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Management Tools for Aquatic Systems: The Role of Periodic Hydraulic Disturbances on Planktonic Communities

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INTRODUCTION

Environmental disturbances in aquatic systems alter phytoplankton community structure, diversity and biomass (Hutchinson, 1961). For example, laboratory experiments and field studies have shown that episodic flushing and nutrient loading can result in enhanced phytoplankton species diversity (Padisak, 1993; Sommer, 1995; Hambright and Zohary, 2000; Buyukates and Roelke, 2002; Lovejoy et al., 2002). Competitive abilities of phytoplankton species vary as a function of the physicochemical environment. It follows that, high species diversity can then be maintained in systems where conditions fluctuate, thereby preventing competitive exclusion. Fluctuating conditions can also affect phytoplankton biomass in systems where phytoplankton and zooplankton interactions become decoupled, i.e., systems where phytoplankton response times are much less than that for zooplankton (Sommer et al., 1986; Reynolds, 1984; Lehman, 1988).

Because disturbances influence the structure of the phytoplankton community, the zooplankton community is also affected (Sommer et al., 1986; Steiner, 2001; Buyukates and Roelke, 2002). For example, succession from less-edible, slower growing, k-selected phytoplankton species to more edible, rapidly growing, r-selected species may occur following a favorable disturbance, and this may stimulate secondary productivity (Sommer, 1981; Reynolds, 1984; Sommer et al., 1986). Zooplankton population shifts might also occur, e.g., increased productivity of small, rapidly growing phytoplankton may result in enhanced performance of zooplankton of small body-size with short generation times (Sommer et al., 1986; Reynolds, 1984). Additionally, high phytoplankton species diversity may favor zooplankton forms that have adopted preferential grazing strategies (Reynolds, 1984; Reynolds, 1989).

Disturbances might affect zooplankton in another way, i.e., through enhanced food-quality. For example, under conditions of pulsed flushing and nutrient loading some phytoplankton species uptake and store nutrients at a rate greater than their reproductive rate (Ketchum, 1939; Droop, 1968; Droop, 1983; Sommer, 1989; Pinckney et al., 1999; Worm and Sommer, 2000). Higher cell-quotas for nutrients that limit zooplankton growth may result in enhanced secondary productivity (Sterner and Hessen, 1994; Hessen and Bjerkeng, 1997; Roelke et al., 1999; Roelke 2000). Conversely, low frequency and magnitude of inflows may lead the system toward steady-state conditions, where cell quotas might approach critical levels. Under these conditions, previously suitable prey might become unsuitable because of the nutritional

mismatch between predator and prey. In this scenario, classical Lotka-Volterra predator-prey theory, where predator abundance increases with increasing food abundance, would fail to describe interactions between zooplankton and phytoplankton (Lotka, 1932). In other words, regardless of high food quantity, poor food quality would result in decreased performance of some zooplankton populations (Sommer, 1992; Roelke, 2000; Urabe et al., 2002).

The structure of the zooplankton community might enhance or mask the effects of disturbances on phytoplankton community structure and food quality. For example, a well-established population of preferential grazers may exert strong top-down control on some phytoplankton populations, which would have otherwise proliferated following a disturbance (MacKay and Elser, 1998; Saunders et al., 2000). Similarly, non-selective grazers might exert a controlling top-down force on accumulated biomass. This would result in a continual recycling of nutrients to inorganic pools, thereby preventing phytoplankton cell quotas from declining to levels unsuitable for some grazers (Sterner and Hessen, 1994; Gulati and DeMott, 1997).

In a previous numerical modeling study, Roelke (2000) indicated that pulsed flushing and nutrient loading events would result in greater phytoplankton species diversity and greater secondary productivity. In order to prove this concept, we conducted experiments of a flow-through design, and rotifers and ciliates numerically dominated the zooplankton. Synchronous with these experiments, and using the same natural assemblages, we conducted experiments using semi-continuous design. In these experiments turbulence was less, and typically copepods were more prevalent and rotifers were much less abundant. Here we compare succession patterns between the two types of experiments and evaluate how the differing zooplankton community structure influenced the role of pulsed inflows on phytoplankton species diversity and secondary productivity.

MATERIALS AND METHODS

Three semi-continuous and flow-through design experiments were performed on March 15, June 7 and September 8, 2001 to test the influence of pulsed inflows of varying frequency on phytoplankton and zooplankton population size, as well as phytoplankton diversity. Here, “semi-continuous” refers to experiments conducted in flasks where the volume was held constant.

Natural plankton assemblages were collected from surface waters in 20 L Nalgene carboys from the Rincon Delta, Texas (27°52' N; 97°31' W). The samples were transported to the

laboratory located in College Station, Texas. This process took ~4 h. During this time samples were kept shaded and cool. At the laboratory, an aliquot of the water was filtered through 47 mm Whatman GF/F glass fiber filters. The aliquot was then autoclaved at 121ºC and 15 PSI for 30 min, then left to cool. Solid standards were then dissolved into the aliquot to prepare media following a f/2 recipe (Guillard and Ryther, 1962), except for nitrogen and phosphorus, which were set according to previous studies (Roelke et al., 1997; Roelke, 2000; discussed more below). This process took ~2 h. To avoid bias from large zooplankton (Sommer, 1985), a 200 µm mesh-size plankton net was used to pre-filter the remaining water, which was then used as an inoculum for the batch experiments. Each experiment was started ~6 h after water was collected from the delta.

Each of the three experiments was comprised of two treatments, with each treatment performed in triplicate. The treatments were 1-day and 3-day pulsed inflows. In our analyses semi-continuous design, we assumed that volume displacement occurring daily was analogous to continuous flow. Chamber volumes were constant, so plankton were subjected to flushing losses as a function of the inflow. The incubators used in the experiments allowed control of temperature, irradiance and photoperiod (see Buyukates, 2003). The degree of flushing and nutrient loading (for nitrogen and phosphorus only) was chosen according to earlier studies (Roelke et al., 1997; Roelke 2000). This scheme replicated likely conditions in a target tidal creek where freshwater flow was replaced with the discharge from a nearby sewage treatment plant in the Rincon Delta.

Temperature was held constant at 20°C for the batch experiments, which was the average seasonal temperature in the delta. Based on photoperiod range of the delta a 12-h L/D cycle was selected. Cool white fluorescent bulbs were used as a light source and irradiance was 200 $\mu Em^{-2}s^{-1}$. This value was in the range of typical light saturated photosynthesis rates of many phytoplankton (Kirk, 1994).

While the two experiment designs were very similar in regards to their physicochemical environment, a major difference was the level of turbulence. In the flow-through design, turbulence was controlled using an aerator powered through a time-delay relay (5 seconds on / 40 seconds off). In the semi-continuous design, chambers were gently swirled twice each day. Consequently, turbulence was greater in the fflow-through experiments.

Periphyton growth on the sides of the incubators was avoided in both experimental designs. In the flow-through design experiments, horizontal surfaces, where periphyton growth was a problem in preliminary studies, were covered with aluminum foil, thereby inhibiting growth. The gentle swirling of the semi-continuous design experiments inhibits periphyton growth as well. In all the experiments reported below, periphyton did not accumulate in any of the chambers. Therefore, shading or nutrient uptake by periphyton was minimal.

The water used for the inoculum was drawn from the same well-mixed carboy that contained the natural plankton assemblage in each experiment. Thus, initial phytoplankton and zooplankton community structures were assumed to be very similar in each of the treatments in a given experiment.

Samples for microscopic analysis were collected at three-day intervals and preserved immediately with 5% glutaraldehyde, v/v. Plankton identification and counts were conducted using an inverted light microscope by the Utermöhl method (1958). Phytoplankton was identified to the taxonomic level of genus (Prescott, 1978). Zooplankton was categorized into copepods (adult, nauplii), rotifers, and ciliates. Phytoplankton cell volumes were estimated by measuring cell dimensions and using common geometric shapes (Wetzel and Likens, 1991). Shannon-Weaver index was used to estimate species diversity (Shannon, 1949),

$$H' = \sum_{i=1}^{n} p_i \log_2 (p_i)$$

where p_i = biomass of species *i* / total biomass, and n = number of species at a specific time. The biovolume for each of the size classes (<20, 20-100, 100-200, >200 µm) were estimated by summation of the population biovolume of algal species whose maximal linear dimensions fell within the classes (Havens 1991a).

