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Vertical flux regulation and plankton composition in a simple ecological system: snapshots from the small marine Lake Rogoznica (Croatia)

Camilla SVENSEN [1*], Christian WEXELS RISER [1], Ivona CETINIĆ [2,3] and Marina CARIĆ [4]

[1] Norwegian College of Fishery Science, University of Tromsø, 9037 Tromsø, Norway

**Corresponding author, e-mail: Camilla.svensen@nfh.uit.no*

[2] Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10000 Zagreb, Croatia
[3] Current address: University of Southern California, 3616 Trousdale Blvd., Los Angeles, CA 90089-0371, USA
e-mail: icetinic@usc.edu

[4] University of Dubrovnik, Institute for Marine and Coastal Research, Kneza D. Jude 12, 20101 Dubrovnik, Croatia
e-mail: marina.caric-gluncic@unidu.hr

Vertical flux regulation was investigated in the small, shallow, marine and partly anoxic Lake Rogoznica (eastern coast of the Adriatic Sea) by studying plankton composition, zooplankton fecal pellet (FP) production and vertical carbon flux. The lake is naturally eutrophicated with high nutrient and particulate organic carbon (POC) concentrations and relatively low species diversity. However, the few species found can be highly abundant. Due to a simple ecological structure and low physical forcing, Lake Rogoznica may be regarded as a natural laboratory especially suitable for plankton studies. Only one copepod species, Acartia italica, *was found in the lake and had a maximal abundance of 140 animals* L^{-1}. *The mixotrophic dinoflagellate* Ceratium furca *and the diatom* Chaetoceros curvisetus *accounted for ~90% of the phytoplankton biomass. Phytoplankton made up 30% of the POC flux at 5 m and 10% at 10 m depth and was dominated by* C. curvisetus *and* C. furca. *Average export of POC was 730 ± 40 mg* m^{-2} d^{-1} *at 5 m and 750 ± 90 mg* m^{-2} d^{-1} *at 10 m depth, and detritus comprised 68 and 86 % at 5 and 10 m depth, respectively. Despite high copepod abundance and high suspended FP concentration, FP only contributed 4 – 5% of the vertical POC flux. The highest contribution to vertical carbon flux was in terms of detritus, and high retention was likely due to FP grazing or fragmentation by* A. italica *copepodites above 5 m depth. It is concluded that Lake Rogoznica is a productive system where organic material is rapidly transformed to detritus.*

Key words: Vertical carbon flux, *Ceratium furca, Chaetoceros curvisetus, Acartia italica*, fecal pellets, Croatia, Central Adriatic, Lake Rogoznica

INTRODUCTION

Vertical flux of carbon from the upper to the deeper compartments of the sea and the pelagic-benthic coupling do not only influence the quality and quantity of food for benthic organisms, but also act as a sink for atmospheric CO_2. However, the dynamic nature of marine systems makes it difficult to investigate mechanisms controlling vertical carbon-fluxes, and advective processes often complicate further. One possible approach to overcome the problem of advection is the use of large mesocosm enclosures where physical parameters can be controlled. However, the main disadvantage of mesocosms is that large-scale processes such as vertical carbon export could be biased due to enclosure-effects (SVENSEN *et al.*, 2001). Another possibility is to use natural laboratories such as coastal lagoons. For instance, lakes have been intensively used as natural laboratories in freshwater biology (SCHINDLER, 1998), although such an approach is rare for marine research. Lake Rogoznica is a small (5300 m^2) and shallow (max 15 m) saline lake located at the eastern Adriatic coast (Croatia) that can serve as a natural laboratory.

Lake Rogoznica is separated from the sea by 100 m of porous karstic rock and tidal amplitudes can be observed in it with a certain delay. Salinity in the sub-surface layer is influenced by the surrounding Adriatic Sea, while the surface layer is usually less saline due to the influence of local precipitation. High banks protect the lake from wind, with the result that the lake is stratified throughout most of the year, with hypoxia/anoxia occurring in the bottom layer (ĆOSOVIĆ *et al.*, 2000). Phytoplankton, zooplankton nauplii and larvae of benthic organisms may enter the lake through fissures between the rocks (KRŠINIĆ *et al.*, 2000), yet Lake Rogoznica appears suitable for only a few species. Diatoms and dinoflagellates are the most important groups, with *Chaetoceros* sp., *Ceratium furca* and *Hermesinum adriaticum* as frequent representatives (BARIĆ *et al.*, 2003; VILIČIĆ *et al.*, 1996/97). The only copepod species recorded in the lake is *Acartia italica*, which is the least known of the genus *Acartia* (KRŠINIĆ *et al.*, 2000). This species usually occurs in high abundances in Lake Rogoznica and is well adapted for fluctuating environments as it was observed to quickly re-establish after a mass mortality event caused by complete anoxia in 1997 (KRŠINIĆ *et al.*, 2000).

Due to its physical characteristics, such as weak influence from the sea and relatively permanent vertical stratification, as well as it's simple ecological structure with low species diversity, Lake Rogoznica is an ideal study site for observing planktonic processes. The community corresponds to the low diversity that can be expected under high productivity conditions (IRIGOIEN *et al.*, 2004) and provides a natural simple ecosystem where the effect of trophic links on carbon flux may be studied.

The main objective of this study was to investigate plankton community and vertical carbon flux in an ecosystem dominated by one copepod species (*Acartia italica*), one mixotrophic dinoflagellate (*Ceratium furca*) and one autotrophic diatom species (*Chaetoceros curvisetus*). The parameters investigated were biochemical properties of the lake, species distribution and biomass, copepod grazing and fecal pellet egestion and composition and magnitude of the vertical carbon flux.

MATERIAL AND METHODS

Suspended samples

During the investigated period from May 11-18, 2004 a detailed suspended profile was sampled three times (11, 14 and 17th). Water was collected with 5 L Niskin bottles at 0, 2, 5, 7, 8, 9, 10, 11, 12 and 13 m depths for measurements of chlorophyll *a* (Chl *a*), phaeopigments, particulate organic carbon and nitrogen (POC, PON) and nutrients. Sub-samples for analyses of Chl *a* and phaeopigments were filtered in triplicates onto GF/F filters and analyzed after methanol extraction according to PARSONS *et al.*, (1984). Aliquots for analyses of POC and PON were filtered onto pre-combusted GF/F filters and analyzed on a Lab Leeman 440 Elemental

Analyzer after fuming with concentrated HCl to remove inorganic carbonates.

