Vol. 339: 185–198, 2007 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published June 6

Effects of a blue mussel *Mytilus edulis* bed on vertical distribution and composition of the pelagic food web

Torkel Gissel Nielsen[1,*], Marie Maar[1,2,]**

[1]**The National Environmental Research Institute, Department of Marine Ecology, Frederiksborgvej 399, PO Box 358, 4000 Roskilde, Denmark**

[2]**Bolding & Burchard Hydrodynamics, Strandgyden 25, 5466 Asperup, Denmark**

ABSTRACT: The impact of a mussel bed on the neighbouring pelagic food web is investigated by a comparative study of the vertical distribution of plankton above a mussel bed with that above a bare sandy bottom. The use of conventional water bottles did not reflect the near-bed dynamics. However, use of a high-resolution water sampler in the bottom 1 m of the water column above the sea floor revealed statistically significant differences. The results document for the first time *in situ* grazing on all major components of the pelagic food web. The vertical distributions of phytoplankton, bacteria, protozoa, meroplankton and copepods were statistically significantly different above the mussel and sand beds. The mussel bed recycled nutrients back to the water column as waste products. The present investigation stresses the need for a more diverse view of the trophic role of suspension-feeding bivalves in shallow coastal ecosystems.

KEY WORDS: *Mytilus edulis* · Bentho–pelagic coupling · Bacteria · Phytoplankton · Zooplankton

INTRODUCTION

Dense populations of benthic suspension feeders play a key role in coastal ecosystems, where their large grazing potential strongly influences the plankton community through depletion of phytoplankton and detritus above the sea bed (Loo & Rosenberg 1989, Petersen & Riisgaard 1992), forcing phytoplankton succession towards small, fast-growing species (Riemann et al. 1988, Noren et al. 1999). At the same time, bivalve populations fertilise the phytoplankton community by excreting nutrients (Jordan & Valiela 1982).

Traditionally, research on suspension feeders assumes that phytoplankton are the main source of nutrition. Knowledge about the prey size spectra of bivalves is primarily available for a small size range of about 4 to 10 µm, and it is reported that particles >4 µm are completely filtered by *Mytilus edulis* (Møhlenberg & Riisgaard 1978). Knowledge about the upper prey size limit of the prey size is based on stomach content analysis (Davenport et al. 2000) and grazing experiments with mesozooplankton or large detritus particles offered as food (Davenport et al. 2000, Karlsson et al. 2003). Recently, Davenport et al. (2000) reported that the upper size limit for prey of *M. edulis* was above 1000 µm, stressing the need for consideration of mesozooplankton as potential prey for this species. So far, little attention has been given to *in situ* effects of mussel populations on the structure and composition of the pelagic food web, including the heterotrophic components. However, all heterotrophic plankton organisms often comprise a significant fraction of the total plankton biomass (Andersen & Sørensen 1986) and consequently to the potential food for suspension-feeding bivalves. Additionally, by using zooplankton as a food source, mussels also remove these competitors for phytoplankton prey. The ecological implications of this link have not so far been investigated.

*Email: tgn@dmu.dk
**Present address: Roskilde

The functional triangle between mussel grazing, phytoplankton and zooplankton has hitherto received little attention, but knowledge thereof is crucial to understanding planktonic community structure and the fate of coastal primary production. In the present paper, the effects of the suspension-feeding *Mytilus edulis* on the pelagic food web are investigated *in situ* by comparison of the plankton community above a mussel bed with that above a bare sand bed. Companion paper (Maar et al. 2007, this volume) investigates the observed functional triangle forced by turbulence and elucidates it using a dynamic model.

MATERIALS AND METHODS

Sampling. The study site was the shallow Limfjord located in northern Denmark (micro-tidal amplitude 0.1 to 0.2 m) (Fig. 1). The fjord is connected with the North Sea on the west coast and the Kattegat on the east coast. The fjord is eutrophic and supports a high biomass of benthic suspension feeders; the mussel fishery is primarily based on a wild population of blue mussels *Mytilus edulis* L. (Kristensen & Hoffmann 2004). Sampling took place on a sand bottom and a blue mussel bed at Løgstør Bredning (Fig. 1) from 26 May to 5 June 2003. The distance between the 2 sites was 950 m and the water column depth was 5.5 m at the sandy site and 6.0 m at the mussel site.

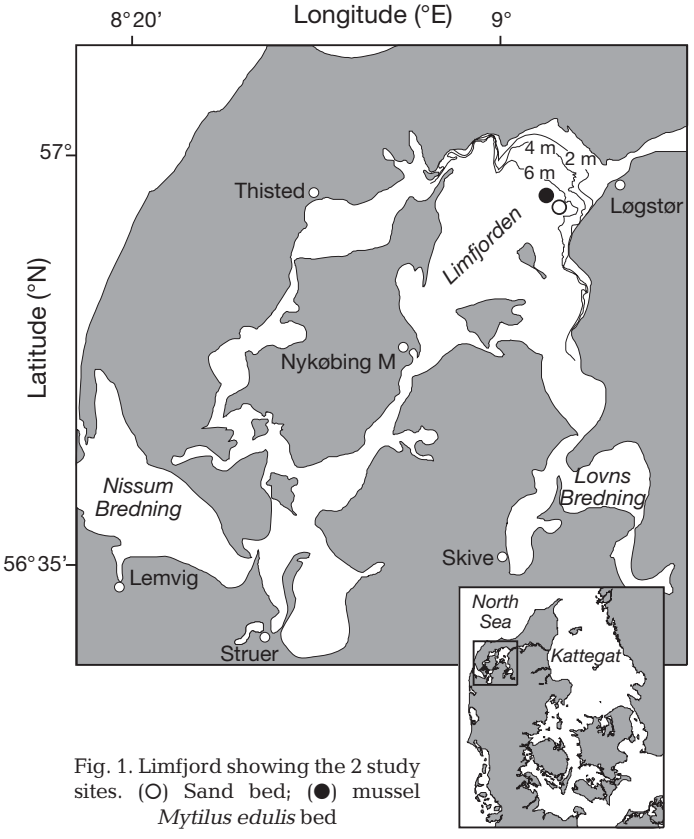

Fig. 1. Limfjord showing the 2 study sites. (○) Sand bed; (●) mussel *Mytilus edulis* bed

Vertical profiles of temperature, salinity and fluorescence were recorded using a CTD (GMI AROP2000) equipped with an *in situ* fluorometer (Type Q300 No. 18, Copenhagen) immediately before and after biological sampling from RV 'Genetica II', (University of Aarhus) anchored to the study sites. Vertical profiles of flow velocity were measured every 13 min by two 1200 kHz RDI $ADCPs_{up}$ (acoustic doppler current profiler, RDI, configured to 'look upward' through the water column above the beds). The ADCPs were provided by the University of Wales, Bangor, UK and measured water currents in 0.30 m bins and covered the water column from 1.66 m (sand bed) and from 0.56 or 0.86 m (mussel bed) above bottom to the surface. It was not possible to determine turbulent parameters with the ADCPs using the variance method, due to the low energy levels during the study period (Wiles et al. 2006). For more detailed information about the physics in the Limfjord during the investigation period see Wiles et al. (2006).

Biological parameters were sampled on 27, 28, 29 May and 1 and 4 June from 9:00 to 11:00 h local time at the centre of each site. Water sampling was on 2 scales: (1) a metre-scale using 30 l Niskin water bottles 1 m (near-bottom), 3 m (middle) and 5 m (surface) above the bottom, and (2) a decimetre scale by a high-resolution sampler, HRS (Fig. 2) standing on the sea floor and overlapping the deepest Niskin bottle depth. The HRS sampler consists of eight 1.5 l polycarbonate syringes (Linatex) mounted at 0.19 m intervals on a metal frame, and syringes from 0.14 to 1.47 m above the sea floor with a total height of 1.8 m. The plungers of the syringes are mounted on a central wire that is connected to a release system in the top of the sampler. When the HRS is loaded, the syringes are empty and a Volvo spring is kept in position by a trigger. Dropping a messenger along the wire releases the trigger and the syringes are simultaneously and instantaneously filled. Prior to release, the HRS was inspected and adjusted by divers to ensure that the sampler was correctly positioned, that the mussels were filtering, and that the syringes were pointing towards the current. Current patterns were allowed to stabilise before release of the trigger and the HRS was immediately retrieved, drained and sampled for the variables described below.

Variables measured. ***Nutrients*:** Samples for the determination of nutrient concentrations (PO_4^{3-}, NO_3^-, NH_4, SiO_4^{3-}) were frozen onboard the ship. Measurements were carried out later at the National Environmental Research Institute (NERI) on an automatic nutrient analyser (Dansk Havteknik) following Grasshoff (1976). All nutrient samples were analysed in duplicate with a precision of 0.06, 0.1, 0.3, and 0.2 µmol l^{-1} for phosphorus, nitrate, ammonia and silicate, respectively.

