1. Hilbeck, A., Baumgartner, M., Fried, P. M. & Bigler, F. *Environ. Entomol.* **27,** 480–487 (1998).
2. Losey, J. E., Rayor, L. S. & Carter, M. E. *Nature* **399,** 214 (1999).
3. Schuler, T. H., Poppy, G. M., Kerry, B. R. & Denholm, I. *Trends Biotechnol.* **17,** 210–216 (1999).
4. Stewart, C. N. Jr *et al. Plant Physiol.* **112,** 115–120 (1996).
5. Talekar, N. S. & Shelton, A. M. *Annu. Rev. Entomol.* **38,** 275–301 (1993).
6. Tabashnik, B. E. *et al. Proc. Natl Acad. Sci. USA* **94,** 12780–12785 (1997).
7. Chilcutt, C. F. & Tabashnik, B. E. *Environ. Entomol.* **26,** 38–45 (1997).
8. Turlings, T. C. J., Tumlinson, J. H. & Lewis, W. J. *Science* **250,** 1251–1253 (1990).
9. De Moraes, C. M., Lewis, W. J., Paré, P. W., Alborn, H. T. & Tumlinson, J. H. *Nature* **393,** 570–573 (1998).
10. Du, Y. *et al. J. Chem. Ecol.* **22,** 1591–1606 (1996).

Prelude or requiem for the 'Mozart effect'?

Rauscher *et al.* reported that listening to ten minutes of Mozart's music increased the abstract reasoning ability of college students, as measured by IQ scores, by 8 or 9 points compared with listening to relaxation instructions or silence, respectively[1]. This startling finding became known as the 'Mozart effect', and has since been explored by several research groups. Here I use a meta-analysis to demonstrate that any cognitive enhancement is small and does not reflect any change in IQ or reasoning ability in general, but instead derives entirely from performance on one specific type of cognitive task and has a simple neuropsychological explanation.

Results from 16 studies on the effect of Mozart's music on the performance of cognitive tasks are summarized in Table 1. Meta-analysis[2] combining the effect sizes reported for all 20 published Mozart-to-silence comparisons (Table 1, top), involving a total of 714 subjects, yields an average cognitive enhancement of $d = 0.09$ standard deviations, or only 1.4 IQ points.

Most of the tasks listed can be classified as stressing either 'abstract reasoning' (Raven's Advanced Progressive Matrices, Stanford–Binet matrices, backwards digit span) or 'spatial–temporal processing'[3] (Paper Folding and Cutting, Revised Minnesota Paper Form Board). The Mozart effect for abstract reasoning is $d = -0.04$, whereas for spatial–temporal processing it is $d = 0.14$ (or 2.1 IQ points). Accordingly, exposure to ten minutes of Mozart's music does not seem to enhance general intelligence or reasoning, although it may exert a small improving effect on the ability to transform visual images.

However, this enhancement is essentially restricted to a single task, is one-quarter as large as that originally reported for a broader class of cognitive abilities, is not statistically significant (combined $Z = 1.14$, $P = 0.26$), and is smaller than the average variation of a single person's IQ-test performance (assuming a test reliability of 0.95, the 50% confidence interval would be 4.5 IQ points wide).

To account for the Mozart effect, Rauscher's group appealed to a model of cortical computation whose operations at the columnar level are compatible with qualities presumed to be present in Mozart's music and with the cognitive processing presumed to be involved in spatial–temporal tasks[1,3,4]. But any improvement in performance with music can also be explained by the fact that the complex visual transformation processes involved in three-dimensional mental rotation and similar difficult spatial tasks (such as paper folding and cutting) are associated with function of the right cerebral hemisphere[5], as is cognitive arousal[6,7].

In support of this, one study found that listening either to Mozart or to a passage from a Stephen King story enhanced subjects' performance in paper folding and cutting, but only for those who enjoyed what they heard[8]. Another experiment found that 8,120 British schoolchildren performed better in response to (presumably enjoyable) popular music than to Mozart's music, relative to a control group that heard a discussion of scientific experiments[9].

Mozart's effect on mood has been verified in standard questionnaires[10]. In a meta-analysis of eight comparisons (with 201 subjects) of auditory relaxation instructions with Mozart's music (Table 1, bottom), the music effect appears to be larger: $d = 0.20$ overall, and $d = 0.56$ for spatial–temporal processing. But as relaxation instructions aim to reduce arousal, it is not surprising that they should impair subsequent cognitive performance, especially on tasks that depend on the right hemisphere.

