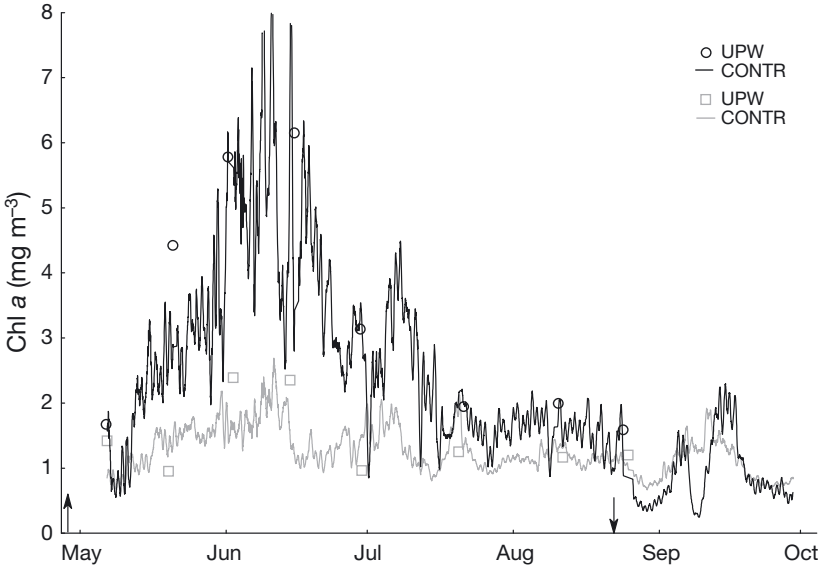

Fig. 3. Time series of estimated chl *a* from *in situ* fluorometers (black and grey lines) and from water samples (○ and □) at 7 m depth within the upwelling area (UPW) and at the control site (CONTR). *In situ* instrument measurements are presented on a daily basis (running mean of 24 hourly samples). Arrows on *x*-axis indicate when the pump was started and shut down

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 significantly higher at the UPW than at the CONTR site for the 2008 cohort, but not for the 2009 cohort (Table 2, 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 µm d^{-1}. High daily shell growth (>80 µm 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 DFW 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 & 8). The main site-specific differences in DFW occurred in the last 2 wk in June, when the mass of the 2009 cohort at the UPW site increased by almost 3 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 mg d^{-1}, CONTR: 15 mg d^{-1}) corresponded in time with the rapid DFW growth of the 2009 cohort in mid-June, and

