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# Impact of introduced juvenile mussel cultures on the pelagic ecosystem of the western Wadden Sea, The Netherlands

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ABSTRACT: Pelagic mussel collectors provide an alternative to fishing for mussel seed from natural beds. These collectors, which have been recently introduced in the Dutch part of the Wadden Sea, facilitate the settlement and survival of blue mussel *Mytilus edulis* larvae. We assessed the removal of plankton by juvenile mussels and the recovery of plankton after filtration. A mesocosm experiment, using natural sea water, was executed on 12 occasions from June to October in 2010 and 2011. Mussel filtration resulted in large reductions in nanophytoplankton, ciliate and total chlorophyll biomasses (65–62%), while picophytoplankton and bacterial biomasses were reduced to a lower extent (38 and 18%). After filtration, mussels were removed and the plankton community was allowed to recover for 8 d, which is the average residence time of water in the area. During this recovery period, net growth rates of bacteria, pico- and nanophytoplankton increased initially in the mussel-filtered mesocosms, but at the end of the recovery period, growth rates were similar in mussel-filtered and control mesocosms. At the end of the recovery period, plankton concentrations between control and mussel mesocosms were not statistically different despite the initial large reduction due to mussel filtration. Our results suggest that nutrients released by mussels during filtration might have stimulated the filtered plankton community, enabling recovery to filtration within 8 d.

KEY WORDS: Bivalves · Filtration · Mesocosm · *Mytilus edulis* · Autotrophic · Heterotrophic · Plankton · Wadden Sea

## INTRODUCTION

In the Wadden Sea, a shallow estuarine system, benthic bivalves are considered key components of the ecosystem (e.g. Verwey 1954, Dankers & Zuidema 1995, Piersma et al. 2001), with the blue mussel *Mytilus edulis* as one of the most abundant species in terms of biomass (Dekker 1989, Beukema & Cadée 1996, Dekker & Waasdorp 2007). In the Wadden Sea, mussels can be found on natural intertidal and subtidal beds as well as on subtidal culture lots (Dankers & Zuidema 1995). Due to the recent introduction of pelagic collectors, mussels are now also present in the water column. Pelagic mussel seed collectors consist of nets or ropes and facilitate the settlement and survival of mussel larvae. After settlement, which takes place in June, the settled larvae grow up to a size of ~25 mm within 4 mo. After being harvested in October the juvenile mussels are sown on culture lots. The pelagic collectors provide an alternative to fishing for juvenile mussels (mussel seed) from natural mussel beds. Both the decrease in

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the supply of juvenile mussels harvested from natural beds as well as governmental policy regulations to protect these beds led to the introduction of artificial mussel collectors. The policy aim is to upscale the number of collectors to a yearly harvest of 40 million kg of mussels by 2020 (Meijer et al. 2009). In this study, we describe the potential impact of filtration by these juvenile mussels on plankton in the Wadden Sea.

Filtration by mussels results in depletion of plankton at a local scale. Whether depletion will be detectable on larger spatial or temporal scales depends on the density of filter feeders, the residence time of an ecosystem and the production capacity of the primary producers or, in other words, whether losses due to filtration can be balanced by growth (Dame & Prins 1997). In systems where primary production is limited by nutrient availability, enhanced recycling of nutrients by filter feeders can result in increased growth rates of primary producers (Newell 2004); these enhanced growth rates might be large enough to compensate for loss of biomass through grazing. In these nutrient-limited systems, compensation mechanisms might thus result in little or no change in phytoplankton biomass, and even an increase in primary production has been recorded (Prins & Smaal 1994, Caraco et al. 1997). In systems where primary production is light limited, the removal of suspended particles by filter feeders will increase light penetration in the water column, potentially increasing phytoplankton growth rates (Filgueira et al. 2015). However, a small increase in light might initially stimulate phytoplankton growth, but the resulting increase in biomass is likely to again reduce light penetration (Caraco et al. 1997). The stimulation of phytoplankton growth with increased light penetration is thus expected to be minimal.

Several studies have illustrated this variable response to filtration in the different systems; Alpine & Cloern (1992) reported a decrease in both chlorophyll and primary production after the invasion of the clam *Putamocorbula amurensis* in San Francisco Bay, USA, while in the same system, 15 yr later, a decrease in total bivalve biomass coincided with an increase in chlorophyll and primary production (Cloern et al. 2007). San Francisco Bay is a turbid, nutrient-rich system, where primary production is limited by light (Alpine & Cloern 1988, Cloern & Dufford 2005). In other systems, where primary production was limited by available nutrients, such as Grande-Entrée Lagoon, Canada (Trottet et al. 2007), or Narragansett Bay, USA (Oviatt et al. 2002), an increase in bivalve density was related to an increase in primary production, while chlorophyll concentration did not change (Doering et al. 1986, Trottet et al. 2008a).

The response of a system to filtration is complicated by the impact bivalves might have on heterotrophic plankton. Heterotrophic organisms can serve as an important food source for bivalves, and filtration can thus result in (local) depletion of heterotrophs like rotifers, heterotrophic nanoflagellates and ciliates (Horsted et al. 1988, Kreeger & Newell 1996, Wong et al. 2003, Nielsen & Maar 2007, Maar et al. 2007, Trottet et al. 2008a). Since these heterotrophs are the main predators on bacteria and small phytoplankton, the removal of these predators by bivalves might alter the competitive outcome between small and larger algae. Since smaller algal cells (<3 µm) are less well retained compared to larger cells (>3 µm; Riisgård & Møhlenberg 1979, but see Strohmeier et al. 2012) and since the small cells are assumed to be better competitors for light and nutrients (Riegman et al. 1993), an increase in small-sized phytoplankton abundance could be expected to occur under heavy filtration pressure. The few studies that included heterotrophic plankton when examining the effect of bivalves on the plankton community found a decrease in microzooplankton as a result of bivalve grazing (Lam-Hoai et al. 1997, Pace et al. 1998, Nielsen & Maar 2007, Maar et al. 2007, Trottet et al. 2008b, Froján et al. 2014). A decrease in heterotrophic nanoflagellate predators was suggested as an explanation for the increase in picophytoplankton (<2 µm) (Cranford et al. 2009), while in other areas a decrease in nano-sized predators (2–20 µm) did not result in an increase of the picoalgae (Froján et al. 2014). More insight in the effect of bivalves on heterotrophic plankton is needed to fully understand the overall impact of suspension feeders (Greene et al. 2011, Froján et al. 2014).

The aims of this study were to (1) estimate the impact of filtration by pelagic juvenile mussels on the plankton in the Wadden Sea and (2) to investigate the recovery potential of the different plankton groups after mussel filtration. To meet these aims, we conducted a mesocosm experiment on 12 occasions. In this experiment, natural sea water was exposed to mussel filtration for a few hours after which the mussels were removed from the mesocosms. This set-up mimicked the passage of a volume of water through a (series of) mussel collector(s). The removal of the mussels marked the end of the 'filtration period' and the onset of the 'recovery period'; during 8 to 9 d, a period comparable to the average resident time in the Wadden Sea (Ridderinkhof et al. 1990), the

plankton community was allowed to recover. For bacteria, pico- and nanophytoplankton and, on some occasions, ciliates, the response to mussel filtration is described.