Differences between mode of inflow among the three experiments conducted on March, June and September were determined by integrating the variables, i.e., bulk phytoplankton and zooplankton taxonomic categories, over the duration of each experiment, then applying a two-factor repeated measures ANOVA (SPSS Inc., 1994). These analyses tested for significant differences between the inflow treatments, i.e., continuous and pulsed inflow, time of year, and the interaction between the mode of inflow and time of year. Statistically significant differences among treatments were assessed at the 5 % level of confidence.

RESULTS

Treatments receiving 3-day pulses showed greater accumulation of adult copepod and nauplii populations in all experiments (Figs. 1, 2, 3, Table 1 and 2) and reduced accumulation of phytoplankton biovolume in all experiments of semi-continuous design and March and June experiments of the flow-through design (Figs. 4, 5 and Table 1 and 2).

Zooplankton abundance in 1-day and 3-day pulse treatments

Zooplankton community structure was different for each of the experiments. Numerically, adult copepods and nauplii dominated the macro-zooplankton in the March and June experiments (Figs. 1, 2) while rotifers were abundant in the September experiment (Fig. 3).

Despite the varying zooplankton community structures, similar responses to the treatments were observed. Adult copepod and nauplii densities were significantly greater in 3-day pulsed treatments in all experiments (Table 1). Rotifer densities did not differ among treatments in the March and June experiments, but did show significantly greater densities in the September experiment (Table 1). Protozoa abundance showed no differential response to variable inflow regime in any of the experiments (Table 1).

Zooplankton abundance and structure in continuous vs. pulsed treatments

Despite differences in zooplankton community structure for each of the experiments, rotifers dominated the macro-zooplankton in flow-through design in all experiments (Figs. 1, 2, 3). In all experiments similar responses to the treatments were observed. Adult copepod and rotifer biovolume were significantly greater in pulsed flow treatments in all experiments (Table 2). Nauplii and protozoa did show significantly greater densities in the March and June experiments but did not differ among treatments in the September experiment (Table 2).

Phytoplankton biovolume in 1-day and 3-day pulse treatments

Phytoplankton community structure also varied between experiments (Fig. 6). Initial phytoplankton community was comprised of diatoms, green algae, cyanobacteria, dinoflagellates and euglena in March and June while diatoms, green algae, cyanobacteria and cryptomonads dominated in September. Although cryptomonads were existent in September their contribution to the total phytoplankton biovolume was small. Some genera were found in all three experiments, others were only found in the third experiment. For example, *Anabaena* sep.,

Peridinium sp., other dinoflagellate species, *Euglena* sp., *Coscinodiscus* sp., *Skeletonema* sp., and *Odontella* sp. were present only in March and June. *Cryptomonad* sp., *Chlamydomonas* sp. and small centric diatoms were present only in September.

As with the zooplankton, similar responses to the treatments were observed in the phytoplankton, despite differences in community structures between experiments. The 1-day pulsed treatments showed higher total phytoplankton biovolume (~2 fold) in all experiments compared to 3-day pulsed treatments (Fig. 4). But at the 5% level, this trend was not significant in the June experiment (Table 1).

Closer examination of each experiment showed that diatoms, *Nitzschia closterium* and *Entomoneis* sp., and coccoid forms of green algae dominated the phytoplankton in March, and both showed significantly greater accumulation of biomass in the 1-day pulsed treatments. Diatoms, *N. closterium* and *Entomoneis* sp., and dinoflagellates, *Peridinium* sp., dominated in June, but only dinoflagellates showed significantly greater accumulation of biomass in the 1-day pulsed treatments. And finally, diatoms, *Entomoneis* sp. and *Chaetoceros* sp., dominated the third experiment. In March and June there were not significant size differences between diatom species. In September small sized phytoplankton dominated the assemblage.

In all experiments, 1-day pulses resulted in decreased species diversity relative to 3-day pulses (Fig. 7). Abrupt dips in diversity during the March and June experiments coincided with population shifts.

Phytoplankton biovolume and composition in continuous vs. pulsed treatments

Phytoplankton community composition varied between experiments. Despite differences in community structure similar responses were observed in the phytoplankton as with the zooplankton. The continuous flow treatments showed higher integrated total phytoplankton biovolume (~ 2 fold) in all experiments compared to pulsed treatments (Figs. 5). But at the 5 % level, this trend was not significant in the September experiment (Table 2).

More detailed analysis of the phytoplankton community structure in each experiment (see Buyukates and Roelke, 2005) showed that coccoid and oblong forms of green algae and diatoms, *Pleurosigma* sp., *Gyrosigma* sp. and *Navicula* sp. dominated the phytoplankton in March, and both showed significantly greater accumulation of biomass in the continuous flow treatment. Dinoflagellates did not show significant differences and chrysophytes did only occur at the last

sampling time in pulsed flow treatments. *Gloeocystis* sp., coccoid and oblong forms of green algae, diatoms, *Nitzschia* sp. and *Skeletonema* sp., an unidentified dinoflagellate species dominated in June. Dinoflagellates and diatoms showed significantly greater accumulation in continuous flow treatments. Finally, various species of green algae and centric forms of diatoms, *Nitzschia* sp., and *Navicula* sp. dominated in September, but only diatoms showed significantly greater accumulation of biomass in the continuous flow treatments (Table 2).

Phytoplankton species diversity showed similar trends in the March and June experiments (Fig. 7). During the March experiment, continuous flow resulted in a continued decrease in phytoplankton species diversity, while the chambers receiving pulsed flows showed a dramatic decrease after the first pulse, then an increase in phytoplankton species diversity (Fig. 7). This dramatic decrease in diversity at the first pulsed flow event coincided with a rapid increase in *Navicula* sp. and coccoid forms of green algae. Continued decrease of phytoplankton species diversity observed in the continuous flow chambers was due to the gradual accumulation of large diatoms, especially *Pleurosigma* sp. and *Gyrosigma* sp. In the June experiment, continuous flow resulted in decreased phytoplankton species diversity while higher diversity was observed in the pulsed flow chambers (Fig. 7). An abrupt decrease in diversity in the fourth sampling time of pulsed flow coincided with the accumulation of *Nitzschia* species, especially *Nitzschia closterium* and *Nitzschia longissima*. Low diversity in the continuous flow chambers was due to the abundance of an unidentified dinoflagellate species. In the September experiment as the diatom and green algal bloom ensued phytoplankton species diversity decreased in both treatments (Fig. 7). Accumulation of phytoplankton biovolume in the September experiment varied from the first two experiments (Fig. 5). In both treatments of the third experiment diatoms and green algae dominated the phytoplankton, and accumulated in biovolume to a level that was an order of magnitude greater than the previous two experiments.

Except for the continuous flow treatment in the September experiment, variability within treatments was low. In this experiment, however, the magnitude and the timing of the maximum biovolume, and the phytoplankton composition at the genus level differed sp., *Navicula* sp., *Characium* sp. and *Ankistrodesmus* sp. were the prevalent genera. In the second chamber phytoplankton structure was comprised of a combination of centric diatoms, *Nitzschia* sp., *Navicula* sp., *Characium* sp., *Entomoneis* sp., *Tetraedron* sp., *Gloeocystis* sp. and *Franceia*

droescheri. In the third chamber *Nitzschia* sp., *Entomoneis* sp. and *Franceia droescheri* were the prevalent genera.

Comparison of semi-continuous and flow-through design experiments

Overall response, in terms of zooplankton abundance, phytoplankton biovolume and phytoplankton species diversity, was consistent between the semi-continuous experimental design and the flow-through incubation design. Phytoplankton and zooplankton community composition, however, varied between the experimental designs, despite the near-identical initial conditions. For example, diatoms dominated in all treatments using the semi-continuous experimental design, whereas green algae, dinoflagellates and diatoms dominated in the March, June and September experiments of flow-through design, respectively (Figs. 8, 9, 10).

In the March and June experiments, adult copepods and nauplii dominated the semi-continuous design, and rotifers dominated the September experiment. In the flow-through design experiments, rotifers were dominant in all experiments (Figs. 1, 2, 3). Finally, protozoa did not do well in experiments of semi-continuous design relative to the experiments of flow-through design (Figs. 8, 9, 10).

Grazing pressure induced shifts in phytoplankton cell-size was observed in both types of designs (Figs. 8, 9, 10). However, the shift from smaller to larger cell-size
was more prevalent in the semi-continuous experiments, in which the adult copepods
among chambers within the continuous flow treatment. In the first chamber *Nitzschia* and nauplii were dominant, compared to flow-through experiments, where rotifers dominated.

