Linkage of the shear features to flow and fragmentation dynamics is more difficult and will require an expanded experimental and simulation basis. Nevertheless, recent experimental studies of the fragmentation of tube pumices at high temperature and pressure indicate that stresses of the order of several megapascals are sufficient to overcome the strength of these volcanic materials[30]. Such stresses should be easily achievable in explosive eruptions where the strain rate criterion is likely to be the deciding factor in the ease of fragmentation. Those experiments[30], in which fragmentation is demonstrably brittle, also generate tube pumice fragments with characteristic terminations at 90° and 45°–60° to the tube elongation. Shear bands are not seen in those single-stress-pulse experiments;this leads us to propose a multiple-stress-pulse origin for the shear bands observed here in Ramadas pumice.

Thus, the textures observed in the tube pumices from Ramadas are consistent with the proposal that the bubble stretching, bubble shearing and fragmentation of this pumice have occurred under strain rates that correspond to viscous, viscoelastic and brittle response regimes of the magma, respectively. Tube pumices are common products of explosive eruptions of silicic magmas, frequently appearing together with spherical pumices. Such shear bands have also been observed in phonolitic pumice indicating that eruptive conditions, not chemistry, control their generation. Further experimental and theoretical work is needed to quantify these aspects of magma fragmentation in order to understand one of the most enigmatic aspects of volcanic eruptions. ☐

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Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments

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Ecological theory predicts that stable populations should yield to large-amplitude cycles in richer environments[1–3]. This does not occur in nature. The zooplankton *Daphnia* and its algal prey in lakes throughout the world illustrate the problem[4–6]. Experiments show that this system fits the theory's assumptions[7–9], yet it is not destabilized by enrichment[6]. We have tested and rejected four of five proposed explanations[10]. Here, we investigate the fifth mechanism: inedible algae in nutrient-rich lakes suppress cycles by reducing nutrients available to edible algae. We found three novel results in nutrient-rich microcosms from which inedible algae were excluded. First, as predicted by theory, some *Daphnia*-edible algal systems now display large-amplitude predator-prey cycles. Second, in the same environment, other populations are stable, showing only small-amplitude demographic cycles. Stability is induced when *Daphnia* diverts energy from the immediate production of young. Third, the system exhibits coexisting attractors—a stable equilibrium and large-amplitude cycle. We describe a mechanism that flips the system between these two states.

Analyses of many natural populations show that *Daphnia* strongly suppresses its edible algal food supply and thus *Daphnia* density is, in turn, limited as a result of reduced fecundity[4,5,10]. We compared[10] observed edible algal equilibrial densities, in lakes covering a wide range of nutrient levels, with algal densities predicted by a well parameterized model based on *Daphnia* energetics. We rejected four explanations for the absence of large-amplitude predator–prey cycles (predator-dependent functional response[11], inedible algal interference[5], density-dependent[12] or productivity-dependent herbivore mortality[5,13]). We suggested that, instead, inedible algae compete successfully with edible algae in richer environments, thereby reducing the effective carrying capacity of *Daphnia*'s prey in productive environments. This would explain the mismatch between theory[14–16] and empirical results[6]. Similar mechanisms involving edibility of prey have been proposed for other communities[17]. It was impossible to test this idea using equilibrium relationships because inedible algal biomass in an enriched system[18] increases with productivity, and therefore obscures its effect. We therefore examined *Daphnia*-edible algal dynamics in nutrient-rich environments from which inedible algae were completely excluded.

