

Interactions between algae and the microbial loop in experimental microcosms

Florence D. Hulot, Peter J. Morin and Michel Loreau

Hulot, F. D., Morin, P. J. and Loreau, M. 2001. Interactions between algae and the microbial loop in experimental microcosms. – *Oikos* 95: 231–238.

We conducted a short-term microcosm experiment to study the direct and indirect effects of a bacterivore on bacteria and the dynamics of two species of green algae. We introduced *Scenedesmus*, *Chlorella* and *Colpidium*, a bacterivorous ciliate, successively in a carbon-rich medium. Bacteria were introduced with *Scenedesmus*, *Chlorella* and *Colpidium*. The experiment lasted 40 days, preventing us from detecting whether the populations had reached equilibrium. The bacterivore had a positive effect on both species of algae by limiting the abundance of bacteria. In absence of the bacterivore, bacteria did not exclude the two algal species, despite the high carbon:nutrient ratio of the medium. Unexpectedly, by the end of the experiment the bacterivore declined in all microcosms. Also, *Chlorella* growth was impeded by the presence of *Scenedesmus*. These two observations might be explained by allelopathic interactions. Our experiment suggests that the functioning of such a simple community is far more complex than assumed in previous theoretical and experimental models. Studying the dynamics of the system, however, allowed us to disentangle species interactions.

F. D. Hulot and M. Loreau, *Laboratoire d'Ecologie, CNRS-UMR 7625, Ecole Normale Supérieure, 46, rue d'Ulm, F-75230 Paris Cedex 05, France (hulot@biologie.ens.fr)*. – P. J. Morin, *Dept of Ecology, Evolution and Natural Resources, Rutgers Univ., New Brunswick, NJ 08903-0231, USA*.

During the last decade, the importance of food-web structure for its functioning has been widely recognised (Leibold and Wilbur 1992, Abrams 1993, Polis and Strong 1996, Hulot et al. 2000). But the nature of the interactions between producers and decomposers and their importance for the dynamics of the whole food web are less studied. Producers and decomposers form the basis of all ecosystems, of which they are two key functional groups (Harte and Kinzig 1993, Loreau 1998). In aquatic systems, bacteria and algae are competitors for limiting nutrients (Currie and Kalff 1984, Harte and Kinzig 1993) and also indirect mutualists because bacteria recycle nutrients and algae are an important carbon provider (Harte and Kinzig 1993). Hence, understanding and predicting food-web dynamics require taking into account the total array of interactions between producers and decomposers.

Thingstad and Pengerud (1985) analysed a chemostat model in which the dynamics of algae, bacteria and bacterial predators depend on the carbon:nutrient ratio of the medium. They made several predictions. (1) Algae should competitively exclude bacteria when the carbon:nutrient ratio is low because bacteria tend to be carbon-limited. In contrast, bacteria should exclude algae at high carbon:nutrient ratios because algae are less competitive than bacteria for mineral nutrients. Algae and bacteria may coexist at intermediate carbon:nutrient ratios because algae are nutrient-limited and bacteria are carbon-limited. (2) The introduction of a bacterial predator leads bacteria to face both competition and predation. This might lead to an increased algal density when algae are limited by competition with bacteria and even allow the persistence of algae when they would otherwise have been excluded by

Accepted 4 May 2001

Copyright © OIKOS 2001

ISSN 0030-1299

Printed in Ireland – all rights reserved

bacteria. In addition, the density of the predator should be greater in chemostats with only bacteria than in a chemostat with both bacteria and algae because of nutrient competition between algae and bacteria (Thingstad and Pengerud 1985). The results of a chemostat experiment containing two species of bacteria, the diatom *Skeletonema costatum* and a marine bacterivorous nanoflagellate with a carbon:phosphorus ratio ranging from 16.8:1 to 672:1, agreed with these predictions (Pengerud et al. 1987). Rothhaupt (1992) conducted batch experiments with phytoplankton, bacteria and a flagellate and compared phytoplankton and bacterial dynamics in the presence and absence of bacterivores. His results showed that with a high carbon:phosphorus ratio (i.e., 412:1) algae were able to grow when bacteria were controlled by the flagellate. In a chemostat experiment where bacteria depended on phytoplankton as a carbon provider, algae and bacteria reached an equilibrium. But algae still benefited from the presence of bacterivores (Rothhaupt 1992). Recently Naeem and Li (1998) also showed that bacteria, bacterivores and predators of bacterivores can be as important as the grazing chain (algae, herbivores, and top predators) in determining autotroph biomass. In their experiment, the addition of bacterivores (*Colpidium* sp. and *Chilomonas* sp.) induced a sharp rise in autotroph biomass (Naeem and Li 1998).

