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Temporal and spatial variation in food availability and meat ratio in a longline mussel farm (*Mytilus edulis*)

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Abstract

The influence of temporal and spatial variation in food availability on mussel meat ratio and biomass was studied in a longline mussel farm (100 m wide and 250 m long, *Mytilus edulis*) during an eight-month period. Current velocity and phytoplankton concentration were measured and mean mussel biomass, density, wet weight and meat ratio were determined. The longline farm aligned the current direction lengthwise through the farm and reduced the current speed and flow to approximately one half to one third of reference station. The mean fluorescence depletion in the centre of the farm was 11 % and the phytoplankton concentration (cells L^{-1}) was 20 to 91 % less in the centre of the farm compared to the reference station. The mean meat ratio increased 1.8 times through the spring phytoplankton bloom. The mean meat ratio (%) and biomass (kg) was spatially variable through the farm with low values in the centre and increasing values towards the edges of the farm. This variation in meat ratio and biomass was observed at all natural phytoplankton concentrations and attributed to spatial variation in food availability through the farm.

Keywords

Bivalve aquaculture, current velocity, food availability, meat content, mussel, *Mytilus edulis*, seston depletion.

Introduction

The development of the mussel (*Mytilus edulis*) farming industry in Norway is based on the technology and methods of suspended longline culture and large sheltered coastal areas are potentially suitable for farming. However, the anticipated expansion and export volumes have not been realized, in part because of low meat ratio, probably related to overcrowded stocks and lack of husbandry knowledge.

The growth of suspension-feeding bivalves is largely controlled by food availability (Winter 1978, Bayne and Newell 1983, Soniat and Ray 1985, Berg and Newell 1986), which in turn is affected by seston concentration, composition and transport rate (Incze and Lutz 1980, Frechette et al. 1989, Blanco et al. 1996). Food availability is often coupled to phytoplankton dynamics (Rosenberg and Loo 1983, Smaal and Stralen 1991) and large volumes of mussels are typically farmed in areas with a high concentration of phytoplankton. Examples of high chlorophyll *a* (Chl *a*) concentrations are 4-12 mg m^{-3} in Ria de Arousa (Figueiras et al. 2002), 8 mg m^{-3} in Benguela Bay (Pitcher and Calder 1998), 7.5 mg m^{-3} in Oosterschelde, 4-22 mg m^{-3} in Marennes-Oléron Bay (Dame and Prins 1998) and 6.9 mg m^{-3} in Chesapeake Bay (Dame and Prins 1998). Several of these farming sites are shallow bays with high tidal amplitude leading to resuspension of organic material and an additional increase in food availability.

In comparison, farming sites along the western coast of Norway are considerably deeper and resuspension of organic material available to mussels in suspension-culture is likely to be insignificant since phytoplankton constitutes the major component of the seston in western Norwegian fjords (Erga 1989, Erga et al. 2005). The biomass of phytoplankton along the

Norwegian coast follows a seasonal pattern with a period of algal blooms in late winter/early spring, late spring/early summer and occasional autumn blooms.