DISCUSSION

The experiments showed that despite differences in zooplankton structure and phytoplankton community composition between the two experiment designs, trends in the model predictions by Roelke (2000) were supported. That is, secondary productivity and phytoplankton species diversity was higher under pulsed inflow and nutrient loading conditions. It may be that in both experimental designs, phytoplankton was of higher quality in the 3-day pulsed treatments, and this resulted in enhanced zooplankton growth. Another alternative explanation is that the increased diversity in 3-day pulsed treatments might have offered selective grazers a better environment, i.e., a broad range of phytoplankton to choose from.

In the March and June experiments of semi-continuous design and flow-through design, adult copepods and nauplii dominated the former, while rotifers dominated the latter. This result was likely due to the lower turbulence in the experiments of semi-continuous design, which might have favored copepod feeding and growth (Saiz and Alcaraz 1991; Alcaraz 1997; Petersen et al. 1998; Quintana et al. 1998). In addition, copepod adults can graze on rotifers, and also protozoa (Sterner 1989; Ingrid et al. 1996). It is likely that grazing by adult copepods contributed to the lower abundance of rotifers and protozoa in the March and June semi-continuous experiments.

In the September experiment, both designs were dominated by rotifers. Water was collected for this experiment shortly after a heavy rain event in the watershed. Salinity was low and nutrient concentrations were high. Various species of rotifers, and small, fast growing, r-selected phytoplankton dominated the plankton assemblage at this time. Previous studies showed that when food sources and physical conditions are favorable for rotifers, they could reproduce rapidly (Reynolds 1984; Gilbert 1985; Sterner 1989). In this way, rotifers can out-pace grazing pressure exerted by slower growing copepods, and come to numerically dominate the zooplankton community. Consequently, for the September semi-continuous design and flow-through design experiments, grazer pressure as a function of zooplankton community structure, were similar.

Because zooplankton structure varied between the March and June experiments of semi-continuous design and flow-through design, the phytoplankton assemblages were subjected to different selective grazing pressure. For example, copepod adults and nauplii can graze on the same size and structure range of phytoplankton that are susceptible to rotifer grazing, but copepods are able to graze on larger phytoplankton species as well (Reynolds 1984; Sterner 1989).

Effects of differing grazing pressure between the two experiment designs for the March and June experiments were reflected in the phytoplankton succession trajectories. Although strong grazing pressure caused an increase in phytoplankton cell size in both types of experimental designs, shifts from smaller to larger cell-size was more prevalent in the semi-continuous design, in which the adult copepods and nauplii were dominant, compared to flow-through design, where rotifers dominated. This trend was strongest in the 3-day pulse treatments, where large diatoms were main survivors in the semi-continuous design (see Buyukates and

Roelke, 2005), and some combination of large diatoms, colonial green algae and dinoflagellates dominated the flow-through design. Even though zooplankton community structure was alike in both designs, the same phytoplankton cell-size shift observed in the March and June experiments was observed in the September experiment. Although rotifers dominated both semi-continuous and flow-through designs, the semi-continuous design had a more pronounced phytoplankton cell-size shift. Most likely, this was due to the presence of some copepods in the semi-continuous experiment, although not as much as the previous two semi-continuous experiments. These results are consistent with the hypothesis that phytoplankton community structure moves toward dominance of larger species under strong grazing pressure due to increased body size or biomass of zooplankton population (Carpenter and Kitchell 1984; Bergquist et al. 1985; Carpenter et al. 1993). Again consistent with the model predictions of Roelke (2000), accumulation of grazer populations and phytoplankton species diversity was higher in the 3-day pulse treatments in both types of experiment designs.

Higher phytoplankton species diversity in treatments receiving pulsed inflows might be a result of top-down control and fluctuating abiotic conditions. For example, selective feeding on the most abundant phytoplankton species would prevent exclusion of slower-growing species, thereby maintaining diversity (Sommer et al. 1986; Gismervik and Andersen 1997; Sommer and Stibor 2002). This process would exert greater influence on phytoplankton diversity with higher zooplankton populations. Similarly, fluctuating physicochemical conditions, which would have occurred in the pulsed inflow treatments, are known to constrain competitive exclusion and promote coexistence (Hutchinson 1961; Sommer et al. 1986; Sommer et al.1993).

In summary, through comparison of experiments of semi-continuous and flow-through design, I showed that pulsed inflows supported greater accumulation of some grazer populations and higher phytoplankton species diversity, when zooplankton were dominated by rotifers or by copepods. The results of this study are consistent with previous model predictions (Roelke 2000). Further experiments are needed to determine whether this relationship holds true when non-selective grazers dominate the zooplankton community structure.

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Table 1. Zooplankton and phytoplankton biovolume accumulation in 1-day and 3-day flow treatments in March, June and September experiments. The table lists the zooplankton and phytoplankton groups and results of two-factor repeated measures ANOVA. Here, flow treatments (1-day vs. 3-day) are repeated measures and different experiment periods (March, June, September) are between–subjects measures that used variables of integrated zooplankton and phytoplankton population over the entire period of experiment. The mean difference is significant at the .05 level; n.s. = is not significant; BSEP = Between Subjects Experiment period; WSFT = Within Subjects Flow treatments; EPFT = Experiment per. x Flow treatment.

Zooplankton groups	Source	SS	DF	MS	F	p
Copepodids	BSEP	1.93E+17	2	9.66E+16	107.32	.000
	WSFT	8.85E+16	1	8.85E+16	26108.92	.000
	EPFT	4.63E+15	2	2.32E+15	683.33	.000
Nauplii	BSEP	6.26E+15	2	3.13E+15	263.09	.000
	WSFT	3.31E+15	1	3.31E+15	1768.22	.000
	EPFT	3.44E+14	2	1.72E+14	91.87	.000
Rotifer	BSEP	1.99E+17	2	9.97E+16	308.87	.000
	WSFT	5.49E+15	1	5.49E+15	195.04	.000
	EPFT	9.54E+15	2	4.77E+15	169.37	.000
Protozoa	BSEP	1.28E+17	2	6.41E+16	435479.79	.000
	WSFT	8.54E+14	1	8.54E+14	3204056.70	.000
	EPFT	1.79E+15	2	8.96E+14	3360922.00	.000

Phytoplankton groups	Source	SS	DF	MS	F	p
Cyanobacteria	BSEP	3.27E+18	2	5.45E+17	169.23	.000
	WSFT	4.27E+17	1	4.27E+17	.58	.474 n.s.
	EPFT	4.17E+18	2	2.09E+18	2.58	.135 n.s.
Green algae	BSEP	1.27E+21	2	6.33E+20	294.49	.000
	WSFT	1.84E+20	1	1.84E+20	71.24	.000
	EPFT	7.14E+19	2	3.57E+19	13.82	.006
Diatoms	BSEP	3.52E+23	2	1.76E+23	161.81	.000
	WSFT	3.37E+22	1	3.37E+22	106.27	.000
	EPFT	3.82E+22	2	1.91E+22	60.20	.000
Dinoflagellates	BSEP	9.98E+20	2	4.99E+20	724.76	.000
	WSFT	3.65E+20	1	3.65E+20	269.11	.000
	EPFT	6.72E+20	2	3.36E+20	248.02	.000
Total	BSEP	3.95E+21	2	1.98E+23	194.22	.000
	WSFT	4.65E+22	1	4.65E+22	159.48	.000
	EPFT	3.24E+22	2	1.62E+22	55.59	.000

Table 2. Zooplankton and phytoplankton biovolume accumulation in continuous and pulsed flow treatments in March, June and September experiments. The table lists the dominant zooplankton and phytoplankton groups and results of two-factor repeated measures ANOVA. Here, flow treatments (continuous vs. pulsed) are repeated measures and different experiment periods (March, June, September) are between–subjects measures that used variables of integrated zooplankton and phytoplankton population over the entire period of experiment. The mean difference is significant at the .05 level; n.s. = is not significant; BSEP = Between Subjects Experiment period; WSFT = Within Subjects Flow treatments; EPFT = Experiment per. x Flow treatment.

