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Deadly competition and life-saving predation: the potential for alternative stable states in a stage-structured predator–prey system

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Predators often undergo complete ontogenetic diet shifts, engaging in resource competition with species that become their prey during later developmental stages. Theory posits that this mix of stage-specific competition and predation, termed life-history intraguild predation (LHIGP), can lead to alternative stable states. In one state, prey exclude predators through competition (i.e. juvenile competitive bottleneck), while in the alternative, adult predators control prey density to limit competition and foster coexistence. Nevertheless, the interactions leading to these states have not been demonstrated in an empirical LHIGP system. To address this gap, we manipulated densities of cannibalistic adult cyclopoid copepods (*Mesocyclops edax*) and their cladoceran prey (*Daphnia pulex*) in a response-surface design and measured the maturation and survival of juvenile copepods (nauplii). We found that *Daphnia* reduced and even precluded both nauplii maturation and survival through depletion of a shared food resource. As predicted, adult copepods enhanced nauplii maturation and survival through *Daphnia* consumption, yet this positive effect was dependent on the relative abundance of *Daphnia* as well as the absolute density of adult copepods. Adult copepods reduced nauplii survival through cannibalism at low *Daphnia* densities and at the highest copepod density. This work demonstrates that predation can relax a strong juvenile competitive bottleneck in freshwater zooplankton, though cannibalism can reduce predator recruitment. Thus, our results highlight a key role for cannibalism in LHIGP dynamics and provide evidence for the interactions that drive alternative stable states in such systems.

1. Introduction

Many species shift ecological interactions over the course of ontogenetic development [1–4]. Continuous growth in body size, for example, allows the consumption of progressively larger food resources [5], while metamorphosis entails discrete physical and behavioural changes that drive diet differences among pre- and post-metamorphic stages [6,7]. As a result of such ontogenetic diet shifts, the juveniles of a variety of predatory species compete for resources with species that are simultaneously preyed upon by adults, a simple food web configuration termed life-history intraguild predation (LHIGP; figure 1). Predators involved in LHIGP may undergo a complete diet shift (i.e. juveniles and adults feed on separate resources; e.g. figure 1) or broaden their diet over ontogeny (i.e. adults continue to feed on the juvenile resource). Size- or stage-dependent interactions can lead to different long-term dynamics, including the types and ranges (in terms of system productivity, e.g.) of alternative stable states than in systems unstructured by body size or life-history stage [3,4,8]. While LHIGP is common in nature [2] and potentially important for the dynamics of human-harvested populations [9,10], theory has outpaced empirical work and there is limited empirical evidence [8,11–13] for the interactions that drive alternative stable states in such systems.
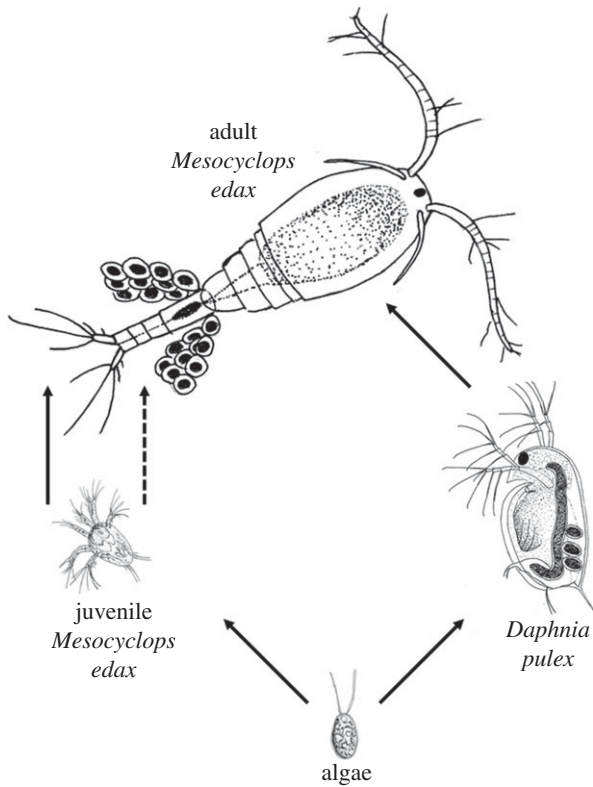
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Figure 1. Life-history intraguild predation food web configuration with study organisms (not drawn to scale). Arrows indicate pathways of energy flow throughout the system. Solid arrows depict feeding relationships (including cannibalism) while dotted line indicates the maturation of juvenile predators to the adult stage. Adult reproduction is omitted because egg-bearing females were removed in this study. Illustrations by V.H.W.R.