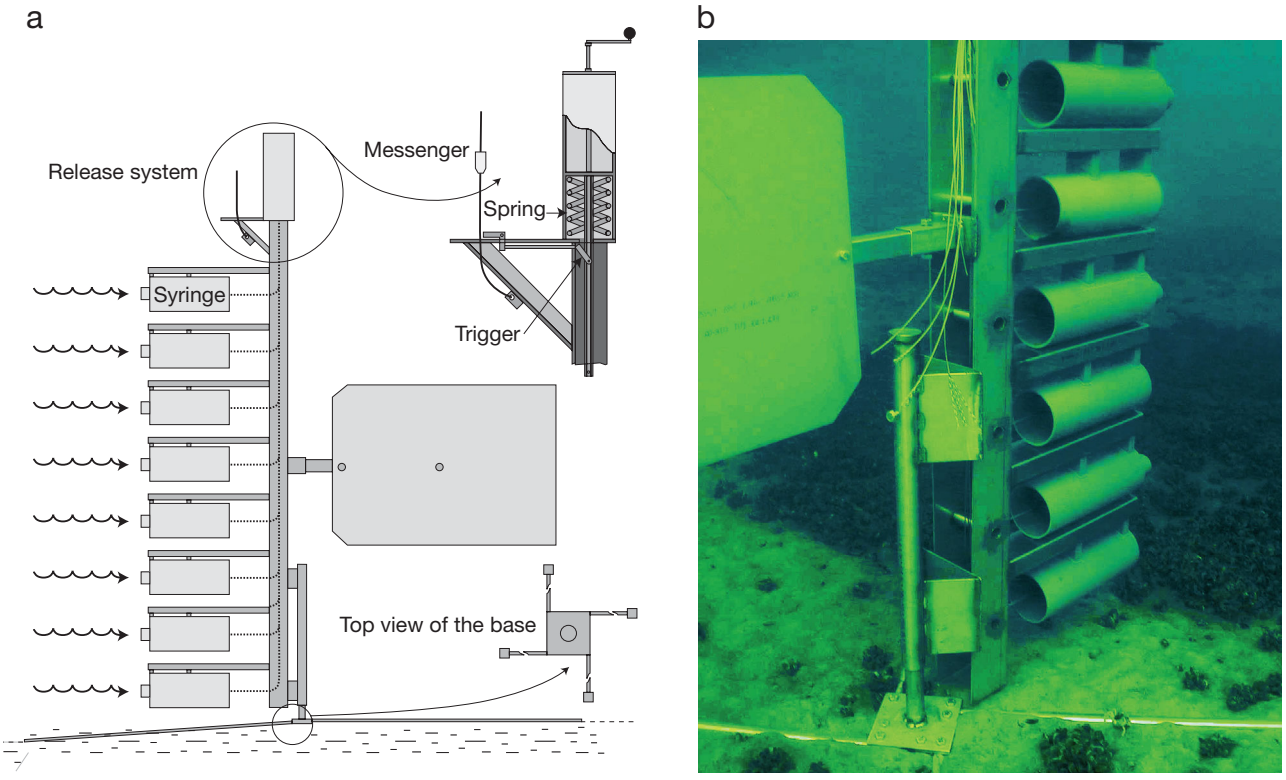

Fig. 2. High-resolution sampler (HRS) in sampling position on sea bed. Photograph by J. Larsen

***Chlorophyll a* (chl *a*):** Three replicates of 50 ml each were filtered onto GF/F filters. Chl *a* was extracted overnight in 5 ml 96% ethanol in the dark and measured before and after acid addition on a Turner Designs Model 700 fluorometer (Yentsch & Menzel 1963).

***Bacterial abundance*:** For quantification of bacteria, 10 ml samples from each depth were preserved with 1 ml formalin in 20 ml glass vials and stored cold until processing. The bacteria were enumerated on a FACS Calibur flow cytometer (Becton Dickinson) after staining of fixed cells with the nucleic acid stain SYBR Green 1 (Molecular Probes) according to Marie et al. (1997). A 1 ml sample was added to 10 µl of a 100× dilution of stock SYBR Green 1, and 10 µl of a suspension of 2 µm fluorescent beads (Polyscience). The number of cells was converted to biomass (µg C l^{-1}) applying 20 fg C $cell^{-1}$ (Lee & Fuhrman 1987).

Bacterial production: This was measured from incorporation of ^{3}H-thymidine (Fuhrman & Azam 1982). Four replicates of 10 ml unfiltered seawater from each sampling depth were sampled in 20 ml plastic vials and incubated with ^{3}H-thymidine for 2 h; one of the 4 replicates was a 10 ml control sample pre-killed with 500 µl trichloroacid (TCA), 100%. The samples were filtered on 0.2 µm cellulose-nitrate filters and washed 10 times with ice-cold TCA (5%). The filters were transported and stored frozen in 20 ml plastic vials before addition of 10 ml Filtercount and processed on an automatic scintillation counter. The incorporated thymidine volume was converted to cell production (µg C l^{-1} h^{-1}) by the factor 1.1×10^{18} cells mol^{-1} ^{3}H incorporated according to Riemann et al. (1987).

Protozooplankton abundance and species composition: We preserved 100 ml seawater with acidified Lugol's solution (2% final concentration). The samples were allowed to settle for 24 h in 10 or 50 ml chambers before counting the protozooplankton under an inverted microscope at 200× magnification. The identification of species or morphological types was based on Nielsen & Hansen (1999).

***Zooplankton* >45 µm:** We fixed 600 ml of sample in 2% buffered formalin (final concentration). In the laboratory, the zooplankters were counted, identified and their length measured.

Benthic community: Abundances and size composition of blue mussel and other benthic species (>0.1 cm) were quantified from bottom samples taken with a 'HAPS' (a small box-corer taking cores with a diameter of 10 cm (Kanneworff & Nicolaisen 1973)); 25 such cores were taken randomly at each site and additional video surveys were used to estimate mussel coverage (Ysebaert pers. comm.).

Statistics. Differences in the mean values of nutrients, chl *a*, phaeopigments, bacterial abundance and

production and zooplankton abundances between the sand and mussel beds were tested by each sampling method using pooled data from all 5 sampling days (see Tables 2 & 3). The Niskin bottle samples were tested for each measured parameter by 2-way ANOVAs with depths (1, 3 and 5 m above bottom) and bed type as fixed factors. At a decimetre scale, we assumed that the effects of mussel filtration on the measured parameters would emerge either as differences in slopes with depth or in means above the sand and mussel beds. Vertical distributions of these parameters sampled by the HRS <1 m above the bottom were empirically tested against the general model $C = \alpha \ln(z) + C_0$, where C is the concentration or abundance of the relevant parameter at Depth z, α is the slope, and C_0 is the concentration at the bottom ($z = 0$). These parameters were tested for significant differences in slopes (i.e. interaction term of depth × bed type) between the sand bed and the mussel bed by ANCOVAs using ln (z) as the covariate. If the interaction term was not significant (i.e. the slopes were parallel) the test was repeated for means without the interaction term. To obtain more detailed information on the parameters at a decimetre scale in the lower 1 m of the water column, the HRS samples were further tested for differences in means and slopes between the sand and mussel beds as described above, but for each separate sampling day (see Tables 4 & 5).

Finally, the sampling efficiency of zooplankton by the 2 sampling devices was tested by comparing all zooplankton abundances measured at 1.09 m (HRS) and 1 m (Niskin) above the beds by a 1-way MANOVA for each site. All statistics were conducted assuming a Type I error of 5% and using SPSS (Version 11.5) for Windows.

