



Predation and priority effects in experimental zooplankton communities

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During colonization of new habitats, the sequence of arrival among species is in many cases determined by chance. Priority effects imply that differences in arrival time may lead to long-lasting differences in species dominance. To evaluate the importance of priority effects, we performed a community assembly experiment, manipulating the inoculation order of three large cladoceran zooplankton species. The inoculation treatments were crossed with a predation treatment to test whether the presence of a predator (larvae of the phantom midge *Chaoborus*) results in changes in the strength of species sorting and priority effects. Our results clearly demonstrate priority effects, but also that the presence of a predator impacts both community assembly and the strength of priority effects. In the predation-free treatments, communities were dominated by either *Daphnia magna* or *Daphnia obtusa*, depending on the species arrival sequence. Whenever *D. obtusa* was inoculated after *D. magna*, the species displayed negative growth. In the presence of *Chaoborus* predation, the communities were generally dominated by the third species, *Simocephalus vetulus*. Here, the growth of *D. magna* was negative when the species was inoculated as second or third. Overall, our results underscore the importance of both priority effects and species sorting during community assembly.

Community assembly is influenced by both regional and local factors (Shurin et al. 2000, Chase 2003). At the regional scale, species must arrive (successful dispersal) into the habitat. Once present, they must cope with the local environmental conditions and the resident community in order to settle successfully (Leibold et al. 2004, Ricklefs 2004). During community assembly, the importance of both factors changes through time. Regional factors are expected to be most important during early community assembly, while local factors will increase in significance because of growing interactions with the local community (Jenkins and Buikema 1998, Mouquet et al. 2003). In the presence of sufficient dispersal, one expects the ultimate composition of the community to be predictable, being determined by the local environmental characteristics, and reflecting efficient species sorting (Cottenie and De Meester 2004, Hodkinson et al. 2004, Urban 2004).

Dispersal limitation may, however, interfere in two ways with this scenario. First, some species may not reach a given, suitable habitat or do so late (Ricklefs

2004). In addition, dispersal limitation may also influence the order in which new species arrive in the habitat. It has been shown that the ultimate composition of the community can in some cases be dependent on the time of arrival of the different species in the habitat (Drake 1991, Samuels and Drake 1997, Beisner et al. 2003, Schroder et al. 2005). Such priority effects result when species that are already present in a community inhibit or facilitate the establishment of other species that arrive in the community at some later time (Morin 1999).

The occurrence of priority effects during community assembly has been observed in a variety of experimental studies and taxa, such as reef fish (Almany 2003, 2004), phytoplankton (Robinson and Dickerson 1987, Robinson and Edgemon 1988), amphibians (Alford and Wilbur 1985), dragonflies (Morin 1984), mosquito larvae (Sunahara and Mogi 2002), *Drosophila* flies (Shorrocks and Bingley 1994), mosquito and amphibian larvae (Blaustein and Margalit 1996), ciliates (Price and Morin 2004), protists and rotifers (Fukami

2004), and aquatic plankton species (Drake 1991). Arriving at the very start of community assembly in some cases thus seems to be a crucial factor in determining whether species will become a dominant member of the community.

Priority effects imply that early colonists can monopolize habitat resources and dominate communities for a long period of time by interactions such as inhibition of other species' development (Connell and Slatyer 1977). The success of early colonists can be due to a purely numerical effect. Rapid population growth then leads to strong exploitation of resources, and the carrying capacity of the habitat is reached before later immigrants can have much impact. An alternative mechanism is that the presence of a species in the beginning of community assembly can alter the environment in such a way that other species arriving at some later time may not establish successfully. A classical example of a priority effect on long-term community structure is shading by growing plants, which inhibits germination of seeds and growth of seedlings in plant communities (Harper 1961).

