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The stability of ecosystems: A brief overview of the paradox of enrichment

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In theory, enrichment of resource in a predator–prey model leads to destabilization of the system, thereby collapsing the trophic interaction, a phenomenon referred to as "the paradox of enrichment". After it was first proposed by Rosenzweig (1971), a number of subsequent studies were carried out on this dilemma over many decades. In this article, we review these theoretical and experimental works and give a brief overview of the proposed solutions to the paradox. The mechanisms that have been discussed are modifications of simple predator–prey models in the presence of prey that is inedible, invulnerable, unpalatable and toxic. Another class of mechanisms includes an incorporation of a ratio-dependent functional form, inducible defence of prey and density-dependent mortality of the predator. Moreover, we find a third set of explanations based on complex population dynamics including chaos in space and time. We conclude that, although any one of the various mechanisms proposed so far might potentially prevent destabilization of the predator–prey dynamics following enrichment, in nature different mechanisms may combine to cause stability, even when a system is enriched. The exact mechanisms, which may differ among systems, need to be disentangled through extensive field studies and laboratory experiments coupled with realistic theoretical models.

1. Introduction

Emergence of the classical predator–prey models dates back to the pioneering work of Lotka (1925). Substantial developments have been made in the field of predator–prey evolution by numerous theoreticians and ecologists over the past decades (May 1972; Abrams 2000). However, some controversies related to classical predator–prey interactions still await consensus among investigators. One of these enigmas is popularly known as Rosenzweig's paradox of enrichment. Rosenzweig (1971) showed that, if the carrying capacity of the prey population of a simple predator–prey model is increased sufficiently, the time evolution of the model system deviates from the steady state and exhibits cycles (i.e. limit cycles). For further increase of the carrying capacity, these cycles grow gradually, bringing the abundance of either the prey or the predator or both populations closer and closer to zero; in other words, leading to the extinction of one or more trophic level. On the basis of these observations, Rosenzweig made the following conclusions:

> "*...increasing the supply of limiting nutrients or energy tends to destroy the steady state. Thus man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance.*"

This exciting and innovative result predicted theoretically by Rosenzweig, has attracted the attention of numerous empiricists and theoreticians for the past four decades. A number of theoretical and empirical studies have been done to explain the paradox of enrichment. In this article, our objective is to review, within the boundary of our knowledge, these theoretical and experimental works and give a brief overview of the solutions proposed. Although Rosenzweig's paradox has been well accepted as a classic example of an ecological paradox, the word "paradox" in the phrase "paradox of enrichment" is not yet universally accepted and is interpreted in different ways (Jensen

and Ginzburg 2005). Rosenzweig used "paradox" to express an apparently contradictory role of enrichment in ecosystems: enrichment that is perceived as beneficial for the growth of populations might have the potential to cause destabilization of the ecosystem and eventually extinction of the predator–prey populations. However, in subsequent articles "paradox" has been used to express the discrepancy between the dynamic behaviour of the real predator–prey systems and that predicted by simple predator–prey models (*see* Jensen and Ginzburg 2005). Without dwelling on this dilemma, we intend to give an overall view of the empirical and theoretical works that are directly related to the phrase "paradox of enrichment".

2. Experiments and field observations on the paradox

A number of experiments were carried out to observe the effect of enrichment on the dynamics of simple predator–prey systems. However, most of these experiments rejected the hypothesis that enrichment would essentially destabilize community dynamics.

The handful of experiments cited by many authors which claim destabilization of ecosystems following enrichment include those by Huffaker *et al* (1963), Luckinbill (1973), Veilleux (1979) and Fussmann *et al* (2000). Huffaker *et al* (1963) showed that an increase in the supply of food to herbivorous mites destabilized their interaction with predatory mites, which eventually led to the extinction of both species.

Luckinbill (1973) and Veilleux (1979) conducted their experiments with *Didinium nasutum* as the predator and *Paramecium aurelia* as its prey. In Luckinbill's experiment, when *Paramecium* and *Didinium* were allowed to grow in 6 ml of standard cerophyl medium, the *Didinium* consumed all the prey in a few hours. However, when the medium was thickened with methyl cellulose, the *Didinium–Paramecium* pair went through two or three diverging oscillations over a period of 10–18 days before the *Didinium* became extinct. Harrison (1995) used these data to test the applicability of predator–prey models with different functional responses, and produced an important result: "...reduction of the food supply for the *Paramecium* and/or thickening of the medium could produce a nonoscillating stable steady state for the population densities". In other words, the system was shown to shift from instability to stability when the pressure of the input prey was reduced (Harrison 1995).

