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Phytoplankton reduction in near-bottom water caused by filter-feeding *Nereis diversicolor*—implications for worm growth and population grazing impact

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ABSTRACT: Studies of vertical profiles of phytoplankton in the field combined with laboratory experiments demonstrated that reduction in phytoplankton concentrations in the near-bottom water layer, 5 to 10 cm in thickness on calm days, may play a significant role for the filter-feeding polychaete *Nereis diversicolor* in realizing its grazing capacity (estimated at $13.8 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ in the shallow bay of Kertinge Nor, Denmark, in July 1994). Field-growth experiments were performed with worms transferred to U-shaped glass tubes placed at different heights (0, 4, 10 and 20 cm) above the seafloor. A considerably reduced specific growth rate of worms at the sea floor ($0.2 \pm 1.1\% \text{ d}^{-1}$), compared to worms elevated just 10 cm above the sediment surface ($2.5 \pm 0.8\% \text{ d}^{-1}$), indicates that extremely meagre food conditions may be prevailing at the bottom. Experimental laboratory data on the development of vertical algal cell profiles were compared with predicted values obtained by means of a simple diffusion model.

KEY WORDS: Grazing impact · Vertical phytoplankton profiles · Ingestion layer · Specific growth rate

INTRODUCTION

Benthic filter-feeding macro-invertebrates may have a pronounced grazing impact on phytoplankton biomass in many shallow marine areas. A number of studies have shown that densities of filter-feeding bivalves (Jørgensen 1980, Cloern 1982, Officer et al. 1982, Nichols 1985, Loo & Rosenberg 1989), ascidians (Petersen & Riisgård 1992) and different species of polychaetes (e.g. Davies et al. 1989, Riisgård 1994) based on known filtration rates have the potential for filtering the total volume of water of their environment several times per day. If the water column is well mixed the filter-feeding bottom fauna may thus theoretically be able to control the pelagic primary production in many shallow and coastal waters.

During recent years a number of studies have been carried out to address questions dealing with the facul-

tative filter-feeding polychaete *Nereis diversicolor* (Riisgård 1991, Riisgård et al. 1992, Vedel & Riisgård 1993, Vedel et al. 1994, Nielsen et al. 1995; for an overview of recent findings see Riisgård 1994). *N. diversicolor* may meet its food requirements on a pure diet of phytoplankton and may be an undervalued key organism in the control of phytoplankton in many shallow brackish water areas. Because *N. diversicolor* may utilize different feeding methods depending on season, phytoplankton biomass and local conditions, it is important to determine to what extent this polychaete filter-feeds. Such data were obtained by Vedel et al. (1994) using a refined monitoring system to obtain continuous, long term field measurements of the filter-feeding activity of this worm. They found that filter-feeding was 'triggered' by the presence of phytoplankton in the water, and that *N. diversicolor* utilized filter-feeding 50 to 100% of the time during the summer period. The grazing impact of *N. diversicolor* was potentially $5.6 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ in May, representing a volume 11 to 55 times greater than the overlying water

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column in the field. However, there was not always a clear correlation between filtration activity and chlorophyll *a* (chl *a*) measured in surface water samples. This phenomenon was assumed to be due to a restriction of the filtration activity on calm days because of the development of phytoplankton-depleted bottom water. The frequency of such incidents was suggested to have an important effect on the filter-feeding potential of *N. diversicolor*.

The present work describes a phytoplankton-reduced boundary layer over dense populations of *Nereis diversicolor*. Data was obtained through studies of vertical profiles of phytoplankton in the field combined with laboratory simulation experiments carried out with algal cells over filter-feeding *N. diversicolor*. Further, the presence of near-bottom reduced algal biomass was assessed through growth experiments in the field with worms placed in glass tubes at different heights above the bottom. These results show that phytoplankton-reduced boundary layers do occur and may significantly reduce the potential grazing impact and growth of *N. diversicolor* in nature.

MATERIALS AND METHODS

Study areas. Field experiments were conducted in 2 study areas during 1993 and 1994: the more eutrophic Odense Fjord (average water depth 0.3 m at sampling site, tidal amplitude ~0.4 m, 10 to 18‰ S) and the less eutrophic Kertinge Nor (average water depth 0.4 m at sampling site, tidal amplitude ~0.3 m, 13 to 24‰ S), Denmark (for localities see Fig. 1 of Vedel & Riisgård 1993). Both localities are characterized by dense populations of *Nereis diversicolor*.

Population investigations. Sampling during this study was carried out at a site in the southern Kertinge Nor where previous sampling had shown high densities of worms. Once a month during parts of 1993–94, 10 or 15 randomly chosen sediment core samples (92 or 143 cm²; 25 cm deep) were taken. Polychaetes that were retained by the sieve (1 mm mesh size) were individually weighed (mg wet wt) to determine population size distribution. These data were used to estimate population filtration rate using methods of Riisgård (1991) and Riisgård et al. (1992) for combining field data with laboratory data on filtration rates.

