

Near-bed gradients in particles and nutrients above a mussel bed in the Limfjorden: influence of physical mixing and mussel filtration

Jens Kjerulf Petersen¹, Marie Maar^{2,*}, Tom Ysebaert^{3,4}, Peter M. J. Herman³

¹Dansk Skaldyrcenter, Øroddevej 80, 7900 Nykøbing Mors, Denmark

²Aarhus University, Department of Bioscience, PO Box 358, Frederiksborgvej 399, 4000 Roskilde, Denmark

³Royal Netherlands Institute for Sea Research (NIOZ), PO Box 140, 4400 AC Yerseke, The Netherlands

⁴Institute for Marine Resources and Ecosystem Studies (IMARES), PO Box 77, 4400 AB Yerseke, The Netherlands

ABSTRACT: The aim of this field study was to investigate the role of mussels on near-bed layer characteristics at different hydrodynamic regimes in a micro-tidal system. At Løgstør Broad, the Limfjorden, Denmark, we deployed 'siphon mimics' to sample chlorophyll *a* (chl *a*), particulate organic carbon (POC) and inorganic nutrients at different distances above the bottom. This was done without disturbing water column gradients and in a manner similar to mussel incurrent flow. Mimics were deployed at 2 sites: a site with a relatively dense mussel bed and a nearby sandy site without mussels. During the 2 wk field campaign, physical conditions in the fjord varied from extremely calm weather with low waves to quite windy with high waves. Results showed that under all conditions, the vertical concentration profiles of chl *a* were significantly depleted towards the mussel bed due to mussel filtration, whereas the degree of chl *a* depletion was correlated to wave height. Nutrient profiles consistently showed increasing concentration profiles towards the bed, identifying the mussel bed and the sediment as a source of nutrients with the highest gradients during the period with high waves. In conclusion, the near-bed concentrations of seston and nutrients in this study were temporally variable and closely linked to the physical structure of the water column.

KEY WORDS: Depletion · Nutrient flux · Mixing · Mussel filtration · Wind forcing · *Mytilus edulis*

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INTRODUCTION

In shallow, coastal ecosystems and estuaries, benthic plants and animals play an active role in the benthic-pelagic coupling of inorganic nutrients and organic matter (Heip et al. 1995). This is in contrast to deep, stratified systems, where the benthic communities are receiving organic matter through sedimentation. Benthic suspension feeders play an important part of this role in coastal ecosystems because they feed directly on (re)suspended phytoplankton and other organic particles in the water column. It has previously been shown that in systems with high bio-

mass of suspension feeders, the typical time scale of filtration (calculated as the time required by the benthos to filter a volume of water equal to the system's volume) is the same order of magnitude as the typical time scale of phytoplankton turnover (i.e. days) (Dame & Prins 1998, Møhlenberg et al. 2007). Thus, the benthos may directly control the phytoplankton standing stock, leading to a shift from bottom-up (nutrient) to top-down (grazing) control of phytoplankton dynamics (Cloern 1982, Norén et al. 1999, Petersen 2004). Besides their possible effect on pelagic primary producers, bio-deposits produced by these benthic suspension feeders enhance transport

of suspended particulate organic matter to the bottom fuelling deposit feeders and altering biogeochemical processes at the sediment-water interface (Newell 2004, Cranford et al. 2007, Maar et al. 2009). The enhanced nutrient regeneration due to biodeposits and excreta from the suspension feeders increases the water column dissolved nitrogen pool, and this may counterbalance the removal of phytoplankton biomass by stimulating new phytoplankton production (Dame 1996, Prins et al. 1998, Newell 2004).

Control of the pelagic primary production by benthic suspension feeders is only possible under mixed conditions of the water column. Benthic suspension feeders, as opposed to the pelagic herbivores, do not take their food from a homogeneous medium, but from the near-bed water layer. Near-bed velocity and turbulence fields are important for the small-scale vertical transport of food particles (Frechette & Bourget 1985). In areas with tidally driven currents (and thus more or less unidirectional flow during prolonged periods of time), depletion of seston above beds of benthic suspension feeders has been demonstrated both in the field (Frechette et al. 1989, Muschenheim & Newell 1992) and in flume studies (Butman et al. 1994, O'Riordan et al. 1995). Modelling these observations gives a clear picture of depletion being dependent on current velocity, mussel bed path length and water depth (Frechette et al. 1989, Wildish & Kristmanson 1997). Heterogeneous roughness due to differences in 3D structure of the suspension feeder community (van Duren et al. 2006) and excurrent jets (Jonsson et al. 2005, Lassen et al. 2006) may, however, alter this picture. In micro-tidal areas with less clear current patterns and low current velocities, depletion of phytoplankton above suspension feeder populations has also been documented (Dolmer 2000, Nielsen & Maar 2007). The limited lateral advection and hence food supply does not allow the mussels to concentrate on relatively small, high-density beds as observed in tidal areas (van de Koppel et al. 2008). Instead the mussels are spread all over the area at relatively low local biomass but a high standing stock on the system scale (Maar et al. 2010). Wind and wave generated mixing is an important feature that can provide food to dense populations of benthic suspension feeders (Frechette & Grant 1991, Møhlenberg 1995, Petersen et al. 2012), especially in shallow areas. Under low-mixing conditions during stratification of the water column, the supply of planktonic algae to the near-bed layer is insufficient to meet the demand of benthic suspension feeders. They may starve at times, even in

eutrophic environments (Maar et al. 2010). At the same time, this relative isolation between benthic grazers and pelagic phytoplankton releases the phytoplankton from grazing pressure and allows it to bloom in the surface layer (Møhlenberg 1995, Petersen et al. 2012). During the subsequent mixing events, the water column may be rapidly depleted due to efficient filtration by the benthic suspension feeders. The optimal conditions for growth of benthic suspension feeders are suggested to be found in this alternation between periods of stratification and mixing. Stratification periods must be long enough to allow the phytoplankton to bloom at the surface layer and short enough to prevent benthic suspension feeders from starving or suffering from hypoxia (Wiles et al. 2006, Maar et al. 2010).