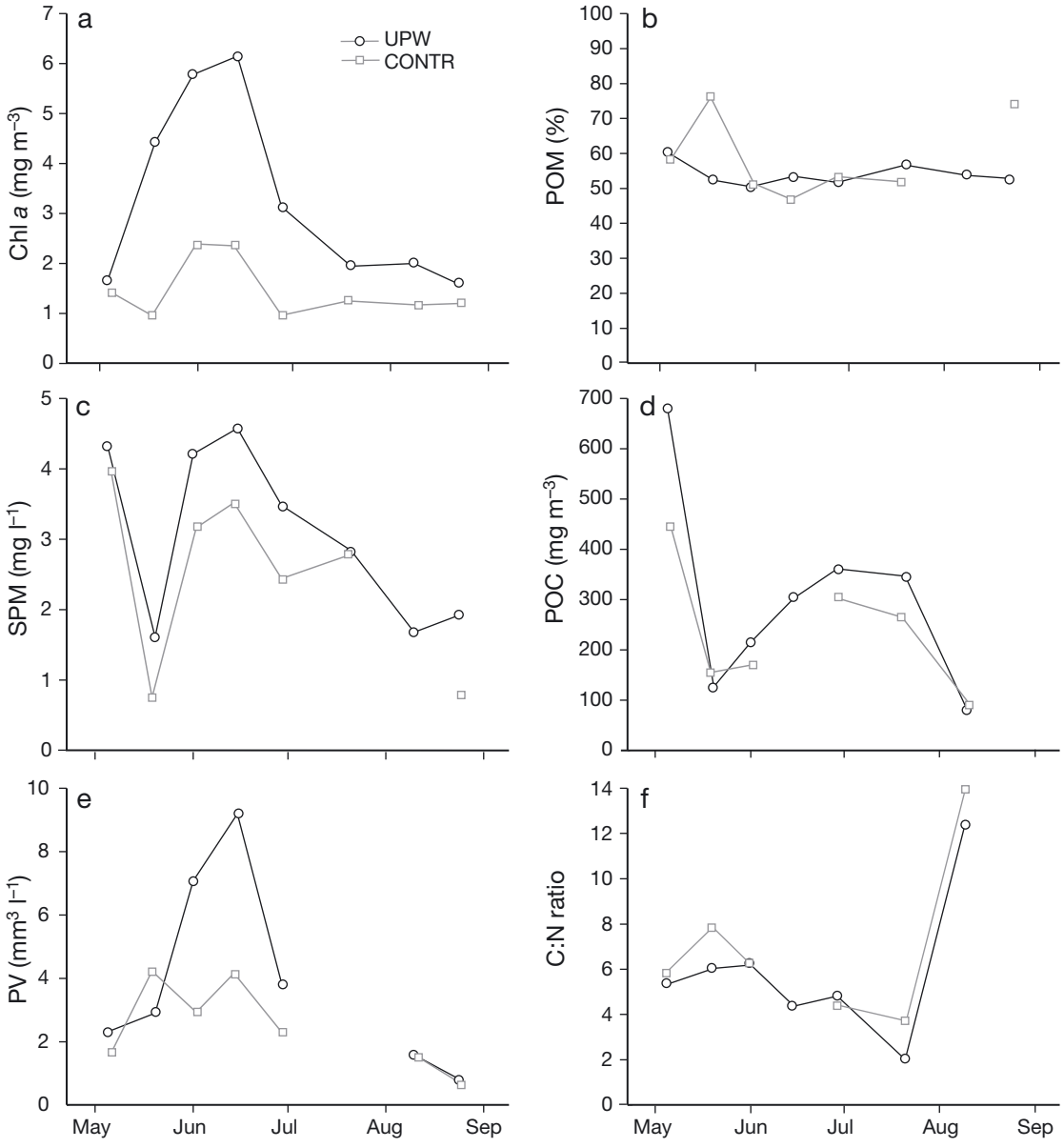

Fig. 4. Time series of (a) chl *a* from water samples, (b) organic matter fraction (POM%), (c) suspended particulate matter (SPM), (d) particulate organic carbon (POC), (e) mean particle volume concentration (PV; total for 1–60 µm particles), and (f) the ratio of carbon to nitrogen (C:N) at 7 m depth at upwelling (UPW) and control (CONTR) sites. Missing data points were due to lack of sampling (PV) and disrupted filters (SPM, POM, POC, and C:N ratio)

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 2 mo 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 2 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

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 2 mussel (*Mytilus edulis*) cohorts. Separate test results are shown for the indicated mussel cohort, and significant mean effects (*p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001) and adequate statistical power at α = 0.05 (*; (1 – β) ≥ 0.8) are indicated

Parameter (cohort)	SS	df	MS	*F*	p	1 – β
SL (2008)						
Intercept	1485174	1	1485174	419475	<0.001***	1.000*
Sampling date	1082	11	98	28	<0.001***	1.000*
SL × Site	303	1	303	104	<0.001***	1.000*
SL × Sampling date	171	11	16	5.4	<0.001***	1.000*
SL (2009)						
Intercept	485303	1	485303	33255	<0.001***	1.000*
Sampling date	14064	11	1279	88	<0.001***	1.000*
SL × Site	20	1	20	1.8	0.179	0.269*
SL × Sampling date	15	11	1.4	0.1	0.999	0.092*
***C* (2008)**						
Intercept	2727	1	2727	855	<0.001***	1.000*
Sampling date	145	6	24	8	<0.001***	0.999*
C	38	1	38	21	<0.001***	0.996*
C × Sampling date	173	6	29	21	<0.001***	1.000*
***R* (2008)**						
Intercept	124	1	124	2657	<0.001***	1.000*
Sampling date	6.2	6	1.03	22	<0.001***	1.000*
R	0.00	1	0.00	0.04	0.840	0.055
R × Sampling date	0.88	6	0.15	2.60	<0.026*	0.815*