## MATERIALS AND METHODS

In order to measure the response of the plankton community to filtration by juvenile mussels, an experiment was performed in several blocks during 2010 to 2011. Natural sea water was incubated with mussels for a few hours ('filtration period'). At the end of this period, mussels were removed and the plankton community was allowed to recover for a period of 8 to 9 d ('recovery period'). Within the plankton community, 4 groups were distinguished; bacteria, picophytoplankton (defined here as 0.2 to <3 µm), nanophytoplankton (3–20 µm), and ciliates (20–200 µm). Larger zooplankton were not included in the current study, as we assumed that juvenile mussels do not effectively filter out larger heterotrophs (Horsted et al. 1988).

### Study animals

In 2010 and 2011, a small collector was placed in the Marsdiep (Fig. 1). This collector consisted of filamentous ropes facilitating mussel settlement. After settlement around June, mussels increase in size up to ~25 mm when harvested in October. Mussel sizes used in this study were between 1.5 and 25 mm. The day before each incubation experiment, ropes with juvenile mussels were collected, transported in sea water and stored in a protective cage suspended in the Royal Netherlands Institute for Sea Research (NIOZ) harbour (Fig. 1). Water temperature in this location was comparable to their original location (±2°C). After each experiment, the number of mussels, average length (± 0.01 mm) and dry weight (dried at 60°C for 48 h, ± 0.1 mg) were established. Dry weight included both shell and flesh.

### Experimental set-up

In 2010, juvenile mussels on pieces of rope were incubated in mesocosms, and the experiment was repeated with a modified mesocosm (see below) in 2011. In 2010, the round mesocosms had a height of 83 cm and a diameter of 39 cm, and the maximum volume they could contain was 99 l. On each date

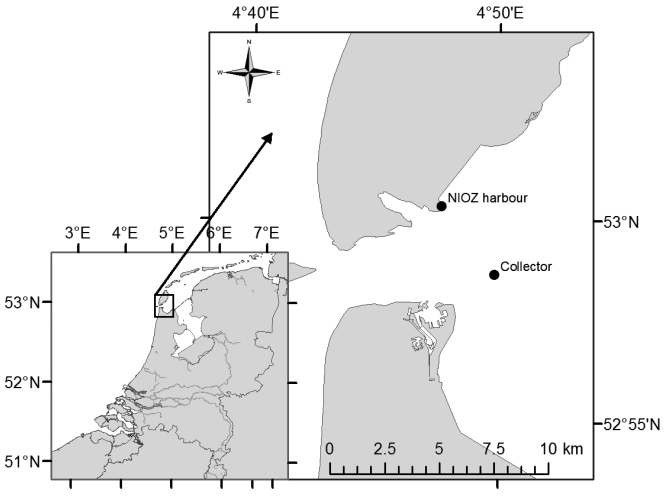


Fig. 1. Location of the pelagic mussel collector and the experimental site (Royal Netherlands Institute for Sea Research [NIOZ] harbour) in the Marsdiep (western Wadden Sea), The Netherlands

(Table 1) 5 mesocosms (4 for block 1) were filled with natural seawater by submersion and placed in the NIOZ harbour (Fig. 1). The distance from the water level to the rim of the mesocosm was measured to determine the exact water volume for each mesocosm on each date, which in 2010 was on average 85 l. Both before and after the incubation, complete mixture of the water was checked by comparing the readings of a miniature submersible fluorometer (microFlu, TriOS) at different depths within the mesocosm. Mussels were added to 3 mesocosms (2 for block 1), while 2 were not incubated with mussels and served as controls. For each block, we verified that the initial plankton concentrations in all mesocosms were not statistically different from each other. Mussel ropes were placed in the mesocosm and a slow rotating mixer enabled gentle mixing of the water while avoiding damage of the fragile microzooplankton community. The removal rate of phytoplankton biomass by juvenile mussels was monitored using the fluorometer. To establish reliable clearance rates on the different components of the plankton community, it is important that plankton concentrations do not get too depleted, since this will result in an underestimation of the clearance rate (Riisgård 2001). Based on trial experiments, we decided to terminate the experiment when the fluorescent signal was 30% of the start value or above. At the end of the incubation, mussels were removed and the mesocosms were closed off using a transparent lid in 2010. First results seemed to indicate that phytoplankton bloomed in both the mussel-filtered and the control mesocosms. These blooms were attributed to higher column irradiance received by

Table 1. General characteristics (means over all mesocosms ± SD) for each block at the start of the filtration experiment. $K_d$: attenuation coefficient, Tchl: total chlorophyll concentration, T: average water temperature (temperature changes during the recovery experiment were always within 0.5°C); Inc. time: average incubation time of blue mussels *Mytilus edulis* in the mesocosms; Length: shell length of mussels; DW: total dry weight of mussels, including the shell (see 'Materials and methods' for details)

| Block | Date | $K_d$ ($m^{-1}$) | Tchl (µg $l^{-1}$) | T (°C) | Inc. time (h) | Length (mm) | DW (g) |
|---|---|---|---|---|---|---|---|
| 1 | 21-Jun-10 | 0.86 ± 0.06 | 5.10 ± 0.97 | 17 | 2.6 | 1.71 ± 0.72 | 174 ± 13.6 |
| 2 | 5- Jul-10 | 1.18 ± 0.11 | 4.53 ± 0.43 | 21 | 2.5 | 3.13 ± 2.08 | 60 ± 31 |
| 3 | 19- Jul-10 | 1.28 ± 0.19 | 4.68 ± 1.05 | 19 | 2.0 | 4.65 ± 2.80 | 244 ± 117 |
| 4 | 3-Aug-10 | 0.58 ± 0.15 | 3.08 ± 0.69 | 19 | 0.5 | 7.17 ± 2.69 | 192 ± 111 |
| 5 | 16-Aug-10 | 0.86 ± 0.06 | 5.02 ± 0.70 | 19 | 2.4 | 17.49 ± 7.90 | 144 ± 90 |
| 6 | 21-Sep-10 | 0.23 ± 0.01 | 1.45 ± 0.08 | 16 | 1.5 | 13.27 ± 4.73 | 122 ± 23 |
| 7 | 13-Oct-10 | 0.48 ± 0.06 | 9.14 ± 1.95 | 15 | 1.1 | 15.32 ± 6.34 | 178 ± 22 |
| 8 | 28-Jun-11 | 0.48 ± 0.03 | 2.93 ± 0.19 | 19 | 2.1 | 8.15 ± 0.58 | 21 ± 0.5 |
| 9 | 12-Jul-11 | 0.85 ± 0.01 | 4.83 ± 0.08 | 19 | 2.5 | 11.81 ± 0.48 | 15 ± 1 |
| 10 | 27-Jul-11 | 0.89 ± 0.03 | 4.18 ± 0.22 | 18 | 3.1 | 13.49 ± 0.07 | 33 ± 0.4 |
| 11 | 9-Aug-11 | 0.66 ± 0.04 | 2.36 ± 0.08 | 15 | 3.2 | 17.49 ± 2.05 | 36 ± 1 |
| 12 | 7-Sep-11 | 0.80 ± 0.01 | 3.83 ± 0.63 | 17 | 2.8 | 19.92 ± 0.17 | 48 ± 1 |

algae in the mesocosms compared to the average irradiance received by algae in the Wadden Sea (see 'Discussion'). In 2011, incoming light was reduced by covering the lids with shading foil, and the mesocosms were adjusted to make the walls less transparent. These adjustments resulted in a smaller volume, and the average volume the mesocosms contained in 2011 was 65 l. Average column irradiances in 2011 were more comparable to column irradiances in the Wadden Sea (Table 2).

