LETTERS

Small-amplitude cycles emerge from stage-structured interactions in *Daphnia*–algal systems

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A long-standing issue in ecology is reconciling the apparent stability of many populations with robust predictions of large-amplitude population cycles from general theory on consumer–resource interactions[1]. Even when consumers are decoupled from dynamic resources, large-amplitude cycles can theoretically emerge from delayed feedback processes found in many consumers[2,3]. Here we show that resource-dependent mortality and a dynamic developmental delay in consumers produces a new type of small-amplitude cycle that coexists with large-amplitude fluctuations in coupled consumer–resource systems. A distinctive characteristic of the small-amplitude cycles is slow juvenile development for consumers, leading to a developmental delay that is longer than the cycle period. By contrast, the period exceeds the delay in large-amplitude cycles. These theoretical predictions may explain previous empirical results on coexisting attractors found in *Daphnia*–algal systems[4,5]. To test this, we used bioassay experiments that measure the growth rates of individuals in populations exhibiting each type of cycle. The results were consistent with predictions. Together, the new theory and experiments establish that two very general features of consumers—a resource-dependent juvenile stage duration and resource-dependent mortality—combine to produce small-amplitude resource–consumer cycles. This phenomenon may contribute to the prevalence of small-amplitude fluctuations in many other consumer–resource populations[6,7].

Incorporating size- or age-structured interactions into theory on the dynamics of biological populations has provided new insight into the causes of population fluctuations and patterns in natural systems. Theory on single-species dynamics reveals that interactions among life-history stages or age classes and the resultant feedback on demographic rates[2,8] can generate a diversity of cycle types. Many of these findings carry over to situations with indirect interactions among stages, for example through competition for food.

The range of possible mechanisms for explaining cyclic dynamics expands markedly once models include explicit interactions with other species. For example, stage-structure and explicit consumer–resource interactions can each destabilize an equilibrium, leading to population cycles[3,9–11]. Intuitively one might think that combining these sources of instability would enhance instability in dynamics. Here, we demonstrate that this combination does not simply increase the amplitude of cycles, but introduces new phenomena that arise from the interaction of the various sources of instability. We show that combining one of the most general life histories for a predator with consumer–resource dynamics produces new types of cycles that may help to explain the rarity of large-amplitude cycles in many systems.

Our approach combines theory on the dynamics of stage-structured populations of the herbivore *Daphnia pulex* and their algal prey with experiments conducted in microcosms to test mechanisms producing different types of cycles. By coupling small-volume flow-through systems to microcosms containing the *Daphnia*–algal populations, we measure the growth rate of individual herbivores experiencing food fluctuations set by the dynamic interactions unfolding in the microcosms, and compare these estimates to model predictions for different types of cycles.

Previous work[3,11,12] has identified three types of cycles that can emerge from stage-structured competition for food in a population being reared under semi-chemostat conditions. Which cycles are found depends on the relative feeding rates of juveniles and adults, fecundity, and relative ability to withstand starvation of juveniles and adults. Here we add to the previous models two general features of natural consumer–resource systems: density-dependent dynamics of resources and a saturating functional response for the consumers. This broadens the range of potential outcomes, including previously undiscovered types of cycle, and defines new empirical tests using consumer–resource systems, reported below. Our analysis exploits a new numerical bifurcation approach for stage-dependent delayed integro-differential models that facilitates resolution of regions of hysteresis, and allows us to identify robust properties of the different types of cycles that emerge.

Our stage-structured model for resource–consumer dynamics (Box 1 and Supplementary Information) is motivated by the extensive work on dynamics of *Daphnia* populations interacting with algal prey. Juvenile and adult predators (stages of *Daphnia*) differ in their feeding rates, energy allocation patterns, and resource-dependent mortality. We assume that the prey population is unstructured and prey cannot evolve. The resulting model that describes interactions of a 'structured' predator population with a simple prey has received relatively little previous attention[13], in contrast with a large body of theory that includes 'structure' in the prey or resource[14–16], used in studies of host–parasitoid interactions or disease dynamics[2]. Yet it contains the key features of many systems where prey complexity can be controlled.