I conclude that a shared right-hemisphere locus provides a plausible explanation for an intermittent, small positive 'enjoyment arousal' effect of Mozart's music on difficult spatial tasks. It also explains the failure to find an effect from other stimulation, which may not be sufficiently enjoyable or arousing to subjects,

Table 1 Studies of the effect of Mozart's music on the performance of cognitive tasks

Task	*N*	*d*	*P*
Comparisons with silence			
Raven's Advanced Progressive Matrices[11]	78	−0.065	0.778
Raven's Advanced Progressive Matrices[12]*	20	0.00	1.000
Matrices (Stanford–Binet)[1,3]*	8	0.097	0.909
Matrices (Stanford–Binet)[13]*	12	−0.048	0.941
Matrices (Stanford–Binet)[14]*	16	−0.308	0.574
Backwards digit span[15]	24	0.149	0.730
Paper Folding and Cutting (Stanford–Binet)[1,3]*	8	1.389	0.140
Paper Folding and Cutting (Stanford–Binet)[16]	136	0.218	0.209
Paper Folding and Cutting (Stanford–Binet)[13]*	12	−0.356	0.586
Paper Folding and Cutting (Stanford–Binet)[14]	45	0.017	0.956
Paper Folding and Cutting (Stanford–Binet)[14]*	16	−0.989	0.085
Paper Folding and Cutting (Stanford–Binet elaborated)[4]*	53	0.724	0.013
Paper Folding and Cutting (Stanford–Binet elaborated)[17]*	38	−0.151	0.653
Paper Folding and Cutting (Stanford–Binet elaborated)[10]	86	0.057	0.795
Paper Folding and Cutting (Stanford–Binet elaborated)[14]	35	−0.011	0.975
Paper Folding and Cutting (computerized)[8]*	28	0.272	0.494
Revised Minnesota Paper Form Board[18]	51	0.082	0.775
Maze completion (paper-and-pencil)[19]*	14	0.000	1.000
Pattern Analysis (Stanford–Binet)[1,3]*	8	0.289	0.735
Short-term memory (character strings)[4]*	26	−0.072	0.861
Comparisons with auditory relaxation instructions			
Raven's Advanced Progressive Matrices[11]	77	−0.176	0.447
Matrices (Stanford–Binet)[1,3]*	8	0.000	1.000
Paper Folding and Cutting (Stanford–Binet)[1,3]*	8	1.622	0.094
Paper Folding and Cutting (Stanford–Binet elaborated)[14]	36	−0.032	0.925
Paper Folding and Cutting (Stanford–Binet elaborated)[20]*	8	0.489	0.571
Paper Folding and Cutting (Stanford–Binet elaborated)[21]*	32	0.814	0.033
Paper Folding and Cutting (Stanford–Binet elaborated)[22]*	24	0.867	0.054
Pattern Analysis (Stanford–Binet)[1,3]*	8	−0.685	0.434

N is the number of subjects in the comparison; *d* is the effect size measure, defined as the number of standard deviations by which the Mozart group performance mean is greater than the control group mean, based on the pooled variance of the two groups (performance for most tasks is measured by the number of test items correctly completed in a fixed time); and *P* is the two-tailed probability associated with affirming the null hypothesis (of $d = 0$). When effect sizes were combined in the meta-analysis, each was weighted by its associated degrees of freedom, or $N-2$; when probabilities were combined, they were first converted to Z-values[2]. To be included, a study must have been published or submitted for publication, and had to compare the effects on the task of a Mozart composition (usually his sonata for two pianos, K.448) and either silence or auditory relaxation instructions, not different types of music or other non-musical auditory stimuli, any of which could be the source of the effect rather than Mozart[15]. To ensure that none of the measurements could have been contaminated by prior tasks or listening conditions, all comparisons are between two separate groups of adult human subjects, each performing the first cognitive task in a testing session, one listening to Mozart and the other to silence or relaxation instructions of equal duration beforehand.
*Extra information needed for these computations was obtained from the authors.

or on abstract reasoning or other cognitive abilities, which do not depend critically on those brain areas.