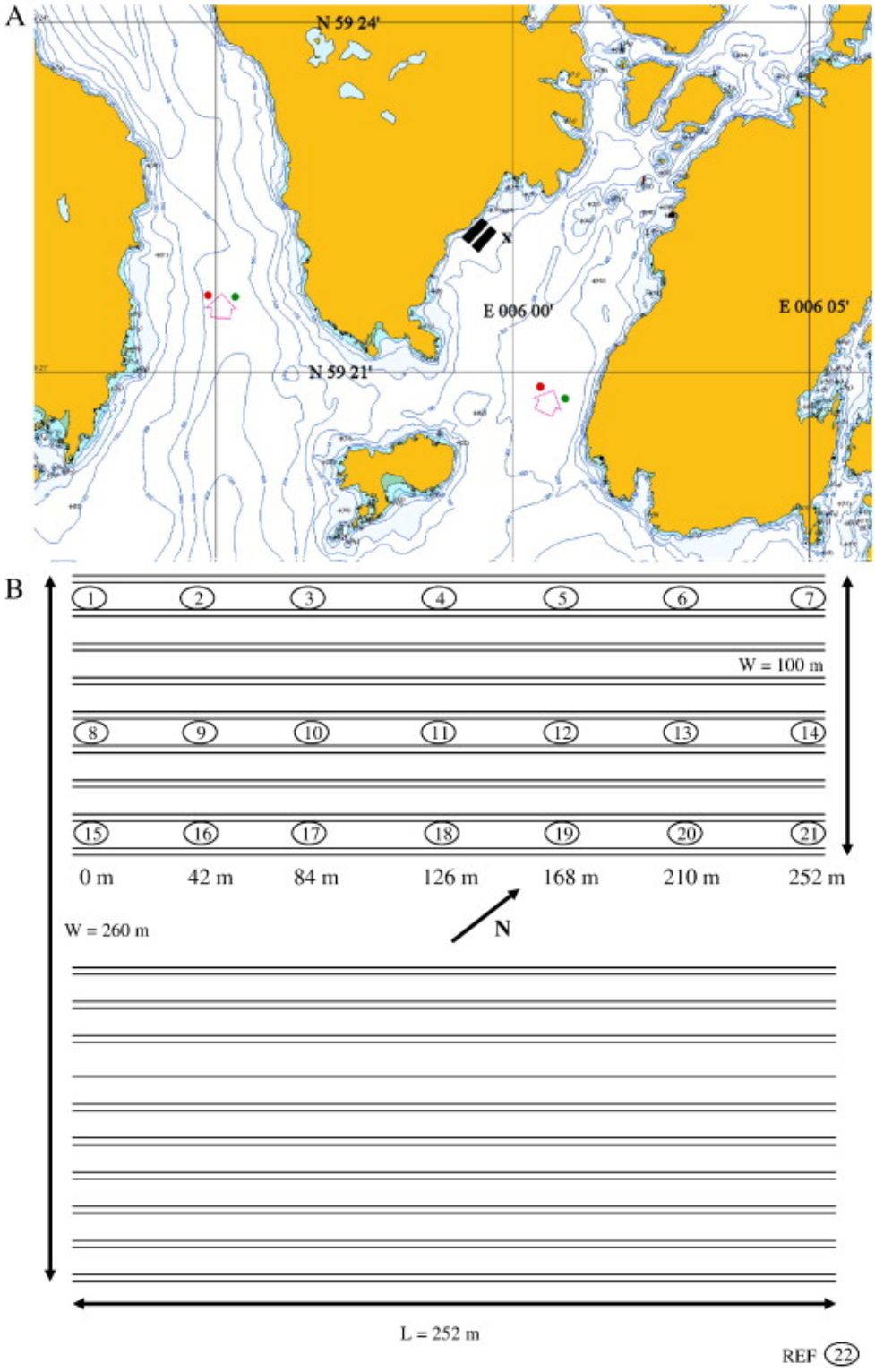


Fig. 1. (A) Site map of the farm area and the investigated mussel farm in the Sandsfjord. Surface area of the inner and outer farm blocks indicated in black and fjord reference site indicated by X. (B) Mussel sampling station overview. Mussel samples were only taken from the inner block of the farm as the outer block was harvested. Sampling stations 1 to 7 on longline 1 are towards the shore, sampling stations 8–14 on longline 5 are referred to as the mid section and sampling stations 15–21 on longline 9 are towards the outer farm

block. The arrow between the blocks indicates north. W is width of block and farm and L is length of farm. Station 22 is the reference station

On regional or local scales blooms may occur from wind generated upwelling of nutrient-rich deep water. For extended periods the concentration of Chl *a* along the Norwegian coast is less than 1-2 mg m^{-3} (Erga 1989, Frette et al. 2004), due to nutrient limitation (Paasche and Erga 1988, Erga et al. 2005). Hence, Norwegian fjords and coastal waters are considered low seston environments compared to sites where most studies on mussel feeding on natural seston have been carried out (Grant et al. 1997, Smaal et al. 1997, Pitcher and Calder 1998, Dame and Prins 1998, Cranford and Hill 1999, Figueiras et al. 2002, Hawkins et al. 2002).

