

Primary production enhancement by artificial upwelling in a western Norwegian fjord

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ABSTRACT: To enhance primary production rate for shellfish cultivation in fjords, a large-scale artificial upwelling experiment was carried out in a western Norwegian fjord during the summers of 2004 and 2005. Pumping $2 \text{ m}^3 \text{ s}^{-1}$ brackish surface water to a depth of 30 m created an artificial upwelling of nutrient-rich deeper water. The entrainment of deeper water into the buoyant brackish plume resulted in a transport of about 450 kg d^{-1} nitrate, 760 kg d^{-1} silicate and 75 kg d^{-1} phosphate to an intrusion depth of 8 to 10 m. The artificial upwelling approximately tripled mean chlorophyll *a* (chl *a*) concentration and related primary production rate during the summer within an influence area of 10 km^2 near the head of the fjord. The size of the area of influence and the relative increase of the algae biomass within it depend on both the water exchange and the photosynthetic effectiveness. The relatively high silicate content of the deeper water stimulated diatom growth inside the area influenced by the artificial upwelling. A higher stable level of phytoplankton biomass, dominated by nontoxic species, would probably increase the carrying capacity of seston-feeding shellfish and could form the basis of more predictable mussel cultivation in fjords.

KEY WORDS: Artificial upwelling · Phytoplankton biomass · Primary production rate · Fjord · Mussel culture

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INTRODUCTION

Physical processes regulating the vertical structure of the ocean determine marine productivity, as exemplified by the importance of coastal upwelling systems in global fisheries (Ryther 1969). In many coastal waters primary production rates benefit from upwelling of deep water. In this process surface waters are displaced offshore by a one-sided horizontal divergence caused by surface Ekman transport and are replaced by nutrient-rich deep water (Smith et al. 1983). The upwelling circulation operates on a wide range of time scales, which include short (hours), intermediate (days) and long (seasonal and inter-annual) scales. The large-scale coastal upwelling regions are among the most productive in the world, with annual primary production rates of more than $700 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Mann & Lazier 1996). These systems favour growth of diatoms. Coastal upwelling also supports some of the most productive and successful mussel farming areas

(Pitcher & Calder 1998, Figueiras et al. 2000). Typical annual primary production rates in Norwegian fjords and coastal waters are 110 to $140 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Eilertsen & Taasen 1984, Erga & Heimdal 1984, Erga 1989b, Erga et al. 2005), where about 60% takes place after the spring bloom during March and April.

In summer fjords are stratified primarily as a result of freshwater runoff and calm wind conditions that restrict vertical mixing of nutrients into the euphotic layer (Aure et al. 1996, Asplin et al. 1999). Nutrients derived from freshwater runoff, or intermediate water inflow from the outer fjord or coastal waters, are generally less important than the vertical nutrient flux (Aksnes et al. 1989). Consequently, the euphotic zone is nutrient-depleted during summer and the primary production rates, which are mainly based on nutrients regenerated in the water column (Skjoldal et al. 2004), are typically reduced to one-third of spring bloom levels (Erga et al. 2005). Primary production rate based upon new nutrients (e.g. an upward nutrient flux from

deeper waters or supported by drainage from the land) is called 'new production' and primary production rate based upon regenerated nutrients in the upper mixed layer is called 'regenerated production' (Dugdale & Goering 1967, Paasche 1988). Total production is the sum of new production and regenerated production. Wassmann (1990) found that total production was about 2.5 times as high as new production in south Norwegian coastal and fjord waters. For the summer upwelling events on the Iberian shelf, northwest Spain, a mean R-value of 2.8 was found (Joint et al. 2002).

The Norwegian research programme MARICULT (1996 to 2000) aimed to provide a basis for the evaluation of environmental constraints and the potential for greater supplies of food, raw materials and energy from the ocean (Olsen 2002). One of the research topics in this programme was enhancement of the production potential in fjords by the creation of artificial upwelling systems. There are a number of simulated or small-scale enrichment experiments using deep water, and it has been proposed to use artificial upwelling in enclosed fjord areas to develop safe production of toxin-free, high-quality shellfish (Aksnes et al. 1985, Berntsen et al. 2002, Olsen 2002). The possibility of moving shellfish into such areas for quality enhancement (increased meat content) and toxicity treatment has also been considered. To the best of our knowledge, the first full-scale experiment on artificial upwelling in coastal waters was carried out in Japan, where concrete panels were installed on the sea bottom to divert deep water (40 to 50 m) into the euphotic zone of the water column (Morikawa 2001). A significant enhancement of phytoplankton and zooplankton production was obtained.

On the basis of the results from observations and models simulating upwelling scenarios (Aure et al. 2000, Berntsen et al. 2002, McClimans et al. 2002), the MARICULT programme recommended further work to validate these results at a fjord-scale testing site to determine the potential of artificial upwelling of deeper nutrient-rich seawater in mariculture applications. Using a numerical buoyant flume model and laboratory simulations, McClimans et al. (2002) demonstrated the effectiveness of a submerged discharge of freshwater to force vertical transport of nutrient-rich deep water to the euphotic zone in fjords. Berntsen et al. (2002) employed a coupled physical–chemical–biological model to study primary production rate in an idealized 60 km long, 4 km wide fjord subjected to various submerged freshwater discharge scenarios. They concluded that primary production rate could be enhanced by a factor of 3. Due to the higher silicate content of the deeper water, the artificial upwelling tends to stimulate diatom more than flagellate growth

(Egge & Aksnes 1992), thereby reducing the problem in fjords of diarrhetic shellfish toxin (DST) caused by *Dinophysis* spp. (Aune et al. 1996). In view of these results the inner part of Lysefjord in western Norway was selected to be suitable for a large scale experiment, since stratification persists throughout the summer and early autumn months. Conditions there provide sufficient quantities of brackish surface water, easily accessible nutrient-rich deeper water and limited water exchange with the open fjord system. We present the results of our first attempt to perform a large-scale experiment aimed to determine the potential impacts of artificial upwelling on phytoplankton biomass, production and composition.

MATERIALS AND METHODS

Study site. The Lysefjord is located on the southwest coast of Norway (59° 0' N, 6° 16' E) (Fig. 1). The fjord is approximately 40 km long and 0.5 to 2 km wide. The sill depth is 14 m, maximum depth is 460 m and the surface area is 44 km². The mean tidal range is 0.4 m and the freshwater supply to the Lysefjord varies between 40 and 90 m³ s⁻¹, with the highest discharges occurring in May. Since hydropower plants became operational in 1935 and 1952, the mean freshwater input to the fjord during April through September has decreased by 30 to 40 %.

Forced upwelling. The artificial upwelling system is mounted on a moored platform located outside the freshwater discharge of a hydropower plant near the head of the Lysefjord (Fig. 1). Brackish water, taken from depths of between 0 and 3 m, is forced down through a vertically mounted pipe by an electrical pump (ITT Flygt pump) (Fig. 2). The diameter of the pipe is 1.25 m and the pump power output of 60 kW produces a flow of about 2 m³ s⁻¹ from the outlet at 30 m depth. Due to the buoyancy of the submerged brackish water it rises to the surface and mixes with the more saline and nutrient rich deeper water. The equilibrium depth (Z_0) is defined as the depth at which the density of the rising plume is equal to the density of the ambient water, and the intrusion depth (Z_i) is expected to be a few metres above Z_0 (McClimans et al. 2002). The mean mixing rate of the brackish water and seawater and related intrusion level was estimated by adding fluorescein dye to the submerged brackish water.

