

Inducible defences and the paradox of enrichment

Matthijs Vos, Bob W. Kooi, Donald L. DeAngelis and Wolf M. Mooij

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In order to evaluate the effects of inducible defences on community stability and persistence, we analyzed models of bitrophic and tritrophic food chains that incorporate consumer-induced polymorphisms. These models predict that intra-specific heterogeneity in defence levels resolves the paradox of enrichment for a range of top-down effects that affect consumer death rates and for all possible levels of primary productivity. We show analytically that this stability can be understood in terms of differences in handling times on the different prey types. Our predictions still hold when defences also affect consumer attack rates. The predicted stability occurs in both bitrophic and tritrophic food chains.

Inducible defences may promote population persistence in tritrophic food chains. Here the minimum densities of cycling populations remain bound away from zero, thus decreasing the risk of population extinctions. However, the reverse can be true for the equivalent bitrophic predator–prey model. This shows that theoretical extrapolations from simple to complex communities should be made with caution. Our results show that inducible defences are among the ecological factors that promote stability in multitrophic communities.

M. Vos and W. M. Mooij, Dept of Food Web Studies, Netherlands Institute of Ecology (NIOO-KNAW), Centre for Limnology, Rijksstraatweg 6, NL-3631 AC, Nieuwersluis, the Netherlands (m.vos@nioo.knaw.nl). MV also at: Dept of Multitrophic Interactions, Netherlands Institute of Ecology (NIOO-KNAW), Centre for Terrestrial Ecology, Boterhoeksestraat 48, NL-6666 GA, Heteren, the Netherlands. – B. W. Kooi, Dept of Theoretical Biology, Faculty of Earth and Life Sciences, Vrije Univ., De Boelelaan 1087, NL-1081 HV, Amsterdam, the Netherlands. – D. L. DeAngelis, US Geological Survey, Biological Resources Division and Dept of Biology, Univ. of Miami, PO Box 249118, Coral Gables, FL 33124, USA.

Understanding the forces that maintain the integrity and persistence of complex natural communities is a key task in ecology and of great relevance to society. Ecologists have studied mechanisms that promote or destroy population stability for decades (Rosenzweig and MacArthur 1963, Rosenzweig 1971, 1973, Luckinbill 1973, Armstrong 1976, Schaffer and Rosenzweig 1978, Yodzis 1981, McCauley and Murdoch 1987, Abrams and Walters 1996, Kirk 1998, Kooi et al. 1998, McCann et al. 1998, Boer et al. 1999, Genkai-Kato and Yamamura 1999, Scheuring 2000, Jansen 2001, Fussmann et al. 2000, Persson et al. 2001, Vos et al. 2001, Vos et al. 2002, Shertzer et al. 2002).

A recurring theme is the prediction that enrichment will destabilise predator–prey interactions and result in high amplitude population oscillations, which entail a risk of local extinctions. Several laboratory studies have shown such population oscillations and extinctions as a result of enrichment (Huffaker et al. 1963, Luckinbill 1973, Fussmann et al. 2000). These experiments show that the paradox of enrichment is more than a model result and beg for further evidence from the field. However, field evidence for the paradox of enrichment is in short supply, even in planktonic systems that would seem to be good candidates (Murdoch et al. 1998). This suggests that one or more of the ecological factors that

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prevent such destabilisation in the field have been overlooked in laboratory studies of population dynamics.

Empirical studies show that inducible defences act as an important ecological factor with both direct and indirect effects at the community level (Raimondi et al. 2000, Turner et al. 2000), but the effects of inducible defences on stability and persistence have hardly been studied theoretically. Empirical work shows three key aspects and consequences of inducible defences that have not been investigated in concert in previous theoretical studies: First, the induction process is consumer density-dependent, often through infochemical cues (Anholt and Werner 1999, Van Donk et al. 1999). Secondly, both prey with induced defences and undefended individuals will be present at a given moment in time, even across a range of consumer densities (Hessen and Van Donk 1993, Lampert et al. 1994). This has intraspecific and within-trophic level heterogeneity as a consequence. Thirdly, defended individuals are hardly ever invulnerable and are therefore still attacked and handled as prey (Jeschke and Tollrian 2000). Several studies have called for theoretical work that links such well-understood individual level processes with their population level consequences (Tollrian and Harvell 1999a, Vet 1999, 2001).