Theory suggests that the outcome of LHIGP and its effects on community dynamics are largely dependent on the balance of competition and predation [14,15]. In systems where predators exhibit a complete diet shift, no alternative stable states exist when the predator is competitively superior; dynamics are instead expected to follow a simple top-down food chain [14]. However, if the prey is competitively superior (as is often the case with fish: [16]), prey can limit the maturation of juvenile predators by depressing abundance of the shared resource (termed a juvenile competitive bottleneck). In this scenario, coexistence of predator and prey is only possible if adult predators become abundant enough to reduce the juvenile competitive bottleneck and increase predator recruitment (i.e. the cultivation effect: [9,14]). Thus competition-dominated versus predation-dominated dynamics can lead to alternative stable states in LHIGP systems [4,8,11,14,15].

Alternative stable states are only possible in complete diet shift LHIGP systems when two specific conditions are met: (i) prey have to be able to competitively exclude juvenile predators through resource competition (i.e. prevent recruitment to the adult stage) and (ii) a relative increase in adult predator density has to reduce prey density and increase predator recruitment [14,17]. While studies of fish communities have supported the basic premise that competitively dominant prey can reduce growth rates of juvenile predators [10,18,19], empirical evidence demonstrating a prey's ability to eliminate predator recruitment through resource competition is scant (but see [11,12]). Furthermore, the effects of changes in adult predator abundance, relative to the prey,

in regulating juvenile competitive bottleneck dynamics (condition (ii)) have received little attention. This represents a major gap in our understanding of LHIGP systems, because theory posits that strong top-down control is necessary to drive an alternative stable state in which predators coexist with their prey [14].

One additional factor that could influence top-down control (and thus the potential for alternative stable states) is cannibalism. Many predators that exhibit size-dependent predation (such as those engaged in LHIGP) are cannibalistic [16,20,21]. If adult predators are unselective in consuming heterospecific versus conspecific prey (i.e. feed according to their relative abundance), then adult predators should benefit juveniles by consuming prey at high relative prey densities. However, at low relative prey densities, cannibalism should further reduce juvenile predator recruitment, adding to the effects of the juvenile competitive bottleneck. Thus, the strength of cannibalism should be a major influence on LHIGP dynamics [20].

The purpose of this study was to test predictions of current theory on how adult predators and prey regulate predator recruitment in LHIGP systems with complete ontogenetic diet shifts. Specifically, we used a response-surface design to establish functional relationships between adult predator–prey densities and juvenile predator recruitment in a stage-structured zooplankton system (figure 1). In this system, the cannibalistic cyclopoid copepod (*Mesocyclops edax*) consumes the cladoceran prey (*Daphnia pulex*), which simultaneously competes with juvenile predators (nauplii) for a shared food resource (algae) (figure 1). This experiment allowed us to test the specific predictions required for the existence of alternative stable states in LHIGP systems: (i) competition for a shared resource between juvenile predator and prey that increases with prey density, reducing and ultimately preventing predator recruitment at high prey density and (ii) a relative increase in adult predator density that reduces competition and increases predator recruitment at high prey density. However, because of cannibalism, high predator densities can reduce or eliminate the positive effect of competitive release, and even reduce juvenile recruitment to the adult predator stage at low prey density.

In general, our results support these predictions: we demonstrate predator exclusion by the prey and provide some of the first experimental evidence for the importance of predation, including cannibalism, in mediating a complete diet shift LHIGP system. This work thus provides novel empirical insights into the capacity of LHIGP to drive alternative stable states predicted by theory [4,14,17].