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1. Rauscher, F. H., Shaw, G. L. & Ky, K. N. *Nature* **365,** 611 (1993).
2. Rosenthal, R. *Meta-Analytic Procedures for Social Research* (Sage, Newbury Park, 1991).
3. Rauscher, F. H. & Shaw, G. L. *Percept. Motor Skills* **86,** 835–841 (1998).
4. Rauscher, F. H., Shaw, G. L. & Ky, K. N. *Neurosci. Lett.* **185,** 44–47 (1995).
5. Ditunno, P. L. & Mann, V. A. *Cortex* **26,** 177–188 (1990).
6. Heller, W. & Nitschke, J. B. *Cogn. Emot.* **11,** 637–661 (1997).
7. Robertson, I. H., Mattingley, J. B., Rorden, C. & Driver, J. *Nature* **395,** 169–172 (1998).
8. Nantais, K. M. & Schellenberg, E. G. *Psychol. Sci.* **10,** 370–373 (1999).
9. Hallam, S. *Psychol. Music* (submitted).
10. Steele, K. M., Bass, K. E. & Crook, M. D. *Psychol. Sci.* **10,** 366–369 (1999).
11. Newman, J. *et al. Percept. Motor Skills* **81,** 1379–1387 (1995).
12. Stough, C., Kerkin, B., Bates, T. & Mangan, G. *Personal. Individ. Diff.* **17,** 695 (1994).
13. Kenealy, P. & Monsef, A. *Psychologist* **7,** 346 (1994).
14. Steele, K. M. *et al. Nature* **400,** 827 (1999).
15. Steele, K. M., Ball, T. N. & Runk, R. *Percept. Motor Skills* **84,** 1179–1184 (1997).
16. Steele, K. M., Brown, J. D. & Stoecker, J. A. *Percept. Motor Skills* **88,** 843–848 (1999).
17. Carstens, C. B. & De Fruscio, D. M. *Percept. Motor Skills* (submitted).
18. Carstens, C. B., Huskins, E. H. & Hounshell, G. W. *Psychol. Rep.* **77,** 111–114 (1995).
19. Wilson, T. L. & Brown, T. L. *J. Psychol.* **131,** 365–370 (1997).
20. Rideout, B. E. & Laubach, C. M. *Percept. Motor Skills* **82,** 427–432 (1996).
21. Rideout, B. E. & Taylor, J. *Percept. Motor Skills* **85,** 112–114 (1997).
22. Rideout, B. E., Dougherty, S. & Wernert, L. *Percept. Motor Skills* **86,** 512–514 (1998).

Rauscher *et al.* reported[1] that brief exposure to a Mozart piano sonata produces a temporary increase in spatial reasoning scores, amounting to the equivalent of 8–9 IQ points on the Stanford–Binet IQ scale[2]. Early attempts to confirm this 'Mozart effect' were unsuccessful[3–6]. Rauscher *et al.* subsequently restricted their account to an improvement in spatial–temporal reasoning, as measured by the Paper Folding and Cutting task[7]. We use procedures modelled on the original report to show that there is little evidence for a direct effect of music exposure on reasoning ability.

We tested the performance of subjects on the same task (a 16- or 18-item paper folding and cutting task) after listening to the same Mozart music as in the original experiment. Control conditions were either the same or chosen to broaden the comparison set, and consisted of silence, relaxation instructions, minimalist music (*Music with Changing Parts* by P. Glass) or relaxation music (*The Shining Ones* by P. Thorton). The experimental designs replicated the original study at the University of Montreal (UM); other standard designs were used at the Appalachian State University (ASU) and the University of Western Ontario (UWO).

Table 1 shows the results of the experiments in either Stanford–Binet standard age scores (SAS) or as raw scores when conversion was not appropriate. SAS values in the UM and UWO studies are quite similar to the original report, indicating that the subjects had similar intellectual skills. The results show that listening to the Mozart sonata produced no differential improvement in spatial reasoning in any experiment. The sonata had no effect on performance, as revealed by analyses for main effects (ASU, $F(4, 81) = 0.33$, $P = 0.86$; UM, $t(30) = 1.14$, $P = 0.263$; UWO, $F(2, 64) = 1.99$, $P = 0.145$) and several interactions, and for individual improvement from the pretest (ASU, $F(4, 80) = 0.24$, $P = 0.91$). When SAS scores were translated into IQ-point equivalents, listening to Mozart produced a 3-point increase relative to silence in one experiment (UWO, 111 versus 108) and a 4-point decrease in the other experiment (UM, 114 versus 118). Conversion of the Mozart and silence comparisons into a measure of effect size indicated that the music had little impact (mean $d = 0.003$). A requiem may therefore be in order.