Observations. Four sampling stations were set up within the main observation area A_0 (Stns 11, 16, 17 and 01) (Fig. 1). The surface area and average width of the fjord inside A_0 are 10 km² and 1 km, respectively. Outside this area we set up Stns 18, 02, 14 in the central and outer part of the fjord and Stn 03 in the Høgs-

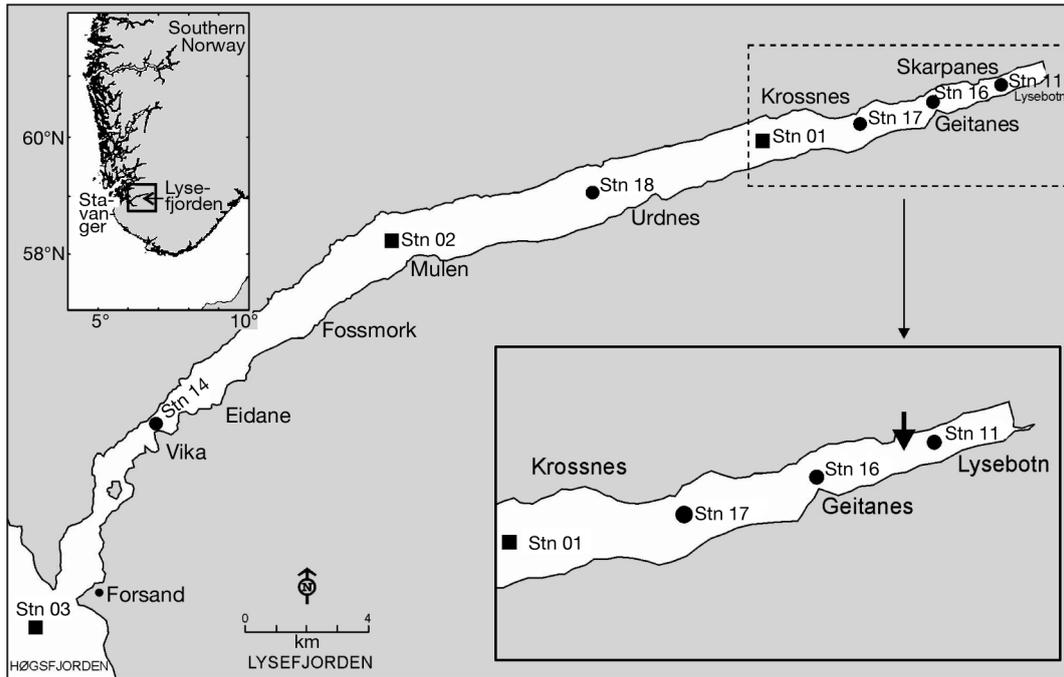


Fig. 1. The Lysefjord, located on the southwest coast of Norway, showing the positions of sampling stations. The enlarged map shows the main observation area A_0 (10 km²). The arrow between Stns 11 and 16 indicates the location of the anchored artificial upwelling platform

fjord outside the Lysefjord. The artificial upwelling experiments were executed during the periods 19 May to 24 August 2004 and 18 June to 27 August 2005.

Measurements of temperature, salinity, *in situ* fluorescence and turbidity were made and samples of phytoplankton were gathered weekly from May to June and from late July to September in 2004, and from June to September in 2005. On three 5-d cruises (May/June, August and September) in 2004 and 2005, additional samples were taken for analyses of inorganic nutrients (nitrate, nitrite, phosphate and silicate), particulate organic carbon (POC) and chlorophyll *a* (chl *a*). To examine the time-scale of the phytoplankton response to the increased supply of nutrients to the euphotic layer, daily observations were carried out

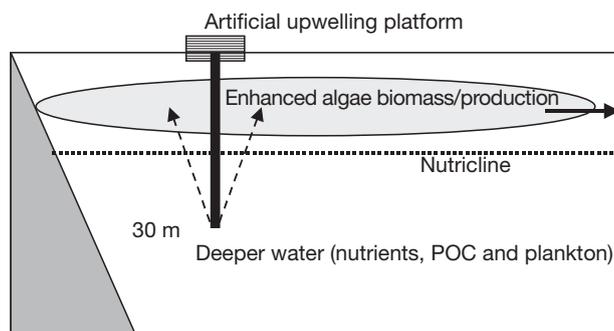


Fig. 2. Relative position of the anchored artificial upwelling system in the water column in the Lysefjord

between 18 and 27 June 2005. Measurements of temperature, salinity, *in situ* fluorescence, turbidity and nutrients on selected stations were also conducted in the Lysefjord in August 2002, and in the period June to September 2003 (7 dates) and 2006 (10 dates). Samples for chl *a* analysis were filtered onto GF/F filters and stored at -20°C . The samples were analysed fluorometrically (Turner Designs-10) according to Parsons et al. (1992) using 90% acetone as solvent and acid corrections for phaeopigments. The fluorometer was calibrated with known concentrations of Sigma chl *a* (Sigma Chemicals) measured spectrophotometrically. Fluorescence-chl *a* (FC), turbidity (Seapoint type), salinity and temperature were measured by a CTD (SD 200 W, SAIV A/S). Measurements were recorded every second while the CTD was lowered at a rate of $<0.5 \text{ m s}^{-1}$ from the surface to 30–50 m. The FC data were calibrated against chl *a* concentrations, and FC values were converted to chl *a* using the equation $y = 0.9x + 0.25$ ($r^2 = 0.75$), where y is chl *a* and x is measured FC. Particulate organic carbon was analysed in a Carlo-Erba analyser. Dissolved inorganic nutrients were analysed according to standard methods (Parsons et al. 1992) adapted for an auto-analyser. Primary production rate, measured as carbon assimilation rates, was obtained from 24 h *in situ* incubations at Stns 17 and 03, starting in the afternoon on 22 June and 24 June 2005, respectively. They were conducted in accordance with the ^{14}C -method (Steemann Nielsen

1952). Phytoplankton abundance was determined according to Utermöhl (1931) using neutralized formalin and Lugol as preservative. Phytoplankton is expressed as biovolume (or plasma volume), i.e. cell volume minus vacuole volume.

Water currents were measured at depths of 5, 8, 10 and 15 m by current meters (SD6000, Sensor Data AS). Current direction and speed were recorded every 10 min at Stn 16 from 1 to 20 May and late July to September in 2004, and from June to September in 2005. Wind direction and speed were measured at the upwelling platform 5 m above sea level from 21 June to 18 August 2005. Subsurface irradiance in the visible part of the spectrum (PAR) was obtained with a PUV 500 from Biospherical Instruments at vertical profiles down to depths of 25 to 30 m. Measurements were made at around local noon at Stns 02 and 03 between 22 and 24 June 2005.

RESULTS

Physical conditions

A typical vertical and horizontal salinity distribution of the upper 25 m of the inner part of the Lysefjord is represented by the measurements made on 22 July 2005 (Fig. 3). From May to September in 2004 and 2005, the mean depth of the brackish layer (salinity < 25.0 psu) at Stn 11 was 5.0 m (SD = 1.3, n = 18). Within the depth interval of 0 to 3 m, where the pump takes its water, the mean salinity was 14.0 psu (SD = 4.6, n = 18). Below the brackish layer salinity gradually increased to about 33.0 psu at 30 m depth. From May to September temperatures gradually increased from 8.5 to 18.0°C in the brackish layer (0 to 5 m), from 7.5 to 10.5°C at 10 m and from 7.0 to 8.5°C at 15 m depth.

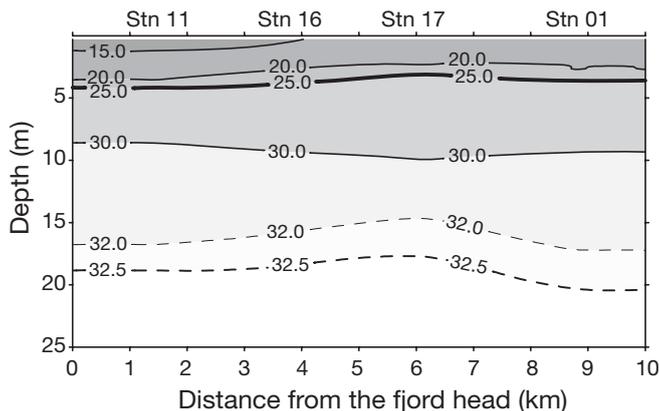


Fig. 3. Typical vertical distribution of salinity (psu) between 0 and 25 m depths in the inner 10 km of the Lysefjord in summer (22 July 2005)

In 2004 the residual currents (24 h running mean) at depths between 5 and 15 m at Geitaneset (Stn 16) were heading out of the fjord, except at the 8 m depth during late August when residual currents were heading inwards. In 2005 outward currents dominated at depths of 5, 10 and 15 m, and inwards at 8 m. The 5-d mean current speed between 5 and 15 m depths, before May to September 2004 observation dates, varied between 2.5 and 6.2 cm s⁻¹, and from June to September 2005 between 2.2 and 7.0 cm s⁻¹.