2. Material and methods

(a) Study system

We examined the effects of competition and predation on LHIGP dynamics using a freshwater zooplankton system consisting of the cyclopoid copepod *M. edax* and the cladoceran *D. pulex* (figure 1). Zooplankton provide a tractable system that allows precise manipulation of predator and prey densities with high replication, and are thus ideal for examining the mechanistic basis of LHIGP. Both species frequently coexist in natural populations but have very distinct life histories. *Mesocyclops* exhibit an ontogenetic diet shift where larval copepods (nauplii) feed on algae before metamorphosing into primarily carnivorous

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pre-adults (copepodites: [22,23]). Owing to this diet shift, nauplii potentially compete with herbivorous zooplankton, such as *Daphnia*, which additionally serve as prey for adults [24–27] (figure 1). Furthermore, *Daphnia* are strong resource competitors within freshwater communities [28] and are substantially larger than nauplii, even as neonates. This probably makes *Daphnia* superior to nauplii in algae resource competition. In addition to consuming cladocerans, adult *Mesocyclops* cannibalize nauplii [22], a common feeding strategy across cyclopoid copepods [23,29]. Thus, this system meets the requisites for a potential juvenile competitive bottleneck (see also [30]) and allows examination of the effects of cannibalism on LHIGP.

We collected adult *Mesocyclops* from a small pond in Sam Houston National Forest, Texas using a plankton net thrown from shore. *Daphnia* came from a laboratory population (originating from a small pond in Huntsville, TX, USA) that had been maintained in filtered (1 μ) pond water for 3 years and fed regularly with *Spirulina* powder and laboratory-cultured *Scenedesmus obliquus* (a green alga) to maintain asexual reproduction.

(b) Experimental design

Our experiment was designed to test the effects of prey and adult predator densities on juvenile predator maturation and survival. Specifically, we manipulated the density of *Daphnia* (0, 3, 9, 18, 27, 36 individuals per 200 ml experimental unit) and adult *Mesocyclops* (0, 1, 2, 4, 8 individuals per 200 ml experimental unit) in an orthogonal design, resulting in 30 unique treatments. This experiment followed a response-surface design by factorially manipulating the densities of two species [31]. The experiment was blocked temporally and three blocks were run in total with 24 experimental units per block. In total, 12 of 30 treatments were replicated in each block (three replicates per treatment), while half of these 12 treatments were additionally replicated within a block, yielding a maximum of four replicates per treatment. Treatments with a single adult copepod were not replicated (predation effects were too variable at this adult density). This experiment was conducted from July to September 2015.

For each block, adult *Mesocyclops* (approx. 830 μm length) were collected from the field and brought back to the laboratory. Egg-bearing females were isolated and held in fresh pond water filtered through 60-μm nylon mesh (collected at the same time and from the same pond as *Mesocyclops* adults). On the following day, nauplii that hatched from eggs were isolated from adults to avoid cannibalism. This procedure was repeated on the second day to harvest nauplii from eggs that had not hatched on the first day. Thus, nauplii used in the experiment were 1–2 days old (approx. 80 μm length). All nauplii were held together in a single large 4 l beaker filled with 60 μm-filtered pond water.

Nauplii were added to 250 ml experimental beakers (containing 200 ml of fresh pond water filtered through 60 μm nylon mesh) on this second day at a density of 25 nauplii per beaker. The mesh size used to filter pond water removed *Mesocyclops* nauplii and larger organisms but retained smaller organisms (seston) including naturally occurring algae, which served as food for nauplii and *Daphnia* during the experiment. On the third day, adult copepods and *Daphnia* were added to beakers marking the start of the experiment. We also added 0.5 ml of a mixture of *Spirulina* powder and artificial pond water (Provosoli medium [22]: 100 mg *Spirulina* powder per 30 ml artificial pond water) to each beaker to provide an additional food source. Adult copepods used were the same females that nauplii were harvested from. Only copepods without external egg sacs were used to avoid adding additional nauplii. To minimize the possibility of parental recognition (i.e. females exhibiting cannibalistic preference towards non-offspring), adults were randomly assigned to beakers of nauplii from mixed-parentage. *Daphnia* were added to beakers in a balanced size-structure

(i.e. equal numbers of small, medium and large individuals) at each *Daphnia* density. *Daphnia* size classes were separated using a 700 μm mesh (to isolate large individuals), and a 440 μm mesh (to isolate medium individuals). Large *Daphnia* individuals always contained eggs or neonates in their brood chambers.

