Inducible defenses and rotifer food chain dynamics

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Abstract Theoretical studies have predicted that inducible defenses affect food chain dynamics and persistence. Here we review and evaluate laboratory experiments that tested hypotheses developed from these theoretical studies. This review specifically focuses on the effects of inducible defenses in phytoplankton-rotifer food chain dynamics. First, we describe the occurrence of colony formation within different strains of green algae (Scenedesmaceae) in response to infochemicals released during grazing by the herbivorous rotifer *Brachionus calyciflorus*. Then we examined the effects of inducible defenses on the population dynamics of this planktonic system in which algal strains that differed in their defense strategies were used. Simple food chains were composed of green algae (Scenedesmaceae), herbivorous rotifers (*Brachionus calyciflorus*) and carnivorous rotifers (*Asplanchna brightwellii*). In this system *B. calyciflorus* exhibits an inducible defense against predation by developing long postero-lateral spines. Experimental studies showed that inducible defenses, as opposed to their absence, could prevent high-amplitude population fluctuations. We discuss the dual effects of induced defenses on extinction probabilities and consider the fit of a theoretical model to experimental data to understand the mechanisms that underlie the observed dynamics.

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Introduction

Inducible defenses are phenotypic changes in prey organisms in response to cues associated with presence of a predator. Their aim is to reduce loss rates in subsequent attack by these predators. These strategies are used by a variety of aquatic organisms including algae and both vertebrate and invertebrate animals. Inducible defenses include responses in (1) morphology, e.g., increased body depth in crucian carp in response to piscivorous fish, such as pike

(Brönmark & Miner, 1992), (2) behavior, e.g., diel vertical migration in daphnids in response to visually hunting zooplanktivorous fish (Ringelberg, 1991) and (3) life history, e.g., a reduced size at first reproduction in daphnids against fish predation (Stibor & Lüning, 1994).

Linking levels of integration

Inducible defenses modify the interaction strength between predator and prey and are as such individual-level responses that affect the functioning of populations and communities (e.g., Vos et al., 2002). Interesting research topics at the individual level include the costs and benefits of inducible defenses and the resulting contribution of these defenses to fitness. Benefits manifest themselves in reduced predation rates if the defense is actually effective at preventing ingestion. In many cases, however, the defense provides only a partial protection against predation (Vos et al., 2004a, b). Moreover, in several cases it has been difficult to document the actual costs of the induced defenses. This raises the question as to why these defenses have not evolved into constitutive defenses. It could be the case that costs manifest themselves more clearly in nature than in the lab.

At the food web and community levels, most attention has been directed at the effects of inducible defenses on stability and persistence. In an unstable system that shows strong population oscillations species might for instance be lost in the troughs of population cycles.

Theoretical predictions

Vos et al. (2004a, b) made a theoretical study of the effects of inducible defenses on bi- and tritrophic food chains using a model parameterized specifically for algae-rotifer dynamics. These researchers employed values from the literature as well as experimental data and made qualitative predictions about the consequences of inducible defenses for the stability and persistence of these food chains. Presence of inducible defenses as opposed to no inducible defenses or constitutive defenses increased the area of stable coexistence of algae and rotifers over a range of environmental conditions (Vos et al., 2004a) (Fig. 1). Theoretical predictions also showed that inducible defenses increased the relative impor-
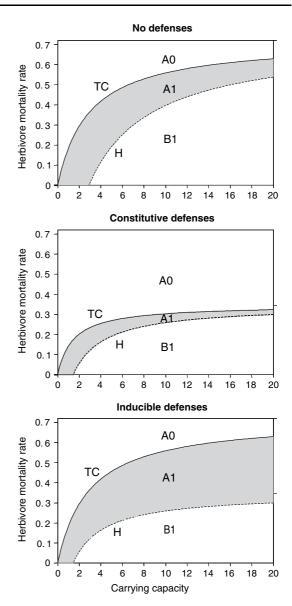

Fig. 1 The stability boundaries of bitrophic food chains without defenses (top), with permanent defenses (middle), or with inducible defenses (bottom), for a range of the carrying capacity and the herbivore mortality rate. The transcritical (TC) and Hopf (H) bifurcation curves separate areas with qualitatively different dynamics. Area A0: only algae exist. Grey area A1: stable coexistence of algae and herbivores. Area B1: algae and herbivores fluctuate. Reproduced, with permission, from Vos et al. (2004a)

tance of bottom-up control. In addition, variation in consumption rates on defended and undefended prey types caused the biomass of all trophic levels to increase simultaneously in response to enrichment (Vos et al., 2004b).