Wind observations at the anchored upwelling platform (Fig. 1) in June to August 2005 showed that an inwards wind direction from the west was dominant and the wind speed (24 h running means) varied between 0 and 5 m s⁻¹. The exception was a period from 1 to 6 July when the dominant wind direction was outwards from the east, with maximum wind speeds (24 h running means) of about 10 m s⁻¹. The strongest currents observed during the artificial upwelling period in 2005 occurred during this windy period. In 2004 there were no current observations at Geitaneset (Stn 16) before 29 May, 6 June and 13 June. Wind observations at a meteorological station just north of the Lysefjord showed strong northwesterly winds (10 to 15 m s⁻¹) before 29 May and calm weather (<2 m s⁻¹) between 1 and 13 June. On the basis of mean current observations together with accompanying wind conditions at this station, we estimated that the 5-d average current speed in the 5 to 15 m layer was about 6 cm s⁻¹ on 29 May and 3 cm s⁻¹ on 6 and 13 June. The 5-d mean of water transport between 5 and 15 m depth previous to observation dates in 2004 and 2005 (Q_v) varied between 160 and 460 m³ s⁻¹, giving a mean transport of 260 m³ s⁻¹.

In June 2005 the irradiances (PAR) at 0.5 m depth at Stn 02 and outside Lysefjord at Stn 03 were 1950 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (clear weather) and 707 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (cloudy). The 1% light depths, at which PAR irradiances are reduced to 1% of the surface values, were about 15 and 24 m, respectively.

Nutrients and particulate organic carbon

In the upper 50 m of the water column in the inner part of the Lysefjord, concentrations of nitrate (N) ranged from 0 to 17 mmol m⁻³, silicate (Si) from 0.3 to 23 mmol m⁻³ and orthophosphate (P_i) from 0 to 1.5 mmol m⁻³ from May to September in 2004 and 2005. Typical of this period were low nutrient concentrations in the upper 10 m of the water column and increasing concentrations below 10 m depth, exemplified by the profile at Stn 17 on 21 June 2005 (Fig. 4). The relatively stable vertical distribution of nutrients below 10 m depth is an effect of the shallow sill depth

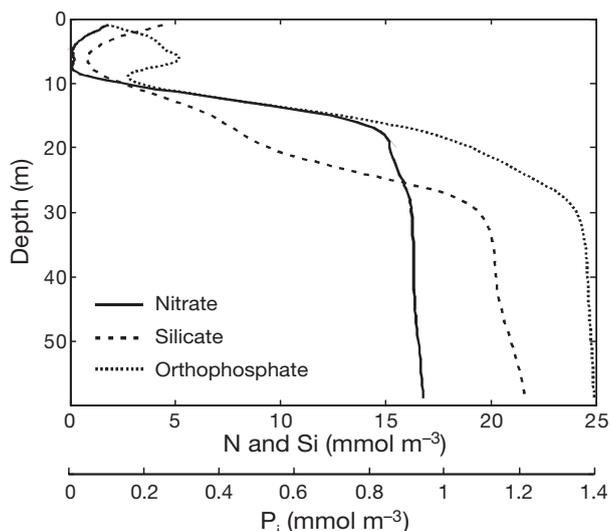


Fig. 4. Typical vertical profiles of nitrate (N), silicate (Si) and orthophosphate (P_i) in the inner part of the Lysefjord during the artificial upwelling experiments (Stn 17 on 21 June 2005)

of 14 m at the inlet of the Lysefjord. In the mixing layer of the artificial upwelling between 10 and 30 m, where the submerged brackish water rises upwards, the mean nutrient values were considerably higher than in the upper 10 m layer (Table 1). In the 10 to 30 m layer the elemental ratios ($N:Si:P_i = 13:11:1$) were quite close to ratios observed in deep waters in other Norwegian fjords ($N:Si:P_i = 11:14:1$) (Stigebrandt & Aure 1988).

At Stns 02, 01, 17, 16 and 11, the POC values varied between 38 and 517 $mg\ m^{-3}$. Maximum values of POC in the water column were found between 3 and 7 m, but the maxima were most frequent at about 7 m. The highest POC value of 517 $mg\ m^{-3}$ during the upwelling period in 2005 was at 7 m at Stn 11 on 17 August. The high correlation between POC and *in situ* turbidity in 2005 ($R^2 = 0.8$, $n = 43$) shows that the upper 20 m of the Lysefjord was dominated by organic particles such as phytoplankton and detritus. In the main artificial upwelling influence layer between 5 and 15 m depth, the R^2 between POC and *in situ* chl *a* was 0.8, and the mean POC:chl *a* ratio was 80:1 ($n = 43$).

Intrusion depth and supply of deep water

The average mixing rate, $M^* = (Q_s/Q_b)/(Z_{30} - Z_i)$, between brackish (Q_b , $m^3\ s^{-1}$) and seawater (Q_s , $m^3\ s^{-1}$) from the outlet depth (Z_{30}) to the intrusion depth (Z_i) was estimated as $0.8\ m^{-1}$. On the basis of vertical density profiles in 2004 and 2005, the density of the submerged brackish

water and M^* , the intrusion depths (Z_i) were estimated to vary between 7 and 11 m in 2004 and 2005, with an average of 8 to 9 m. This fits well with the observed mean chl *a* maximum depth of 7.0 m at Stn 11 during the upwelling period from June to September 2005. The total mixing (Q_s/Q_b) between 30 and 10 m depth at the platform location was about 14.0. With $Q_b = 2\ m^3\ s^{-1}$ the supply of deeper seawater (Q_s) to 10 m depth was then $28\ m^3\ s^{-1}$. This is about 12% of the total observed mean water exchange between 5 and 15 m depths in the inner part of the fjord. Based on both the mean concentrations of nutrients in 2004 and 2005 (Table 1) and the estimated transport of water between 30 to 10 m depths, the artificial upwelling supply of nutrients was estimated to $450\ kg\ d^{-1}\ N$, $750\ kg\ d^{-1}\ Si$ and $70\ kg\ d^{-1}\ P_i$.

Primary production rates June 2005

The daily integrated primary production rate between surface and 20 m depths in the Lysefjord at Stn 17 on 22 June and at Stn 03 (Fig. 1) on 24 June were approximately $350\ mg\ C\ m^{-2}\ d^{-1}$. Carbon assimilation rates at fixed depths varied between 0 and $2.8\ mg\ C\ m^{-3}\ h^{-1}$ at Stn 17 and between 0 and $2.3\ mg\ C\ m^{-3}\ h^{-1}$ at Stn 03, with the highest values occurring within the upper 0 to 3 m layer. From this we conclude that the difference in primary production rate between the Lysefjord and Høgsfjord was insignificant before the onset of the artificial upwelling in late June 2005 (see Fig. 7a).

Estimated artificial upwelling primary production rate

The primary production rate (P_{upw}) measured as $kg\ C\ d^{-1}$ due to the artificial upwelling is estimated by:

$$P_{upw} = PHOS_{upw} \cdot (POC/POP) \cdot R \quad (1)$$

where $PHOS_{upw}$ ($70\ kg\ d^{-1}$) is the mean supply of phosphate to the photic layer due to artificial upwelling,

Table 1. Mean concentrations of nitrate (N), phosphate (P_i) and silicate (Si) ($mmol\ m^{-3}$) and N/P_i , Si/P_i at depths of 0 to 10 m and 10 to 30 m at Stn 11, from May to September in the Lysefjord in 2004 and 2005

Year	Depth (m)	N ($mmol\ m^{-3}$)	Si ($mmol\ m^{-3}$)	P_i ($mmol\ m^{-3}$)	N/P_i	Si/P_i
2004	0–10	0.9	2.1	0.1	6.9	16
2005	0–10	1.8	4.4	0.3	5.4	13.3
2004	10–30	10.3	8.1	0.8	13.2	10.4
2005	10–30	12.7	11.3	0.9	13.9	12.4

POC/POP = 41 according to the Redfield ratio and R is the ratio between total and new production; $R = 2.3$ is a typical value for southern Norwegian marine waters (Wassmann 1990, Skjoldal & Wassmann 1986). Using Eq. (1) P_{upw} is estimated to be 6600 kg C d^{-1} .

The natural production rate (P_n) measured as kg C d^{-1} inside a given area (A , km^2) is:

$$P_n = p_n \cdot A \quad (2)$$

where p_n is the average primary production rate per m^2 below the upper brackish layer. The total primary production rate (PT) is then the sum of P_{upw} and P_n , since the water and related natural phytoplankton exchange with the external fjord system is not significantly influenced by the artificial upwelling (see previous explanation). Typical mean daily integrals of carbon assimilation in the euphotic zone in fjords for the period from April to September are 500 to $600 \text{ mg C m}^{-2} \text{ d}^{-1}$, with about one-half occurring below the upper brackish layer ($p_n = 300 \text{ mg C m}^{-2} \text{ d}^{-1}$) (Erga 1989b, Erga et al. 2005).