Trials lasted 6 days over which a temperature of 20°C and a 12 L : 12 D cycle was maintained. Every other day, 0.5 ml of the previously described mixture of *Spirulina* powder and artificial pond water was added to beakers. Once per day, each beaker was checked for egg-bearing and dead adult *Mesocyclops*. The number of egg-bearing and dead adults per beaker was recorded and these individuals were replaced with live females without eggs from remaining females used to collect nauplii. Egg-bearing females were replaced to avoid adding additional nauplii to beakers during the experiment. Adult female mortality was low (mean proportion of dead females per survey day ± 1 s.e. = 0.016 ± 0.003) throughout the experiment.

On the sixth and final day of the experiment, all remaining nauplii were counted and the stage (nauplius (pre-metamorphosis) or copepodite (post metamorphosis)) of each was recorded. Nauplii undergo complete metamorphosis, transitioning from the nauplius to the copepodite stage, which closely resembles adults in morphology but is smaller [22]. All *Daphnia* were isolated from beakers and preserved in 70% ethyl alcohol (following [32]) for later enumeration.

(c) Statistical analysis

(i) Predator recruitment

We examined the independent and potentially interactive effects of *Daphnia* and adult copepod density on nauplii maturation and survival using generalized linear mixed models (GLMM; lme4 package: [33]) in the statistical software R [34]. Separate models were constructed for maturation and survival data. Both maturation (final matured nauplii (copepodites)/initial nauplii per beaker) and survival (final nauplii + copepodites/initial nauplii per beaker) responses were proportional and therefore modelled with a binomial error distribution and logit link [35]. *Daphnia* density and adult copepod density were modelled as fixed effects, and an interaction between these effects was included in both models. This interaction would be expected if, for example, copepods consume nauplii when *Daphnia* are rare (i.e. negative effect on nauplii) but consume *Daphnia* when *Daphnia* are abundant (i.e. positive effect on nauplii). Copepod density was treated as an ordinal predictor (*Daphnia* density as a continuous predictor) to aid in the visualization of the hypothesized interaction between copepod and *Daphnia* density, though treating copepod density as a continuous predictor did not alter qualitative results of the analysis. These models also included experimental block as a random intercept and slope that varied among copepod factor levels. We used fitted versus Pearson's residual plots to assess model fits and additionally checked for overdispersion in all models. To test the significance of fixed effects, we dropped these terms and compared nested models using likelihood ratio tests [36]. Random effects were retained in all model comparisons.

(ii) Prey mortality/regulation

Daphnia reproduced over the course of the experiment, in part because the largest size class of *Daphnia* added to beakers always carried eggs or neonates. Thus to examine the consumptive effects of adult copepods on *Daphnia*, we tested the effects of initial copepod density (held constant over the course of the experiment) on the final number of *Daphnia* per beaker using a GLMM (lme4 package) with a Poisson error distribution and log link. Initial copepod density was treated as an ordinal predictor, while initial *Daphnia* density was included as an additional continuous predictor to account for different *Daphnia* starting

densities. Again, treating copepod density as a continuous predictor did not alter qualitative results of the analysis. Experimental block was modelled as a random intercept and slope that varied among individual treatments. The effect of copepod density on final *Daphnia* density was tested by dropping this effect from the full model, and comparing nested models (fit with maximum-likelihood estimation) using a likelihood ratio test.

