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Depletion of plankton in a raft culture of *Mytilus galloprovincialis* in Ría de Vigo, NW Spain. II. Zooplankton

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ABSTRACT: Depletion of chl *a* has previously been observed within cultivation rafts of mussels, whereas the effect of mussel filtration on the zooplankton community is unknown. Therefore we investigated the distributions of both chl *a* and zooplankton across a cultivation raft of blue mussel *Mytilus galloprovincialis* during summer in the Ría de Vigo, NW Spain. Our hypothesis was that zooplankton is depleted in the immediate region of the raft, but that the degree of depletion varies between prey types and therefore differs from that of chl *a*. We observed a significant average depletion of 57% for chl *a* and of 26 to 77% for different zooplankton groups at the lower edge and downstream of the raft. At the lowest current speeds, removal rates of protozooplankton, nauplii and copepodites were lower than for chl *a*, indicating that zooplankton escaped filtration. In contrast, removal rates of zooplankton >150 µm increased with current speed and exceeded those of chl *a* at the highest current speeds. This was due to additional filtration by passive filter feeders such as barnacles and hydroids. The present study demonstrates the effect of the raft epifaunal community on the structure of the zooplankton community in the upper productive layer, and stresses the importance of including heterotrophic plankton in estimates of potential bivalve production.

KEY WORDS: Current speed · Depletion · Epifauna · Filtration · Mussels · Raft · Zooplankton

INTRODUCTION

Raft farming of blue mussels *Mytilus galloprovincialis* has become economically important due to high production, relatively low operating costs and high prices for mussels, and the Galician upwelling systems in NW Spain are among the most productive in the world (Pérez-Camacho et al. 1991). Raft farming optimizes production by cultivating mussels in the upper parts of the water column, thereby creating direct contact between filter-feeding bivalves and the pelagic food web (Pérez-Camacho et al. 1991). In contrast, benthic mussel cultures may suffer from food limitation during stratification (Wiles et al. 2006). However, raft farming has the potential to impact the surrounding pelagic food web by removing plankton in the upper productive surface layer.

Mussels feed on phytoplankton (Riisgård 2001), detritus (Navarro et al. 1991, 1996) and zooplankton in the size range from 3 to 3000 µm (Kreeger & Newell 1996, Davenport et al. 2000, Wong et al. 2003, Lehane & Davenport 2006). A depletion of phytoplankton and detritus was previously observed around rafts (Navarro et al. 1996, Heasman et al. 1998, Petersen et al. 2008, this issue), whereas, to our knowledge, depletion of zooplankton in relation to raft farming has not been investigated. The retention efficiency and hence ingestion of different prey types by mussels may vary due to differences in prey sizes, shapes, motility patterns and escape responses (Cowden et al. 1984, Kiørboe et al. 1999, Jakobsen 2002, Wong et al. 2003), causing different depletion patterns in prey types. This was observed above a blue mussel *Mytilus edulis* bed in a Danish estuary (Nielsen & Maar 2007), where the

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depletion of zooplankton was lower than that of chl *a* and depended on zooplankton sizes and species. In marine enclosure experiments, blue mussels also reduced the number of ciliates and rotifers, while larger zooplankton such as adult copepods were less affected (Horsted et al. 1988). Raft farming is therefore expected to deplete various zooplankton taxa to different degrees and thereby to change the structure of the pelagic food web.

In the present study, we tested the hypothesis that both chl *a* and different zooplankton taxa are depleted in the immediate region of the studied cultivation raft of blue mussels, but that the degree of depletion varies between prey types. In the accompanying paper by Petersen et al. (2008), the physical properties and depletion of phytoplankton at different scales of cultivation rafts are discussed.

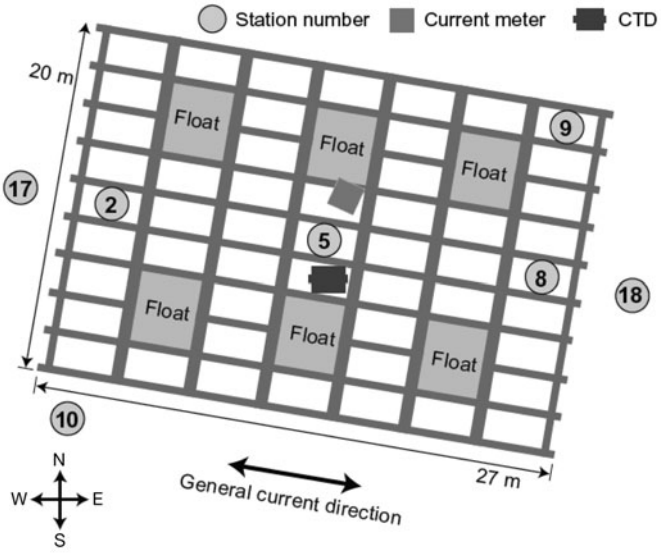

Fig. 1. Sampling stations and deployment sites of current meter and CTD within the area of a cultivation raft

MATERIALS AND METHODS

Sampling. A blue mussel *Mytilus galloprovincialis* farm located on the northern shore of the Ría de Vigo, NW Spain, was studied from 19 to 28 July 2004 (see Petersen et al. 2008, their Fig. 1). The Ría de Vigo is a coastal upwelling system characterised by predominant upwelling conditions from April to September and downwelling conditions the rest of the year. During the upwelling period, the system supports a high production of blue mussels (Navarro et al. 1991). The sampling period was characterised by a relaxation between the summer upwelling events, the water column was mainly stratified, and chl *a* values were relatively low (Arbones et al. 2008). A series of measurements was conducted along a single raft according to the tidal cycle of either ingoing (oceanic) or outgoing (estuarine) water on 5 occasions (Table 1). Temperature and salinity profiles were measured by a CTD (ME-profiler, Meerestechnik), with 0.5 m intervals in a water column of 25 m depth. The current-meter (Aanderaa RCM9) measured mean current speeds and directions at 10 min intervals at the centre of the raft at 2 m depth. Niskin water bottles and a modified WP-2 net (45 µm mesh size) samples were taken upstream 2 to 3 m before the raft, followed by sampling at the centre, at the lower edge and 2 to 3 m downstream of the raft (Table 1, Fig. 1). A depletion ratio was defined as the proportion of plankton removed compared to upstream of the raft (control). On 27 July, at ingoing tide, the downstream depletion of plankton was masked, because water sampling accidentally overlapped the transition to slack water in the tidal cycle and current direction changed. These values were therefore ignored in the calculation of depletion ratios.

Phytoplankton and protozooplankton. Samples for estimation of chl *a* and protozooplankton were taken at the surface (3 m), 9 m and below the ropes at 18 m depth (7 m above bottom) and analysed according to Petersen et al. (2008). The chl *a* size fraction >2 µm was assumed to be available for mussels (Møhlenberg & Riisgård 1978). During the sampling period, 95 and 77% of total chl *a* was >2 and >20 µm, respectively (Arbones et al. 2008). Phytoplankton carbon biomass was calculated assuming a C:chl *a* ratio of 43 estimated

Table 1. Sampling time, current direction, mean ± SE current speed, mean ± SE upstream chl *a* concentration at 3 and 9 m depth and the station numbers according to Fig.1. UTC: universal time coordinated

Date	UTC	Tide	Direction (degrees)	Current speed (m s^{-1})	Chl *a* (mg m^{-3})	Station no.			
						Upstream	Centre	Edge	Downstream
21 Jul	15:30	Ingoing	98 ± 7	0.025 ± 0.006	0.78 ± 0.09	10	5	9	–
24 Jul	8:00	Outgoing	286 ± 10	0.034 ± 0.006	0.60 ± 0.05	18	5	2	17
24 Jul	14:00	Ingoing	105 ± 2	0.041 ± 0.002	0.56 ± 0.03	17	5	8	18
27 Jul	8:00	Ingoing	116 ± 8	0.016 ± 0.002	1.50 ± 0.23	17	5	8	18
27 Jul	14:00	Outgoing	163 ± 5	0.015 ± 0.002	1.95 ± 0.52	17	5	8	18

for micro-phytoplankton (<20 µm) at the surface layer in the same area (Cermeño et al. 2005). For abundance and species composition of ciliates and heterotrophic dinoflagellates, 100 ml seawater was preserved with acidic Lugol's solution (2% final concentration). The samples were allowed to settle for 24 h in 50 ml chambers before quantification under an inverted microscope. The identification of species or morphological types was based on Nielsen & Hansen (1999). Cell volume was calculated from measurements of linear dimensions and simple geometric shapes, and the carbon biomass was estimated from volume according to the equations in Menden-Deuer & Lessard (2000).

