Research

Enrichment can damp population cycles: a balance of inflexible and flexible interactions

Akihiko Mougi and Kinya Nishimura

A. Mougi (mougi@bio-math10.biology.kyushu-u.ac.jp) and K. Nishimura, Graduate School of Fisheries Sciences, Hokkaido Univ., JP–041-8611 Hakodate, Japan. Present address for AM: Dept of Biology, Kyushu Univ., JP–812-8581 Fukuoka, Japan.

Destabilization of one predator–one prey systems with an increase in nutrient input has been viewed as a paradox. We report that enrichment can damp population cycles by a food-web structure that balances inflexible and flexible interaction links (i.e. specialist and generalist predators). We modeled six predator–prey systems involving three or four species in which the predators practice optimal foraging based on prey profitability determined by handling time. In all models, the balance of interaction links simultaneously decreased the amplitude of population oscillations and increased the minimum density with increasing enrichment, leading to a potential theoretical resolution of the paradox of enrichment in non-equilibrium dynamics. The stabilization mechanism was common to all of the models. Important previous studies on the stability of food webs have also demonstrated that a balance of interaction strengths stabilizes systems, suggesting a general rule of ecosystem stability.

The paradox of enrichment has been a central issue of ecosystem stability since Rosenzweig published his influential paper on that subject in 1971 (Rosenzweig 1971). Various models have predicted that environmental enrichment would destabilize one predator–one prey systems, paradoxically leading to species extinction (Rosenzweig 1971, Gilpin 1972, May 1972, Yodzis and Innes 1992). The results of several laboratory studies have supported with these theoretical predications (Huffaker et al. 1963). In contrast, several natural field studies show counterexamples, that is, a nondestabilizing pattern (McCauley and Murdoch 1990). Ecological theory must therefore explain why the paradox of enrichment is observed in simple laboratory communities but not in complex natural systems (Vos et al. 2004).

Theoretical studies have sought to resolve the paradox of enrichment by modifying Rosenzweig's original one predator–one prey system by introducing additional realistic factors. Density-dependent mortality of the predator species (Gilpin 1975, Gatto 1991) and ratio-dependent predation (Arditi and Ginzburg 1989) are examples of possible simple, general stabilizing factors. In actual complex natural systems, however, many factors can complicate the simple one predator–one prey system. For example, McCauley and Murdoch (1990) suggested that the paradox of enrichment does not occur in natural planktonic systems.

Recent theoretical studies involving model systems with three species, such as a tritrophic food chain and a one predator–two prey system/two subpopulation system, have identified several factors that can lead to resolution of the paradox. Resolving factors are a top predator with a type II

functional response (Abrams and Roth 1994) and prey heterogeneity, such as an inedible prey (Kretzschmar et al. 1993), an invulnerable prey (Abrams and Walters 1996), an unpalatable prey (Genkai-Kato and Yamamura 1999), or a prey with an inducible defense (Vos et al. 2004). A few studies have succeeded in showing a non–paradoxical pattern (Kretzschmar et al. 1993, Abrams and Walters 1996, Vos et al. 2004), but others have not (Abrams and Roth 1994, Genkai-Kato and Yamamura 1999).

Different studies use different stability criteria to analyze the stability of systems. Those mentioned above that can resolve the paradox use a local stability analysis (Abrams and Walters 1996, Vos et al. 2004). Classically, many theoretical studies on the paradox of enrichment that have used a local stability analysis have shown a shift from limit cycles to a stable equilibrium point, that is, resolution of the paradox of enrichment, mainly in one predator–one prey systems. It is important and unavoidable for scientists, including ecologists, to understand systems that exhibit non-equilibrium dynamics (Prigogine and Stengers 1984, Huisman and Weissing 1999, Vandermeer 2006). Therefore, several recent studies have tackled the problem of the paradox of enrichment by using non-equilibrium dynamics (Abrams and Roth 1994, Genkai-Kato and Yamamura 1999).