(iii) Predator reproduction

To examine a potential positive effect of *Daphnia* consumption on copepod reproduction, we tested whether the proportion of egg-bearing female copepods was influenced by the relative initial abundance of *Daphnia*. Individual beakers were checked for egg-bearing females and dead females (both replaced with non-reproductive females) daily (i.e. six times) over the course of the experiment. Because observation day had no effect on the proportion of egg-bearing females, we summed the total number of egg-bearing females as well as the total number of females per beaker over the six observations and used these sums to calculate the proportion of egg-bearing females. Dead females were subtracted from the total number of adult females in calculating this proportion. A single outlier (36 *Daphnia* per one adult copepod; the highest relative *Daphnia* abundance) was removed prior to analysis, because its position on *x*-axis and low proportional response drove an unrealistic hump-shaped relationship between relative *Daphnia* abundance and the proportion of egg-bearing females, but we additionally present the analysis including this data point for completeness. We used a GLMM with a binomial error distribution and logit link to model proportional copepod reproduction data. The ratio of *Daphnia* : adult copepods was modelled as a fixed effect, while experimental block was modelled as random intercept. We tested the effect of the *Daphnia* : adult copepod ratio on copepod reproduction by dropping this term from the full model, and comparing this null model (random intercept only) to the full model using a likelihood ratio test.

3. Results

(a) Predator recruitment

Daphnia and adult copepods had an interactive effect on both nauplii maturation (GLMM comparison (likelihood ratio test): $\chi^2 = 61.05$, $p < 0.001$; figure 2a) and survival (GLMM comparison (likelihood ratio test): $\chi^2 = 93.31$, $p < 0.001$; figure 2b). In the absence of adult predators, maturation and survival rates of juvenile predators declined with increasing *Daphnia* density until no juvenile predators survived in most replicates (mean proportion survived (± 1 s.e.) $= 0.01 \pm 0.01$; 100% mortality in three of four replicates; figure 2b), indicating that *Daphnia* can completely prevent predator recruitment under these conditions. Notably, initial *Daphnia* density had a greater effect on maturation than survival: in the absence of copepods, the proportion of matured nauplii was reduced to nearly zero at an initial density of 18 *Daphnia* per beaker, while the proportion of surviving nauplii was reduced to nearly zero at only the highest initial *Daphnia* density (36 *Daphnia* per beaker).

Effects of adult predators were contingent on *Daphnia* density. At low *Daphnia* densities (less than or equal to three *Daphnia* per beaker), adult copepods reduced nauplii maturation (figure 2a). In contrast, adult copepods enhanced maturation at intermediate–high initial *Daphnia* densities (more than three *Daphnia* per beaker; figure 2a), probably

through heterospecific predation. This interactive effect, however, only occurred at intermediate copepod densities: at the highest copepod density (eight copepods per beaker), copepods reduced maturation across *Daphnia* densities (figure 2a).

Survival data followed a similar pattern: adult copepods reduced nauplii survival at low-intermediate *Daphnia* densities (less than or equal to 18 *Daphnia* per beaker; figure 2b), but increased nauplii survival at high initial *Daphnia* densities (more than or equal to 27 *Daphnia* per beaker; figure 2b). Importantly, the presence of just four adult copepods increased nauplii survival from nearly 0 to 30%, indicating that even a small number of adults can prevent the inevitable competition-mediated 'extinction' of juvenile predators that would occur in their absence. However, at the highest copepod density (eight copepods per beaker), copepods again reduced nauplii survival across *Daphnia* densities (figure 2b).

(b) Prey mortality/regulation

Copepods reduced final *Daphnia* density across initial *Daphnia* densities (GLMM comparison (likelihood ratio test): $\chi^2 = 177.97$, $p < 0.001$; figure 3).

(c) Predator reproduction

Daphnia consumption had a positive effect on adult copepod reproduction: the percentage of females bearing eggs increased with initial *Daphnia* density per copepod (GLMM comparison (likelihood ratio test): $\chi^2 = 6.62$, $p = 0.010$; figure 4). Including the one outlier (see Material and methods) did not alter the general pattern but not surprisingly weakened statistical power (GLMM comparison (likelihood ratio test): $\chi^2 = 3.36$, $p = 0.067$).