RESULTS

Physical properties

The sampling period was generally calm, and winds were only consistently higher than 5 m s^{-1} on 26 to 28 May and 2 to 3 June, while on 31 May to 1 June there was moderate wind but with a relatively large fetch (Wiles et al. 2006). There was a gradual increase in temperature during the sampling period due to solar heating, resulting in a sea surface temperature of 17°C on 4 June (Figs. 3a & 4a). Salinity increased concurrently (Figs. 3b & 4b) and the effects of temperature and salinity counteracted each other so that the density of the water remained approximately constant over the period (Figs. 3c & 4c). The water column was stratified over the period except on 31 May and 3 June, when the water column was mixed by wind-driven wave

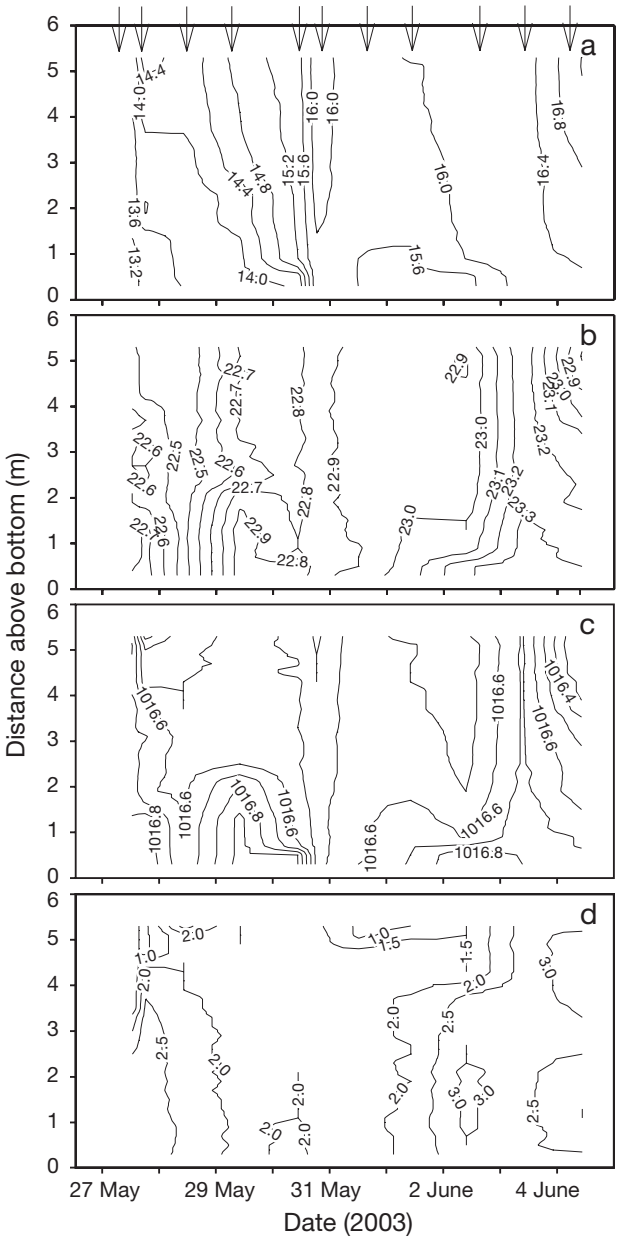

Fig. 3. Water column properties from CTD casts above sand bed showing (a) temperature (°C), (b) salinity (psu), (c) density (kg m^{-3}), (d) fluorescence (arbitrary units). Arrows (top abscissa) indicate samplings

motion (Wiles et al. 2006). On 29 May, a cold high-salinity patch was observed close to the bottom. The depth distribution of chl *a* fluorescence decreased towards the mussel bed on 27 and 28 May, but this pattern was not consistent with that observed on the other sampling days (Figs. 3d & 4d). Above the sand bed, chl *a* fluorescence levels were generally higher in the lowest 3 m of the water column, except on 31 May (total mixing) and 4 June, when there was a bloom at the surface. Mean (±SD) flow velocities were weak,

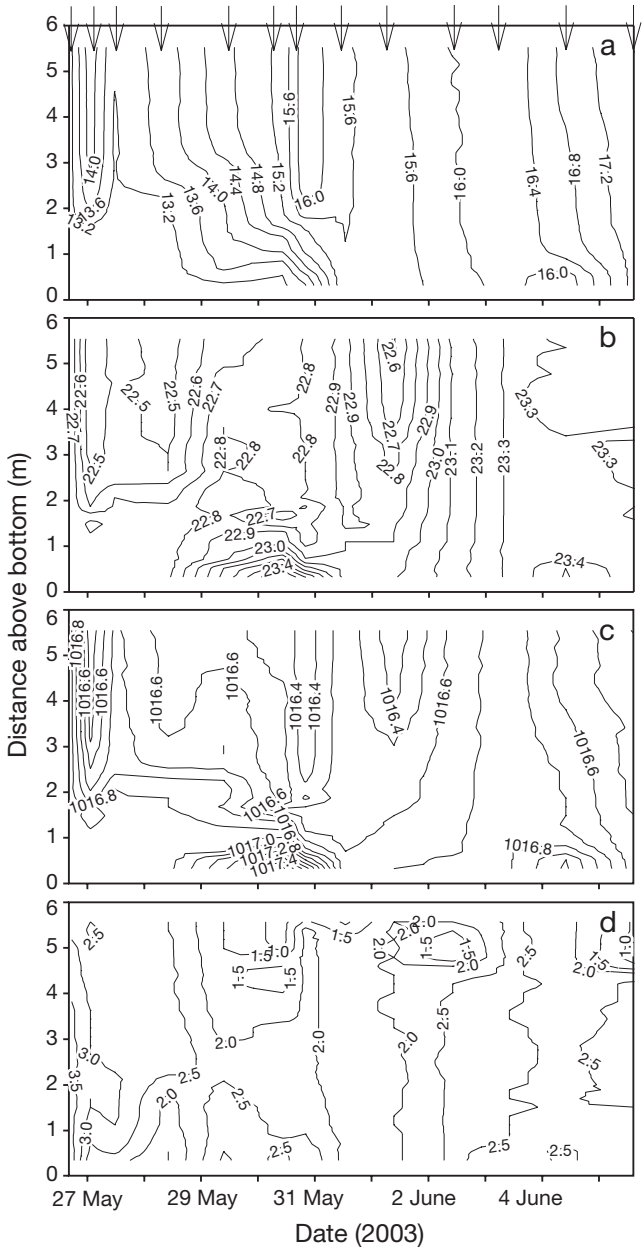

Fig. 4. Water column properties from CTD casts above mussel bed showing (a) temperature (°C), (b) salinity (psu), (c) density (kg m^{-3}), (d) fluorescence (arbitrary units). Arrows (top abscissa) indicate samplings

0.05 ± 0.1 m s^{-1} 1.66 m above the sand bed and 0.04 ± 0.1 m s^{-1} 0.86 m above the mussel bed (Fig. 5). When the water column was stratified, the flow frequently exhibited a 2-layer structure with opposing flows in surface and near-bed layers (Wiles et al. 2006). The general direction of water currents near the beds was N to NW from the sand bed towards the mussel bed on 28, 29 May and 1 June, while on 27 May and 4 June the flow direction was southerly during sampling (Fig. 5). There was a statistically significantly higher chl *a* concentration above the sand bed on 4 June than on the other days (ANCOVA, $F_{1, 4, 15}$, $p < 0.05$), indicating that chl *a* was not depleted by upstream mussels even though the flow direction was southerly. Chl *a* concentrations in the low-salinity patch on 29 May tended to be lower than for the other days, but this was not statistically significant (ANCOVA, $F_{1, 4, 15}$, $p > 0.05$).

Benthic community

As expected, a pronounced difference was observed between the benthic communities of the 2 sites (Table 1). Blue mussels *Mytilus edulis* totally dominated the mussel site with an average abundance and biomass of 3911 ind. m^{-2} and 300 g ash-free dry wt (AFDW) m^{-2}, respectively; on average they covered 27 % of the sea bed. The size range of the blue mussel population was 0.2 to 5.8 cm shell length with an average (± SD) of 2.2 ± 0.9 cm and a median of 23 cm. Area-specific population filtration capacity F_{pop} was 94 m^3 m^{-2} d^{-1} using a clearance of 1.0 l h^{-1} ind.$^{-1}$ (Kiørboe & Møhlenberg 1981) with linear temperature correction (Riisgaard & Seerup 2003). At the sandy site, the benthic biomass was 1 order of magnitude lower, since no blue mussels were present and the benthic community was composed of infauna spp. such as *Ensis* spp., *Venerupis senegalensis* and different species of polychaetes. For *Ensis* spp., F_{pop} = 0.4 m^3 m^{-2} d^{-1} was calculated from Shumway et al. (1985) using a dry-weight to AFDW ratio of 2 and a scaling exponent of 0.66. This corresponds to less than 0.5 % of filtration capacity at the mussel bed and can therefore be ignored.