Mesozooplankton. Mesozooplankton was collected using a modified WP-2 net (45 µm) from 10 m to the surface on all days, while an additional sample was taken from 20 m to the surface upstream of the raft on 27 July (ingoing current). The content of the cod end was concentrated on a 30 µm sieve, rinsed to a beaker and preserved in 2 to 4% buffered formalin, and stored for later enumeration and biomass estimation. The samples were split by a plankton splitter to obtain sample sizes of approximately 500 individuals. On 19 July, additional samples were taken upstream of the farm at 2, 5, 10 and 18 m depth by 5 l Niskin bottles and preserved as described above. All identifiable zooplankton were catagorised to either species or genus, and developmental stage. Prosome lengths were measured on 10 individuals from each copepodite stage, and total body length was measured on 25 to 50 nauplii. Likewise, the lengths of cladocerans and different meroplankton organisms were measured. If the upstream sample had <10 counts of a species, this series (centre, edge, downstream) was ignored. Biomass was estimated from abundance, and weight:length relationships, according to literature values (Hansen & Ockelmann 1991, Hansen 1993, Sabatini & Kiørboe 1994, Mauchline 1998, Fotel et al. 1999, Satapoomin 1999) using a carbon to dry weight (DW) ratio of 0.45 (Mauchline 1998).

Fauna on the raft. A blue mussel abundance of 750 mussels m^{-3} was calculated from a wet weight (WW) of 15 kg mussels m^{-1} of rope (Pérez-Camacho et al. 1991), assuming that 1 m rope covered a volume of 1 m^3 and using a WW:DW ratio of 5% and a typical individual DW of 1 g (F. G. Figueiras unpubl. data). From inspection of digital photos, several epifaunal species on the mussels were observed (Fig. 2). Therefore, 12 mussels with mean ±SE shell lengths of 80 ± 3 mm were collected from the submerged ropes in July 2006 and preserved in formalin, and the dominant epifauna on the shells was identified and enumerated. The numbers of hydroid stems and barnacles per mussel shell were quantified in the laboratory, and hydrotheca length and diameter of the hydroids were measured under an inverted microscope at 50× magnification.

Fig. 2. Submerged ropes overgrown with mussels and epifauna (Photo: J. N. Larsen)

Depletion model. The depletion rate, ∂t, of chl *a* (mg m^{-3}) or zooplankton (ind. m^{-3}), C, downstream of a mussel raft in the main current direction can be described by a horizontal, 1-dimensional depletion model assuming that the surface layer of the water column is totally mixed and that dispersion is negligible (Bacher et al. 2003):

$$\partial t = -u\frac{dC}{dx} + C(x,t)\times N\times CR \quad (1)$$

where u (m s^{-1}) is the current speed, x (m) is the distance along the main current direction, N (ind. m^{-3}) is the abundance of mussels and CR (m^3 ind.$^{-1}$ d^{-1}) is the individual clearance rate. Eq. (1) can be solved analytically assuming steady-state conditions ($\partial t = 0$), and the downstream food concentration C_x at distance x can then be estimated as:

$$C_x = C_0\times\exp\left(\frac{-N\times CR\times x}{u}\right) \quad (2)$$

where C_0 is the upstream food concentration. Since we have measured current velocity and upstream and downstream food concentrations at $x = l = 27$ m, this can be used to estimate the 'actual' CR in the field as:

$$CR = \frac{-\ln\left[\frac{C_l}{C_0}\right]\times u}{l\times N} \quad (3)$$

which is otherwise difficult to estimate, since it depends on population size structure, physical transport, food concentration and quality. The actual CR also takes refiltration into account and will probably be lower than observed in experiments conducted under optimal conditions (Wildish & Kristmanson 1997). Filtration by the mussel population F_C (d^{-1}) can finally be estimated as:

$$F_C = CR\times N \quad (4)$$

For comparison of filtration rates of phytoplankton F_{chl} and zooplankton F_{zoo}, we defined a retention efficiency *RE* as:

$$RE = \frac{F_{zoo}}{F_{chl}} \quad (5)$$

Ingestion rates of plankton were calculated as F_C multiplied by the average carbon biomass $\overline{C}$ (mg C m^{-3}) for each plankton group:

$$\overline{C} = \frac{C_0 - C_l}{\ln\left(\frac{C_0}{C_l}\right)} \quad (6)$$

Maximum specific growth rates (d^{-1}) of mussels were calculated from ingestion rates using a maximum absorption efficiency of 0.81% (Navarro et al. 1991) and a C:DW ratio of 0.40 for mussels (Smaal & Vonck 1997). Total ingestion ING (g C d^{-1}) of phytoplankton and zooplankton by the farm was calculated as:

$$ING = \overline{C}\times F_C\times R\times A_{raft} \quad (7)$$

where the raft volume A_{raft} was 6480 m^3 (27 × 20 × 12 m) and the number of rafts was R = 68. Required specific phytoplankton and zooplankton growth rates G (d^{-1}) to sustain the zooplankton biomass within the farm with volume A_{farm} of 108×10^5 m^3 (600 × 1500 × 12 m) was estimated as:

$$G = \frac{ING}{(A_{farm} - R\times A_{raft})\times C_0} \quad (8)$$

assuming that C_0 is representative for the concentration between rafts.

Statistics. Depletion ratios at the centre, edge and downstream stations were tested for differences from the upstream depletion ratio of 1 by 1-sample *t*-tests using a Type I error of 5%. Zooplankton species were aggregated into larger groups according to their size and swimming abilities. The 6 groups were: (1) dinoflagellates, (2) ciliates, (3) copepods <300 µm (all nauplii), (4) copepods 300 to 600 µm (all C_I to C_{III} and C_{IV} to C_{VI} of *Oithona similis*), (5) copepods >600 µm (C_{IV} to C_{VI} of *Paracalanus parvus*, *Temora longicornis*, *Pseudocalanus* spp. and *Acartia clausi*, and C_I to C_{VI} of harpacticoid copepods), and (6) other mesozooplankton including cladocerans (*Evadne nordmanni*) and meroplankton (cirriped nauplii, bivalve, gastropod and polychaete larvae). Chl *a* >2 µm, ciliates and dinoflagellates at 18 m depth were likewise tested as 1 group, because their size and depletion ratios were similar. In the case of zooplankton groups with a depletion ratio significantly different from 1, we tested whether the retention ratio (Eq. 5) was significantly different from 1 at the different current speeds listed in Table 1. Simple linear and non-linear regression lines were calculated using the least squares method and a Type I error of 5%. All statistical tests were conducted using SPSS (Ver. 11.0) for Windows.

RESULTS

Local environment

The water column was thermally stratified on the 3 sampling days, and the depth of the upper surface mixed layer was 6 to 10 m. Diurnal tidal currents were easterly for ingoing oceanic water and south-easterly or westerly for outgoing estuarine waters (Table 1). The current speed measured from 0.5 h before to the end of sampling (1 to 2 h) varied from 0.015 to 0.041 m s^{-1} (Table 1).