Nutrient concentrations (NO_2, NO_3, NH_4, SiO_4 and PO_4) were measured by standard methods (IVANČIĆ & DEGOBBIS, 1984; STRICKLAND & PARSONS, 1972) within one month after sampling. NH_4 concentrations were measured in samples preserved with phenol, while NO_2, NO_3, SiO_4, PO_4 were measured on frozen samples.

Temperature, salinity and pH were measured *in situ* with a CTD probe (Idronaut). Samples for oxygen were collected with a 5 L Niskin water sampler at 0, 2, 5, 7, 8, 9, 10, 11, 12 and 13 m depths. To preserve anoxic conditions, the Niskin sampler was attached to a N_2 cylinder to maintain N_2 over the sample while it was transferred to glass bottles. The bottles had previously been flushed with N_2. Dissolved oxygen was measured immediately after sampling in samples preserved with Fahling reagent, according to the standard method by Winkler (STRICKLAND & PARSONS, 1972).

Samples for suspended phytoplankton determination were preserved in neutralized formaldehyde (2% final concentration). Sub-samples (50 mL) were microscopically investigated after 24 h sedimentation in Utermöhl chambers (UTERMÖHL, 1958). Microphytoplankton cells (> 20 μm) were counted at 200 and 400x magnification. Nanophytoplankton cells (2-20 μm) were counted in 20 randomly selected fields of vision, under magnifications of 400 and 1000x. Bio-volume was calculated using geometric shapes of each phytoplankton species according to VILIČIĆ (1985). Average bio-volumes (BV) were converted into carbon biomass using previously published conversion factors: for diatoms pg C $\mu m^{-3} = 0.288 \times BV^{0.811}$, for dinoflagellates pg C $\mu m^{-3} = 0.76 \times BV^{0.819}$ (MENDEN-DEUER & LESSARD, 2000), and for other flagellates pg C $\mu m^{-3} = 0.433 \times BV^{0.863}$ (VERITY *et al.*, 1992).

Zooplankton abundance and vertical distribution

Mesozooplankton were collected daily (6 samplings in total) with a vertical net haul from 7 m depth to the surface using a WP-2 net (180 μm mesh size, diameter 52 cm) and preserved with buffered formaldehyde at a final concentration of 4%. *Acartia italica* was the only copepod species present, and abundance was obtained by diluting the sample and counting 5 sub-samples (200–400 individuals per sub-sample) using a stereomicroscope (Leica M-60) at 40-100x magnification. Stage composition was investigated on two occasions, May 12 and May 17, by counting and measuring prosome lengths of 218 and 350 individuals, respectively, at 100x magnification.

On May 18 *A. italica* (nauplii, CI-CIV and adult females), copepod fecal pellets (FP) and *Ceratium furca* were sampled with Niskin bottles from 2, 5, 7, 10 and 12 m depths. The content of the Niskin bottle was concentrated over a 20 μm mesh and preserved with buffered formaldehyde (4% final concentration). Nauplii and copepodites were counted in 1-5 sub-samples corresponding to 20% of the total sample volume. *Ceratium furca* and copepod FP were counted in triplicate sub-samples of 0.5-2% of the total sample.

Vertical flux of organic matter

Vertical flux of organic matter was measured daily throughout the investigated period using sediment traps (produced by KC-Denmark) at 5 and 10 m depths. The traps consisted of parallel cylinders with inner diameter 72 mm, height 450 mm (aspect ratio 6.25) and volume 1.8 L. The cylinders were mounted in a gimbaled frame equipped with a vane to obtain stability. Sediment traps of this type are especially suitable in shallow areas due to the low aspect ratio and easy handling. Their catchment efficiencies, evaluated using the ^{234}Th method, is 70-100% (COPPOLA *et al.*, 2002). Data obtained from this type of sediment trap can therefore be considered reliable, especially in systems without advection such as Lake Rogoznica.

The traps were deployed for approximately 24 h without preservation to avoid swimmer contamination (migrating zooplankton). Upon retrieval the content of the two parallel cylinders were gently mixed and triplicate sub-samples

were taken for analyses of Chl *a*, POC and PON. These samples were analyzed as described for the suspended samples.

Sub-samples for enumeration of phytoplankton (20 mL) and zooplankton FP (100 mL) were also collected from the sedimented material. Phytoplankton and FP samples were preserved with buffered formaldehyde (2% and 4% final concentration, respectively) and enumerated using a light-microscope by a combination of methods as described by RATKOVA *et al.* (1999). Briefly, three different size-classes were counted in 3 steps using the appropriate sample volume and magnification. Phytoplankton cells were measured and bio-volumes were calculated according to Smayda (1978). Carbon-content of individual cells (PPC) was converted from cell-volume (MENDEN-DEUER & LESSARD, 2000). Fecal pellet length and width was measured and volume was converted to carbon (FPC) using a volumetric carbon-conversion factor of 69.4 µg C mm^{-3} (RIEBESELL *et al.*, 1995).

Acartia italica grazing and fecal pellet production experiment

A grazing experiment was performed on May 14. Copepods collected with a WP-2 net (180 µm mesh-size) were gently diluted in water from 5 m depth sieved through a 20 µm mesh size. In the laboratory a sub-sample of the zooplankton catch corresponding to the approximate *in situ* concentrations (50–100 animals L^{-1}) were incubated in 1100 mL Schott bottles in 5 replicates. Five bottles without animals served as controls.

Incubation water for the experiment was collected from 5 m depth. The water was gently sieved through a 90 µm mesh prior to incubation to remove large grazers. Initial (T_0) samples were taken for analyses of Chl *a* (triplicates), POC (duplicates) and phytoplankton composition (1 sample). The bottles were incubated *in situ* hanging at 2 m depth from a floating buoy to allow gentle movements of the bottles. The bottles were wrapped in aluminum foil to avoid phytoplankton growth during the experiments. After 18 h the bottles were taken up and 300 mL were removed from each bottle for analyses of Chl *a*. The rest of the content was concentrated through a 10 µm mesh and fixed with formaldehyde for quantification of zooplankton and FP enumeration and measurements (length and width). The volume removed from each bottle was noted when calculating copepod abundance and FP production.