The area of influence (A_{infl}) is defined as the area where the phytoplankton biomass and the primary production rate are significantly stimulated by the artificial upwelling. Investigation of the longitudinal distribution of chl a in the Lysefjord during artificial upwelling in 2004 and 2005 (Fig. 5a) showed that in all cases, except on 29 May 2004 and 6 June 2005, the area of influence was 10 km^2 or less, e.g. inside Stn 01 (Fig. 1). On 29 May and 6 June 2005 currents and water exchange were considerably increased and a greater proportion of chl a existed outside the area of 10 km^2 . On basis of these observations our main fixed observation area (A_o) is selected to be the inner 10 km^2 of the Lysefjord (Fig. 1). Using $A = A_o$ in Eq. (2), the natural production (P_n) is estimated to be 3000 kg C . The total primary production rate $PT = P_{\text{upw}} + P_n$ caused by the increased supply of nutrients to the euphotic layer is then calculated to be 9600 kg C d^{-1} , i.e. an increase of the primary production rate (PT/P_n) by a factor of about 3.

In a steady-state situation the total upwelling primary production rate (PT) measured as kg C d^{-1} inside A_o is balanced with the transport of carbon ($Q_v \cdot Cm_{\text{upw}}$) leaving A_o , where Q_v is the water transport in the layer influenced of the artificial upwelling and Cm_{upw} is the mean carbon concentration inside A_o , i.e.

$$PT = Q_v \cdot Cm_{\text{upw}} \quad (3)$$

With $Cm_{\text{upw}} = CT_{\text{upw}} / (A_o \cdot H_a)$ we get:

$$PT = \text{ChlT}_{\text{upw}} / (A_o \cdot H_a) \cdot Q_v \cdot (\text{POC}/\text{chl } a) \quad (4)$$

where CT_{upw} and ChlT_{upw} are the total carbon and chl a inside A_o , H_a is the mean thickness of the plankton layer influenced by the artificial upwelling and

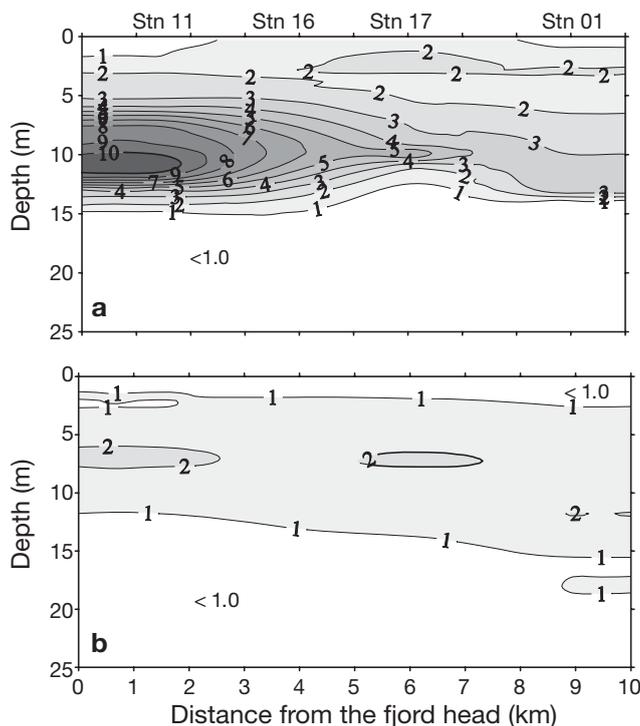


Fig. 5. Typical vertical distribution of chl a (mg m^{-3}) between 0 and 25 m depths in the inner 10 km of the Lysefjord (a) with artificial upwelling (22 July 2005) and (b) during natural conditions (30 August 2005)

POC/chl a is the ratio between particulate organic carbon and chl a . The total chl a inside A_o (ChlT_{upw} , measured as $\text{kg chl } a$) is then:

$$\text{ChlT}_{\text{upw}} = PT \cdot (A_o \cdot H_a) / (\text{POC}/\text{chl } a) / Q_v \quad (5)$$

This relation shows that ChlT_{upw} inside A_o is also expected to increase by a factor of 3 during the artificial upwelling experiment.

Observed effects of artificial upwelling

Mean chl a values in the 4 to 15 m layer at Stn 11 in the inner part and at Stn 2 in the middle of the Lysefjord (Fig. 1) were, respectively, 1.7 mg m^{-3} ($\text{SD} = 0.7$, $n = 335$) and 1.6 mg m^{-3} ($\text{SD} = 0.6$, $n = 335$) during the May to September periods from 2002 to 2006, excluding the artificial upwelling periods in 2004 and 2005. Chl a values in the range 1 to 2 mg m^{-3} are typical for the upper 10 m of the water column in fjords during summer when nutrients are scarce (Aure et al. 2000). This confirms that the horizontal differences of chl a between the inner and middle fjord are insignificant during natural conditions. To examine the effects of the artificial upwelling experiment, observed chl a was integrated in the 4 to 15 m layer within A_o , both in

situations with (ChIT_{upw}) and without (ChIT_n) artificial upwelling. Examples of typical vertical distributions of chl *a* inside A_o , both with artificial upwelling and during natural conditions are shown in Fig. 5.

In 2004 the artificial upwelling was started on 19 May. After a period with strong northerly winds and currents in late May, weather conditions became calmer, and ChIT_{upw} values increased from 167 kg on 29 May to 400 to 500 kg in June (Fig. 6a). On 27 July and 3 August ChIT_{upw} was still at the same level as in June. On 17 August ChIT was reduced to about 130 kg even though the current and wind conditions were still moderate. This anomalously low value was related to a collapse in the diatom stock inside A_o (discussed later). The artificial upwelling system stopped on 24 August. After this date the integrated chl *a* inside A_o decreased to about 100 kg. In the artificial upwelling period from 6 June to 3 August 2004 the mean ChIT_{upw} was about 480 kg (48 mg m^{-2}), excluding 29 May 2004 when A_{infl} was much greater than A_o , and the diatom collapse on 17 August 2004. The mean chl *a* concentration (chl_{upw}) inside A_o was 4.8 mg m^{-3} . Outside the

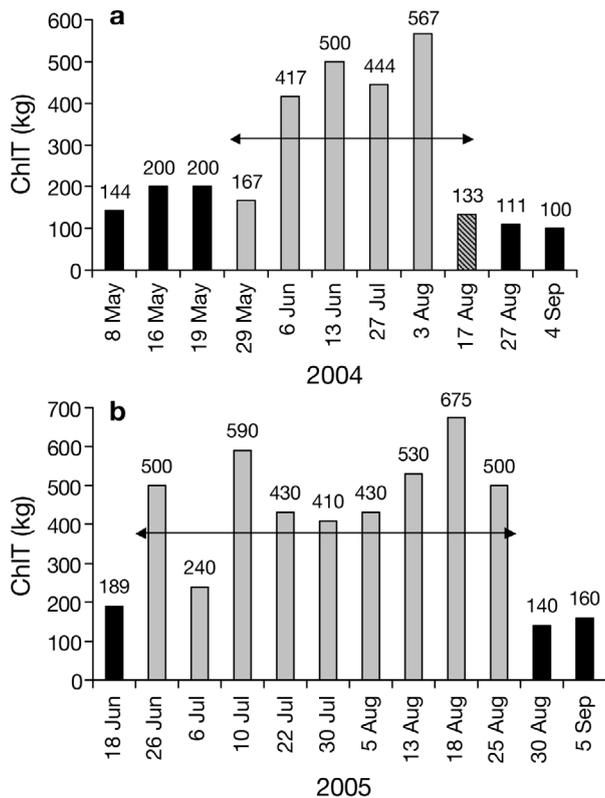


Fig. 6. Integrated chl *a* (ChIT , kg) from below the surface layer to 15–20 m depth inside A_o ($= 10 \text{ km}^2$) in the inner part of the Lysefjord. (a) 8 May to 4 September 2004 and (b) 18 June to 5 September 2005 (grey columns and horizontal arrow = artificial upwelling response periods, black columns = natural conditions, hatched column = phytoplankton [diatom] collapse on 17 August 2004)

upwelling period in May and late August to September 2004 the mean ChIT_n was 155 kg (15.5 mg m^{-2}) and the mean chl *a* concentration (chl_{n}) was 1.9 mg m^{-3} inside A_o . ChIT_{upw} then increased by a factor of about 3.0 and chl_{upw} increased by a factor of about 2.5 in the artificial upwelling period from June to the first part of August 2004.