Pelagic community

There was no statistically significant difference in mean zooplankton abundances sampled at approximately 1 m above the bottom between the 2 sampling devices, illustrating that they collected zooplankton with the same efficiency (MANOVA, $F_{8, 1}$, $p > 0.05$). For the water samples taken 1, 3 and 5 m above bottom with the 30 l Niskin bottles, there were only significant differences between the 2 sites for ammonium, silicate and for bivalve larvae (Tables 2 & 3). Nutrient concentrations were, in general, close to the detection level except for silicate (Tables 2 & 3, Fig. 6a–e). Chl *a* concentrations varied between 2 and 6 mg m^{-3} (Fig. 6f–j) and the size-fraction >2 µm available to mussels contributed 82 ± 7 % to total chl *a* (data not shown). Bacterial abundance was in the order of 3 to 8 × 10^9 cells l^{-1} and bacterial production varied from 20 to 72 µg C l^{-1} d^{-1} (Fig. 7). The protozooplankton consisted of athecate dinoflagellates *Gymnodinium* spp., thecate

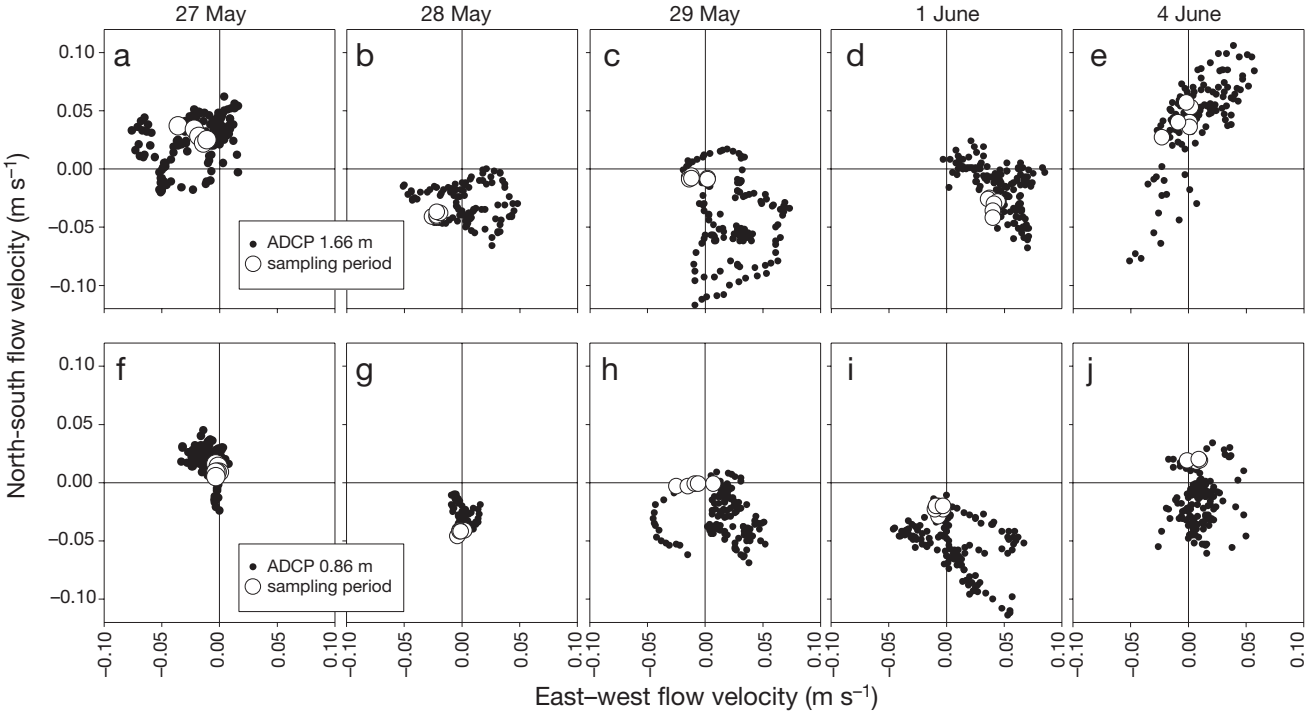

Fig. 5. East–west and north–south velocities (m s^{-1}) 1.16 m above sand bed and 0.86 m above mussel *Mytilus edulis* bed on the 5 sampling days. (○) 2 h sampling periods with HRS. ADCP: acoustic doppler current profiler

Table 1. Average ± SE abundance and biomass of benthic community above sand and mussel *Mytilus edulis* beds in the Limfjord, Denmark. AFDW: ash-free dry weight

Species	Sand bed		Mussel bed	
	Abundance (ind. m^{-2})	Biomass (g AFDW m^{-2})	Abundance (ind. m^{-2})	Biomass (g AFDW m^{-2})
Bivalvia				
Mytilus edulis	3 ± 3	0.001 ± 0.001	3911 ± 717	300.0 ± 59.11
Ensis spp.	17 ± 10	28.43 ± 15.95	0	0
Venerupis senegalensis	3 ± 3	4.199 ± 4.199	0	0
Gastropoda				
Hinia reticulata	0	0	10 ± 8	0.943 ± 0.718
Polychaeta				
Heteromastus filiformis	1941 ± 177	0.146 ± 0.014	130 ± 92	0.011 ± 0.009
Nephtys hombergii	66 ± 10	1.613 ± 0.256	68 ± 11	1.217 ± 0.235
Nereis virens	3 ± 3	1.469 ± 1.469	0	0
Pectinaria (*Lagis*) *koreni*	234 ± 34	4.085 ± 0.656	431 ± 54	6.500 ± 0.869
Scoloplos armiger	138 ± 21	0.336 ± 0.066	0	0
Total	2405	40.28	4551	308.6

dinoflagellates *Protoperidinium* spp., *Strombidium*-like naked oligotrich ciliates and the mixotrophic ciliate *Myrionectra rubra*. Their overall abundance varied from 0.5 to 177 × 10^3 cells l^{-1} (Fig. 8). The larger zooplankton (>45 µm) were dominated by copepodites and nauplii of *Centropages hamatus*, bivalve larvae and polychaete trochophores, and their overall abundance varied between 7 to 1500 ind. l^{-1} (Fig. 9). The abundance of bivalve larvae was statistically significantly higher above the mussel bed than over the sand bed (Table 3).

The higher vertical resolution towards the seabed achieved by the high-resolution sampler (Fig. 2) gave a totally different impression of near-bed plankton dynamics than the Niskin bottle and chl *a* fluorescence samples (Figs. 3d & 4d). Samples taken by the HRS revealed statistically significant differences between the 2 sites for most of the measured parameters (Tables 2 & 3). Thus,

Table 2. Average ± SE nutrient concentrations (mmol m^{-3}), chlorophyll *a* (mg m^{-3}), phaeopigments (mg m^{-3}), bacterial abundance ($\times 10^9$ cells l^{-1}) and production (µg C l^{-1} d^{-1}) 5, 3 and 1 m above bottom, ab, (2-way ANOVA, $F_{1, 2, 24}$) and from high-resolution sampler (HRS) <1 m above bottom (ANCOVA, $F_{46\text{-}47, 1}$). *, **: statistically significant differences in means* and slopes** (interaction term) between sand and mussel *Mytilus edulis* beds

m (ab)	PO_4^{3-}	NO_3^-	NH_4	SiO_4^{3-}	Chl *a*	Phaeopigments abundance	Bacterial abundance	Bacterial production
Sandy bottom								
5	0.08 ± 0.01	0.20 ± 0.10	0.31 ± 0.01	2.25 ± 0.38	3.66 ± 0.59	4.46 ± 0.54	6.32 ± 0.54	1.41 ± 0.18
3	0.07 ± 0.00	0.18 ± 0.08	0.42 ± 0.07	2.29 ± 0.35	3.66 ± 0.41	4.79 ± 0.74	6.15 ± 0.66	1.69 ± 0.28
1	0.07 ± 0.00	0.22 ± 0.12	0.45 ± 0.08	2.66 ± 0.53	3.98 ± 0.41	5.34 ± 1.07	6.36 ± 0.63	1.75 ± 0.24
HRS	0.11 ± 0.03	0.11 ± 0.04	0.62 ± 0.12	3.22 ± 0.66	5.55 ± 0.82	7.93 ± 0.90	6.53 ± 0.49	1.33 ± 0.23
Mussel bed								
5	0.07 ± 0.01	0.11 ± 0.01	0.40 ± 0.09*	1.18 ± 0.37*	3.68 ± 0.42	4.55 ± 0.70	5.81 ± 0.45	1.45 ± 0.17
3	0.07 ± 0.01	0.12 ± 0.02	0.50 ± 0.11*	1.74 ± 0.49*	3.82 ± 0.41	5.61 ± 0.68	5.77 ± 0.62	1.51 ± 0.18
1	0.10 ± 0.02	0.13 ± 0.02	0.74 ± 0.12*	1.89 ± 0.22*	3.88 ± 0.36	6.64 ± 1.40	6.14 ± 0.44	1.42 ± 0.09
HRS	0.15 ± 0.03*	0.16 ± 0.02	2.03 ± 0.37**	5.25 ± 1.32*	3.21 ± 0.67**	5.72 ± 1.12*	5.82 ± 0.63*	1.20 ± 0.11**