Zooplankton groups	Source	SS	DF	MS	F	p
Copepodids	BSEP	5.76E+15	2	2.88E+15	2.84	.136 n.s.
	WSFT	1.74E+14	1	1.74E+14	8.36	.028
	EPFT	6.14E+15	2	3.07E+15	147.22	.000
Nauplii	BSEP	1.72E+15	2	8.60E+14	12.07	.008
	WSFT	1.07E+15	1	1.07E+15	30.18	.002
	EPFT	8.66E+14	2	4.33E+14	12.27	.008
Rotifer	BSEP	5.77E+17	2	2.89E+17	687.92	.000
	WSFT	1.47E+17	1	1.47E+17	5019.94	.000
	EPFT	4.26E+16	2	2.13E+16	728.40	.000
Protozoa	BSEP	1.09E+19	2	5.46E+18	6193224.00	.000
	WSFT	1.00E+18	1	1.00E+18	8699585.00	.000
	EPFT	5.91E+18	2	2.96E+18	25697295.00	.000

Phytoplankton groups	Source	SS	DF	MS	F	p
Cyanobacteria	BSEP	2.80E+20	2	1.40E+20	309.37	.000
	WSFT	7.30E+18	1	7.30E+18	18.85	.005
	EPFT	1.88E+19	2	9.40E+18	24.28	.001
Green algae	BSEP	9.99E+23	2	3.10E+22	16.11	.004
	WSFT	2.28E+22	1	2.28E+22	.76	.417 n.s.
	EPFT	3.68E+22	2	1.84E+22	.61	.573 n.s
Diatoms	BSEP	2.85E+24	2	1.43E+24	140.01	.000
	WSFT	1.15E+23	1	1.15E+23	15.50	.008
	EPFT	2.81E+23	2	1.40E+23	18.96	.003
Dinoflagellates	BSEP	2.66E+22	2	2.12E+19	627.49	.000
	WSFT	9.70E+21	1	9.70E+21	120.66	.000
	EPFT	1.91E+22	2	9.57E+21	119.01	.000
Total	BSEP	6.87E+24	2	3.43E+24	51.51	.000
	WSFT	8.11E+22	1	8.11E+22	1.35	.289 n.s.
	EPFT	8.82E+22	2	4.41E+22	.73	.518 n.s.

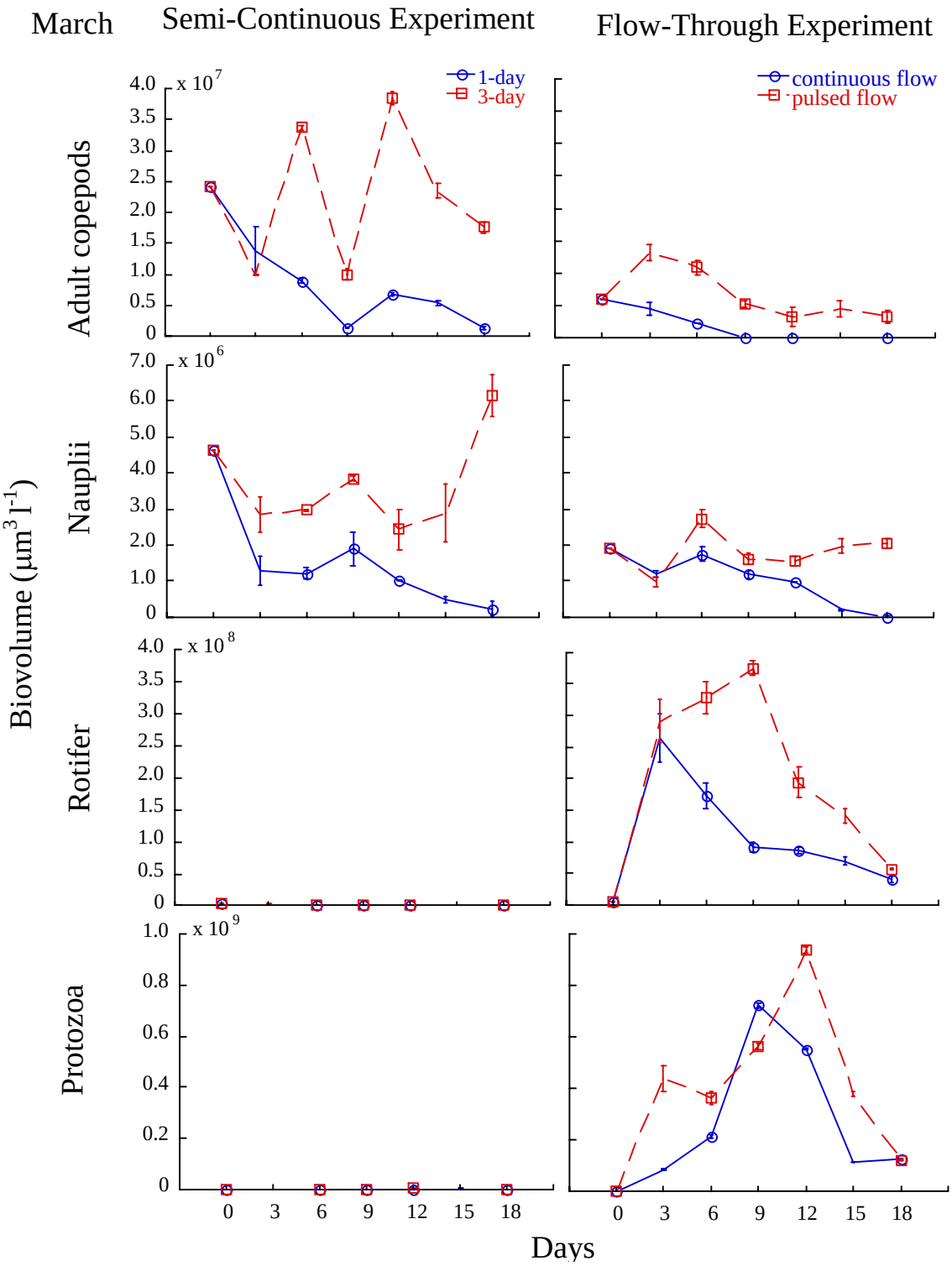

Figure 1. Accumulation of adult copepods, nauplii, rotifer and protozoa in semi-continuous and flow-through design experiments conducted in March. Symbols and error bars indicate the mean ± 1 SD from triplicate chambers. In both experimental designs, zooplankton performed better in the three incubators receiving 3-day pulse inflows.