In 2005 the artificial upwelling was started on 18 June and was closed down on 27 August. The daily observations during the first week of upwelling (Fig. 7a) showed that chl *a* integrated between the surface layer and 15 m depth (ChII , mg m^{-2}) at Stn 11 inside A_o increased from 20 mg m^{-2} on 18 June to a maximum of 60 to 70 mg m^{-2} on 25–26 June. The time needed to establish a fully developed artificial upwelling, thus, appears to be about 1 wk. During this period ChII at Stn 11 increased by a factor of about 3 relative to Stn 02 outside A_o , and the mean daily increase of ChII after 21 June was about 23%.

During the period from 26 June to 25 August 2005, while the artificial upwelling was in progress, ChII (mg m^{-2}) values were significantly higher at Stn 11 than at the reference station, Stn 02 (Fig. 7b). At Stn 11, ChII varied between 53 and 73 mg m^{-2} , with the exception

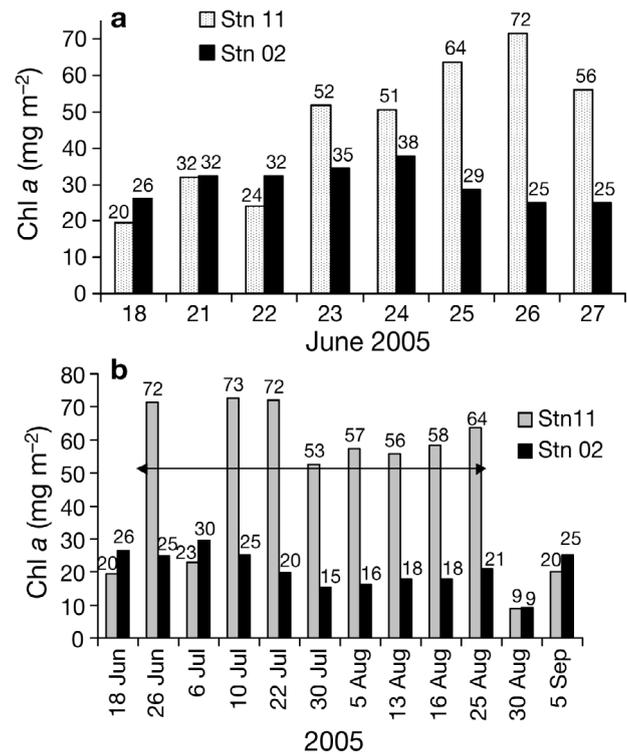


Fig. 7. (a) Vertical integrated chl *a* (mg m^{-2}) at Stns 11 and 02 during the period 18 to 27 June 2005 (artificial upwelling commenced on 18 June). (b) Vertically integrated chl *a* (mg m^{-2}) at Stns 11 and 02 from 18 June to 5 September 2005 (horizontal arrow = artificial response upwelling period)

of 6 July when ChlI was reduced to 23 kg due to a considerable increase in out-fjord wind speed and consequently higher water exchange ($A_{\text{infi}} \gg A_o$). At the reference station (Stn 02) ChlI varied between 15 and 30 mg m^{-2} in the same period. Mean ChlI values at Stn 11 (excluding 6 July when $A_{\text{infi}} \gg A_o$) and Stn 02 during the artificial upwelling period were about 60 and 20 mg m^{-2} , respectively. The mean chl *a* concentration (chl_m) showed a similar pattern as ChlI, and at Stn 11 it varied between 5.3 and 10.5 mg m^{-3} , with the exception of 6 July where chl_m was 3.3 mg m^{-3} . At Stn 02 chl_m varied between 1.7 and 3.3 mg m^{-3} . The average chl_m was 6.5 mg m^{-3} at Stn 11 and 2.2 mg m^{-3} at Stn 02. Both mean ChlI and chl_m inside A_o were then about 3 times as high at Stn 11 as at the reference station, Stn 02. In the artificial upwelling period the typical thickness of the phytoplankton layer (H_a) and the mean chl *a* maximum depth at both Stn 11 and 02 were 9 to 10 m and 7 m, respectively.

In the upwelling period from 26 June to 25 August 2005 the integrated chl *a* inside A_o (ChlT_{upw}) varied between 410 and 675 kg, except on 6 July when A_{infi} was much greater than A_o (Fig. 6b). The mean ChlT_{upw} , excluding 6 July ($A_{\text{infi}} \gg A_o$), was 510 kg (51 mg m^{-2}) and the mean chl *a* concentration ($\text{chl}_{\text{m,upw}}$) was 5.3 mg m^{-3} . During natural conditions, the integrated chl *a* inside A_o (ChlT_n) was 163 kg (16 mg m^{-2}) and the mean natural chl *a* concentration ($\text{chl}_{\text{m,n}}$) was 1.7 mg m^{-3} . Both ChlT_{upw} and $\text{chl}_{\text{m,upw}}$ inside A_o increased, therefore, by a factor of about 3 in the artificial upwelling period from June to August 2005. The observed mean natural ChlT_n of 160 kg between the 4 and 15 m depths in 2004 and 2005 was almost identical to the observed mean ChlT_n of 165 kg (SD = 35 kg, $n = 16$) at Stns 11, 16, 17 and 01 inside A_o from May to September in 2002, 2003 and 2006.

Fig. 8 shows that there is a high correlation between observed ChlT inside A_o and the water transport (Q_v , $\text{m}^3 \text{ s}^{-1}$). ChlT_{upw} , and the difference between ChlT_{upw} and ChlT_n are decreasing with increasing Q_v and with the largest relative changes appearing at low Q_v . When Q_v is less than $260 \text{ m}^3 \text{ s}^{-1}$ the observed influence area of the artificial upwelling is less than $A_o = 10 \text{ km}^2$. The mean total primary production rate (PT) inside A_o ($A_{\text{infi}} \leq A_o$) during artificial upwelling is calculated using the observed mean of ChlT_{upw} (500 kg) and Q_v ($235 \text{ m}^3 \text{ s}^{-1}$) in Eq. (4). Natural production, P_n , is calculated using $\text{ChlT}_n = 180 \text{ kg}$ and the related mean $Q_v = 225 \text{ m}^3 \text{ s}^{-1}$. When $H_a = 9 \text{ m}$ and $\text{POC}/\text{chl } a = 80$, PT and P_n are estimated to be approximately 9000 kg C d^{-1} ($900 \text{ mg C m}^{-2} \text{ d}^{-1}$) and 3000 kg C d^{-1} ($300 \text{ mg C m}^{-2} \text{ d}^{-1}$), respectively. PT and P_n measured as kg C d^{-1} may also be expressed as:

$$\text{PT } (P_n) = k \cdot \text{ChlT}_{\text{upw}} \text{ (n)} \quad (6)$$

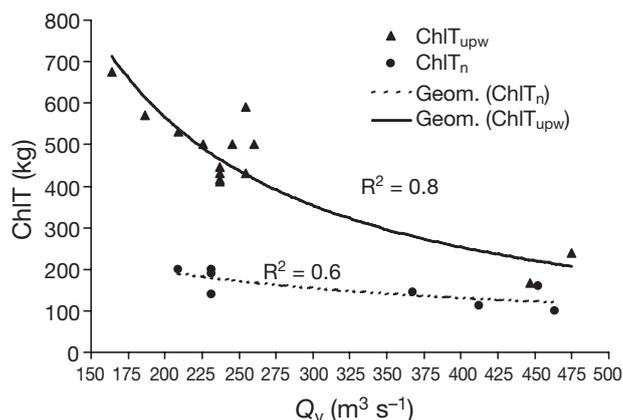


Fig. 8. Observed relationships between the water transport (Q_v) and the total chl *a* inside A_o (ChlT) in the inner part of the Lysefjord. ChlT from artificial upwelling = ChlT_{upw} , and ChlT from natural conditions = ChlT_n . Geometric regression lines and related R^2 are included