During the recovery period, temperature (±0.5°C), oxygen, salinity (Hach multimeter) and light attenuation (Wetlab CST) were measured, and samples were taken for total chlorophyll, pico-and nanophytoplankton and ciliate cell counts. In 2010, sampling and measurements were performed only at the end of the recovery period, whereas in 2011, measurements were performed every day, while sampling took place every other day. In 2011, bacteria were sampled in addition to all other parameters. Ciliates were sampled for all 12 blocks, but not all samples were analysed due to lack of time and money. The total volume sampled per block was always less than 10% of the original volume. At the end of the 8 to 9 d recovery period, mesocosms were emptied, cleaned and stored for the next occasion.

## Plankton

### Bacteria

Triplicate subsamples (1 ml) for enumerating free-living bacteria were fixed with glutaraldehyde (0.5% final concentration), mixed and then stored at –80°C until analysis. Analysis of samples, which always took

Table 2. Mean column irradiances (Eq. 1) in the mesocosms (depth, $z = 0.8$ m) at the start and end of the recovery period. Average column irradiances in the western Wadden Sea (see Fig. 1) are also given for the start date of each experiment. Light above 200 µE $m^{-2}$ $s^{-1}$ is considered saturating for phytoplankton growth (Gieskes & Kraay 1975, Colijn 1982). Non-saturating levels are in *italics*; nd: not determined

| Block | Start date | Recovery period (d) | Control | | Mussel | | Wadden Sea |
|---|---|---|---|---|---|---|---|
| | | | Start | Recovery | Start | Recovery | Start |
| 1 | 21-Jun-10 | 9 | 522 | nd | 550 | nd | 295 |
| 2 | 5-Jul-10 | 9 | 387 | 415 | 474 | 481 | *123* |
| 3 | 19-Jul-10 | 9 | 390 | 381 | 536 | 424 | *118* |
| 4 | 3-Aug-10 | 8 | 363 | 292 | 422 | 359 | *163* |
| 5 | 16-Aug-10 | 9 | 289 | 272 | 342 | 301 | *113* |
| 6 | 9-Sep-10 | 8 | *51* | 245 | *54* | 244 | *39* |
| 7 | 13-Oct-10 | 9 | *192* | 158 | *216* | *169* | *96* |
| 8 | 28-Jun-11 | 8 | *153* | 253 | *172* | 265 | *154* |
| 9 | 12-Jul-11 | 8 | *148* | *167* | *176* | *185* | *113* |
| 10 | 27-Jul-11 | 8 | *199* | *148* | 257 | *168* | *143* |
| 11 | 9-Aug-11 | 8 | *182* | *152* | 220 | *154* | *153* |
| 12 | 7-Sep-11 | 8 | *28* | *98* | *36* | *100* | *19* |

place within 1 mo after sampling, were performed using a flow cytometer (C6, BD Accuri, excitation with 488 nm laser). Samples were diluted with 10% TE buffer, SYBR green I (Invitrogen) stain was added (0.1% final concentration), and samples were incubated in the dark for 15 min. The 530 nm laser (FL1) was used to detect the stained cells.

### Pico- and nanophytoplankton

Phytoplankton cell counts were performed by means of flow cytometry (BD Accuri C6). Triplicate water samples (1 ml) were processed unfixed, immediately after collection. Fluorescence at wavelengths >670 nm (FL3) was ascribed to chlorophyll. Forward scatter, calibrated with beads (spherotech, BD Accuri) was used as an indication of cell size. Based on the relative fluorescence to size, a distinction between phytoplankton and debris was made. It is generally assumed that mussels effectively retain particles larger than 3 µm and that for smaller particles the efficiency rapidly drops (Møhlenberg & Riisgård 1978). We decided to make a distinction between small-sized cells that are assumed to be less well retained (here called picophytoplankton and defined as <3 µm) and well retained cell sizes (here called nanophytoplankton, 3–20 µm). Note that the definition of pico- and nanoplankton deviates from the conventional definition of <2 µm and 2–20 µm, respectively.

### Ciliates

For enumeration of ciliates, 1 subsample (0.5–1 l) was fixed in 2 to 4 ml of acid Lugol and stored in brown glass bottles at 4°C until analysis. Samples were concentrated (10–20×) using the Utermöhl sedimentation technique (Verweij et al. 2010). Per sample, a minimum of 100 individuals or, at very low abundances, all individuals in a maximum of 10% of the concentrated sample, were counted and divided in 5 length classes (<20 µm, 20–40 µm, 40–60 µm, 60–80 µm and >80 µm), using an inverted microscope. To reduce the variability in counts, numbers were converted into carbon biomass according to the following approach; an oblate spheroid (volume: $4/3\pi ab^2$) was chosen to best represent the average shape of ciliates (cf. Putt & Stoecker 1989). The middle of the length class/2 = $a$ and the middle of the length class/4 = $b$. The estimated average volumes were then converted into carbon biomass (µg) using 0.326 volume $(\mu m^3)^{0.891}$ (Putt & Stoecker 1989).

### Chlorophyll

For the determination of total chlorophyll, duplicate subsamples (200–300 ml) were filtered through Whatman GF/F filters using low vacuum pressure (maximum −0.4 bar). Filters were stored in the dark at −80°C for no more than 2 mo. Chlorophyll was extracted by homogenisation of filters in 90% acetone with the addition of glass pearls, and the concentration of chlorophyll was determined fluorometrically (Holm-Hansen et al. 1965) using spinach chlorophyll *a* (Sigma) as a reference.

## Equations and statistics

### Column irradiances

Average column irradiances ($I_C$, PAR µE $m^{-2}$ $s^{-1}$) in the mesocosms were calculated according to Eq. (1) (Riley 1957). The average column irradiances in the western Wadden Sea during the mesocosm experiments (Table 2) were calculated by assuming an average depth ($z$) for the western Wadden Sea of 4.1 m. Daily surface irradiances ($I_0$, J $cm^{-2}$) available from the Royal Netherlands Meteorological institute (KNMI) station De Kooy (www.knmi.nl/klimatologie) were converted in PAR µE using a conversion factor of 0.24. Attenuation coefficients ($K_d$, $m^{-1}$) were measured during a regular sampling programme in the western Wadden Sea (see Jacobs et al. 2014).

$$I_C = \frac{I_0 (1 - e^{-K_d z})}{K_d z} \quad (1)$$

### Filtration losses and recovery rate

During the filtration period, mussels were incubated in natural sea water. The filtration losses ($F_P$, dimensionless), which is the fraction removed by mussels, was calculated according to:

$$F_P = \left( \frac{N_{c,0} - N_{m,0}}{N_{c,0}} \right) \quad (2)$$

where $N_{c,0}$ and $N_{m,0}$ are the concentrations of cells at the end of the filtration period in the control and mussel treatments, respectively. For each experiment, we verified that the cell concentrations did not differ significantly between the mesocosms before filtration started.