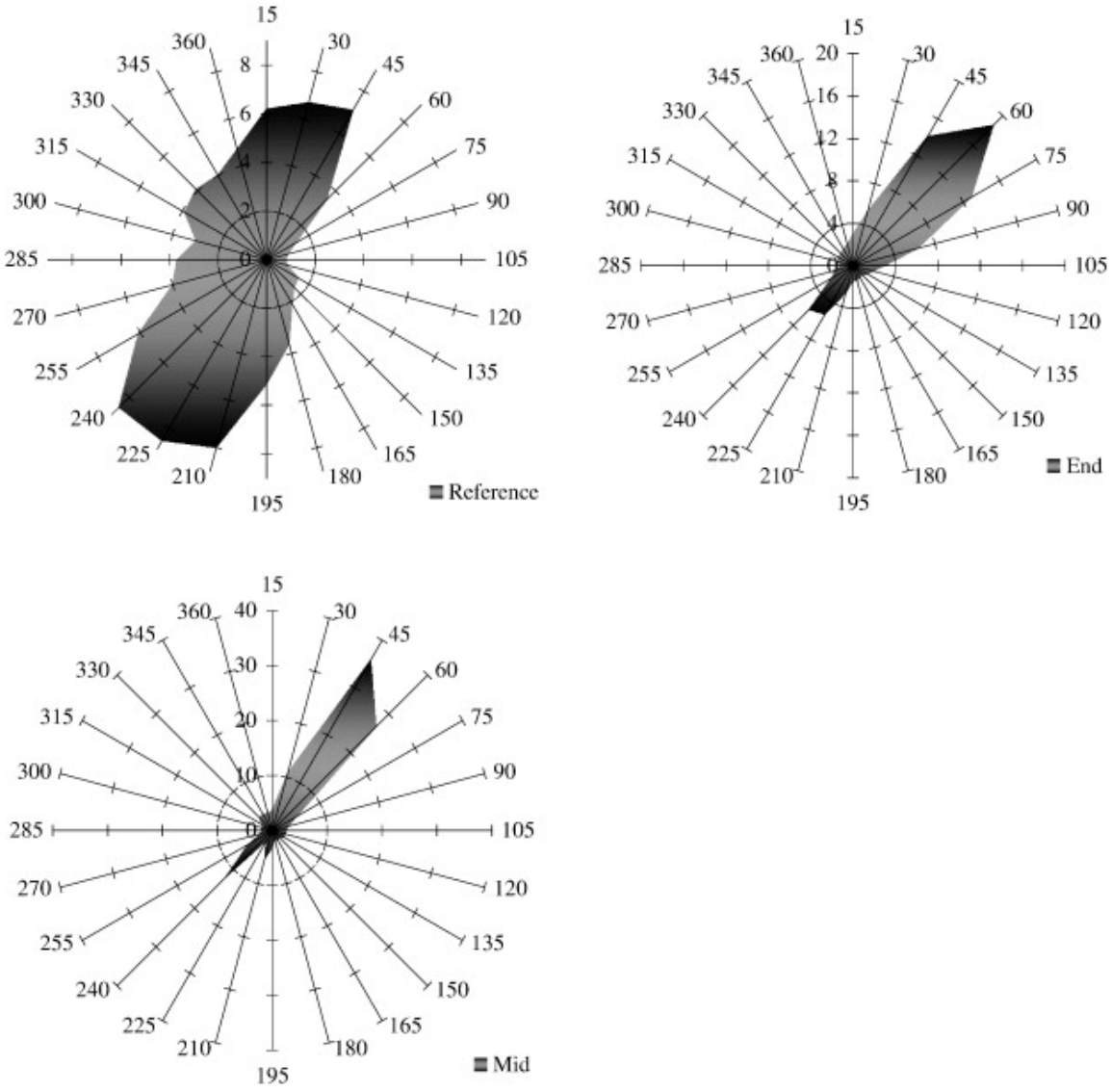


Fig. 2. The distribution of water flow (%) per 15-degree sector at the reference station, the ends of the mid section (mean of position 0 (station 8) and 252 (station 14) and the mean of water flow at positions 63 m, 126 m (station 11) and 189 m. Note the different scale on the *y*-axis

Mussel farming in low seston environments is vulnerable to seston depletion, which may cause tissue wasting and lead to low meat ratio during extended periods of the year.

Table 1. Current direction, mean current speed, standard deviation (SD), number of observations and flow at the sampling stations.

Distance from SW end (m)	Direction (degree)	Mean current speed (cm s^{-1})	SD	Number of observations (n)	Flow ($m^3 m^{-2}$)
0	15-75 (NE)	5.49	4.85	2065	67832
63	15-75 (NE)	4.65	4.37	2634	73376
126	15-75 (NE)	2.92	3.25	1905	33265
189	15-75 (NE)	2.88	2.8	2441	42110
252	15-75 (NE)	2.63	2.04	2504	38992
REF	15-75 (NE)	3.31	2.33	963	19072
0	195-255 (SW)	2.62	1.74	855	4606
63	195-255 (SW)	3.64	2.30	583	12714
126	195-255 (SW)	2.48	2.19	757	10888
189	195-255 (SW)	4.24	2.76	704	17534
252	195-255 (SW)	3.29	2.50	936	18347
REF	195-255 (SW)	3.73	2.24	1450	32151

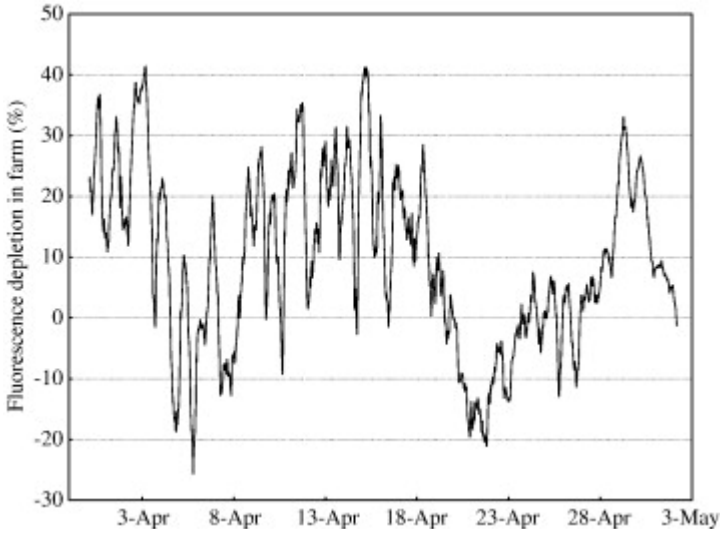


Fig. 3. Time series of the relative fluorescence depletion in the farm calculated from the fluorescence concentration (6 hour running mean, *n* = 8898) in the centre of the farm (station 11) and on the reference station (station 22)

Reduced growth rates are generally observed in areas of low current speed and/or high population densities. Seston depletion has been recorded in the water overlaying natural beds

of filter feeding bivalves (Frechette et al. 1989, Noren 1999, Dolmer 2000), in mussel rafts (Navarro 1991) and in a longline mussel farm (Strohmeier et al. 2005).