It is indeed important to consider the effects of inducible defences at higher levels of ecological organisation, as they occur in a wide range of ecosystems (Havel 1987, Karban and Baldwin 1997, Tollrian and Harvell 1999b). Such inducible defences include refuge use, reduced activity, adaptive life history changes, the production of toxins and synomones and the formation of colonies, helmets or spines. Inducible defences occur in many terrestrial plant species (Havel 1987, Karban and Baldwin 1997), freshwater phytoplankton (chlorophytes, Van Donk et al. 1999), zooplankton (protozoa, rotifers, cladocera, Havel 1987, DeMeester et al. 1999, Gilbert 1999, Kuhlman et al. 1999, Tollrian and Dodson 1999), snails (Turner et al. 2000), insects (mayfly larvae, Dahl and Peckarsky 2002; dragonfly larvae, Johansson and Wahlström 2002), amphibia (Anholt and Werner 1999), fish (Brönmark et al. 1999), marine colonial invertebrates (bryozoa and gorgonacea, Harvell 1984, 1999) and barnacles (Lively 1999).

We aim at bridging the gap between current theory and empirical data by including density-dependent inducible defences, intraspecific heterogeneity and reduced maximum ingestion rates on induced prey in a classical food chain model that was conceived by Rosenzweig and MacArthur (1963) and formalised and developed by Rosenzweig (1971, 1973), Oksanen et al. 1981 and Kretzschmar et al. (1993). We parameterise this model for a well-studied system to investigate the effects of inducible defences in an ecologically relevant domain.

In this respect a food chain consisting of algae, herbivorous rotifers and carnivorous rotifers is a good

model system. For example, strains of *Scenedesmus* spp. algae differ in edibility to *Brachionus* spp. rotifers, owing to inducible colony formation (Hessen and Van Donk 1993, Lampert et al. 1994, Lüring 1999). Different *Brachionus* spp. rotifers vary in edibility to consumers like *Asplanchna* spp. rotifers, owing to inducible spine formation or size differences (Gilbert 1999). Colonies and spines effectively lower the maximum ingestion rates achieved by gape-limited consumers. Of the above mentioned organisms different strains exist that 1) always have the undefended phenotype, 2) have inducible defences, or 3) are permanently defended. Intraspecific heterogeneity will be present in both the plant (Hessen and Van Donk 1993, Lampert et al. 1994) and the herbivore population (Gilbert 1967), at a certain concentration of consumer-released infochemicals.

In the current paper we focus on two key consequences of inducible defences: stability and persistence. Here stability carries the meaning that a system of populations tends to return to its equilibrium state following a small perturbation away from that state (Case 2000). Minimum population densities are used as a measure for persistence. When minimum population densities stay farther away from zero, populations run a lower risk of extinction and thus have a higher probability to persist (McCann et al. 1998). We study both bitrophic and tritrophic food chains to include the possible effects of feedback across trophic levels on stability and persistence.

Model

We use a classical food chain model (Oksanen et al. 1981, Kretzschmar et al. 1993) with a slight modification to include natural mortality in the plants, as the basic model for the no defence and permanent defence scenarios. Density-dependent induction and decay of defences are incorporated for the food chain scenario with inducible defences. Hereafter we will refer to the different trophic levels as plants (P), herbivores (H) and carnivores (C). Below we show the bitrophic version of the food chain model and explain how the tritrophic version is a simple extension. Our standard food chain model is defined by

$$\begin{aligned} \frac{dP_i}{dt} &= P_i \left(r_i \left(1 - \frac{P_i}{k} \right) - \frac{v_{i1} H_i}{1 + v_{i1} h_{i1} P_i} - s_{i1} \right) \\ &= \text{logistic plant growth} - \text{Holling type II herbivory} \\ &\quad - \text{natural mortality} \end{aligned} \quad (1a)$$

$$\begin{aligned} \frac{dH_i}{dt} &= H_i \left(\frac{c_{i1} v_{i1} P_i}{1 + v_{i1} h_{i1} P_i} - s_{i2} \right) \\ &= \text{herbivore growth} - \text{natural mortality} \end{aligned} \quad (1b)$$

where t is time, subscript i is 1 for the undefended case and 2 for the defended case, r and k are the intrinsic

growth rate and carrying capacity of plants, v_{i1} is the herbivore search rate, h_{i1} its handling time, s_{i1} and s_{i2} are the death rates for the plant and herbivore, respectively and c_{i1} is the efficiency of plant conversion into herbivore biomass. Permanently defended plants P_2 impose an increased handling time h_{21} on herbivores, relative to the lower h_{11} of undefended plants P_1 . This decreases the maximum ingestion rate of herbivores. The attack rate v_{21} on defended plants may be lower than or equal to the attack rate v_{11} on undefended plants.

