scribed[10], might have been altered in mutant embryos[11,12]. Furthermore, ultrastructural abnormalities affect mainly the nuclei of embryos from null females at the 2-cell stage, indicating that, even with transcriptional activity, reduced survival is in part related to the decrease in structural integrity of the early embryonic nucleus (Fig. 1e–h).

The key role for control by maternal-origin HSF1 in early development raises the possibility that in defective form it may be a cause of post-fertilization abnormalities associated with infertility in mammals, including humans.

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1. McMillan, D. R., Xiao, X., Shao, L., Graves, K. & Benjamin, I. J. *J. Biol. Chem.* **273,** 7523–7528 (1998).
2. Xiao, X. *et al. EMBO J.* **18,** 5943–5952 (1999).
3. Schupbach, T. & Wieschaus, E. *Genetics* **121,** 101–117 (1989).
4. Jedlicka, P., Mortin, M. A. & Wu, C. *EMBO J.* **16,** 2452–2462 (1997).
5. Greenhouse, S., Rankin, T. & Dean, J. *Am. J. Hum. Genet.* **62,** 1282–1287 (1998).
6. Schultz, R. M. *BioEssays* **15,** 531–538 (1993).
7. Bensaude, O., Babinet, C., Morange, M. & Jacob, F. *Nature* **305,** 331–333 (1983).
8. Christians, E., Campion, E., Thompson, E. M. & Renard, J. P. *Development* **121,** 113–122 (1995).
9. Christians, E. *et al. Mol. Cell Biol.* **17,** 778–788 (1997).
10. Bevilacqua, A., Fiorenza, M. T. & Mangia, F. *Development* **127,** 1541–1551 (2000).
11. Latham, K. E., Garrels, J. I., Chang, C. & Solter, D. *Development* **112,** 921–932 (1991).
12. Davis, W. Jr & Schultz, R. M. *Dev. Biol.* **218,** 275–283 (2000).

Biodiversity

Coexistence and resource competition

How large numbers of species coexist on a seemingly limited number of different resources is a classic problem in ecology[1], and attempts have been made to solve it experimentally. But we are not convinced that Huisman and Weissing's[2] proposal to add non-stationary dynamics in species abundance to the list of possible explanations offers any new insight into this biodiversity enigma.

Early ideas were based on competitive exclusion, in which two (or more) species compete for shared resources but only the more proficient survives[3], and the number of coexisting species, n, does not exceed the number of available resources, k. But these ideas based on competitive exclusion cannot explain how rich ensembles of species can coexist on a limited number of resources (that is, $n > k$), as in aquatic ecosystems.

A solution to this biodiversity problem has been suggested by Huisman and Weissing[2] in the form of a model demonstrating the possibility of coexistence of two or more competitors under conditions of fluctuating (periodic or chaotic) community dynamics, a finding central to contemporary ecological theory[4]. However, we believe that their solution to the $n > k$ puzzle has long been known[5–13].

It was first inferred from a computer simulation over 25 years ago[5] that two species can coexist on one biotic resource, with coexistence occurring along what appeared to be a periodic orbit, as was also shown by Huisman and Weissing[2]. This was confirmed analytically and expanded to cover the more general case of n species coexisting on one biotic resource[9]. The fact that coexistence depends on the nonlinearity of the species-specific growth functions and on the lack of system equilibrium — the central issue discussed by Huisman and Weissing[2] — has also been demonstrated earlier[8]. The plankton paradox (whereby $n > k$) was thus resolved about two decades after it was first posed as a biodiversity problem.

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1. Hutchinson, G. E. *Am. Nat.* **95,** 137–145 (1961).
2. Huisman, J. & Weissing, F. J. *Nature* **402,** 407–410 (1999).
3. Gause, G. J. *The Struggle for Existence* (Williams & Wilkins, Baltimore, 1934).
4. Sommer, U. *Nature* **402,** 366–367 (1999).
5. Koch, A. L. *J. Theor. Biol.* **44,** 387–395 (1974).
6. Armstrong, R. A. & McGehee, R. *J. Theor. Biol.* **56,** 499–502 (1976).
7. Armstrong, R. A. & McGehee, R. *Theor. Popul. Biol.* **9,** 317–328 (1976).
8. Armstrong, R. A. & McGehee, R. *Am. Nat.* **115,** 151–170 (1980).
9. McGehee, R. & Armstrong, R. A. *J. Diff. Equns* **23,** 30–52 (1977).
10. Kalan, J. L. & Yorke, J. A. *Am. Nat.* **111,** 1032–1036 (1977).
11. Ebenhöh, W. *Ecol. Modell.* **75/76,** 83–98 (1994).
12. Yodzis, P. *Introducton to Theoretical Ecology* (Harper & Row, New York, 1989).
13. Fryxell, J. M. & Lundberg, P. *Individual Behavior and Community Dynamics* (Chapman & Hall, London, 1997).

Huisman and Weissing reply — How can we explain the biodiversity of rainforests and coral reefs if we do not understand the species diversity of phytoplankton in a droplet of water[1]? In our attempt[2] to solve the plankton paradox, we showed that multispecies competition may generate oscillations and chaos and that these fluctuations create opportunities for the coexistence of many species. Lundberg *et al.* question the novelty of our findings and argue that the plankton paradox was resolved 25 years ago.

The earlier findings[3–5] quoted by Lundberg *et al.* are interesting because they show that multiple species can coexist on a single biotic resource. However, biotic resources are irrelevant to an explanation of the plankton paradox. This paradox is concerned with phytoplankton[1], and phytoplankton species do not compete for biotic resources — they use abiotic resources such as nitrogen, phosphorus, silicon, iron and light.

Also, the mechanisms that generate the fluctuations differ. The models to which Lundberg *et al.* refer consider predators competing for biotic prey. It is well known that predator–prey interactions easily generate fluctuations[6]. The fluctuations that we investigated, however, are not predator–prey oscillations. We discovered that models of competition for abiotic resources[2,7] may also generate fluctuations, and that these competitive fluctuations allow a high species diversity. We have therefore shown that competition itself can generate the fluctuations that favour species coexistence. This resolves the plankton paradox.

Apart from these differences with the earlier findings[3–5] in terms of the type of resource and the source of the fluctuations, there is an important similarity, as pointed out by Lundberg *et al.* All of these studies indicate that non-equilibrium dynamics generated by species interactions can have a major impact on biodiversity.

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1. Hutchinson, G. E. *Am. Nat.* **95,** 137–145 (1961).
2. Huisman, J. & Weissing, F. J. *Nature* **402,** 407–410 (1999).
3. Koch, A. L. *J. Theor. Biol.* **44,** 387–395 (1974).
4. Armstrong, R. A. & McGehee, R. *J. Theor. Biol.* **56,** 499–502 (1976).
5. Armstrong, R. A. & McGehee, R. *Am. Nat.* **115,** 151–170 (1980).
6. Volterra, V. *Nature* **118,** 558–560 (1928).
7. Tilman, D. *Resource Competition and Community Structure* (Princeton Univ. Press, 1982).

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