Here we review both theoretical and experimental studies on inducible defenses and their impact on bi- and tritrophic food chains that involve algae-rotifer relationships. We describe population level effects of the inducible morphological response of green algae (Scenedesmaceae) against predation by the herbivore *Brachionus calyciflorus*.

Observed predator-induced defenses in rotifers and algae

Defenses in herbivorous rotifers

Rotifers are preyed upon by a variety of invertebrate predators including protists, cnidarians, cladocerans, cyclopoid, calanoid and harpacticoid copepods, mysids, insect larvae (species of Chaorboiridae), and other rotifers (Williamson, 1983). Williamson's review of invertebrate predation on rotifers was updated by Brandl (2005) who discussed various factors determining predation rates, as well as the impact of freshwater copepods on rotifers. These and other works demonstrate numerous examples of defenses in rotifers including the following: (1) changes in morphology (e.g., spine development or elongation; reviewed in Gilbert, 1999); (2) behavioral response (e.g., vertical migration or escape reactions; Gilbert & Kirk, 1988); (3) life history changes (e.g., high maximum growth rate; Walz, 1995); and (4) chemical deterrents (Felix et al., 1995; Walsh et al., 2006). One of the first reports of inducible defenses in rotifers was the induction of spine formation in *B. calyciflorus* by *Asplanchna* (Gilbert, 1966; Gilbert, 1967). The observations by Gilbert (1967) suggested that the chemical signal (a kairomone) involved in this induction of defenses is a heat-stable protein. More on the chemical ecology of rotifers can be found in Snell (1998).

Juvenile *B. calyciflorus* and adults with no or short postero-lateral spines are highly susceptible to *Asplanchna* predation, but those with long spines are relatively protected from being captured or ingested (Gilbert, 1966; Gilbert, 1967; Halbach, 1971). These authors demonstrated that *Asplanchna* must orient the long-spined prey in such a way as to allow passage of the relatively large prey into its mouth. Time spent swallowing spined prey therefore increases, and ingestion attempts can be unsuccessful.

Young *Asplanchna* especially have difficulty ingesting spined *B. calyciflorus* (Gilbert, 1967; Gilbert, 1980). The effects of prey vulnerability on the functional response and growth have been tested for *Asplanchna* preying on *B. calyciflorus* and several other rotifer species (Iyer & Rao, 1996; Nandini et al., 2003). The capture success and ingestion of *Asplanchna* on spined *B. calyciflorus* is much lower than on non-spined *B. calyciflorus* (Iyer & Rao, 1996). However, a direct comparison of functional responses of *Asplanchna* on spined and non-spined *B. calyciflorus* has not yet been made. The effectiveness of *Brachionus* spines in preventing ingestion is likely to differ for different *Asplanchna* species.

Response to rotifer predation in *Scenedesmus*

Inducible defenses are common among herbivorous rotifers that often fall prey to carnivorous zooplankton, but even the prey of herbivorous zooplankton are well known to exhibit their own form of inducible defense. For example, species in the Scenedesmaceae, a group of green algae, show striking phenotypic plasticity when in the presence of the microcrustacean *Daphnia magna* (Hessen & Van Donk, 1993). The authors observed induction of colony-formation in an algal species that is now called *Desmodesmus subspicatus*. Subsequently, induction of colony-formation was also found in a *Scenedesmus acutus* (now *S. obliquus*) (Lampert et al., 1994). In response to the presence of infochemicals released, due to grazing by this herbivore, the alga formed four- to eight-celled colonies. This response also occurs when *Scenedesmus* is exposed to grazing-released infochemicals of the rotifers *Brachionus* and *Keratella* (Lürling & Van Donk, 1997; Van Donk et al., 1999). A whole range of different *Scenedesmus* strains was used in bio-assays to test their response to *B. calyciflorus* (Verschoor et al., 2004a). Most algal strains showed a similar response to infochemicals released by *B. calyciflorus* and *D. magna*; colony-formation may, therefore be a general response to herbivory in these algae.