In a study on the community assembly of cladoceran zooplankton species in newly created habitats, a systematic pattern of occurrence of three large cladoceran species was observed (Louette and De Meester 2005, Louette et al. unpubl.). *Daphnia obtusa* was found to rapidly colonize new habitats and dominate the community during the first year. The larger congener *Daphnia magna*, believed to be a superior competitor (Gliwicz 1990), was found in relatively few of the new habitats. The third species, *Simocephalus vetulus*, became a dominant member of the zooplankton communities in most habitats during the second year. This pattern raises the question why *D. obtusa* is dominant in so many habitats in the first year, and why *S. vetulus* becomes co-dominant in the second year. Is this purely an effect of deterministic species sorting influenced by local environmental conditions, or does it reflect an important impact of priority effects? Furthermore, larvae of the phantom midge *Chaoborus* were observed to be important predators in these newly formed communities, raising the question whether and how the presence of this predator affects the occurrence of priority effects.

We present here the results of a community assembly experiment with the above-mentioned cladoceran zooplankton species, in which the time of arrival is manipulated between the different species in order to investigate the relative importance of priority effects and species sorting in determining community structure (similar to Robinson and Dickerson 1987, Robinson and Edgemon 1988). The specific influence of predation on community assembly has so far rarely been examined (Shurin 2001), although several studies have shown that the impact of priority effects can be reduced

in the presence of predation (Morin 1984, 1999). We incorporated the effect of predation in our experiment, and tested whether the presence of phantom midge larvae changes the strength of species sorting and priority effects in our simplified zooplankton communities.

Material and methods

We performed the experiment at the Aquatic Research Experimental Area (ARENA) of the Laboratory of Aquatic Ecology (K.U.Leuven, Heverlee, Belgium). The experiment started in the beginning of May 2004 and ran for 60 days until the end of June 2004. White plastic conical barrels (height 68 cm, upper diameter 54 cm; water volume of 80 l) were filled with non-fertilized tap water (nitrate concentration: 14 mg l^{-1} , phosphorus concentration: $72 \text{ } \mu\text{g l}^{-1}$) two weeks before the actual start of the experiment. After filling the barrels, they were immediately covered with fine mesh-sized nets (1 mm) to prevent natural colonization by zooplankton species (through excluding potential dispersal vectors) and potential predators (e.g. *Chaoborus*, odonates and *Notonecta*). A few days later, an inoculum of the unicellular alga *Scenedesmus obliquus* (1.10^{10} cells) was added to all units in order to provide a food source for the zooplankton species that were to be inoculated. The three large cladoceran species we worked with (*D. obtusa*, adult body size approximately 2 mm; *D. magna*, adult body size approximately 3 mm; and *S. vetulus*, adult body size approximately 2 mm), all known to be among the first colonizing species of newly created habitats (Louette and De Meester 2005), were raised in the laboratory for 6 months prior to the start of the experiment.

The experiment consisted of 10 different inoculation treatments (six different inoculation sequences, three control treatments with pure cultures of each of the three species, and one mixture of all three species inoculated at the same time; Table 1). These treatments were crossed with two predation regimes (presence/absence of *Chaoborus obscuripes* instar III and IV larvae). *C. obscuripes* is one of the largest chaoborids in Europe (together with *Chaoborus crystallinus*), displays no diurnal vertical migration, and is typical for fishless habitats (Berendonk and Bonsall 2002, Wissel and Benndorf 1998). *Chaoborus* is an ambush predator which stays motionless in the water column and detects its prey by mechanoreceptors (Riessen et al. 1984).

The 20 different treatments were replicated three times, resulting in 60 experimental units. Experimental units were organized in a randomized block design. Species were inoculated as 20 egg-bearing adult females per unit. The first species was inoculated on day 1, the second species on day 15 and the third species on day

Table 1. The experimental set-up consisted of 6 different inoculation sequence treatments, three control single species treatments, and 1 mixture treatment with all three species inoculated together. Two different predation regimes (with/without *Chaoborus* predation) were created, resulting in 20 different combinations, each time with a threefold replication.