In Veilleux's experiment, the outcome of the predator–prey interaction (again with methyl cellulose in the medium) depended upon the concentration of the bacterial nutrient cerophyl present in the medium. Veilleux observed the following: at low cerophyl concentrations the predator and prey coexisted at a numerically stable equilibrium; at intermediate cerophyl concentrations, although the species

coexisted over time, the population densities oscillated with an amplitude related to the cerophyl level. However, at high cerophyl concentrations, the species were unable to coexist (Veilleux 1979). Hence, similar to Luckinbill's experiment, Veilleux's experiment also demonstrated that for a stable coexistence of the predator and prey populations, a reduction in the supply of available prey is needed.

Fussmann *et al* (2000) reported the dynamic behaviour of a two-species aquatic community in a laboratory containing a rotifer–algae system. This experiment also showed that reduction of high nutrient input shifted the system from a region of consistent predator extinction to a region of coexistence.

On the other hand, a number of observations including those by Walters *et al* (1987), Watson and McCauley (1988), Leibold (1989), McCauley and Murdoch (1990), Kirk (1998), Persson *et al* (1993), Persson *et al* (2001), Mazumder (1994), could not support the paradox of enrichment. Analysis of phytoplankton–zooplankton systems with different nutrient inputs demonstrated that the equilibrium density of phytoplankton increases with an increase of total phosphorus (Walters *et al* 1987; McCauley *et al* 1988; Leibold 1989; Mazumder 1994).

McCauley and Murdoch (1990) tested the dynamic behaviour of the freshwater zooplankton *Daphnia* and its algal prey. They reported that the biomass data of these populations collected from lakes and ponds depicted stable and cyclical dynamics caused by interactions between the populations. The cycles in the field data were not of the paradox-of-enrichment type due to the following reasons: the amplitude of the cycles was small, the period equal to a *Daphnia* generation was short, and the cycles were generated by the developmental delay of *Daphnia* (McCauley and Murdoch 1990). Further, they grew the field-collected *Daphnia* and algae populations in nutrient-rich and nutrient-poor tanks. They demonstrated that the addition of nutrients to the experimental tanks had no effect on the amplitude of population cycles of the cladoceran *Daphnia*, and that *Daphnia*–algae populations exhibited similar dynamics in both nutrient-rich and -poor tanks. Moreover, "*Daphnia* populations displayed time-lag cycles in both treatments with amplitudes, periods, and demographic details similar to those observed in field and other tank populations". They concluded that in natural lakes and ponds the biomass of phytoplankton (prey) has no correlation with the amplitude of *Daphnia* (predator) cycles.

However, in 1999, a paper published in *Nature* by McCauley *et al* reported that they found large amplitude cycles in enriched algae–*Daphnia* systems. Their experiment demonstrated that the dynamics of the *Daphnia*–algal system essentially flipped between two coexisting attractors—a stable equilibrium and large amplitude cycles. Only the presence of inedible algae and the production of ephippia

(resting eggs) seemed to be able to change the nature of these cycles towards dynamics with less profound fluctuations in population density.

To test the hypothesis that enrichment of phytoplankton prey will increase the variability and complexity of predator dynamics, Kirk (1998) conducted a laboratory experiment with microcosms containing planktonic rotifer (*Synchaeta pectinata*) as predators and phytoplankton as prey. Prey enrichment was done by directly increasing the input concentration of prey into predator chemostat flasks. Such enrichment reduced the population variability thereby stabilizing the predator–prey dynamics. The reason for this stability, as Kirk found, was the production of some unidentified autotoxin by the rotifers that reduced the population growth rate and individual survival. The result of the experiment showed that enrichment stabilized the population oscillations, and thereby rejected the hypothesis of the paradox of enrichment.

Persson *et al* (2001) conducted experiments in three aquatic food-web configurations with high or low nutrient additions. For this experiment, the basic food web chosen included bacteria, heterotrophic flagellates, algae and small grazers (small cladocerans and rotifers). The three food webs were designed by keeping the basic web unaltered (web I), adding large grazers (web II), and adding both large grazers and fish (web III). The results demonstrated that although the predator–prey dynamics were destabilized by enrichment, changes in both resource edibility and consumer mortality stabilized the dynamics. Moreover, it was found that for a certain degree of enrichment, vulnerable prey responded in accordance with the paradox of enrichment, however, destabilization of the invulnerable prey was insignificant.