4. Discussion

In many taxa, predators have to compete with their 'future' prey during early developmental stages [2,4]. Theory suggests that such LHIGP systems can give rise to alternative stable states in ecological communities [4,9,14], yet the stage-specific competitive and predatory relationships that drive these states are empirically understudied. Here, we show that predator recruitment in LHIGP is driven by a delicate balance of competition, predation and cannibalism. Competitively superior *Daphnia* reduced nauplii recruitment and even precluded nauplii survival at the highest *Daphnia* density, demonstrating the potential for predator exclusion by prey [9,14]. As hypothesized, adult copepods alleviated this competitive bottleneck by consuming *Daphnia*, an interaction that could potentially facilitate predator persistence in the long-term (i.e. the cultivation effect: [9]). This positive effect of adults on juveniles, however, only occurred at intermediate to high *Daphnia* densities and at an intermediate copepod density. At low *Daphnia* densities, copepods compounded any negative effects of *Daphnia* on nauplii through cannibalism, while at the highest copepod density, copepods consistently reduced nauplii survival through cannibalism. Thus, our results demonstrate that the relative abundances of predators and prey and the cannibalistic propensity of adults are critical factors mediating LHIGP dynamics.
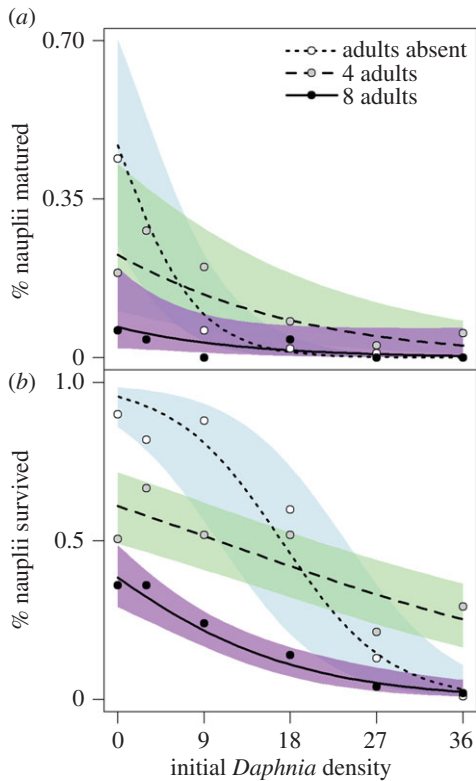
Figure 2. Effects of initial *Daphnia pulex* density (individuals per beaker) and adult copepod (*Mesocyclops edax*) density (individuals per beaker) on proportional nauplii (juvenile copepod) maturation (*a*) and survival (*b*). Initial nauplii density was 25 individuals per beaker. Points represent means of replicated treatments. Two adult copepod factors levels (one and two copepods per beaker) were omitted for clarity. Lines and colour bands depict generalized linear mixed model fits and 95% confidence intervals, respectively. (Online version in colour.)

Figure 3. Effects of adult copepod (*Mesocyclops edax*) density (individuals per beaker) on *Daphnia pulex* final density (individuals per beaker) across initial *Daphnia* densities (individuals per beaker). Points represent means of replicated treatments. Two adult copepod factor levels (one and two copepods per beaker) were omitted for clarity. Lines and colour bands depict generalized linear mixed model fits and 95% confidence intervals, respectively. (Online version in colour.)