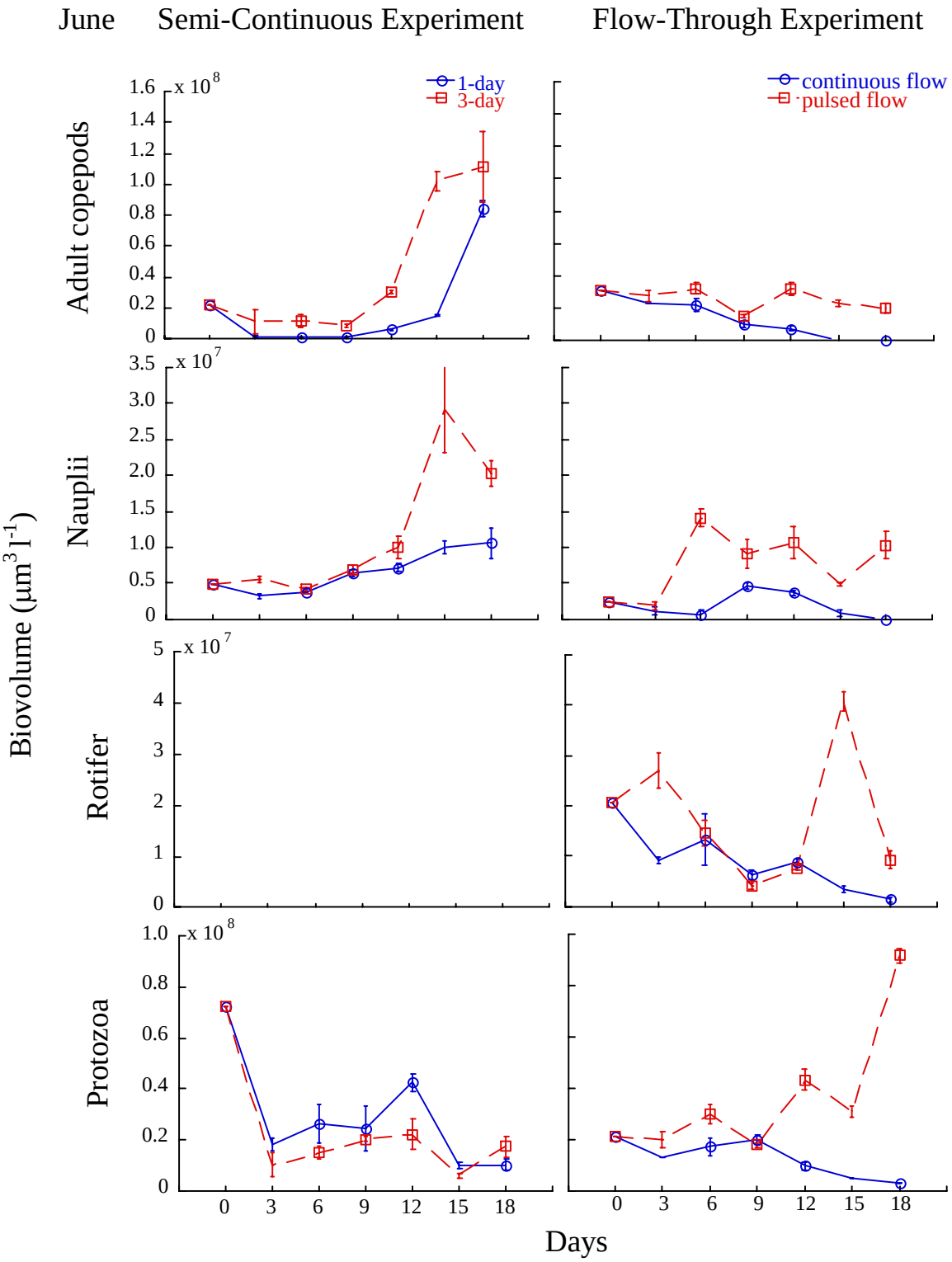

Figure 2. Accumulation of adult copepods, nauplii, rotifer and protozoa in semi-continuous and flow-through design experiments conducted in June. Symbols and error bars indicate the mean ± 1 SD from triplicate chambers. Zooplankton performed beter in the three incubators receiving 3-day pulse inflows compared to the three incubators receiving 1-day inflows.

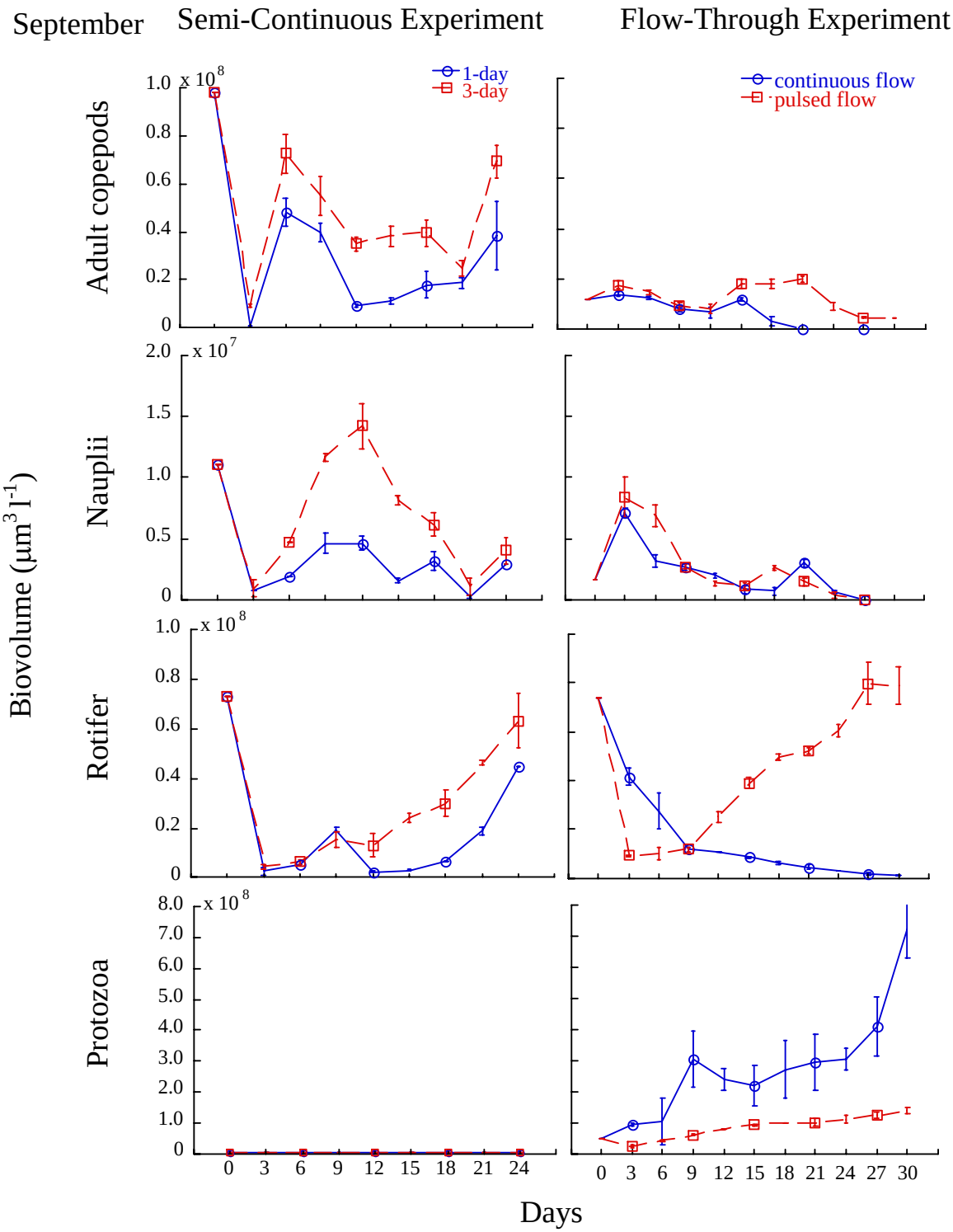

Figure 3. Accumulation of adult copepods, nauplii, rotifer and protozoa in semi-continuous and flow-through design experiments conducted in September. Symbols and error bars indicate the mean ± 1 SD from triplicate chambers. Except for the protozoa in the flow-through design, zooplankton performed better in the three incubators receiving 3-day pulse inflows.