Empirically, the *Daphnia*–algal system displays an extraordinary range of dynamics that includes fluctuations around a stable equilibrium, and a combination of small- and large-amplitude cycles[4,6,7,17]. As predicted by previous theory, large-amplitude consumer–resource cycles can be found under nutrient-rich conditions, the so-called 'paradox of enrichment'[4]. However, in these same environmental conditions, small-amplitude cycles not predicted by previous theory were present and there is evidence that these periodic attractors coexist[4,5]. This suggests that there is some fundamental feature of this system that produces these small-amplitude cycles even under nutrient-rich conditions where only large-amplitude cycles are expected.

Bifurcation analysis of the stage-structured predator–prey model parameterized for the *Daphnia*–algal system (Fig. 1 and Supplementary Information) reveals new dynamics as the algal carrying capacity is increased. In environments with low algal carrying

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Box 1 | A structured model of the dynamics of a consumer and its resource

Population balance equations are shown for processes and interactions, along with equations for juvenile development and survival. The top three equations describe the dynamics of resource (F) and juvenile (J) and adult (A) consumers, respectively. The dynamics of juvenile development time and juvenile survival are determined by integral equations (bottom two equations). Further model details, parameter definitions and estimation, and bifurcation analysis is provided in Supplementary Information.

Resource dynamics:

$$\frac{dF(t)}{dt} = \overbrace{qF(t)\left(1 - \frac{F(t)}{k}\right)}^{\text{logistic resource growth}} - \overbrace{I_J \frac{F(t)}{F(t) + f_h} J(t)}^{\text{ingestion by juveniles}} - \overbrace{I_A \frac{F(t)}{F(t) + f_h} A(t)}^{\text{ingestion by adults}}$$

Juvenile dynamics:

$$\frac{dJ(t)}{dt} = \overbrace{\frac{\chi I_A \sigma_A}{\gamma} \frac{F(t)}{F(t) + f_h} A(t)}^{\text{birth}} - \overbrace{\frac{\chi I_A \sigma_A}{\gamma} \frac{F(t)}{F(t) + f_h} A(t - \tau(t)) S(t)}^{\text{maturation}}$$
$$ - \overbrace{\frac{\mu_J}{I_J \sigma_J} \frac{F(t) + f_h}{F(t)} J(t)}^{\text{juvenile mortality}}$$

Adult dynamics:

$$\frac{dA(t)}{dt} = \overbrace{\frac{\chi I_A \sigma_A}{\gamma} \frac{F(t)}{F(t) + f_h} A(t - \tau(t)) S(t)}^{\text{maturation}} - \overbrace{\frac{\mu_A}{I_A \sigma_A} \frac{F(t) + f_h}{F(t)} A(t)}^{\text{adult mortality}}$$

$$\frac{w}{\sigma_J I_J} = \overbrace{\int_{t - \tau(t)}^{\tau} \frac{F(\xi)}{F(\xi) + f_h} d\xi}^{\text{juvenile development}}$$

$$S(t) = \overbrace{\exp\left(-\frac{\mu_J}{I_J \sigma_J} \int_{t - \tau(t)}^{\tau} \frac{F(\xi) + f_h}{F(\xi)} d\xi\right)}^{\text{juvenile survival}}$$

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capacity the model has a stable equilibrium, as is found in unstructured predator–prey models. Increasing algal carrying capacity beyond ~0.3 mg C l^{-1}, we encounter a bifurcation near which two cycles appear: a new small-amplitude resource–consumer cycle and, via a subcritical fold of periodic orbits, a large-amplitude resource–consumer cycle. Notably, the two cycles are coexisting attractors over a broad range of algal carrying capacities corresponding to nutrient-rich environments (Fig. 1a). Bifurcation analysis also reveals that the cycles are separated by an unstable limit cycle. This causes the transition between the large- and small-amplitude cycles to occur abruptly (Supplementary Information), which is a common feature of laboratory and field experiments.