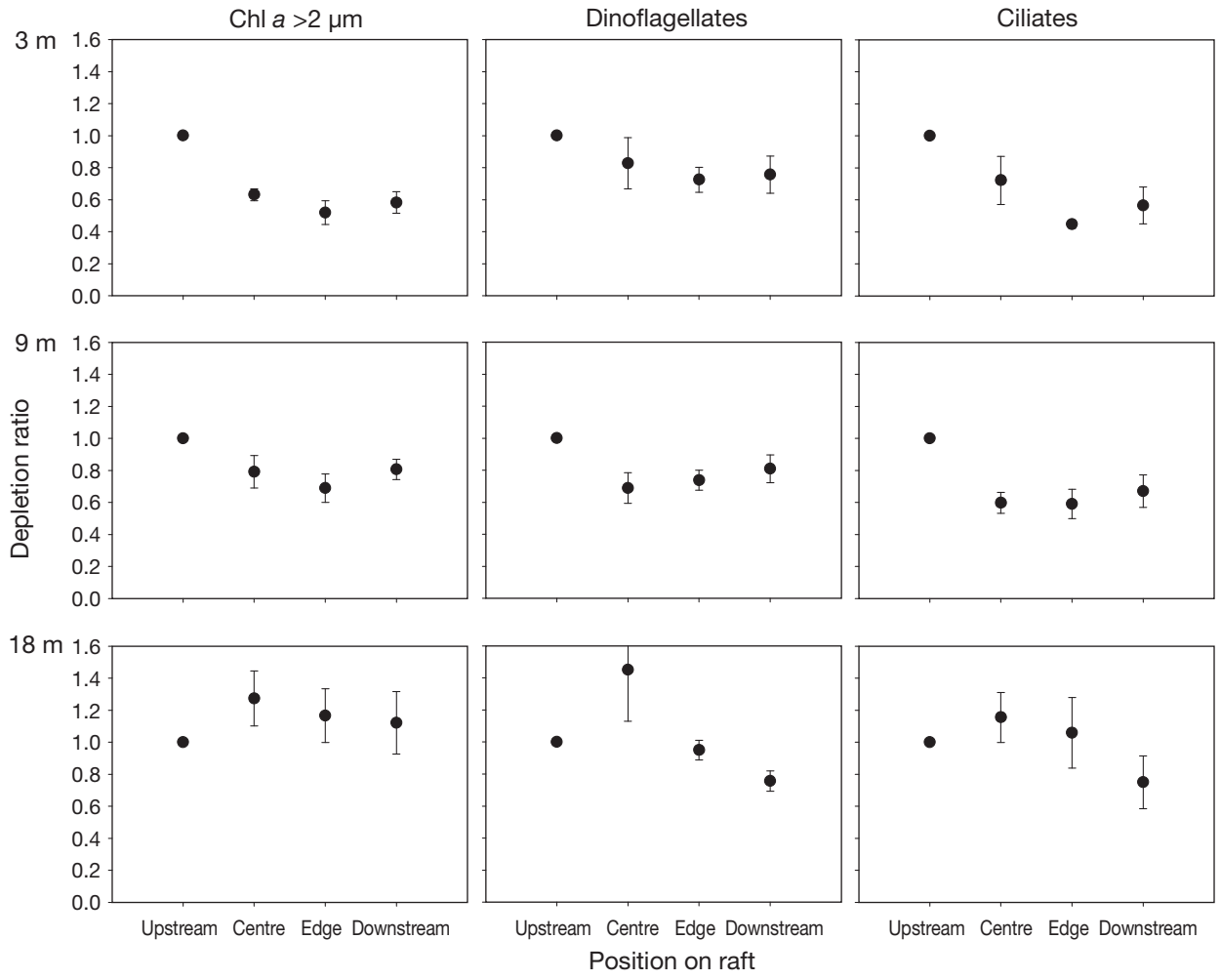

Fig. 3. Mean (±SE) depletion ratio of chl *a* >2 µm, dinoflagellates and ciliates at 3, 9 and 18 m depth on all sampling days

A significant depletion of chl *a* was observed at the centre, edge and downstream of the raft at 3 and 9 m depth (Fig. 3, Table 2) and was 57 ± 5% (mean ± SE) downstream (Table 3). There was no difference in means of F_{chl} between 3 and 9 m depth (paired *t*-test, $t_3 = 1.400$, $p > 0.05$) and the overall mean (±SE) F_{chl} was 52 ± 6 d^{-1} (Eq. 4). There was no significant correlation between F_{chl} and upstream chl *a* concentration (Spearman, n = 8, p = 0.60). The estimated CR of chl *a* was 2.9 l h^{-1} using an abundance of 750 mussels m^{-3} (Eq. 3). The growth rate was <0.5 d^{-1} based on the estimated CR and phytoplankton carbon biomass.

Table 2. One-sample *t*-tests of depletion ratios at the centre, edge and downstream stations; *significantly different from the upstream value of 1

	Centre		Edge		Downstream	
	p	df	p	df	p	df
Chl *a* >2 µm (3 and 9 m)	<0.001*	9	<0.001*	9	<0.001*	7
Dinoflagellates (3 and 9 m)	0.026*	9	0.001*	9	0.041*	7
Ciliates (3 and 9 m)	0.002*	9	0.001*	9	0.004*	7
Chl *a* >2 µm, dinoflagellates and ciliates (18 m)	0.045* (>1.00)	11	0.311	11	0.476	8
Nauplii (<300 µm)	<0.001*	24	<0.001*	22	<0.001*	19
Copepodites (300–600 µm)	<0.001*	26	<0.001*	26	<0.001*	20
Copepodites (>600 µm)	0.825	23	0.022*	23	0.002*	18
Meroplankton, *Evadne nordmanni*	<0.001*	23	<0.001*	21	<0.001*	19

Table 3. Mean (±SE) length and depletion ratio estimated at the edge (21 July) and downstream (24 to 27 July) of the raft

	Stages	Length	$C(l):C(0)$
Chl *a* >2 µm (3 and 9 m)	–	–	0.57 ± 0.05
Dinoflagellates (3 and 9 m)	–	31 ± 1	0.70 ± 0.04
Ciliates (3 and 9 m)	–	50 ± 2	0.55 ± 0.08
Oithona similis	Nauplii	150 ± 10	0.46 ± 0.19
	CI–CIII	277 ± 10	0.26 ± 0.10
	CIV–CVI	432 ± 6	0.49 ± 0.22
Paracalanus parvus	Nauplii	160 ± 10	0.26 ± 0.10
	CI–CIII	382 ± 14	0.33 ± 0.10
	CIV–CVI	727 ± 22	0.44 ± 0.18
Temora longicornis	Nauplii	264 ± 14	0.39 ± 0.08
	CI–CIII	469 ± 14	0.49 ± 0.07
	CIV–CVI	777 ± 21	0.55 ± 0.14
Pseudocalanus spp.	Nauplii	280 ± 10	0.46 ± 0.13
	CI–CIII	543 ± 34	0.56 ± 0.15
	CIV–CVI	792 ± 29	0.77 ± 0.08
Acartia clausi	Nauplii	238 ± 15	0.32 ± 0.14
	CI–CIII	467 ± 12	0.39 ± 0.10
	CIV–CVI	734 ± 21	0.71 ± 0.40
Harpacticoid copepods	CI–CVI	686 ± 48	0.61 ± 0.25
Evadne nordmanni	–	700 ± 38	0.33 ± 0.15
Cirriped nauplii	–	404 ± 39	0.31 ± 0.10
Bivalve larvae	–	174 ± 17	0.52 ± 0.10
Gastropod larvae	–	208 ± 16	0.43 ± 0.18
Polychaete larvae	–	715 ± 98	0.42 ± 0.14

Protozooplankton

Dinoflagellates dominated the protozooplankton community with up to 58 000 cells l^{-1}, whereas the abundance of ciliates was <12 000 cells l^{-1} (Fig. 4). There was a significant depletion within the raft area, while below the ropes (18 m) there was no significant depletion of chl *a*, dinoflagellates or ciliates (Tables 2 & 3, Fig. 3). Average filtration rates were 38 ± 11 and 66 ± 15 d^{-1} for dinoflagellates and ciliates (3 and 9 m), respectively. The filtration rates were not significantly different from each other or from filtration of chl *a* >2 µm, and there was no significant difference between 3 and 9 m depth (paired sample *t*-tests, df = 7, $p > 0.071$). The retention efficiency (RE) of dinoflagellates and ciliates (3 and 9 m) was significantly <1 at the lowest current speed (Table 4), but there was no significant regression between removal rate and current speed (Fig. 5).