Abrams and Roth (1994) and Genkai-Kato and Yamamura (1999) used the amplitude of population oscillation and minimum density as stability indices instead of a local stability analysis, but they did not succeed in a resolution of the paradox. Abrams and Roth (1994) showed that the changes in the amplitude and period of population density
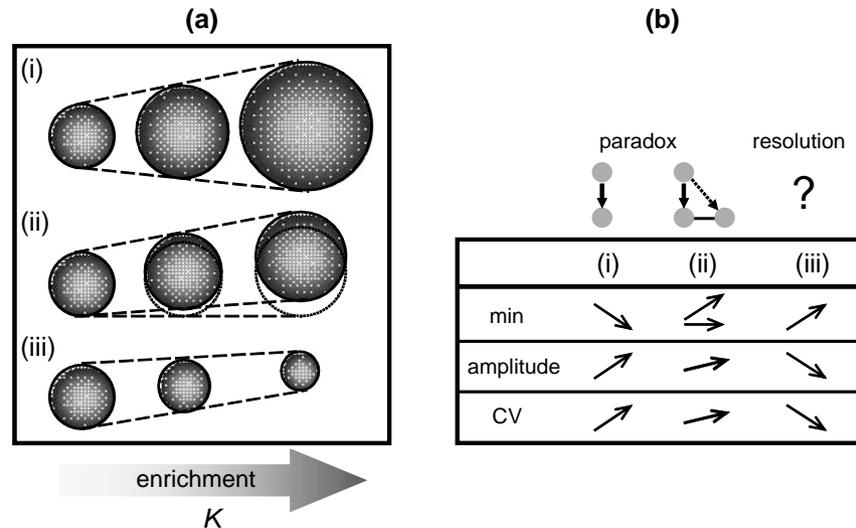
Figure 1. Schematic diagram (a) and summary table (b) of the paradox of enrichment pattern (paradox) and the pattern when the paradox is resolved (resolution). In panel (a), (i)-(iii) are qualitative diagrams of the pattern of oscillation of population densities as the carrying capacity of the basal resource, K, increases (degree of enrichment). Circles qualitatively represent the amplitude of cycles of population density oscillation, and the position of the circles above the horizontal baseline reflects the minimum population density. (i) The paradox of enrichment pattern. (ii) The pattern described by Genkai-Kato and Yamamura (1999). The increase in the amplitude of oscillation with enrichment is less, and the minimum density of populations, except that of one species, increases with enrichment (the dotted circle represents the one species whose minimum density remains constant with the change in K). (iii) The pattern of resolution of the paradox of enrichment. (b) Food-web structures and table summarizing the patterns in panel (a): min, minimum population density; amplitude, amplitude of population density oscillation; CV, coefficient of variation of population density.

oscillation were not monotonic, and that the lowest amplitudes were sometimes associated with greater enrichment. Genkai-Kato and Yamamura (1999) showed moderation of the destabilization pattern with increasing enrichment but did not show a stabilization pattern or resolve the paradox in non-equilibrium dynamics (Fig. 1).

Previously, we identified a single example of a pattern showing resolution of the paradox of enrichment in non-equilibrium dynamics in a two predator–two prey system in which the predator species practiced optimal diet use (Mougi and Nishimura 2007). Under certain conditions, the amplitude of population density oscillations decreased and minimum population density increased with increasing enrichment, thus resolving the paradox of enrichment in a non-equilibrium dynamics system (Fig. 1). Furthermore, we found that the food-web structure of a system is crucial for resolution of the paradox. For the paradox to be resolved, the system must have a flexible and specific food-web structure that involves high exploitative competition between specialist and generalist predators (heterogeneity of predator type). However, we cannot conclude from this finding that this mechanism for resolution of the paradox is generally applicable to a wide range of food-web configurations.

In this paper, we demonstrate resolution of the paradox of enrichment as a theoretical problem using non-equilibrium dynamics in multi-species predator–prey systems, which are configured by adding complexity in some simple basic systems. In these systems, three or four species interact in a flexible food-web resulting from optimal diet use of the predator species, which is modeled by Genkai-Kato and Yamamura (1999) and Mougi and Nishimura (2007). Adding system complexity is a proven method and a first step toward ascertaining the general requirements for

resolution of the paradox. We show that the conditions for resolution of the paradox of enrichment shown in the previous analysis (Mougi and Nishimura 2007) form the core requirements in a wide range of simple food-web configurations, and discuss what this underlying food-web structure has in common with the stable food-web structures modeled by previous studies on food-web stability.