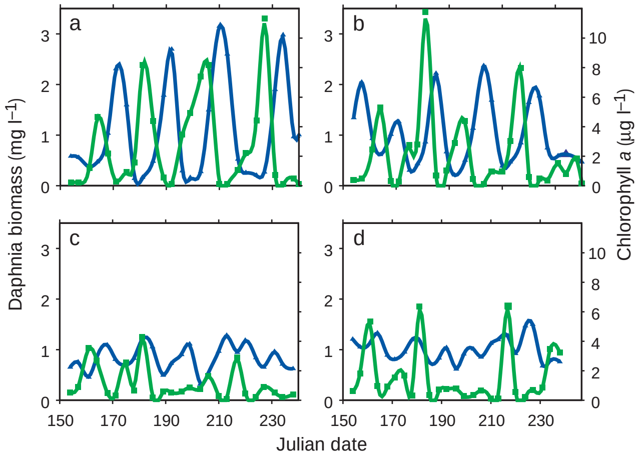

Figure 1 Large- and small-amplitude cycles in the same global environment. Population dynamics of *Daphnia* (blue triangles) and their edible algal prey (green squares) in four nutrient-rich systems from one treatment. The solid lines are spline fits to the time series (d.f., degrees of freedoms 20). **a**, **b**, Examples of large-amplitude predator–prey cycles. **c**, **d**, Examples of small-amplitude stage-structured cycles. The initial biomass of the replicates is similar. *Daphnia* biomass is calculated from estimates of density and size-structure, using length–weight relationships measured for the clone used in the experiment. Algal biomass is measured as chlorophyll *a* concentration.

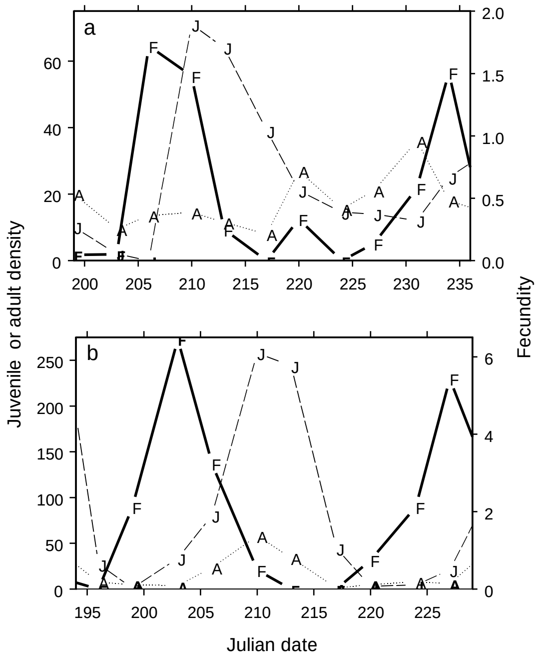

Figure 2 Suppression of *Daphnia*'s fecundity in predator–prey cycles and stage-structured cycles. In stage-structured cycles (**a**), *Daphnia*'s fecundity (F = eggs per adult) is suppressed primarily by the over-production of juveniles (individuals <1.4 mm in length), whereas both juveniles (J) and adults (A) effect suppression in predator–prey cycles (**b**). Juveniles and adults co-vary positively during the predator–prey cycles, but not in the stage-structured cycles.

We achieved this manipulation in a series of replicate microcosms containing diverse plankton communities (bacteria, edible algal species, *Daphnia pulex*) minus inedible algae. In enriched systems containing inedible algae, our observations from lakes[4,6], mesocosm experiments[6], and two sets of new experiments (data not shown; E.M. *et al.*, manuscript in preparation), have shown that *Daphnia*-edible algal dynamics do not display large-amplitude cycles. These systems are stable and can display stage-structured small-amplitude cycles. In contrast, results from our nutrient-rich microcosms without inedible algae reveal new features of the dynamics. First, as predicted by theory, *Daphnia* and their algal prey can indeed display large-amplitude predator–prey cycles at high nutrient levels and in the absence of inedible algae (Fig. 1). Fluctuations in *Daphnia* biomass exceeded a factor of five between peaks and troughs, with densities of more than 400 individuals per litre at the zenith of the cycles. Four systems in total exhibited this type of cycle. These large-amplitude cycles have never been observed before in the *Daphnia*–algal system. Second, under the same global environmental conditions (Fig. 1), some (6) of the populations display small-amplitude cycles (maximum/minimum *Daphnia* biomass less than 2). The difference in dynamics is not merely quantitative (that is, differing amplitudes); the two types are also characterized by differences in demography (Fig. 2). In the large-amplitude predator–prey (PP) cycles, juvenile and adult *Daphnia* fluctuate in synchrony ($P < 0.05$ cross-correlation time-series analysis) and suppression of fecundity results from increases in both juvenile and adult densities. By contrast, the small-amplitude cycles are stage-structured (SS) with a negative covariance between juveniles and adults, and fecundity suppression occurs as a result of the over-production of juveniles[4]. Thus large changes in amplitude and their demographic structure are distinguishing characteristics of the cycles.