Table 3. Average ± SE zooplankton abundance (cells or individuals l^{-1}) 5, 3 and 1 m above bottom, ab, (2-way ANOVA, $F_{1, 2, 24}$) and from HRS <1 m above bottom (ANCOVA, $F_{46\text{-}47, 1}$). *, **: statistically significant differences in means* and slopes** (interaction term) between sand and mussel *Mytilus edulis* beds

m (ab)	Athecate dinofl. $\times 10^3$	Thecate dinofl. $\times 10^2$	Oligotrich ciliates $\times 10^2$	*Myrionectra rubra* $\times 10^2$	Bivalve larvae	Trochophores	Nauplii	Copepodites
Sandy bottom								
5	83 ± 21	40 ± 14	69 ± 11	44 ± 6	246 ± 109	55 ± 15	56 ± 20	24 ± 5
3	91 ± 25	40 ± 18	83 ± 17	60 ± 16	378 ± 71	52 ± 10	66 ± 13	34 ± 8
1	84 ± 11	22 ± 7	78 ± 15	94 ± 26	638 ± 140	65 ± 17	66 ± 17	39 ± 6
HRS	99 ± 26	30 ± 8	79 ± 22	17 ± 5	586 ± 224	23 ± 6	28 ± 10	23 ± 10
Mussel bed								
5	53 ± 13	25 ± 4	83 ±23	46 ± 14	611 ± 211*	37 ± 9	82 ± 24	33 ± 8
3	71 ± 14	50 ± 19	120 ± 24	58 ± 12	967 ± 179*	50 ± 5	78 ± 17	40 ± 6
1	84 ±20	45 ±10	107 ± 23	69 ± 16	1024 ± 212*	55 ± 14	52 ± 11	32 ± 8
HRS	76 ± 34**	23 ± 7	33 ± 14*	13 ± 3**	299 ± 71**	23 ± 17	14 ± 5*	10 ± 5*

mussel filtration only affected the pelagic food web in the lower 1 m of the water column. The concentrations of phosphate, ammonium and silicate were statistically significantly higher above the mussel bed than the sand bed (Tables 2 & 4); this was most prominent in the case of ammonia (Fig. 6a–e). Chl *a* concentrations varied between 3 and 10 mg m^{-3} and increased towards the sand bed (Fig. 6f–j). Above the mussel bed, chl *a* concentrations declined towards the bed and were significantly lower at 1 to 8 mg m^{-3} compared with the sand bed. There was significantly lower bacterial abundance and production above the mussel bed on most days (Tables 2 & 4, Fig. 7), but no significant difference in specific growth rates (= production:biomass) between the sites (ANCOVA, $F_{6, 1}$, $p > 0.05$). There was also a statistically significantly lower abundance of ciliates and dinoflagellates above the mussel bed in 14 out of 16 cases when testing the days separately (Table 5, Fig. 8). In the case of the larger zooplankton (trochophores, bivalve larvae, nauplii and copepodites), the pattern was less clear, with a significantly lower abundance above the mussel bed in 7 out of 20 cases for the different days (Table 5, Fig. 9). However, on 28 May the abundances of all larger zooplankters were statistically significantly lower over the mussel bed than over the sand bed.

DISCUSSION

Conventional oceanographic sampling with profiling equipment and Niskin water bottles does not resolve the near-bed distributions of nutrients and plankton, and therefore near-bottom depletion can be overlooked, as documented here (Tables 2 & 3, Figs. 3d, 4d & 6–9). This is partly because bottom contact was avoided to protect the equipment, but also because the pressure wave in front of the sampling device creates mixing and resuspension and consequently obscures details of near-bed distribution patterns. In this context, the application of stationary, bottom operated samplers

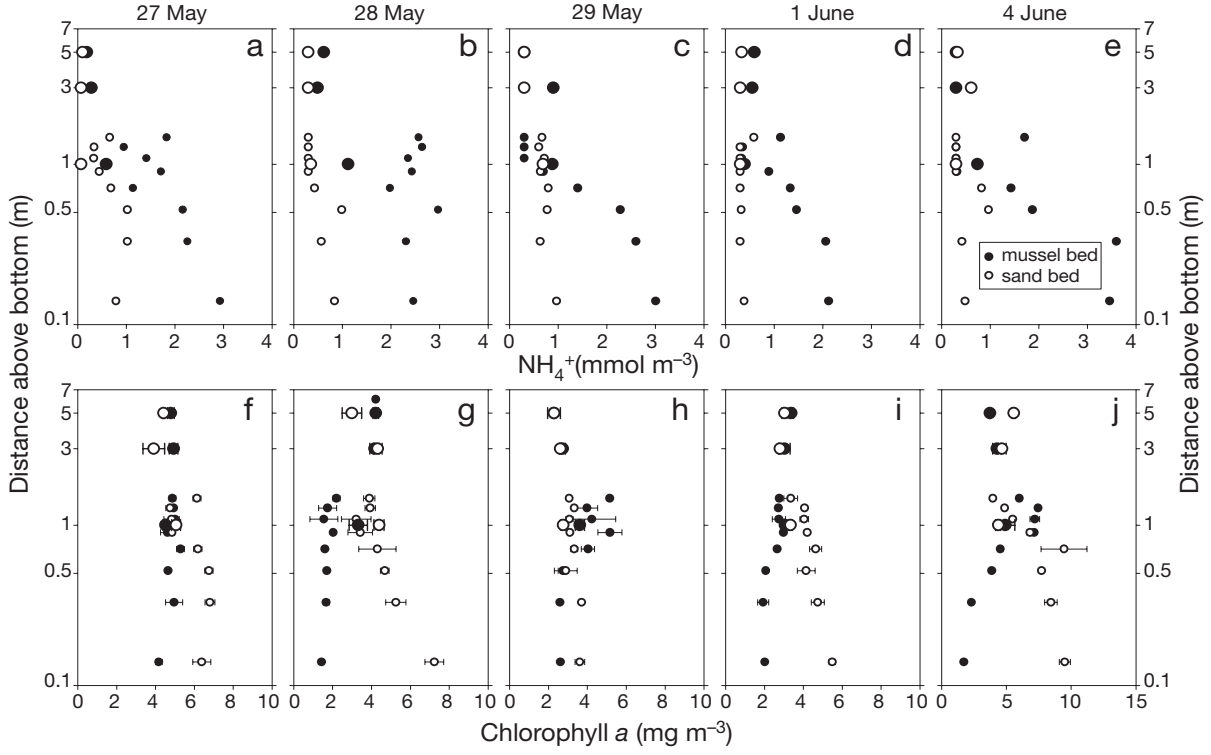

Fig. 6. Vertical distributions of ammonia (mmol m^{-3}) and chlorophyll *a* (mg m^{-3}) above sand and mussel *Mytilus edulis* beds sampled by Niskin bottles (large data points) and HRS (small data points). No error bars given in top panels as there was only 1 measurement per depth

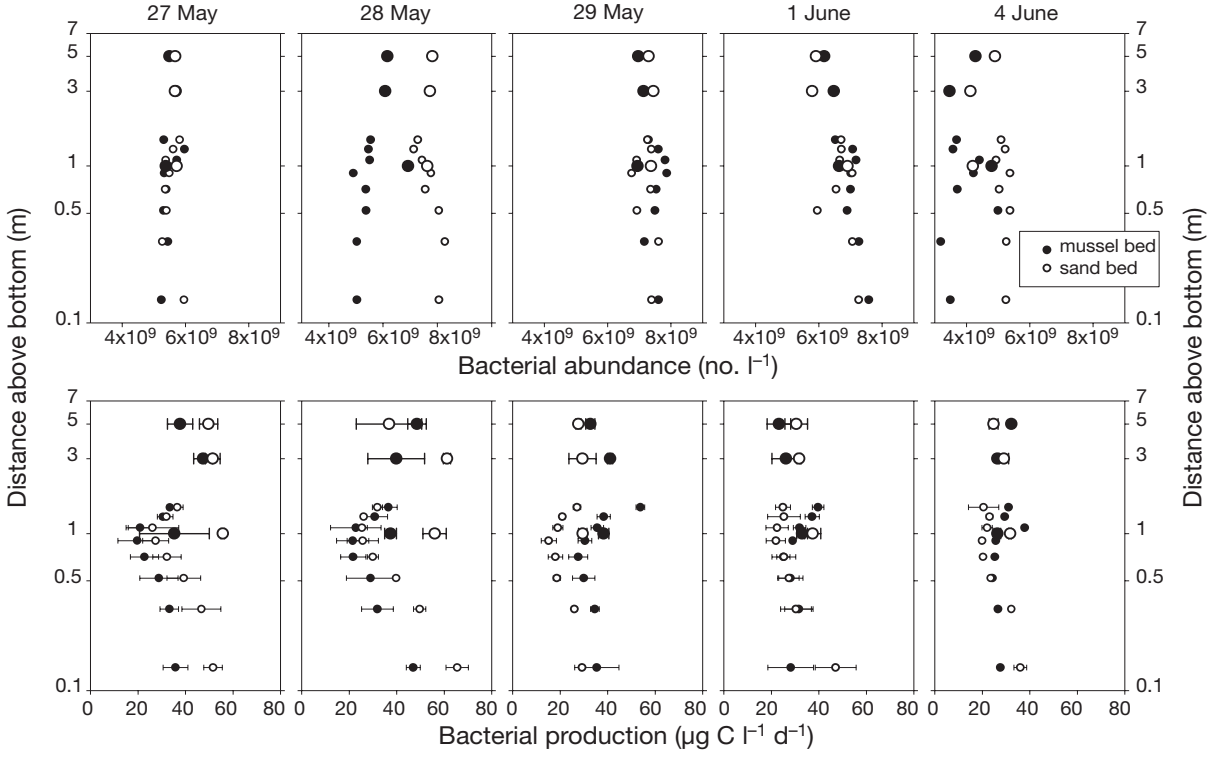

Fig. 7. Vertical distributions of bacterial abundances (no. l^{-1}) and production (µg C l^{-1} d^{-1}) above sand and mussel *Mytilus edulis* beds sampled by Niskin bottles (large data points) and HRS (small data points). No error bars given in top panels as there was only 1 measurement per depth