We incorporate inducible defences in the above system by allowing a herbivore density-dependent flow of plants from the undefended part of the population to the defended part (Fig. 1). Similarly, decay of defences is included as a density-dependent flow from the defended portion to the undefended part. These rates of inter-change depend on herbivore density in a sigmoidal fashion: Induction is minimal at low herbivore densities and maximal at high herbivore densities. The reverse is true for the decay of defences. The following set of differential equations represents the rates of change of undefended and defended plants and their herbivores:

$$\begin{aligned} \frac{dP_1}{dt} = & P_1 \left(r_1 \left(1 - \frac{P_1}{k} - \frac{P_2}{k} \right) - s_{i1} \right) \\ & - \frac{v_{11} H_1 P_1}{1 + (v_{11} h_{11} P_1 + v_{21} h_{21} P_2)} \\ & - i_1 P_1 \left(1 - \left(1 + \left(\frac{H_1}{g_1} \right)^{b_1} \right)^{-1} \right) \\ & + i_1 P_2 \left(1 + \left(\frac{H_1}{g_1} \right)^{b_1} \right)^{-1} \end{aligned} \quad (2a)$$

$$\begin{aligned} \frac{dP_2}{dt} = & P_2 \left(r_2 \left(1 - \frac{P_2}{k} - \frac{P_1}{k} \right) - s_{i2} \right) \\ & - \frac{v_{21} H_1 P_1}{1 + (v_{11} h_{11} P_1 + v_{21} h_{21} P_2)} \\ & + i_1 P_1 \left(1 - \left(1 + \left(\frac{H_1}{g_1} \right)^{b_1} \right)^{-1} \right) \\ & - i_1 P_2 \left(1 + \left(\frac{H_1}{g_1} \right)^{b_1} \right)^{-1} \end{aligned} \quad (2b)$$

$$\frac{dH_1}{dt} = H_1 \left(\frac{c_{i1} v_{11} P_1 + c_{21} v_{21} P_2}{1 + (v_{11} h_{11} P_1 + v_{21} h_{21} P_2)} - s_{i2} \right) \quad (2c)$$

where g_1 is the density of herbivores at which induction reaches half its maximum rate, while b_1 is a shape parameter of the induction and decay functions. The herbivore attack rate is v_{11} on undefended plants and v_{21} on defended plants. Similarly herbivore handling times are h_{11} and h_{21} on undefended and defended plants. System (2) ensures that eventually all plants become undefended when no herbivores are present. When herbivores are present, a balance of defence induction

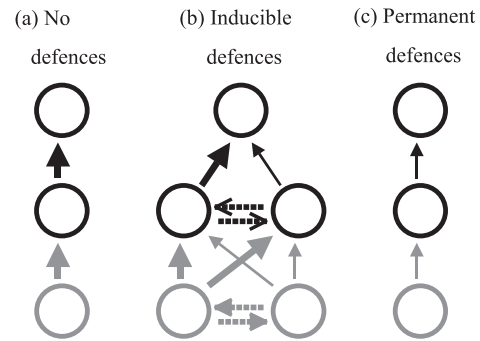


Fig. 1. Food chains with different types of defences. (a) no defences. (b) inducible defences. (c) permanent defences. Solid arrows show the strength of per capita feeding interactions. Dashed arrows reflect intraspecific transitions between the defended and undefended state. Food chains were analysed as bitrophic plant-herbivore systems (shown in black), or as tritrophic plant-herbivore-carnivore systems (added trophic level in dark grey).

and decay will be approached at a rate that depends on parameter i_1 .

This bitrophic system can be expanded to a tritrophic system by including a defended herbivore H_2 and a carnivore C , with their respective death rates s_{22} and s_3 . Now the induction of plants will depend on the total herbivore density ($H_1 + H_2$). Herbivores have the same defence induction and decay functions as in system (2), but depend on carnivore density C and have their own parameters i_2 , b_2 and g_2 . Carnivore attack rates are v_{12} and v_{22} on undefended and defended herbivores, respectively. Similarly, carnivore handling times are h_{12} and h_{22} on undefended and defended herbivores. The conversion efficiency from herbivores to carnivores is c_2 .

The model was parameterised using values from the literature and our own experimental data. We used laboratory studies on algae and rotifers that concerned defence induction in response to consumer-released infochemicals, the effects of inducible defences on functional responses, population growth rates and mortality rates and measurements of conversion efficiencies, carbon contents and dry-weights. Van Donk et al. (1999) and Gilbert (1999) provide access to the extensive literature on this well-studied plankton system. The parameters, dimensions, interpretations and literature sources of all used parameter values are listed in Table 2 of a separate paper that investigates the effects of inducible defences on trophic structure (in press). In the current paper we show the parameter values used in the captions of Fig. 2, 3. In this model system no costs of inducible defences in terms of reduced growth rates can be detected (Gilbert 1999, Lüring and Van Donk 2000). However, colonial algae have increased sedimentation rates, which are incorporated in our study as an increased natural mortality s_{21} . For the sake of generality and because theory predicts trade-offs to be impor-

tant in systems with inducible defences, we also include alternative cost scenarios for defended plants and herbivores in our analysis.