The aim of this field study was to investigate the role of mussels on near-bed layer characteristics at different hydrodynamic regimes in a micro-tidal system. This was tested by comparing vertical profiles of seston and dissolved inorganic nutrients at the near-bed layer under different physical conditions in the presence and absence of mussels. The hypothesis is that the vertical profiles will be significantly affected by the interactions between mussel bed filtration and physical forcing.

MATERIALS AND METHODS

The study site was located in Løgstør Broad in the central part of the Limfjorden, Denmark (Fig. 1). The Limfjorden is a large shallow body of water connecting the North Sea with the Kattegat. The Limfjorden consists of several basins, called broads, and connecting channels or straits. Løgstør Broad has an average depth of 5.8 m and a maximum depth of approx. 9 m. There is constant intrusion of high saline water (salinity 32 to 34) from mainly the North Sea passing through Løgstør Broad and an input from the Kattegat of low saline water (salinity 19 to 25). Furthermore, there is a freshwater input of $2.7 \text{ km}^3 \text{ yr}^{-1}$ from the catchment area. Throughout most of the year the main wind direction is westerly or south-westerly, but during summer prolonged periods of easterly winds may prevail. Limfjorden is a micro-tidal system (tidal amplitude 0.1 to 0.2 m), where the combination of a strong salinity gradient and westerly wind is responsible for a net flow from the North Sea (Thyborøn Kanal) through the Limfjorden to the Kattegat (Hofmeister et al. 2009). The Limfjorden is generally eutrophic, receiving a high nutrient load from the surrounding watershed, which results in

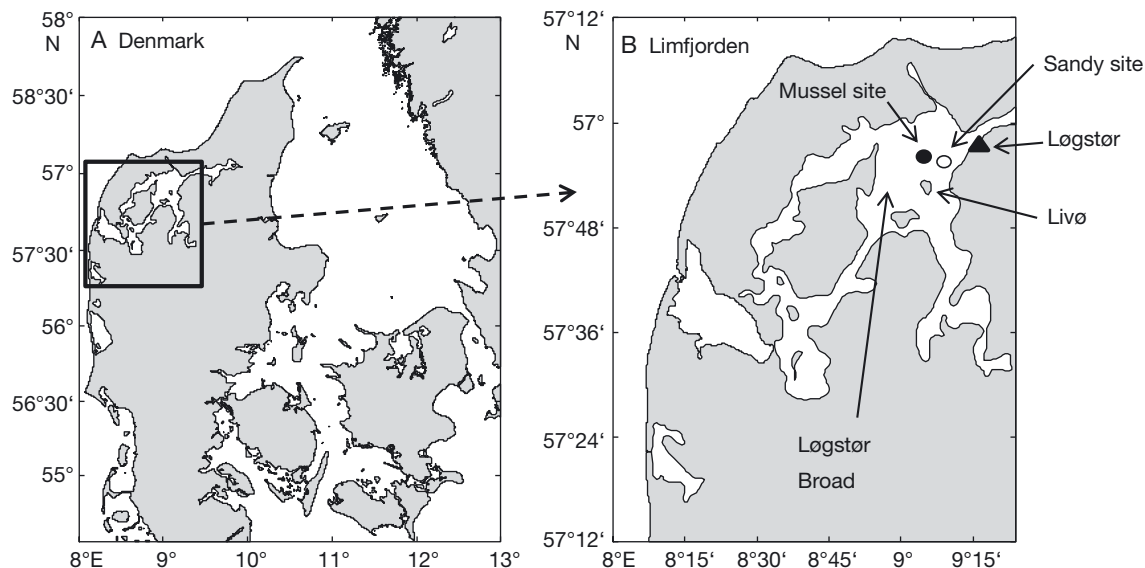


Fig. 1. (A) Position of the Limfjorden, Denmark, and (B) field sites: mussel site (black) and sandy site (white) in Løgstør Broad, as well as the meteorological station at Livø

high primary production rates of up to $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Krause-Jensen et al. 2011). The high primary production supports a large mussel fishery on wild stocks using bottom trawling amounting to 70 000 to 110 000 t of blue mussels *Mytilus edulis* yr^{-1} (Hoffmann 2005), although catches have been decreasing for the entire Limfjorden to around 30 000 to 40 000 t yr^{-1} in the last 5 to 6 yr (Dolmer et al. 2011). A large part of the fishery takes place in the Løgstør Broad.

