

7. Tilman, D. *Resource Competition and Community Structure* (Princeton Univ. Press, Princeton, 1982).
8. Rothhaupt, K. O. *Nature* **333**, 660–662 (1988).
9. Ciro-Perez, J., Carmona, M. J. & Serra, M. *Limnol. Oceanogr.* **46**, 1511–1523 (2001).

10. Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F. & Hairston, N. G. Jr *Nature* **424**, 303–306 (2003).

doi:10.1038/nature04526

ECOLOGY

Nelson et al. reply

Replying to: T. Yoshida, L. E. Jones, S. P. Ellner & N. G. Hairston Jr
Nature doi:10.1038/nature04526 (2005).

We have demonstrated that qualitatively different consumer–resource dynamics can have a large impact on natural selection in a consumer population, and proposed that the change in selection is generated by the juvenile–adult stage–structure of the consumer¹. Yoshida *et al.*² propose an alternative mechanism to explain our results, but, on the basis of other evidence collected at the time of our experiments¹, we can refute this explanation. We also discuss theoretical results that show how simple stage–structure in a consumer population can modify selection.

The consumer–resource interaction between *Daphnia* and algae shows two qualitatively different classes of population cycle: small-amplitude, stage-structured cycles and large-amplitude, consumer–resource cycles³. These cycles are characterized by different amplitudes, frequencies and juvenile development rates. Among competing genotypes of *Daphnia*⁴, we found that small-amplitude, stage-structured cycles reduce the amount of selection compared with large-amplitude, consumer–resource cycles — a result that we explained in terms of the interaction between resource dynamics and resource-dependent juvenile development, which emerges from general competition models based on *Daphnia* and algal ecology^{4–7}.

Yoshida *et al.*² propose that the observed change in selection results from the difference in algal diversity between treatments, rather than a difference in population dynamics. They suggest that the four algal species provided in the stage-structured treatment allows for trade-offs among genotypes, whereas the single algal species in the consumer–resource treatment does not. This mechanism would require that *Daphnia* genotypes have different performance (relative to one another) with each algal species, and that selection is slow when multiple algal species are present and rapid when only one is present.

However, these features do not exist in our experiments. The algae we used are easily ingested by *Daphnia* and, as *Daphnia* are gen-

eralist filter-feeders⁸, differential ingestion of algal species is unlikely. Furthermore, *Daphnia* genotypes do not show the required trade-off in performance among algal species⁹. A more direct test is to compare the rate of selection among genotypes against the dynamics of each algal species. In our experiments, the algal community became dominated by a single species at around day 50 (Fig. 1a) — a common observation in *Daphnia*–algal aquaria experiments¹⁰. As this does not lead to the required rapid competitive exclusion (Fig. 1b), the mechanism suggested by Yoshida *et al.* can be rejected.

We agree that it is challenging to identify the mechanisms that maintain diversity, particularly when they involve life-history features that are difficult to manipulate. However, the alternative mechanism proposed by Yoshida *et al.*² cannot capture the main result of our experiments — selection is reduced under small-amplitude population cycles¹. Theoretical work on physiologically structured models in *Daphnia* has tightly linked the models to experiments^{5–7}. Based on those results, we have developed a competition model to test the influence of structured *Daphnia*–algae population dynamics on selection among *Daphnia* genotypes⁴. This independently parameterized model predicts both of the two classes of population cycle. Selection among competing consumer genotypes changes depending on the class of dynamics — selection under large-amplitude cycles is greater than under small-amplitude cycles.

As we proposed¹, the difference in selection is caused by the influence of resource dynamics on mortality and juvenile development. Our experimental and theoretical results both indicate that structured population dynamics can have a strong influence on natural selection through a potentially general equalizing mechanism.

William A. Nelson[†], Edward McCauley^{*},
 Frederick J. Wrona[‡]

^{*}Ecology Division, University of Calgary, Calgary, Alberta T2N 1N4, Canada

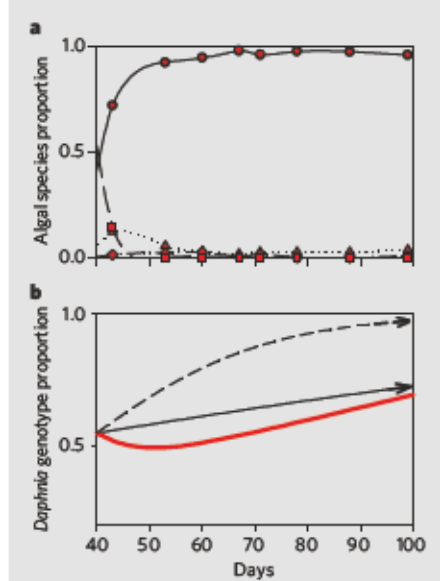


Figure 1 | Algal composition and genotype selection. **a**, Example of species composition of the algal community changing with time (see also Fig. 2a in ref. 1). Lines represent individual algal species and symbols indicate times at which samples were taken. **b**, Selection dynamics for genotype '9H'. Red line shows selection for example shown in **a**; black line shows average selection under stage-structured cycles; and dashed line shows the faster selection under consumer–resource cycles. The genotype dynamics in stage-structured cycles do not show rapid competitive exclusion when the algal population is dominated by a single species.

[†]Present address: Centre for Mathematical Biology, University of Alberta, Edmonton, Alberta T6G 1G1, Canada

e-mail: wnelson@math.ualberta.ca

[‡]Water & Climate Impacts Research Centre, National Water Research Institute, University of Victoria, Victoria, British Columbia V8W 3P5, Canada

1. Nelson, W. A., McCauley, E. & Wrona, F. J. *Nature* **433**, 413–417 (2005).
2. Yoshida, T., Jones, L. E., Ellner, S. P. & Hairston, N. G. Jr *Nature* **438**, doi:10.1038/nature04526 (2005).
3. McCauley, E., Nisbet, R. M., Murdoch, W. W., de Roos, A. M. & Gurney, W. S. C. *Nature* **402**, 653–656 (1999).
4. Nelson, W. A., McCauley, E. & Nisbet, R. M. *Ecol. Lett.* (submitted).
5. McCauley, E., Nisbet, R. M., de Roos, A. M., Murdoch, W. W. & Gurney, W. S. C. *Ecol. Monogr.* **66**, 479–501 (1996).
6. Noonburg, E. G. *et al.* *Funct. Ecol.* **12**, 211–222 (1998).
7. Nisbet, R. M., McCauley, E., Gurney, W. S. C., Murdoch, W. W. & Wood, S. N. *Ecology* **85**, 3132–3139 (2004).
8. DeMott, W. R. *Limnol. Oceanogr.* **27**, 518–527 (1982).
9. Repka, S. *Freshwat. Biol.* **38**, 675–683 (1997).
10. Nelson, W. A., McCauley, E. & Wrona, F. J. *Proc. R. Soc. Lond. B* **268**, 1223–1230 (2001).

doi:10.1038/nature04527