3. Theories proposed to resolve the paradox

The serious discrepancy between theoretical expectations and observations in natural predator–prey systems promoted investigators to propose a number of theoretical mechanisms for resolving the paradox of enrichment. Some of these mechanisms followed directly from the experiments conducted previously, others were drawn from theoretical analysis of plausible mathematical models of predator–prey interactions.

3.1 *Presence of inedible prey*

To explain the mismatch between theory and observation, a general class of mechanisms has been developed by expanding the original model of Rosenzweig and MacArther (1963). A common division of prey was made on the assumption that the prey consists of two types of species, only one of which is edible by the predator; the other is inedible (Phillips 1974, Leibold 1989, Kretzschmar *et al* 1993). Grover (1995) studied detailed theoretical analyses on the effects of neutral inedible prey, interfering inedible prey and nutritionally valueless prey. A neutrally inedible prey is generally not consumed by the predator and thus does not directly influence the interaction between the predator and the edible prey. However, these inedible prey can exert control over the nutrient content of edible producers, and it has been shown that the presence of such inedible prey may overturn destabilization following nutrient enrichment (Grover 1995). The experimental work by McCauley and Murdoch (1990) also demonstrated that the presence of inedible prey that acts as a nutrient sponge (Kretzschmar *et al* 1993; Murdoch *et al* 1998) may provide a plausible mechanism to resolve the paradoxical outcome of ecosystem enrichment (McCauley *et al* 1999).

3.2 *Presence of invulnerable prey*

Due to several reasons some individuals among the prey population may appear to the predator in a transitional state between the vulnerable and invulnerable classes. Invulnerability of an individual prey may be either due to its physiological/behavioural state, or its spatial location (Abrams and Walter 1996). Sometimes immobile prey occupy a spatial location where predators cannot gain access and, in such conditions, the predatory risks are greatly reduced thereby making the individual prey invulnerable (Werner and Anholt 1993). Incorporating in the predator–prey models such a dynamic class of prey population that is invulnerable due to spatial location, or has a greatly reduced vulnerability to predators due some potential survival activity associated with its physiology, Abrams and Walter (1996) showed that enrichment cannot destabilize the predator–prey system. When predator–prey systems consisting of an invulnerable class of prey are enriched, the invulnerable class increases in number resulting in an increase in the biomass of the entire prey population. However, increased numbers of invulnerable prey result in an increase in the input of individuals into the vulnerable class making the predator–prey interaction a "donor-controlled" system, and the dynamics of such systems have been shown to be strongly stabilizing (Pimm 1982). The experimental work by Persson *et al* (2001) (discussed in Section 2) supported these theoretical analyses, showing that invulnerable prey may stabilize trophic-level dynamics by replacing more vulnerable prey.

3.3 *Presence of unpalatable prey*

Apart from the class of profitable (edible) and inedible prey, in the context of enrichment of predator–prey systems, some

investigators have emphasized the presence of another class of prey that is less profitable but edible. Because the profitability of such prey is lower than a critical value, even if these prey are consumed at high biomass, the nutritional requirement of the predator population is unfulfilled. These prey are referred to as "unpalatable" (Genkai-Kato and Yamamura 1999, 2000). Analysis of one-predator, two-prey systems (Genkai-Kato and Yamamura 1999) demonstrated that if the predator exhibits optimally selective feeding (e.g. calanoid copepods), the presence of an unpalatable prey efficiently reduces the amplitude of dynamic oscillation following enrichment. Moreover, in an enriched ecosystem the presence of an unpalatable prey prevents the minimum abundance of species from falling below certain values (Genkai-Kato and Yamamura 1999), and thus increases the robustness of stability of the predator–prey systems against enrichment. Following these results they concluded that the profitability of unpalatable prey has the potential to act as a key predictor for the dynamic behaviour of predator–prey systems in nature. Experiments have shown that due to some physical and biological constraints, the quality of food both in planktonic and terrestrial ecosystems sometimes decreases at high biomass. For example, Urabe and Sterner (1996) demonstrated that, though the biomass of algae increases in response to light availability, the P:C ratio of algae, which might be considered as a potential measure of its food quality for the grazer zooplankton, remains fixed up to a certain critical light intensity, and decreases beyond it. There are also examples among plant herbivores which demonstrate that the quality of prey decreases at high abundance due to certain moisture conditions (e.g. Olff *et al* 2002). Recently, Roy and Chattopadhyay (2006a) have proposed a simple phenomenological relationship to describe the degradation of energy value at increased levels of carrying capacity. Theoretical analysis has demonstrated that incorporation of the proposed relationship in simple predator–prey models overturns the possibility of destabilization of community dynamics following enrichment (Roy and Chattopadhyay 2006a).