Investigations were carried out during a field campaign from May 26 to June 6 2003 at 2 sites in the north-eastern part of the Løgstør Broad (Fig. 1). Based on a prior dive survey, we selected a mussel bed at approx. 6 m depth (hereafter called 'mussel site') and a nearby (approx. 900 m southeast) sand bed at approx. 5.5 m depth (hereafter called 'sandy site'). The mussel site was characterized by a patchy coverage of mussel clumps varying from a few centimeters up to several meters, with an average coverage of 27% (Ysebaert et al. 2009). The length frequency distribution showed that mainly mussels of a single cohort were present (2 yr olds), with a few individuals of an older cohort. At the mussel bed, average (\pm SE) abundance and biomass of mussels were $3911 \pm 615 \text{ ind. m}^{-2}$ and $300 \pm 89 \text{ g ash free dry weight (AFDW) m}^{-2}$, respectively. Average length of the mussels was $22.26 \pm 0.32 \text{ mm}$. At the mussel site, mussels comprised 97.4% of benthos biomass (Nielsen & Maar 2007). At the sandy site, macrobenthic biomass was much lower than at the mussel site

with an average of $41 \pm 15 \text{ g AFDW m}^{-2}$ (Ysebaert et al. 2009). No mussels were present at the sandy site, and the benthos community was composed of infauna species such as *Ensis* spp., *Venerupis senegalensis* and different species of polychaetes (Nielsen & Maar 2007). The filtration potential is in the order of 84 m d^{-1} for a mussel population of 3911 ind. m^{-2} with an average size of 22 mm (Riisgård 2001, Ysebaert et al. 2009), or $15\times$ the water column per day. The filtration capacity of *Ensis* spp. at the sandy site was estimated to be $<0.5\%$ of the mussel bed filtration and could therefore be ignored (Nielsen & Maar 2007).

A meteorological station on the island of Livø (Fig. 1) measured wind speed and direction, temperature, humidity and solar radiation. Current velocity and turbulence were measured by Acoustic Doppler Current Profilers (ADCPs) above the sand bed and the mussel bed. Surface waves were obtained from a Directional Wave Rider Buoy (Datawell), which was moored over the mussel study site to determine the period and amplitude of waves passing through the system. Conductivity, temperature and depth (CTD) profiles were collected daily over both sampling sites. For further information on measurements of physical parameters see Wiles et al. (2006).

'Siphon mimics' (Petersen et al. 2012) were installed by divers to sample water and seston in a manner similar to mussel incurrent flow. We used this method to gently sample chlorophyll *a* (chl *a*), particulate organic carbon (POC) and inorganic

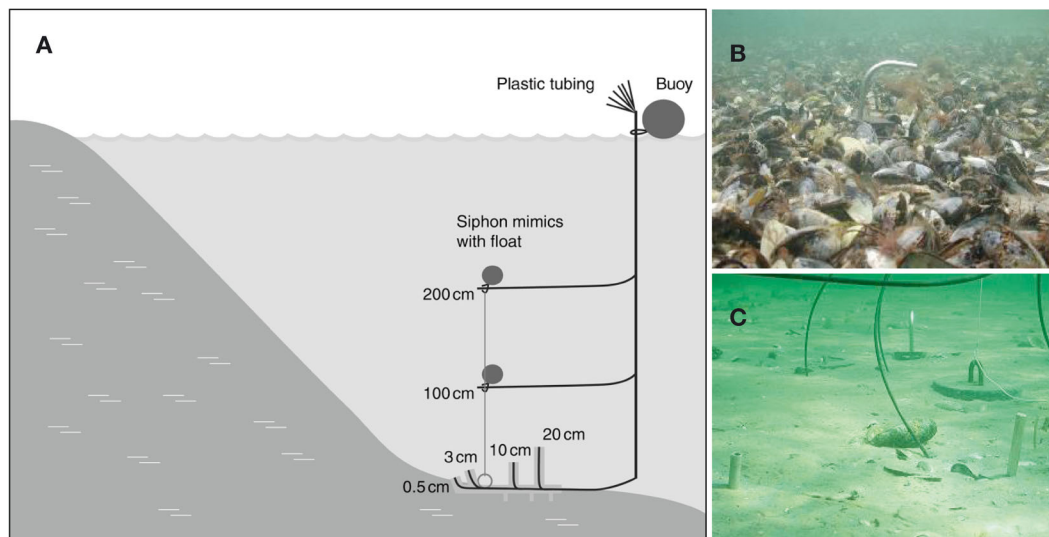


Fig. 2. (A) Siphon mimics set-up, (B) the mussel site, and (C) the sandy site. The siphon mimics near the bottom were enforced with an aluminium tube

nutrients very close to the bottom and at different heights in the water column without eroding vertical gradients. The siphon mimics consisted of small tubes by which water was pumped at rates typical for mussel filtration rates (Fig. 2). There was no excurrent flow to avoid mixing of the water. Water was sampled with a pumping rate of 150 to 180 ml min⁻¹, and sampling took place 0.5, 3, 10, 20, 100 and 200 cm above the mussel bed (not from the sediment underneath) or above the bottom at the sandy site. At the mussel site, siphon mimics were placed above a large patch of mussels. The water samples were collected in 0.5 l polyethylene bottles, and 3 replicates were taken sequentially at each depth. On 5 June, rough weather conditions prevented sampling with the siphon mimics, and samples were instead collected by divers using syringes placed in a frame at identical heights as the siphon mimics. There were 10 total sampling occasions at the mussel site and 6 sampling occasions at the sandy site due to rough weather. Subsamples on all sampling occasions were analysed for chl *a* as a measure of phytoplankton biomass and phaeopigments as an indicator of degeneration products (Strickland & Parsons 1972). In addition, 7 subsamples from the mussel site and 5 subsamples from the sandy site were analysed for suspended POC. Dissolved inorganic nutrients (NH₄ and dissolved inorganic nitrogen [DIN] = NO₃ + NO₂ + NH₄) were analysed for 5 and 3 sampling occasions from the mussel site and sandy site, respectively. For the analysis of chl *a* and phaeopigments, 100 ml of water was pre-filtered through a 100 µm screen