Table 1 Effect of listening condition on scores from the Paper Folding and Cutting task

Listening condition	Mean	s.e.	*N*
UM, Stanford–Binet SAS scores			
Mozart	57.31	1.26	32
Silence	59.06	0.88	32
UWO, Stanford–Binet SAS scores			
Mozart	55.58	0.64	24
Silence	54.27	0.67	21
Relaxation music	54.14	0.31	22
ASU, number correct from 16 items			
Mozart	10.78	0.74	18
Silence	11.42	0.91	17
Minimalist music	10.83	0.78	18
10 min relaxation	10.89	0.86	18
20 min relaxation	11.07	0.98	15

In the Paper Folding and Cutting (PFC) task, the subject chooses the appearance of unfolded paper from five alternatives. At UM, subjects listened to music or silence and were then given the Stanford–Binet PFC or Matrices task. After 10 min rest, they had the other treatment and were given the other task. Task order and treatment order were counterbalanced across subjects. Only results from the PFC task are shown; there was no significant effect of treatment on Matrices results, $t(30) = 0.40$, $P = 0.69$. At UWO, after being randomly assigned a listening condition, subjects were tested with the Stanford–Binet PFC task. At ASU, subjects were pretested with 16 PFC items. After 48 h, they were exposed to a treatment condition and tested with 16 new PFC items, followed by a 20-item mood questionnaire. PFC tasks were counterbalanced across subjects. Pretest results indicated no pre-existing difference among groups, $F(4, 81) = 0.66$, $P = 0.62$. There was a significant 'practice' effect of improvement from the first to the second test, $F(1, 81) = 33.6$, $P < 0.001$, but this did not interact with treatment condition, $F(4, 81) = 0.59$, $P = 0.67$, indicating that no treatment had a differential effect on improvement.

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1. Rauscher, F. H., Shaw, G. L. & Ky, K. N. *Nature* **365,** 611 (1993).
2. Thorndike, R. L., Hagen, E. P. & Sattler, J. M. *The Stanford–Binet Intelligence Scale,* 4th edn (Riverside, Chicago, 1986).
3. Carstens, C. B., Huskins, E. & Hounshell, G. W. *Psychol. Rep.* **77,** 111–114 (1995).
4. Kenealy, P. & Monsef, A. *Psychologist* **7,** 346 (1994).
5. Newman, J. *et al. Percept. Motor Skills* **81,** 1379–1387 (1995).
6. Stough, C., Kerkin, B., Bates, T. & Mangan, G. *Personal. Individ. Diff.* **17,** 695 (1994).
7. Rauscher, F. H. & Shaw, G. L. *Percept. Motor Skills* **86,** 835–841 (1998).

Rauscher replies — Our results on the effects of listening to Mozart's *Sonata for Two Pianos in D Major K. 448* on spatial–temporal task performance[1–3] have generated much interest but several misconceptions, many of which are reflected in attempts to replicate the research. The comments by Chabris and Steele *et al.* echo the most common of these: that listening to Mozart enhances intelligence. We made no such claim. The effect is limited to spatial–temporal tasks involving mental imagery and temporal ordering.

Chabris' oversight led him to include in his analysis abstract reasoning tasks other than spatial–temporal tasks, which are a subset of the former. Four other studies (refs 4,5 and F.H.R. *et al.*, manuscripts in preparation) all demonstrate a Mozart effect, and Chabris has excluded comparisons of scores following the playing of Mozart with scores obtained with other composers[2,4,6,7]. The effect works for not just one spatial–temporal task, as claimed by Chabris, but for three (refs 5,8 and F.H.R. and L. J. Hayes, manuscript in preparation). Chabris attributes our account of the Mozart effect to IQ-test variation, a fair hypothesis if the Mozart effect had anything to do with overall IQ. Test and retest reliability of spatial–temporal scores must be significantly smaller than that of general IQ score, which represents a composite of many unrelated subtests.

Chabris dismisses the neural model[9] that motivated the original report[1] by proposing that Mozart produces 'enjoyment arousal', a right-hemisphere function like spatial–temporal task performance. Other abstract reasoning tasks (Ravens Matrices) are left-hemisphere functions, Chabris claims. Music therefore improves spatial–temporal tasks, not matrix tasks, as a result of a shared right-hemisphere locus. But listening to music also includes processing rhythmic information, for example, which is a left-hemisphere function[10]. Chabris' reasoning would thus predict that music improves left-hemisphere tasks, such as Ravens Matrices, because of a shared left-hemisphere locus, which it does not.