Thingstad and Pengerud's model, however, does not take into account the mutualistic aspect of algae-bacteria interactions or nutrient recycling. Daufresne and Loreau (in press) recently studied a stoichiometrically explicit model that includes the recycling role of decomposers (bacteria here) and the energy-providing role of primary producers (algae here) in addition to the competition for nutrients between these two functional groups. In particular, with Lotka-Volterra recipient-controlled functions for nutrient uptake, they showed that the coexistence of bacteria and algae is possible only if decomposers are carbon-limited and if the carbon:nutrient ratios of primary producers and decomposers are sufficiently similar. The latter condition determines the competitive ability of decomposers for nutrients and therefore the system's persistence. The model shows that if decomposers are nutrient limited, algae are excluded and the system collapses.

The effects of producer diversity and decomposer diversity on ecosystem functioning has been studied recently both theoretically (Loreau 2001) and experimentally (Naeem et al. 2000). Naeem et al. (2000) found a significant positive correlation between microbial diversity and the diversity of organic compounds used. According to Loreau (2001), this result might be explained by a low niche overlap between decomposers, that is, a high niche complementarity leading to a low number of unused compounds. On the other hand, Naeem et al. (2000) found higher proportions of algal biomass when algal species diversity was intermediate

to high and bacterial species diversity was low. This nonlinear effect of algal diversity on primary production highlights the fact that the productivity of aquatic ecosystems depends on more than the diversity of primary producers (Morin 2000).

This recent work shows that the interactions between primary producers and the microbial loop are still poorly understood. In this paper we present the results of a microcosm experiment on the interactions between two algal species (*Scenedesmus armatus* and *Chlorella vulgaris*), bacteria and a bacterivorous ciliate (*Colpidium striatum*) in a medium with a high carbon:nutrient ratio. The experiment investigates both the effects of the bacterivore on the two algal species and the effects of the two algae on bacteria and the bacterivore.

Material and methods

Experimental design

All food webs were assembled in 250-ml screw-cap Erlenmeyer flasks containing 100 ml of initially sterile medium (0.55 g of Carolina Biological Supply protozoan pellets per litre of well water). The medium contained DOC, NO₃ and PO₄ at, respectively, 125.9 μmol l⁻¹, 4.7 μmol l⁻¹ and 0.17 μmol l⁻¹. Thus, the medium C:N and C:P were 119:1 and 2220:1, respectively, which should ensure nutrient competition between algae and bacteria. In a previous experiment (Pengerud et al. 1987), the bacterium *Pseudomonas putida* excluded the alga *Skeletonema costatum* when the medium C:P was 250:1. The low concentration of phosphorus might also induce competition between *Chlorella* and *Scenedesmus*. Phosphorus competition experiments where phosphorus concentration was 1.2 μmol l⁻¹ (Grover 1991a) between the two algal species showed that *Chlorella* outcompeted *Scenedesmus* in both continuous and phosphorus-pulsed cultures. Moreover light competition experiment between phytoplankton species showed that *Chlorella* was a superior competitor for light (Huisman et al. 1999).

Five food webs were assembled: *Scenedesmus* + bacteria, *Scenedesmus* + bacteria + *Chlorella*, *Scenedesmus* +

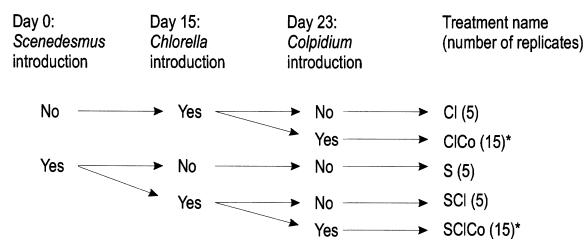


Fig. 1. Sequence of species introductions and treatment abbreviations with replicate numbers. The asterisk indicates that in 10 out of 15 cultures additional introductions were made.

Table 1. Duration and treatments involved in repeated-measure ANOVAs.