Copepods

The 5 dominant copepods were *Oithona similis*, *Paracalanus parvus*, *Temora longicornis*, *Pseudocalanus* spp. and *Acartia clausi*. Total upstream abundance was highest on 24 July during the ingoing current, with up to 41 200 ind. m^{-3}, and lowest on 21 July, with <4500 ind. m^{-3}, including all copepod stages (Fig. 6). The majority of *O. similis*, *P. parvus*, *T. longicornis* and *Pseudocalanus* spp. were found in the surface layer (<10 m depth; Fig. 7a to d), while the abundance of *A. clausi* was highest below the ropes at 10 to 20 m depth (Fig. 7e). Upstream of the farm on 19 July, total surface abundance was 14 000 nauplii m^{-3}, 12 400 and 3400 ind. m^{-3} for copepodite stages CI to CIII and CIV to CVI, respectively, and decreased with depth. Depletion ratios of nauplii and CI to CIII and CIV to CVI of *O. similis* were significantly different from 1 at the centre, edge and downstream stations, whereas the depletion ratios of copepodites >600 µm (CIV to CVI of *P. parvus*, *T. longicornis* and *Pseudocalanus* spp., *A. clausi* and harpacticoid copepods) were only significantly <1 at the edge and downstream stations (Fig. 8, Table 2). The RE values were significantly <1 for copepod nauplii and copepodites >600 µm at the lowest current speed and for copepodites 300 to 600 µm at a current speed of 0.025 m s^{-1}. On the contrary, the RE values were significantly >1 at the 2 highest current speeds for nauplii and at the highest current speed for copepodites >300 µm (Table 4). There was a significant positive non-linear correlation between removal rates and current speed for all 3 groups of copepods (Fig. 9).

Other mesozooplankton

Bivalve larvae occurred in high numbers, with up to 77 000 ind. m^{-3}, especially during the upwelling period (Fig. 10). Other mesozooplankton present were the cladocerans *Evadne nordmanni*, different meroplankton (cirriped nauplii, gastropod and polychaete larvae) and harpacticoids copepods (CI to CVI). There was significant depletion at the centre, edge and downstream stations for all mesozooplankters examined (Fig. 11, Tables 2 & 3). Harpacticoid copepods were tested together with the other copepodites >600 µm (see above). The RE values were significantly >1 at the highest current speed (Table 4), and there was a positive non-linear correlation between filtration rate and current speed (Fig. 12). There was a significant positive correlation between depletion ratio and length of all mesozooplankton including copepods ($n = 20$, $r^2 = 0.35$, $p < 0.01$).

Fauna on the raft

The total biomass of blue mussels *Mytilus galloprovincialis* was 750 g DW m^{-3} using the estimated abundance of 750 mussels m^{-3} and an individual DW of 1 g. Epifauna was established on the mussel shells

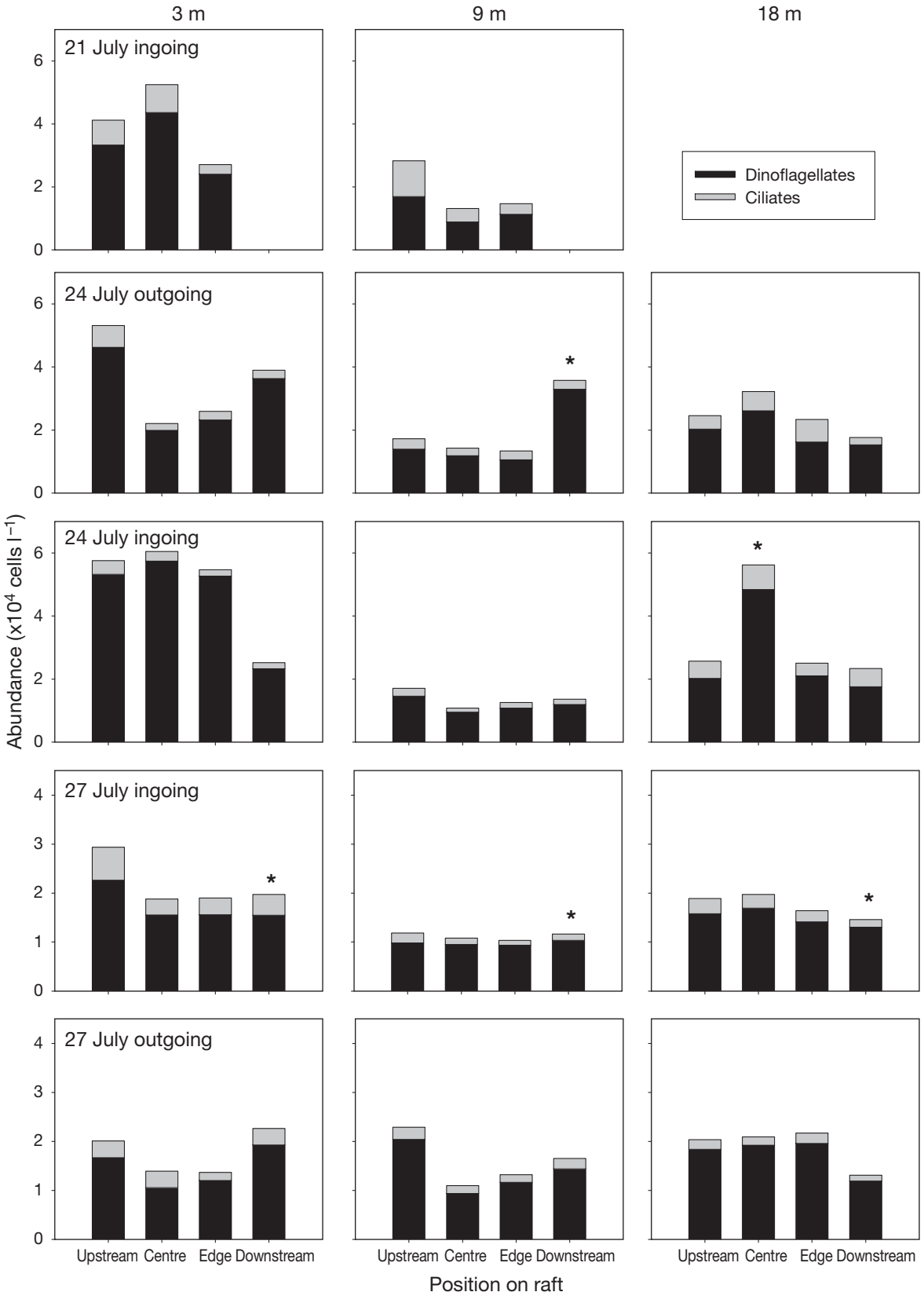

Fig. 4. Abundance (ind. l^{-1}) of protozooplankton (ciliates and dinoflagellates) at 3, 9 and 18 m depth on the 5 sampling days. The data marked with asterisks are not included in the average depletion ratio

Table 4. One-sample *t*-tests of retention efficiency at different current speeds; *significantly different from 1

	1–2 cm s^{-1}			2–3 cm s^{-1}			3–4 cm s^{-1}			4–5 cm s^{-1}		
	Mean ± SE	p	df	Mean± SE	p	df	Mean± SE	p	df	Mean ± SE	p	df
Dinoflagellates and ciliates (3 and 9 m)	0.57 ± 0.09	0.02*	3	0.93 ± 0.31	0.84	3	0.81 ± 0.35	0.63	3	2.16 ± 0.61	0.16	3
Copepod nauplii	0.45 ± 0.11	0.01*	4	1.27 ± 0.40	0.53	4	2.09 ± 0.39	<0.05*	4	8.06 ± 2.16	0.04*	4
Copepodites 300–600 µm	0.69 ± 0.13	0.07	5	0.62 ± 0.11	0.02*	5	1.78 ± 0.88	0.48	2	6.59 ± 1.32	0.01*	5
Copepodites >600 µm	0.55 ± 0.10	0.01*	5	0.69 ± 0.25	0.28	5	0.57 ± 0.47	0.43	4	5.26 ± 1.49	<0.05*	5
Meroplankton, *Evadne nordmanni*	1.11 ± 0.18	0.55	5	0.61 ± 0.15	0.05	5	1.50 ± 0.49	0.08	5	7.19 ± 1.26	0.01*	5

(Fig. 2), especially the thecate hydroid *Plumularia setacea* and the barnacles *Balanus perforatus* occurred in high numbers. There were 22 ± 6 (mean ± SE) hydroid stems $mussel^{-1}$, with a hydrotheca diameter of 0.10 ± 0.009 mm and a length of 0.17 ± 0.014 mm. The corresponding biomass was 126 g DW m^{-3} using 0.003 g DW $ind.^{-1}$ (Orejas et al. 2000). *B. perforatus* were present with 21 ± 5 ind. $mussel^{-1}$, and their basal diameter varied from 2 to 12 mm, with a median of 3.0 mm (n = 60). The biomass of *B. perforatus* was 229 g DW m^{-3}, using 0.007 g C $ind.^{-1}$ (Dahl et al. 2005) and a DW:C ratio of 2. The biomass of *M. galloprovincialis* thus accounted for 68% and other epifauna for 32%. The abundance of epifauna should be used with care, since the epifauna was sampled in the same month but 2 yr later than the original data. From digital photos and mussel shells, other predators were observed, but not quantified, such as sea urchins, bryozoans and fish (mullets *Mugil* sp.).