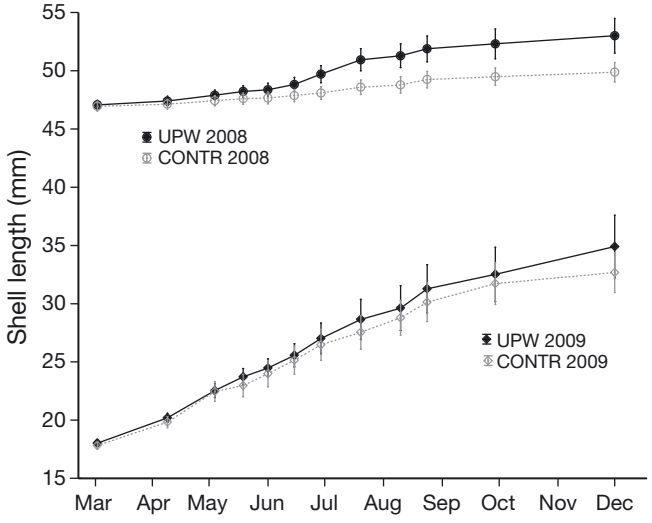

Fig. 5. Temporal changes in mean shell length (mm) for individually marked *Mytilus edulis* from 2 mussel cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) sites. Error bars indicate ±95% confidence limits

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 from 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 2 sites (Table 2, 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* × chl *a*) was 7.8 and 4.7 µg chl *a* h^{-1} at the UPW and CONTR sites, respectively. Average *C* values measured on each sampling date were not significantly 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 30–40% 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* was 0.95 and 0.96 mg O_2 h^{-1} g^{-1} at the UPW site 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 & 8) and increased *C* (Fig. 9). *R* was linearly correlated with particle volume ($r = 0.71$, $p < 0.004$), phaeopigment concentration ($r = 0.64$, $p < 0.014$), SPM concentration ($r = 0.60$, $p < 0.029$), and POM concentration ($r = 0.57$, $p < 0.047$), but not to temperature or salinity.

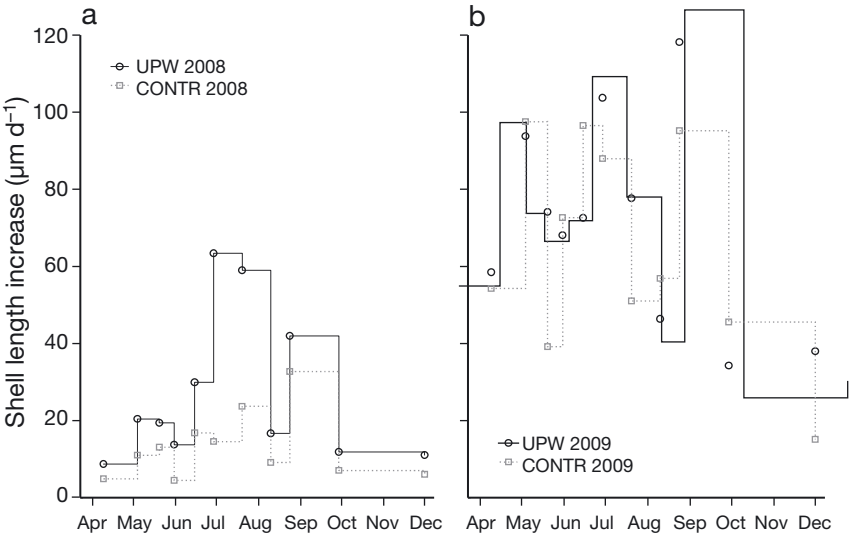

Fig. 6. Temporal changes in the mean daily growth of *Mytilus edulis* shell from 2 cohorts (a: 2008; b: 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) sites