Several studies suggest that the 'enjoyment arousal' explanation is unlikely. First, rats exposed to the Mozart sonata *in utero* and for 60 days post-partum during their waking cycles learned a spatial maze faster and with fewer errors over days than did controls[11]. It is unlikely that learning improved in these animals as a result of pleasure they derived from the treatment. Second, students who listened to Mozart, Mendelssohn, relaxation instructions or silence demonstrated a Mozart effect despite ratings of the Mendelssohn work as being maximally arousing[4]. Third, students who listened to the Mozart sonata scored higher on a spatial–temporal task than after they listened to other stimuli, regardless of their preference (F.H.R. *et al.*, manuscript in preparation). Finally, investigation of the Mozart effect on epileptiform activity showed that the sonata produced a reversal of the epileptic state in comatose patients[12]. No effects were found after exposure to control music. According to these authors, this finding strongly suggests that the effect is not caused by emotional state or arousal.

Steele *et al.* find no Mozart effect in three differently designed studies. Not one design replicated the original reports[1–3], and they introduced several methodological concerns. For example, spatial–temporal task performance varies widely between individuals, making randomization an inefficient way to ensure uniform before-treatment task proficiency[2]. What measures were taken by the two studies using between-subjects designs to tackle this? Was testing done blind, as in other replications (refs 1,3,4 and F.H.R. *et al.*, manuscript in preparation)?

Chabris' analysis is incomplete and includes studies not relevant to the effect he was exploring. Although the Mozart effect cannot be found under all laboratory conditions, as discussed by Steele *et al.*, several studies have successfully replicated it (refs 1–8,11,13,14 and F.H.R. *et al.*, manuscripts in preparation). Because some people cannot get bread to rise does not negate the existence of a 'yeast effect'.

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1. Rauscher, F. H., Shaw, G. L. & Ky, K. N. *Nature* **365,** 611 (1993).
2. Rauscher, F. H., Shaw, G. L. & Ky, K. N. *Neurosci. Lett.* **185,** 44–47 (1995).
3. Rauscher, F. H. & Shaw, G. L. *Percept. Motor Skills* **86,** 835–841 (1998).
4. Rauscher, F. H. & Ribar, R. J. *Percept. Motor Skills* (submitted).
5. Siegel, S. *Percept. Motor Skills* (submitted).
6. Rideout, B. E., Dougherty, S. & Wernert, L. *Percept. Motor Skills* **86,** 512–514 (1998).
7. Nantais, K. M. & Schellenberg, E. G. *Psychol. Sci.* **10,** 370–373 (1999).
8. Wilson, T. L. & Brown, T. L. *J. Psychol.* **131,** 365–370 (1997).
9. Leng. X. & Shaw, G. L. *Concepts Neurosci.* **2,** 229–258 (1991).
10. Peretz, I. *Brain* **113,** 1185–1205 (1990).
11. Rauscher, F. H., Robinson, K. D. & Jens, J. J. *Neurol. Res.* **20,** 427–432 (1998).
12. Hughes, J. R., Daaboul, Y., Fino, J. J. & Shaw, G. L. *Clin. Electroencephalogr.* **29,** 109–119 (1998).
13. Rideout, B. E. & Laubach, C. M. *Percept. Motor Skills* **82,** 427–432 (1996).
14. Rideout, B. E. & Taylor, J. *Percept. Motor Skills* **85,** 112–114 (1997).

Ubiquitous dispersal of microbial species

The biosphere supports astronomical numbers of free-living microorganisms that belong to an indeterminate number of species. One view[1–3] is that the abundance of microorganisms drives their dispersal, making them ubiquitous and resulting in a moderate global richness of species. But ubiquity is hard to demonstrate, not only because active species have a rapid turnover, but also because most species in a habitat at any moment in time are relatively rare or in some cryptic state[4]. Here we use microbes that leave traces of their recent population growth in the form of siliceous scale structures to show that all species in the chrysomonad flagellate genus *Paraphysomonas* are probably ubiquitous.