3.4 *Ratio-dependent functional response*

Dynamic instability due to enrichment of resource supply is generally an outcome of those simple predator–prey models that incorporate functional responses which are fully dependent on prey density. These functional responses are based on the assumptions that predators encounter prey species at random, and that the probability of this encounter depends on prey abundance only. Arditi and Ginzburg (1989) argued that these assumptions may not always be appropriate. They proposed that, if the time scale of population dynamics, at which the models operate differs from the behavioural time scale, it would be reasonable to

assume that trophic function depends on the ratio of prey to predator abundance. Arditi and Ginzburg (1989) termed these uptake functions "ratio-dependent functional response". A number of empirical observations conducted earlier (e.g. Bernstein 1981; Katz 1985) supported the argument of ratio-dependent trophic function. If "ratio-dependent" uptake functions are incorporated, oscillatory instability of the dynamics following an enrichment in carrying capacity does not arise in simple predator–prey models (Arditi and Ginzburg 1989; Arditi and Berryman 1991). However, the acceptance of ratio-dependent functional forms is debated by some ecologists (Okasanen *et al* 1992; Diehl *et al* 1993; Abrams 1994; Gleeson 1994), and a detail of this debate, which is out of the scope of this review, may be found in Abrams and Ginzburg (2000), and Jensen and Ginzburg (2005).

3.5 *Spatial interaction or spatiotemporal chaos*

To study the effects of space and time on interacting species Jansen (1995) extended the scope of the simple Lotka–Volterra system and the Rosenzweig-MacArthur model to a patchy environment. Analysis has demonstrated that spatial interaction can bound the fluctuations of a predator–prey system and regulate the abundance of the populations (Jansen 1995). Moreover, the laboratory experiment of Holyoak (2000) and theoretical works by Jansen and Lloyd (2000) and Jansen (2001) also showed that spatial patches protect predator–prey systems from collapsing due to population extinction following enrichment. Using a standard diffusion-reaction system and a diffusion-reaction system with a cut-off at low population densities, Petrovskii *et al* (2004) demonstrated theoretically that transition to spatiotemporal chaos can prevent species extinction in an enriched ecosystem. Thus, consideration of time and space may efficiently alter the paradoxical outcome of the regular dynamics predicted by simple predator–prey models.

3.6 *Inducible defense*

To study the effects of inducible defences on community stability and persistence, Vos *et al* (2004a, 2004b) analysed models of bitrophic and tritrophic food chains that incorporate consumer-induced polymorphism. They showed that intra-specific heterogeneity in defence levels can overturn the instability following enrichment. Essentially, inducible defenses represent a predator-dependent effect (i.e. indirect interference). These effects are caused by differences in handling times and/or conversion efficiencies between defended and undefended prey. Vos *et al* (2004a) found that the stabilizing effect remains unchanged even if the inducible defences affect the attack rates of consumers.

By bounding the minimum abundance of populations from falling below a minimum value, inducible defences may promote the persistence of predator–prey species in tritrophic food chains (Vos *et al* 2004). Induced defences have also been shown to decelerate the rapid population decline of *Daphnia* under peak predation by fish. Induced defences can thus contribute to the persistence of prey populations in the face of high predation risk by efficient predators (Vos *et al* 2002).

3.7 *Density-dependent predator mortality*

The experiment conducted by Kirk (1998) (discussed in §2) demonstrated that, at high population density rotifers produced some unidentified autotoxin that acted as a source of density-dependent mortality, where the death rate of the predator increases in direct response to an increase in the biomass of the predator (Bazykin 1974). This density-dependent mortality has been shown to stabilize predator–prey dynamics. In general, introduction of a density-dependent mortality term in a simple predator–prey model also theoretically provides a stabilizing effect on enrichment. Gatto (1991) discussed such stability using a predator–prey model with a Holling type II functional response. Apart from autotoxins produced by the predator, density-dependent mortality in the predator can, for other reasons also stabilize predator–prey dynamics (Gatto 1991). A likely situation, as Gatto argued is as follows. For a *Daphnia* algal system, when *Daphnia* are more abundant, either some other predators that are specialized on other prey might switch to *Daphnia*, or *Daphnia* account for a higher proportion of all their predators' diets. In such situations, consideration of density-dependent predator mortality might be reasonable in simple predator–prey models.