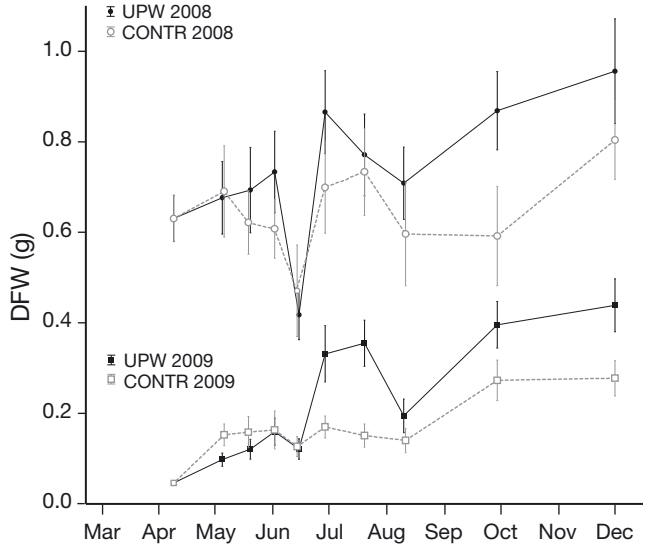

Fig. 7. Temporal changes in mean dry flesh weight (DFW) of 2 *Mytilus edulis* cohorts (2008 and 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) sites. Error bars indicate ±95% confidence limits

DISCUSSION

The results of this study show that controlled upwelling in a stratified oligotrophic environment can significantly increase phytoplankton biomass. Although upwelling was limited to a 4 mo period in the present study, it resulted in a significant enhancement of blue mussel growth performance over the mussel growth period. This demonstrates that anthropogenic enhancement of bivalve dietary conditions may facilitate cultivation of bivalves in oligotrophic environments that have previously been considered to be of limited use for human food production. Phytoplankton biomass at the upwelling site in Lysefjord approximately doubled as a result of the upwelling of nutrient-rich water. This is in accordance with previous studies in Lysefjord that showed approximately tripled phytoplankton concentration (Aure et al. 2007a). The lower response to the upwelling of nutrient-rich deep water in the present study is likely due to a lower pumping rate of brackish water to force the upwelling, estimated at 0.7–0.9 m^3 s^{-1}, compared to the 2 m^3 s^{-1} used in the study by Aure et al. (2007a). The differences in chl *a* concentration between sites disappeared as the pump was shut down in August.

The enhanced tissue growth at the upwelling site compared to the control site resulted in 24% (2008 cohort) to 95% (2009 cohort) higher tissue mass after 2 mo of upwelling. Since these values do not include weight loss through spawning and since reproductive output was greater at the upwelling site, the cumulative growth enhancement at the upwelling site was underestimated. As an example of maximal differences: harvesting 1 yr old mussels from the upwelling site in mid-July (before spawning) would result in 2.4 times more DFW compared to the control site (Fig. 7). The present study is the first to demonstrate how enhanced phytoplankton biomass, driven by controlled upwelling of nutrients at their natural concentrations and composition, can improve mussel growth performance. Enhanced phytoplankton concentrations by forced upwelling may also affect other grazers and higher trophic levels in coastal ecosystems (Yanagi & Nakajima 1991, Jeong et al. 2013).