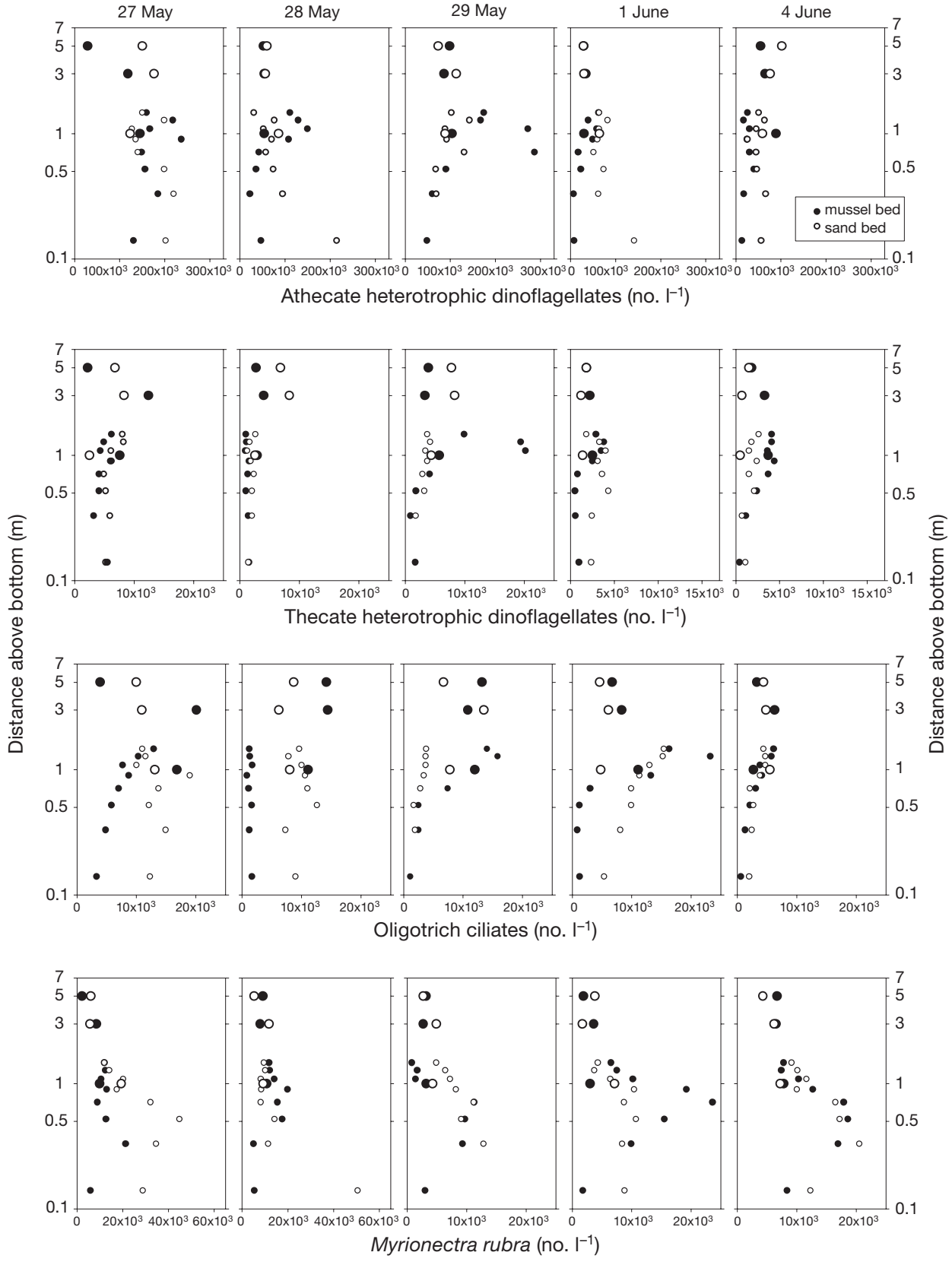

Fig. 8. Vertical distributions (cells l^{-1}) of different protozooplankton groups above sand and mussel *Mytilus edulis* beds sampled by Niskin bottles (large data points) and HRS (small data points)

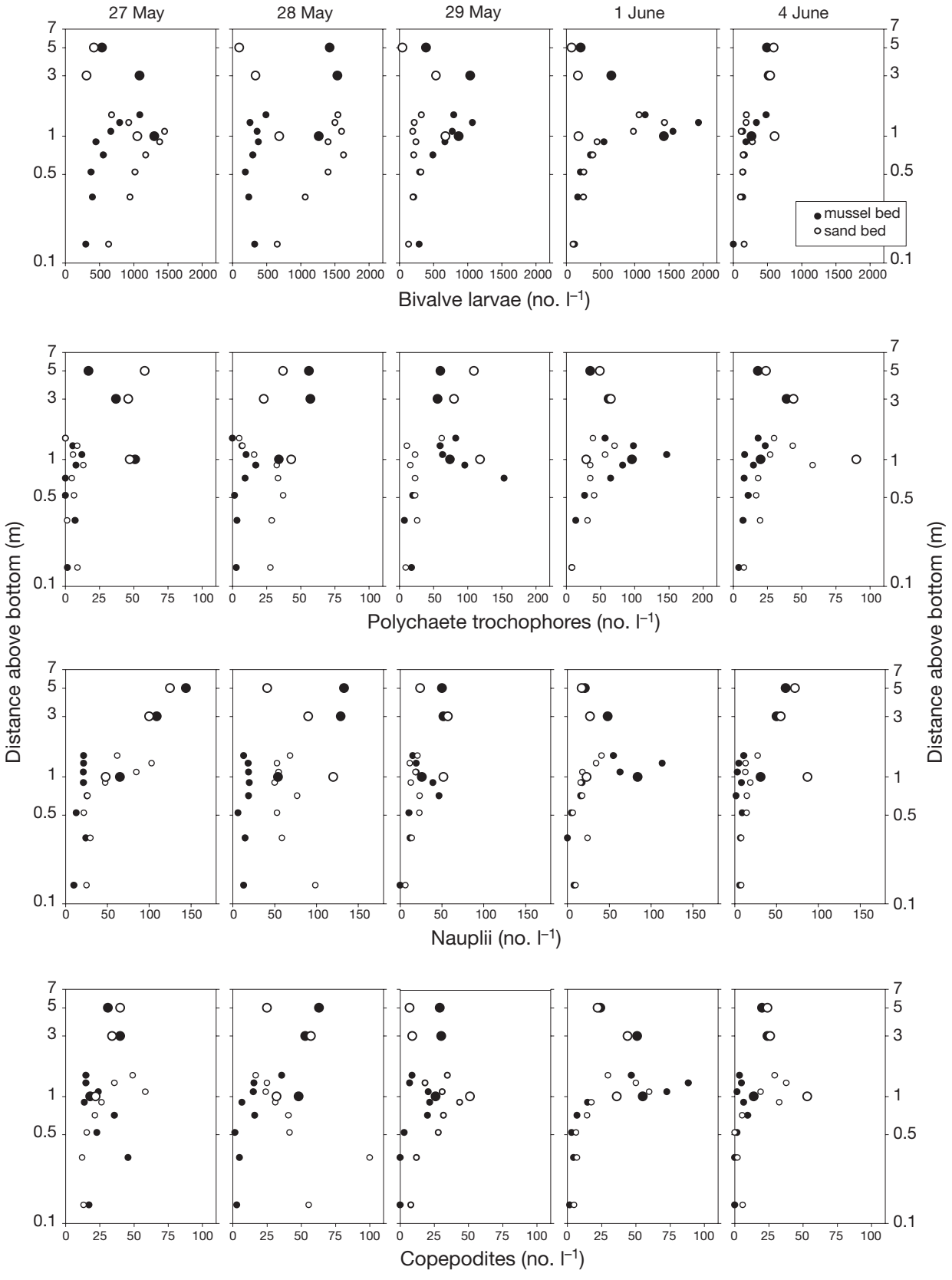

Fig. 9. Vertical distributions (ind. l^{-1}) of different mesozooplankton groups above sand and mussel *Mytilus edulis* beds sampled by Niskin bottles (large data points) and HRS (small data points)