After the filtration period, mussels were removed from the mesocosms, and this marked the beginning

of the recovery period. The recovery period lasted 8 to 9 d. Based on the changes in concentration of the different plankton groups, a net growth rate ($k$, $d^{-1}$) was calculated after 2 d and at the end of the recovery period according to:

$$k = \left(\frac{1}{t}\right)\ln\left(\frac{N_t}{N_0}\right) \quad (3)$$

where $t$ is the duration of the recovery period (2 or 8–9 d), and $N_0$ and $N_t$ are the concentration of a plankton group directly after the filtration period and on Day $t$ during the recovery period, respectively.

The recovery rate ($R_R$, $d^{-1}$) is defined as

$$R_R = \left(\frac{1}{t}\right)\ln\left(\frac{N_{m,t} / N_{c,t}}{N_{m,0} / N_{c,0}}\right) \quad (4)$$

where $N_{m,t}$ and $N_{c,t}$ represent the concentration of cells on Day $t$ in the mussel and control mesocosms, respectively.

### Statistical analysis

The chosen mesocosm set-up had as a consequence that there were, apart from the introduced factors like mussel size, several random factors throughout the experiment like water temperature, plankton community and suspended matter concentration. The influence of these extraneous factors can be eliminated by grouping the data in blocks using a randomized block design. In a randomized block design, only 1 primary factor is under consideration. In the current experiment, this is the difference in response of the plankton community in water filtered by mussels and a control treatment (no filtration). All analyses were performed using the R free statistical software environment (R Development Core Team 2011), and a significance level of $\alpha = 0.05$ was used for all tests.

## RESULTS

Mussel filtration resulted in the removal of plankton, but the losses were not equal for the different plankton groups distinguished in this study. On average, a larger fraction of the available nanophytoplankton, ciliates and total chlorophyll (0.62–0.65) was removed compared to picophytoplankton (0.38) and especially bacteria (0.18; Table 3). The removal of mussels from the mesocosms ended the filtration period and marked the onset of the recovery period. During 8 to 9 d, which is the average residence time of water in the Wadden Sea, the plankton community was allowed to recover.

In 2011, plankton samples were collected every other day during the recovery period. The plankton concentration shows fluctuations over time. Despite differences between the blocks and the increasing variation between mesocosms with time, some general patterns emerged (Fig. 2). For both bacteria and picophytoplankton, concentrations in both mussel and control treatments reached a peak on Day 2 (Fig. 2). Nanophytoplankton generally showed a peak on Day 2 in the control mesocosms, while for the mussel-filtered mesocosms the highest concentration were found on Day 8. For ciliates, no general pattern was detected.

Table 3. Fraction of plankton cells (means ± SD) removed by blue mussels *Mytilus edulis* (Eq. 2) for bacteria, picophytoplankton, nanophytoplankton and total chlorophyll (Tchl). Bacteria removal was only measured in 2011; empty cells indicate that losses were not determined for that block

| Block | Start date | Bacteria | Pico | Nano | Ciliates | Tchl |
|---|---|---|---|---|---|---|
| 1 | 21-Jun-10 | | 0.59 ± 0.08 | 0.72 ± 0.07 | 0.65 ± 0.05[a] | 0.65 ± 0.05 |
| 2 | 5-Jul-10 | | 0.36 ± 0.15 | 0.61 ± 0.21 | | 0.47 ± 0.24 |
| 3 | 19-Jul-10 | | 0.58 ± 0.06 | 0.74 ± 0.03 | | 0.71 ± 0.05 |
| 4 | 3-Aug-10 | | 0.38 ± 0.07 | 0.63 ± 0.03 | 0.70 ± 0.08 | 0.63 ± 0.04 |
| 5 | 16-Aug-10 | | 0.14 ± 0.09 | 0.47 ± 0.25 | 0.74 ± 0.06[a] | 0.63 ± 0.04 |
| 6 | 21-Sep-10 | | 0.23 ± 0.31 | 0.56 ± 0.13 | 0.59 ± 0.08 | 0.65 ± 0.16 |
| 7 | 13-Oct-10 | | 0.34 ± 0.03 | 0.46 ± 0.12 | | 0.61 ± 0.02 |
| 8 | 28-Jun-11 | 0.23 ± 0.00 | 0.55 ± 0.02 | 0.77 ± 0.02 | 0.71 ± 0.04[a] | 0.76 ± 0.02 |
| 9 | 12-Jul-11 | 0.08 ± 0.01 | 0.33 ± 0.06 | 0.48 ± 0.08 | 0.54 ± 0.04 | 0.57 ± 0.08 |
| 10 | 27-Jul-11 | 0.04 ± 0.01 | 0.46 ± 0.01 | 0.75 ± 0.01 | 0.63 ± 0.40[a] | 0.77 ± 0.03 |
| 11 | 9-Aug-11 | 0.10 ± 0.01 | 0.24 ± 0.01 | 0.84 ± 0.01 | 0.42 ± 0.25[a] | 0.79 ± 0.01 |
| 12 | 7-Sep-11 | 0.11 ± 0.01 | 0.41 ± 0.01 | 0.81 ± 0.01 | 0.74 ± 0.12 | 0.77 ± 0.03 |
| | **Mean** | **0.12 ± 0.07** | **0.38 ± 0.17** | **0.62 ± 0.19** | **0.62 ± 0.15** | **0.65 ± 0.12** |

[a]Filtration losses were determined for these blocks, but concentrations were not determined for the recovery period

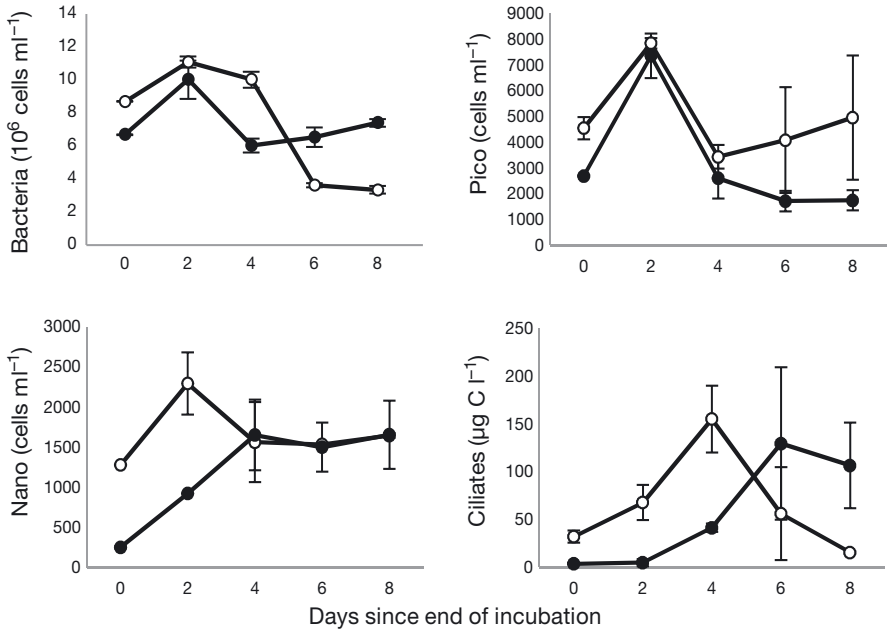


Fig. 2. Mean ± SD concentrations during the recovery period for bacteria, picophytoplankton, nanophytoplankton and ciliates. The *x*-axis indicates the days since the filtration experiment had ended; Day 8 marks the end of the recovery period. White symbols indicate the controls; black symbols indicate the blue mussel *Mytilus edulis* treatment. For this example, data from 7 September 2011 were used

During the recovery period, net growth rates ($k$) were calculated after 2 d (2011) and 8 d (both years; Eq. 3). The peaks in concentration previously described were reflected in the net growth rates (µg d$^{-1}$); 2 d after mussel filtration had ended, bacteria and pico- and nanophytoplankton responded with an increased growth rate, while after 8 d, this effect of filtration had disappeared (Table 4).