Research has shown that induction of colony formation in unicellular algae can have a large effect on feeding efficiency in *B. calyciflorus*. The maximum ingestion rate of this rotifer was lower when feeding on algae with an induced defense than on
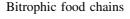
undefended algae (Verschoor et al., in press). This difference in maximum ingestion rates was, due to a difference in handling time rather than a difference in capture efficiency. Alternatively, algae that exhibited constitutive defenses not only reduced the maximum ingestion rate, but also seemed to be assimilated less efficiently by rotifers. Growth experiments provided further support that larger algae caused reduced *Brachionus* growth (Mayeli et al., 2004; Lürling et al., 2005).

Observations on bi- and tritrophic food chains with induced defenses

Overview of population level experiments

Algal-rotifer systems are ideal models to study effects of defenses on the population dynamics of higher trophic levels. Mayeli et al. (2004) presented data on the growth rates of *B. calyciflorus* and *Brachionus patulus* using two species of Scenedesmaceae. Here *B. calyciflorus* was able to grow on cells of *S. obliquus* as it did on the green alga *Chlorella* (Lucía Pavón-Meza et al., 2001). However, it had a lower or even negative population growth coefficient when feeding on the large, colonial and spined *D. quadricauda*. On the other hand, *B. calyciflorus* grown with the unicellular *Chlorella* showed different types of population dynamics, including predator–prey cycles, coexistence at equilibrium, or extinction, depending on the conditions of the chemostat set-up (Fussmann et al., 2000). The rotifer-algal cycles in this system seemed to be affected by rapid evolution in response to oscillating predator density (Yoshida et al., 2003). Population dynamics are not only governed by predation, but likely also by initiation of sexual reproduction and diapausing resting eggs in monogonont rotifers (Schröder, 2005). This feature can be adaptive for survival in varying environmental conditions. In laboratory populations rotifers tend to lose the ability to reproduce sexually. The evolution of the rotifer population toward asexual reproduction was a critical component in laboratory studies of algal-rotifer dynamics (Fussmann et al., 2003). Recent advances of other mechanisms underlying plankton population dynamics such as complex interactions, and ecological stoichiometry are reviewed in Yoshida (2005).

Bitrophic food chains

Van der Stap et al. (2006) assessed how different algal defenses can lead to qualitatively different patterns in population dynamics. They conducted a bitrophic experiment using food chains composed of four strains of Scenedesmaceae, differing in their defense strategies and an herbivorous species of *Brachionus* (Fig. 2a). Population fluctuations and herbivore persistence were observed in bitrophic food chains without defenses in algae (Fig. 3a). In the treatment with the constitutively defended algal strain, an increase in population density was followed by extinction of the rotifers in all replicates (see for example Fig. 3d). Such extinctions occurred in only half of the replicates that had algae with induced defenses (as exemplified in Figs. 3b–c). However, the herbivores persisted throughout the experiment in food chains with undefended algae. There were some population fluctuations in this treatment, but without the very low minimum densities that would endanger *Brachionus* persistence. Statistical analysis of the data showed that herbivore persistence was positively related to the proportion of small highly edible algae present (Van der Stap et al., 2006).