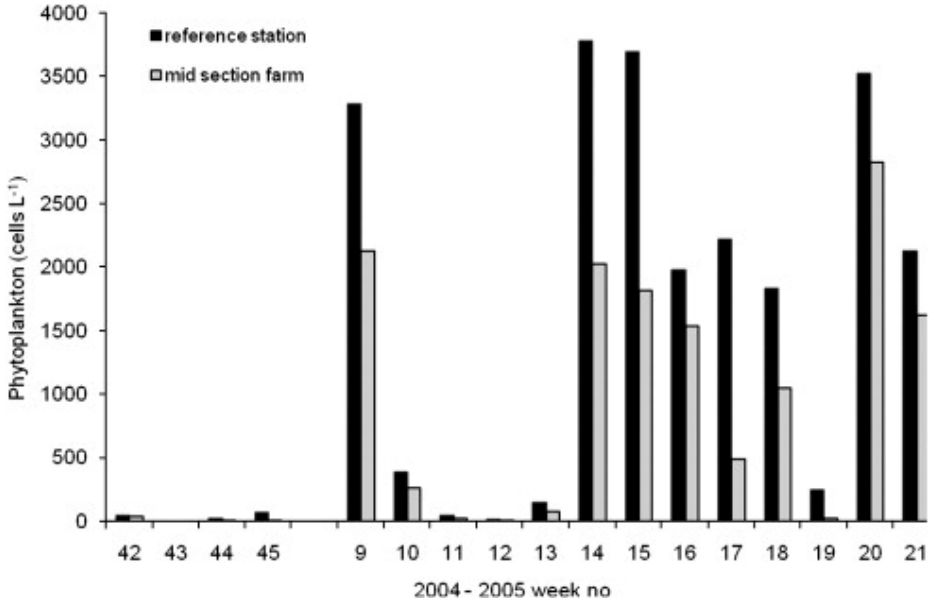


Fig. 4. Phytoplankton concentration on the reference station (dark bars, station 22) and in the centre of the farm (grey bars, station 11). Note the time scale break on the *x*-axis.

We have previously studied a long and narrow mussel farm situated in a low seston environment and reported spatial Chl *a* depletion and decreasing meat ratio towards the mid section of the farm (Strohmeier et al. 2005). The investigated farm was found to be unsuitable for mussel farming in low seston environment as friction from the mussel ropes greatly reduced flow and thereby the seston supply. The reduction in flow was explained by the narrow spacing between longlines. Compared to the previous description of a narrow farm, in which the measurements were taken during a time scale of days, the present study includes time-series of measurements over 8 months in a farm with enlarged spacing between the longlines. The aim of this study was to measure food availability and somatic growth in a commercial longline mussel farm during a shift in food concentration to determine the influence of temporal and spatial food availability on mussel meat ratio. The study was conducted from October 2004 to May 2005 to avoid sampling in the period of gamete release.

Materials and methods

Study site and the longline mussel farm

The Sandsfjord is located on the southwest coast of Norway (Fig 1A). The fjord is approximately 55 km long, 0.5 - 14 km wide and a part of a larger fjord system. The maximum depth is 420 m. The mean tidal range is 0.4 m. The maximum depth in this section of the fjord is 220 m. The depth under the inner part of the farm was 30 m and 90 m under the outer part of the farm. The investigated longline mussel farm was located in the outer part of the fjord (N 59º 22', E 006º 00'). The farm comprised two blocks; each 252 m long, 100 – 110 m wide and had 9 and 10 double longlines running lengthwise. The mussels in the outer block were harvested and all measurements were conducted in the inner block of the farm (Fig 1B). In the following text is the term "farm" used synonymous to the inner block of the farm. We denoted the SW edge of the farm as position 0 m and the NE edge as the end of the farm at 252 m. The distance between the longlines was 10 - 12 m. The distance between the two sections was 40 m. There was 6.14 km mussel rope per longline, arranged in 5 m deep bights hanging from the surface. The investigations were carried out from October 2004 to May 2005.

Water velocity, phytoplankton biomass and composition

Water velocity was measured simultaneously with six current meters (SD 6000, Sensordata AS, Norway), deployed at 2.5 m depth. Water velocities were recorded every 10 minutes from 12th October to 23rd November 2004. Five current meters were placed between longline four and five and at position 0 (station 8), 63, 126 (station 11), 189 and 252 m (station 14, Fig 1B). One current meter was situated on the reference station (station 22) to record ambient current velocities. Water flow (Y, m^3m^{-2}) was calculated as: $[(x_1\ (ms^{-1}) * t\ (s)) + (x_2\ (ms^{-1}) * t\ (s)) +$

126 (x_n (ms^{-1}) * t (s))] * m^2m^{-2}, where x is the measured current speed in a 15 degree interval and t
127 is the time interval for the measurement.

128

129 Table 2 a. Temporal variation in mean (n = 21) biomass (kg m^{-1}), density (mussels m^{-1} rope), wet weight (g $individual^{-1}$) and
130 meat ratio (%) within the longline mussel farm. Number in parenthesis is standard deviation.