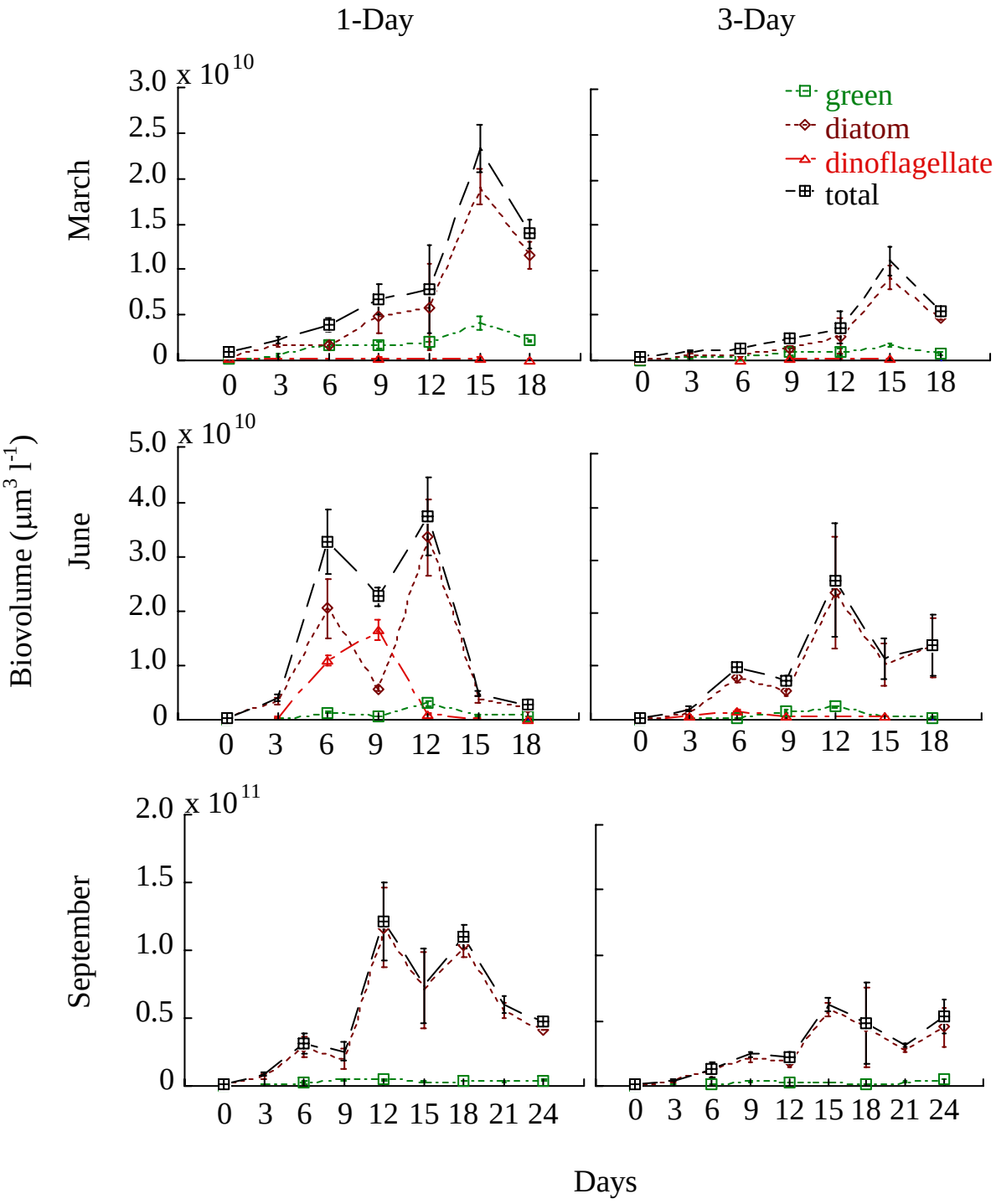

Figure 4. Accumulation of phytoplankton biovolume in the semi-continuous design experiments conducted in March, June and September. Symbols and error bars indicate the mean ± 1 SD from triplicate chambers. Total biovolume was lower in the three flasks receiving 3-day pulse inflows compared to the three flasks receiving 1-day pulse inflows.

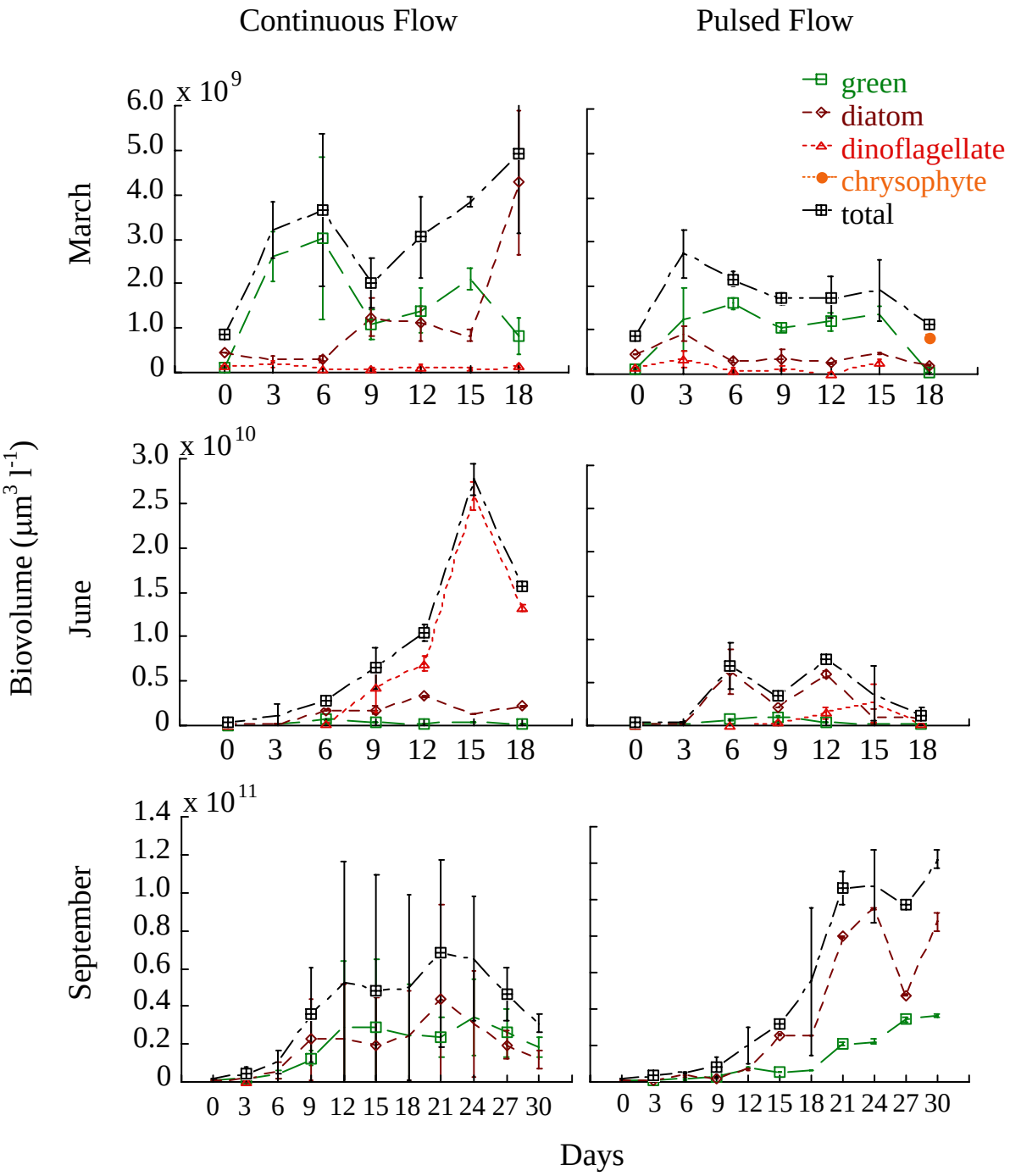

Figure 5. Accumulation of phytoplankton biovolume in the flow-through design experiments conducted in March, June and September. Symbols and error bars indicate the mean ± 1 SD from triplicate chambers. Except for the September experiment total biovolume was lower in the three incubators receiving 3-day pulse inflows compared to the three incubators receiving 1-day pulse inflows.

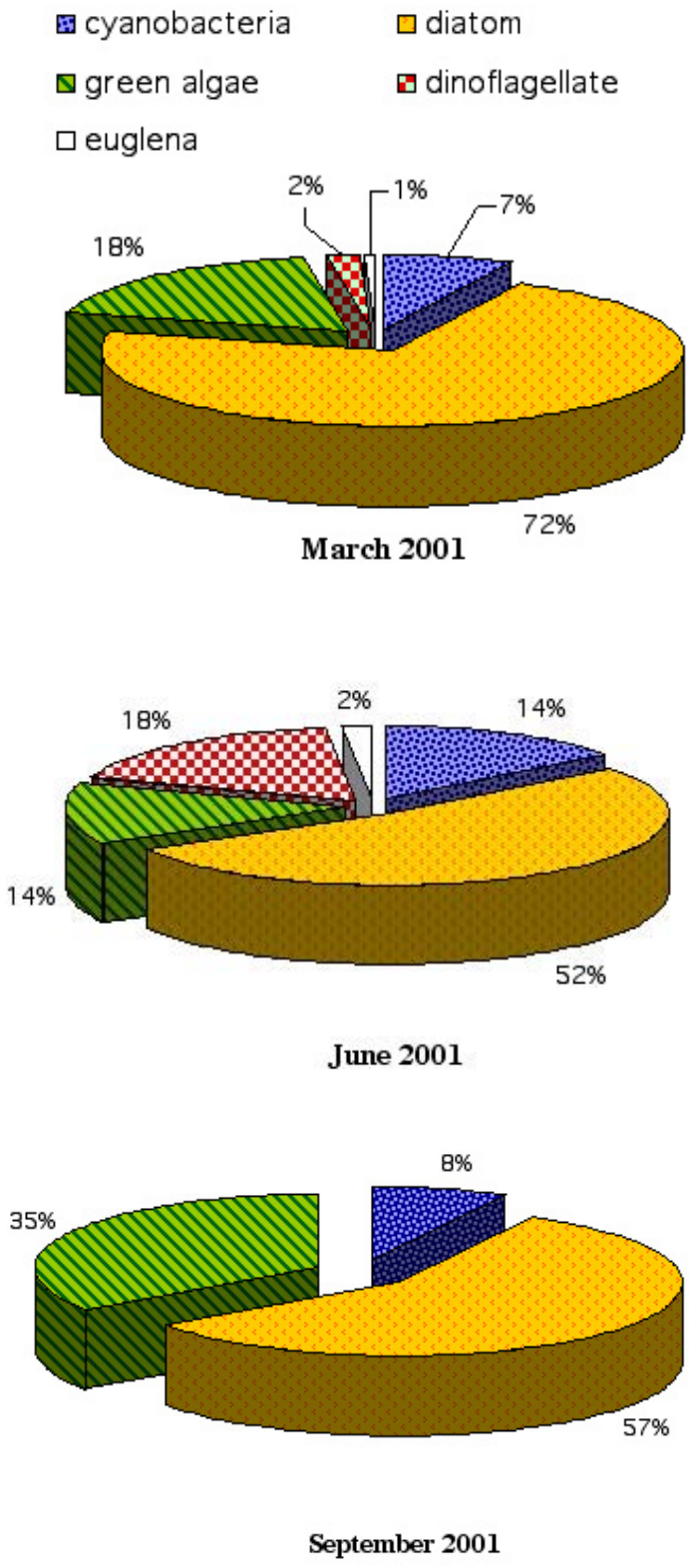

Figure 6. Initial phytoplankton community composition placed into generic taxonomic groups of diatoms, cyanobacteria, green algae, dinoflagellates and *Euglena* in March, June and September samplings. Graph shows only the abundant groups in each month.