We used a simple analytical approach in the case of the bitrophic food chain. It is well-known that three qualitatively different behaviours of a bitrophic food chain occur in the following order as the carrying capacity of the system is increased: 1) only plants exist; 2) plants and herbivores coexist in a stable equilibrium; 3) plant and herbivore populations fluctuate. These qualitatively different behaviours are separated by bifurcations: herbivores can exist as the transcritical (TC) bifurcation is crossed and limit cycles of plants and herbivores appear as the Hopf (H) bifurcation is crossed. It is well-known that the transcritical bifurcation occurs in this system when the vertical herbivore isocline intersects the right end of the hump-shaped plant isocline where herbivore density is zero and that the Hopf bifurcation occurs when the vertical herbivore isocline intersects the apex of the plant isocline (Rosenzweig and MacArthur 1963, Scheffer 1998). We will show bifurcation curves for different combinations of the carrying capacity, a bottom-up effect and herbivore mortality, a top-down effect. Using the equations for TC and H bifurcation curves, we will show that the paradox of enrichment can be absent in a food chain with inducible defences. We will make clear how this stabilising effect of inducible defences results from differences in handling times on defended and undefended prey. We also show that permanent defences do not have such a stabilising effect.

A numerical bifurcation analysis was used to investigate areas of stability in the tritrophic food chain model. Again the carrying capacity was taken as a measure for primary productivity, to stay close to the original approach by Rosenzweig and MacArthur (1963) and Rosenzweig (1971). Mortality of the carnivore was taken as a top-down effect on the food chain. Bifurcations were calculated with the software packages locbif (Khibnik et al. 1993), CONTENT (Kuznetsov and Levitin 1997) and Auto (Doedel et al. 1997).

We checked the sensitivity of our tritrophic stability results to several changes in our assumptions and model components. Changes in the incorporated costs of defences allow us to draw more general conclusions. The sensitivity analysis also allowed us to check whether the observed phenomena in the more complex tritrophic case are due to the same mechanism as in the analytically transparent bitrophic case. The following changes were made: 1) plant defences entail no costs ($s_{11} = s_{21}$); 2) plant defences result in a reduced intrinsic growth rate r_2 for induced plants and not in an increased natural mortality; 3) herbivore defences entail costs that result in an increased natural mortality (s_{22}); 4) defences decrease the attack rates (v_{21} , v_{22}); 5) defences do decrease

consumer attack rates, but do not increase handling times; 6) functional responses are linear instead of Holling type II and defences cause reduced attack rates; 7) plants and herbivores with induced defences have a lower conversion efficiency to consumer biomass; 8) plants with induced defences are inedible ($v_{12} = 0$); 9) both induced plants and herbivores are inedible; 10) a simultaneous increase or decrease of the values of the induction function parameters b_i and g_i . The above increases and decreases accounted for 5 to 30% of the value that was estimated for the real system and were implemented in steps of 5%.

Results

Stability of the bitrophic food chain

In the bitrophic food chains three qualitatively different types of dynamics occur, depending on the bottom-up effects of enrichment and top-down effects that determine herbivore death rates (Fig. 2). Changes in the existence and stability properties of the food chain are shown across a range of plant carrying capacities (k) and herbivore death rates (s_{12}). The scenarios with no defences, permanent defences and inducible defences are shown in the top, middle and bottom panels of Fig. 2. In case of small carrying capacities and high herbivore mortality rates only plants can exist (area A0). For intermediate values of both factors plants and herbivores coexist in a stable equilibrium (area A1). Low herbivore death rates and high carrying capacities, familiar in the paradox of enrichment, lead to instability of the system in all cases (area B1). The TC curves separate area's A0 and A1, marking so-called transcritical bifurcation points. These TC curves are described by

$$s_{12} = - \frac{c_{il} v_{il}}{\frac{1}{k - \frac{s_{il} k}{r_i}} + v_{il} h_{il}} \quad \text{and consequently} \quad \lim_{k \rightarrow \infty} s_{12} = \frac{c_{il}}{h_{il}} \quad (3)$$

The H curves mark so-called Hopf bifurcation points, where the system starts to oscillate when the carrying capacity is increased (Fussmann et al. 2000). These H curves are described by

$$s_{12} = - \frac{c_{il} v_{il}}{\frac{1}{\frac{k}{2} - \frac{ks_{il}}{2r_i} - \frac{1}{2h_{il}v_{il}}} + v_{il} h_{il}} \quad \text{and consequently} \quad \lim_{k \rightarrow \infty} s_{12} = \frac{c_{il}}{h_{il}} \quad (4)$$