	October	December	March	May
Biomass	7.1 (2.0)	6.0 (1.8)	7.0 (2.1)	8.1 (2.2)
Density	425 (105.4)	338 (77.0)	359 (84.0)	426 (148.0)
Wet weight	16.7 (3.5)	18.1 (3.0)	18.3 (3.3)	18.6 (3.7)
Meat ratio	47.6 (5.2)	42.3 (5.3)	58.0 (6.9)	75.1 (9.0)

131

132 Table 2 b. Results from repeated measures ANOVA testing differences between mean biomass, density, wet weight and meat
133 ratio over time. Significant ANOVAs were followed by a Tukey post hoc test and when relevant these p values are given in
134 the text.

Source of variation	SS	df	MS	*F*	*p*
Biomass	47.7	3	19.9	5.8	0.000
Density	130122	3	4.3	4.3	0.008
Wet weight	43.4	3	2.6	2.6	0.059
Meat ratio	13116	3	104.9	104.9	0.000

135

136 Fluorescence, temperature and salinity were measured at station 11 and 22, at 2.5 m depth by
137 two STD/CTD instruments (SD 204, SAIV A/S, Norway). The instruments recorded every 5
138 minutes during two periods: 1) from 12th October to 1st December 2004 and 2) from the 30th
139 March to 2nd May. The data in period 1 from the reference station was not logged due to
140 instrument failure.

141

142 Phytoplankton was sampled weekly, at station 11 and 22 in two periods: 1) from the 14th
143 October to the 7th November 2004 and 2) from the 2nd of March to the 23rd of May 2005.
144 Approximately 1.5 L seawater was sampled by a hose from 1 – 3 m depth. Phytoplankton
145 counts were performed on 200 ml preserved water samples (1% neutral formaldehyde and
146 neutral Lugol). Phytoplankton species were identified using a light microscope or an
147 epifluorescence microscope. Filtration on 0.45 µm pore size filter and sedimentation

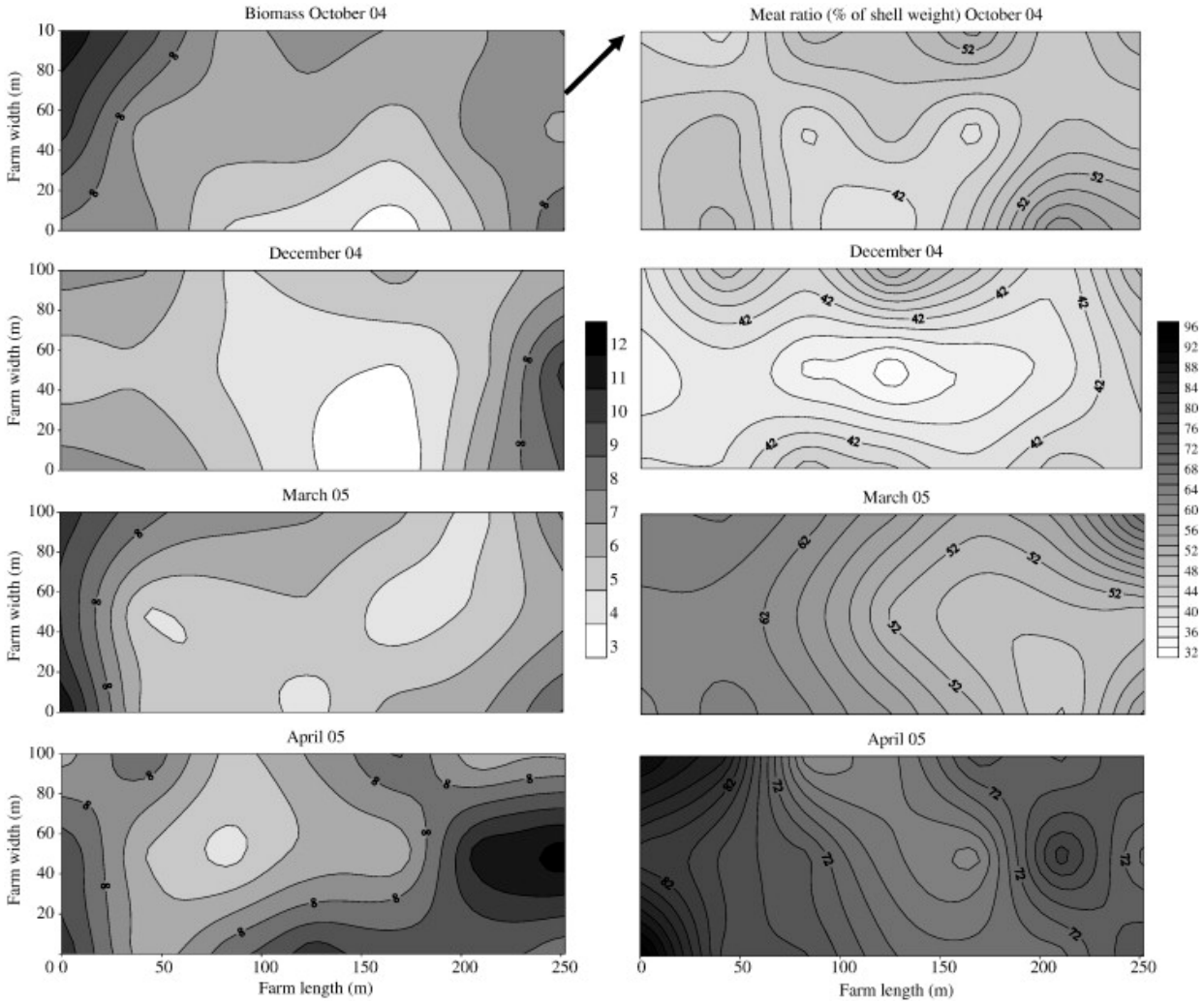
techniques was adapted to the present plankton abundance and composition with detection limits 100 - 10 000 cells L^{-1} (Sournia 1978).