before being filtered through GF/C filters. Filters were extracted in ethanol and analysed on a Turner fluorometer. Fluorescence units were converted to weight of chl *a* (µg l⁻¹) by correlation with standards. The filtered water was subsequently stored frozen and later analysed for dissolved inorganic nutrients. Nutrients were determined by standard methods on a SKALAR segmented flow autoanalyzer. For analysis of POC, between 500 and 1000 ml was filtered on pre-combusted (6 h, 550°C) and pre-weighted Whatman GF/F filters. After being rinsed with Milli-Q water, the filters were dried in an oven at 70°C and stored until analysis. POC was determined using a Carlo Erba Elemental Analyzer after Cr₂O₃ and AgCo₃O₄ catalysed oxidation and segregation on a Haysep-Q-column.

Vertical profiles of seston and nutrients above benthic filter feeders often follow a logarithmic distribution with depth due to the occurrence of a concentration boundary layer that is shaped by the activity of the benthic filter feeders and hydrodynamic forcing (Frechette et al. 1989, Wildish & Kristmanson 1997, Ackerman et al. 2001). The concentration C_z of seston and inorganic nutrients at sampling depth z (log scale) in the near-bed layer can therefore be described as a linear function:

$$C_z = \alpha \ln(z) + C_0 \quad (1)$$

where C_0 is the concentration 1 m above the bed where $\ln(z) = \ln(1.0) = 0.0$ and α is the gradient. A positive gradient of a substance indicates a depletion gradient (sink) towards the bottom, whereas a nega-

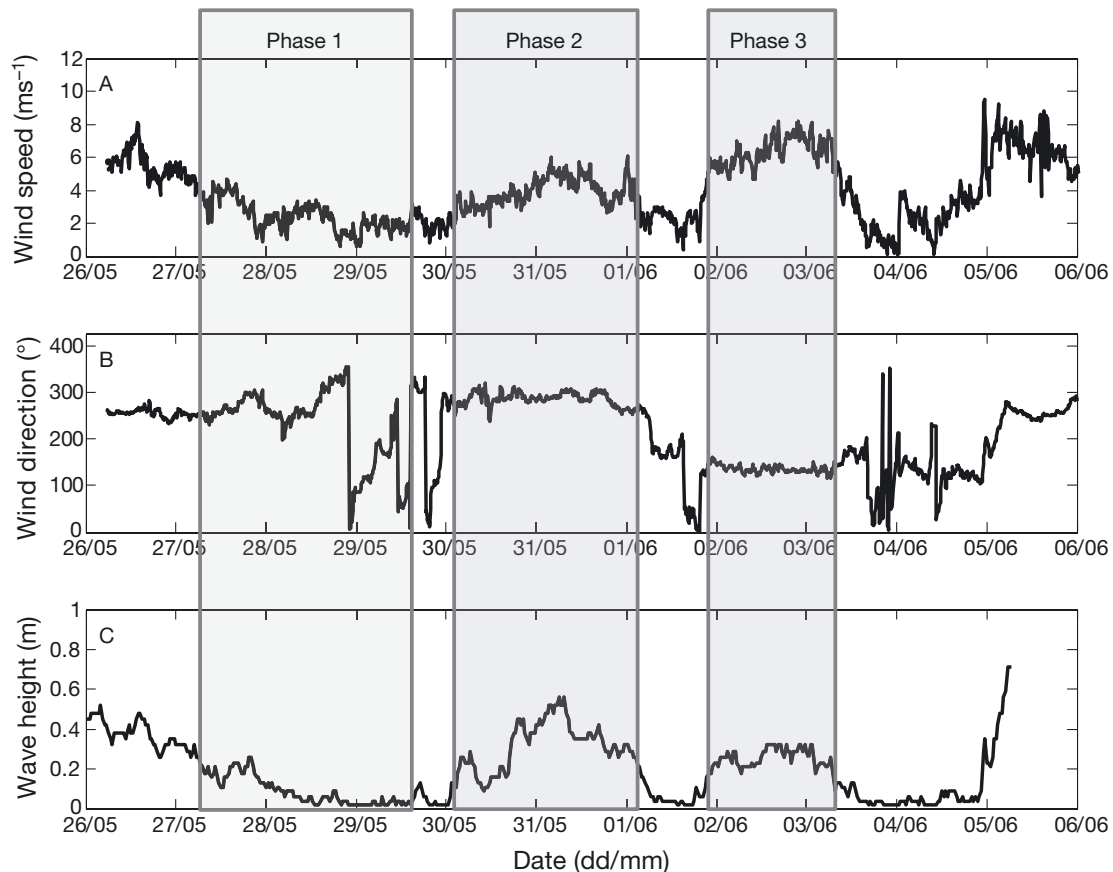


Fig. 3. Temporal patterns of (A) wind speed, (B) wind direction and (C) wave height. Data on wave height is modified from Wiles et al. (2006). The 3 phases of physical forcing are indicated