Tritrophic food chains

Since natural communities are usually constructed of more than two trophic levels, a third trophic level was added to the model system (Verschoor et al., 2004b) (Fig. 2b). The simple food webs were composed of green algae (Scenedesmaceae), herbivorous rotifers (*B. calyciflorus*) and carnivorous rotifers (*Asplanchna brightwellii*). In this system *B. calyciflorus* exhibits an inducible defense against predation by developing long posteriolateral spines. At high phosphorus levels, we observed strong population fluctuations in all food chains with undefended algae (Fig. 4a). In one out of three cases this led to the extinction of the top predator. When this treatment was repeated in time, again one out of three replicates ended in extinction of the top-predator after a very low population minimum of its prey. These fluctuations did not occur when algae had inducible defenses (Fig. 4b). At low phosphorus levels, deterministic consumer extinctions were observed, while the algae grew to carrying capacity. Herbivores in food chains with undefended algae showed an oscillatory ten-
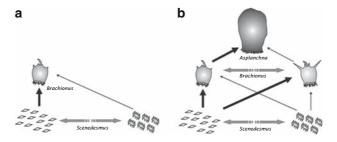
Fig. 2 Composition of bitrophic (**a**) and tritrophic (**b**) food chains. Solid arrows show the strength of the interactions. Dashed arrows reflect shifts in morphology between defended and undefended state
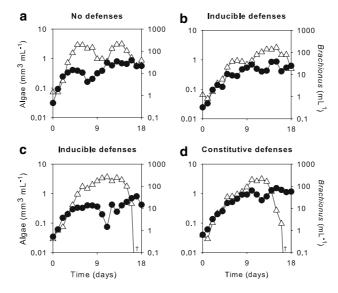

Fig. 3 Population dynamics of bitrophic food chains composed of the herbivorous rotifer *Brachionus calyciflorus* and the undefended algae *Desmodesmus subspicatus* (**a**), inducible defended algae *Scenedesmus obliquus* II (**b**), and *Scenedesmus obliquus* I (**c**), and constitutively defended algae *Desmodesmus*

quadricauda (**d**). The left axis is used for the density of algal volumes (*filled circles*), the right axis for the density of herbivores (*open triangles*); one replicate shown. Herbivore extinctions are marked with †. Reproduced, with permission, after Van der Stap et al. (2006)
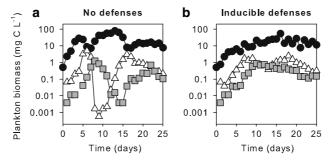

Fig. 4 Population dynamics of tritrophic food chains in the high phosphorus treatments, with densities expressed as mg C l⁻¹. Circles denote phytoplankton, triangles herbivorous zooplankton (*Brachionus*) and squares carnivorous zooplank-

ton (*Asplanchna*). (**a**) Food chain with undefended phytoplankton (*Desmodesmus*); (**b**) food chain with inducible defenses in phytoplankton (*Scenedesmus*); one replicate shown. Reproduced, with permission, after Verschoor et al. (2004b)

dency before going extinct. In the low phosphorus treatment with inducible defenses, herbivores went extinct in a more monotonical way (Verschoor et al., 2004b).

Chemostat

Predator–prey dynamics stabilized in a one-reactor chemostat with a mixed culture of *B. calyciflorus* and *S. obliquus*. This coincided with the induction of colony-formation in the algal prey. In contrast, high-amplitude population fluctuations were observed in the second reactor of a two-stage chemostat where prey were unable to form protective colonies (Lürling et al., 2005). Thus, we see that the use of continuous culture systems, especially for rotifers, is highly useful for the study of general population regulation principles (Walz, 1993).

Linking experimental observations and the theoretical work

The model by Vos et al. (2004a) predicted stability of predator–prey interactions for only a narrow range of parameter values when food chains were based on undefended algae. In contrast, for food chains with inducible defenses, stable coexistence of predator and prey was predicted for a relatively wide range of conditions. The experimental observations of Verschoor et al. (2004b) can be interpreted in this context. Here we note that the actual dynamics were high-amplitude fluctuations, which seemed to dampen out in the case of undefended algae at the base of the food chain, while a monotonic approach to a stable equilibrium was seen in the case of algae protected by inducible defenses (Fig. 4). The latter agrees directly with our expectation as based on the model: inducible defenses seem to stabilize dynamics. However, the dynamics in food chains with undefended algae can be explained in two alternative ways. The first possibility is that dynamics were truly cyclic, but some factor (such as increased heterogeneity through accumulation of detritus) stabilized the system late in the experiment. This explanation is consistent with our observations. However, it is also possible that the dynamics were inherently stable, but approached equilibrium through a damped oscillation, instead of monotonically. In this case, the