Mussel samples, biomass and meat ratio

All mussels from a 0.15 m section on the rope at 2.4 m depth were collected. Samples were taken at 21 stations (Fig 1B) on four occasions: 16 - 17th October 2004, 8 - 13th December 2004, 21 - 23rd March 2005 and 25 April - 6th May 2005. The mussels were 2.5 years old at the start of the experiment. The whole weight of the sample was determined on mussels at the day of sampling. The mussel biomass was estimated by multiplying the mean wet weight of 21 samples per m with the total length of mussel rope. Following weight measurements, the sample was mixed and a sub-sample of approximately 500 g was taken. These mussels were cleaned and then steamed according to the standard protocol for preparing mussels for food safety analyses (pers. comm. Tore Aune, Norwegian School of Veterinary Science). The meat (somatic tissue) was removed and the weight of the shells determined. The meat ratio was calculated as: (weight of steamed meat / shell weight) * 100.

Statistics

The mean daily change in meat ratio was calculated as: (meat ratio at $_{t+1}$ – meat ratio $_{t}$ / $_{t+1 - t}$). Kriging was used as interprolation to map meat ratio and biomass contours. Repeated measures ANOVA (Zar 1996) was use to test differences in mussel- biomass (kg m^{-1}), density (No m^{-1}), wet weight (g $individual^{-1}$) and meat ratio (% of shell weight), and was followed by a Tukey HSD test in cases with significant repeated measures ANOVA. The relationship between the wet weight, density of mussels and meat ratio was examined by a regression analyses. Statistica version 8.0 (StatSoft inc., 2007, USA) was used for all statistical analyses. The significance level (α) of 0.05 was accepted in all analyses.



174

175 Fig. 5. Temporal and spatial variation in mean biomass (kg m^{-1}) and meat ratio (%) through the mussel farm at 2.4 m depth. Each plot is
176 based on the 21 stations. The arrow indicates north.

177

178 # Results

179 *Temperature and salinity*

180 The temperature fluctuated between 10 and 12 °C from October to mid November and
181 thereafter it fluctuated around 10 °C until December. The temperature increased from 5 to 9
182 °C from April to May. The salinity fluctuated between 20 – 30 ‰.

183

Current velocity and phytoplankton biomass

The water flow at the reference station was mostly in the N-NE and the SW direction (Fig 2), although water flow was also frequently recorded in the W direction. The mean current speed and the water flow in the NE direction were 3.3 cm s^{-1} and 19000 m^3 m^{-2} and in the SW direction 3.7 cm s^{-1} and 32000 m^3 m^{-2} (Table 1). The water flow through the mussel farm and at the edges of the mussel farm was along the long axis of the farm and mainly in the NE direction (Fig 2). The mean current speed and water flow in the NE direction decreased within the farm, from 5.5 cm s^{-1} and 68000 m^3 m^{-2} at position 0 to 2.6 cm s^{-1} and 39000 m^3 m^{-2} at position 252 (Table 1). The water flow in the SW direction decreased with increasing distance into the farm and was 3 to 4 times lower compared to the flow in the NE direction (Table 1). Within the farm, at stations 63 m, 126 m and 189 m, the lateral mean current speed (normal to the long axis of the farm) was always less than 1.5 cm s^{-1}.

The fluorescence concentration measured in the farm from mid October to December was generally lower than 1 mg m^{-3} but some peaks up to about 2 mg m^{-3} were recorded. The mean concentration from October to December was 0.71 mg m^{-3} (SD = 0.41, n = 14364). The mean fluorescence concentration measured in the farm in April was 2.06 mg m^{-3} (SD 0.78, n = 9018) and 2.30 mg m^{-3} (SD 1.15, n = 9018) at the reference station. This indicates 10.6 % fluorescence depletion in the centre of the farm. The relative fluorescence concentration in the farm fluctuated from -25 % to 40 % during April, but most often between 0 to 30 % (Fig 3). The mean fluorescence concentration calculated for the measurements in which the farm concentration was ≤ reference concentration gave 2.00 mg m^{-3} (SD 1.11, n = 6664) in the farm and 2.36 mg m^{-3} (SD 1.24, n = 6664) at the reference station, indicating a 15.4 % depletion.