Field measurements. The importance of employing sampling protocols with realistic pumping rates and incurrent tube diameters (to mimic the pumping rate of filtering worms) has been emphasized by Judge et al. (1993). Therefore, the sampling tubes used in the present work had an inner diameter of 4 mm that matches the diameter of burrows of the 'standard' *Nereis diversicolor* (300 to 450 mg wet wt), and the sampling vol-

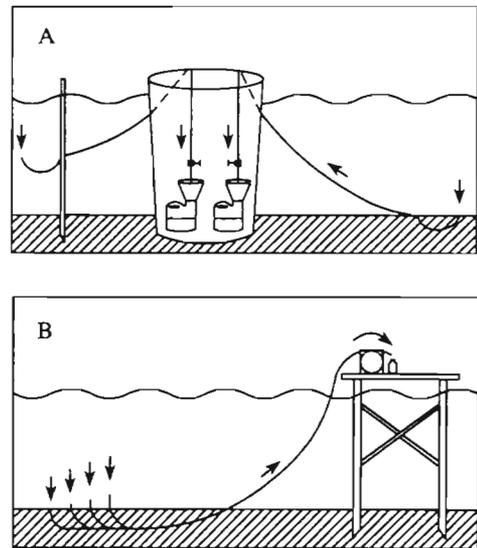


Fig. 1 Devices used for field sampling water at different heights above the sediment

ume rate did not exceed the pumping rate of the worms (i.e. 10 ml min^{-1}). The devices used for sampling water at different heights above the sediment are shown in Fig. 1. Water samples were collected simultaneously either (Fig. 1A) by siphoning the samples into plastic bottles placed on the bottom in an empty barrel, or (Fig. 1B) by using an adjustable multiple-canal peristaltic pump placed on a platform and powered by an electric generator ashore. A glass tube was fixed at the end of each sampling tube and positioned at a certain height above bottom. The water sampling rate was adjusted to equal the pumping rate of a 'standard' *N. diversicolor*.

Water samples for chl *a* measurement were immediately filtered (Whatman GF/C, 0.3 bar) and the filters put in 10 ml 96% ethanol and placed on ice in the dark for 24 h. The extracted chl *a* content was measured according to standard procedures (Arvola 1981) by measuring the absorption at 665 nm on a Perkin-Elmer model 554 spectrophotometer. Water samples (50 ml) for fluorescence measurement were gently passed through GF/C filters and the extracted chl *a* was determined fluorometrically (Sequoia-Turner model 450) the following day.

Laboratory experiments. The experimental aquarium (50 × 50 × 100 cm) was first filled with 20 cm of low organic sediment stripped of macrofauna, and *Nereis diversicolor* (individual biomass of 300 to 600 mg wet wt) was added to obtain the desirable density. In the laboratory sampling device, thin tubes (inner diameter = 1.19 mm) were employed to minimize unwanted mixing in the aquarium. The tube entrances were projecting at different heights from a vertically placed pipe-

Table 1. *Nereis diversicolor* Population density, biomass and estimated population filtration capacities at actual field temperatures (cf. Riisgård et al. 1992) of worms in Kertinge Nor (1993-94) and in Odense Fjord (June 1993*)

1993	March	April	May	June	June*	August	October
Population density (ind. m ⁻²)	273	434	986	1091	1427*	1179	1845
Biomass (g m ⁻²)	29	124	106	163	68*	136	215
Filtration capacity (m ³ m ⁻² d ⁻¹)	at: 4.8°C 0.2	7.5°C 3.5	14.5°C 3.1	18.0°C 5.1	17.0°C 2.4*	17.1°C 2.3	12.9°C 4.6
1994	February	March	May	June	July	August	September
Population density (ind. m ⁻²)	1223	1397	1405	1303	1550	1376	1252
Biomass (g m ⁻²)	145	222	297	273	328	255	219
Filtration capacity (m ³ m ⁻² d ⁻¹)	at: 3.8°C 0.9	4.6°C 1.7	17.7°C 9.3	19.1°C 9.1	23.6°C 13.8	25.5°C 11.1	15.7°C 5.8

rack. At the start of an experiment the through-flowing seawater was cut off and a known concentration of the flagellate *Rhodomonas* sp. (mean diameter 5 to 7 µm) was added. Water samples were collected at appropriate time intervals and the algal concentration was either measured on an electronic particle counter (Elzone 180xy) or with a fluorometer. In a number of cases the population filtration rate of worms held in the aquarium was measured previous to a profile experiment (in still water after cutting off mixing with air bubbles) by means of the clearance method (i.e. volume of water cleared of algal cells per unit of time) according to Riisgård (1991).