The observed changes in tissue mass between sampling dates provides information on both somatic and reproductive tissue growth. We assume that rapid (<2 wk) and large decreases (exceeding the DFW loss during winter starvation, >1–4 mg d^{-1}; Strohmeier 2009) in mean DFW represents spawning. Temporal variations in tissue growth were typically positive through most of the year, except during spawning periods. Tissue growth rate was highest in the pre-spawning period for the 2009 cohort at the

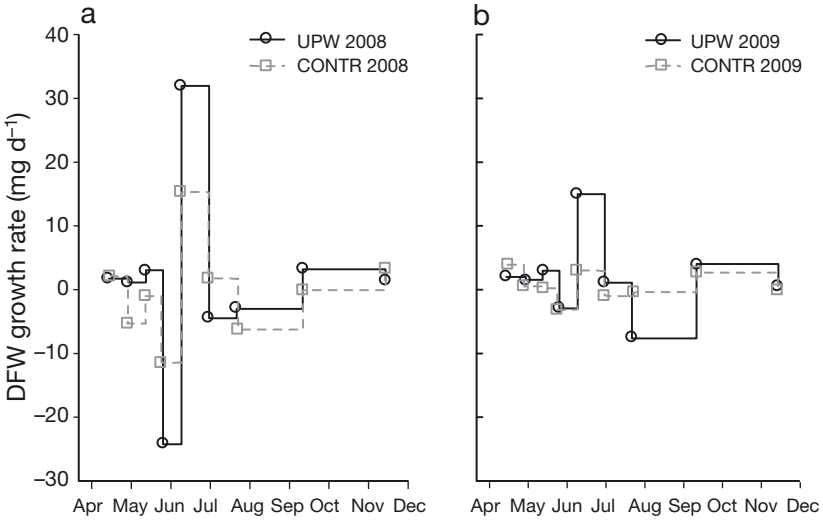

Fig. 8. Temporal changes in estimated mean daily dry flesh weight (DFW) growth rate of 2 *Mytilus edulis* cohorts (a: 2008; b: 2009) held at 7 m depth at the upwelling (UPW) and control (CONTR) sites

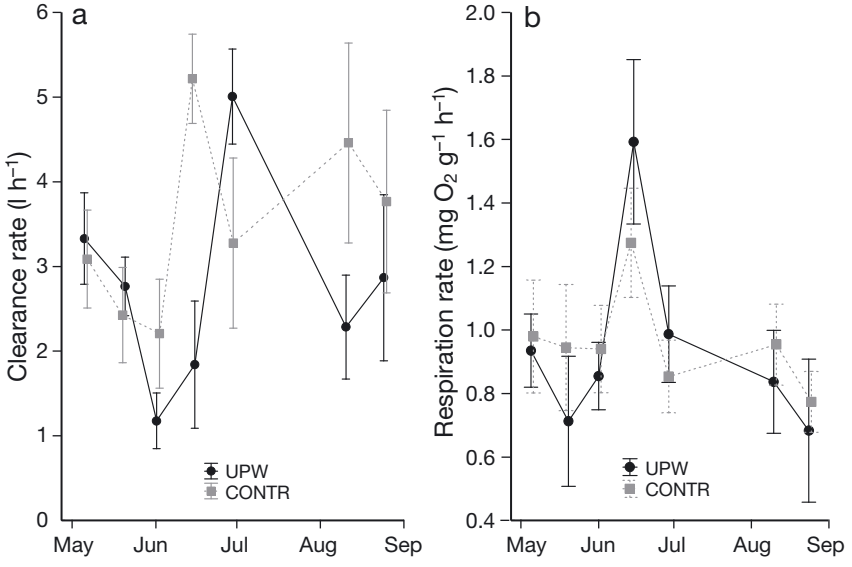

Fig. 9. Temporal changes in mean (a) clearance rate standardized to a 50 mm shell length individual and (b) dry flesh weight standardized respiration rate for the 2008 *Mytilus edulis* cohorts held at the upwelling (UPW) and control (CONTR) sites. Error bars indicate ±95% confidence limits

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 1 yr 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 of enhanced tissue growth, reproductive output, and meat yield in the 2 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 & 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 indicates 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 the possibility for the structural weight to be more closely 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 2 yr 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 *Mytilus 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).

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

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