The model

Consider a flexible food web that includes a predator species practicing optimal diet use. We model six tri- or tetra-trophic food chains with flexible omnivorous (a predator can eat two prey species, each of which belongs to a different trophic level) or nonomnivorous (a predator can eat two prey species belonging to the same trophic level) links through optimal diet use by the predators. The possible food-web structures of each model are illustrated on the left or right sides of each of the panels in Fig. 2. Panels (a)–(f) correspond to models numbered 1–6, respectively. In the species connection diagrams in Fig. 2, solid arrows represent fixed links between a predator and a prey species. Dotted arrows represent potentially flexible links between a predator and the less profitable prey species through optimal diet use. The lines linking the two circles in the lowest trophic level represent the presence of interspecific competition.

The dynamics of the density of species i (1, ..., N; N = 3 or 4), X_i, is described by modified versions of the original Rosenzweig model. In each model, species number i is defined in the order shown in Fig. 2; that is, the highest number is the top predator. The basal resource species
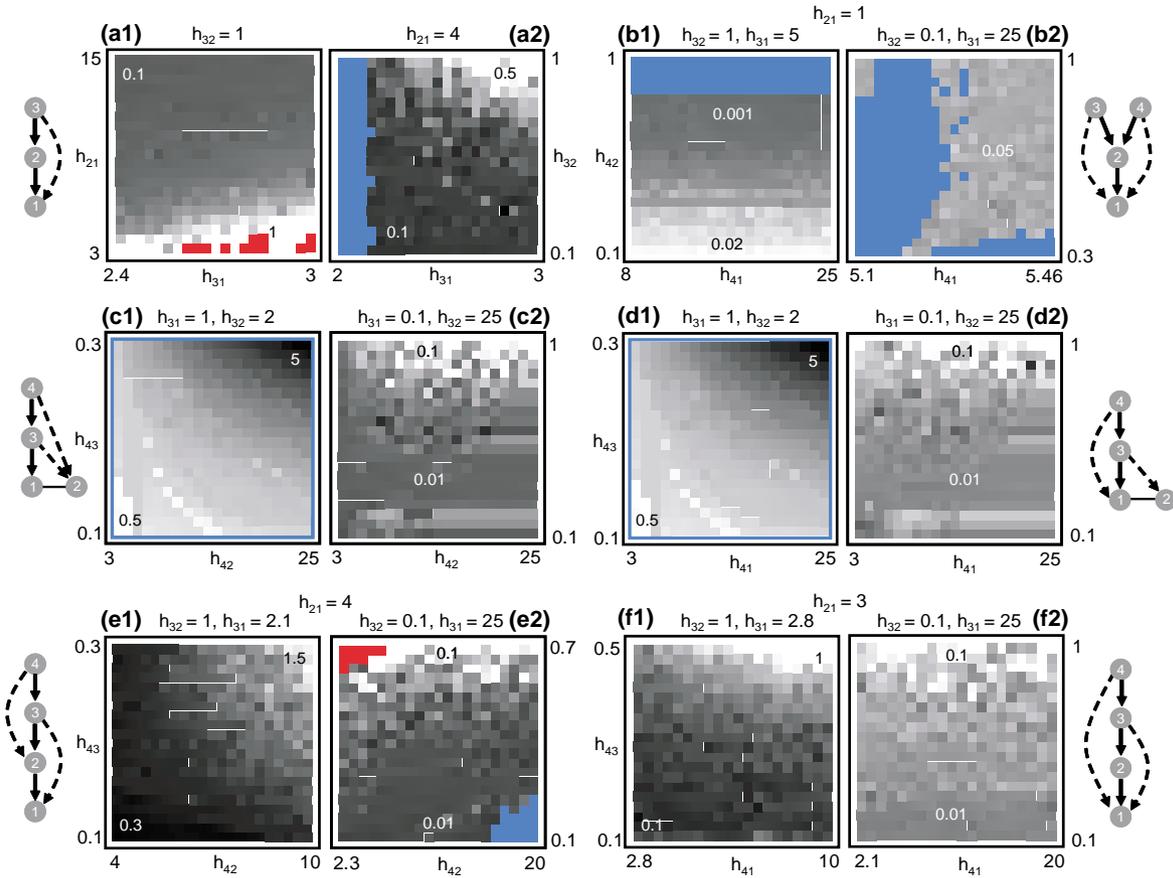
Figure 2. Change in the amplitude of oscillation with increasing enrichment in h_{ij} (handling time) space. We manipulated the enrichment by changing K from 8 to 32 (each pixel represents the outcome of a shift of K). This arbitrary selection of values of K does not influence our results. The parameter settings of h_{ij} are shown above each panel. The other parameter values used in the calculations are $\alpha_{12} = 0.5$, $\alpha_{21} = 0.1$, $\varepsilon = 1$, $b = 1$, $d = 0.25$ (0.1 only in model 2), $r = 0.25$, $g = 0.5$ (the parameter settings does not change our main result). (a)–(f) correspond to models 1–6, respectively. The area surrounded by the blue frame (c1 and d1) or colored blue represents the region where the paradox of enrichment exists. In the area colored red or outside of the parameter space, coexistence cannot occur (but coexistence would occur in (b1), (c), (d), (e2), and (f2) even if larger outlying values on the horizontal axis were shown). In the remaining area, the paradox is resolved. The relative lightness of the gray shading in the panels (except in c1 and d1) represents the degree of stabilization with increasing enrichment (the lighter the shading, the higher the degree of stabilization). In panels (c1) and (d1), the darkness of the shading indicates the degree of destabilization that occurs with increasing enrichment (the darker the shading, the higher the degree of destabilization). The numerical values on the panels indicate the degree of stabilization (or destabilization in c1 and d1). Although the values are relatively small because the calculations are for a limited range of K, they can be larger. The irregular patterns in several panels reflect the chaotic or complex dynamics behavior of those systems.