Ingestion by mussels and other epifauna

Ingestion rates of plankton by the raft faunal community (mussels and other epifauna) were estimated for the 24 July ingoing current and the 27 July outgoing current (Table 5), representing 2 extremes in chl *a* concentration and current speeds (Table 1). On 27 July during low current speeds and high chl *a* concentrations, the contribution of phytoplankton to total plankton carbon-ingestion was the greatest, at 77%. In contrast, ingestion of zooplankton (86%) was most important on 24 July, during high current conditions and low chl *a* concentrations. Especially copepodites and gastropod larvae were important in the diet on both days. Total ingestion rates were 43708 and 35327 g C $raft^{-1}$ d^{-1} on 24 and 27 July, respectively. The required zooplankton growth rates to sustain their biomass in the farm area were several times higher on 24 July than on 27 July, with a maximum of 5.4 d^{-1}, while it was 1.8 to 2.1 d^{-1} for phytoplankton (Table 5).

DISCUSSION

Both chl *a* and zooplankton were depleted at the centre, edge and downstream of the raft but at different degrees, supporting our hypothesis. The present study is the first to demonstrate depletion of zooplankton caused by cultivation rafts, although depletion of chl *a* and zooplankton have previously been observed above a natural blue mussel bed in a Danish estuary (Nielsen & Maar 2007). Mussel farming not only removed zooplankton, but it also changed the composition of the zooplankton community, since depletion was most severe for nauplii, copepodites CI to CIII and *Evadne nordmanni* and overall decreased with zooplankton size. The observed depletions suggest that zooplankton were efficiently removed by the raft epifaunal community (mussels and other epifauna) and that zooplankton may be important in their diet. However, blue mussels *Mytilus galloprovincialis* have the ability to sort and reject particles from their labial palps prior to ingestion, and zooplankton can be rejected in pseudofaeces (Laabir & Gentien 1999, Wong & Levinton 2006). In this case, the ingestion by mussels would be less than the estimated removal of zooplankton. In addition, the absorption efficiency of zooplankton may be different from that of chl *a* (Wong et al. 2003), and the contribution of zooplankton ingestion to the growth of blue mussels is therefore difficult to estimate without further experiments.

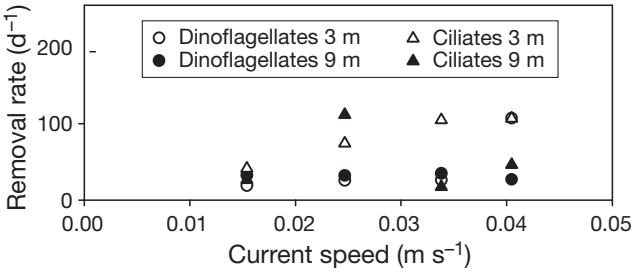

Fig. 5. Removal rates of dinoflagellates and ciliates versus current speed. A significant regression line could not be obtained (n = 16, r^2 = 0.12, p = 0.23)

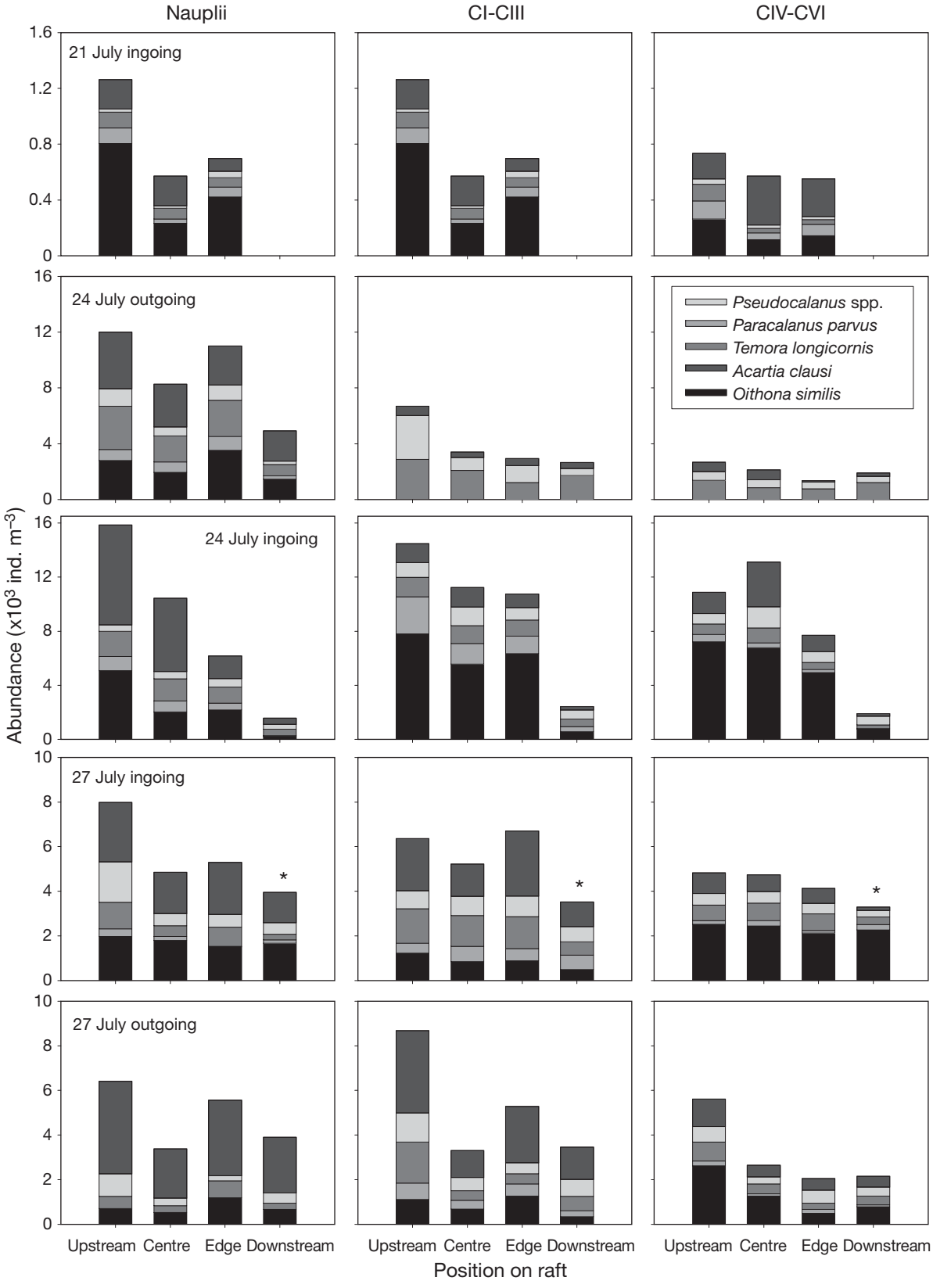

Fig. 6. Abundance (ind. m^{-3}) of the different stages (nauplii, CI to CIII and CIV to CVI) of the dominant copepods on the 5 sampling days. The data marked with asterisks are not included in the average depletion ratio