dynamics of systems with undefended versus algae protected by inducible defenses are not separated by a Hopf bifurcation, but by a stable focus-node boundary, which is situated within the stability area itself (Yodzis & Innes, 1992; Vos et al., 2005). On one side of this line a stable equilibrium is approached monotonically, on the other side this occurs through a damped oscillation (Vos et al., 2005). We cannot formally exclude this possibility based on current evidence, but further chemostat experiments will be helpful in teasing these alternative explanations apart. The experimental results of Verschoor et al. (2004b) clearly showed that inducible defenses in algae prevented high-amplitude population fluctuations in both bitrophic and tritrophic food chains, but the exact nature of these fluctuations remains unclear. The experiments showed that the algae-rotifer model system is very reproducible within batch, semi-continuous and continuous cultures, but dynamics may differ between these experimental systems; therefore, caution is warranted when making extrapolations to nature based on any of these systems alone. A particularly interesting observation is that inducible defenses at the herbivore level had little or no effect on stability in the model of Vos et al. (2004a; b). Exactly the same surprising result was obtained in the experiments by Verschoor et al. (2004b). These results await an ecological explanation.

In order to identify, whether phenotypic plasticity at the individual level has consequences for community dynamics, a more quantitative approach was taken and mechanistic predator–prey models were fitted to experimental population dynamics data collected in batch cultures by Van der Stap et al. (unpublished observations). They started off by using the inducible defense model by Vos et al. (2004a; b), however, realizing that this model assumes constant conditions, it was modified for application to the transient dynamics in a batch experiment. A good match was obtained between model and data, with 77% of the variance in the data being accounted for by the model. Moreover, results from the model showed that quantitative differences in handling times of prey placed the system at different locations in parameter space, in particular relative to the predator existence boundary. Long handling times on defended prey brought predators closer to the existence boundary, where they can go extinct earlier when nutrients are being depleted in the system than

predators that are further away from the existence boundary.

Other predator–prey interactions

Where predators and prey live together, predator responses to prey defenses may be expected. *Asplanchna priodonta* is able to grow larger jaws (Fontaneto & Melone, 2005) and this may be one way of how a predator can respond to spines in brachionid prey. A response in jaw size has not yet been studied or observed for the experimental predator species *A. brightwellii*. Besides the inducible defense of spines in *B. calyciflorus*, two other species in this genus employ predatory defense strategies. *Brachionus rubens* does not exhibit these morphological defenses, rather it has the ability to attach to cladocerans, which may serve, as an alternative escape mechanism from predation by *Asplanchna* (Iyer & Rao, 1996). Rotifers of the *Brachionus plicatilis* complex differ in body size and vulnerability to copepod predation. This differential sensitivity to predation promoted coexistence in a situation, where the competitively dominant species were preferred as prey (Ciros-Pérez et al., 2004).

Conclusion

Phenotypic plasticity in individual prey can have profound effects on population dynamics, affecting both consumers at higher trophic levels and the prey themselves. Plasticity in defenses creates variation in handling times and/or attack rates of predators on different prey types. This can cause prey with inducible defenses, as opposed to those without defenses, to prevent strong population fluctuations in both bi- and trirophic food chains. However, these differences in prey also place model predators at distinct locations in parameter space, which in turn confer different risks of extinction. Whereas induced defenses clearly promote stability and persistence under high nutrient conditions, this is no longer the case when these nutrients become depleted and the environment becomes harsher for predators. In such an environment, predators may actually go extinct sooner, when basal preys in the food chain are more strongly defended.

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