increases by a growth term, $r_i(1 - f(X_i)/K_i)$ and decreases by a predation term $\sum_{j \in \text{predators}} \mu_{ji}X_j$, where r_i is the per capita intrinsic growth rate; K_i is the carrying capacity, which reflects the degree of enrichment (we follow the classical theory that the effect of enrichment influences only the carrying capacity of prey to maintain comparability with previous studies); and $f(X_i)$ equals X_i in the absence of interspecific competition within a trophic level (models 1, 2, 5 and 6), or $\sum_{k \in \text{resources}} \alpha_{ik}X_k$ in the presence of such competition (models 3 and 4), where α_{ik} are the intra- and interspecific competition coefficients ($\alpha_{ii} = 1$). The term μ_{ji} implies the instantaneous exploitation rate of resource species i by predator species j, defined by a functional response (below).

A predator species belonging to trophic levels above the second trophic level increases by a birth term, $b_i \sum_{j \in \text{preys}} g_{ij}\mu_{ij}X_j$ and decreases by a death term, $\sum_{j \in \text{predators}} \mu_{ji}X_j$,

if the predator is in a middle trophic level, or d_i, if the predator is the top predator. b_i is the conversion efficiency, which relates the predator's birth rate to prey consumption, and d_i is the death rate of predator species i. We assume that the predators are optimal foragers and select their diets based on optimal diet utilization theory (Stephens and Krebs 1986). Each predator includes a prey species in its diet menu, or excludes a species from its diet, on the basis of the prey's profitability in order to maximize its net rate of energy intake while foraging. A predator species that can utilize multiple prey (two prey) consumes its diet according to a prey-dependent type II functional response, $\mu_{ij} = p_{ij}\varepsilon_{ij}/(1 + \sum_{j \in \text{preys}} p_{ij}h_{ij}\varepsilon_{ij}X_j)$, where ε_{ij} is the searching efficiency for prey j; h_{ij} is the handling time of prey j; g_{ij} is the energy value of an individual of prey j; and p_{ij} ($0 \le p_{ij} \le 1$) is the capture probability of an individual of prey species j given an encounter.

Profitability of prey items is ranked by the net energy gain, g, relative to handling time, h, upon an attack. The higher ranked prey species is unconditionally included in the diet menu (i.e. $p = 1$). If the density of the more profitable prey drops below a critical threshold (below), the less profitable prey is also included in the diet menu ($p = 1$). Otherwise, the less profitable prey is excluded from the diet menu ($p = 0$). Inclusion or exclusion of the less profitable prey (i.e. menu variety) depends on the difference in profitability between the prey items and the density of the higher ranked prey item (Stephens and Krebs 1986). The critical threshold is $X_{iH}^{ct} = g_{iL}/\{\varepsilon_{iH}h_{iH}h_{iL}(g_{iH}/h_{iH} - g_{iL}/h_{iL})\}$, where the subscripts H and L represent the ranking of the prey's profitability, indicating the higher and lower ranked prey species, respectively (after Genkai-Kato and Yamamura 1999). In addition, a predator species that cannot utilize multiple prey species (e.g. species 2 in model 1) consumes its diet according to a type II functional response, $\varepsilon_{ij}/(1 + \varepsilon_{ij}h_{ij}X_j)$.