The two types of cycles can be distinguished by a key diagnostic feature[18,19]: the ratio of the cycle period to juvenile stage duration (hereafter referred to as the delay). This is illustrated in Fig. 1b–e. In the large-amplitude cycles (Fig. 1b, c), the period exceeds the delay, a property that is characteristic of previously studied resource–consumer systems. By contrast, in the small-amplitude cycle (Fig. 1d, e), the juvenile stage duration is always larger than the cycle period, yielding cycles with a period/delay ratio less than one. The small-amplitude cycles are caused by the interaction between the instability caused by the resource–consumer interaction and the resource-dependent juvenile stage duration in the consumer *Daphnia*. Numerical experiments (not shown) established that removing the type II functional response that is the source of the instability in nutrient-rich algal environments, decoupling the prey dynamics by replacing density-dependent growth with semi-chemostat dynamics,

or fixing the juvenile stage duration at time periods longer than the cycle period, all cause the coexisting attractors to disappear.

Our structured model thus apparently explains one of the major empirical results reported previously[4]: the *Daphnia*–algal system can display both large- and small-amplitude cycles under the same nutrient-rich environment. This hypothesis can be rigorously tested by measuring the period/delay ratio in dynamic interacting populations. There are some major challenges in measuring the development time of individuals (stage durations) non-destructively in a population where individuals cannot be marked to follow their growth or performance. Some attempts to dye individual *Daphnia* have been tried, but feeding performance is affected. We overcame these challenges by designing new bioassay experiments whereby we can measure growth of individuals in populations experiencing food dynamics set by the interaction between predators and prey (Fig. 2 and Supplementary Information). Estimates of growth rates from these bioassays were validated through comparisons with 'artificial cohort' experiments (Supplementary Information).