tive gradient indicates a production gradient towards the bottom. We first tested the null hypothesis that vertical concentration profiles were not significantly affected by the interactions between mussel bed filtration (depth as the covariate) and physical forcing on the different sampling days (days as factor). This was done using 2-way crossed ANOVA (Matlab v. 2010b). If gradients were different between days due to the interactions between hydrodynamics and mussel filtration (i.e. interaction term = day \times depth), then a post hoc multiple comparison test (Tukey-Kramer) was conducted by Matlab (Type 1 error of 0.05). If gradients were not different between days (i.e. no interaction), we tested the null hypothesis that vertical profiles were not significantly affected by mussel bed filtration. The interaction term was removed and the test repeated for the overall gradient and intercept. Simultaneously taken samples at the different depths were be considered a single 'profile' where values are likely more correlated to one another than for randomly taken samples. Such grouping was not taken into account when consider-

ing the 3 samples for a depth as independent replicates. We tested for this possible bias by comparing the 2-way crossed ANOVA with a 3-level nested ANOVA, where 'profile' was nested within 'day', and 'day' was crossed with 'depth'. In all cases the factor 'profile' was very insignificant ($p > 0.6$). We therefore decided to pool it with the overall error and present the results of the factorial ANOVA. The relation between gradients and wave height was tested with linear correlation coefficients.

RESULTS

Meteorological conditions varied greatly during the campaign period, ranging from light winds to almost no wind in the middle of the period to strong winds from southeast shifting to south and west by the end of the period (Fig. 3). The wind speed could be correlated to wave height, but the relation was not straightforward due to differences in wind direction and thus fetch. Three periods with different forcing

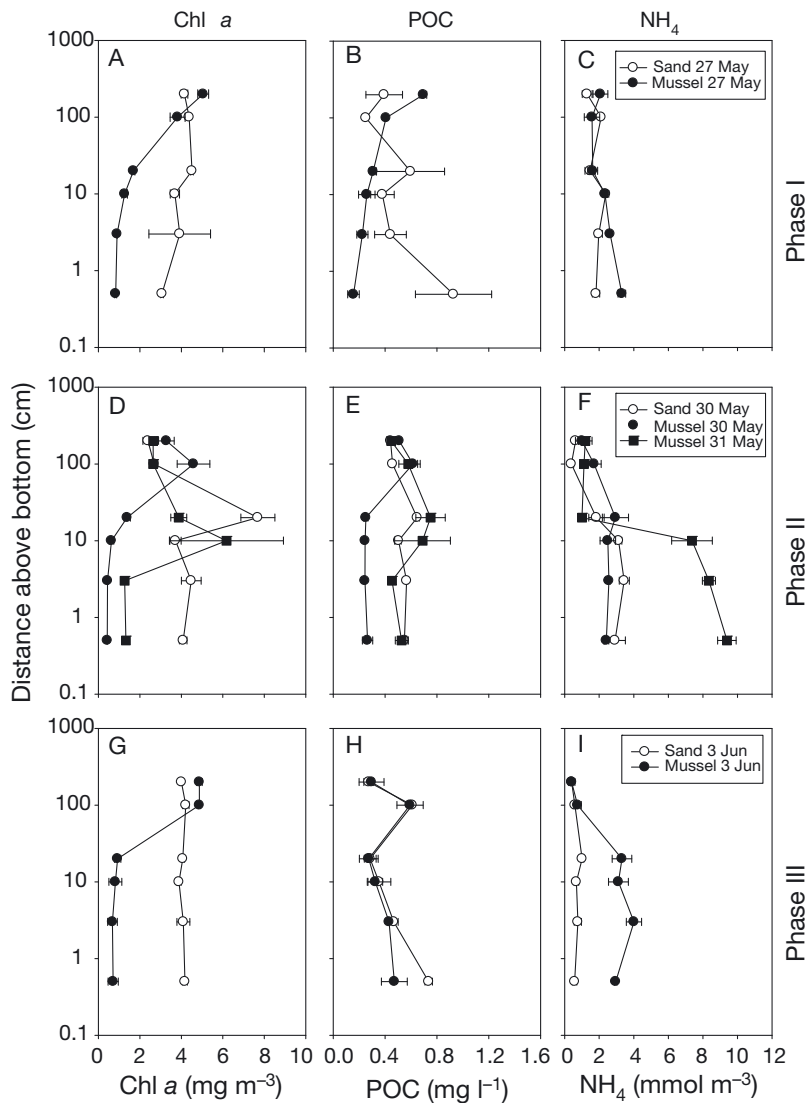


Fig. 4. Vertical profiles of chlorophyll *a*, particulate organic carbon (POC) and NH₄ (average \pm SD) above the mussel bed site and the sandy site during (A–C) Phase 1 with stratification of the water column (low wind, small waves), (D–F) Phase 2 with medium wind conditions but high waves, and (G–I) Phase 3 with strong wind conditions but medium waves

could be identified during the campaign period. Phase 1 had low wind speeds and small waves, Phase 2 comprised medium wind speeds and high waves, and Phase 3 had high wind speeds and moderate waves (Fig. 3).