For simplicity, we assume identical values of the parameters b, d (except for model 4), r, g, ε, and K among predators and/or prey (Fig. 2), but the relaxation of this assumption does not influence our story. We manipulate the parameters h_{ij} and K and examine the population dynamics behavior in each model system. As mentioned above, the manipulation of the handling time h_{ij} changes the relative profitability of a prey species or the interaction strength of the predators with their prey. Our main purpose was to investigate how food webs determined by different values of the handling time parameter respond to a change in K.

The handling time h_{ij} reflects the potential interaction strength of a predator species with its prey species ($h_{iH} < h_{iL}$) caused by varying relative densities of prey species (Stephens and Krebs 1986). Hence, we refer to the adaptive predator species with a relatively shorter handling time for the more profitable prey ($h_{iH} \ll 1$) and a relatively longer one for the less profitable prey ($h_{iL} \gg 1$) as a potential specialist (or simply 'specialist'), and the predator with relatively similar, medium-length handling times for both prey ($1 \approx h_{iH} \approx h_{iL}$ or not $h_{iH} \ll 1$ and $h_{iL} \gg 1$) as a potential generalist (or simply 'generalist') (we add 'potential' because the realized food-web links (below) can differ from those predicted from the values of the handling time parameter).

Results

In all systems, the stability of equilibrium changes from stable to unstable (oscillation) at a critical value of K through a Hopf bifurcation. In our analysis, we focus on non-equilibrium dynamics that is realized above the critical value of K that generates a Hop bifurcation, and examine how the oscillation changes with increasing K. The density of each species in the predator–prey communities potentially displays cyclic or chaotic behavior at larger values of K. With a sufficiently long simulation run for evaluation of system stability in the non-equilibrium state, we obtained asymptotic behavior. We numerically calculated changes in population oscillation amplitude (difference between the maximum and minimum densities), minimum density, and the coefficient of variation of population density (CV), each of which is a stability index, with an increase in K in the

wide parameter space of the prey handling time of each predator. Since the trends of changes in stability indices with a change in K were identical for all species, we arbitrarily chose stability changes of a single species (species 1) by which to evaluate the paradox of enrichment.

First, we found that in all models the amplitude of density oscillations can decrease with increasing enrichment (Fig. 2), with a simultaneous increase in the minimum density and a simultaneous decrease in the CV (data not shown), implying a reversal from the paradox of enrichment pattern to a stabilization pattern (Fig. 1); that is, the paradox is completely resolved. Importantly, we note that the amplitude (minimum density) always decreases (increases) with an increase in K after bifurcation. In contrast, Jansen's spatial model shows a rapid increase (decrease) in the amplitude (minimum density) with an increase in K after bifurcation, although the pattern is reversed for larger values of K and the amplitude of oscillation decreases (Jansen 1995).