	Effects of <i>Scenedesmus</i> on:	Effects of <i>Chlorella</i> on:	Effects of <i>Colpidium</i> on:
<i>Scenedesmus</i>	Duration: days 3 to 15 Treatments: S, SCI, SCICo*	Duration: days 18 to 39 Treatments involved: S, SCI	Duration: days 24 to 39 Treatments involved: SI, SCICo
<i>Chlorella</i>	Duration: days 18 to 39 Treatments involved: CI, SCI	–	Duration: days 24 to 39 Treatments: CI, CICO, SCI, SCICo
<i>Colpidium</i>	Duration: days 28 to 40 Treatments involved: CICO, SCICo	–	–

* In this analysis, 15 replicates for the SCICo treatment were considered.

bacteria + *Chlorella* + *Colpidium*, *Chlorella* + bacteria and *Chlorella* + bacteria + *Colpidium* (see Fig. 1 for the sequence of species introductions and treatment abbreviations). Each food-web combination was replicated 5 times. On day 0, 302 000 *Scenedesmus* coenobia (four-celled colony) were introduced to allow population establishment. A first introduction of *Chlorella* (755 cells) was attempted on day 8. A second introduction was done on day 15 (76 000 *Chlorella* cells). On day 23, about 2 500 *Colpidium* individuals were added. In 10 of the 15 treatments containing *Chlorella* and *Colpidium*, with or without *Scenedesmus* (i.e., CICO and SCICo), a predator of *Colpidium* was introduced on day 30 but did not establish in any replicate. These cultures will be considered as replicates of treatments containing *Colpidium* only in statistical analyses involving the period before day 30. All algal and ciliate inocula contained bacteria. Thus bacteria were introduced in microcosms with algae. Bacteria were plated on agar on day 38. The experiment ended on day 40.

A fraction of 1% of the medium was daily replaced with fresh sterile medium. The experimental microcosms were maintained under 22°C in 14:10 light-dark cycle incubators and all replicates were rotated daily. Cells were counted every 2–3 d. Algal cells were counted using a hemacytometer and a compound microscope. Protists were counted under a stereoscopic microscope in subsamples of the withdrawn medium (Lawler and Morin 1993).

Statistical analyses

Repeated-measures analysis of variances (RMANOVA) tested for effects of a particular species on the dynamics of another species. Species abundances were log-transformed before statistical analyses to correct for heteroscedasticity. The analysis covered different periods of the experiment depending on which species were being analysed (Table 1).

First, we tested whether treatment effects were present when only *Scenedesmus* was present (days 3 to 15). Second, we tested for the reciprocal effects of the two algal species on each other (days 18 to 39). Comparing the *Chlorella* + bacteria (CI) and *Scenedesmus* + bacteria + *Chlorella* (SCI) treatments showed the effects

of *Scenedesmus* on *Chlorella*, and comparing *Scenedesmus* + bacteria (S) and *Scenedesmus* + bacteria + *Chlorella* (SCI) treatments showed the effects of *Chlorella* on *Scenedesmus* (Table 1).

The *Colpidium* treatment was nested within the *Chlorella* treatment, and the *Chlorella* treatment itself was nested in the *Scenedesmus* treatment. The reciprocal effects of *Scenedesmus* and *Colpidium* on each other could not be tested with nested RMANOVAs because the nested experimental design was not completely balanced. Consequently, we assessed effects of *Scenedesmus* on *Colpidium* dynamics by comparing the *Chlorella* + bacteria + *Colpidium* (CICO) and *Scenedesmus* + bacteria + *Chlorella* + *Colpidium* (SCICo) treatments with RMANOVA. Similarly we tested for effects of *Colpidium* on *Scenedesmus* dynamics by comparing *Scenedesmus* + bacteria + *Chlorella* (SCI) and *Scenedesmus* + bacteria + *Chlorella* + *Colpidium* (SCICo) treatments with RMANOVA (Table 1). Lastly, we tested for effects of *Colpidium* on *Chlorella* dynamics by comparing *Chlorella* + bacteria + *Colpidium* (CICO), *Scenedesmus* + bacteria + *Chlorella* + *Colpidium* (SCICo), *Scenedesmus* + bacteria + *Chlorella* (SCI) and *Scenedesmus* + bacteria + *Chlorella* + *Colpidium* (SCICo) treatments in a nested RMANOVA (Table 1).

An ANOVA and a post-hoc Bonferroni *t* test were used to test for treatment effects on bacterial abundance.

Results

Treatment effects on *Scenedesmus*

The RMANOVA performed on *Scenedesmus* coenobial abundances during the first phase from days 3 to 15 did not reveal any initial differences between cultures assigned to different treatments (Table 2). There was a significant effect of time on *Scenedesmus* populations. Note that the first introduction of *Chlorella* on day 8 had no effect on *Scenedesmus* dynamics.

There was no significant *Chlorella* or *Chlorella* × time effect but a significant time effect on *Scenedesmus* dynamics (Table 2, Fig. 2). Indeed, *Scenedesmus* coenobial abundances increased from day 15 to 22 in both treatments (Table 2, Fig. 2). We expected a negative effect

Table 2. Effects on *Scenedesmus* dynamics. RMANOVA results on (A) Treatment homogeneity during the period *Scenedesmus* alone (days 3 to 15); (B) *Chlorella* effects from days 18 to 39; (C) *Colpidium* effects from days 24 to 39.