Paraphysomonas consists of 50 species, which can be distinguished by the morphology of their surface scales[5], although oligonucleotide sequence (small-subunit ribosomal RNA) data indicate that the morphospecies are also genetically distinct[6]. The scales remain recognizable for several months after cell death, so looking at their remains in the sediment of a pond provides evidence of the preceding species succession. We used transmission electron microscopy to examine the superficial ~2 mm of sediment collected from a one-hectare freshwater pond (Priest Pot, Cumbria, UK[7]). ^{210}Pb dating indicated that this sediment layer had been deposited within the previous three months. We identified and quantified all the scales and cell remains of *Paraphysomonas* species present, and used this information to reconstruct whole cells. Our examination of 25.2 µl of sediment yielded data on the relative abundance of 32 species.

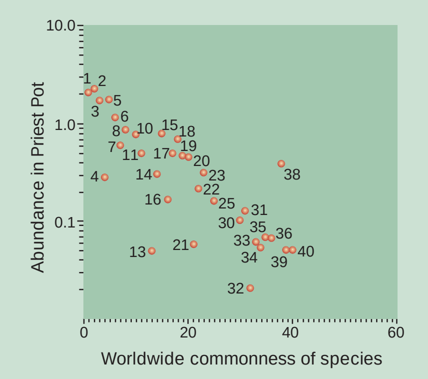

Figure 1 The abundance of each *Paraphysomonas* species in 25.2 µl (equivalent to ~0.1 cm^2) of superficial Priest Pot sediment, plotted against its worldwide commonness. Commonness data are ranked in order, decreasing from left to right. Species 1 and 2 are *P. vestita* and *P. imperforata*, respectively. Further details are available from the authors.

We compared our data with information in 73 published surveys of *Paraphysomonas* species from biogeographic regions across the world. These surveys recorded a total of 41 species, 78% of which were detected in our small volume of pond sediment. The pattern of relative abundance of species in Priest Pot is similar to the global one (Fig. 1). Species that are frequently recorded globally are also abundant in sediment from Priest Pot, and species that are rarely found globally are not abundant in Priest Pot.

We think that globally abundant species will, through neutral migration, 'seed' the pond more frequently than rare species. They are probably capable of population growth in a broad range of conditions, so they will more frequently find suitable conditions. Finally, termination of population growth is accompanied by the production of resting cysts. As the size of the 'cyst bank' for each species is likely to be proportional to its global abundance, repeated cyst production will effectively strengthen the pattern of relative abundance of species that results from neutral migration.

It is widely believed that most microbial species have yet to be discovered, which follows from the general rule that, for each tenfold reduction in body length, the global number of taxa increases roughly 100-fold[8]. But this relation breaks down for organisms smaller than about 1 mm (refs 1,8,9), probably because the enormous number of microorganisms (the water column of Priest Pot typically supports $\sim 4 \times 10^{14}$ living *Paraphysomonas*) drives large-scale dispersal across the physical and geographical barriers that halt the migrations of larger animals and plants. As ubiquity will limit rates of local speciation and extinction[1], the global number of species less than 1 mm long will be relatively small.

Free-living bacteria sustain all the important ecosystem functions. They are about three orders of magnitude more numerous than heterotrophic flagellates, so it is even more likely that they too are ubiquitous, and that the global richness of free-living microbial species is moderate.

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1. Fenchel, T. *Oikos* **68,** 375–378 (1993).
2. Roberts, M. S. & Cohan, F. M. *Evolution* **49,** 1081–1094 (1995).
3. Finlay, B. J., Esteban, G. F. & Fenchel, T. *Nature* **383,** 132–133 (1996).
4. Fenchel, T., Esteban, G. F. & Finlay, B. J. *Oikos* **80,** 220–225 (1997).
5. Preisig, H. R., Vørrs, N. & Hällfors, G. in *The Biology of Free-living Heterotrophic Flagellates* (eds Patterson, D. J. & Larsen, J.) 361–399 (Syst. Assoc. Special Volume No. 45; Clarendon, Oxford, 1991).
6. Rice, J. *et al. Microbiology* **143,** 1717–1727 (1997).
7. Finlay, B. J., Maberly, S. C. & Cooper, J. I. *Oikos* **80,** 209–213 (1997).
8. May, R. M. *Phil. Trans. R. Soc. Lond. B* **330,** 293–304 (1990).
9. Lawton, J. H. *Oikos* **81,** 3–5 (1998).