Clearance rates were calculated for Chl *a*, a parameter showing statistically significant differences between treatment and control bottles (Student t-test, $p < 0.05$). Ingestion rates of carbon were obtained from clearance rates by utilizing a PPC:Chl *a* ratio of 61.5 from the incubation water of the experiment. Ingestion rates were also calculated based on FPC production of *A. italica* copepodites in the 5 treatment bottles by utilizing the expression I= E/(1-AE), where I is the ingestion rate (µg C $copepod^{-1}$ d^{-1}), E is the measured egestion rate (µg C $copepod^{-1}$ d^{-1}) and AE the assimilation rate (BÅMSTEDT *et al.*, 2000). An AE of 60% was assumed, since low assimilation rates have been found for *A. tonsa* feeding in carbon-rich environments (KIØRBOE *et al.*, 1985).

Six sub-samples of copepods were taken for carbon-analyses. Each sub-sample was poured into a small beaker and animals were counted and placed one by one in a new beaker with filtered seawater. The animals were then transferred to a pre-burned GF/F filter and analyzed as described for POC samples. Each filter contained from 69–110 *A. italica* copepodites (mix of all stages). Three filters containing 8 or 9 females were also analyzed for carbon-content of *A. italica* females.

RESULTS

Hydrography, nutrients and suspended biomass

Data from the three profiles (11, 14 and 17th of May) are merged and presented as an average ± SD due to low variation between the samplings. From 0 to 5 m depth the salinity increased from 25 S to 35 S. Below 5 m depth the salinity was relatively uniform with an average of 36 ± 0.2

S (Fig. 1A). Temperature ranged from 21°C at the surface to 14.5 °C at 13 m. A maximum temperature of 23.5 °C was measured at 5 m depth. Oxygen concentrations were low at the surface (5.5 mL L^{-1}) and peaked at 5 m depth (11 mL L^{-1}). Below 5 m the O_2 concentration decreased sharply and at 13 m depth anoxic conditions were recorded (Fig. 1A).

Total nitrogen (NH_4, NO_2 and NO_3) concentrations ranged from 10-15 µM at 0 and 2 m, but nitrogen was consumed between 2 and 5 m depth (Fig. 1B). All nutrient concentrations

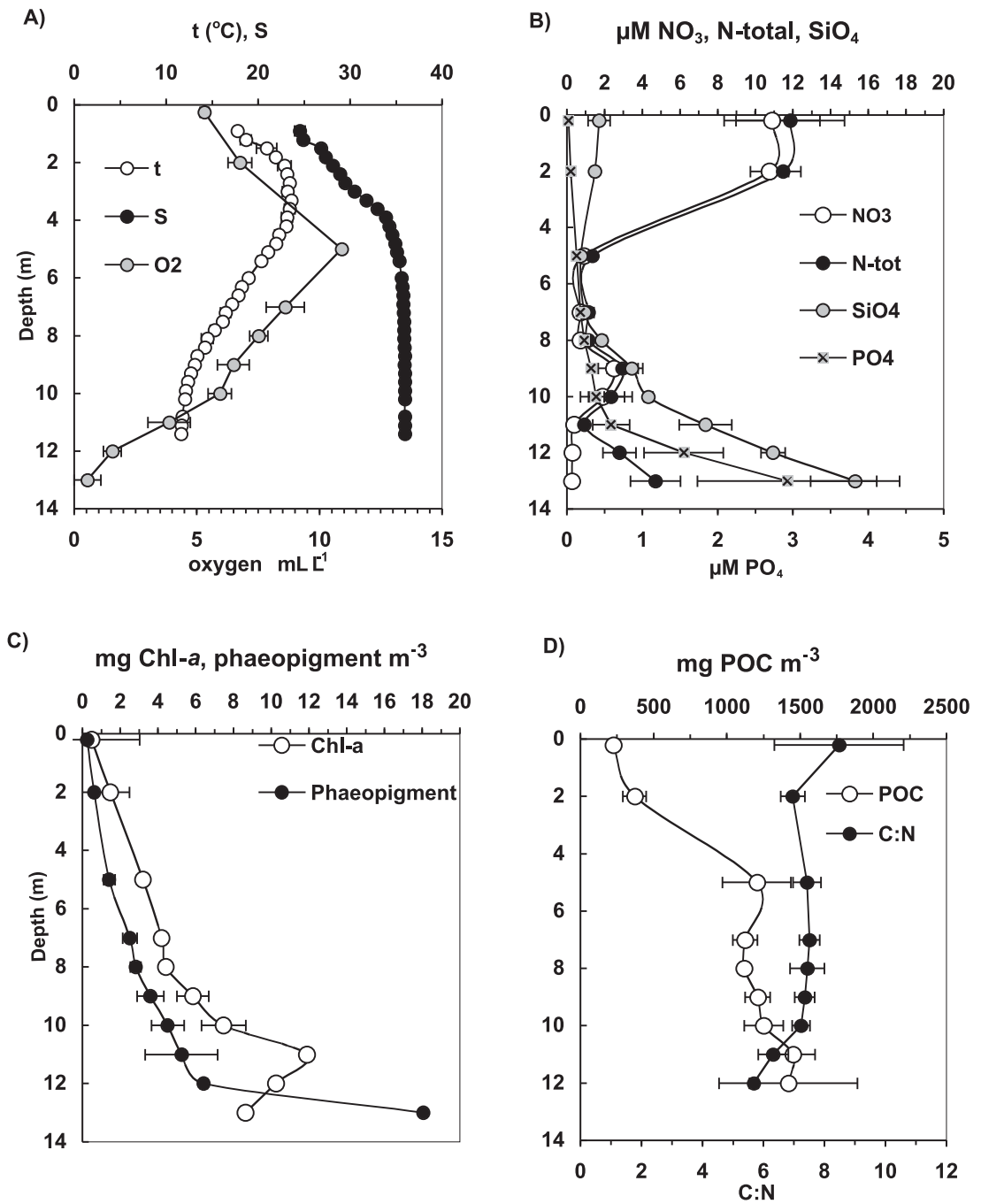

Fig. 1. Vertical profiles of mean temperature (°C), salinity and oxygen (mL O_2 L^{-1}) (A), nutrients (µM) (B), chlorophyll a *and phaeopigments (mg m^{-3}) (C), and particulate organic carbon (POC, mg m^{-3}) and C:N (atomic) ratio (D). Bars represent ± SD*

were low between 5 and 8 m depth and increased from 9 m to the bottom. Silicate concentrations of 1-2 µM were homogenously distributed to 8 m depth, from where the concentration increased to >14 µM at 13 m. Phosphorous concentrations were <0.5 µM above 5 m and increased closer to the bottom sediments (Fig. 1B).