Source	MS	DF	F value	P
A. Treatment homogeneity (days 3 to 15)				
Time	0.38	6	24.9	0.0001
Treatment	0.01	4	0.64	0.65
Time × Treatment	0.02	24	1.18	0.30
B. <i>Chlorella</i> effects				
Time	0.10	8	10.91	0.0001
<i>Chlorella</i>	0.0006	1	0.02	0.90
Time × <i>Chlorella</i>	0.0078	8	0.80	0.53
C. <i>Colpidium</i> effects				
Time	0.18	5	16.93	0.0001
<i>Colpidium</i>	0.52	1	27.74	0.0008
Time × <i>Colpidium</i>	0.05	5	4.62	0.002

of *Chlorella* on *Scenedesmus* dynamics (Grover 1991a, b, Huisman et al. 1999); thus the absence of such an effect is noteworthy.

Scenedesmus coenobial abundance clearly increased after *Colpidium* introduction in the culture on day 23 (significant time, *Colpidium* and time × *Colpidium* effects on *Scenedesmus* dynamics; Table 2, Fig. 2).

In conclusion, the establishment of *Chlorella* populations had no effect on *Scenedesmus* cultures during the course of the experiment whereas the presence of *Colpidium* had a significant positive effect on *Scenedesmus* coenobial abundance.

Treatment effects on *Chlorella*

First, *Chlorella* abundance was significantly higher in the treatment without *Scenedesmus* (significant time and treatment effects but no significant interaction between time and treatment; Table 3, Fig. 3). During the course of the experiment (days 18 to 39), *Chlorella* populations exhibited an exponential growth in the two treatments involved (CI, SCI).

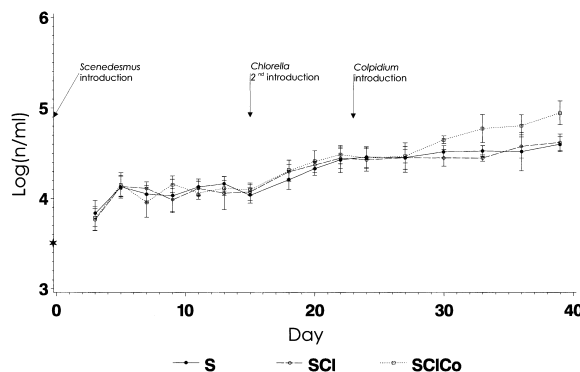


Fig. 2. *Scenedesmus* mean abundances through time in the various treatments. Error bars represent standard deviations and the star indicates the initial density of *Scenedesmus* (see Fig. 1 for abbreviations).

The nested RMANOVA revealed significant time and *Colpidium* effects and a significant interaction between time and *Colpidium* (Table 3). *Colpidium* had a positive effect on *Chlorella* abundance (Fig. 3). *Chlorella* abundance increased markedly after *Colpidium* introduction in comparison with the two treatments without *Colpidium*. This increased abundance was more striking in treatments with *Scenedesmus*. But this effect was dependent on time: just after *Colpidium* introduction, *Chlorella* dynamics showed a slight inflection followed by a marked increase. The inflection might be due to consumption of *Chlorella* by *Colpidium*. Indeed, at the onset of the *Colpidium* population growth phase, some *Chlorella* cells could be identified inside *Colpidium*.

In summary, there was a negative effect of *Scenedesmus* and a positive effect of *Colpidium* on *Chlorella* abundance during the course of the experiment.

Treatment effects on *Colpidium*

Colpidium abundance increased after its introduction in cultures and decreased towards the end of the experiment (Fig. 4). *Colpidium* abundance was higher and reached its maximum value sooner in the treatment with *Scenedesmus* (significant effects of treatment and time and significant interaction between time and treatment; Table 4, Fig. 4).

From day 23 to 28 *Colpidium* had a growth rate of $0.438 \pm 0.014 \text{ d}^{-1}$ in *Scenedesmus* + *Chlorella* + bacteria + *Colpidium* cultures and a growth rate of $0.258 \pm 0.039 \text{ d}^{-1}$ in *Chlorella* + bacteria + *Colpidium* cultures. These two growth rates were significantly different ($n = 10$; $t = 132$; $P < 0.001$). *Colpidium* cell size decreased strikingly while *Colpidium* abundances decreased towards the end of the experiment. No *Chlorella* cells were observed inside *Colpidium* individuals when their size was decreasing, perhaps because the smaller *Colpidium* were unable to ingest *Chlorella*.