where k is the photosynthetic effectiveness (daily integrals of vertically integrated carbon assimilation over chl *a*, $\text{mg C mg chl } a^{-1} \text{ d}^{-1}$) (Prasad et al. 1995, Erga et al. 2005) and $\text{ChlT}_{\text{upw}} \text{ (n)}$ is the mean total chl *a* inside A_o . Possible losses of chl *a* due to sedimentation are not taken into account, but they are probably low under continuous upwelling and stratified conditions (Riebesell 1989). The restricted residence time of the phytoplankton layer (5 d) inside A_o and the low sinking velocity of healthy algae ($< 1 \text{ m d}^{-1}$) support this assumption. The mean PT and P_n inside A_o are calculated using the observed mean of ChlT_{upw} (500 kg) in 2004 and 2005 and ChlT_n (165 kg) in the period from 2002 to 2006 in Eq. (6). Using $k = 18 \text{ mg C mg chl } a^{-1} \text{ d}^{-1}$, a value representative of average growth conditions during the summer season in southwestern Norwegian fjords (Erga et al. 2005, S. Erga unpubl. data from adjacent fjords), Eq. (6) gives a total artificial upwelling production (PT) of 9000 kg C d^{-1} ($900 \text{ mg C m}^{-2} \text{ d}^{-1}$) and a natural production (P_n) of 2950 kg C d^{-1} ($295 \text{ mg C m}^{-2} \text{ d}^{-1}$).

Both methods give a total artificial upwelling production (PT) of approximately 9000 kg C d^{-1} ($900 \text{ mg C m}^{-2} \text{ d}^{-1}$) and a natural production (P_n) inside A_o of approximately 3000 kg C d^{-1} ($300 \text{ mg C m}^{-2} \text{ d}^{-1}$). The estimated P_n is close to the observed typical natural production of 3000 kg C d^{-1} ($300 \text{ mg C m}^{-2} \text{ d}^{-1}$) below the surface layer in the summer period. The primary production rate due to the artificial upwelling ($P_{\text{upw}} = \text{PT} - P_n$) is then 6000 kg C d^{-1} ($600 \text{ mg C m}^{-2} \text{ d}^{-1}$) and close agreement with the previously estimated $P_{\text{upw}} = 6600 \text{ kg C d}^{-1}$ ($660 \text{ mg C m}^{-2} \text{ d}^{-1}$) based on the increased supply of nutrients to the photic layer.

Phytoplankton composition

Some days before the artificial upwelling started on 19 May 2004, the phytoplankton stock inside the area of influence of artificial upwelling was dominated by dinoflagellates (Fig. 9a). During June and in the first part of August 2004 there was a considerable relative increase of diatoms with *Chaetoceros* spp. as the dominant genus. The diatom biomass increased from about 4% of the total phytoplankton biovolume (sum of diatoms and flagellates) on 29 May to about 41% on 13 June. During this period the diatom volume biomass increased by $20\% \text{ d}^{-1}$. On 3 August the diatom biovolume still constituted 84% of the total biovolume inside A_0 . Outside A_0 at Stn 02, and in the adjacent Høgsfjord (Stn 03), no diatoms were observed. Here, flagellates including dinoflagellates were the dominant group of phytoplankton in terms of biomass. On 17 August the

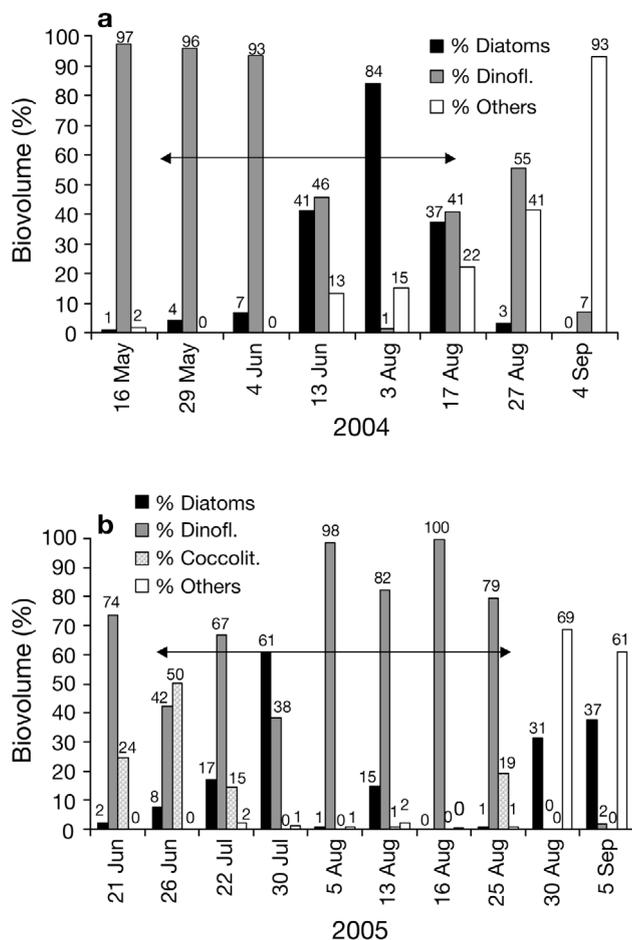


Fig. 9. Percentage biovolume of the most important groups of phytoplankton within the depth interval 7 to 15 m in the inner part of the Lysefjord during (a) 16 May to 4 September 2004 at Stns 11 and 16, and (b) 21 June to 5 September 2005 at Stn 17, inside the main observation area A_0 (horizontal arrow = artificial response upwelling period, Dinofl. = dinoflagellates, Coccolit. = coccolithophorids)

diatom stock was greatly reduced. After the artificial upwelling was stopped in late August, flagellates $<20 \mu\text{m}$ (i.e. dinoflagellates plus others) became the dominant phytoplankton fraction. From June to September 2004, *Dinophysis* species were only encountered in very low concentrations ($<300 \text{ cells l}^{-1}$) within the depth interval 5 to 20 m in the Lysefjord. The normal species succession in western Norwegian fjords during summer is that flagellates and dinoflagellates dominate, but occasionally diatoms may occur (Erga 1989a, Erga et al. 2005).

During the initial phase of the artificial upwelling period in late June 2005, a more detailed study of the quantitative distribution of the most important groups of phytoplankton with respect to biomass was carried out. In this phase the phytoplankton inside the area of influence was dominated by dinoflagellates (74% of the biovolume), while diatoms made up only 2% of the total (Fig. 9b). The main difference between 2004 and 2005 was the mass occurrence of the coccolithophorid, *Emiliania huxleyi*, in 2005, which was by far the most important species in late June 2005. The abundance of *E. huxleyi* increased inwards in the Lysefjord, a pattern that was also observed for the dinoflagellates. Among the dinoflagellates, nontoxic *Ceratium lineatum* was dominant, while *Dinophysis* species were present in low concentrations only, both inside and outside the area of influence. The highest concentration of phytoplankton was situated below the brackish layer, from 6 m and deeper, where *E. huxleyi* was totally dominant, with concentrations of around 10 to $12 \times 10^6 \text{ cells l}^{-1}$. Among the diatoms, the pennate forms dominated, with *Pseudonitzschia* spp., *Cylindrotheca closterium* and *Nitzschia longissima* being the most important species.

During the first month of the artificial upwelling period (from 21 June to 22 July), diatom concentrations within and outside the area of influence, Stns 17 and 02, respectively, increased from about 10^3 to $10^4 \text{ cells l}^{-1}$ to about $10^6 \text{ cells l}^{-1}$, but on 30 July the concentrations of diatoms decreased markedly in Stn 02, while they continued to increase to a maximum of $1.5 \times 10^6 \text{ cells l}^{-1}$ at Stn 17. Now the dominating species had changed from *Pseudonitzschia* spp. to *Skeletonema* sp. In late July the contribution of diatoms rose to about 60% of the total biovolume (Fig. 9b). In August dinoflagellates once again took over as the dominant fraction in terms of biovolume, with *Ceratium lineatum* as the dominant species. As in 2004, *Dinophysis* species were now present in only very low concentrations. In late August when the artificial upwelling was stopped, small flagellates $<5 \mu\text{m}$ (others) dominated and the chl *a* content of the water column decreased to the same levels as outside the area of influence (Figs. 9b & 6b).