Table 4. Statistically significant differences in means (*) or slopes (**) of nutrients (mmol m^{-3}), chlorophyll *a* and phaeopigments (mg m^{-3}), bacterial abundance ($\times 10^9$ cells l^{-1}) and production (µg C l^{-1} d^{-1}) between sand bed and mussel *Mytilus edulis* beds sampled on the different days by HRS <1 m above the bottom (ANCOVA $F_{6\text{-}7,\,1}$). ns: not significant; –: below detection limit at sandy site

Date d/mo	PO_4^{3-}	NO_3^-	NH_4	SiO_4^{3-}	Chl *a*	Phaeo-pigments	Bacterial abundance	Bacterial production
27/5	ns	–	*	ns	*	ns	ns	*
28/5	ns	*	*	ns	**	*	*	**
29/5	*	**	**	*	**	*	ns	*
1/6	ns	–	**	ns	**	*	ns	**
4/6	*	–	**	*	**	**	*	**

such as artificial siphons (Jonsson et al. 2005) and the present HSR (Fig. 2) has clear advantages. The HSR allows undisturbed sampling across sharp interfaces (Maar et al. 2003) once the water column structure is re-established and the bivalves have resumed filtering. The samples taken with the HRS sampler made it possible to analyse all components of the pelagic food web above a mussel bed and sandy reference site, resolving the implication of mussel suspension-feeding on the near-bed distribution pattern of plankton.

Field studies have shown that mussel populations in shallow waters can deplete a water layer of several metres thickness within 1 d (Dolmer 2000b, Ackerman et al. 2001). This intuitively implies that mussels significantly influence the plankton concentration in the water column above them. However, a depleted boundary layer near the bed prevents full realization of the filtration potential of the benthic filter-feeders (Wildish & Kristmanson 1997). Consequently, the actual grazing impact depends on the processes that supply plankton to mussels, e.g. sedimentation, advective transport (Frechette et al. 1989, Wildish & Kristmanson 1997) and wind-driven vertical mixing (Møhlenberg 1995). In coastal, micro-tidal estuaries such as the Limfjord, these processes are primarily controlled by the competition between density-driven stratification and wind-driven mixing which occurs indirectly through wave motion (Wiles et al. 2006). Flow velocities were weak (<0.10 m s^{-1}) and advection was therefore less important than vertical mixing for the supply of food to mussels in the Limfjord, as suggested by Dolmer (2000a). Accordingly, the supply of plankton to the benthic communities is pulsed, depending on the physical regime, on a time scale of 1 to 4 d (Figs. 3c & 4c). Benthic feeding activity then generates feed-back processes that regulate the pelagic food web through bottom–up (nutrient recycling) or top–down (grazing) effects.

Effects of mussel bed on phytoplankton and bacteria

The bulk of the substantial literature addressing the ecological role and implication of mussels considers grazing on phytoplankton. During the present investigation we observed a significant near-bed depletion of chl *a* above the mussel bed and an increase in chl *a* concentration towards the bottom on the sandy reference site (Fig. 6f–j). This depletion caused by mussel filtration has previously been documented in well-mixed tidal areas (Frechette et al. 1989, Wildish & Kristmanson 1997), but is often more pronounced in micro-tidal areas with periods of strong stratification (Møhlenberg 1995, Dolmer 2000a).

In the present study, bacterial abundances on 2 d were statistically significantly reduced above the mussel bed compared with the sandy bottom (Table 4). In general, most free-living marine bacteria are <1 µm (Wright et al. 1982) and consequently too small to be efficiently retained by mussels (Møhlenberg & Riisgaard 1978). Previous field studies have also found a statistically significant removal of phytoplankton but no reduction in bacterial abundance (Wright et al. 1982, Wildish & Kristmanson 1984). In a series of seawater enclosures in Danish fjords, Riemann et al. (1988) demonstrated that addition of mussels in concentrations comparable to their *in situ* biomass did influence the bacterial community. However, the direct predation

Table 5. Statistically significant differences in means (*) or slopes (**) of zooplankton (cells or individuals l^{-1}) between sand bed and mussel *Mytilus edulis* beds sampled on the different days by HRS <1 m above bottom (ANCOVA, $F_{6\text{-}7,\,1}$). ns: not significant. 29 May was not tested for protozooplankton because 2 samples were missing

Date d/mo	Athecate dinofl. $\times 10^2$	Thecate dinofl. $\times 10^2$	Oligotrich ciliates $\times 10^2$	*Myrionectra rubra* $\times 10^2$	Bivalve larvae	Trochophores	Nauplii	Copepodites
27/5	**	*	*	*	*	ns	ns	ns
28/5	*	*	*	ns	*	*	*	*
29/5	–	–	–	–	ns	ns	ns	*
1/6	*	*	*	**	ns	ns	ns	ns
4/6	**	*	ns	**	ns	ns	*	ns

effect on the bacteria was difficult to distinguish from the indirect effect of reduced phytoplankton biomass and production (Bjørnsen et al. 1988). Most reports on mussel grazing on bacteria are based on laboratory experiments using cultured strains of bacteria that are 1 order of magnitude larger than those in natural bacterial populations (Birkbeck & McHenry 1982). We therefore assume that the lower bacterial abundance found in the present study above the mussel bed was caused by ingestion of bacteria in association with particles (Wildish & Kristmanson 1984), but this needs to be verified under controlled laboratory conditions. Bacterial biomass can thereby be a potentially important food source for mussels, since bacteria constitute a large heterotrophic pelagic carbon pool in the Limfjord (Andersen & Sørensen 1986).

Through their grazing activities, the mussel populations recycle nutrients to the water column as waste products. In the present study, excretion of nutrients by mussels exceeded the consumption by osmotrophic organisms, and an accumulation of ammonium, phosphate, and silicate was observed <1 m above the mussel bed during the stratified periods (Table 2). The recycled nutrients are released to the nutrient-depleted phytoplankton community in the upper water column during wind- or wave-generated mixing events (Møhlenberg 1995). This probably caused the significantly higher ammonium concentrations at the surface compared with the sand bed. This replenishment of nutrients favours fast-growing species such as diatoms, thereby performing bottom–up control of the pelagic system (Riemann et al. 1988). Conversely, the higher silicate concentrations above the sand bed were interpreted as reflecting resuspension of settled diatoms.

Effects of mussel bed on zooplankton

The availability of bacterial production to higher trophic levels depends on the magnification of the average cell size up through the microbial food web (roughly 1 order of magnitude for each trophic level). In contrast to bacterial cells, the succeeding links in the food web (i.e. heterotrophic flagellates and ciliates) are of a size that is efficiently retained by mussels (Møhlenberg & Riisgaard 1978). So far most research on microbial food webs has considered the trophic link to mesozooplankton, while trophic coupling with benthic suspension feeders has received much less attention. To our knowledge, the present study is the first report describing *in situ* observations of zooplankton vertical distributions above a mussel bed. In general, there was a statistically significantly lower abundance of ciliate and heterotrophic dinoflagellates above the mussel bed than above the bare sand. Heterotrophic flagellates also contributed to the carbon requirements of *Geukensia demissa* and *Mytilus edulis* in grazing experiments, although assimilation efficiency of flagellates was lower than for phytoplankton (Kreeger & Newell 1996). The role of pelagic protists as a link between picophytoplankton and the filter-feeding bivalve *Crassostrea gigas* was documented by Le Gall et al. (1997) and Dupuy et al. (1999), who concluded that the protozoan community significantly contributes to the food supply of *C. gigas*.

Hitherto, most research has focused on the implications of suspension-feeding bivalves on phytoplankton and the lower limit of the retention spectra, although the recent work of Davenport et al. (2000) has demonstrated that mussels easily ingest mesozooplankton (<100 µm) in the laboratory and occasionally larger animals (300–600 µm). Herein we have documented a statistically significantly lower abundance of trochophores, bivalve larvae, nauplii and copepodites in 7 out of 20 cases above the mussel bed than at the reference site — most markedly on 28 May (Table 5). Protozooplankton and bivalve larvae seemed more vulnerable to predation than either trochophores or copepods on most days. Bivalve larvae were however more abundant higher in the water column above the mussel bed than in the sand bed, illustrating that some of the larvae can survive here. The escape success of different zooplankton above a mussel bed and the interference by turbulence was investigated using a dynamic model which showed that enhanced turbulence considerably increased the grazing impact on all size classes (Maar et al. 2007, this volume). Hence, the suspension feeder *Mytilus edulis* has the potential to exploit all size classes of zooplankton as long as these are accessible (e.g. when the supply of zooplankton is mediated by turbulent mixing of the water column caused by physical forcing of the system). In the laboratory, mussels fed on a mixture of phyto- and zooplankton (rotifers) had a 2 times higher growth than mussels fed on phytoplankton alone (Wong & Levinton 2004). The importance of microzooplankton in the *in situ* diet of mussels is not known, but outside the main phytoplankton blooms, heterotrophic prey contributes significantly to the plankton biomass in coastal waters (Andersen & Sørensen 1986) and potentially constitutes an important trophic link to the benthic grazers in marine ecosystems in shallow estuaries such as the Limfjord.