In model 1, the paradox is resolved in the wide parameter space that allows coexistence (Fig. 2a). In addition, the paradox is likely to be resolved (higher degree of stabilization) if the top predator (species 3) is a generalist (h_{3j} has similar, medium values ($h_{32} \approx 1$; $2.3 < h_{31} < 3$) (Fig. 2a2). In model 2, the paradox is resolved if one top predator (species 3) is a generalist ($h_{32} = 1$; $h_{31} = 5$) and the other (species 4) is a specialist (h_{4j} has dissimilar values, one small and one large ($h_{42} \ll 1$; $h_{41} \gg 1$)) (Fig. 2b1), or vice versa (Fig. 2b2). In addition, the paradox is likely to be resolved at higher levels of specialization of the specialist predator ($h_{42} \ll 1$) (Fig. 2b1). The patterns are quite similar between models 3 and 4 (5 and 6), because the realized food-web structure is the same for the two models (Fig. 3). In both models (3 and 4), if the non-top predator (species 3) is a generalist ($h_{31} = 1$; $h_{32} = 2$), then the paradox of enrichment pattern is found in the entire region of coexistence when the top predator (species 4) specializes in the more profitable prey species (species 3) (Fig. 2c1, 2d1). However, the paradox pattern is moderated at higher levels of specialization of the specialist predator (species 4) ($h_{42} \ll 1$). In contrast, when the non-top predator (species 3) is a specialist ($h_{31} = 0.1$; $h_{32} = 25$), the region of coexistence broadens and a range within which the paradox is resolved appears (Fig. 2c2, 2d2). In addition, the paradox is likely to be resolved when the top predator (species 4) behaves as a generalist ($h_{43} \approx 1$) compared with the non-top predator (species 3). In models 5 and 6, the paradox is resolved over the wide parameter spaces that allow coexistence. In both models, the paradox is resolved if the predator in the third trophic level (species 3) is a generalist ($h_{32} = 1$; $h_{31} = 2.1$ in model 5, and $h_{32} = 1$; $h_{31} = 2.8$ in model 6) and the top predator is a specialist ($h_{43} \ll 1$; $h_{42} > > 1$ in model 5, and $h_{43} \ll 1$; $h_{41} \gg 1$ in model 6) (Fig. 2e1, 2f1). In contrast, when the predator in the third trophic level (species 3) is a specialist ($h_{32} = 0.1$; $h_{31} = 25$), the range within which resolution is achieved broadens (Fig. 2e2, 2f2), and the paradox is likely to be resolved when the top predator (species 4) behaves as a generalist ($h_{43} \approx 1$) compared with the non-top predator (species 3). Finally, note that some parameter spaces of coexistence region are rectangular because the predation pressure on the
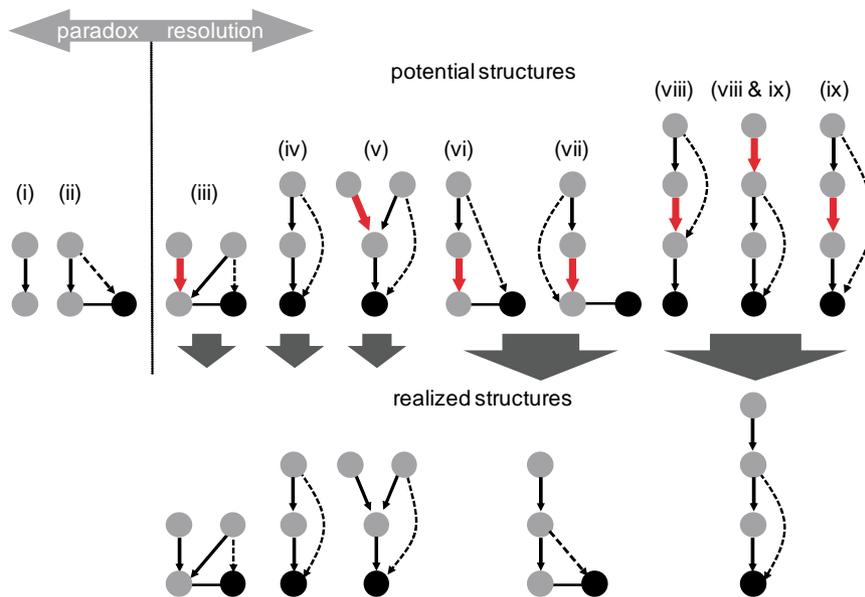
Figure 3. Food-web structures when the paradox of enrichment is not resolved (i-ii) or resolved (iii-ix). (i) and (ii) the structures of the Rosenzweig system and the Genkai-Kato and Yamamura system, respectively. (iii) the system that we analyzed previously (Mougi and Nishimura 2007). (iv)–(ix) models 1–6, respectively, in this study. The structures shown in (iii)–(ix) (upper row) are potential structures reflecting the magnitudes of the handling times. The red arrow indicates a strong link, solid black a weak link, dotted black a flexible weak link. The color of the circles indicates the population density: black circles indicate a much higher density than the gray circles. (viii and ix) the structure for resolution common to models 5 and 6. In structures (vi), (vii), (viii), and (ix), the realized structures (lower row) can differ from the potential structures (upper row). In the realized structures, note that only flexible or inflexible links are indicated.

less profitable prey becomes constant (zero) if the handling time of the less profitable prey is more than a certain value.