208 The mean phytoplankton concentration on the reference station in October and November
209 2004 was 34 000 cells L^{-1} (SD = 30 000) and always less than 100 000. This period was
210 dominated by the diatoms *Skeletonema costatum* and *Chaetoceros* spp. except week number
211 42 that had 6000 to 8000 cells L^{-1} of *Prorocentrum minimum*. On the 2nd of March 2005
212 (week 9) the phytoplankton concentration was 3 200 000 cells L^{-1} followed by four weeks
213 with concentration less than 400 000 cells L^{-1}. From April (week 14) to last half of May
214 (week 21) there were more than 1 500 000 cells L^{-1} except for week 19 (Fig 4). In 2005
215 *Skeletonema costatum, Chaetoceros* spp. and occasionally *Pseudonitzschia* spp. (week 9)
216 constituted the phytoplankton community. The phytoplankton concentration was 20 to 91 %
217 less in the centre of the farm compared with the reference station (Fig 4). The mean
218 phytoplankton concentration from February to May was 1 793 000 cells L^{-1} (SD = 1 485 000).
219 The mean phytoplankton depletion in the farm was 45 % (SD = 24.5)
220
221 *Biomass, density, wet weight and meat ratio.*
222 The mean shell length was 53.3 mm in October, 55.6 mm in December, 57.1 mm in March
223 and 56.6 mm in May (Table 2). The increase in mean farm biomass (kg mussel m^{-1} rope) from
224 December to May was considerable (Table 2, $p < 0.001$). The estimated total biomass was
225 784 000 kg in October, 663 000 kg in December, 773 000 kg in March and 895 000 kg in
226 May. The largest biomass was consistently recorded at 0 and 252 m but varied between these
227 sites over time (Fig 5).

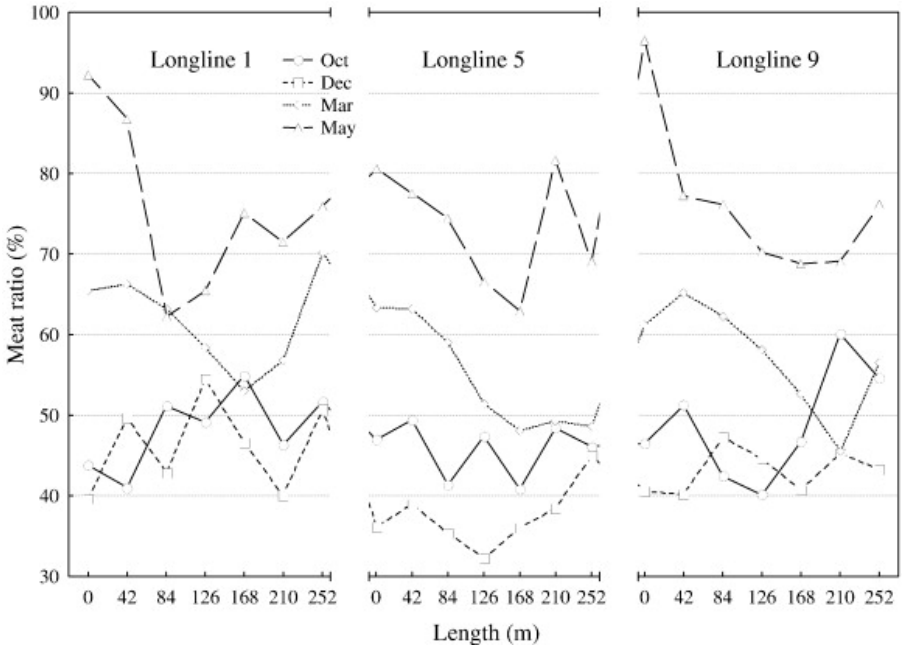


Fig. 6. Mean meat ratio along longline 1 (stations 1–7), longline 5 (stations 8–14) and longline 9 (stations 15–21) from October to May.

The decrease in mean density (mussels m^{-1}) from October to December and increase in mean density from December to May was significant (Table 2, $p = 0.03$ for both). The estimated decrease in number of mussels was 197 000 day^{-1} from October to December. There were no significant changes in wet weight during the sampling period (Table 2, $p > 0.05$).

The decrease in mean meat ratio (% of shell weight) from October to December was significant (Table 2, $p = 0.046$). The increase in mean meat ratio from December to March and March to May was significant ($p < 0.001$ for both). There was a tendency to lower mean meat ratio in the mid section of the farm (Fig 5 and Fig 6). In March and May the meat ratio was highest in the SW edge (Fig 5). Linear regression showed no significant correlation between the density of mussels and the meat ratio at the four sampling times (October $r^2 = 0.004$, $p = 0.79$, December $r^2 = 0.03$, $p = 0.45$, March $r^2 = 0.13$, $p = 0.11$, May $r^2 = 0.001$, $p = 0.89$). The mean daily estimated change in meat ratio (%) was -0.23 from October to December, 0.15 from December to March and 0.36 from March to May.