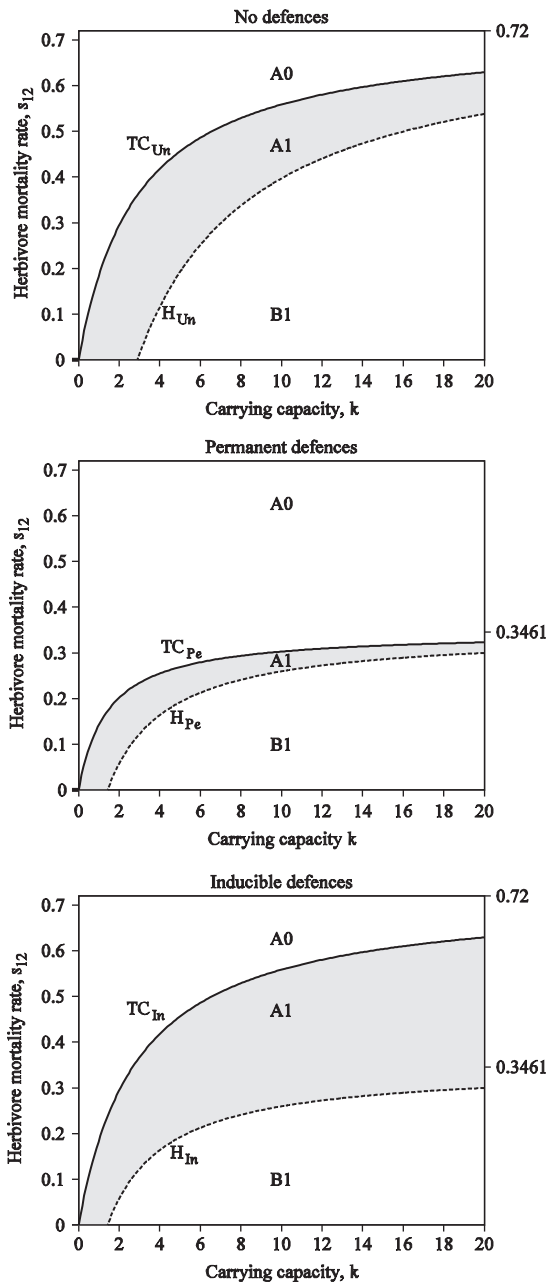


Fig. 2. The stability boundaries of bitrophic food chains without defences (top), with permanent defences (middle), or with inducible defences (bottom), for a range of the carrying capacity k and the herbivore mortality rate s_{12} . The transcritical (TC) and Hopf (H) bifurcation curves separate areas with qualitatively different dynamics. Area A0: only plants exist. Grey area A1: stable coexistence of plants and herbivores. Area B1: plants and herbivores fluctuate. Parameter values used: $b_1 = 2.05$, $c_{11} = c_{21} = 0.36$, $g_1 = 0.06$, $i_1 = 1.0$, $r_1 = r_2 = 1.42$, $s_{11} = 0.145$, $s_{21} = 0.18$, $s_{12} = 0.17$, $h_{11} = 0.5$, $h_{21} = 1.04$, $v_{11} = v_{21} = 0.77$. See the Methods section for the sensitivity analysis.

So, the TC and H curves converge to the same values c_{11}/h_{11} when the system is enriched to an infinite

carrying capacity ($k \rightarrow \infty$). Note that this convergence constricts the possibilities for a stable equilibrium to an exceedingly narrow range of conditions as k increases (Fig. 2, top, middle). Defences increase the handling time of resource species and consequently $h_{21} > h_{11}$. Consequently, curve TC_{Un} for the undefended scenario lies above curve TC_{Pe} for the permanent defence scenario (Fig. 2, top, middle).

The curves for the inducible defence case (Fig. 2, bottom) are special because the TC_{In} curve coincides with the TC_{Un} curve of the undefended scenario (no plants are induced in the absence of herbivores) while the H_{In} curve almost coincides with the H_{Pe} curve of the permanent defence scenario (almost all plants are induced at high carrying capacities and herbivore densities). As a consequence, for a food chain with inducible defences the transcritical curve TC_{In} and the Hopf curve H_{In} will not converge to the same value for $k \rightarrow \infty$. For the estimated parameters of the real system TC_{In} is equal to TC_{Un} and converges to $c_{11}/h_{11} = 0.72$ while H_{In} is approximately equal to H_{Pe} and converges to a value close to $c_{21}/h_{21} = 0.3461$. This range between c_{11}/h_{11} and c_{21}/h_{21} shows the range of s_{12} for which the paradox of enrichment is absent in the food chain with inducible defences.

Stability of the tritrophic food chain

As in the bitrophic case, the conditions for stability of the tritrophic food chain are restricted to a limited range of carrying capacities (k) and top consumer mortalities (s_3) for the no defence and permanent defence scenarios (Fig. 3, top and middle, grey stability area A2). The tritrophic food chain with permanent defences has the most restricted stability area (Fig. 3, middle).