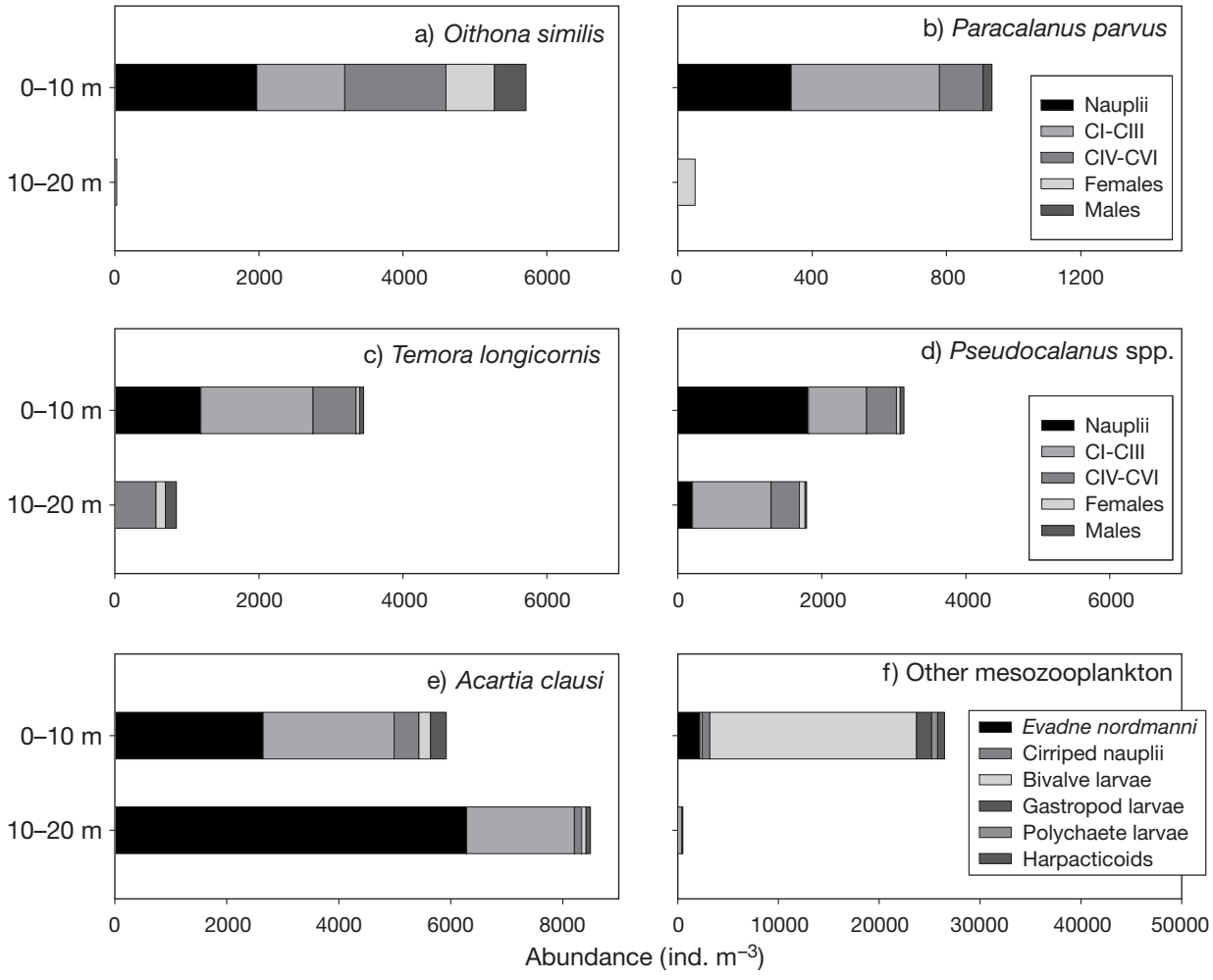

Fig. 7. Upstream vertical distributions (0 to 10 and 10 to 20 m) of the abundance (ind. m^{-3}) of copepods (a to e) and mesozooplankton other than calanoid copepods (f) on 27 July (ingoing current, Station 17)

Removal of zooplankton was significantly lower than that of chl *a*, except for meroplankton, but only at the lowest current speed. Removal decreases if zooplankton exhibits fast escape responses by jumping away from the predator. Active suspension feeders such as blue mussels generate a feeding current that zooplankton may detect and react to in calm water (i.e. low current speed) and this has been observed for protozooplankton, nauplii and copepods (Kiørboe et al. 1999, Jakobsen 2002, Titelman & Kiørboe 2003). In contrast, at higher current speeds, the escape success may be reduced due to interference by turbulence (Kiørboe et al. 1999, Maar et al. 2007, Waggett & Buskey 2007). On the other hand, meroplankton shows no escape reactions or slowly changes to a swimming direction away from the predator (Singarajah 1975, André et al. 1993), which is in agreement with our results. Another possibility is that removal rate decreases if zooplankters are of about the same size as the inhalant apertures of mussels. The prey size of blue mussels varies from 120 to 6000 µm based on stomach content analysis, but only prey sizes <3000 µm are retained in high numbers (Lehane & Davenport 2006). However, we reasoned that size was unimportant for filtration because maximum zooplankton length was <800 µm and because removal rates of protozooplankton were lower than for phytoplankton, even though they were of the same size. Structural defences by meroplankton, such as spines and shells, have no significant effect on ingestion by *Mytilus edulis* (Cowden et al. 1984). We therefore think that ingestion of protozooplankton, nauplii and copepodites was lower than for phytoplankton because they performed successful escape jumps at the lowest current speeds, while meroplankton and *Evadne nordmanni* were unable to escape.

In contrast, removal rates for all zooplankton except for protozooplankton were higher than for phytoplankton at the highest current speed. Since it is unlikely

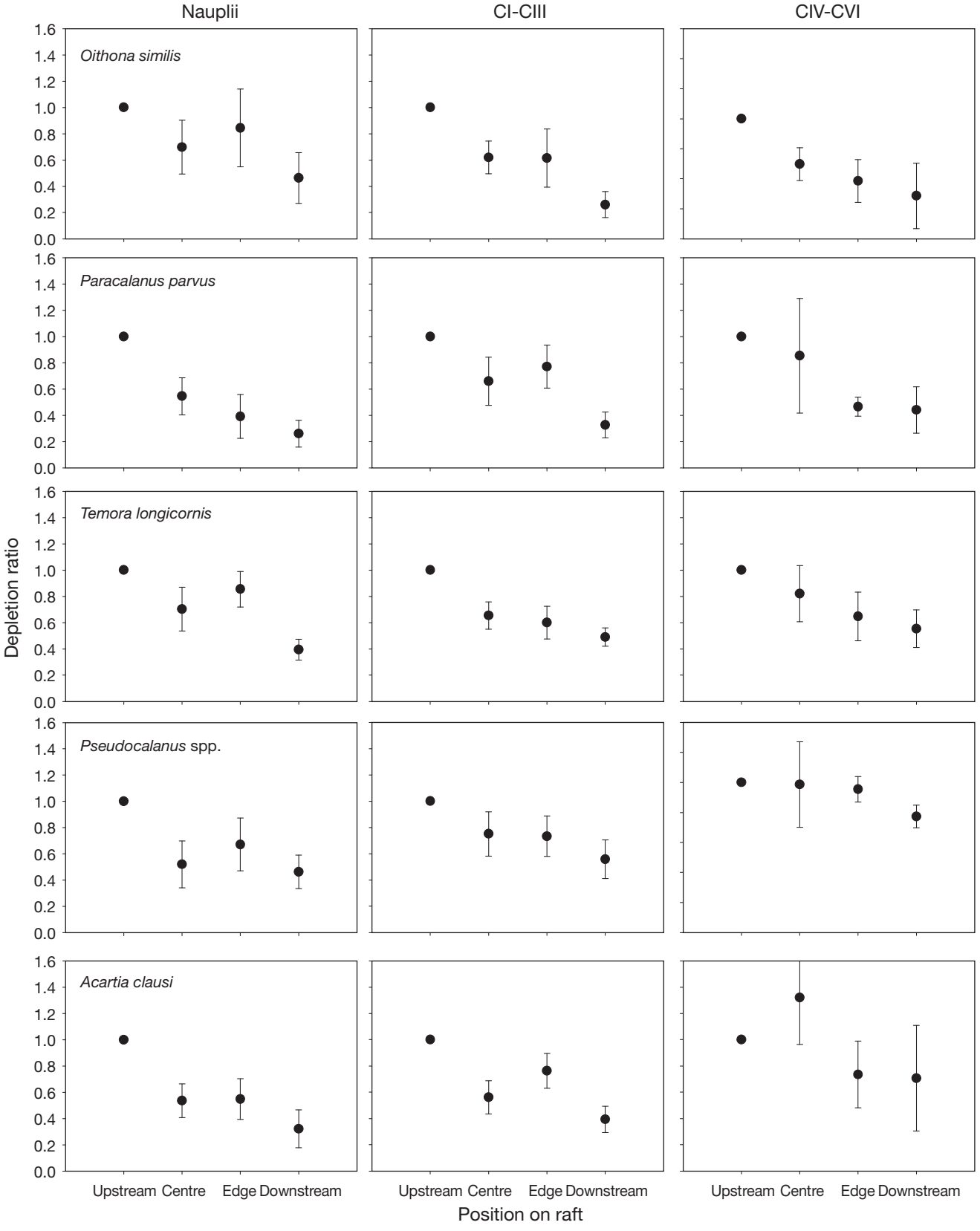

Fig. 8. Mean (±SE) depletion ratio of different stages (nauplii, CI to CIII and CIV to CVI) of the dominant copepods