Growth experiments. Worms (307 to 429 mg wet wt, n = 48) were placed in U-shaped, black-painted, glass tubes (4.0 mm inner diameter) and buried on the study location in Kertinge Nor with the tube entrances at 0, 4 and 10 cm above the bottom. The sediment surface was covered with plastic to prevent the worms from deposit-feeding. Another 12 tubes were placed on a rack 20 cm above the bottom. Initial and final wet wts after a 14 d growth period were determined (after 24 h

starvation to empty the gut and 2 min drainage on filter paper). The specific growth rate (μ , d⁻¹) was calculated according to the equation: $\mu = \ln(W_t/W_0)t^{-1}$, where W_t and W_0 are the individual body wet wt of polychaetes on Days t and 0, respectively.

Growth experiments in the laboratory were performed using ad libitum feeding of shrimp meat or 2 to 3 × 10⁴ *Rhodomonas* sp. cells ml⁻¹. The specific growth rates were determined after 14 d.

RESULTS

Grazing impact

Population densities, biomass, and estimated population filtration capacities of *Nereis diversicolor* in Kertinge Nor during 1993 and 1994 are shown in Table 1. The grazing capacity reached a maximum level during summer due to a combination of high population biomass and high temperatures. In July 1994 the estimated population filtration rate was 13.8 m³ m⁻² d⁻¹, corresponding to a volume 35 times that of the overlying water column. In Odense Fjord the number was 2.4 m³ m⁻² d⁻¹ in June 1993 (Table 1), corresponding to 5 to 24 times that of the water column.

Vertical profiles

The laboratory experiments demonstrate the formation of a water layer with reduced phytoplankton concentrations over a population of filter-feeding *Nereis diversicolor* (Figs. 2 to 5) with no advective flow. Worm densities, measured population filtration capacities (F_{pop}), individual filtration rates (F_{ind}), and water temperatures are given in Table 2.

Table 2. *Nereis diversicolor*. Density, estimated population filtration capacity (F_{pop}) and individual filtration rate (F_{ind}) at different temperatures in laboratory experiments

Expt	Density (ind. m ⁻²)	F_{pop} (m ³ m ⁻² d ⁻¹)	F_{ind} (ml min ⁻¹)	Temperature (°C)
Fig. 2A	120	1.3	7.4	8.5
Fig. 2B	120	1.3	7.5	10.2
Fig. 3A	160	1.8	8.1	10.1
Fig. 3B	160	1.3	6.0	15.0
Fig. 4	186	1.3	4.9	4.4
Fig. 5A	186	2.1	7.7	10.2
Fig. 5B	186	2.1	7.7	10.7