Table 4. Net growth rate (d$^{-1}$, mean ± SD) for bacteria, pico- and nanophytoplankton in both the control and blue mussel *Mytilus edulis* mesocosms, on Days 2 and 8 during the recovery period. Day 2 net growth rates as well as bacterial net growth rates were only determined for 2011. Results from the paired *t*-test to detect differences between the 2 treatments are given; *denotes a significant ($p < 0.05$) difference

| | Control | Mussel | *t* | df | p |
|---|---|---|---|---|---|
| **Day 2** | | | | | |
| Bact | 0.10 ± 0.18 | 0.28 ± 0.14 | 3.62 | 4 | 0.02* |
| Pico | 0.09 ± 0.19 | 0.35 ± 0.25 | 3.68 | 4 | 0.02* |
| Nano | −0.03 ± 0.47 | 0.32 ± 0.42 | 3.56 | 4 | 0.02* |
| **Day 8** | | | | | |
| Bact | 0.01 ± 0.08 | 0.04 ± 0.03 | 1.01 | 4 | 0.37 |
| Pico | −0.07 ± 0.09 | −0.05 ± 0.17 | −0.08 | 10 | 0.94 |
| Nano | 0.04 ± 0.09 | 0.09 ± 0.14 | −1.15 | 10 | 0.28 |

Filtration resulted in a reduced biomass for most plankton groups, and also in a changed relative abundance within the plankton community. One of the main questions in this study was whether a mussel-filtered plankton community could recover to pre-filtered concentrations within 8 to 9 d. Therefore, for the 4 plankton groups (bacteria, pico- and nanophytoplankton and ciliates) and for total chlorophyll, the concentrations at the end of the recovery period for the control and mussel-filtered mesocosms is indicated (Fig. 3). At the end of the recovery period, bacterial concentrations are comparable to the concentrations before mussel filtration (treatment: $F = 0.014$, df = 1, $p = 0.91$ and block: $F = 0.43$, df = 4, $p = 0.08$).

Picophytoplankton concentrations generally decreased during the recovery period in the mussel mesocosms (data points below 1:1 line) (Fig. 3B), but there was no significant difference between the response in the different blocks or between the control and mussel-filtered mesocosms (block: $F = 1.16$, df = 11, $p = 0.41$ and treatment: $F = 1.34$, df = 1, $p = 0.27$). On 1 occasion, 19 July 2010, a picophytoplankton bloom was observed in the mussel-filtered mesocosms.

Mussels severely reduced the concentration of nanophytoplankton on most occasions, with only between 60 and 20% of the original concentration present at the onset of the recovery period (Table 3). Despite these substantial reductions, in 8 out of 12 blocks, nanophytoplankton concentrations attained concentrations comparable to or even much higher than the concentration before filtration, but concentration in the control mesocosms also increased during the recovery period for most blocks (Table 5). Comparing the concentration of nanophytoplankton at the end of the recovery period between the mussel-filtered and control mesocosms, no significant differences between control and mussel-filtered mesocosms were detected (treatment: $F = 2.60$, df = 1, $p = 0.14$, block: $F = 1.10$, df = 11, $p = 0.44$). For total chlorophyll, the same pattern was observed as for nanophytoplankton (Fig. 3E, Table 5).

The recovery of ciliate biomass was determined for 4 blocks only (Tables 3 & 5, Fig. 3D). In 2 blocks, cili-