	ma-ob-ve	ma-ve-ob	ob-ma-ve	ob-ve-ma	ve-ma-ob	ve-ob-ma	ma	ob	ve	mix
day 1	<i>D. magna</i>	<i>D. magna</i>	<i>D. obtusa</i>	<i>D. obtusa</i>	<i>S. vetulus</i>	<i>S. vetulus</i>	<i>D. magna</i>	<i>D. obtusa</i>	<i>S. vetulus</i>	combination
day 15	<i>D. obtusa</i>	<i>S. vetulus</i>	<i>D. magna</i>	<i>S. vetulus</i>	<i>D. magna</i>	<i>D. obtusa</i>				
day 30	<i>S. vetulus</i>	<i>D. obtusa</i>	<i>S. vetulus</i>	<i>D. magna</i>	<i>D. obtusa</i>	<i>D. magna</i>				
day 45										
day 60										

30. During the progress of the experiment, predation pressure of *Chaoborus* was maintained at high level by adding each month (day 1 and day 30) 20 instar III and IV larvae. Samples were taken on day 30, 45 and 60 at four random locations in each barrel with a tube sampler (length 1 m, diameter 75 mm), which was positioned vertically in the water column and was then closed at the bottom by a magnetic lid. This resulted in a sample of 12 l of water, which was filtered through a 64 µm plankton net. Cladoceran density values were transformed to biomass values using published length-weight relationships (McCauley 1984). Environmental variables (pH, temperature, oxygen concentration, chlorophyll a levels, and conductivity) were measured every two weeks during the course of the experiment in each of the units.

A first approach to assess the impact of priority effects is to compare the biomass of each of the three species in the communities on day 60 in relation to the sequence of inoculation. Biomass values on day 60, however, may merely reflect the fact that the different species were given a different amount of time to grow in the different treatments. We therefore also calculated for each species the rate of population biomass increase (r_b) from day 45 to day 60. We used this time interval to calculate the rate of population biomass increase as all the species were inoculated by then, and effects of treatments could be assessed equitably. Rate of population biomass increase per day was calculated as follows:

$$r_b = (\ln(B_t + 1) - \ln(B_0 + 1))t^{-1}$$

where: B_0 = population biomass at the beginning of time-interval (day 45); B_t = population biomass at the end of time-interval (day 60); t = duration of time-interval in days (15 days).

We then performed an analysis of variance on the rate of population biomass increase on each of the species in the different treatments in which it was inoculated, with inoculation sequence and predation as factors. Significant differences in the rate of population biomass increase for a given species in relation to its inoculation sequence (reduced population growth of later colonists), and especially a negative rate of population biomass increase of species that were inoculated as second or third species (negative popula-

tion growth of later colonists), provide strong evidence for priority effects.

Results

Values of the measured environmental variables were stable throughout the experiment, and were in the range of natural water bodies; dissolved oxygen: 8.4 mg l⁻¹ (SE 0.2), temperature: 18.2°C (SE 0.4), conductivity: 423 µS cm⁻¹ (SE 14), pH: 8.7 (SE 0.1), and chlorophyll a: 5.9 µg l⁻¹ (SE 0.6). *Chaoborus* density levels remained constant among all the predation treatments and throughout the experiment (repeated measures analysis of variance, all $p > 0.05$).

The biomass of the three species in each treatment is presented in Fig. 1. In the presence of predation, *S. vetulus* always dominated community structure (except in ma-ob-ve). In the absence of predation, *D. obtusa* was only dominant when it was inoculated as the first species. In all the other cases, *D. magna* dominated the community. The mixture treatment (all three species inoculated together) showed dominance of *Daphnia* species in the absence of predation, and co-dominance of *D. magna* and *S. vetulus* in the presence of predation.

There was a significant effect of predation on the rate of population biomass increase of each of the three species (Table 2, Fig. 2). The rate of population biomass increase of *D. magna* and *D. obtusa* was significantly lower in the experimental units with predation than in those without predation. Especially *D. obtusa* suffered from high predation rates, as populations disappeared almost completely in the presence of *Chaoborus* (Fig. 1). In contrast, the rate of population biomass increase of *S. vetulus* was higher in the experimental units with predation than in those without predation (Fig. 2).