(a) Resource competition: the juvenile competitive bottleneck

Resource depletion was a likely mechanism driving negative effects of *Daphnia* on nauplii. While the actual alga consumed by nauplii in this study is unknown, coarsely filtered pond water provided the resources necessary for nauplii growth and maturation over the 6-day experimental duration (0 *Daphnia*/0 adult copepods: mean proportion matured (± 1 s.e.) = 0.44 $\pm$ 0.12, survived = 0.81 $\pm$ 0.05). For comparison, *Mesocyclops* nauplii mature in approximately one week when fed with the flagellated alga *Cryptomonas ozolini* under ideal laboratory conditions [22]. We additionally added *Spirulina* to beakers every other day to supplement food resources. Though there is no evidence that *Mesocyclops* nauplii utilize *Spirulina* as a food resource (B.J.T. 2015, unpublished data), additional work shows that an even greater addition of *Spirulina* in the present experimental system alleviates the competitive effects of *Daphnia* on nauplii (B.J.T. 2015, unpublished data), perhaps through a reduction in *Daphnia* feeding rate concomitant with higher resource density. Thus, had we not added this additional resource for *Daphnia*, competitive effects would have probably been even stronger.

Daphnia reduced nauplii maturation at a lower initial *Daphnia* density than survival, indicating that development is more sensitive to food limitation. This finding is consistent with net production models of individual growth, which assume that energy can only be allocated to growth once
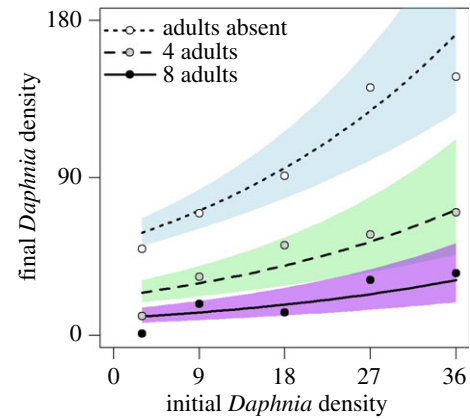
maintenance (i.e. survival) costs are met [37]. In the field, reduced growth rates could prolong the period at which nauplii are susceptible to size-dependent predators [19], such as other carnivorous zooplankton or cannibalistic adults. Interestingly, we measured almost complete nauplii mortality at the highest initial *Daphnia* density (36 *Daphnia*/0 adult copepods, mean proportion survived (± 1 s.e.) = 0.01 $\pm$ 0.01; 100% mortality in three of four replicates), which probably occurred via nauplii starvation. Thus, under our experimental conditions, it appears that *Daphnia* have the capacity to drive the extinction of their predator through competition. This result coincides with the theoretical finding that LHIGP can lead to an alternative stable state in which competitively dominant prey exclude predators [14]. The strength of this competitive effect was at least partially due to the rapid population growth of *Daphnia* over the course of experiment, where in the absence of adult copepods, *Daphnia* increased by a factor of approximately 7 on average from initial densities, magnifying their competitive superiority.

Competitive dominance of prey is generally predicted for systems where predators simply increase in size while their functional morphology changes little (e.g. fish: [16]), but this pattern is not necessarily true for systems with metamorphosis. With metamorphosis, predators completely 'rebuild' their morphology and thus do not necessarily face a morphological trade-off that renders them competitively inferior. Yet our results provide clear evidence that even when predators undergo complete metamorphosis, prey can be competitively dominant and even exclude their predator. Given that metamorphosis is common in many animal taxa [6], our results indicate that competition could play an important role in regulating predator recruitment across a much broader taxonomic range than previously suggested.

(b) Heterospecific and conspecific predation

Heterospecific and conspecific predation were critical interactions mediating the magnitude of predator recruitment. Size-dependent predators, such as those involved in LHIGP, are often cannibalistic [38–40], yet the effects of cannibalism on LHIGP are rarely considered (but see [20]). In this study,
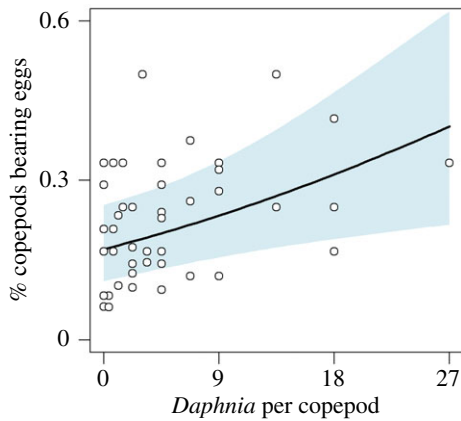
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Figure 4. Proportion of egg-bearing copepods as a function of initial *Daphnia pulex* relative abundance (i.e. *Daphnia* per copepod). Points represent proportion of egg-bearing copepods calculated from six observations per beaker made daily over the duration of the experiment. Line depicts generalized linear mixed model fit and colour band depicts 95% confidence interval. (Online version in colour.)