Chl *a* concentration increased gradually from <0.5 µg L^{-1} at the surface to >10 µg L^{-1} at 12-13 m depth (Fig. 1C). The concentration of Chl *a* was twice as high at 10 m than at 5 m depth. The distribution of phaeopigments followed that of Chl *a*, although with a higher concentration at 13 m (Fig. 1C). The suspended biomass of POC was generally high, although lower at the surface than below 5 m (Fig. 1D). Between 5 and 10 m depth the POC concentrations were in the range of 1100–1200 mg C m^{-3}. The highest concentrations of POC were found at 11 and 12 m with 1450 mg C m^{-3}. Concentrations of PON were homogenously distributed with depth, and did not vary much during the sampled period (data not shown), and C:N ratios (atomic) decreased from 8.5 at the surface to < 6 at 12 m depth (Fig. 1D).

Phytoplankton

Phytoplankton carbon (PPC) in Lake Rogoznica was dominated by the diatom *Chaetoceros curvisetus* and the dinoflagellate *Ceratium furca* (Fig. 2). Due to its large size, *C. furca* was the species contributing most to the total PPC biomass, although *C. curvisetus* was more abundant (Table 1). The peak concentrations of *C. curvisetus* cells were found at 5 or 7 m depth, with abundances in the range of 154 - 974 cells mL^{-1} (Table 1). The relative contribution of *C. curvisetus* to the total diatom abundance was > 50%, and generally close to 100%. The dinoflagellate group was mainly represented by *C. furca*, although unidentified dinoflagellates of 10-20 µm size were also present (dinoflagellates other than *C. furca*

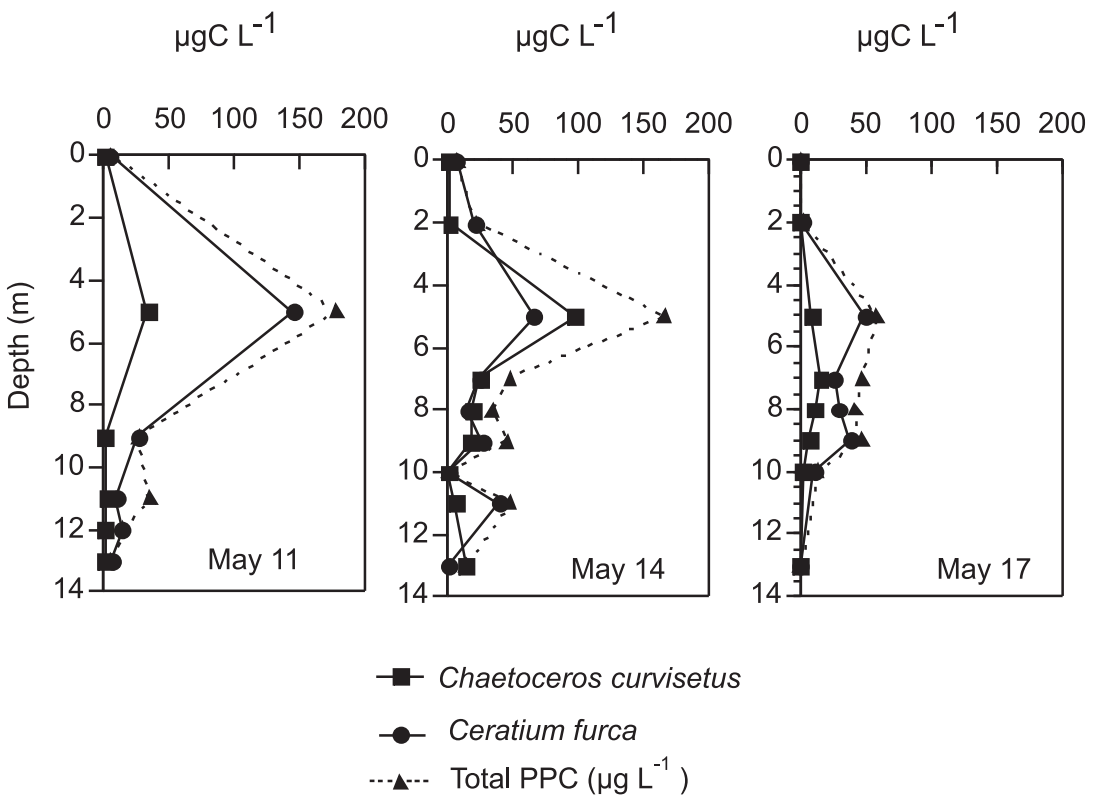

Fig. 2. Vertical distribution (µg C L^{-1}) of Chaetoceros curvisetus*,* Ceratium furca *and total phytoplankton carbon (PPC) in Lake Rogoznica on May 11, 14 and 17*

in Table 1). The maximum concentration of *C. furca* was 41 cells mL^{-1} and the peak was always found at 5 m depth (Table 1). The highest concentrations of other dinoflagellates were generally found at 9 m depth or deeper, resulting in a lower relative contribution of *C. furca*.

Vertical distribution of *Acartia italica*, *Ceratium furca* and fecal pellets

The abundances of *A. italica* copepodites (CI-CVI) sampled with the WP-2 net varied from 17 - 48 individuals L^{-1}, with a mean of 30 ± 15 (95 % confidence interval). In comparison, abundance based on integrated samples obtained with Niskin bottles (2, 5, 7, 10 and 12 m) was 44 copepods L^{-1}. The community consisted of <1% CII, 1-7% CIII, 3-8% CIV, 70-80% CV and 14-15% adult females. CI copepodites were absent, probably due to low sampling efficiency of the smallest stages of the 180 µm net. Stage CV and females comprised the majority of the community and contributed 95% and 84% of the total abundance on May 12 and 17, respectively.

The average carbon-weight of *A. italica* females was 2.6 ± 0.4 µg (n=3), while the average carbon-weight for the whole community (representing the average carbon-content of animals used in the experiment) was 1.0 ± 0.06 µg (n=6) (Table 4).