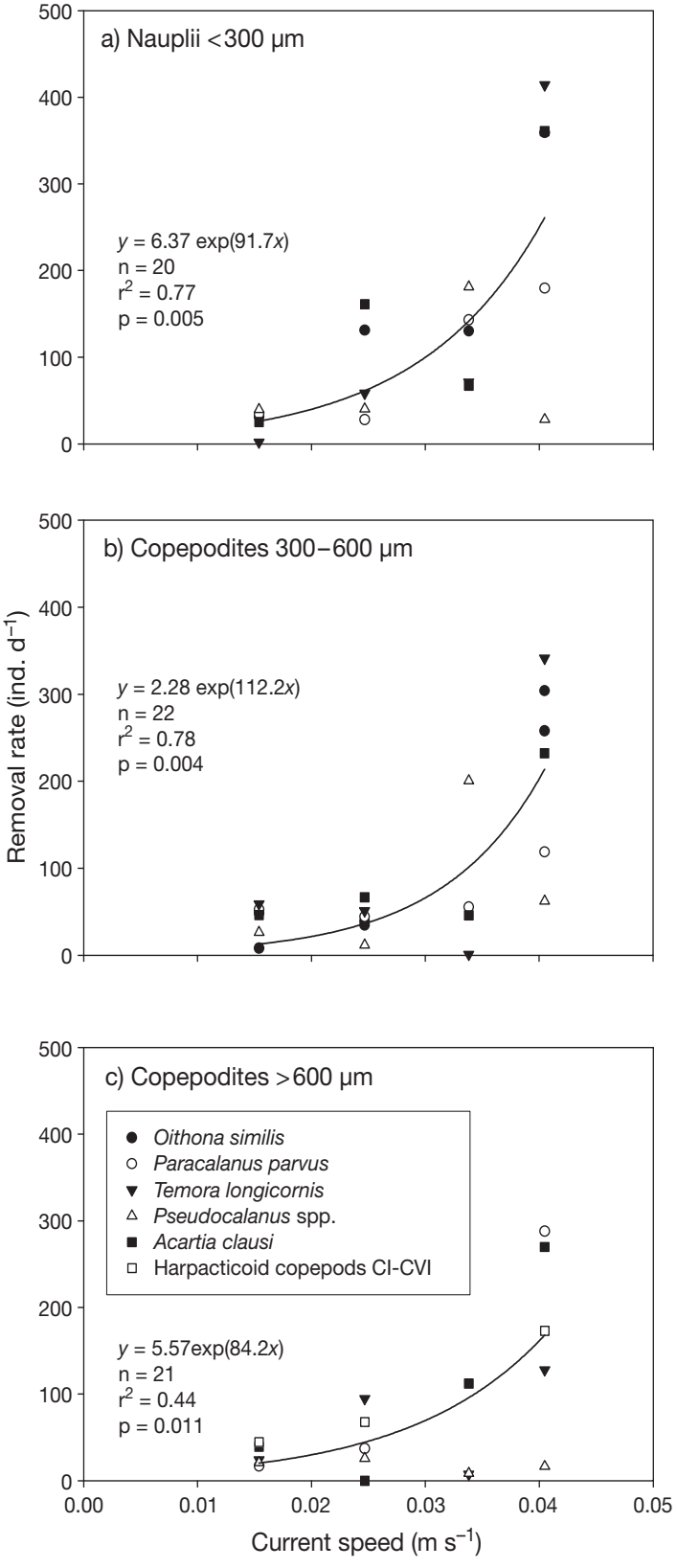

Fig. 9. Removal rates (d^{-1}) of: (a) nauplii (<300 µm), (b) copepodites 300 to 600 µm and (c) copepodites >600 µm versus current speed

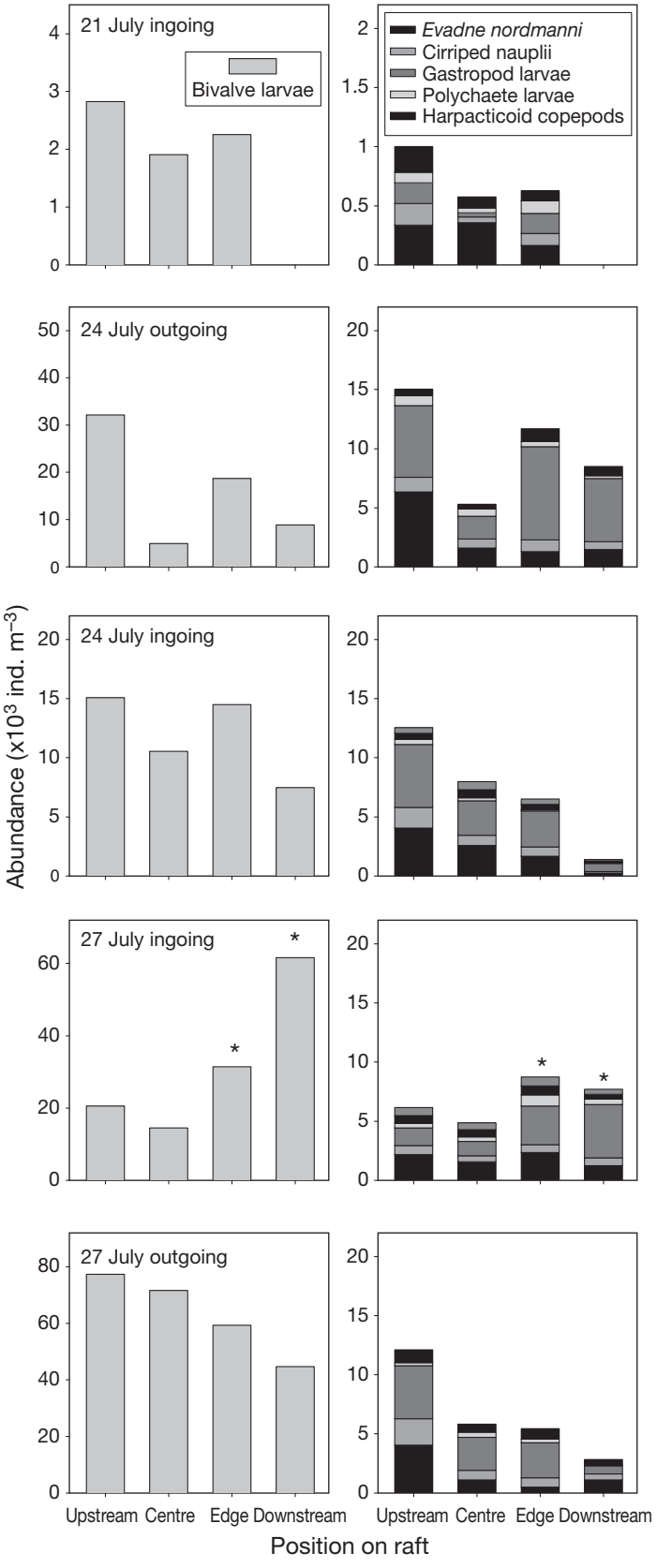

Fig. 10. Abundance (ind. m^{-3}) of mesozooplankton other than calanoid copepods on the 5 sampling days