Ecological consequences

The present investigation documents a diverse trophic interaction between suspension-feeding bivalves and the pelagic food web. First, although the

suspension-feeding bivalves remove plankton from the water column above them, they recycle nutrients back to the water column as waste products. In addition, mussels also impact the zooplankton community indirectly through reduction in the abundance of their plankton prey, and directly by preying on other zooplankters and thereby eliminating pelagic competitors. Consequently, mussels have a very diverse role in shallow water ecosystems, where they mediate nutrient cycling and exert a bottom–up control on the pelagic food web. Hence, mussels have the potential to simultaneously regulate the pelagic food web by performing both bottom–up and the top–down control. The relative importance of these 2 mechanisms strongly depends on the interplay between zooplankton swimming potential, benthic filtration capacity and the physical regime.

Acknowledgements. This study was supported by a Managing Benthic Ecosystems (MaBenE) grant (EKV3-2001-00144) and the Danish National Research Council (Grant No. 21-04-0391). B. Søborg, J. Larsen, J. D. Nielsen and V. D. Hansen are thanked for technical assistance. L. Gissel Nielsen and K. Moser are thanked for design and construction of the HRS. S. Gooding is acknowledged for counting the protozooplankton samples. We are grateful to T. Ysebaert for providing data for the benthic community and J. Simpson and P. Wiles for providing ADCP data. We also thank 2 anonymous referees for detailed comments on the manuscript.

LITERATURE CITED

Ackerman JD, Loewen MR, Hamblin PF (2001) Benthic–pelagic coupling over a zebra mussel reef in western Lake Erie. Limnol Oceanogr 46:892–904

Andersen P, Sørensen H (1986) Population dynamics and trophic coupling in pelagic microorganisms in eutrophic coastal waters. Mar Ecol Prog Ser 33:99–109

Birkbeck TH, McHenry JA (1982) Degradation of bacteria by *Mytilus edulis*. Mar Biol 72:7–15

Bjørnsen PK, Riemann B, Horsted SJ, Nielsen TG, Pock-Steen J (1988) Trophic interactions between heterotrophic nanoflagellates and bacterioplankton in manipulated seawater enclosures. Limnol Oceanogr 33:409–420

Davenport J, Smith RW, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Mar Ecol Prog Ser 198:131–137

Dolmer P (2000a) Algal concentration profiles above mussel beds. J Sea Res 43:113–119

Dolmer P (2000b) Feeding activity of mussels *Mytilus edulis* related to near-bed currents and phytoplankton biomass. J Sea Res 44:221–231

Dupuy C, Le Gall S, Hartmann HJ, Bréret M (1999) Retention of ciliates and flagellates by the oyster *Crassostrea gigas* in French Atlantic coastal ponds: protists as a trophic link between bacterioplankton and benthic suspension feeders. Mar Ecol Prog Ser 177:165–175

Frechette M, Butman CA, Geyer WR (1989) The importance of boundary layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol Oceanogr 34:19–36

Fuhrman JA, Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar Biol 66:109–120

Grasshoff K (1976) Methods of seawater analysis. Verlag Chemie, Weinheim

Jonsson PR, Petersen JK, Karlsson Ö, Loo LO, Nilsson S (2005) Particle depletion above experimental bivalve beds: *in situ* measurements and numerical modelling of bivalve filtration in the boundary layer. Limnol Oceanogr 50:1989–1998

Jordan TE, Valiela I (1982) A nitrogen budget of the ribbed mussel, *Geukansia demissa*, and its significance in nitrogen flow in a New England salt-marsh. Limnol Oceanogr 27: 75–90

Kanneworff E, Nicolaisen W (1973) The HAPS. A frame supported bottom corer. Ophelia 10:119–129

Karlsson Ö, Jonsson PR, Larsson AI (2003) Do large seston particles contribute to the diet of the bivalve *Cerastoderma edule*? Mar Ecol Prog Ser 262:161–173

Kiørboe T, Møhlenberg F (1981) Particle selection in suspension-feeding bivalves. Mar Ecol Prog Ser 5:291–296

Kreeger DA, Newell RIE (1996) Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa* and *Mytilus edulis* (Bivalvia, Mollusca). Aquat Microb Ecol 11:205–214

Kristensen PS, Hoffmann E (2004) Bestanden af blåmuslinger i Limfjorden 1993–2003. DFU-Rapp No. 130-04, Danmarks Fiskeriundersøgelser, Charlottenlund

Lee S, Fuhrman JA (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. App Environ Microbiol 53:1298–1303

Le Gall S, Hassen MB, Le Gall P (1997) Ingestion of a bactivorous ciliate by the oyster *Crassostrea gigas:* protozoa as a trophic link between picoplankton and benthic suspension-feeders. Mar Ecol Prog Ser 152:301–306

Loo LO, Rosenberg R (1989) Bivalve suspension-feeding dynamics and benthic-pelagic coupling in a eutrophicated marine bay. J Exp Mar Biol Ecol 130:253–276

Maar M, Nielsen TG, Stips A, Visser AW (2003) Microscale distribution of zooplankton in relation to turbulent diffusion. Limnol Oceanogr 48:1312–1325

Maar M, Nielsen TG, Bolding K, Burchard H, Visser AW (2007) Grazing effects of blue mussel *Mytilus edulis* on pelagic food web under different turbulence conditions. Mar Ecol Prog Ser 339:199–213

Marie D, Partensky F, Jacquet S, Vaulot D (1997) Enumeration and cell cycle analysis of natural populations of marine picoplankton by flow cytometry using the nucleid acid stain SYBR Green I. Appl Environ Microbiol 63(1): 186–193

Møhlenberg F (1995) Regulating mechanisms of phytoplankton growth and biomass in a shallow estuary. Ophelia 42:239–256

Møhlenberg F, Riisgaard HU (1978) Efficiency of particle retention in 13 species of suspension-feeding bivalves. Ophelia 17:239–246

Nielsen TG, Hansen PJ (1999) Dyreplankton i danske farvande. Tema-Rapp No. 28, DMU, Miljø- og Energiministeriet, Copenhagen

Noren F, Haamer J, Lindahl O (1999) Changes in the plankton community passing a *Mytilus edulis* mussel bed. Mar Ecol Prog Ser 191:187–194

Petersen JK, Riisgaard HU (1992) Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. Mar Ecol Prog Ser 88:9–17

Riemann B, Bjørnsen PK, Newell S, Fallon R (1987) Calculation of cell production of coastal marine bacteria based

on measured incorporation of [^{3}H]thymidine. Limnol Oceanogr 32:471–476
Riemann B, Nielsen TG, Horsted SJ, Bjørnsen PK, Pock-Steen J (1988) Regulation of the phytoplankton biomass in estuarine enclosures. Mar Ecol Prog Ser 48:205–215
Riisgaard HU, Seerup DF (2003) Filtration rates in the soft clam *Mya arenaria*: effects of temperature and body size. Sarsia 88:415–428
Shumway SE, Cucci TL, Newell RC, Yentsch CM (1985) Particle selection, ingestion and absorption in filter-feeding bivalves. J Exp Mar Biol Ecol 91:77–92
Wildish D, Kristmanson D (1984) Importance to mussel of the benthic boundary layer. Can J Fish Aquat Sci 41:1618–1625
Wildish D, Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambrige
Wiles PJ, van Duren LA, Häese C, Larsen J, Simpson JH (2006) Stratification and mixing in the Limfjorden in relation to mussel culture. J Mar Syst 60:129–143
Wong WH, Levinton JS (2004) Culture of the blue mussel *Mytilus edulis* (Linnaeus 1758) fed both phytoplankton and zooplankton: a microcosm experiment. Aquac Res 35: 965–969
Wright RR, Coffin RB, Ersing CP, Pearson D (1982) Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. Limnol Oceanogr 27:91–98
Yentsch CS, Menzel DW (1963) A method for the determination of phytoplanton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res 10:221–231

Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

Submitted: June 12, 2006; Accepted: October 16, 2006
Proofs received from author(s): April 20, 2007