During the campaign period there was a general trend for warming of the water and a more or less simultaneous increase in salinity (Wiles et al. 2006) leading to approximately constant density. A shift in stratification from stratified to mixed waters coincided with the change in physical forcing. During Phase 1, with little wind and small waves, the water

column was stratified with the pycnocline situated around 2 m above the bottom, whereas there was no stratification during Phases 2 and 3 (higher waves and higher wind speeds). In intermediate periods, a pycnocline appeared to be building up from the bottom. The velocity components, as observed by the ADCPs, varied substantially from close to zero and up to 0.2 m s⁻¹ depending on whether the water column was mixed or not (Wiles et al. 2006). However, velocities close to the bed were always extremely low at both sites, ranging around 0.01 m s⁻¹ and too low to generate significant turbulence from bottom shear (Wiles et al. 2006). It can be concluded that during the campaign period, mixing was primarily generated by wind and wave action, and stratification by solar heating (Wiles et al. 2006).

In Fig. 4, vertical profiles of chl *a*, POC and NH₄ from the siphon mimics over the 2 sampling sites are shown for the 3 phases of physical forcing. NH₄ constituted in all cases the major part of the DIN pool. During Phase 1 (stratification and low wind and waves), there was a decrease in particulate suspended matter, noticeably chl *a* and POC, and an increase in NH₄ towards the mussel bed (Fig. 4a–c). In contrast, there was no gradient over the sand bottom for chl *a* or NH₄ (except for POC, which increased towards the bottom). During Phase 2 (medium winds but strong waves), there was a strong mixing of the water column. Over the mussel bed, there was still a decrease towards the bed in chl *a* and POC, but this depletion only occurred in the layer very near to the bed (<20 cm) (Fig. 4d,e). A strong increase in NH₄ was observed above the mussel site especially on 31 May, but also above the sandy site on 30 May (Fig. 4f). Phase 3 represents conditions with the strongest winds, but medium waves (3 June). Again, less steep gradients were observed for chl *a* and POC, but depletion was still noticeable in the lower water layer, whereas an increase in NH₄ was observed

could be identified during the campaign period. Phase 1 had low wind speeds and small waves, Phase 2 comprised medium wind speeds and high waves, and Phase 3 had high wind speeds and moderate waves (Fig. 3).

Table 1. ANOVA results of differences in gradients between sampling days and with depth above the bottom for chlorophyll *a*, particulate organic carbon (POC) and NH_4 . The *p*-values below the Type 1 error threshold (0.05) are indicated in **bold**. For post hoc results see Fig. 5

	Mussel site			Sandy site		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Chl <i>a</i>						
Depth × Day	9	1.26	0.291	5	6.29	7×10^{-4}
Depth	1	50.53	2×10^{-9}	–	–	–
Day	9	1.34	0.239	–	–	–
POC						
Depth × Day	6	3.31	0.014	4	3.20	0.035
NH_4						
Depth × Day	4	7.79	6×10^{-4}	2	6.68	0.011

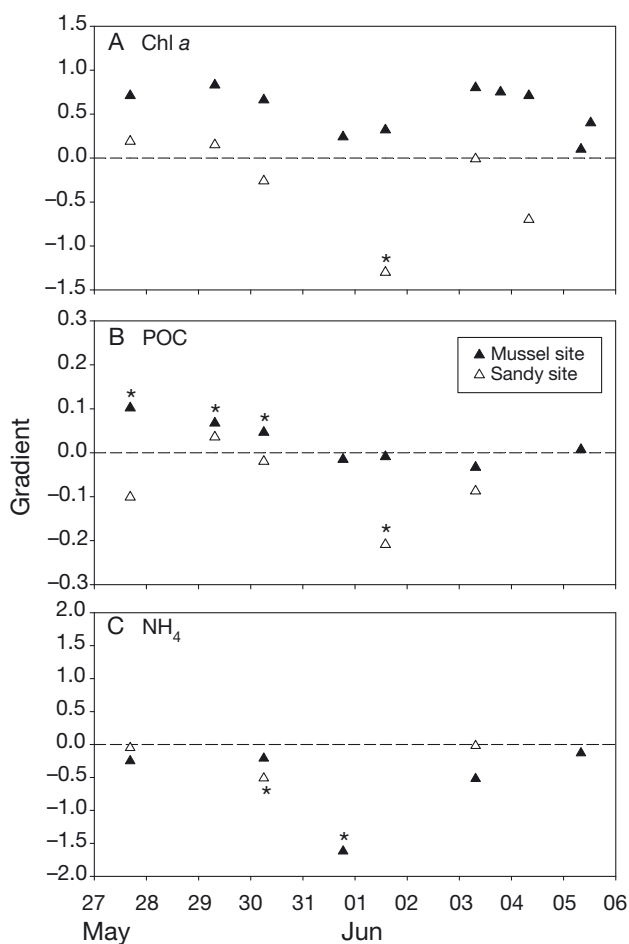


Fig. 5. The estimated gradients from Eq. (1) of (A) chlorophyll *a*, (B) particulate organic carbon (POC), and (C) NH_4 in the near-bed layer at the mussel site and the sandy site. Days that are significantly different from at least one of the other days at the same site are indicated with an asterisk ($p < 0.05$). See also Table 1 for more statistical results