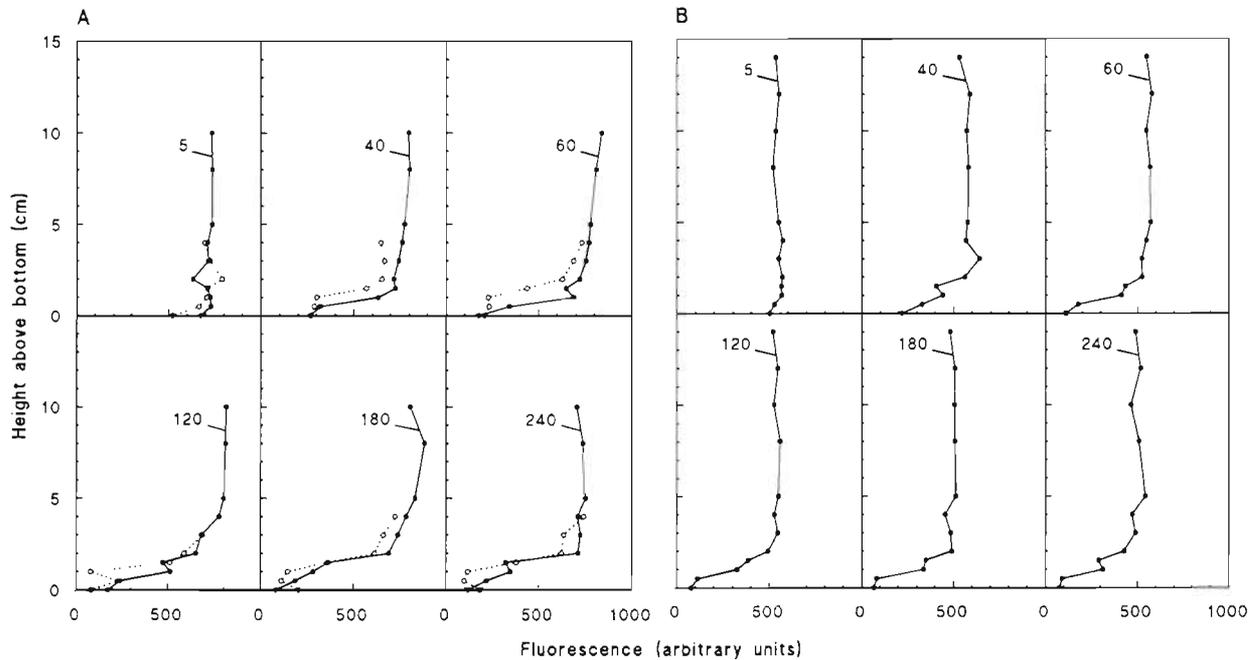


Fig. 2. Development of vertical fluorescence profiles in 2 laboratory experiments (A and B) with filter-feeding worms *Nereis diversicolor* buried in sediment on the bottom of an aquarium (see Table 2). Time (min) after stoppage of mixing with air is shown. Open circles in Expt A represent measurements of parallel samples taken at a different site in the aquarium

To examine the effect of these parameters on the thickness of the phytoplankton-reduced water layer it is convenient to introduce the concept of concentration displacement thickness, referred to as the ingestion

layer. It is defined by the integral $\int_0^L [1 - C(y)/C_0] dy$, where C_0 and $C(y)$, respectively, are the initial and instantaneous concentrations, the latter being a function of distance y above the bottom and L being a

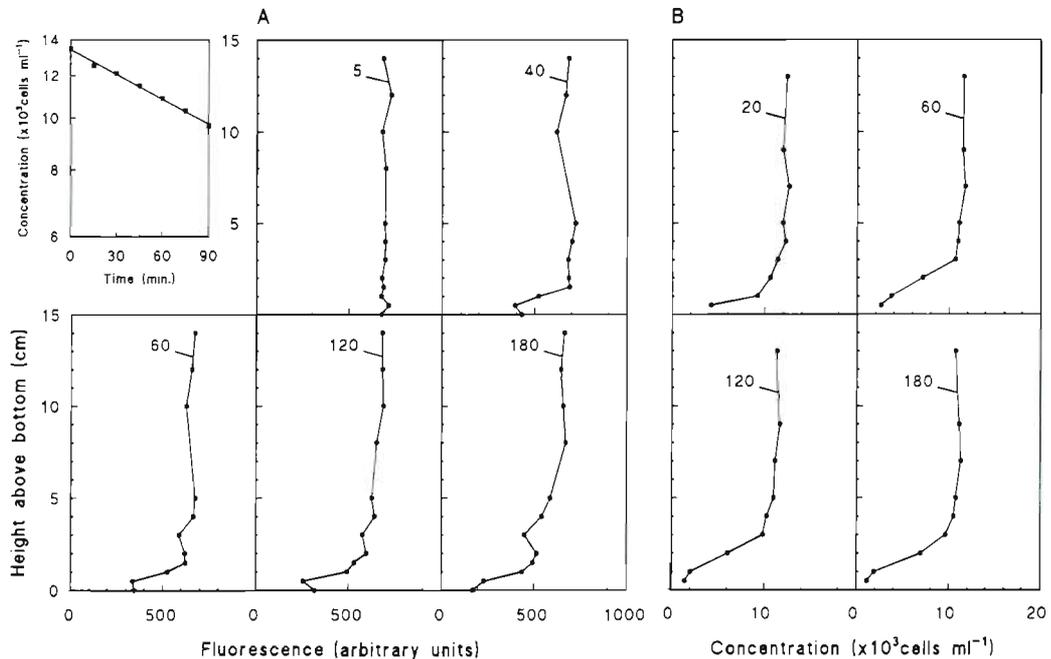


Fig. 3. Development of vertical profiles in (A) fluorescence and (B) algal cell concentration in 2 laboratory experiments (see Fig. 2). Insert shows the exponential reduction in algal concentration used to estimate F_{pop} (see Table 2) previous to stoppage of mixing at time zero

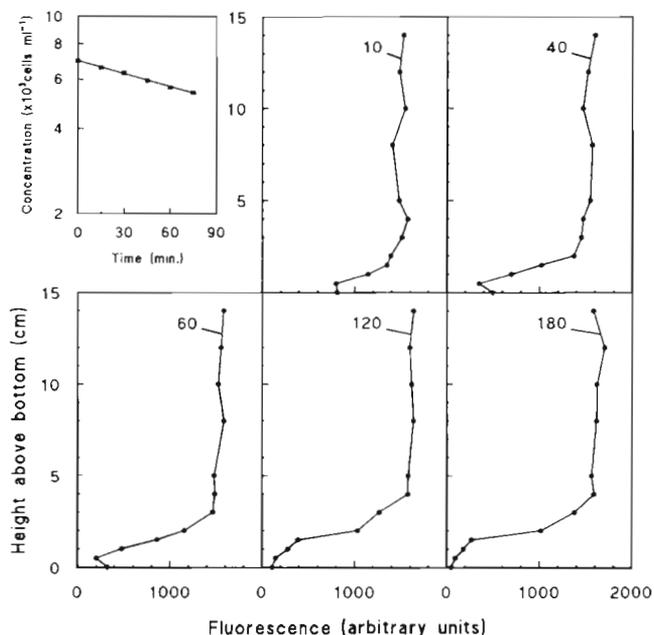


Fig. 4. Development of vertical fluorescence profiles in a laboratory experiment (see Fig. 2). Insert as in Fig. 3