A high-resolution vertical profile was sampled once (May 18) for the distribution of *A. italica* copepodites (CI-CVI), nauplii (NI-NVI), FP and *C. furca*. The results revealed that most of the activity took place at 5 m depth, with 142 *A. italica* L^{-1}, 40 000 *C. furca* L^{-1} and

Table 1. Abundance (cells mL^{-1}) and vertical distribution of Chaetoceros curvisetus *and* Ceratium furca *in Lake Rogoznica. Abundances are rounded to the nearest number. The relative contributions of* C. curvisetus *to the total diatom abundance* (C. cur. /diat.) *and* C. furca *to the total dinoflagellate abundance* (C. fur. /dino.) *are also given*

Date	Depth (m)	*C. curvisetus*	*C. furca*	*C. cur.* / diat.	*C. fur.* / dino.
11 May 2004	0	5	1	1	1
	5	329	41	1	0.9
	9	10	7	1	1
	11	20	3	1	0.03
	12	8	4	1	1
	13	2	1	1	1
14 May 2004	0	3	2	0.7	0.3
	2	12	6	0.9	0.6
	5	974	19	1	0.8
	7	236	7	1	0.9
	8	181	4	1	0.3
	9	176	7	1	0.3
	10	0	0	-	-
	11	55	11	1	0.4
	13	140	0	1	-
17 May 2004	0	3	0	0.5	-
	2	4	0.5	0.5	1
	5	85	14	1	0.6
	7	154	7	1	0.5
	8	112	8	1	0.5
	9	66	11	1	0.5
	10	21	3	1	0.3
	13	0	0	-	0

3500 FP L^{-1} (Fig. 3). Nauplii were relatively homogenously distributed through the water column, although with the highest abundance, of about 100 individuals L^{-1}, at 2 m depth (Fig. 3). All organisms as well as FP decreased in numbers below 5 m depth and few organisms were present in the upper 2 m. The vertical profile indicates less favorable conditions above 5 m and below 7 m depth.

Vertical flux of POC, chlorophyll *a*, phytoplankton and fecal pellets

The vertical flux of POC was high and stable (700-800 mg C m^{-2} d^{-1}) throughout the investigated period both at 5 and 10 m depth (Fig. 4 A, B). Phytoplankton (PPC) made up 32 and 12% of the total POC flux at 5 and 10 m depth, respectively. At 5 m depth the total PPC sedimentation was 220 ± 80 mg C m^{-2} d^{-1} (average ± SD), while at 10 m depth it was reduced to 80 ± 20 mg C m^{-2} d^{-1} (Table 2). The PPC flux was mainly composed of *C. furca* and *C. curvisetus cells*, and the contribution of other phytoplankton (Coccolithophores and small flagellates) was negligible (Fig. 4 C, D). Dinoflagellates as a group comprised 54% and 67% of the total PPC flux at 5 and 10 m depth, respectively (Table 2). The vertical flux of Chl *a* was higher at 10 m than at 5 m depth, 3.6 ± 0.6 mg m^{-2} d^{-1} and 2.0 ± 0.3 mg m^{-2} d^{-1}, respectively (Fig. 4 C, D). This could indicate differences in cellular Chl *a* content for phytoplankton at 5 and 10 m depth.

Despite the high *A. italica* abundance, copepod FP only contributed 4% and 5% of the total POC flux at 5 and 10 m depth, respectively (Table 2, Fig 4 A, B). With the low contribution of both PPC and FPC to the POC flux, it is clear that the main fraction of vertical carbon flux in Lake Rogoznica consisted of degraded, unrecognizable organic material (i.e. detritus).

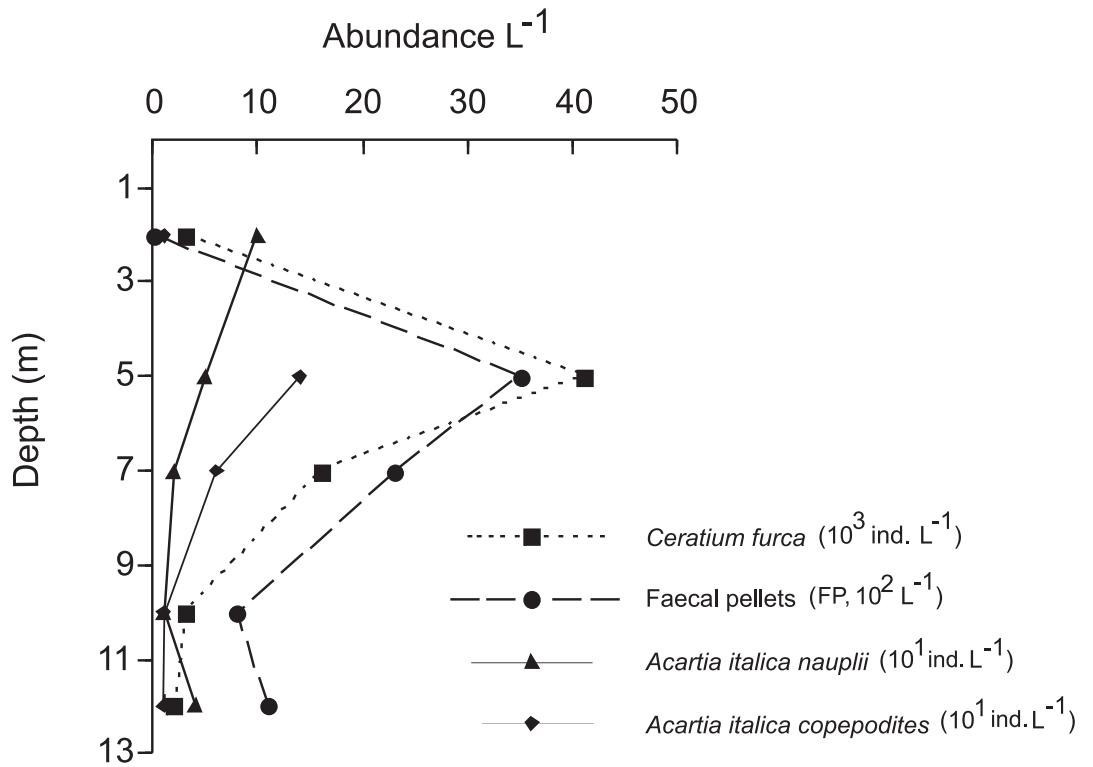

Fig. 3. Abundances of Acartia italica *copepodites (101 ind. L^{-1}), nauplii (101 ind. L^{-1}),* Ceratium furca *(103 cells L^{-1}) and fecal pellets (FP, 102 L^{-1}) in the water column on May 18. Data from each depth are based on counts from the same Niskin bottle*