This system appears to have two coexisting attractors, one associated with SS cycles and the other with PP cycles. This conclusion is reinforced by additional results from the first experiment: more than half of the systems (12 of 22) showed the two classes of dynamics in sequence (Fig. 3). Of these, eight of the

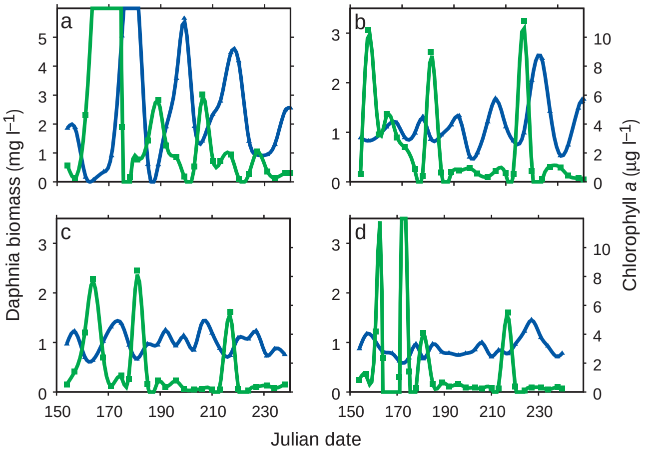

Figure 3 Systems can switch between large-amplitude and small-amplitude cycles. Population dynamics of *Daphnia* (blue triangles) and their edible algal prey (green squares) in four nutrient-rich systems from one treatment. The solid lines are spline fits to the time series (20 d.f.). **a**, **b**, Examples of systems displaying transitions from large-amplitude predator–prey cycle to stage-structured cycle (**a**) and small-amplitude cycle to large-amplitude predator–prey cycle (**b**). **c**, **d**, Systems with similar initial conditions from the same treatment that do not switch dynamics.