We summarize these results as a food-web topology in Fig. 3. The food-web structures in the upper row are the potential structures based on the handling time magnitudes. These structures can change in nature of dynamical oscillations of prey densities and optimal diet use by predators to those shown in the lower row of Fig. 3. Even if the realized food web structures differ from the potential ones, however, they still involve an inflexible and a flexible link (Fig. 3).

Considering all of these results together, the paradox of enrichment in non-equilibrium dynamics is likely to be resolved (higher stabilization with enrichment) when the following conditions hold: (1) the food web has at least one adaptive forager that practices optimal diet use; (2) the adaptive foragers are a potential specialist and a potential generalist (in model 1, the former is not the adaptive forager), leading to realized food web structures that include inflexible and flexible links (Fig. 3); and (3) the food-web system is one in which stable (flexible one predator–two prey subsystem) and unstable (inflexible one predator–one prey subsystem) subsystems are coupled via the trophic chain or by high exploitative competition within a trophic level (Discussion). In the discussion section, we explain why this food-web structure can lead to resolution of the paradox of enrichment by comparing our models with that of Genkai-Kato and Yamamura (1999).

Discussion

Since Rosenzweig suggested that an increase in enrichment paradoxically destabilizes one predator–one prey systems and results in species extinction (Rosenzweig 1971), ecologists have examined empirically and theoretically whether such a paradoxical response of an ecosystem is a universal pattern (McAllister et al. 1972, Luckinbill 1974, Riebesell 1974, Arditi and Ginzburg 1989, McCauley and Murdoch 1990, Yodzis and Innes 1992, Kretzschmar et al. 1993, Abrams and Roth 1994, Grover 1995, Jansen 1995, Abrams and Walters 1996, Kirk 1998, Murdoch et al. 1998, Genkai-Kato and Yamamura 1999, McCauley et al. 1999, Holyoak 2000, Persson et al. 2001, Arditi et al. 2004, Verschoor et al. 2004, Vos et al. 2004, Steiner et al. 2005).

We found that enrichment can damp population cycles (cause stabilization through a decrease in the amplitude of the population density oscillation and an increase in the minimum density with increasing enrichment), provided that the food-web structure behaves flexibly, which depends on optimal diet use by the predator species. Furthermore, and more importantly, stabilization requires a particular food-web structure, which is shared among multiple models. The paradox of enrichment is likely to be resolved in non-equilibrium dynamics when the food web has both a potential specialist (inflexible) predator and a potential generalist (flexible) predator (Fig. 3). Interestingly, the realized food-web structures for resolution of the paradox also involve inflexible and flexible predators, even in those cases in which the realized structure differs from the potential structure, which is based on the magnitudes of the handling times (Fig. 3). The reason why this simple rule regarding inflexible and flexible predators leads to a stabilization pattern with increasing enrichment can be explained by analyzing the population dynamics behavior and comparing the differences in behavior within a model
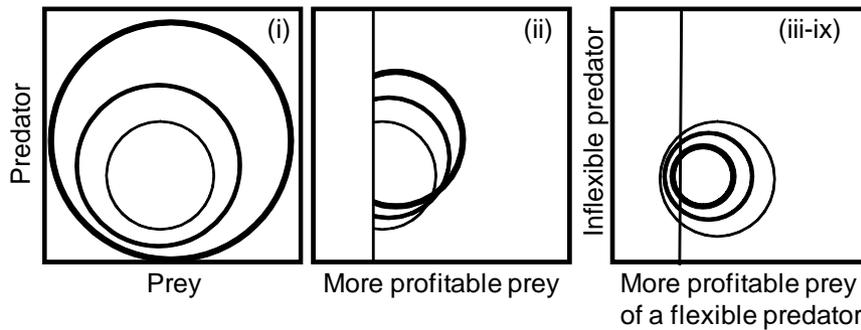
Figure 4. Qualitative patterns of change in population density oscillations with increasing enrichment in the predator–prey systems shown in Fig. 3. The axes are the densities of the indicated species. The diameter of the circles represents the amplitude of the population density oscillation, and the line thickness of the circles represents the value of K: the thicker the line, the higher the enrichment. The vertical lines indicate the critical threshold of prey density, below which the predator switches to use not only the more profitable but also the less profitable prey species (The Model). In (iii–ix), the critical threshold and the more profitable prey shown on the horizontal axis are those for a predator that frequently uses the less profitable prey (flexible predator).

or among models, and then examining each case to determine whether the paradox is maintained or resolved.