Table 2. Budget of suspended (integrated from 0-13 m) and sedimented particulate organic carbon (POC), phytoplankton carbon (PPC), fecal pellet carbon (FPC) and detritus in Lake Rogoznica. Detritus represents the unrecognizable fraction of POC (i.e. detritus= POC-FPC-PPC). All values are rounded averages ± SD, except suspended FPC which is based on suspended FP from the profile obtained on May 18 and FP carbon-content from the experiment

	Suspended (mg m^{-2})	Sedimented 5 m (mg m^{-2} d^{-1})	Sedimented 10 m (mg m^{-2} d^{-1})
POC	14240 ± 2350	730 ± 40	750 ± 90
PPC Total	690 ± 310	220 ± 80	80 ± 20
Diatoms	190 ± 140	100 ± 80	20 ± 20
Dinoflagellates	490 ± 270	120 ± 20	50 ± 20
FPC	270	10 ± 15	20 ± 10
Detritus	13290	500	650

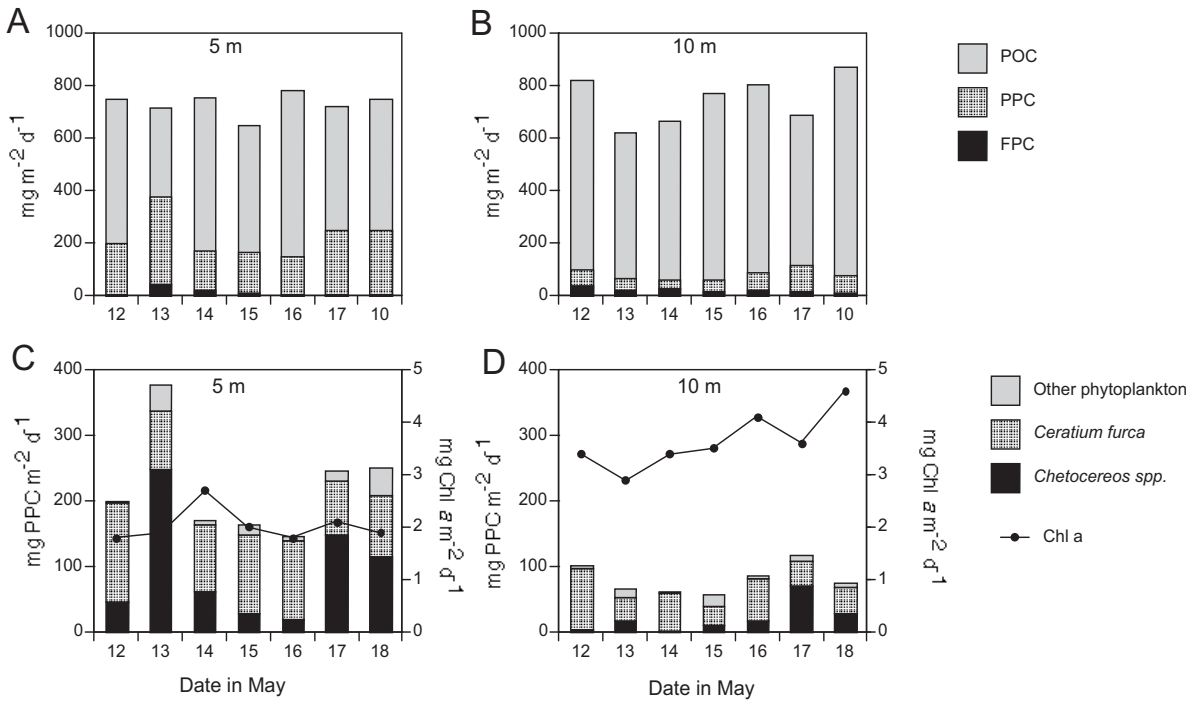

Fig. 4. Vertical carbon flux (POC, PPC, FPC, mg m^{-2} d^{-1}) at 5 m depth (A) and 10 m depth (B). Composition of PPC flux (mg m^{-2} d^{-1}) at 5 m depth (C) and 10 m depth (D)

Fecal pellet production and grazing by *Acartia italica*

The concentration of *A. italica* copepodites per incubation bottle was 89 ± 19 (average ± SD). Adult males and females comprised 69% of the total copepodite abundance (Table 3). Fecal pellet production rates, clearance rates and ingestion rates were based on the number of copepodites in each incubation bottle. The average production of FP was 10 ± 1 copepod^{-1} d^{-1}, corresponding to 0.1 ± 0.4 µg C copepod^{-1} d^{-1} (Table 3). By assuming 60% AE the daily ingestion rate per copepod was 0.35 ± 0.04 µg C. The clearance rate for Chl *a* was 1.1 ± 0.4 mL copepod^{-1} d^{-1}, corresponding to an ingestion rate of 0.27 ± 0.1 µg C copepod^{-1} d^{-1} using a Chl *a* ratio of 61.5 from the experiment (Table 3). Hence,

Table 3. Fecal pellet production and grazing experiment. Abundance of Acartia italica*, content of Chl* a*, POC and phytoplankton, FP production and grazing*

	Average ± SD (n samples)
A. italica (n bottle^{-1})	
Nauplii	13 ± 4 (5)
Copepodites CI – CVI	89 ± 19 (5)
% males/females	69 ± 4 (5)
Chlorophyll *a* (µg L^{-1})	
Initial	3.9 (1)
Stop	3.4 ± 0.1 (5)
POC (µg C L^{-1}) (initial)	1371 (2)
Phytoplankton (µg C L^{-1})	
Total (initial)	240 (1)
Ceratium furca (initial)	207 (1)
Chaetoceros curvisetus (initial)	4 (1)
Clearance rate, Chlorophyll *a*	
mL copepod^{-1} d^{-1}	1.14 ± 0.44 (5)
Fecal pellet production	
# FP copepod^{-1} d^{-1}	10 ± 1 (5)
µg C copepod^{-1} d^{-1}	0.14 ± 0.02 (5)
Ingestion rate (µg C copepod d^{-1})	
From clearance (C:Chl *a* = 61.5)	0.27 ± 0.11 (5)
From egestion (60 % AE)	0.35 ± 0.04 (5)
Animal carbon-content	
A. italica female	2.57 ± 0.37 (3)
A. italica community sample	1.00 ± 0.06 (6)

the two independent estimates of copepod ingestion rates corresponded well and indicated a daily individual carbon ingestion of about 30% of the mean body carbon weight.