In conclusion, *Colpidium* growth was lower in the treatment containing high *Chlorella* abundance and no *Scenedesmus* compared with the treatment containing *Scenedesmus* and a lower *Chlorella* abundance.

Treatment effects on bacteria

An ANOVA on the five treatments (CI, CI_{Co}, S, SCI, SCI_{Co}) showed a significant treatment effect (MS = 1.72, df = 4, $F = 106$, $P = 0.0001$). Bacteria were significantly more abundant in treatments lacking *Colpidium* (Bonferroni post-hoc test; Fig. 5). This is consistent with a strong negative effect of *Colpidium* on its prey (bacteria). *Scenedesmus*, *Chlorella* or the two species of algae together did not have any effect on bacterial abundance (Fig. 5).

Table 3. Effects on *Chlorella* dynamics. RMANOVA results on (A) *Scenedesmus* effects from days 18 to 39; (B) *Colpidium* effects nested in *Scenedesmus* effects from days 24 to 39.

Source	MS	DF	F value	P
A. <i>Scenedesmus</i> effects				
Time	6.23	8	88.13	0.0001
<i>Scenedesmus</i>	7.09	1	11.55	0.0094
Time × <i>Scenedesmus</i>	0.18	8	2.59	0.079
B. <i>Colpidium</i> effects nested in <i>Scenedesmus</i> effects				
Time	12.89	5	271.32	0.0001
<i>Scenedesmus</i>	11.40	1	10.41	0.08
<i>Colpidium</i> nested in <i>Scenedesmus</i>	1.09	2	3.67	0.0487
Time × <i>Scenedesmus</i>	0.06	5	0.24	0.93
Time × <i>Colpidium</i> nested in <i>Scenedesmus</i>	0.28	10	5.86	0.0008

Discussion

Our experiment shows that interactions between three important components of microbial communities (bacteria, algae and bacterivores) can strongly influence species coexistence. Algae coexisted with bacteria despite the high carbon:phosphorus ratio in our experiment. In the *Scenedesmus* + bacteria treatment, *Scenedesmus* populations did not display any change in their dynamics all along the experiment. This suggests a coexistence of bacteria and *Scenedesmus*, although we did not measure the dynamics of bacteria. In *Chlorella* + bacteria cultures, *Chlorella* populations showed an increasing phase of abundance but we cannot be sure whether they reached an equilibrium by the end of the experiment or whether they were in the first increasing phase of an oscillation. Despite the high carbon:nutrient ratio, it seems likely that the growth of bacteria was limited. This limitation might be due to a nutrient or a trace element but it might also be due to carbon. In Pengerud et al.'s (1987) and Rothhaupt's (1992) experiments, bacteria could exclude algae when carbon was provided as glucose, which is easily assimilable. In our experiment, in contrast, carbon was available as dissolved organic carbon, which is more difficult to assimilate. Since algae can provide carbon in a form easily accessible to bacteria (Cole et al. 1982), they might have sustained bacterial growth. According to Daufresne and Loreau's (in press) model, this carbon limitation might have prevented the exclusion of algae by bacteria.

The introduction of *Colpidium* had a positive indirect effect on the two species of algae. These might have benefited from nutrient cycling, which released nutrients bound in bacteria (Rothhaupt 1992). We expected *Colpidium* to reach a steady state and to maintain in the microcosms as previously reported in cultures of bacteria and *Colpidium* (Lawler and Morin 1993). However, *Colpidium* populations decreased drastically after a period of population growth. This effect might be due to a harmful substance released in the medium by *Chlorella*. Indeed, several toxins are synthesised by *Chlorella*. In particular, chlorellin, first described as a

growth inhibitor substance (Pratt 1942), might affect some bacteria (Pratt and Fong 1944). In a review on algal allelopathy, Inderjit and Dakshini (1994) noticed that *Chlorella* has a negative effect on *Asterinoella formosa* and *Nitzschia* but a positive effect on *Scenedesmus* (Inderjit and Dakshini 1994). In our experiment, bacteria did not seem to be affected by *Chlorella* since their density did not differ in treatments with or without *Chlorella*. However, *Colpidium* might have been affected by *Chlorella* allelopathy. *Colpidium* initial growth rate was higher in the *Scenedesmus* + bacteria + *Chlorella* + *Colpidium* treatment than in the *Chlorella* + bacteria + *Colpidium* treatment. This discrepancy might be explained by the higher abundance of *Chlorella* in the latter treatment than in the former, leading to different concentrations of chlorellin or other harmful substances. Moreover, some bacteria degrade dissolved organic matter and thus prevent accumulation of toxins (Maestrini and Bonin 1981). Therefore, in the microcosm experiment *Colpidium* might have indirectly transformed a favourable environment into an unfavourable one for itself. This transformation might also include the modification of the pH of the medium. An alternative hypothesis is that the observed dynamics was the beginning of long-term oscillations.