Replicate *Daphnia*–algal systems display the same collection of dynamics described previously[4]. Under common environmental conditions of nutrient enrichment, temperature and light levels, the predator–prey systems display either large-amplitude or small-amplitude cycles, with transitions between the attractors (Fig. 2 and Supplementary Information). Consistent with dynamics presented previously[4], small-amplitude cycles predominate (~80% of the replicates) when resting egg production is not manipulated. Large- and small-amplitude cycles can be distinguished using two probes: variation in *Daphnia* egg density and in algal biomass (Fig. 3 and Supplementary Information). The cycle periods for these dynamics average 21.4 days with lower and upper 95% prediction intervals of 14.5 and 28.2, respectively (Fig. 4). The bioassay experiments
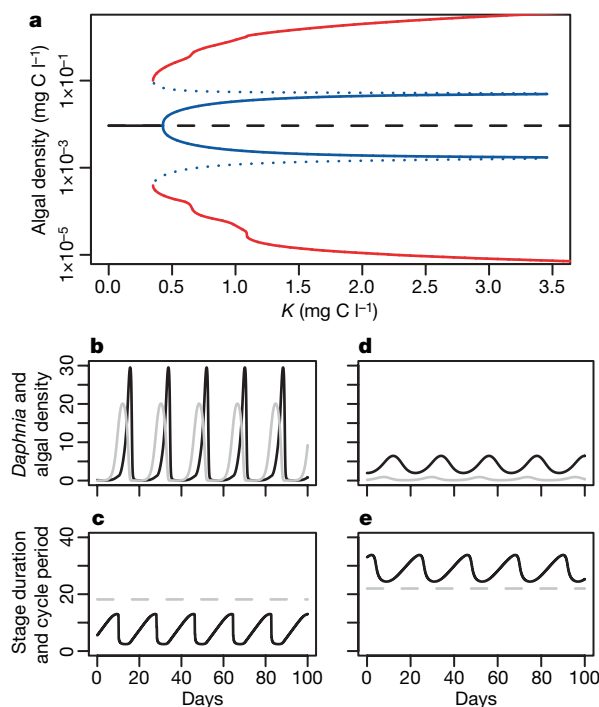
Figure 1 | Multiple limit-cycle attractors in the structured predator–prey model. a, Bifurcation diagram showing the transition from a stable steady state (solid black line) to a region of multiple coexisting limit cycles with increasing algal carrying capacity K (mg C l^{-1}). The range in algal density (mg C l^{-1}) over a cycle is shown. Stable small-amplitude cycles (blue) and large-amplitude cycles (red) are shown, separated by an unstable cycle (dashed blue line). **b**, **d**, Large- and small-amplitude cycles of *Daphnia* (black) and algae (grey). **c**, **e**, Graphs showing a key diagnostic feature: the relationship between cycle period (dashed line) and the stage duration of *Daphnia* (solid line) during large- (**c**) and small-amplitude cycles (**e**).
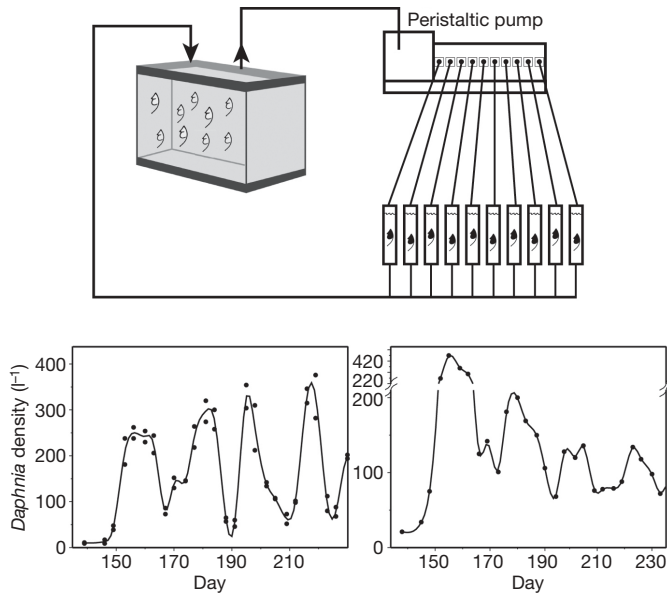
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Figure 2 | Bioassay experiments for resource–consumer systems.
Distinguishing among causes of dynamics often requires observations on the
performance of individuals in interacting populations. For many
populations, individuals cannot be marked or followed, which restricts the
estimation of key rates. Using flow-through systems coupled to microcosms
(upper panel), we can estimate these rates for individuals. As the dynamics
unfold in the microcosm, water containing algal prey flows through the vial
housing an individual whose growth and reproduction can be observed
during cyclic dynamics. Lower panels illustrate examples of large- and small-
amplitude dynamics from which individuals were drawn to estimate length-
specific growth rates.

Figure 3 | Egg density dynamics during cycles. Dynamics of egg density in
Daphnia populations displaying large-amplitude cycles (**a**) and small-
amplitude cycles (**b**–**d**). The red line shows large-amplitude cycles as
characterized by the fecundity probe (see Supplementary Information). The
blue line shows small-amplitude cycles. The coefficient of variation (CV) in
algal biomass is also presented.

(Fig. 2) show that individual *Daphnia* grow at different rates in the
large-amplitude and small-amplitude cycles (Fig. 4a,b), and thus
the development time bears a fundamentally different relationship
with the cycle period. The juvenile stage duration of individual
Daphnia developing in the large-amplitude cycle is on average
7.2 days, yielding a cycle period/delay ratio of ~3. During the
small-amplitude cycles, juvenile stage durations were estimated to
be 42 days (lower 95% prediction limit 37 days; upper limit 48 days),
which is significantly longer than the cycle period, producing a frac-
tional period/delay ratio. Independent experiments that estimate the
length-specific growth rates of juvenile *Daphnia* in populations at
equilibrium (Supplementary Information) yield comparable values
to those obtained from the individual bioassay experiment (Fig. 4b).
Thus, two key predictions from theory were supported by results
from these new experiments. First, coexisting attractors were
observed in the same enrichment environment. Second, the stage
durations of individual *Daphnia* were significantly shorter than the
cycle period in the large-amplitude cycle, and significantly longer
than the cycle period in the small-amplitude cycle (Fig. 4). To our
knowledge, this is the first empirical support for cycles with a frac-
tional period/delay ratio.