adult copepods benefited juvenile copepods by consuming *Daphnia*, though these positive effects only occurred at an intermediate adult copepod density. At the highest adult copepod density, cannibalism outweighed the indirect benefit (from reduced interspecific competition) to juvenile copepods across *Daphnia* densities. This suggests that in LHIGP systems with cannibalism, there is an optimal adult predator : prey ratio or absolute adult density beyond which adults might actually further reduce recruitment by cannibalizing juvenile predators.

Accordingly, an important factor determining the impact of cannibalism on LHIGP is whether adults exhibit a preference for conspecific versus heterospecific prey. While we could not compute a preference index in this study (the cause of nauplii mortality, either starvation or cannibalism, was unknown), the results of our study are consistent with unselective feeding (i.e. feeding depending on relative abundance): copepods reduced nauplii survivorship when nauplii were abundant relative to *Daphnia*, but enhanced nauplii survivorship through *Daphnia* consumption when nauplii were relatively rare. By contrast, Byström *et al.* [16] found that fish are often preferentially cannibalistic, though other work suggests that cannibalistic propensity can vary both within and among taxa [41–44]. In systems where adult predators are preferentially cannibalistic, we expect the beneficial effects of adults on juveniles to be weaker than in systems where adults exhibit no selectivity or a preference for heterospecific prey. In general, our results highlight the need to consider cannibalism in predicting the dynamics of natural LHIGP systems.

(c) Long-term implications

In complete diet shift LHIGP systems when prey are competitively dominant (e.g. the present zooplankton system), theory predicts alternative stable states: prey either exist alone, feeding on the resource, or coexist with the predator [14]. Coexistence occurs because adult predators rely on prey for food and thus cannot exist without them [14]. By contrast, diet broadening over ontogeny reduces predator dependence on prey, resulting in prey exclusion [4,15]. Thus, the results of our short-term study suggest that by consuming *Daphnia*, carnivorous adult copepods can indeed facilitate coexistence (when occurring at moderate densities), while in the absence of adults, strong competition could drive an alternative consumer–resource equilibrium. Nevertheless, predicting long-term effects will depend in part on the predator's numerical response. Interestingly, while nauplii suffered from higher *Daphnia* density, adult copepods benefited: we recorded a higher proportion of egg-bearing females when *Daphnia* were relatively abundant, despite the short experimental duration. This suggests that had the experiment been run longer, a greater initial larval input would have occurred in high *Daphnia* density treatments. This reproductive response, however, would do little to overwhelm the competitive effect of *Daphnia* in our experimental system that lacked renewed resources for nauplii. Thus, a longer-term study with continuous resource input (e.g. [45]) that allows for multiple copepod generations would be useful in elucidating the population-level effects of the biotic interactions demonstrated here.

While theory makes clear predictions on how the degree of ontogenetic diet shift determines the long-term dynamics of LHIGP, the additional effects of cannibalism remain underexplored (but see [20] for effects on a diet broadening LHIGP scenario). Predators in LHIGP often become cannibalistic at the transition from resource- to prey-feeding [16,20]. Thus with cannibalism, adult predators gain an additional food resource while juveniles experience an additional source of mortality. Recent theoretical work suggests that such stage-specific impacts can have dramatic consequences for the distribution of biomass across stages [4]. Specifically, in LHIGP where juvenile and adult predators take on different ecological roles, shifts in biomass distribution could alter the strength of interspecific interactions with substantial consequences for community dynamics. Theoretical and long-term empirical studies exploring these potential effects of cannibalism provide a clear avenue to advance our understanding of stage-structured species interactions.

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