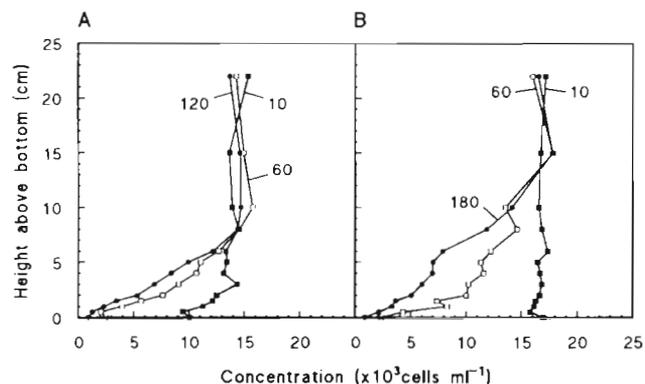


Fig. 5. Development of vertical profiles of algal cell concentration in a laboratory experiment (see Fig. 2)

sufficiently large distance so that $C(L) = C_0$. The ingestion layer has dimension of length and has a simple physical meaning: it is the layer of initial concentration, C_0 , holding as many algal cells as are actually ingested by the benthic filter-feeders up to a given time. Fig. 6 shows the ingestion layer versus time for the data of Figs. 2 to 5. Comparison with Table 2 shows that higher worm density causes higher growth rate of the ingestion layer (Fig. 5A, B compared to other figures). Reducing the temperature from 10 to 4.4°C, at a given worm density, reduces both filtration capacity and ingestion layer growth (Figs. 4 & 5). Similarly, reducing temperature from 15 to 10°C (Fig. 3A, B) reduces ingestion layer growth, despite increasing filtration rate.

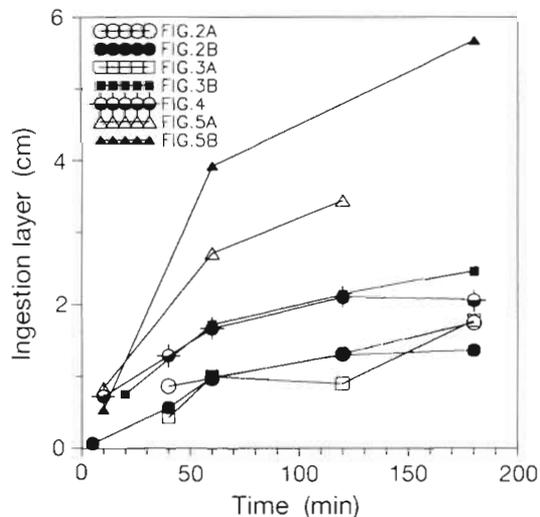


Fig. 6. Growth of ingestion layer versus time for laboratory experiments in Figs. 2 to 5. At any time, the ingestion layer is the layer of initial concentration holding as many algal cells as are actually ingested by benthic filter-feeders up to this time

Phytoplankton densities measured as chl *a* on calm days in surface and near-bottom water of Odense Fjord show a reduction of about 2 times in the bottom water (Table 3). Other measurements performed in Kertinge Nor also demonstrate the presence of phytoplankton reduction in near-bottom water (Figs. 7 to 9). A pronounced phytoplankton-reduced bottom layer, corresponding to the profiles obtained in stagnant water in the laboratory experiments, is seen in Fig. 8, especially

Table 3. Chl *a* concentrations measured in water samples collected in calm weather near the surface and just above the bottom in Odense Fjord in June and July 1993

Date	Temperature (°C)	Salinity (‰S)	Height above bottom (cm)	Chl <i>a</i> ($\mu\text{g l}^{-1}$)
29 June	18.4	—	0	2.0
			40	4.1
	19.4	—	0	2.0
			33	4.0
			17	8.1
14 July	14.8	15.8	0	1.8
			25	2.2
	15.5	15.8	0	1.9
			25	2.3
			10	5.1
18.7	15.0	0	3.2	
		10	5.1	
15 July	19.5	24.3	0	2.4
			34	3.9
	20.7	23.5	0	2.6
			25	4.2