There was a significant inoculation treatment effect for both *Daphnia* species, but not for *S. vetulus*. We observed that in the presence of predation, the population biomass increase rate of *D. magna* was significantly different between the treatment in which it was inoculated as first species and the treatments in which it was inoculated as second or third species, after

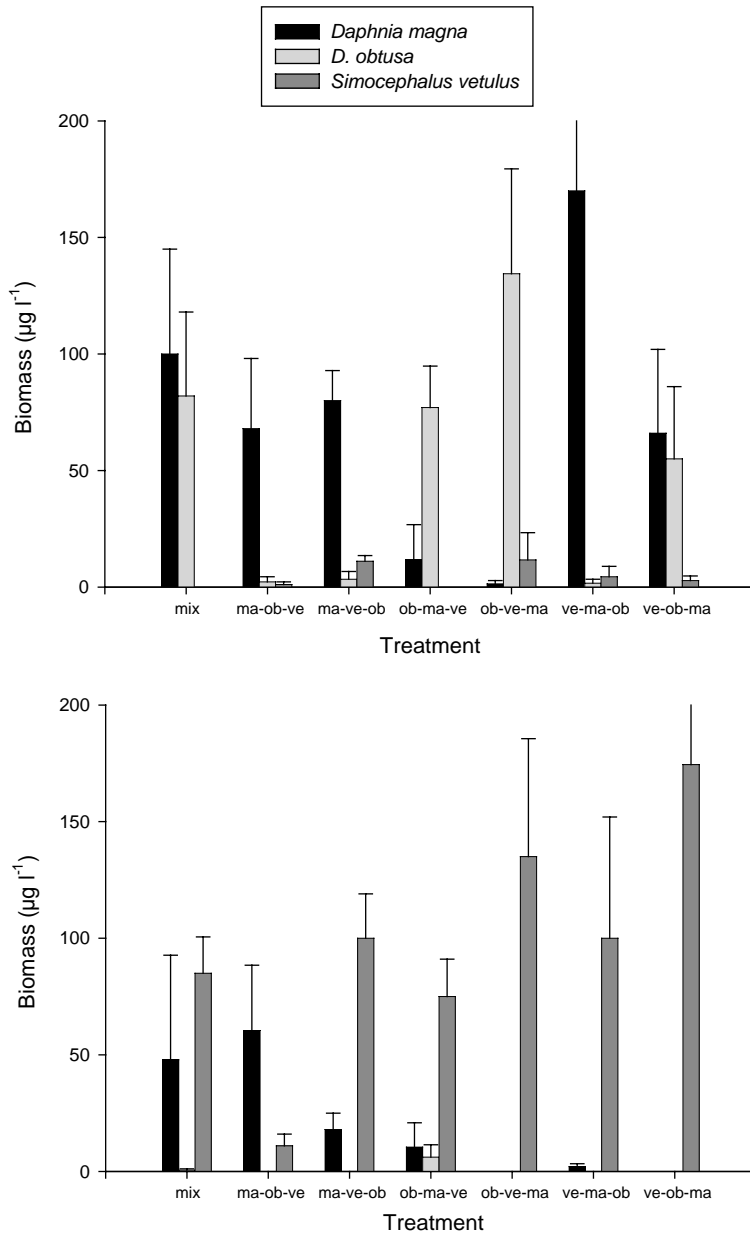


Fig. 1. Average biomass for all three species (*Daphnia magna*, *D. obtusa*, and *Simocephalus vetulus*) on day 60 in the treatments without (upper) and with (lower) *Chaoborus* predation. Error bars represent the standard error of the mean.