DISCUSSION

Physical environment and species distribution

Lake Rogoznica represents a special habitat for marine planktonic organisms due to low and fluctuating salinities in the upper 2 m, and oxygen poor/anoxic conditions below 12 m depth. A high concentration of organic detritus also creates a turbid environment below 5 m depth. Influenced by these physical constraints, the few species capable of surviving in Lake Rogoznica must be distributed through a narrow zone of 10 m depth.

Diatom abundance (mainly *Chaetoceros curvisetus*) peaked between 2 and 7 m depth where light and nutrients could maintain their growth. This is supported by a rapid decline in nutrients between 2-5 m as well as with a peak in O_2 concentration at 5 m depth. Also, the red-tide -forming species *Ceratium furca* peaked at 5 m depth, co-occurring with *C. curvisetus*. Maximum cell concentrations of *C. furca* were 41 cells mL^{-1}, corresponding to 144 µg C L^{-1}. The previous reported maximum abundance of *C. furca* in Lake Rogoznica was 3.6 cells mL^{-1} (ĆOSOVIĆ *et al.*, 2000). There are otherwise few reports of dinoflagellate blooms where *C. furca* is the dominating species. However, a study from the North Sea in August reported a bloom of *C. furca* with 11 cells mL^{-1} (JANSEN *et al.*, 2006), and a bloom concentration as high as 480 cells mL^{-1} has been recorded in Chesapeake Bay (SMALLEY & COATS, 2002).

Since *C. furca* is a mixotrophic species (able to switch between autotrophy and phagotrophy) their abundance was probably not regulated by nutrients to the same degree as for *C. curvisetus*. When cellular nutrient ratios of *C. furca* are low, the species may switch to phagotrophy (SMALLEY *et al.*, 2003) and could thus avoid competing with autotrophs for resources. It is suggested that mixotrophy could give red-tide dinoflagellates a competitive advantage over strictly photosynthetic organisms (SMALLEY & COATS, 2002). It is also reported that nutrient replete cells do not ingest prey and have higher cellular Chl *a* content than cells growing under nutrient-depleted conditions (SMALLEY *et al.*, 2003). We recorded a gradual doubling in suspended Chl *a* concentrations from 5 to 10 m depth in Lake Rogoznica that was not associated with accumulated organic material (POC), and suggest that this could be due to increased cellular Chl *a* content of nutrient replete *C. furca* cells living in the deeper layers of the lake.

Not only were *C. curvisetus* and *C. furca* most abundant at 5 m depth but also *Acartia italica* with a concentration of 142 copepods L^{-1}. 61% of the integrated abundance of copepodites (CI-CVI) stayed at 5 m depth, while a total of 88% were found at 5 and 7 m depth. In contrast,

nauplii were most abundant at 2 m and decreased in concentration with increasing depth. Since there are few natural predators for *A. italica* in Lake Rogoznica, copepodite distribution was probably determined by food availability. The high surface concentration of nauplii indicates that eggs hatch in the surface layer and possibly also that *A. italica* copepodites were preying on their own nauplii at 5 m depth. Both a high surface abundance of nauplii and a strong cannibalistic predation pressure on nauplii by older copepodites in Lake Rogoznica were suggested in a previous study (KRŠINIĆ *et al.*, 2000).

Fecal pellet production by *Acartia italica*

The measured individual fecal pellet (FP) production rate of *A. italica*, 0.14 µg C d^{-1}, was low compared to reported values of *A. tonsa* feeding under optimal conditions (BESIKTEPE & DAM, 2002). Still, a daily FP production rate of 10 ind^{-1} is similar to rates obtained in a study where *A. tonsa* were grazing on a natural dinoflagellate bloom (JANSEN *et al.*, 2006). Although initial total phytoplankton carbon (PPC) was 240 µg L^{-1} in our experiment from Lake Rogoznica, only 33 µgC L^{-1} was phytoplankton other than *C. furca*. Diatoms made up 4 µgC L^{-1} and other phytoplankton (mainly dinoflagellates 10 - 20 µm) made up 29 µgC L^{-1}. Previous studies report that *Acartia* spp. are not able to graze *C. furca* (JANSEN *et al.*, 2006), and that the optimal food size for *A. tonsa* is 10-12 µm (BESIKTEPE & DAM, 2002). We may therefore assume that despite high concentrations of PPC in the incubation water, *A. italica* may have been food limited due to low concentrations of suitable food items. This could also explain the low clearance rates on Chl *a* obtained in our experiment.

A. italica and *C. furca* may have been competing for the same food as *C. furca* may ingest dinoflagellates at a rate of 0 – 0.11 ind^{-1} h^{-1}, corresponding to an average clearance rate of 2.5 ± 0.35 µl ind^{-1} h^{-1}, or a daily average consumption of prey biomass of 4.6% of body carbon (SMALLEY *et al.*, 2003). In our experiment this would correspond to an estimated total ingestion by *C. furca* of 11 µg C d^{-1}, which represents 33% of the phytoplankton biomass at T_0 of the experiment. We suggest that the low FP production rates of *A. italica* obtained in this study were due to low food concentrations of suitable food items as well as competition for prey with *C. furca*.

Carbon budget and vertical flux

Sedimentation rates of POC were high but represented only a 5% daily loss rate of suspended POC. A similar composition of sinking POC at 5 m depth as for suspended POC suggests that decomposition and degrading of material happened below the 5 m trap. This corresponded well with peaks in bacterial production at 7 and 11 m depth on May 17, as well as gradually increasing concentrations of dissolved organic carbon (DOC) with depth (ŠESTANOVIĆ *et al.*, 2005). The large fraction of detritus observed during our study may hence reflect high bacterial activity. High DOC concentrations have frequently been measured in Lake Rogoznica (ĆOSOVIĆ *et al.*, 2000; ŠESTANOVIĆ *et al.*, 2005), while suspended POC has not previously been measured.

Phytoplankton carbon (PPC) contributed on average 30% at 5 m depth and 11% at 10 m depth of the total POC flux. *C. furca* contributed 54 and 67% of sedimented PPC at 5 and 10 m depth, respectively. Since *C. furca* is capable of swimming 0.5–1 m h^{-1} (LEVANDOWSKY & KANETA, 1987), their presence especially in the deeper sediment traps could be due to migration and not passive flux.