Theory on the dynamics of structured populations has provided
new explanations for cycles and has enabled investigators to identify
mechanisms giving rise to cycles of various types. Our experiments
and measurements of individual performance in populations reveal a
new type of small-amplitude cycle that arises from the interaction of
instability in the predator–prey interaction causing fluctuations in
resource density and a dynamically varying life-history feature of the
predator. This interaction constrains the amplitude of the cycle even
under nutrient-rich conditions where large-amplitude cycles prevail
in either unstructured predator–prey models (for example,
MacArthur–Rosenzweig models) or structured models with fixed
stage durations for predators. The new cycles require the interaction
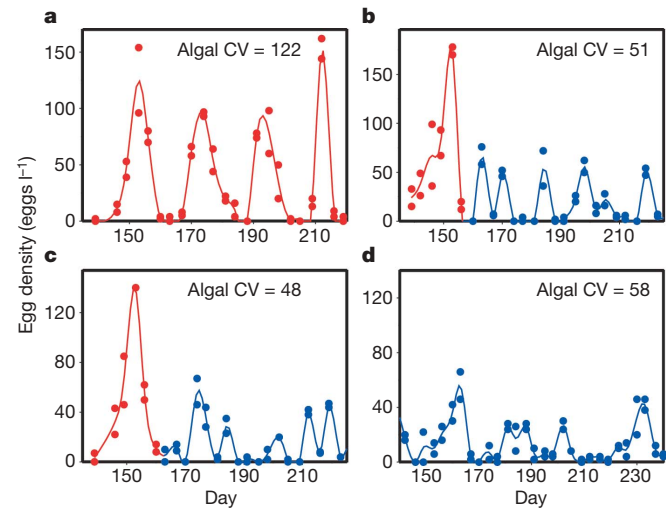of effects to emerge.

Simple models containing nonlinearities in biological processes can
produce phenomena such as alternative stable states or coexisting
attractors, complex transients as dynamics move from the influence
of one basin of attraction to another, and a range of cycles. A key
question is whether these 'rich' results from nonlinear models actually
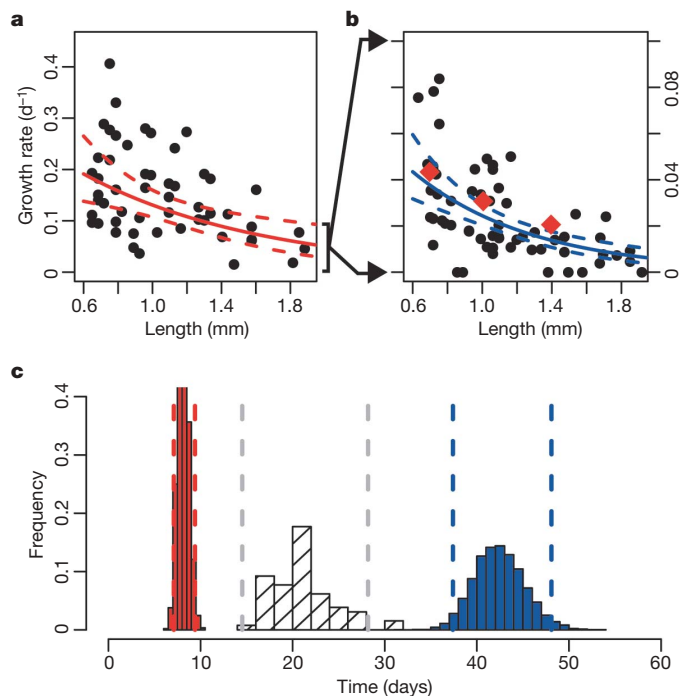provide fundamental insight into the dynamics of ecological