D. obtusa (Table 2, Fig. 2). Moreover, the population biomass increase rate of *D. magna* was negative whenever it was introduced after *D. obtusa*. There was no difference in population biomass increase rate of *D. magna* when inoculated after *S. vetulus* compared to when the species was inoculated first. In the absence of predation, the rate of population biomass increase in *D. magna* was not significantly lower for the combinations with both other species, although there was a marginally significant effect when inoculating *D. magna* as the last

species after *D. obtusa*. For *D. obtusa*, the rate of population biomass increase in the absence of predation differed significantly between the treatment where it was inoculated as first species and the treatments where it was inoculated as second or third species, both in the combinations with *D. magna* and *S. vetulus* (Table 2). Also, the population biomass increase rate of *D. obtusa* was negative whenever it was introduced after *D. magna*. There was no difference in the rate of population biomass increase of *D. obtusa* among the

Table 2. Analysis of variance on the effects of treatment and predation on the rate of population biomass increase (r_b) of *Daphnia magna*, *D. obtusa*, and *Simocephalus vetulus*. Post-hoc tests are presented (p-values) for both predation regimes (NP = no predation, P = predation), and indicate whether the treatment in which the species is inoculated as first differed significantly from the treatments in which the species is inoculated as second or third.

Effect	df	SS	F	p	Inoculation	NP	P
<i>Daphnia magna</i>							
Inoculation	7	0.218	5.087	0.001	ma-ob-ve/ob-ma-ve	0.182	0.001
Predation	1	0.046	7.456	0.010	ob-ve-ma	0.064	0.001
Inoculation \times predation	7	0.068	1.574	0.179			
Error	32	0.196			ma-ve-ob/ve-ma-ob ve-ob-ma	0.131 0.654	0.119 0.289
<i>D. obtusa</i>							
Inoculation	7	0.135	2.573	0.032	ob-ma-ve/ma-ob-ve	0.002	0.177
Predation	1	0.086	11.504	0.002	ma-ve-ob	0.017	0.177
Inoculation \times predation	7	0.073	1.390	0.243			
Error	32	0.240			ob-ve-ma/ve-ob-ma ve-ma-ob	0.048 0.273	0.939 0.742
<i>Simocephalus vetulus</i>							
Inoculation	7	0.098	1.648	0.158	ve-ma-ob/ma-ve-ob	0.668	0.397
Predation	1	0.335	39.322	<0.001	ma-ob-ve	0.370	0.089
Inoculation \times predation	7	0.086	1.436	0.225			
Error	32	0.273			ve-ob-ma/ob-ve-ma ob-ma-ve	0.204 0.272	0.623 0.076

treatments in the presence of *Chaoborus*; in these treatments, population biomass of *D. obtusa* was always very low.

Discussion

The results of our experiment underscore the importance of time of arrival in the habitat in order to become a dominant member of the community. Although the same numbers of individuals were inoculated in the 6 different inoculation treatments and the time difference between the first and second inoculum was short, the resulting community structure differed in a pronounced and repeatable way among treatments.

We observe that *D. obtusa* can only become the dominant member of the community when inoculated as first (treatments: ob-ma-ve and ob-ve-ma) and only in the predation-free environments. In spite of the low propagule numbers (20 adult females were inoculated per unit) and the short interval between subsequent inocula (two weeks), *D. obtusa* is able to establish its population by a rapid monopolization of resources, and prevent the superior competitor (*D. magna*, Gliwicz 1990; see also results of the mixture treatment in our experiment) from dominating, at least on the time-scale of the present study. Whenever *D. obtusa* was inoculated as second immigrant after *D. magna*, its population declined until extinction (Fig. 1, 2). During the colonization of newly created habitats, *D. obtusa* was observed to be generally one of the first species to arrive in the habitat (Louette and De Meester 2005). Its

dominance during early community assembly may be caused by the numerical effects observed in the present experiment. Coexistence of this species on a regional scale with species such as *D. magna* may thus be facilitated by having a good colonization capacity. According to our results, this species seems to have few chances to establish when it arrives after *D. magna* or *S. vetulus*. However, generalization of our results to a broad range of environmental conditions should be done with care, as our experimental design was very simple (forcing the species to coexist simultaneously), while in nature other factors (e.g. spatial and temporal segregation) are important in determining community structure.