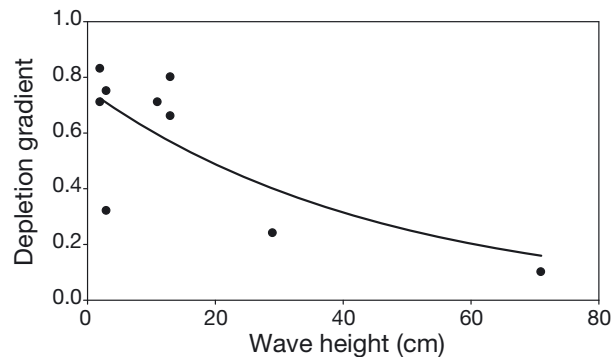


Fig. 6. Correlation between wave height and depletion gradients of chlorophyll *a* at the mussel site. $R^2 = 0.76$, $n = 9$, $p = 0.022$

above the mussel site (Fig. 4g-i). Above the sandy site, there was no pattern with depth for NH_4 and chl *a*, whereas POC increased slightly towards the bottom. The statistical results (Table 1) showed a significant trend for chl *a* × depth (sink due to mussel filtration) and thus a depletion gradient on all days, despite different hydrodynamic conditions (Fig. 5). For POC and NH_4 at the mussel site, there was a significant effect of mussel bed filtration and hydrodynamics on vertical gradients with the highest values on 27 to 30 May (Phase 1, POC) and 31 May (Phase 2, NH_4). At the sandy site, there were significant effects on gradients of chl *a*, POC and NH_4 between days with the highest gradients on 30 May (NH_4) and 1 June (chl *a*, POC).

The depletion gradient of chl *a* concentrations correlated significantly with wave height ($p = 0.022$, Fig. 6) but not with wind speed (average of 3 h preceding sampling). No significant relation was found between NH_4 and POC gradients and wind or wave forcing. The ratio of chl *a* to phaeopigments increased with increasing distance from the bottom (Fig. 7), indicating a higher proportion of degradation products near the bottom.

DISCUSSION

This study clearly demonstrates the presence of a chl *a* and particle depleted benthic near-bed boundary layer above a dense bed of mussels in a semi-enclosed, micro-tidal sound. The use of siphon mimics makes it possible to measure simultaneously near-bed depletion profiles from just a few cm (0.5 to 20 cm) up to 200 cm above the mussels without disturbing the concentration profiles, as opposed to conventional water sampling with bottles (Jonsson et al.

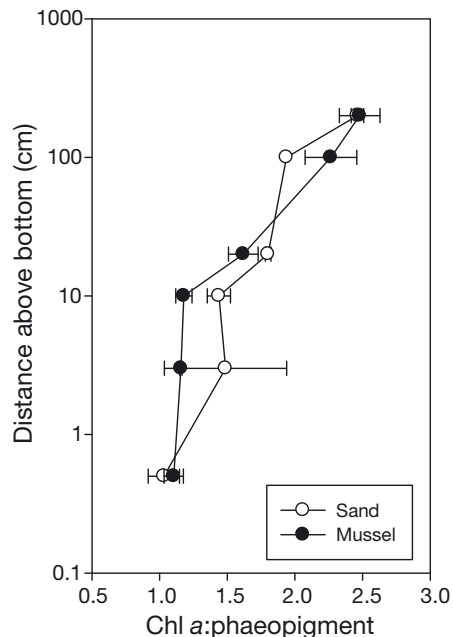


Fig. 7. Vertical profiles of chlorophyll *a*:phaeopigment (average \pm SD) above the mussel bed and the sandy site on 27 May during Phase 1 stratification of the water column (low waves, low wind)

2005, Nielsen & Maar 2007, Petersen et al. 2008). For chl *a*, a significant impact of mussel filtration on vertical gradients was observed for all days despite the varying physical conditions (Table 1, Fig. 5). However, the degree of depletion decreased with increasing wave height (Fig. 6) because higher mixing during conditions with high waves compressed the bottom depletion layer (Fig. 4). For POC, we observed depletion only during periods of low wind and small waves. On days with more mixing, the re-suspension of organic matter probably counteracts the removal by mussel filtration. At the sandy site, vertical gradients were only visible at the highest mixing event (Phase 2) that caused a significant production of chl *a* and POC near the sediment probably due to re-suspension (Fig. 5).

Depletion by benthic suspension-feeders has previously been demonstrated in micro-tidal areas (Riisgård et al. 1998, Dolmer 2000, Nielsen & Maar 2007, Petersen et al. 2012). In this study, we do not only demonstrate this phenomenon, but also show that it is temporally variable and closely linked to the physical structure of the water column. The very low values of the turbulent mixing coefficient, however, make it extremely difficult to measure. ADCPs were not successful at estimating turbulent mixing, which remained under the noise level of the system (Wiles

et al. 2006). However, we can estimate an order of magnitude for the turbulent mixing by assuming that within the range of our measurements, turbulent diffusivity K ($\text{m}^2 \text{s}^{-1}$) is proportional to height above the bed. Moreover, by assuming that within the lowermost water layers production of particles is limited and that sinking of particles is negligible, all particles would be mixed in from above and the vertical flux of particles would be constant over the depth range considered. Thus, at steady state,

$$K \frac{dc}{dz} = \kappa u_* z \frac{dc}{dz} = Q \quad (2)$$

where Q ($\text{mg m}^{-2} \text{s}^{-1}$) is the filtration flux by the mussels, $\kappa = 0.4$ is the von Karman constant, u_* (m s^{-1}) is the friction velocity and z (m) is the water depth. Q can be approximated as $C_1 \times F$, where C_1 (mg m^{-3}) is the concentration at the depth z_1 where mussels filter, and F is the filtration velocity (m s^{-1}). We then have for the concentration profile:

$$C_z = C_1 \left(1 + F \times \ln \left(\frac{z}{z_1} \right) \times \frac{1}{\kappa u_*} \right) \quad (3)$$