3.8 *Effect of toxic food*

It is established that, in the context of ecosystem stability, the energy value or food value of the resource (i.e. prey) is very important (van Baalen *et al* 2001). The caloric content of prey regulates the dynamics of one-predator – two-prey interaction (Roy *et al* 2005). The food value or dietary value is generally determined by the stoichiometry or chemical composition of the resource (i.e. prey) (Jones and Flynn 2005). Thus, a minor change in the stoichiometry of prey may cause a significant change in its quality as a food (Sterner and Elser 2002; Mitra and Flynn 2005). A common reason for this stoichiometric modulation might be the production of toxin (e.g. Flynn *et al* 1996; Calbet *et al* 2002). Toxin-producing phytoplankton in marine ecosystems have a significant role in determining the zooplankton population

density (Chattopadhyay *et al* 2002) and regulating the phytoplankton–zooplankton dynamics (Roy *et al* 2006). Generally, the presence of (common) secondary metabolites in a resource is a major cause for food toxicity (Bartosz 2005). The mixed diets of a predator often contain a measurable amount of toxic chemicals (Bartosz 2005) that act as inhibitory agent for growth. For example, the dietary composition of human food contains some 1.5 g of plant-originated toxic xenobiotics (Dietrich *et al* 2003). Following these observations, Roy and Chattopadhyay (2006b) recently showed that, theoretically, in the context of stability of simple predator–prey systems, the presence of toxic prey is highly significant. Toxic food in a mixed resource may efficiently counteract oscillation (destabilization) arising from enrichment of resource availability. Moreover, at increased resource availability, toxic food that acts as a source of extra mortality may increase the abundance of the predator as well as that of the palatable prey (Roy and Chattopadhyay 2006b).

4. Concluding remarks

A theoretical study predicted that enrichment of an ecosystem may cause dynamic instability leading to extinction of species in a finite time period (Rosenzweig 1971). However, in real ecosystems, destabilization due to enrichment has rarely been observed (Vos *et al* 2004). Also, a number of experiments including those by McCauley and Murdoch (1990), Kirk (1998), Persson *et al* (2001), which directly tested the effect of enrichment, could not support the paradox. Several studies have been conducted over the decades on this popular paradox. The question that has dominated the literature is: "Why is the paradox of enrichment so rarely (if ever) detected in natural systems?" The predominant approach to this question has been to posit novel complexity.

We have summarized the explanations related to the paradox. The mechanisms that have been discussed range from simple extension of the predator–prey model to complex population dynamics, including chaos in space and time. Although the enrichment paradox has been treated as an ecological axiom, a general consensus on the different explanations of the paradox has not been reached. Some theories either directly or indirectly indicate the importance of predator-induced effects. We note that inducible defence is an indirect interference by the predator, density-dependent mortality again is effectively a predator-dependent effect. The proposition of ratio-dependent functional response is a direct incorporation of the predator-dependent effect. It is reasonable to ask whether the phenomenon that was initially proposed by Rosenzweig (1971) is due only to the failure of theoretical understanding of the ecological consequences of simple predator–prey interactions. While most explanations

involve increased and conditional complexity, the suggested shift away from prey-dependent functional responses asks simply for a reconsideration of the basic assumptions of the paradox of enrichment. On the other hand, each of the theories that take into account the presence of an alternative prey (inedible, invulnerable, unpalatable, toxic) are effectively applicable to some specific ecosystems considered.

Despite the fact that a large number of experiments have rejected the hypothesis of the paradox of enrichment, it is interesting to note that certain microsome experiments, as we have already mentioned, do seem to support the paradox of enrichment. The reason is that such systems are suitably simple: they do not have the complexities described by the various "complexity" theories discussed. Moreover, the short generation times of those systems prevent significant interference between predators from emerging. These systems seem to obey the assumptions of Rosenzweig: seemingly all others (including all natural systems) do not.

However, nature is much more complex than models and laboratories. In nature different mechanisms may combine to cause stability, even when a system is enriched, and the exact mechanisms may differ among systems. What we would want is to have a multicausal understanding of important ecological processes (Vos *et al* 2004b). This understanding needs to be achieved through extensive field work and laboratory experiments, coupled with realistic theoretical models. Formulation of a concrete bridge between the response of ecosystems under enrichment and a universally accepted valid model for predator–prey interaction is still an unachieved goal.

Acknowledgement

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