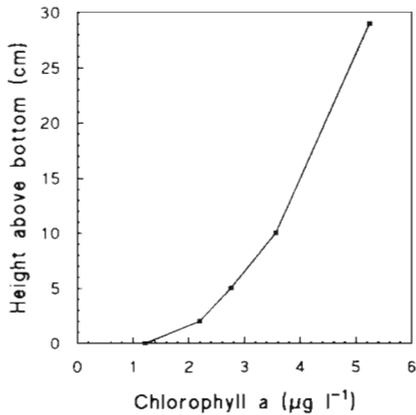


Fig. 7. Chl a concentration profile above the bottom in Kertinge Nor in August 1993

during the first 30 min with no current. However, this was subsequently changed when the tide (Fig. 8; 90 to 180 min) caused a slow current to bring a new water mass with a higher algal content into the area (notice the new chlorophyll scale used to depict the 180 min profile). A similar situation is shown in Fig. 9A.

Growth experiments

The growth experiments (Table 4) suggest that reduced phytoplankton in near-bottom water is a frequently occurring phenomenon that restricts the

growth of *Nereis diversicolor*. Specific growth rate, reflecting food supply, was about 10 times higher in worms raised 10 cm above the bottom. The maximum specific growth rates obtained in the field (2.5% d⁻¹) are considerably lower than growth rates measured on well-fed worms in the laboratory (4.9 to 5.6% d⁻¹).

DISCUSSION

Studies of vertical profiles of phytoplankton both in the field (Figs. 7 to 9) and in controlled laboratory experiments (Figs. 2 to 5) have demonstrated phytoplankton reduction in a near-bottom water layer, 5 to 10 cm in thickness on calm days, caused by filter-feeding *Nereis diversicolor*. Further, a considerably reduced growth rate of *N. diversicolor* at the sediment surface compared to worms elevated just 10 cm above the bottom (Table 4) indicates that extremely meagre food conditions may be prevailing at the bottom. This hitherto unnoticed phenomenon may also explain the observed unexpectedly low *in situ* filter-feeding activity of *N. diversicolor* (cf. Vedel et al. 1994).

The reduction of phytoplankton in the near-bottom water layer is a natural consequence of the activity of benthic filter-feeders. This is readily demonstrated in well-controlled laboratory experiments, involving no

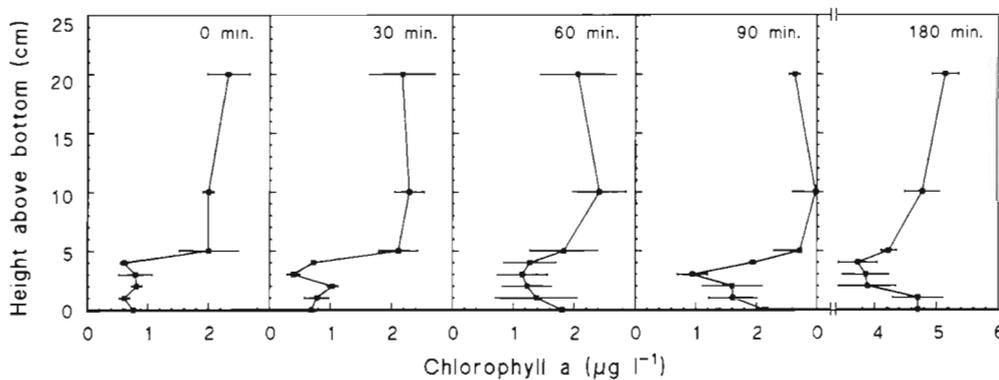


Fig. 8. Chl a concentration profiles measured at different times in Kertinge Nor in October 1993 (water temperature = 12.9°C, wind speed = 0 to 3 m s⁻¹, current speed = 2 to 3 cm s⁻¹). Error bars: ± SD (n = 2)