Fecal pellet carbon (FPC) only made up 4-5% of the total POC flux. From the FP production experiment it is possible to calculate the potential contribution of FP to the POC export. A production rate of 0.14 µg FPC copepod d^{-1} and a total *A. italica* abundance of 528 * 10^3 m^{-2} gives a potential FPC community production of 74 mg C m^{-2} d^{-1}. Given these calculations, only 31% of the FPC production were recovered in the traps at 10 m depth. Hence, the estimated retention rate of FPC was 70% in Lake Rogoznica during our investigation based on the experimentally

obtained FP production rates. However, when comparing sedimented FPC with the standing stock of suspended FP obtained from the vertical profile the retention rate of FPC is even higher. The high retention of FP could either be due to high rates of bacterial degradation or pellet destruction (coprophagy or coprorhexy) by the copepods. Given the high sinking speed of *Acartia* FP of several meters d^{-1} (POULSEN & KIØRBOE, 2006) and the shallowness of the lake, residence time of a pellet would be <1 d and make degradation by bacteria unlikely to explain the high retention of FP.

Recent investigations have documented the ability of *A. tonsa* to feed on, or fragment own, FP with clearance rates of 11–22 mL female d^{-1} (POULSEN & KIØRBOE, 2005). The average concentration of FPC based on the profile from May 18th was 0.022 µg C mL^{-1}. This yields a potential FP ingestion rate from the copepod community of 128–255 mg FPC d^{-1}, representing 48-95% of the suspended biomass of FPC, or 173-344% of the FPC production based on our experimentally obtained rates. Based on this calculation exercise we suggest 1) that the low FPC flux in Lake Rogoznica was mainly due to pellet grazing or destruction by the *A. italica* community, and 2) that the FP production rates obtained in the experiment do not represent optimal production rates. In addition to food limitation, the low FP production rates may be caused by coprophagy or coprorhexy by the copepods in the incubation bottles due to long incubation times (18 h). Instead of sinking to the lake bottom as intact FP, the produced FP rapidly enters the pool of detritus through copepod grazing activity. The high fraction of detritus in the suspended (67%) and sedimented (68 and 86% at 5 and 10 m depth) carbon pool points to a system where biological production is rapidly degraded. The high vertical flux of carbon eventually accumulates at the bottom of the lake, where re-mineralization processes cause anoxic conditions.

CONCLUSIONS

Lake Rogoznica is a naturally eutrophicated marine system and was inhabited by only a few planktonic species during the study. Most biological activity took place between 2 and 12 m depth, with *A. italica*, *C. furca* and *C. curvisetus* abundances peaking at 5 m depth. The contribution of phytoplankton to the vertical carbon flux was high, while the contribution of copepod FP was minor. The low vertical flux of FP was unexpected due to high copepod abundance, shallow depth and no advection in the lake. An FP retention of >70% was calculated from the FP production experiment for *A. italica*. We suggest that this was due to coprophagy or mechanical destruction of FP by the zooplankton in the upper 5 m of the water column. The high contribution of suspended and sedimented detritus points to a system where biological production is rapidly degraded and sinks to the bottom of the lake where anoxic conditions are evolving.

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Regulacija vertikalnog fluksa i sastav planktona u jednostavnom ekološkom sistemu: "snapshots" iz malog slanog jezera Rogoznica (Hrvatska)

Camilla SVENSEN [1], Christian WEXELS RISER [1]* Ivona CETINIĆ [2,3] i Marina CARIĆ [4]

[1] *Norveški ribarstveni fakultet, Sveučilište u Tromsu, 9037 Tromsø, Norveška*

[2] *Prirodoslovni fakultet, Sveučilište u Zagrebu, Rooseveltov trg 6, 10000 Zagreb, Hrvatska*

[3] *Privremena adresa: Sveučilište južne Kalifornije, 3616 Trousdale Blvd., Los Angeles, CA 90089-0371, SAD*
e-mail: icetinic@usc.edu

[4] *Sveučilište u Dubrovniku, Institut za istraživanje mora i priobalja, Kneza D. Jude 12, 20101 Dubrovnik, Hrvatska*
e-mail: marina.caric-gluncic@unidu.hr

** Kontakt adresa, e-mail: Camilla.svensen@nfh.uit.no*

SAŽETAK

Istraživan je vertikalni protok u malom, slanom, plitkom i djelomično anoksičnom jezeru Rogoznica (istočna obala Jadranskog mora) na temelju sastava planktona, produkcije zooplanktonskih fekalnih peleta i vertikalnog protoka ugljika.

Jezero je prirodno eutroficirano s visokim koncentracijama hranjivih soli, a posebito čestičnim organskim ugljikom (POC) i relativno niskoj raznolikosti vrsta. Nekoliko pronađenih vrsta su pokazivale visoke brojnosti. Zbog svoje jednostavne ekološke strukture i slabih fizikalnih sila jezero Rogoznica se smatra prirodnim laboratorijem pogodnim za istraživanje planktona. Pronađena je samo jedna vrsta kopepoda, *Acartia italica*, s maksimalnom brojnošću od 140 jedinki L^{-1}. Miksotrofni dinoflagelat *Ceratium furca* i diatomeja *Chaetoceros curvisetus* su bili zastupljeni s ~90% u fitoplanktonskoj biomasi. Fitoplankton predstavlja do 30% u dotoku čestičnog organskog ugljika na dubini od 5 m, te 10% na dubini od 10 m, a prevladavale su vrste *C. curvisetus* i *C. furca.*

Prosječni dotok čestičnog organskog ugljika iznosio je 730 ± 40 mg m^{-2} d^{-1} na dubini od 5 m i 750 ± 90 mg m^{-2} d^{-1} na dubini od 10 m, dok je detritus obuhvaćao 68% odnosno 86% dotoka na dubinama od 5 i 10 m.

Usprkos visokoj zastupljenosti kopepoda i koncentraciji suspendiranih fekalnih peleta, doprinos fekalnih peleta vertikalnom dotoku čestičnog organskog ugljika je bio samo 4 – 5 %. Najveći doprinos vertikalnom protoku ugljika predstavlja detritus i visoko zadržavanje je vjerojatno posljedica grazing-a fekalnih peleta ili njihove fragmentacije od strane kopepodita *A. italica* na dubini iznad 5 m. Ustanovljeno je da je jezero Rogoznica produktivni sistem u kojem se organski materijal brzo pretvara u detritus.

Ključne riječi: vertikalni protok ugljika, *Ceratium furca, Chaetoceros curvisetus, Acartia italica*, fekalni peleti, Hrvatska, srednji Jadran, jezero Rogoznica