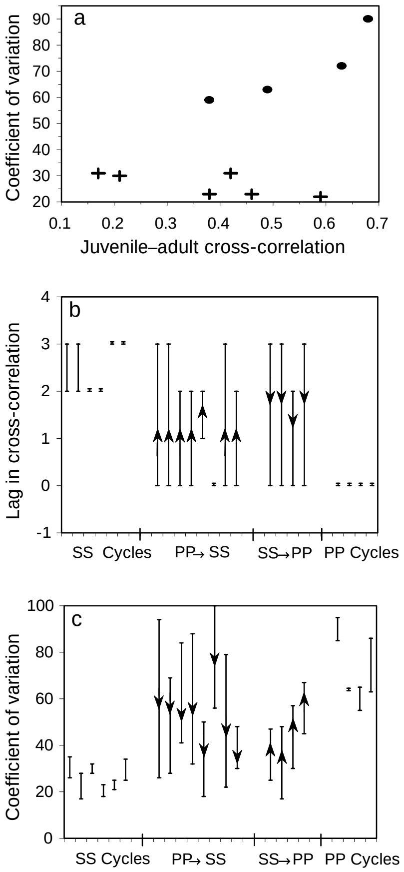

Figure 4 Detecting the different types of cycle. **a**, Shown is the difference between stage-structured cycles (SS) and predator–prey cycles (PP). SS cycles (crosses) have both a low coefficient of variation (reflecting a small amplitude) and peak values of cross-correlation coefficients between juveniles and adults occurring at a phase shift of three sampling periods (10–11 day temporal lag; see Fig. 2a). PP cycles (solid circles) have large amplitude, and juveniles and adults co-vary positively at zero lag (the peak value of the cross-correlation coefficient is at zero lag; see Fig. 2b). **b**, **c**, Shown is a comparison of these features for the first half of each series with the second half of the series. The horizontal bars show the starting and ending values; the lines and arrows show the magnitude and direction of the change that occurs between the first and second half of each series.

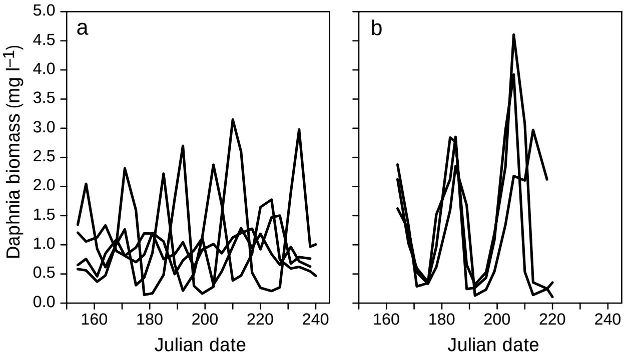

Figure 5 Energy channelling towards asexual reproduction destabilizes dynamics. **a**, Dynamics of replicate *Daphnia* populations illustrating that the replicates are asynchronous in time. **b**, Dynamics of the *Daphnia* populations in which energy channelling towards asexual reproduction is maintained by swapping adult females producing ephippial resting eggs with similarly sized females carrying asexual eggs.

systems showed PP cycles giving way to SS cycles, and four showed SS cycles giving rise to PP cycles (Fig. 4), based on comparing changes in both temporal variation and demographic correlations between juveniles and adults for the first and second half of each *Daphnia* series. As far as we know, this is the first experimental demonstration of coexisting attractors.

Why do only four of these populations show continuing large-amplitude cycles? Unless these systems are different from those analysed previously[4,6,10], the cause is unlikely to be direct density-dependence of *Daphnia*'s vital rates. The alternative is some mechanism that temporarily decouples *Daphnia*'s dynamics from the algal dynamics, and hence stabilizes the interaction, when food is scarce. One possibility is that in the more stable systems *Daphnia*'s rate of increase was reduced by the production of energy-intensive resting eggs (ephippia) that drop to the bottom and do not contribute to population growth. A variable fraction of the *Daphnia* population may produce ephippia in response to declining food supply, so ephippial production could prevent subsequent over-exploitation of the algal population and hence damp the large-amplitude cycle. It is well known that *Daphnia* can display alternate modes of reproduction in response to different environmental stimuli[19] such as declining food per head, but the dynamical consequences of this feature have never been examined experimentally. We established that this mechanism operates in the following experiment.

We experimentally removed ephippia-producing females from one set of populations, replacing them with the same number of asexually-reproducing gravid females. Figure 5a shows the dynamics of replicate *Daphnia* populations where the energy channelling was not manipulated; the waxing/waning of the populations is not coincidental, which eliminates the possibility that common environmental variability drives the cycles. Replicate *Daphnia* populations where energy channelling was artificially directed to asexual reproduction (that is, away from resting egg production) displayed even larger-amplitude predator–prey cycles (Fig. 5b) with no tendency to show small-amplitude fluctuations or demography characteristic of the stage-structure cycles. Thus, ephippial production is one mechanism that can suppress predator–prey cycles at high nutrient levels in the absence of inedible algae.