Predation seems to be a crucial factor in determining the outcome of community assembly and the role of priority effects. First, we observe that *S. vetulus* is strongly favored over the *Daphnia* species in the presence of *Chaoborus*, and no significant priority effects are observed for this species. In general, pure competitive interactions and hence priority effects are expected to be weaker in the presence of selective predation (Allen 1973, Morin 1999). However, we have strong indications for priority effects in the presence of *Chaoborus* for *D. magna*. *D. magna* is only able to establish successfully when it is inoculated as first species and *S. vetulus* is inoculated as third species (ma-ob-ve). In all the other cases, when *D. magna* is inoculated as second or third species, the population of the species has negative growth or attains very small population sizes (Fig. 1, 2). Predation of *Chaoborus* seems thus changing the strength of competitive interactions among species, which leads to alternative priority effects to emerge.

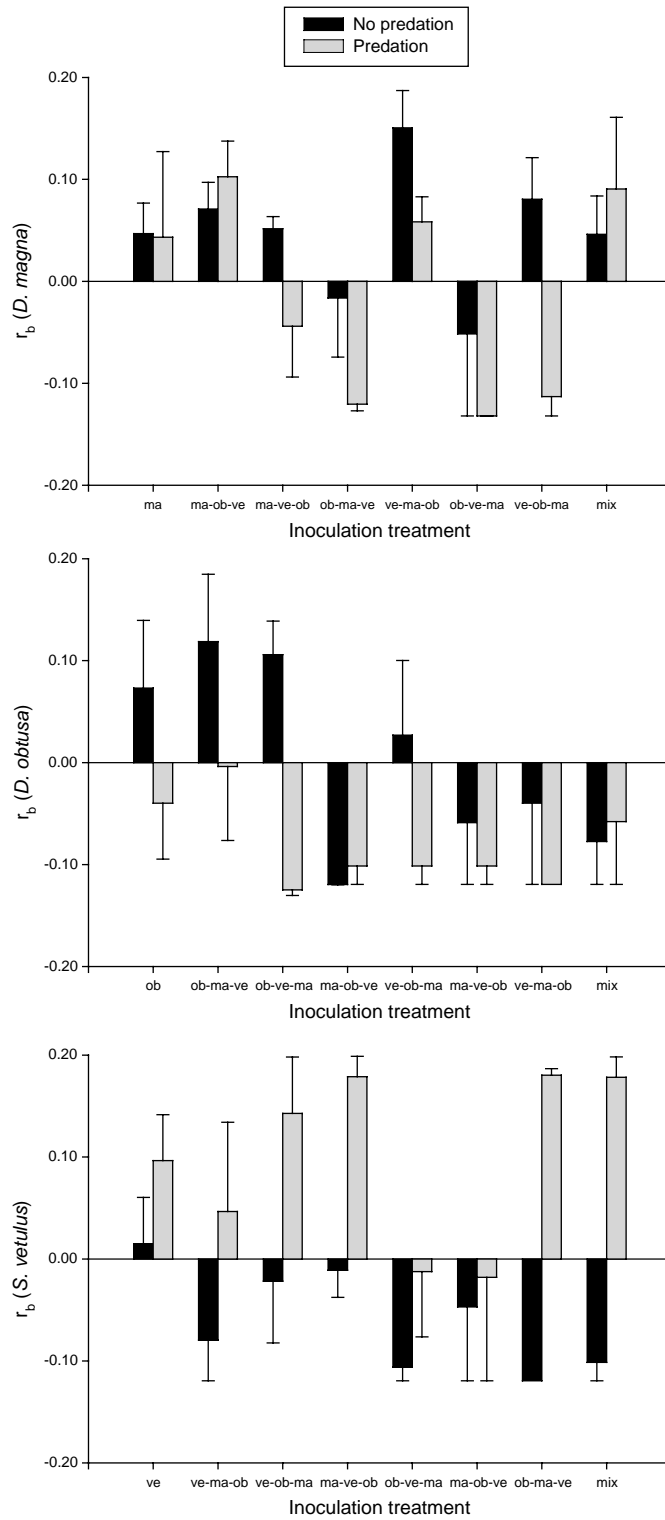


Fig. 2. Rate of population biomass increase (r_b) of *Daphnia magna* (ma), *D. obtusa* (ob) and *Simocephalus vetulus* (ve) for the control, the six different inoculation sequence treatments and the mixture treatment (the interval between 45–60 days in the experiment). Error bars represent the standard error of the mean.

The rate of population biomass increase of both *Daphnia* species was significantly lower in the regimes with predation than in the absence of predation. *D. obtusa* suffered the most from *Chaoborus* predation, and disappeared almost completely. *D. magna* experienced less negative influences of this predator, but its rate of population biomass increase stayed lower in the presence than in the absence of predation. Differences in predation rate on both *Daphnia* species can be attributed to differences in prey selectivity of *Chaoborus*. In contrast to other chaoborids, *C. obscuripes* has a relatively large mouth gape length (approximately 750 µm for fourth instars) which enables the species to feed on a wide range of prey species and sizes (from small rotifers to *Daphnia*) (Wissel and Benndorf 1998). The species is thus able to control populations of *Daphnia* species of moderate sizes like *D. obtusa*, but has more difficulties for the larger *D. magna*. Overall, the rate of population biomass increase of *Simocephalus* was higher in the presence of predation, which suggests that *Simocephalus* experiences no negative effects of predation. It maintained a high rate of population biomass increase in all inoculation sequence treatments in the presence of *Chaoborus*, probably because of the low biomass of competing *Daphnia*, which had difficulties coping with *Chaoborus* predation.