The filtration velocity (m s^{-1}) for the concentration profile can then be estimated from:

$$F = \frac{(C_2 - C_1) \kappa u_*}{C_1 \ln \left(\frac{z_2}{z_1} \right)} \quad (4)$$

where the approximated concentrations $C_2 = 5.0 \text{ mg chl } a \text{ m}^{-3}$ at $z_2 = 2 \text{ m}$ and $C_1 = 0.8 \text{ mg chl } a \text{ m}^{-3}$ at $z_1 = 0.005 \text{ m}$ for calm periods. Turbulence in the water column was modelled for a relatively calm campaign day (28 May) with stratification (Phase 1) and the diffusivity K was estimated to be in the order of $2 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ at a height of 1 m above the bottom (Maar et al. 2007). With these values, we would estimate F to be in the order of 15 m d^{-1} , which corresponds to a clearance rate of $0.004 \text{ m}^3 \text{ ind.}^{-1} \text{ d}^{-1}$ using the above estimated mussel density. This estimate is lower than the theoretical value of $0.021 \text{ m}^3 \text{ ind.}^{-1} \text{ d}^{-1}$ (Riisgård 2001), but our estimate also takes re-filtration into account as it is an integrated measure of bed consumption. In an environment with low levels of water exchange and relatively low levels of ambient concentrations of chl *a*, it is reasonable to assume that around 20% of the filtration potential is realized. In another micro-tidal area, the Kertinge Nor, the realized filtration rate of ascidians was around 50% due to incomplete mixing (Petersen et al. 2012). However, the site in Petersen et al. (2012) is shallower than Løgstør Broad and thus would have better mixing conditions. The estimated total filtration rate by the

mussels using C_1 would amount to $360 \text{ mg C m}^{-2} \text{ d}^{-1}$, which is about twice the measured primary production of $160 \text{ mg C m}^{-2} \text{ d}^{-1}$ estimated on that day (I. G. Teixeira et al. unpubl. data). However, during calm, stratified conditions, mussel filtration is uncoupled from the upper productive layer, a bottom depletion layer is developed and the filtration potential is not fully exploited.

In periods of heavier waves, the POC and chl *a* profiles corresponded less to the model shown in Eq. (3), with concentrations decreasing towards the bed only in the very near-bottom layers. We infer from this observation that turbulent diffusivities very close to the mussel bed are not substantially affected by waves, but that slightly above the bed (between a few cm and 10 cm), a considerable increase in vertical diffusivities would be caused by the wave orbital motions. Wiles et al. (2006) also concluded that mixing is not directly produced by the currents above the bed—and thus not by current shear caused by the orbital motions—but rather as turbulence injected into the water column by the waves. Heterogeneous bottom roughness due to the presence of mussels was also considered unlikely to have significant effect on the food supply to mussels due to the low current velocities (Wiles et al. 2006). Probably during these periods of heavy waves, the near-bed layer is much compressed and turbulent diffusivity only increased linearly with distance from the bed over a much smaller height range.

In general, the profiles of NH_4 and chl *a* mirrored each other above the mussel site, which can be expected since the mussel bed is a source of NH_4 due to excretion and a sink of particles due to filtration. Using the same model as above for chl *a*, one can estimate that a concentration difference of $1.5 \text{ mmol N m}^{-3}$ between bottom and 2 m (Fig. 4c) would correspond to an NH_4 flux of around $7.6 \text{ mmol N m}^{-2} \text{ d}^{-1}$. This seems in reasonable stoichiometric equilibrium with a daily influx of around $30.7 \text{ mmol C m}^{-2}$ (C:N ratio = 5.1) although the N flux would be slightly too high. The profile of NH_4 during the windiest day that sampling was still possible (31 May) deviates strongly from expectations (Fig. 4f, Table 1) based on the profile of particles and chl *a*. Here, the concentration differences were much larger, and this is unexpected since the mixing coefficients are most probably higher on these days, which would lead to a less pronounced concentration gradient. Most probably this strong gradient is caused by an enhanced flux out of the sediment during the wavy period. Mechanisms for ‘wave pumping’ of interstitial water have been described in models (Boudreau 1997) and have

also been observed in the field. The magnitude of this effect depends on wave characteristics and on hydraulic conductivity of the sediment. It is not very likely that the relatively fine material in the Limfjorden sediment has a high hydraulic conductivity. However, the spaces in between the mussels, which in calm conditions contain fine fluffy material derived from degraded phytoplankton according to the relative content of phaeopigments close to the bottom (Fig. 7), could represent an important pool of nutrients that could easily be mobilized by wave action.

In conclusion, this study shows that there is a significant impact of mussel filtration on vertical gradients of chl *a*, POC and NH_4 in a micro-tidal area. Furthermore, the near-bed concentrations of seston and nutrients are temporally variable and closely linked to the physical structure of the water column. During conditions with high waves, the bottom depletion layer of chl *a* and POC was compressed and the vertical gradients above the mussel bed are less steep in comparison with calm conditions. On the contrary, for NH_4 , there was a strong vertical gradient caused by an enhanced flux out of the sediment during the wavy period. During the stratified period with low waves, it is estimated that around 20% of the filtration potential was realized due to the low levels of water exchange near the mussel bed and low ambient chl *a* concentrations. Thus, the transport processes of food and nutrients between the mussel bed and the water column are governed by water column mixing events influencing the near-bed dynamics.

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