DISCUSSION

Physical controls on primary production rate

The large-scale experiment in the Lysefjord showed that artificial upwelling enhanced the observed algae biomass and the estimated primary production rate within an area of about 10 km² during summers in 2004 and 2005. The artificial upwelling also stimulated diatom growth. These results are in accordance with model simulations of primary production rate in a similarly scaled fjord subjected to different scenarios of submerged freshwater discharge (Berntsen et al. 2002). Our study is the first full-scale experiment to use submerged brackish water discharged in a controlled manner to force artificial upwelling in a fjord area and to demonstrate experimentally the significant potential for ecological studies on this topic in fjords.

Previous investigations in western Norwegian fjords have revealed a remarkable consistency with respect to water exchange processes and phytoplankton growth dynamics (Erga & Heimdal 1984, Erga 1989a,b, Erga et al. 2005). Nutrient limitation usually leads to reduced primary production yields and changes in species composition to a predominance of ultraplankton (< 5 µm) flagellates and dinoflagellates during the summer period, but still more than 50% of the annual primary production occurs after the spring diatom blooms. The mean total primary production rate below the surface brackish layer due to artificial upwelling (PT) was determined to be about 900 mg C m⁻² d⁻¹ inside an area of 10 km², about 3 times the natural production rate (P_n). A primary production rate in the euphotic zone of 1500 mg C m⁻² d⁻¹ is often found in western Norwegian fjords during the main spring bloom in March (Erga & Heimdal 1984, Erga et al. 2005). Therefore, it ought to be possible to increase primary production rate rates in the Lysefjord to 1500 mg C m⁻² d⁻¹ during summer by forced upwelling of nutrient rich deeper water. A considerable enhancement of primary production rates due to natural upwelling have also been reported for many of the strong natural upwelling systems in the world, e.g. the northwest coast of South Africa (Brown 1992), northcentral Chile (Rutllant & Montecino 2002) and northwestern Spain (see Álvarez-Salgado et al. 2005). Maximum primary production rates for these highly productive waters are typically 6000 to 8000 mg C m⁻² d⁻¹, considerable higher than primary production rates during the spring bloom in Norwegian fjord waters.

A nutrient enrichment experiment using mesocosms (plastic cylinders) in Lindåspollene, a landlocked fjord system north of Bergen (Aksnes et al. 1985), demonstrated that an artificial upwelling rate corresponding to approximately 1 m d⁻¹ resulted in an 8 to 10-fold

increase in the midsummer primary production rate. The upwelling rate inside A_o (10 km²) in this experiment was approximately 0.3 m d⁻¹, and with an observed production enhancement factor of about 3, this relationship is in accordance with the study of Aksnes et al. (1985).

The observed mean water exchange between 5 and 15 m (Q_{vm}) during the artificial upwelling periods ($A_{infl} \leq A_o$) in the inner part of the Lysefjord was about 240 m³ s⁻¹, which gives a mean residence time (T_r) of about 5 d in the inner 10 km² of the fjord. The time-scale of the phytoplankton response to increased supply of nutrients to the euphotic layer in June 2005 was observed to be 5 to 7 d (Fig. 7a), which is similar to the mean residence time estimated. The area of influence of increased production based on artificial upwelling is dependent on both the residence time of the phytoplankton layer (T_r) and the phytoplankton division rate (A_r). According to Aksnes (1993), the condition for a local or regional effect on new production is dependent upon the ratio $R = 1/(T_r \cdot A_r)$. When R is much less than 1 the new production will be local. In the inner 10 km² of the Lysefjord, R was 0.2 using $A_r = 1$ d⁻¹. This indicates that most of the artificial upwelling production took place inside the fixed observation area A_o of 10 km². Observations of the longitudinal distribution of chl *a* in the Lysefjord during artificial upwelling in 2004 and 2005 support this assumption.

To estimate the area of influence (A_{infl}) of artificial upwelling in a fjord system we use a combination of Eqs. (4, where $A_o = A_{infl}$, measured in km²) & (6):

$$A_{infl} = (CT_{upw}/ChlT_{upw}) \cdot Q_v / (k \cdot H_a) \quad (7)$$

where H_a is the mean thickness (m) of the phytoplankton layer, CT_{upw} and $ChlT_{upw}$ are the total particulate organic carbon and chl *a* biomass, respectively, inside A_{infl} , Q_v is the water flux out of the phytoplankton layer and k is the photosynthetic effectiveness in the phytoplankton layer. $CT_{upw}/ChlT_{upw}$ is the ratio between total particulate organic carbon and chl *a* (i.e. POC/chl *a*). It follows that A_{infl} is proportional to the mean water exchange Q_v and inversely proportional to k when H_a and POC/chl *a* are considered as constants. Water flux, Q_v , is associated with the residence time of the phytoplankton layer (T_r) inside A_{infl} , and k with the phytoplankton division rate (A_r) (see previously). The mean chl *a* concentration ($chl_{m_{upw}}$) inside the A_{infl} is determined by Eqs. (1), (2) & (7):

$$chl_{m_{upw}} = P_{upw} \cdot [(chl\ a/POC)/Q_v] + [P_n/(k \cdot H_a)] \quad (8)$$

In Fig. 10 $chl_{m_{upw}}$ is calculated as a function of Q_v using $P_{upw} = 6600$ kg C d⁻¹, POC/chl *a* = 80, $H_a = 10$ m, $P_n = 300$ mg C m⁻² d⁻¹ and $k = 18$ mg C mg chl *a*⁻¹ d⁻¹. A mean POC/chl *a* ratio of 81 ($n = 288$) was typical for another western Norwegian fjord during the summer

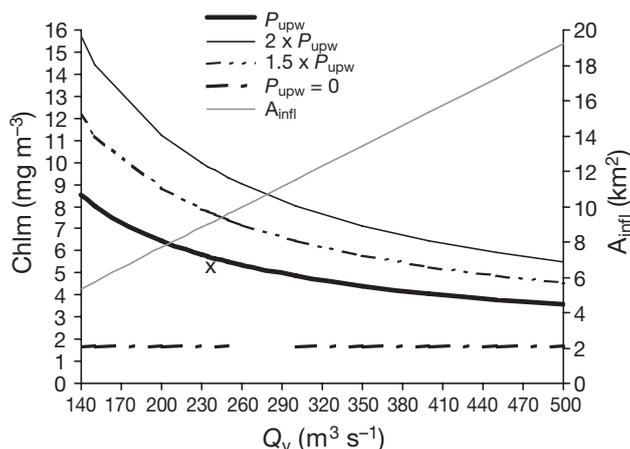


Fig. 10. Calculated area of influence (A_{infl}) and mean chl a (chl_m) inside the area of influence as a function of water transport (Q_v). POC/chl $a = 80$, $H_a = 10$ m, $k = 18$ mg C mg chl $a^{-1} d^{-1}$, $P_n = 300$ mg C $m^{-2} d^{-1}$ and $P_{\text{upw}} = 6600$ kg C d^{-1} . The following cases are shown: $P_{\text{upw}} = 0$, $P_{\text{upw}} \times 1$, $P_{\text{upw}} \times 1.5$ and $P_{\text{upw}} \times 2.0$. Mean observed chl_m and Q_v (shown by x) during artificial upwelling in 2005 inside $A_o = 10$ km 2 ($A_{\text{infl}} < A_o$)

period (Erga et al. 2005). The observed mean $\text{chl}_{m,\text{upw}}$ and Q_v inside A_o in 2005 were 5.3 mg m^{-3} and 235 m^3 s^{-1} , respectively. As shown in Fig. 10, the observed $\text{chl}_{m,\text{upw}}$ was well in agreement with the calculated value of 5.7 mg m^{-3} when $Q_v = 235$ m^3 s^{-1} . As observed, the calculated A_{infl} was less than 10 km 2 when Q_v was below 260 m^3 s^{-1} . During natural conditions ($P_{\text{upw}} = 0$) the mean chl a concentration (chl_n) inside the A_{infl} is calculated to be 1.7 mg m^{-3} (Fig. 10), almost identical to the observed chl_n during natural conditions in 2004 and 2005 (1.8 mg m^{-3}). When the primary production rates due to the artificial upwelling (P_{upw}) are increased by factors of 1.5 and 2.0, $\text{chl}_{m,\text{upw}}$ is increased to 7.8 and 9.8 mg m^{-3} , respectively, when $Q_v = 235$ m^3 s^{-1} . A doubling of P_{upw} represents a mean daily integrated carbon assimilation of about 1.6 g C $m^{-2} d^{-1}$, which is at the same level as the daily integrated carbon assimilation during the main spring bloom in other western Norwegian fjords (Erga & Heimdal 1984, Erga 1989b, Erga et al. 2005). This level is within the natural variability of the fjord ecosystem and probably a reasonable upper limit of enhanced primary production achieved by artificial upwelling.