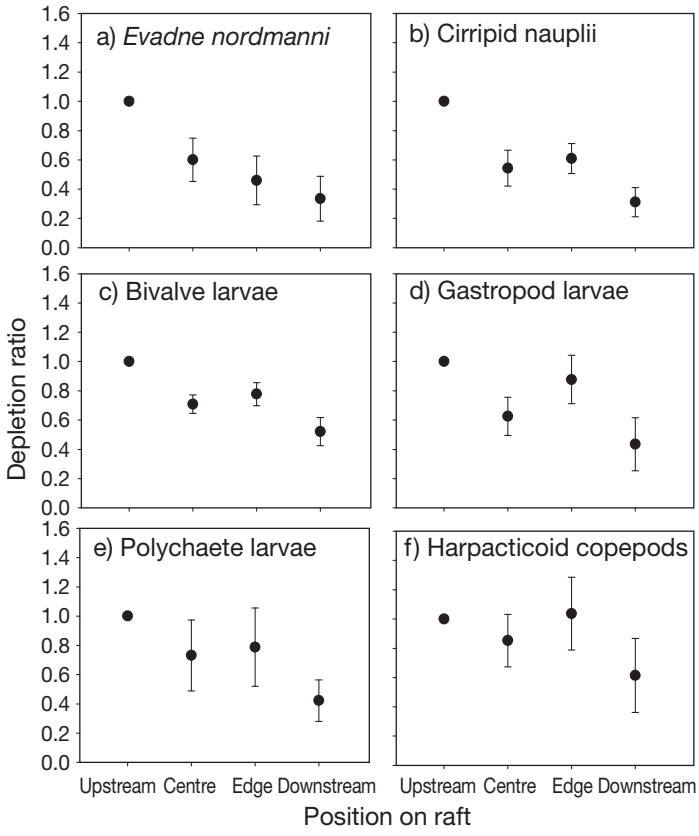

Fig. 11. Mean (±SE) depletion ratios of mesozooplankton other than calanoid copepods

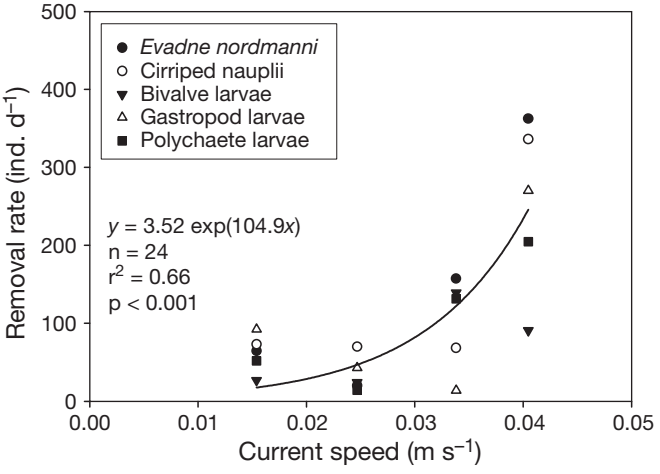

Fig. 12. Removal rates (d^{-1}) of mesozooplankton other than calanoid copepods versus current speed

that mussels should ingest more zooplankton than phytoplankton, we suggest that predators other than mussels were important. Although mussels dominate the biomass within a raft, up to 100 invertebrate species have been observed on the submerged ropes (Pérez-Camacho et al. 1991). Filtering species are believed to be quickly overgrown by mussels and normally comprise <10% of the epifaunal biomass (Pérez-Camacho et al. 1991). Nevertheless, a high biomass (32% of total) of hydroids *Plumularia setacea* and barnacles *Balanus perforatus* was observed on the mussels in the present study. Hydroids and barnacles are passive filter feeders that feed on e.g. invertebrate eggs and larvae, copepod nauplii, copepodites and detritus (Barnes 1959, Lewis 1981, Gili et al. 1996). Passive suspension feeding has a dome-shaped feeding response to current speed (Best 1988), with a maximum at 0.08 m s^{-1} for *Balanus crenatus* (Eckman & Duggins 1993), which is higher than the current speeds in our study. The grazing pressure on zooplankton by the epifaunal raft community is therefore likely to increase with current speed and cause the observed relatively high depletion of zooplankton in comparison to chl *a* within the raft area.

Calculations showed that the observed depletion of plankton around the rafts could not be renewed by local production in the farm area. This can be seen from the required specific growth rates of 1.8 to 2.1 d^{-1} to sustain the local phytoplankton biomass; this is higher than maximum specific growth rates of 0.7 to 1.3 d^{-1} measured in the area during summer (Figueiras

Table 5. Upstream plankton biomass, ingested biomass by the raft community, percentage contribution to total ingestion and required growth rates to sustain the plankton biomass in the farm area

	24 Jul ingoing				27 Jul outgoing			
	Biomass (mg C m^{-3})	Ingested (g C $raft^{-1}$ d^{-1})	Contribution (%)	Growth rate (d^{-1})	Biomass (mg C m^{-3})	Ingested (g C $raft^{-1}$ d^{-1})	Contribution (%)	Growth rate (d^{-1})
Chl *a* >2 µm	22.6	5891	13.5	1.7	84.0	27108	76.7	2.1
Dinoflagellates and ciliates (3 and 9 m)	5.8	2197	5.0	2.5	7.3	1004	2.8	0.9
Copepod nauplii	1.7	1413	3.2	5.4	0.9	113	0.3	0.8
Copepodites 300-600 µm	10.3	7619	17.4	4.9	8.9	1801	5.1	1.3
Copepodites >600 µm	21.2	16222	37.1	5.0	15.8	1558	4.4	0.7
Evadne nordmanni	3.1	2471	5.7	5.2	3.1	731	2.1	1.5
Cirripid nauplii	0.7	546	1.2	5.1	0.9	223	0.6	1.6
Bivalve larvae	1.3	553	1.3	2.8	6.7	905	2.6	0.9
Gastropod larvae	7.0	5107	11.7	4.9	5.8	1575	4.5	1.8
Polychaete larvae	2.5	1688	3.9	4.4	1.5	309	0.9	1.4

et al. 2002). Required zooplankton specific growth rates (2.5 to 5.4 d^{-1}) on 24 July were also considerably higher than previously reported values (Hansen 1993, Mauchline 1998, Fotel et al. 1999). On 27 July, specific growth rates (0.9 to 1.8 d^{-1}) were closer to observed maximum values for copepods, but still much higher than those measured for meroplankton. Although zooplankton caught in pseudofaeces or faeces have been observed to survive in some cases (Laabir & Gentien 1999), they will sink out of the upper productive layer quickly and must be considered as a loss to the pelagic food web. The observed depletion of plankton around single rafts, thus, has the potential to change the structure and production of the whole pelagic community within the farm area, although the 68 rafts only covered 4% of the area. A substantial decline in zooplankton abundance was observed in San Francisco Bay after the introduction of infaunal clams (Kimmerer et al. 1994). A reduction in zooplankton abundance will reduce growth of fish larvae, since they often are food limited and totally dependent on the abundance of copepod nauplii during their early life (Munk 1997, Rowlands et al. 2008).

From the observed depletions, it was possible to estimate the actual CR of mussels in the field by taking refiltration into account. The actual CR of 2.9 l h^{-1} for chl *a* was therefore lower than found in laboratory experiments (Riisgård 2001) and corresponded to a growth rate <0.5% d^{-1} during the study period. In comparison, maximum growth rates of 2.1% d^{-1} were measured during upwelling with high chl *a* concentrations for raft-cultivated mussels in the area (Navarro et al. 1991). We could not estimate the contribution of zooplankton to mussel ingestion and growth in the present study due to the ingestion by passive suspension feeders, the implications of pseudofaeces production and unknown absorption efficiencies for zooplankton. However, ingestion of zooplankton is probably important for mussel growth during periods with low phytoplankton concentrations. This was found in the Limfjord, where the heterotrophic contribution to the diet of natural mussels varied from 17 to 34% during summer and autumn, with relatively low phytoplankton concentrations (Maar et al. 2007). The present investigation stresses the need for considering zooplankton as a potential food source if the bivalve production potential at a locality is to be evaluated and managed correctly.

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