The results of the mixture treatment, in which all three species were inoculated together, demonstrate the outcome of purely competitive interactions. *D. magna* seems to be a good competitor, as it represents a large proportion of the total biomass in both predation regimes. Both *Daphnia* species outcompeted *Simocephalus* completely in the absence of predation in our experiment. Our observations can be explained by the different life history characteristics of the three species. *Daphnia* species are more pelagic and have a superior filtration rate than the more sedentary *Simocephalus* (Balayla and Moss 2004). Overall, habitat conditions in our experiment were simple so that little habitat other than barrel surfaces was present for *Simocephalus* to attach to. However, the tendency of *Simocephalus* to cling to hard surfaces and macrophytes facilitates its survival in the presence of pelagic predators (e.g. *Chaoborus*), as the chance of being captured is reduced for *Simocephalus* compared to *Daphnia*. Corigliano and de Bernardi (1978) similarly showed that *Daphnia* outcompetes *Simocephalus* in the absence of predation. In the presence of predation by *Hydra*, *Simocephalus* was observed to be superior to *Daphnia* (Schwartz and Hebert 1989).

In general, our study provides clear evidence for the importance of an early arrival in the habitat in order to become a dominant member of the community and the risks inherent in a delayed arrival. Under a scenario of strong species sorting, a deterministic outcome of community assembly would be predicted, determined

by the prevalent environmental characteristics. However, differences in arrival time between species can strongly influence community structure, because of priority effects (Morin 1999, Fukami and Morin 2003, Price and Morin 2004). Furthermore, we demonstrate that predation is very important factor in determining community composition and the strength and nature of priority effects. Predation is a key factor involved in species sorting in zooplankton (Cottenie and De Meester 2004), and has been suggested to reduce the impact of priority effects (Morin 1984, 1999). Our results clearly indicate that differences in arrival time during community assembly may lead to the occurrence of priority effects when predators are already present. However, differential strengths and directions of species sorting in the absence and presence of predation interact with the occurrence of priority effects. As a whole, community structure in our experiment was determined in a relatively predictable way, by a combination of local environmental conditions and arrival sequence of the studied species.

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