We draw three conclusions with broad implications. First, given an environment that matched the theory, the *Daphnia*–algal system displayed large amplitude predator–prey cycles. We conclude that simple consumer–resource theory, that predicts such cycles in productive environments, is the appropriate starting point for investigations of population dynamics. Second, inedible algae may well suppress these inherent predator–prey cycles in natural waters. Competitors or other drains on resources may also explain stable consumer–resource interactions in other natural communities. Finally, ephippial production, which is stabilizing, is only one example of a stabilizing life-history feature that uncouples consumer dynamics from a temporarily scarce food supply. Other organisms respond to low resource density by shutting off reproduction and surviving better, which has a similar effect[20]. The identification of uncoupling mechanisms that cause natural populations to maintain stability in enriched environments is a significant challenge for population ecologists. ☐

Methods

Dynamics of *Daphnia pulex* and edible algae were studied in 22 replicate systems under a 12 h light/12 h dark cycle at 22.0 ± 0.3 °C. Additionally, three control tanks were used to estimate the edible algal carrying capacity in the absence of *Daphnia*. Each 20 litre tank was filled with ultra-violet-sterilized water from Glenmore Reservoir, Alberta (pH 8.5). An edible algal 'cocktail' was created from stock cultures: *Selenastrum capricornum* (University of Toronto Culture Collection number 37), *Scenedesmus obliquus* (UTCC no. 5), *Mallomonas papillosa* (UTCCMP), *Ankistrodesmus convolutus* (UTCC no. 304), *Rhodomonas minuta* (UTCC no. 34), *Chlamydomonas reinhardtii* (University of Texas Culture Collection number 90), *Cosmarium* sp. (UTEX), *Cryptomonas erosa* (Freshwater Institute, Winnipeg) and added to each tank. Nutrient additions (KH_2PO_4, $NaNO_3$, $Ca(NO_3)_2{\cdot}4H_2O$) were based on empirical relationships[18] to yield an edible algal carrying capacity exceeding 3.0 mg carbon per litre (see below). After 7 days, the water from all tanks was mixed thoroughly to standardize algal initial conditions. Over the following 7 days, a fixed number of individually sized female *Daphnia pulex* drawn from a single-clone stock population was added to each tank to make starting conditions as uniform as possible.

Each tank was sampled twice weekly. Two replicate 1-litre water samples were drawn; gently filtered onto a 35-μm mesh that was kept moist in a Petri dish. All *Daphnia* individuals in the sample were enumerated and sized, and then gently washed back into their tank. Sampling with replacement ensures that *Daphnia* death rates *per capita* were not shifted in parameter space. *Daphnia* biomass was calculated using density estimates for each size class, along with dry weight of individuals in each size class from length–weight relationships measured for the clone used in the experiment. Algal samples were filtered onto Whatman glass microfibre filters (GF/C), and frozen for later analysis following standard acetone extraction and fluorometric determination of chlorophyll *a* concentrations[18]. Samples preserved with Lugol's solution[18] were inspected using an inverted-phase microscope to ensure that no inedible algal species invaded the tanks. Total phosphorus and soluble reactive phosphorus levels were routinely monitored along with biweekly measurements of pH and water hardness. Phytoplankton in replicate tanks with no *Daphnia* added did not display cyclic fluctuations.

To ensure no alternative food supply (such as algal or bacterial wall growth) was available for *Daphnia* in these nutrient-rich environments, all surfaces of the tanks were scraped daily for the entire duration of the experiments, and detrital material was vacuumed off the bottom every three days and treated to break down the material. The sample was ground using a high-speed micro-tissue grinder (Ultra Turrax Tissue Grinder, Staufen, Germany), sonicated for 20 min, and microwaved at high power for 3–5 min. The water sample was then cooled to the tank temperature and added back to the original tank. These procedures (scraping and regenerating bottom material) were effective in eliminating any wall growth, and any potential sink of organic material on the bottom of each tank.