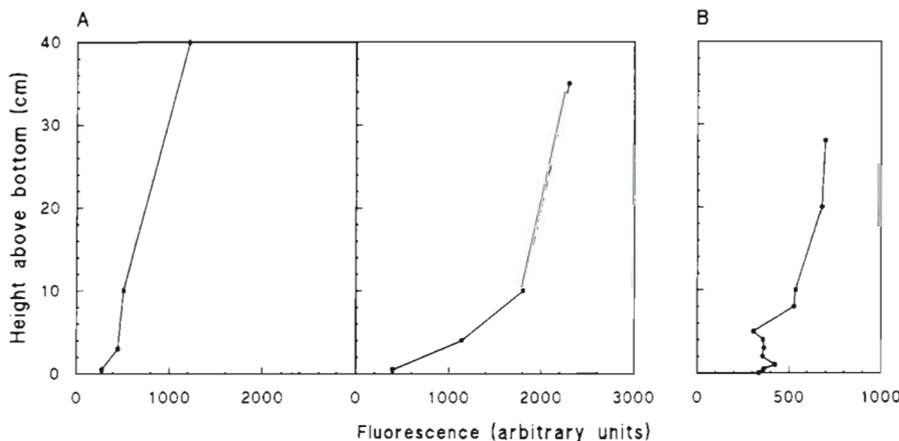


Fig. 9. Fluorescence profiles measured at different times in Kertinge Nor in (A) July and (B) September 1993. (A) First profile (time = 0): temperature = 19.2°C, wind speed = 1 to 2 m s⁻¹. Second profile (time = 5.5 h): 23.0°C, 2 to 4 m s⁻¹, chl a in surface water = 11.0 ± 1.5 µg l⁻¹ (± SD). (B) 17.6°C, 2 to 4 m s⁻¹, chl a in surface water = 2.1 ± 0.2 µg l⁻¹ (± SD)

Table 4. *Nereis diversicolor*. Mean (\pm SD) specific growth rate (μ) of worms placed at different heights (0, 4, 10 and 20 cm) above the bottom in Kertinge Nor in July 1994, and specific growth rates of worms fed algal cells (2 to 3×10^4 *Rhodomonas* sp. cells ml^{-1}) or shrimp meat (to excess). Number of worms on Days 0 and 14 are shown in brackets. Field: $24.4 \pm 0.9^\circ\text{C}$, 16.9 ± 0.6 ‰ S. Laboratory: 15°C , 17 ‰ S

Location	Food source	Body wet weight (mg)		Growth, μ (% d^{-1})	
		Day 0	Day 14		
Field	0 cm	Food source	371 ± 37 (12)	385 ± 56 (11)	0.2 ± 1.1
	4 cm	Phytoplankton	361 ± 34 (12)	454 ± 26 (8)	1.4 ± 0.5
	10 cm	–	342 ± 36 (12)	475 ± 69 (12)	2.5 ± 0.6
	20 cm	–	370 ± 37 (12)	490 ± 71 (10)	2.0 ± 0.8
Laboratory	<i>Rhodomonas</i> sp.		367 ± 41 (12)	728 ± 33 (7)	4.9 ± 0.8
	Shrimp meat		258 ± 31 (9)	566 ± 92 (9)	5.6 ± 1.0
	–		471 ± 84 (7)	942 ± 149 (7)	5.0 ± 0.7

global advection currents. Here the transient evolution of a concentration boundary layer can be modelled as a simple diffusion process, starting from an initially uniform algal concentration and subjected to a flux boundary condition at the bottom and an effective diffusivity in the agitated water. At the bottom, inhalant water, being filtered and subsequently exhaled, represents a net drain of phytoplankton that can be expressed as a flux depending on the actual concentration at the bottom. In addition, inhalant and exhalant currents of the filter-feeders cause a mixing of the water in a region above the bottom. This mixing process involves up-currents of filtered water with a low (or zero) phytoplankton concentration, and down-currents with a higher concentration. Over time the net result is a transport of phytoplankton in the direction of decreasing concentration, a process that may be modelled in the usual way by Fick's law. The effective diffusivity in this law must be determined from experi-

ments, and it is expected to increase with both strength of exhalant currents and population density of filter-feeders. Estimates of the magnitude of the effective diffusivity and actual filtration rates, determined from the present experiments (Figs. 2 to 5), have been used to solve the diffusion problem, assuming algal cells to be neutrally buoyant (P. S. Larsen unpubl.). The results are expressed as the increase with time of the previously defined ingestion layer. In Fig. 10, theory is compared with experimental data from the laboratory.

For the second case in Fig. 10 (the case of Fig. 5), diffusion theory gives a satisfactory prediction. For the first case (the case of Fig. 3B), however, the data fall far below predictions. One explanation for this difference is that organized convective currents still may have been present. It is more likely, however, that the population filtration capacity measured previous to the algal depletion experiment (Table 2) was not fully utilized during this experiment—possibly due to the disturbance of the sensitive filter-feeding worms. The considerable experimental uncertainty should also be noted.

More complicated and general cases of grazing impact by benthic filter-feeders involve turbulent and/or tidal water currents (e.g. Wildish & Kristmanson 1984, Fréchette & Bourget 1985, O'Riordan et al. 1993, Butman et al. 1994). Here, the distribution of phytoplankton concentration may, in principle, be modelled as a convection-diffusion process. The effective diffusive transport through a horizontal current leads to a boundary layer whose spatial development is dependent on: (1) the extent of populated area of bottom, (2) the upstream concentration, and (3) the mixing due to turbulence of the flow and wind-driven circulation, in addition to that induced by the filter-feeders. A suitable model for this situation remains to be developed.