In contrast, inducible defences cause the food chain to be stable across a wide range of carrying capacities (Fig. 3, bottom). The paradox of enrichment is absent for a range of low carnivore mortality rates. In the numerical bifurcation analysis we allowed enrichment up to a carrying capacity of 200 mg algal carbon/l. Even in such a highly eutrophic environment the stability of the food chain is unaffected when defences are inducible.

Population persistence in the bitrophic and tritrophic food chains

It is possible for the bitrophic food chain to show oscillatory periodic behaviour (Fig. 2, area B1). In this case minimum population densities (over one period) of plants and herbivores approach zero as the carrying capacity is increased (Fig. 4, top). Minimum population densities for the inducible defence case (the solid lines) almost coincide with those of the permanent defence

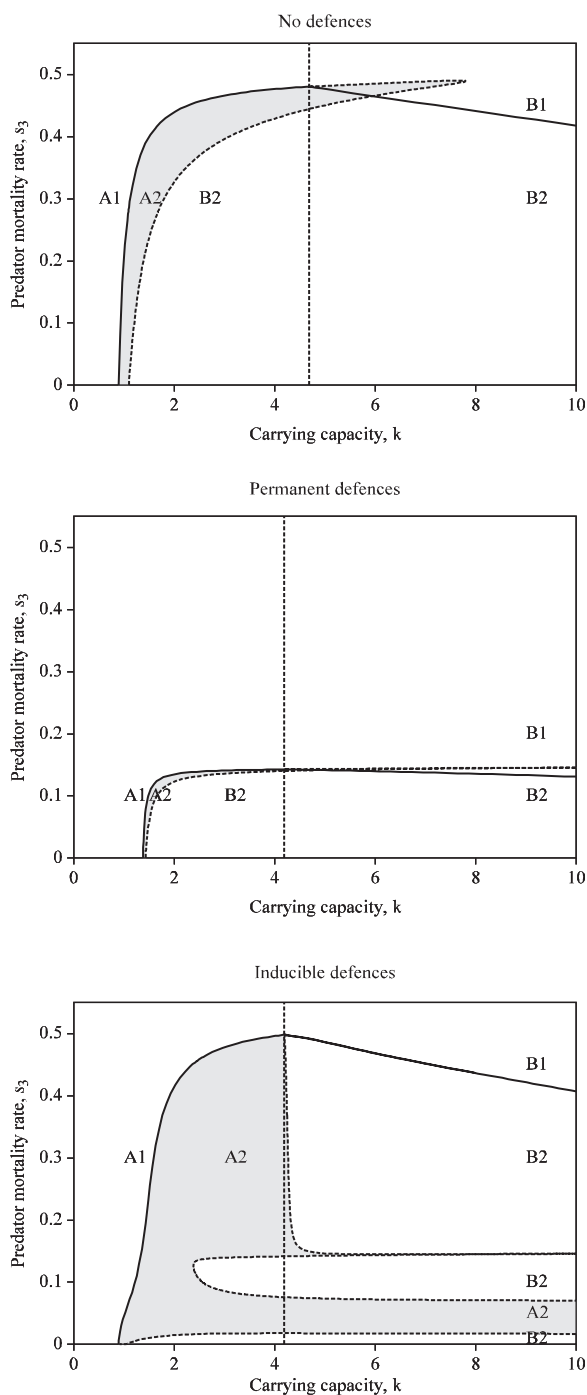


Fig. 3. The stability boundaries of a tritrophic food chain without defences, (top), with permanent defences (middle), or with inducible defences (bottom) for a range of the carrying capacity k and the carnivore mortality rate s_3 . Area A1: stable coexistence of plants and herbivores. Grey area A2: stable coexistence of plants, herbivores and carnivores. Area B1: unstable dynamics of plants and herbivores. Area B2: unstable dynamics of plants, herbivores and carnivores. Parameter values used: The values listed in Fig. 2 and $b_2 = 1.5$, $c_{21} = c_{22} = 0.5$, $g_2 = 0.02$, $i_2 = 1.0$, $s_{22} = 0.17$, $s_3 = 0.125$, $h_{12} = 0.83$, $h_{22} = 3.33$, $v_{12} = v_{22} = 2.71$.