Both simple biomass models[8,21] and stage-structured predator–prey models[7] parameterized using independent physiological data for *Daphnia* predict that large-amplitude prey-escape cycles should occur once the edible algal carrying capacity exceeds levels of approximately 0.2 mg carbon l^{-1}. Levels of nutrient enrichment were chosen[18] to yield edible algal carrying capacities of more than 15 times that level (3.0 mg carbon l^{-1}), thus ensuring that the systems were placed deep in the parameter space that predicts predator–prey limit cycles.

To assess changes in dynamics between the two types of cycles (predator–prey and stage-structured) we compared two statistics—one describing the amplitude and the other describing the covariance of juveniles and adults. The coefficient of variation in *Daphnia* biomass (standard deviation/mean biomass) provides an indication of the relative magnitude of temporal variability as influenced by cycle amplitude, and the magnitude of cross-correlation coefficients between juvenile and adult biomass, estimated while one of the series is shifted (or lagged) in time, can be used to characterize cycle demography. As the demography of stage-structured cycles suggests (Fig. 2a), the cross-correlation between juveniles and adults is weak (in most cases slightly negative) for unlagged series and maximum when the juvenile series is shifted forward in time by approximately three sampling intervals (10–11 days). In predator–prey cycles (Fig. 2b), juveniles and adults co-vary positively, so that the maximum positive correlation occurs without any shifts in the series (that is, with zero lag). Thus, the stage-structured cycles have small coefficients of variation and maximum cross-correlations with a shift of 10–11 days (a lag of three sampling intervals), while the predator–prey cycles have large coefficients of variation and maximum cross-correlation coefficients at zero lag (Fig. 4a). Lags and coefficients of variation for particular systems can be assessed by comparing data from Fig. 4, b and c.

To test whether the production of ephippial resting eggs reduces the amplitude of predator–prey cycles, we set up six additional 20-litre tanks matched in pairs. Inoculations of tanks followed the protocol outlined above, except that the inoculation date for one tank in each pair was staggered by 2 weeks to ensure that the dynamics were out of phase. The exact cues for ephippial egg production are unclear, but appear to be related to rapidly declining food availability. Staggering tanks by 2 weeks helps to create donor tanks that contain asexual ovigerous females. We manipulated the realized energy channelling to asexual reproduction by swapping individual *Daphnia* that had produced ephippial eggs with ovigerous females from the donor tank of the pair. Tanks were checked every day and when a female carrying a resting egg was found, she was removed from the tank and replaced with a female of similar size carrying asexual non-resting eggs. Replacement with similarly sized individuals ensures that the numerical response is maintained without modifying the population-level ingestion rates. The tanks were sampled as described above. Experiments lasted until the supply of egg-bearing females in donor tanks was exhausted.

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Ghrelin is a growth-hormone-releasing acylated peptide from stomach

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Small synthetic molecules called growth-hormone secretagogues (GHSs)[1–3] stimulate the release of growth hormone (GH) from the pituitary[4,5]. They act through GHS-R, a G-protein-coupled receptor for which the ligand is unknown. Recent cloning of GHS-R[6,7] strongly suggests that an endogenous ligand for the receptor does exist and that there is a mechanism for regulating GH release that is distinct from its regulation by hypothalamic growth-hormone-releasing hormone (GHRH)[4,5]. We now report the purification and identification in rat stomach of an endogenous ligand specific for GHS-R. The purified ligand is a peptide of 28 amino acids, in which the serine 3 residue is *n*-octanoylated. The acylated peptide specifically releases GH both *in vivo* and *in vitro*, and *O-n*-octanoylation at serine 3 is essential for the activity. We designate the GH-releasing peptide 'ghrelin' (*ghre* is the Proto-Indo-European root of the word 'grow'). Human ghrelin is homologous to rat ghrelin apart from two amino acids. The occurrence of ghrelin in both rat and human indicates that GH release from the pituitary may be regulated not only by hypothalamic GHRH, but also by ghrelin.