**Figure 4 | Comparison of individual growth rates in large- and small-
amplitude cycles.** Length-specific growth rates in large-amplitude cycles
(**a**) and small amplitude cycles (**b**) yield different estimates of juvenile stage
duration (**c**; Supplementary Information). Diamonds show estimates from
artificial cohort experiments (Supplementary Information). In large-
amplitude cycles, juvenile stage duration (**c**, red) is significantly less than
cycle periods (**c**, grey). In small-amplitude cycles, the juvenile duration is
significantly greater than the cycle period (**c**, blue). Dashed lines show 95%
prediction intervals (Supplementary Information).

systems[20]. As we confront model predictions with well-studied experimental systems, where direct measurements of rates and manipulation of environmental conditions can be coupled quantitatively to models, more often than not, model expectations are upheld and general processes underlying the dynamics are being revealed. Structured population models of ecological interactions in particular are capturing the essence of dynamics of several 'model' systems (for example, *Tribolium*[21], rotifers[22], *Daphnia* and *Bosmina*[12], California redscale[2], Arctic char and brown trout[23]). These models predict the occurrence of different dynamics as we move from one environment to the next, and identify key processes that lead to the different types of fluctuations. Although the models are costly to parameterize, the mechanisms apply to a broad range of organisms that share general life-history features, such as resource-dependent development rates and stage-specific interactions dictated by allometric scaling of energy acquisition and expenditure. Using these confrontations between theory and experiments, we are discovering important linkages between physiological ecology and life-history traits that explain dynamics of interacting populations in different environments.

METHODS SUMMARY

Daphnia–algal dynamics. Microcosms were established using techniques described previously[4] and maintained in a constant environment at 24 °C with a 14:10 light cycle. Replicates were inoculated with a single clone of *Daphnia pulex* used in the previous experiments on food-dependent growth and reproduction[24]. Initial nutrient enrichment with inorganic phosphorus and nitrogen placed the algal carrying capacity deep in parameter space where large-amplitude predator–prey cycles are predicted by theory[4]. Techniques for nutrient regeneration, non-destructive sampling of *Daphnia* populations, and chlorophyll analysis were carried out as described previously[4]. Single clones of each algal species from the University of Toronto Culture Collection were used. Biweekly samples were taken and no manipulations of *Daphnia* egg production were performed. An accurate estimate of periodicity in the population dynamics can be obtained by measuring the time period between reproduction bursts of fecund females in the population (Supplementary Information). Dynamics from 24 tanks were used to estimate this periodicity to compute the distribution shown in Fig. 4c.

Bioassay experiments. To estimate stage duration, we drew individuals of various sizes from *Daphnia* populations executing different types of cycles (large-amplitude and small-amplitude cycles) (Supplementary Information). One individual was placed in each flow-through vial, and each peristaltic pump could supply and remove water and food for ten replicate vials. A typical (1 mm) juvenile *Daphnia*, living at 24 °C, can filter at most $2 \, \mathrm{ml \, h^{-1}}$ (ref. 24). The flow rate through each vial was $40 \, \mathrm{ml \, h^{-1}}$, ensuring that the individual could not significantly alter the food concentration. Each individual experienced the same food concentration as its counterparts in the population of *Daphnia* in the microcosm. Individuals were drawn from populations during the period of egg production and followed for a minimum of 3 days, for individuals <1.4 mm, and 4 days for individuals >1.4 mm. An individual contributed only one estimate (that is, no repeated measures). Length-specific growth rates were calculated as $\ln(L_t/L_0)$/time and regressed against length (mm) using nonlinear regression. Using these regression equations, the juvenile stage durations and 95% prediction intervals were estimated by determining the time required to grow from the size at birth (0.69 mm) to the size at first reproduction (1.6 mm) (Supplementary Information).

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