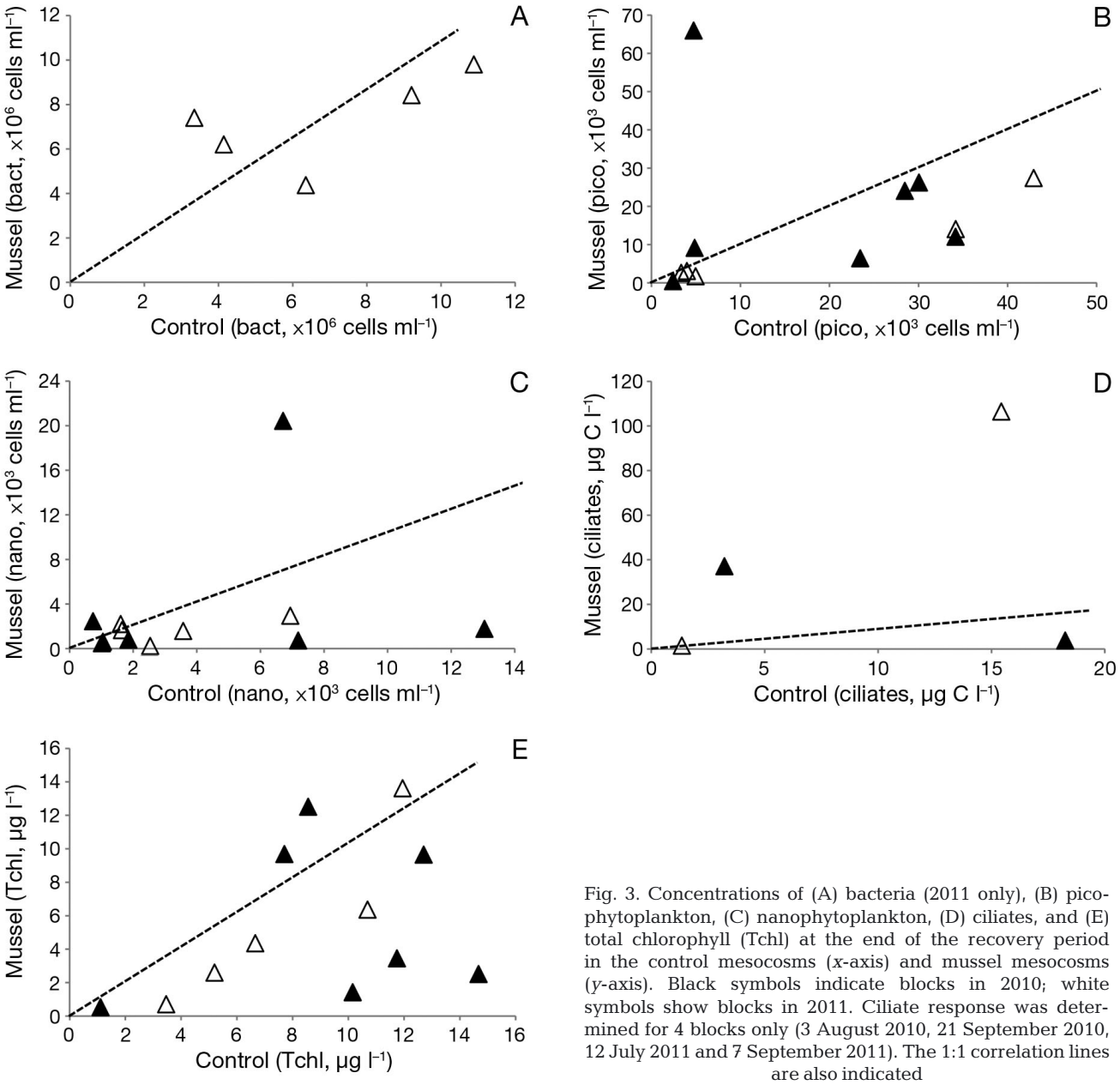


Fig. 3. Concentrations of (A) bacteria (2011 only), (B) picophytoplankton, (C) nanophytoplankton, (D) ciliates, and (E) total chlorophyll (Tchl) at the end of the recovery period in the control mesocosms (*x*-axis) and mussel mesocosms (*y*-axis). Black symbols indicate blocks in 2010; white symbols show blocks in 2011. Ciliate response was determined for 4 blocks only (3 August 2010, 21 September 2010, 12 July 2011 and 7 September 2011). The 1:1 correlation lines are also indicated

ate carbon had increased after 8 d in the mussel-filtered mesocosms, while in the control mesocosms, the biomass was comparable to the initial biomass (September 2010 and September 2011). In the 2 other blocks (August 2010 and July 2011), ciliates barely recovered after mussel filtration (Table 5).

The randomized block design of the experiment does not give insight in causes for the observed variation between blocks and treatments. A closer look at the data might reveal potential factors that help explain the variation. It is expected that at times when the phytoplankton community is light limited, an increase in light penetration due to removal of seston by mussels will stimulate phytoplankton growth. When the algal community is mainly nutrient limited, excreted nutrients by mussels likewise stimulate growth of algae. We therefore investigated the stimulating effect of mussel filtration on phytoplankton by increased light penetration ('light-limitation hypothesis') or increased nutrient availability ('nutrient-limitation hypothesis'). The recovery rate ($d^{-1}$), which is the increase in plankton concentration in the mussel-filtered mesocosm corrected for changes in the controls, was correlated with the average light (PAR µE $m^{-2}$ $s^{-1}$) in the mesocosms during the recovery period (Fig. 4A, Table 2). The correlation coefficients for the relation

Table 5. Mean ± SD concentration in the control and blue mussel *Mytilus edulis* mesocosms directly after mussel filtration ($N_0$) and at the end of the 8 d recovery period ($N_t$) for bacteria, pico- and nanophytoplankton, ciliates and total chlorophyll (Tchl)

| Block | Start date | Bacteria (cells ml$^{-1}$) | | Pico (cells ml$^{-1}$) | | Nano (cells ml$^{-1}$) | | Ciliates (µg C l$^{-1}$) | | Tchl (µg l$^{-1}$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $N_0$ | $N_t$ | $N_0$ | $N_t$ | $N_0$ | $N_t$ | $N_0$ | $N_t$ | $N_0$ | $N_t$ |
| **Control** | | | | | | | | | | | |
| 1 | 21-Jun-10 | | | 6423 | 2422 | 2654 | 1012 | | | 2.9 | 1.1 |
| 2 | 5-Jul-10 | | | 32346 ± 2468 | 23443 ± 7180 | 5535 ± 281 | 7190 ± 2720 | | | 4.7 ± 0.2 | 10.2 ± 0.4 |
| 3 | 19-Jul-10 | | | 8693 ± 20 | 4728 ± 2088 | 3551 ± 258 | 6715 ± 3035 | | | 5.2 ± 0.1 | 8.6 ± 0.3 |
| 4 | 3-Aug-10 | | | 51698 ± 15451 | 34154 ± 15169 | 2810 ± 493 | 13049 ± 2192 | 17.9 ± 15.6 | 18.3 ± 22.0 | 3.2 ± 1.0 | 11.7 ± 7.8 |
| 5 | 16-Aug-10 | | | 40359 ± 2362 | 30045 ± 2710 | 328 ± 168 | 1045 ± 265 | | | 4.8 ± 0.1 | 7.7 ± 3.9 |
| 6 | 21-Sep-10 | | | 2357 ± 610 | 4845 ± 701 | 1467 ± 19 | 734 ± 42 | 6.4 ± 2.4 | 3.2 ± 0.2 | 1.4 ± 0.1 | 14.7 ± 3.9 |
| 7 | 13-Oct-10 | | | 25955 ± 2437 | 28447 ± 3849 | 556 ± 86 | 1849 ± 1680 | | | 9.5 ± 2.1 | 12.7 ± 4.8 |
| 8 | 28-Jun-11 | $8.7\times10^6 \pm 3.1\times10^4$ | $3.3\times10^6 \pm 2.4\times10^4$ | 14043 ± 676 | 3338 ± 675 | 3773 ± 383 | 2530 ± 464 | | | 3.3 ± 0.3 | 3.5 ± 2.0 |
| 9 | 12-Jul-11 | $4.2\times10^6 \pm 6.4\times10^4$ | $4.1\times10^6 \pm 2.0\times10^4$ | 30507 ± 691 | 3966 ± 1404 | 3087 ± 445 | 3567 ± 1082 | 13.3 ± 0.6 | 1.4 ± 1.0 | 4.7 ± 0.1 | 6.7 ± 0.4 |
| 10 | 27-Jul-11 | $5.3\times10^6 \pm 2.8\times10^4$ | $1.1\times10^7 \pm 2.2\times10^5$ | 31466 ± 710 | 42922 ± 665 | 5572 ± 28 | 6940 ± 237 | | | 5.0 ± 0.2 | 5.2 ± 5.8 |
| 11 | 9-Aug-11 | $8.7\times10^6 \pm 6.0\times10^5$ | $9.2\times10^6 \pm 3.1\times10^5$ | 45040 ± 429 | 34158 ± 7473 | 2067 ± 11 | 1604 ± 278 | | | 3.0 ± 0.1 | 10.7 ± 2.5 |
| 12 | 7-Sep-11 | $4.2\times10^6 \pm 8.4\times10^4$ | $6.4\times10^6 \pm 4.4\times10^5$ | 4549 ± 1155 | 4961 ± 2414 | 1276 ± 5 | 1643 ± 30 | 32.0 ± 6.3 | 15.4 ± 1.0 | 3.5 ± 0.8 | 12.0 ± 10.8 |
| **Mussel** | | | | | | | | | | | |
| 1 | 21-Jun-10 | | | 2625 ± 525 | 439 ± 138 | 745 ± 182 | 488 ± 146 | | | 1.0 ± 0.2 | 0.4 ± 0.3 |
| 2 | 5-Jul-10 | | | 20681 ± 4766 | 6441 ± 5352 | 2122 ± 1171 | 724 ± 199 | | | 2.5 ± 1.1 | 1.4 ± 0.4 |
| 3 | 19-Jul-10 | | | 6191 ± 499 | 65965 ± 48617 | 947 ± 89 | 20435 ± 10319 | | | 1.5 ± 0.3 | 12.5 ± 1.5 |
| 4 | 3-Aug-10 | | | 32263 ± 3701 | 12054 ± 6840 | 1039 ± 86 | 1773 ± 1439 | 2.0 ± 1.0 | 3.8 ± 3.2 | 1.2 ± 0.1 | 3.5 ± 3.2 |
| 5 | 16-Aug-10 | | | 34645 ± 3527 | 26220 ± 2175 | 175 ± 97 | 617 ± 353 | | | 2.0 ± 0.1 | 9.7 ± 5.4 |
| 6 | 21-Sep-10 | | | 1830 ± 744 | 9153 ± 4387 | 892 ± 45 | 2461 ± 756 | 1.7 ± 0.3 | 36.1 ± 12.1 | 0.5 ± 0.2 | 1.9 ± 0.5 |
| 7 | 13-Oct-10 | | | 17090 ± 626 | 24062 ± 11680 | 300 ± 68 | 805 ± 142 | | | 3.7 ± 0.1 | 9.7 ± 0.5 |
| 8 | 28-Jun-11 | $6.7\times10^6 \pm 2.5\times10^4$ | $7.4\times10^6 \pm 2.4\times10^5$ | 6318 ± 270 | 2616 ± 1099 | 851 ± 66 | 241 ± 23 | | | 0.8 ± 0.1 | 0.7 ± 0.0 |
| 9 | 12-Jul-11 | $3.9\times10^6 \pm 4.9\times10^4$ | $5.1\times10^6 \pm 1.3\times10^6$ | 20603 ± 1722 | 1974 ± 792 | 1594 ± 243 | 1835 ± 417 | 5.6 ± 0.9 | 1.8 ± 1.1 | 2.1 ± 0.4 | 3.1 ± 1.2 |
| 10 | 27-Jul-11 | $5.1\times10^6 \pm 5.9\times10^4$ | $9.8\times10^6 \pm 2.1\times10^4$ | 17011 ± 397 | 27419 ± 9897 | 1382 ± 61 | 2945 ± 1103 | | | 1.1 ± 0.1 | 2.6 ± 2.5 |
| 11 | 9-Aug-11 | $7.8\times10^6 \pm 1.3\times10^5$ | $8.4\times10^6 \pm 6.7\times10^4$ | 34367 ± 403 | 14071 ± 9510 | 335 ± 19 | 2206 ± 504 | | | 0.7 ± 0.0 | 6.4 ± 4.2 |
| 12 | 7-Sep-11 | $3.7\times10^6 \pm 1.3\times10^4$ | $4.4\times10^6 \pm 2.1\times10^5$ | 2695 ± 33 | 1749 ± 392 | 248 ± 15 | 1654 ± 425 | 3.5 ± 0.0 | 106.5 ± 44.9 | 0.8 ± 0.1 | 13.6 ± 0.2 |