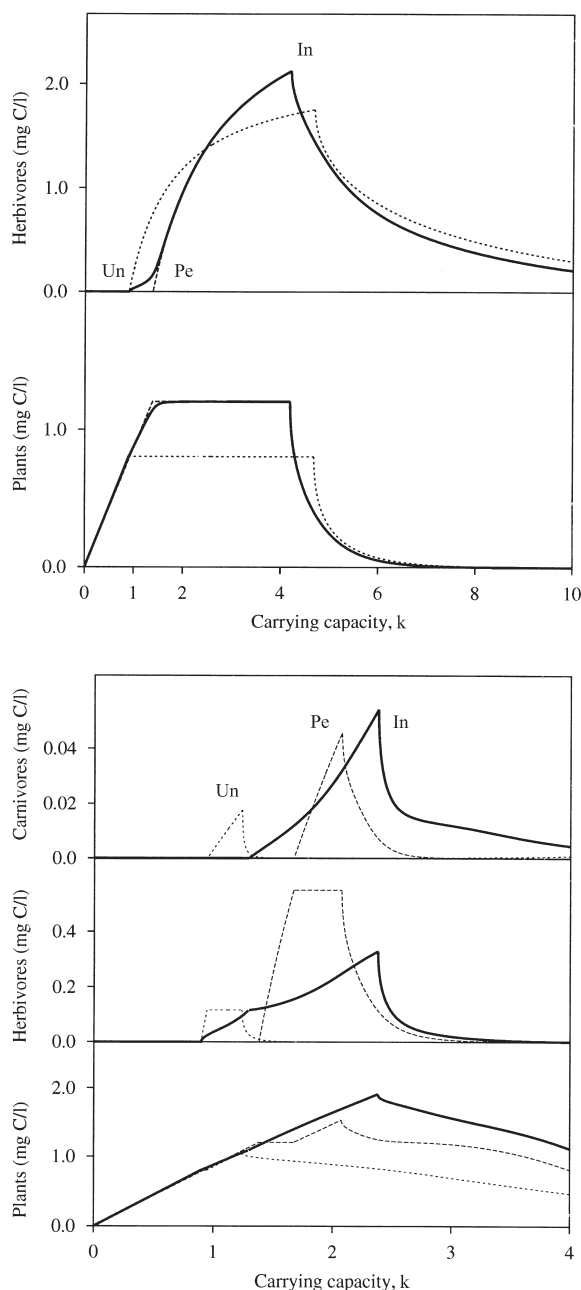


Fig. 4. Minimum population densities, a measure for population persistence, in a bitrophic food chain (top) and a tritrophic food chain (bottom), when defences are absent (Un, dotted lines), permanent (Pe, dashed lines) or inducible (In, solid lines) for a range of the carrying capacity k . For parameter values used, see Fig. 2, 3.

scenario and lie below the minimum densities for the undefended scenario.

In contrast, when the tritrophic food chain exhibits oscillatory behaviour, minimum population densities of all trophic levels remain bound farther away from zero in the inducible defence scenario.

The sensitivity analysis

Our sensitivity analysis focused on the stability of the tritrophic food chain with inducible defences and in particular on stable area A2 at a high level of the carrying capacity. We asked whether the paradox of enrichment remained absent under ten changes in our assumptions and model components. The only scenario where a change resulted in population fluctuations was scenario 5, where inducible defences in prey did not affect handling times, but only reduced attack rates (see Discussion). Changes in the way the costs of defences are incorporated did not eliminate this stable area A2 at a high carrying capacity.

Discussion

Inducible defences caused an absence of the paradox of enrichment in both the bitrophic and tritrophic model food chains, for a range of top-down effects that affect consumer death rates. This stabilisation did not occur when defences were fixed. For the bitrophic food chain with inducible defences we showed that the equilibrium will remain stable under enrichment to an infinite carrying capacity for a range of herbivore mortality rates (s_{12}), namely if $c_{21}/h_{21} < s_{12} < c_{11}/h_{11}$. This means that stability simply depends on the difference between herbivore handling times (h_{11}) on induced and undefended plants. Possibilities for stability increase as the difficulty of handling induced plants increases relative to undefended plants. Our planktonic example is based on the difficulty that gape-limited herbivores experience when handling induced colonial algae, but the same principle applies to terrestrial plants that exhibit herbivore-induced spines or thorns (Gowda 1996, Gomez and Zamora 2002). Here we have assumed that the conversion efficiency from plant biomass to herbivore biomass is identical for defended and undefended plants, which is realistic for single-celled and colonial algae. It is conceivable that inducible defences decrease the digestibility and thus conversion efficiency of defended plants. Differential conversion will in that case also affect the difference between the c_{11}/h_{11} values of defended and undefended plants. From Fig. 2 it is clear that all factors that cause a sufficient increase in herbivore mortality rates will stabilise an oscillating plant–herbivore system, as it is moved from area B1 to A1. However, this stability area A1 is very narrow in the fixed defence scenarios, especially at high carrying capacities (Fig. 2, top and middle) and a slightly increased herbivore mortality will drive the herbivore to extinction (area A0). Our estimated mortality rate for the herbivore with inducible defences was a laboratory value of 0.17 d^{-1} , which is below the value 0.3461 that would cause an absence of the paradox of enrichment. Two additional sources of