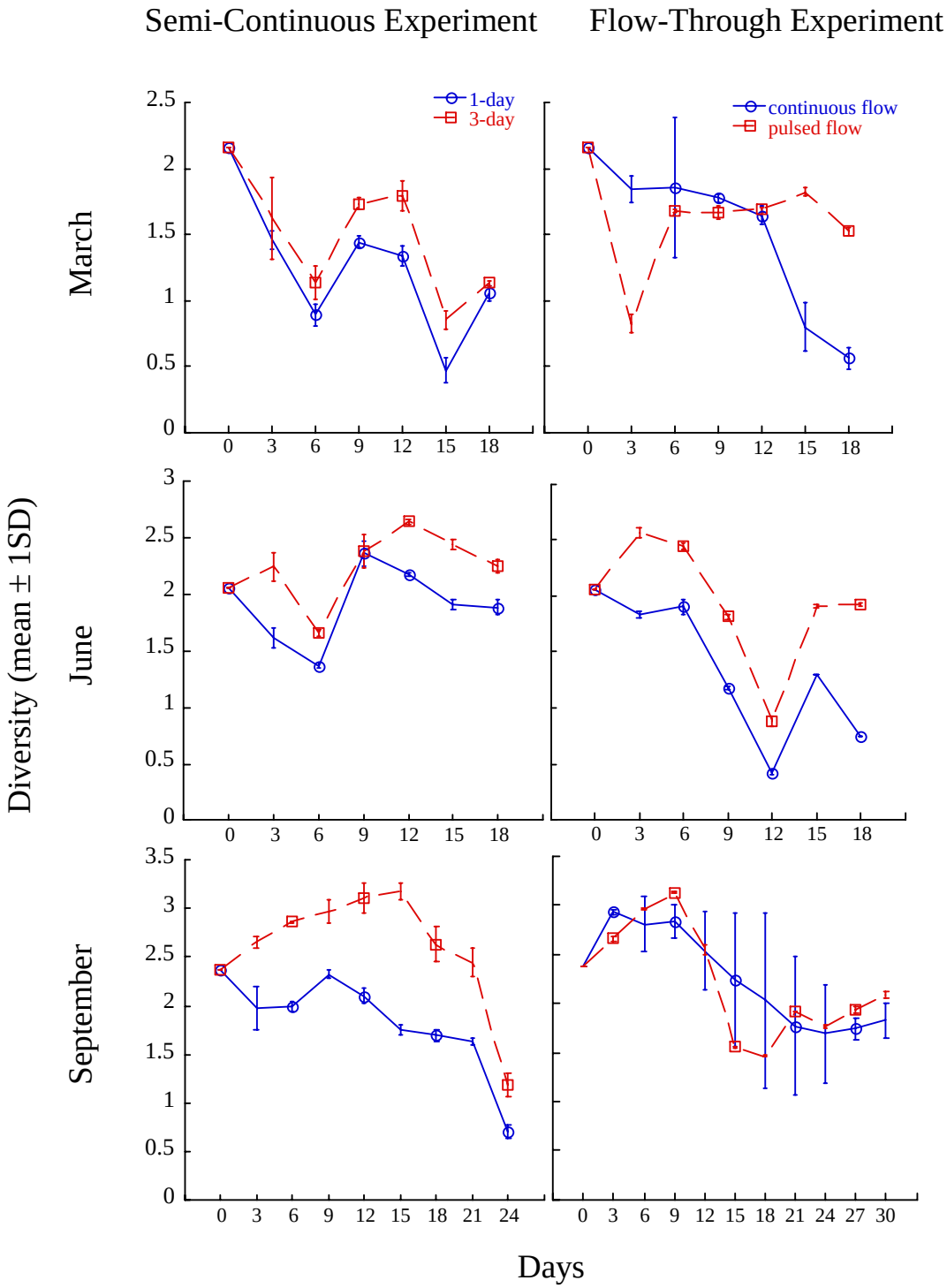

Figure 7. Phytoplankton species diversity in the semi-continuous and flow-through design experiments in March, June and September. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse flow treatments on triplicate incubators. In most cases, 1-day pulses resulted in lower diversity when compared to 3-day pulses.

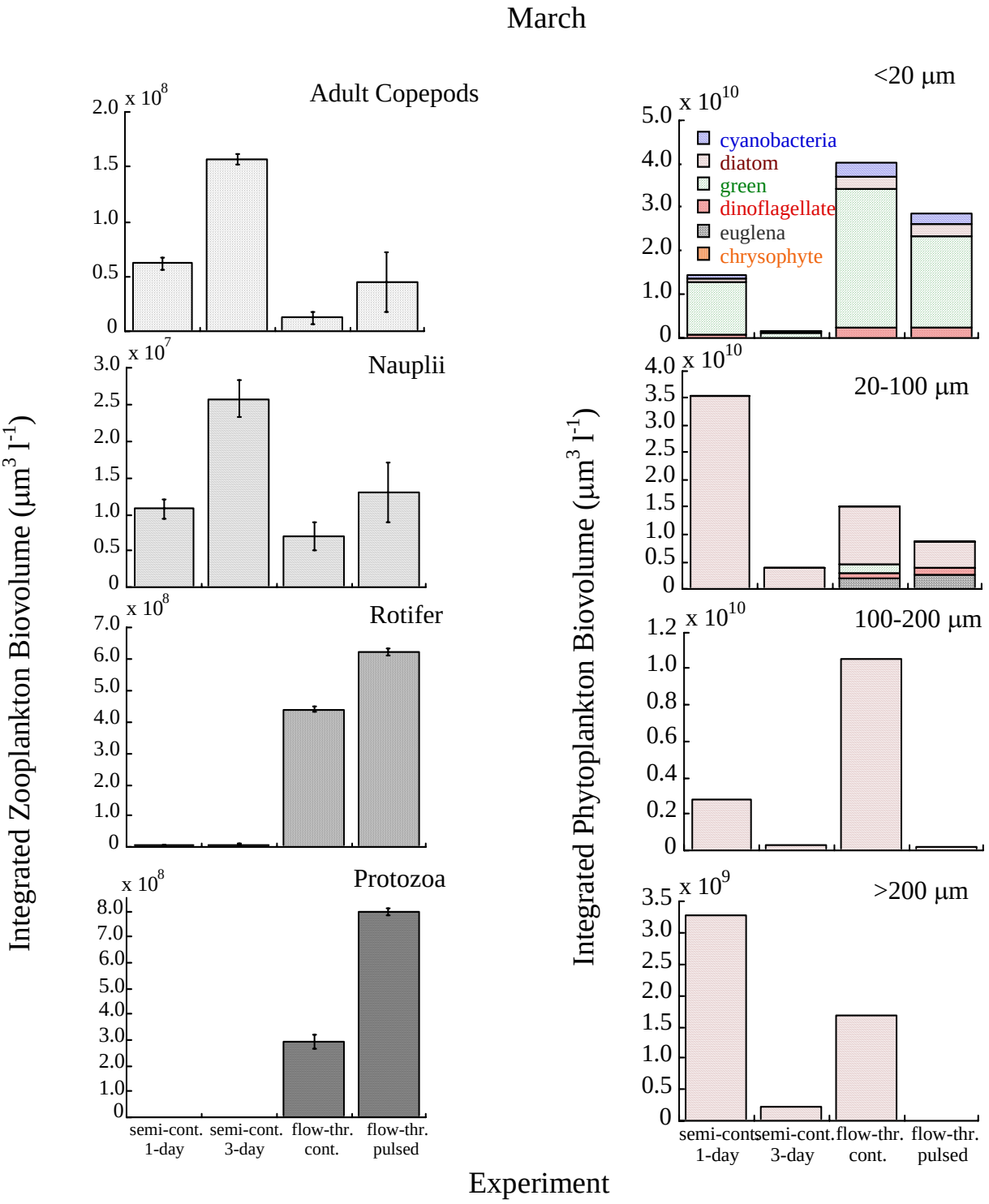

Figure 8. Comparison of zooplankton group structure and phytoplankton cell size structure between the semi-continuous and flow-through design experiments conducted in March.