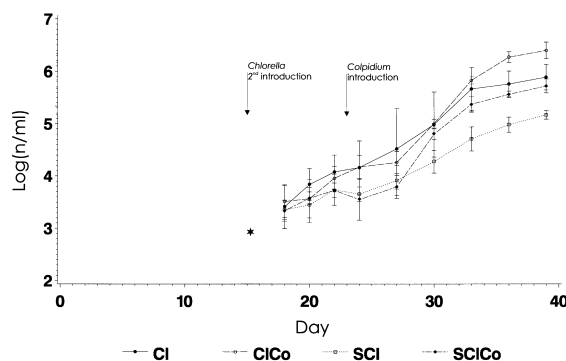


Fig. 3. *Chlorella* mean abundances through time in the various treatments. Error bars represent standard deviations and the star indicates the initial density of *Chlorella* (see Fig. 1 for abbreviations).

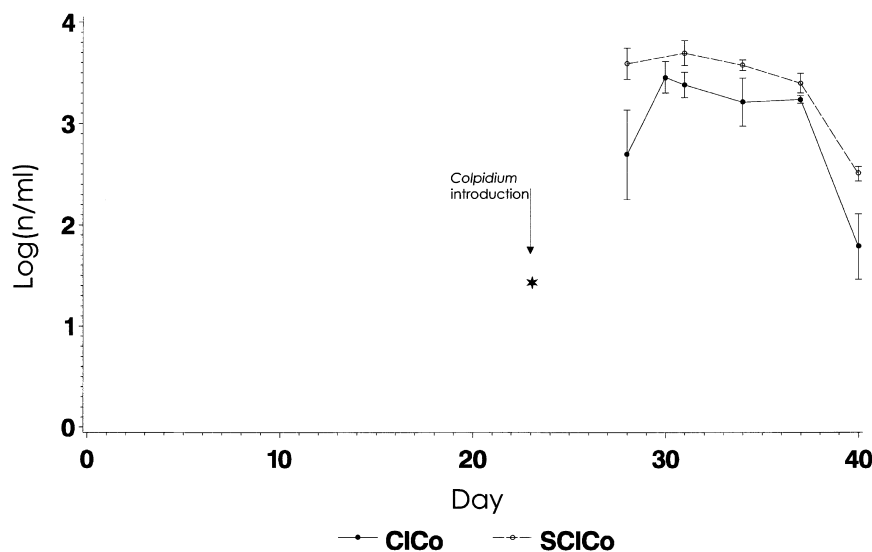


Fig. 4. *Colpidium* mean abundances through time in the various treatments. Error bars represent standard deviations and the star indicates the initial density of *Colpidium* (see Fig. 1 for abbreviations).

The phenomena observed in microcosms might not be directly transposed in real ecosystems. *Chlorella* attained very high abundances in microcosms (up to 4.05×10^6 individuals/ml in one replicate of the CICO treatment) compared with abundances found in situ experiments or in lakes (up to 561 individuals/ml in Post and McQueen 1987), which could lead to high concentrations of harmful substances. Laboratory experiments studying allelopathic substances have generally used nutrient-rich culture media producing dense algal populations in comparison with in situ abundances. During algal blooms in eutrophied waters, however, important quantities of harmful substances might be produced (Maestrini and Bonin 1981). Thus the question remains whether or not antibiotics (Cole 1982) and allelopathic substances are produced in quantities large enough to be effective.

The results regarding the interaction between *Scenedesmus* and *Chlorella* are worth discussing. Jorgensen (1956) carried out crossed experiments to study the production of growth-inhibiting substances by algae and their effects. In particular he showed that *Scenedesmus* formed substances that inhibited the growth of *Chlorella* and that *Chlorella* filtrates stimulated *Scenedesmus* growth rate. Grover (Grover 1991a, b) ran phosphorus-limited cultures where phosphorus was supplied at a constant concentration or with varying periodic pulses leading to non-steady continuous cultures to study competition between *Chlorella* and *Scenedesmus*. In all cases, *Chlorella* outcompeted *Scenedesmus* whatever the order of introduction. In our experiment, when *Chlorella* reached its maximum abundance, no negative effect on *Scenedesmus* could be detected. Conversely, *Chlorella* seemed to suffer during its invasion in a medium already occupied by *Scenedesmus*. These results might be explained by the release of a substance inhibiting *Chlorella* growth by *Scenedes-*

mus. The absence of allelopathic effects during Grover's (1991a, b) experiments might depend on temperature, which is known to play an important role in the production of harmful substances. Grover's experiments were run at 12°C while Jorgensen's at 20°C and ours at 22°C. An alternative hypothesis is that *Chlorella* growth might have been impeded by *Scenedesmus* shading, which, just as the release of growth-inhibiting substances, can generate a priority effect.