mortality would raise the herbivore's death rate under more natural conditions and thus cause an absence of the paradox of enrichment. First, a complex of pathogens, generalist predators and accidents may act together as a rather constant background source of mortality. Secondly, the addition of a carnivore (that has coupled dynamics with the herbivore) may impose a sufficient additional mortality to stabilise the system. In Fig. 3 we can see this happening: a stable area (A2) occurs for a limited range of low carnivore mortality rates (s_3) and a wide range of carrying capacities. In the numerical bifurcation analysis we allowed enrichment up to 200 mg C/l and stability was preserved under these highly eutrophic conditions. Extensive numerical analysis has shown that increasing the herbivore's death rate, either to simulate the above mentioned higher mortality in nature, or to incorporate costs of herbivore defences, will dramatically enlarge stable area A2 in Fig. 3, at the expense of the 'oscillatory' area B2 in the middle of this graph.

Our analysis shows that inducible defences may cause the paradox of enrichment to be absent in both bitrophic and tritrophic food chains, depending on mortality rates at the top trophic level. This conclusion is based on analytical results for the bitrophic case and numerical bifurcation results in the tritrophic case. Bifurcation analysis is a powerful tool, but results will depend on the configuration of the chosen parameter values. We used values from a well-studied system to obtain results in an ecologically relevant domain and additionally performed a sensitivity analysis. The only sensitivity scenario for which the stabilising effect disappeared, was when handling times were identical on defended and undefended plants. This is exactly what we would expect on the basis of our bitrophic analytical results, where the difference between these handling times was essential for an absence of the paradox of enrichment.

Inducible defences also promoted persistence in the tritrophic food chain, as the minimum densities of oscillating plant, herbivore and carnivore populations remained more strongly bound away from zero. Especially the carnivores were much more vulnerable to large amplitude oscillations in the fixed defence scenarios (Fig. 4). Interestingly, persistence was not promoted in the bitrophic food chain with inducible defences, showing that results from simple predator–prey models may not always apply in a more complex multitrophic context. Closer examination of time series revealed that the minimum densities of defended and undefended plants coincided for each period in the bitrophic case but were shifted in the tritrophic case, owing to differential numerical responses to cycling herbivores. This effectively 'buffered' minimum densities of total biomass (induced + undefended) in the tritrophic food chain.

In natural food webs a variety of species occurs at each trophic level. Differential vulnerability of these species to

consumers may have important community level-consequences (Leibold 1989, Power et al. 1992, Kretzschmar et al. 1993, Grover 1995, Abrams and Walters 1996, Bohannan and Lenski 1999, Hulot et al. 2000, Persson et al. 2001, Steiner 2001). Within-trophic level heterogeneity owing to the presence of both vulnerable and invulnerable prey has been shown to promote stability or persistence (Abrams and Walters 1996, Ruxton and Lima 1997, Bohannan and Lenski 1999, Genkai-Kato and Yamamura 1999). Other stabilising factors include density-dependent mortality (Kirk 1998) and the use of spatial refuges (Jansen 2001). The importance of the above factors may vary in different ecosystems. Prey are often not completely invulnerable (Jeschke and Tollrian 2000); natural mortality may be largely density-independent (Doherty and Fowler 1994, Hixon and Carr 1997); consumers may learn not to handle less preferred prey (Vos 2001); and some habitats may provide little shelter or patchiness. Moreover, most of the above mentioned work has considered bitrophic predator-prey interactions, while natural communities are multitrophic. This work has shown that results on population persistence may be less robust to the addition of trophic levels than results on population stability. Inducible defences promoted the stability of both bitrophic and tritrophic food chains. Future studies will have to explore the relative importance of the various stabilising and destabilising forces in natural ecosystems.

This brings us back to the discrepancy between results from laboratory and field studies. One of the original incentives that led Rosenzweig to his (1971) work on the effects of enrichment was an experiment by Huffaker et al. (1963), that reported the destabilisation of a stable predator-prey system after an increase in the prey's food supply. This 'enrichment' treatment caused both the predator and prey to go extinct. Experimental work on a predator-prey system by Luckinbill (1973, 1974) further supported Rosenzweig's idea (May 1976). Fussmann et al. (2000) recently showed consistent predator extinctions due to extreme cycles, that were a response to an elevated nutrient supply. Persson et al. (2001) also showed increased population variability in edible species in response to enrichment. However, a paradox of enrichment can not always be observed in the field: Murdoch et al. (1998) noted that daphnids and algae have a stable interaction in lakes and reservoirs across a wide range of nutrient levels, although planktonic systems seem good candidates for observing a paradox of enrichment. The presence of both inedible and edible algae may be essential in explaining this result (McCaulley et al. 1999). Our results show that inducible defences in algae and zooplankton are a stabilising factor in bitrophic and tritrophic planktonic systems. Our analytical results suggest that this stabilising effect may occur in any system where inducible defences increase handling

times and thus the maximum ingestion rate of consumers.

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