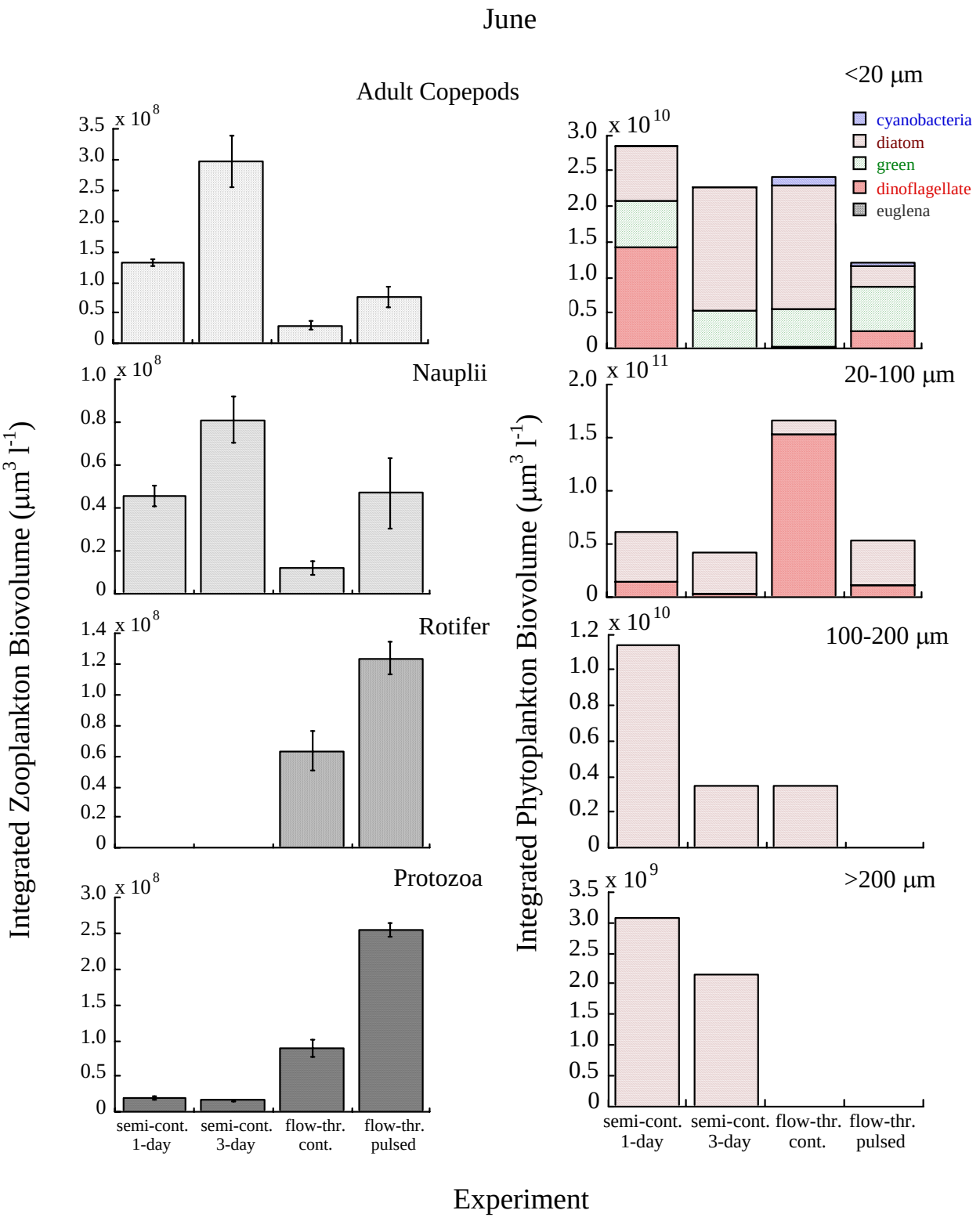

Figure 9. Comparison of zooplankton group structure and phytoplankton cell size structure between the semi-continuous and flow-through design experiments conducted in June.

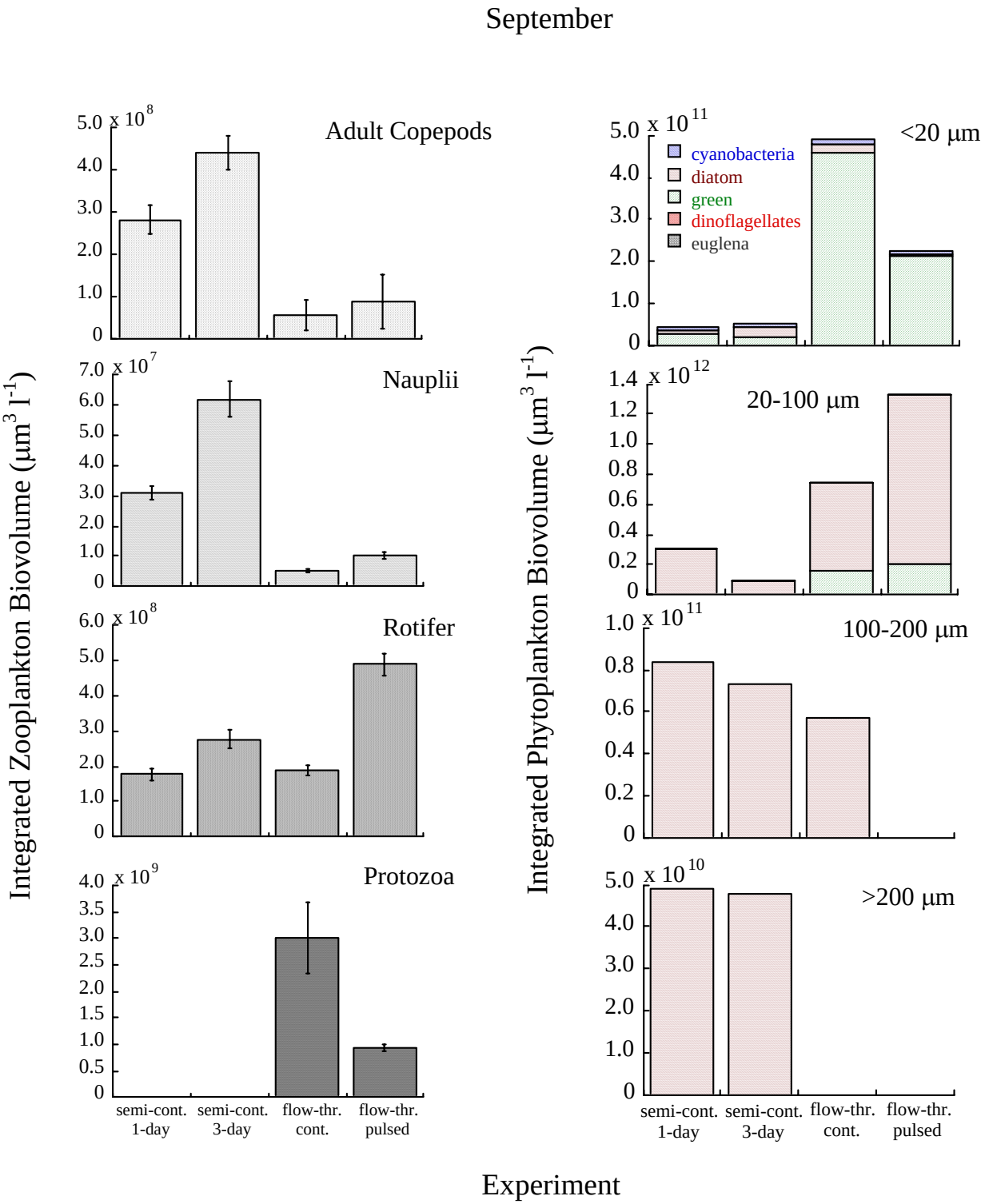

Figure 10. Comparison of zooplankton group structure and phytoplankton cell size structure between the semi-continuous and flow-through design experiments conducted in September.