The k value of 18 mg C mg chl $a^{-1} d^{-1}$ used in our calculations is typical for a chl a maximum at about 10 m depth during the summer in western Norwegian fjords (S. R. Erga unpubl. data). A shallower intrusion depth (Z_i) will result in a higher k value, since the POC/chl a ratio increases upward in the water column during stratified conditions as light conditions improve (Erga 1989a,b). In periods with persistent low solar irradiance at the surface and/or increased upper layer turbidity, we

expect lower k values and, thus, a reduced total primary production rate (PT) (Eq. 6) and increased area of influence (A_{infl}) (Eq. 7). In a comprehensive primary production rate investigation on the Iberian shelf break (northwestern Spain) during periodic upwelling and relaxation events in June through July, k values were found to be within the range 9 to 24 mg C mg chl $a^{-1} d^{-1}$ (primary production rate and chlorophyll concentration, depth-integrated from surface to the base of euphotic zone) (Joint et al. 2002). From their data a mean k value of 16 mg C mg chl $a^{-1} d^{-1}$ can be calculated. However, during a winter upwelling/downwelling sequence in the Ría de Vigo (northwestern Spain), a bloom of *Skeletonema costatum* revealed k values as high as 45 mg C mg chl $a^{-1} d^{-1}$ (Álvarez-Salgado et al. 2005).

Species succession

Physical conditions for large-scale blooms of diatoms typically include persistent upwelling regimes (Brown 1992, Taylor & Haigh 1996, Rutllant & Montecino 2002, Trainer et al. 2002, Ning et al. 2004, Álvarez-Salgado et al. 2005), and dinoflagellate blooms occur most frequently in stratified waters (Delmas et al. 1993, Reguera et al. 1995, Taylor & Haigh 1996). Common for many of these upwelling systems is that the growth stimulating response seems to occur towards the end of the upwelling period or beginning of the relaxation period when the water column start to stabilize and nutrients are replenished. In the Lysefjord a modest artificial upwelling was achieved in both 2004 and 2005, with a mean intrusion depth of 8 to 9 m. It is widely accepted that the coupling between internal biological processes and external physical perturbations plays a key regulatory role in the seasonal succession of phytoplankton (Harris & Trimbee 1986, Taylor & Haigh 1996, Teira et al. 2001).

According to the 'intermediate disturbance hypothesis' (IDH), intermediate disturbance or turbulence will lead to maximum species diversity of phytoplankton (see Sommer 1995), while intense disturbances reduce diversity to a few dominant species (Flöder & Sommer 1999, Huisman et al. 1999). Besides increased production, it was desirable to obtain a dominance of 'healthy' diatoms in our artificial upwelling experiments. One precondition for this is to ensure that sufficient concentrations of 'seed' populations are present in the initial phase of the artificial upwelling at the operational depth of the system (Ishizaka et al. 1983), and that a balance between nutrient supply and the dilution of growing diatoms is obtained. According to Hutchinson (1953), changes in the physical regime on time scales longer than the generation time of the organism, which for phytoplankton is about 1 ± 0.5 d^{-1} , should prevent

competitive exclusion. The main advective processes in the inner 10 km² of the Lysefjord have been shown to operate on a much longer time scale than this (5 to 7 d). The retention time should, therefore, be sufficient for a diatom bloom to develop within the main area of artificial upwelling. The artificial upwelling water transport and associated 'turbulence' was insignificant compared with natural water exchange (12%). Based on this we do not expect any effects of the artificial upwelling water transport on selection of diatoms.

At the head of the Lysefjord, the daily integral of carbon assimilation with *Emiliania huxleyi* as the dominant species was no higher than 350 mg C m⁻² d⁻¹ in June 2005, even if cell concentrations were as high as 10 to 12 × 10⁶ cells l⁻¹. However, such a low rate of carbon assimilation is not representative of the artificial upwelling period, since it only concerns the initial part when no stimulating effect on primary production rate has been obtained. Previous experience has shown that when natural upwelling in fjords occurs during summer, daily integrals of carbon assimilation of about 1 g C m⁻² d⁻¹ could be achieved (Erga 1989b), and that such events may stimulate diatom growth (Aksnes et al. 1985, Paasche & Erga 1988, Erga 1989a). Silicate is an important competitive factor in this context (Egge & Aksnes 1992). Our results for the Lysefjord are in accordance with these findings. The dominance of diatoms, however, was higher in 2004 than in 2005, as revealed by their accounting for 90% and 60%, respectively, of the total biovolume by the end of July. This could be ascribed to the mass occurrence of *Emiliania huxleyi* in the whole fjord system from mid-June until mid-July 2005, which resulted in unfavourable light conditions due to high concentrations of detached coccoliths in the water column. Typical of such situations are increased scattering to absorption ratios (Frette et al. 2004). It is also interesting to note that by the end of July 2005, *Skeletonema* sp. was the major contributor to phytoplankton biomass within the area of influence of the artificial upwelling, while outside this area it was almost absent.

In both 2004 and 2005 the diatom stock was greatly reduced during August (Fig. 9). Possible explanations for the diatom breakdown could be a lack of 'seed' diatoms in the influence region or an incidental unbalance between nutrient supply and diatom biomass. From mid-August 2004 the currents within the area of influence increased, which led to higher rates of water exchange. The effect of this may have been a reduced phytoplankton biomass due to dilution. The phytoplankton may, therefore, have adapted to reduced but stable nutrient concentrations, and to less favourable light conditions. Also, diatoms were scarce outside the area of influence both in August 2004 and 2005. Therefore, if the efficiency of the artificial upwelling, as far

as diatom growth is concerned, depends on 'seed populations' from outside, lower levels of diatoms are to be expected under such conditions (Ishizaka et al. 1983).

The normal seasonal succession pattern of phytoplankton in fjords of western Norway involves a rising incidence of toxic dinoflagellates in the upper brackish layer from June to September (Dahl et al. 2004, Erga et al. 2005), among which *Dinophysis* species are most common. Members of the potentially toxic diatom genus *Pseudonitzschia* (Scholin et al. 2000) are often encountered below the pycnocline in June. This was also the case in the Lysefjord. These 2 genera are also common during the summer in coastal waters throughout the world, and are known to cause problems for the mussel industry (Belin 1993, Reguera et al. 1995, Aune et al. 1996, Taylor & Haigh 1996, Horner et al. 1997, Ryan et al. 2005, Strohmeier et al. 2005).

When *Pseudonitzschia* spp. occur in western Norwegian fjords, they are always accompanied by a several other nontoxic diatoms, of which *Leptocylindrus* spp., *Chaetoceros* spp. and *Skeletonema* sp. are the most common (see Erga & Heimdal 1984, Erga 1989a, Erga & Skjoldal 1990). Representatives of these genera also made up the largest fraction of diatoms in the Lysefjord during the artificial upwelling period. To date, *Pseudonitzschia* spp. has not caused any toxicity problems in Norwegian fjords.

In conclusion, the large-scale experiment in the Lysefjord during summers of 2004 and 2005 demonstrated that artificial upwelling of nutrients from deeper water strata approximately tripled mean algae biomass and the estimated primary production rate below the surface layer within an influence area of 10 km² at the head of the fjord. The concentrations and composition of the upwelling nutrients are identical to those normally encountered during the winter and spring seasons. There were differences in the species composition of the algae within and outside the area of influence, with periodic dominance of diatoms inside the influence area. However, diatom growth seems to be dependent upon 'seed populations' in the adjacent fjord waters. The increase in primary production rate due to artificial upwelling should occur within the natural variability of the fjord ecosystem and be confined to the area of interest. A higher stable level of phytoplankton biomass, dominated by nontoxic species, is likely to increase the fjord's carrying capacity of seston-feeding shellfish and could form the basis of more predictable mussel cultivation in fjords. To investigate this possibility further, a study of the effects of large-scale artificial upwelling on commercial mussel production has now been launched in the Lysefjord. It will also focus more thoroughly on the ecological aspects of artificial upwelling, including implementation of a 3D physical/biological model.

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