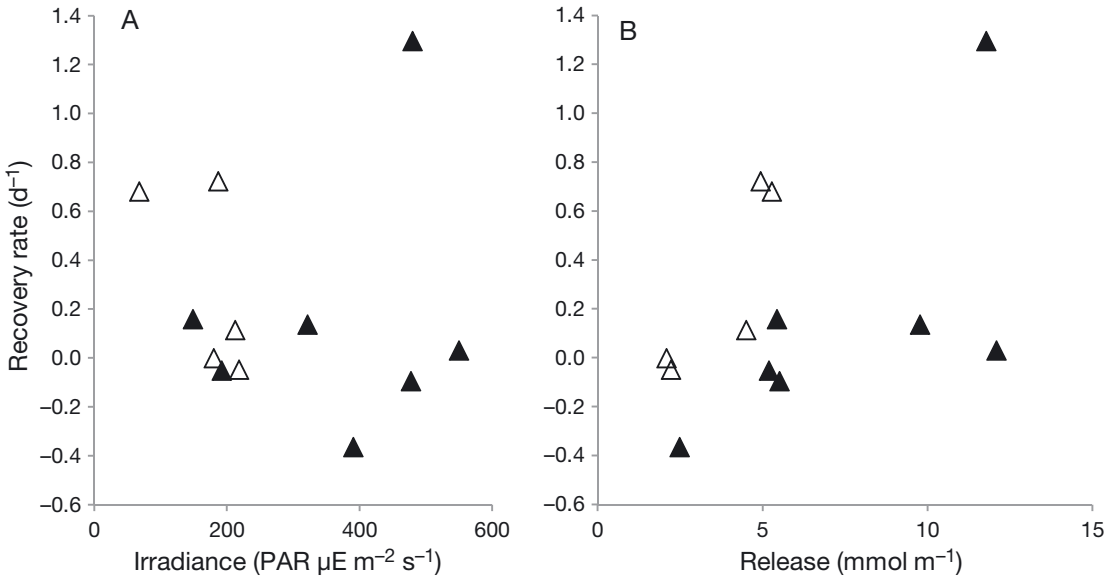


Fig. 4. (A) Relation between the recovery rate (Eq. 4) and the average light received by algal cells during the recovery period (irradiance). (B) Weight-dependent release of nutrients during the incubation, estimated using the relation described by Van Broekhoven et al. (2014) and correlated to the recovery rate. Black symbols indicate the blocks in 2010; white symbols show blocks in 2011. For these figures, the change in nanophytoplankton concentration was used

between light and recovery rate for 2010 and 2011 were 0.21 and –0.65, respectively, but these were not statistically significant (2010: $t = 0.49$, df = 5, p = 0.65, 2011: $t = -1.44$, df = 3, p = 0.24).

Nutrient fluxes are unknown during the filtration and recovery period, and to estimate the released nutrients during the incubation, we used a relation between nutrient release and juvenile mussel biomass as a proxy (Van Broekhoven et al. 2014). The relation between the release of phosphorus and release of ash free dry weight (AFDW) rate is described by the allometric relation: $0.005 \times \text{AFDW}^{0.7}$ with AFDW in mg and release in mmol m$^{-1}$ h$^{-1}$. The dry weights of mussels used in the incubation experiment (Table 1) were converted into using a factor 10 (Palmerini & Bianchi 1994). The estimated total nutrient release (incubation time in h [Table 1] multiplied by the estimated release rate) was correlated with the recovery rate (Fig. 4B). The correlation coefficients for 2010 and 2011 between recovery rate and nutrient release are 0.66 ($t = 1.98$, df = 5, p = 0.11) and 0.85 ($t = 2.84$, df = 3, p = 0.07) respectively.

## DISCUSSION

### Recovery response

The difference in response of the plankton community to mussel filtration was not easily identified. We found large differences in the recovery response in the mussel-filtered mesocosms between blocks and also in the unfiltered control mesocosms, and large changes in plankton concentrations occurred during the recovery period (Table 5). The recovery rate of nanophytoplankton positively correlated with nutrient release (Fig. 4B); for total chlorophyll the same relation was found, while for picophytoplankton the relation was absent (data not shown). More mussel biomass as well as a longer incubation resulted in more excreted nutrients, likely enhancing nanophytoplankton growth, although the correlation, with only 5 data points, was not significant (p = 0.07, 2011). The weak correlation between light penetration in the mesocosms and recovery rate in both 2010 and 2011 does not exclude that the community was (also) light limited during the recovery period. The absence of a stimulating response of mussel filtration on phytoplankton growth could be due to the fact that in 2010 (blocks 1–5), light in the mesocosms was already above saturation levels (see 'Materials and methods') due to the mesocosm design, and increased penetration due to mussel filtration did not have a further stimulating effect. In other blocks, mussel filtration did not raise the irradiances up to saturation levels, so in these cases light was still limiting phytoplankton growth. It is plausible that the phytoplankton community in the Wadden Sea is limited by both nutrients and light between June and October.