Discussion

The lengthwise flow direction in the mid section of the farm was pronounced compared to the more varied flow directions at the reference station. Although there were lateral recordings within the farm, these were associated with low current speeds. The data indicates that the "dense curtain of mussels" underneath the longlines caused the aligned directional flow when the mean current speed exceeded ~ 1.5 cm s^{-1}. The farm structure (including mussels) greatly reduced current speed and flow through the farm. The reduction in current speed and flow was most distinct in the main flow direction through the farm in which current speed and flow leaving the farm was approximately half and one third of inflow. Alignment of current direction and current speed reduction is also reported for mussel rafts (Boyd and Heasman 1998). The degree of current reduction is dependent on the background current speed and the farm properties (friction exerted by the farm) such as farm length, spacing between longlines and size of mussels (Aure et al. 2007). Aligned flow direction is a disadvantage as it delivers a one-dimensional renewal of water, which entails a spatial seston supply with deteriorating seston supply according to current speed reduction and suspension feeding at increasing farm length. A clear front-rear flow, often assumed for mussel suspension culture was found at mid depth (2.4 m depth) in this longline farm, while mussel rafts may diverge from such a flow pattern both inside- and between depth layers (Blanco et al. 1996).

The fluorescent concentration measured in the mid section of the farm showed large variation with up to 40 % depletion and a mean of 11 % depletion compared to the reference station. About 25 % of the fluorescence measurements were higher in the farm compared to the reference station, possibly explained by situations with strong wind moving seston depleted water from the farm to the reference station. When these measurements were excluded a mean of 15 % depletion was recorded in the farm. The phytoplankton concentration in the mid

271 section of the farm was often 20 – 50 % lower but some times as much as 70 – 90 %.
272 Although it seems likely that the fluorescence measurements at the reference station have
273 been influenced by the farm due to the sometimes lower values at this station compared to the
274 farm station, we have no explanation for the discrepancy in results between fluorescent and
275 phytoplankton measurements. When 50 % or more of the phytoplankton is extracted at the
276 mid section of the farm we expect even greater food depletion further down-stream in the
277 farm. This is due to the slower water flow (increased retention time) from the mid section
278 towards the exit end of the farm, which gives the remaining mussels more time to clear the
279 residual phytoplankton. It is also possible that the seston quality decreases (is poorer) down-
280 stream due to the selective feeding ability of mussels (Milke and Ward 2003, Ward et al.
281 2003). Finally, not all of the seston is available as food since mussels do not filter in very
282 dilute suspensions (Gosling 2003). The level of cessation in feeding is likely variable but
283 reported around 0.5 mg Chl *a* m^{-3} (Dolmer 2000, Riisgård 2001, Strohmeier 2005). A spatial
284 gradient in seston quantity and quality can therefore be expected from the inflowing end
285 toward the out flowing end in dense longline mussel farms as a consequence of current
286 reduction and selective filter feeding.
287
288 In November and December the fluorescence concentration in our farm was often under the
289 estimated zero net energy balance suggested for *Perna canaliculus* (as Chl *a*) by Hawkins et
290 al. (1999). The concentration of phytoplankton from mid October to December was less than
291 100 000 cells L^{-1} and altogether these recordings indicate insufficient food concentration
292 inside the mussel farm. Deficient food concentration may explain the observed decrease in
293 meat ratio from October to December. Although there were significant changes over time in
294 mussel density, the large variability in the estimates may indicate modest accuracy. Video
295 observations show an accumulation of mussel shells under the farm (unpubl. data, T.

296 Strohmeier), indicating that the decrease in mussel density from October to December can be
297 caused by strong wave action from the first winter storm. The increase in recorded density
298 from December to May is likely due to shell growth of the autumn settlement of mussels. The
299 food concentration increased at the spring bloom in which the mean fluorescent concentration
300 increased three times and the mean phytoplankton concentration increased 53 times.
301 Following the increase in food concentration at the spring bloom the meat ratio almost
302 doubled. This shows a great temporal variability in meat ratio and that somatic growth of *M.*
303 *edulis* responds rapidly to elevated food concentrations.
304
305 The meat ratio of suspension feeding mussels can be regarded as an integrated measure of
306 food availability over time outside the period of gamete release. The gradual decrease in
307 biomass and meat ratio from the edges and towards the mid section of the farm indicates
308 spatial and insufficient food availability in the mid section of the farm, even at spring bloom
309 concentrations of phytoplankton. The spatial variation in meat ratio was likely caused by the
310 lengthwise reduction in current speed (seston supply) and phytoplankton concentration.
311 Considerations of farm design with special emphasis on farm length and spacing between
312 longlines according to the farm biomass and the location's carrying capacity is therefore
313 particularly important in a low seston environment to avoid spatial food depletion and high
314 variability in meat ratio (consumer quality).
315
316 The development of models to estimate carrying capacity for suspended aquaculture (Smaal
317 and Heral 1998, Aure et al. 2007, Grant et al. 2007) requires data for validation, on a fine
318 scale of spatial and temporal variation in currents, food concentration and mussel biomass.
319 Our results may therefore give new finer-scale information relevant to the understanding and
320 modelling of carrying capacity for suspended bivalve aquaculture.

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