As suggested above, the strength of the exhalant currents created by filter-feeding *Nereis diversicolor* is expected to affect the development of concentration boundary layers. The velocity of exhalant currents (determined by the tube with inner diameter of 4 mm in the laboratory experiments) of *N. diversicolor* pumping 8 ml min^{-1} (10°C ; see Riisgård et al. 1992), can be estimated to be 0.7, 1.1 and 1.5 cm s^{-1} at 5, 10 and 15°C , respectively. Despite the considerable change of temperature in the present experiments, the results do not show a clear effect of it on the thickness of the mixing layer or the deduced effective diffusivity used in the modelling shown in Fig. 10.

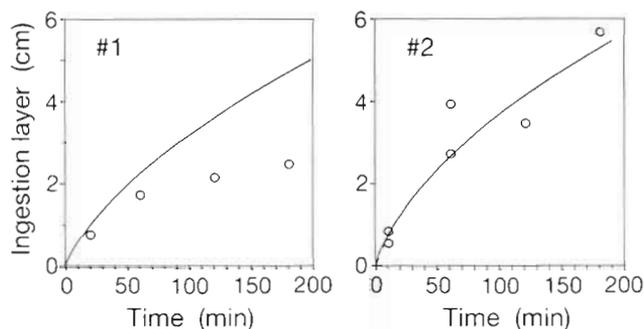


Fig. 10. Ingestion layer versus time for 2 laboratory experiments (#1 as in Fig. 3B, #2 as in Fig. 5). Experimental data (circles) and solutions to diffusion model (curves) are shown. The 1-D transient diffusion problem was solved using an effective diffusivity of $0.3 \times 10^6 \text{ m}^2 \text{ s}^{-1}$ (an average value estimated from flux and concentration gradient near bottom for data of same experiments) as well as F_{top} values from Table 2 and assuming 100% retention

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LITERATURE CITED

- Arvola L (1981) Spectrophotometric determination of chlorophyll *a* and phaeopigments in ethanol extractions. *Ann Bot Fenn* 18:221–227
- Butman CA, Fréchette M, Greyer RW, Starczak VR (1994) Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. *Limnol Oceanogr* 39:1755–1768
- Cloern JE (1982) Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar Ecol Prog Ser* 9: 191–202
- Davies BR, Stuart V, Villiers M de (1989) The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* Fauvel) and its effects on water quality in a coastal marina. *Estuar Coast Shelf Sci* 29:613–620
- Fréchette M, Bourget E (1985) Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. *Can J Fish Aquat Sci* 42:1158–1165
- Jørgensen BB (1980) Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* 34:68–76
- Judge ML, Coen LD, Heck KL Jr (1993) Does *Mercenaria mercenaria* encounter elevated food levels in seagrass beds? Results from a novel technique to collect suspended food resources. *Mar Ecol Prog Ser* 92:141–150
- Loo LO, Rosenberg R (1989) Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *J Exp Mar Biol Ecol* 130:253–276
- Nichols FH (1985) Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976–1977 drought. *Estuar Coast Shelf Sci* 21:379–388
- Nielsen AM, Enksen NT, Iversen JLL, Riisgard HU (1995) Feeding, growth and respiration in the polychaetes *Nereis diversicolor* (facultative filter-feeder) and *N. virens* (omnivorous)—a comparative study. *Mar Ecol Prog Ser* 125:149–158
- Officer CB, Smayda TJ, Mann R (1982) Benthic filter feeding: a natural eutrophication control. *Mar Ecol Prog Ser* 9: 203–210
- O’Riordan CA, Monismith SG, Koseff JR (1993) A study of concentration boundary-layer formation over a bed of model bivalves. *Limnol Oceanogr* 38:1712–1729
- Petersen JK, Riisgård HU (1992) Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. *Mar Ecol Prog Ser* 88:9–17
- Riisgård HU (1991) Suspension feeding in the polychaete *Nereis diversicolor*. *Mar Ecol Prog Ser* 70:29–37
- Riisgård HU (1994) Filter-feeding in the polychaete *Nereis diversicolor*: a review. *Neth J Aquat Ecol* 28:453–458
- Riisgård HU, Vedel A, Boye H, Larsen PS (1992) Filter-net structure and pumping activity in the polychaete *Nereis diversicolor*: effects of temperature and pump-modelling. *Mar Ecol Prog Ser* 83:79–89
- Vedel A, Andersen BB, Riisgård HU (1994) Field investigations of pumping activity of the facultatively filter-feeding polychaete *Nereis diversicolor* using an improved infrared phototransducer system. *Mar Ecol Prog Ser* 103: 91–101
- Vedel A, Riisgård HU (1993) Filter-feeding in the polychaete *Nereis diversicolor*: growth and bioenergetics. *Mar Ecol Prog Ser* 100:145–152
- Wildish DJ, Kristmanson DD (1984) Importance to mussels of the benthic boundary layer. *Can J Fish Aquat Sci* 41: 1618–1625

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