Fig. 6 summarises the interactions that likely occurred in our experiment. Bacteria probably had an indirect negative effect on both algal species via the exploitation of a common resource. *Chlorella* might have an allelopathic-like direct negative effect on *Colpidium*. *Scenedesmus* might have an allelopathic-like direct negative effect on *Chlorella*. Finally, *Colpidium* probably had a direct negative effect on bacteria through consumption and an indirect positive effect on *Scenedesmus* and *Chlorella* via the control of bacteria.

In conclusion, our experiment suggests that the interactions between bacteria and algae, and between different species of algae in the presence or absence of a bacterivore, are far more complex than expected. Therefore we need more long-term experiments allowing population abundances to vary. This approach should highlight the dynamical aspects of species interactions and thereby allow formulating assumptions on the functioning of the community. Despite the complex-

Table 4. Effects on *Colpidium* dynamics. RMANOVA results on *Scenedesmus* effects from days 28 to 40.

Source	MS	DF	F value	P
<i>Scenedesmus</i> effects				
Time	3.09	4	105.44	0.0001
<i>Scenedesmus</i>	3.02	1	31.45	0.0005
Time \times <i>Scenedesmus</i>	0.23	4	7.98	0.0037

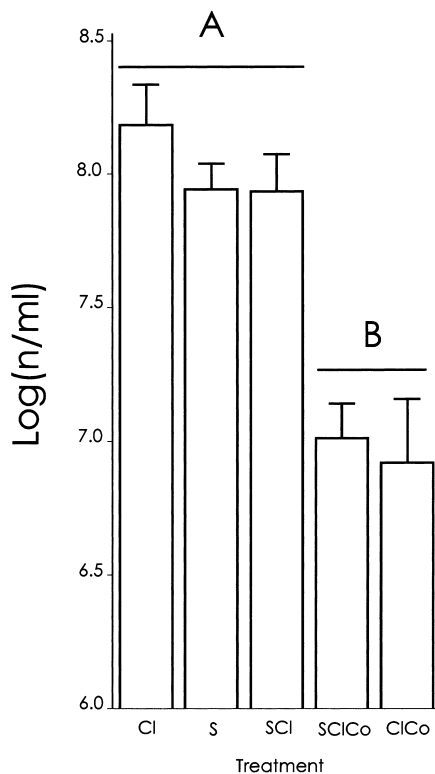


Fig. 5. Bacterial mean abundances on day 38 in the various treatments (see Fig. 1 for abbreviations). Error bars represent 95% confidence intervals.

ity of the community, we were able to disentangle interactions between species in our experiment. As underscored by Rothhaupt (1992), the protist indirectly shifted nutrients from bacteria to primary producers. Further experiments should take higher trophic levels

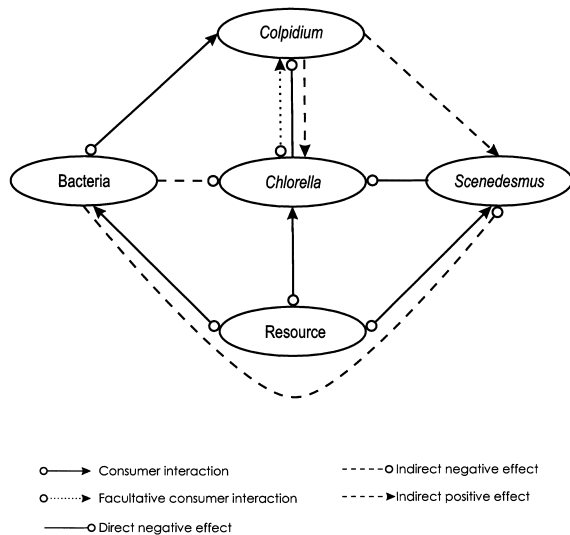


Fig. 6. Summary of the direct and indirect effects in the experimental microbial community.

into account in order to understand the links between species belonging to the so-called microbial loop and species of the so-called classic food web. Moreover, while the diversity of allelopathic substances is related to the diversity of organisms secreting them, the effects of these substances seem to be linked with the abundance of the organisms that secrete them, leading to nonlinear effects of algal diversity on community dynamics. Further experiments should also take into account the effects of organic compounds such as allelopathic substances on community dynamics.