This study confirmed the removal of heterotrophic organisms by juvenile mussels (e.g. Horsted et al. 1988, Kreeger & Newell 1996). Assuming that heterotrophs, like phytoplankton, also serve as a food source for mussels (e.g. Kreeger & Newell 1996, Wong et al. 2003), not only nutrients stored in algal cells are released during the digestion process, but also nutrients stored in heterotrophs become available for new phytoplankton growth. The contribution to total planktonic carbon in the Wadden Sea from heterotrophs increases from June to September (Brussaard et al. 1996, Jacobs 2015), as does the contribution of heterotrophs to the mussels' diet. Hypothetically, more nutrients are thus available for autotrophs later in the season (van Beusekom & de Jonge 2012).

### Species shifts and food web interactions

From previous studies, it was already known that adult mussels are not very efficient suspension feeders on small planktonic components like bacteria and picophytoplankton (<2 µm), while they are generally assumed to better retain larger organisms like nano- and microsized plankton (>2 µm) including both autotrophs and heterotrophs (Lucas et al. 1987, Horsted et al. 1988, Matthews et al. 1989, Kreeger & Newell 1996, Ward & Shumway 2004, Trottet et al. 2008a, Strohmeier et al. 2012). Using a mesocosm set-up in which natural plankton was exposed to mussel filtration, we confirmed for juvenile mussels (<25 mm) that filtration mainly affected the larger components of the plankton community (3–200 µm). We only investigated the impact of mussels on the small planktonic food web (<200 µm), including ciliates but not taking into account larger organisms like copepod nauplii. Although larger mussels can retain mesozooplankton like copepod nauplii, smaller sized mussels do not effectively prey on these larger organisms (Horsted et al. 1988). This 'size-selective' filtration thus led to changes in the relative abundance of the different size classes within the plankton community investigated. Mussel filtration resulted in a reduced abundance of both competitors and predators of picophytoplankton, while the clearance rate of mussels on picophytoplankton was low (Table 3), resulting in very little change in picophytoplankton concentrations after filtration. Reduced competition and lower predation rates give rise to the expectation that mussel filtration in the long run could result in increased picophytoplankton concentrations. Previous mesocosm studies have indeed shown that filtration by mussels can shift the plankton community towards smaller sized cells (Olsson et al. 1992, Prins et al. 1995, 1997). A lower predation rate on picophytoplankton due to a reduced number of heterotrophic organism by mussels was suggested as the most plausible explanation for the observed increase in relative abundance of pico-sized algae in Thau Lagoon in France (e.g. Souchu et al. 2001), as well as in Tracadie Bay, Canada (Cranford et al. 2008). However, contrary to this expectation, we did not observe an increase in picophytoplankton at the end of the recovery period. The main differences between the current mesocosm study and the mesocosm experiments by Olsson et al. (1992) and Prins et al. (1995, 1997) as well as with the observed changes in ecosystems in France and Canada is the high and constant filtration pressure exerted by mussels and a much longer (simulated) residence time in the previous experiments and areas. Froján et al. (2014) investigated the impact of a mussel culture in Ría de Vigo, a productive area in Spain, and reported a reduction in heterotrophic predators due to mussel filtration, but no change in pico-sized plankton biomass. The ultimate effect of bivalves can thus be very different between different areas, depending on factors like the plankton composition, filtration pressure and residence time.

Several studies including this one have reported on the removal of both autotrophic as well as heterotrophic plankton by *Mytilus edulis.* To understand the impact of bivalve cultures on the surrounding plankton community, it is therefore important to include the heterotrophic organisms and food web interactions in bivalve impact studies (Greene et al. 2011, Froján et al. 2014). In the current study, we found that even though bacterial concentrations were hardly affected by mussel filtration in itself (Table 3) and concentrations before filtration were comparable to concentrations at the end of the 8 d recovery period, it cannot be concluded that this group is unaffected by filtration. After all, their net growth rate showed an initial increase in the mussel-filtered mesocosms (Table 4). The most likely explanation for this increased net growth rate is the organic material excreted by mussels. A previous study indicated that higher specific growth rates for bacteria after mussel filtration resulted in an increased biomass of microzooplankton and in particular increased biomass heterotrophic nanoflagellates (Jacobs et al. 2015). In the mussel treatments for 2 out of 4 blocks for which ciliate recovery was determined, a large increase in ciliate biomass was seen, while for the control treatments there was a loss of ciliate biomass at the end of the recovery period (Fig. 3D, Table 5). Prins & Escaravage

(2005) reported the opposite result; in their mesocosm experiment, biomasses of larger algae, heterotrophic dinoflagellates and copepods were strongly reduced in the presence of adult mussels, while ciliate biomass was not affected. According to those authors, ciliates experienced a reduced predation rate due to a declining abundance of copepods. As discussed earlier, the differences between our study and that by Prins & Escaravage (2005) are numerous, and the outcome of both experiments largely depends on both the presence of a continuous filtration pressure as well as on the (simulated) residence time.

The water in the presented study was not prefiltered and therefore large zooplankton was expected to be present in the mesocosms. Copepod nauplii are known predators on ciliates, and the presence of mesozooplankton could potentially have had an impact in the mescosms, reducing ciliate numbers. However, our time series (Fig. 2C,D) indicate that the ciliate biomasses follow the dynamics of bacteria with a delay of 2 d, which seems to suggest that in our study the presence of prey, potentially from bacteria via heterotrophic nanoflagellates, rather than predation by mesozooplankton plays a more dominant role. It can now be hypothesised that the organic carbon excreted by mussels ends up in ciliate biomass, especially later in the season. Since ciliates are the most important food source for copepods (Calbet & Saiz 2005), the introduction of mussels might indirectly enhance the food availability for copepods and thus for trophic levels that depend on copepods as food, like fish larvae.

### Impact of juvenile mussel cultures on plankton communities

Juvenile mussel filtration resulted in the removal of a large part of the plankton community. Directly after filtration, nanophytoplankton, ciliate and total chlorophyll biomasses remaining were between 38 and 35% of biomasses present at the start of the incubation. Picophytoplankton and bacterial biomasses were reduced to a much lower extent, and at the end of the filtration period, on average 62 and 82% of the start concentration were still present. During the recovery period, net growth rates of bacteria and pico- and nanophytoplankton increased initially in the mussel-filtered mesocosms, but at the end of the recovery period, this difference in growth rates between mussel-filtered and control mesocsms had disappeared again. At the end of the recovery period, the plankton concentrations between control and mussel mesocosms were no longer statistically different despite the initial large reduction due to mussel filtration. The results from this study suggest that nutrients released by mussels during filtration might have stimulated the filtered plankton community to recover to filtration within 8 d.

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