Acknowledgements – The early drafts of the manuscript benefited greatly from comments by Christina Kaunzinger, Andy Gonzalez, Gérard Lacroix, Owen Petchey and Minus van Baalen. F.D.H. thanks Jeremy Fox, Lin Jiang, Jennifer Johnson, Yoko Kato, Christina Kaunzinger, Zac Long, Timon McPhearson, Jon Norberg and Owen Petchey for their welcome during her stay at Rutgers University. This work was supported by NSF grant 9806427 to Peter Morin and Timothy Casey.

References

- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. – *Am. Nat.* 141: 351–371.
- Cole, J. J. 1982. Interactions between bacteria and algae in aquatic ecosystems. – *Annu. Rev. Ecol. Syst.* 13: 291–314.
- Cole, J. J., Likens, G. E. and Strayer, D. L. 1982. Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. – *Limnol. Oceanogr.* 27: 1080–1090.
- Currie, D. J. and Kalff, J. 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. – *Limnol. Oceanogr.* 29: 298–310.
- Daufresne, T. and Loreau, M. in press. Ecological stoichiometry, indirect interactions between primary producers and decomposers, and the persistence of ecosystems. – *Ecology*.
- Grover, J. P. 1991a. Algae grown in non-steady continuous culture: population dynamics and phosphorus uptake. – *Verh. Int. Verein. Limnol.* 24: 2661–2664.
- Grover, J. P. 1991b. Dynamics of competition among microalgae in variable environments: experimental tests of alternative models. – *Oikos* 62: 231–243.
- Harte, J. and Kinzig, A. P. 1993. Mutualism and competition between plants and decomposers: implications for nutrient allocation in ecosystems. – *Am. Nat.* 141: 829–846.
- Huisman, J., Jonker, R. R., Zonneveld, C. and Weissing, F. J. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. – *Ecology* 80: 211–222.
- Hulot, F. D., Lacroix, G., Lescher-Moutoué, F. and Loreau, M. 2000. Functional diversity governs ecosystem response to nutrient enrichment. – *Nature* 405: 340–344.
- Inderjit and Dakshini, K. M. M. 1994. Algal allelopathy. – *Bot. Rev.* 60: 182–196.
- Jorgensen, E. G. 1956. Growth inhibiting substances formed by algae. – *Physiol. Plant.* 9: 712–726.
- Lawler, S. P. and Morin, P. J. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. – *Am. Nat.* 141: 675–686.
- Leibold, M. A. and Wilbur, H. M. 1992. Interactions between food-web structure and nutrients on pond organisms. – *Nature* 360: 341–343.
- Loreau, M. 1998. Ecosystem development explained by competition within and between material cycles. – *Proc. R. Soc. Lond. B* 265: 1–7.

- Loreau, M. 2001. Microbial diversity, producer-decomposer interactions and ecosystem processes: a theoretical model. – Proc. R. Soc. Lond. B 268: 303–309.
- Maestrini, S. Y. and Bonin, D. J. 1981. Allelopathic relationships between phytoplankton species. – Can. Bull. Fish. Aquat. Sci. 210: 323–338.
- Morin, P. J. 2000. The complexity of co-dependency. – Nature 403: 718–719.
- Naeem, S. and Li, S. 1998. Consumer species richness and autotrophic biomass. – Ecology 79: 2603–2615.
- Naeem, S., Hahn, D. R. and Schuurman, G. 2000. Producer-decomposer co-dependency influences biodiversity effects. – Nature 403: 762–764.
- Pengerud, B., Skjoldal, E. F. and Thingstad, T. F. 1987. The reciprocal interaction between degradation of glucose and ecosystem structure. Studies in mixed chemostat cultures of marine bacteria, algae, and bacterivorous nanoflagellates. – Mar. Ecol. Prog. Ser. 35: 111–117.
- Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – Am. Nat. 147: 813–846.
- Post, J. R. and McQueen, D. J. 1987. The impact of planktivorous fish on the structure of a plankton community. – Freshwat. Biol. 17: 79–89.
- Pratt, R. 1942. Studies on *Chlorella vulgaris*. V. Some properties of the growth-inhibitor formed by *Chlorella* cells. – Am. J. Bot. 29: 142–148.
- Pratt, R. and Fong, J. 1944. Chlorellin, an antibacterial substance from *Chlorella*. – Science 99: 351–352.
- Rothhaupt, K. O. 1992. Stimulation of phosphorus-limited phytoplankton by bacterivorous flagellates in laboratory experiments. – Limnol. Oceanogr. 37: 750–759.
- Thingstad, T. F. and Pengerud, B. 1985. Fate and effect of allochthonous organic material in aquatic microbial ecosystems. An analysis based on chemostat theory. – Mar. Ecol. Prog. Ser. 21: 47–62.