Paradox or resolution?

For convenience, we explain the stabilization mechanism by comparing the dynamics behavior among three models, the classic Rosenzweig model (hereafter 'RM'), the Genkai-Kato and Yamamura model ('KYM'), and our general model, which includes all six models described in this study and one model from our previous study (Rosenzweig 1971, Genkai-Kato and Yamamura 1999, Mougi and Nishimura 2007). The three models exhibit qualitatively distinguishable dynamics (Fig. 4). In RM and KYM, the paradox of enrichment is universal. In KYM, the destabilization with increasing enrichment is mitigated to some extent, although the paradox pattern does not disappear. A simple stability mechanism can regulate population oscillations. When the less profitable prey is edible (the authors' term is 'unpalatable'), an optimal forager can stop the decrease in the density of the more profitable prey at a critical threshold (X_{iH}^{ct}); therefore, the minimum density of the predator may become moderately higher, resulting in a decrease in the amplitude of the density oscillations (Genkai-Kato and Yamamura 1999). However, this stability mechanism cannot resolve the paradox of enrichment.

The reason that it cannot is as follows (Fig. 5). When enrichment is low (low K), the less profitable prey functions poorly as supplemental prey because of its relatively low density (even though its density is higher than that of the more profitable prey). Thus, the predator cannot recover until its density decreases enough to allow the density of the more profitable prey to increase above the critical threshold. When enrichment is high (high K), in contrast, the less profitable prey functions nicely as supplemental prey because of its higher density. Thus, the more profitable prey experiences much lower predation pressure when the predator uses both preys, based on a type II functional response, because of the paucity of the more profitable prey, resulting in the rapid recovery of the populations of both the more profitable prey and the predator.

This mechanism can explain the increase in the minimum density of the predator with enrichment. In addition, the unilateral gain of benefit from an increase in enrichment by the less profitable prey can explain the increase in the minimum density of the less profitable prey. However, the amplitudes of the population density oscillations do not decrease but increase with increasing enrichment, because the constant minimum density of the more profitable prey (which is equal to the critical threshold) with increasing
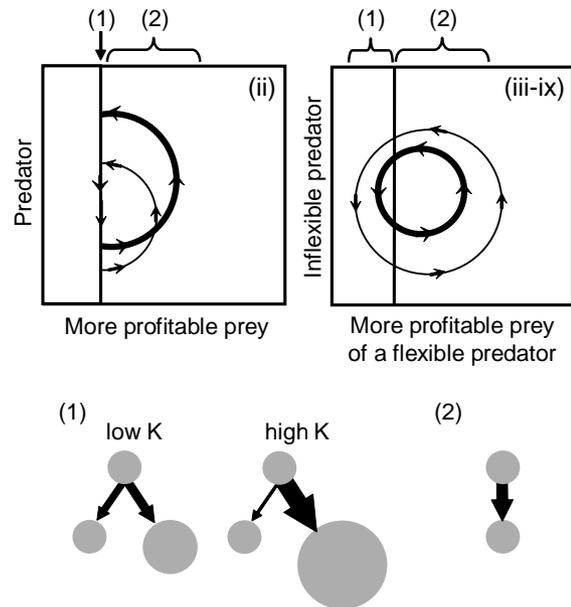

Figure 5. Mechanism for resolution of the paradox of enrichment. The upper two panels correspond to the diagrams for (ii) and (iii-ix) in Fig. 4. (1) and (2) represent the two phases during which a flexible predator uses both prey or only the more profitable prey, respectively. The food webs of phases (1) and (2) are shown below the panels. During phase (1), for both low and high K, the circle at the lower left represents the more profitable prey and that on the lower right represents the less profitable prey (in (iii-ix), whether the two prey species belong to the same trophic level or not depends on the model). The size of each circle qualitatively represents the population density. The arrow size qualitatively represents the degree of predation pressure.

enrichment is not high enough for the predator to suppress increases in the populations of the prey species; thus, the system can be approximately characterized as a one predator–one prey system, which shows the paradox of enrichment.

Food-web structure for resolution of the paradox of enrichment

Our general model is qualitatively different from KYM. Structurally, we model a system in which stable (one flexible predator–two prey subsystem) and unstable (one inflexible predator–one prey subsystem) subsystems are coupled via the trophic chain (models 1 and 3–6) or by high exploitative competition within a trophic level (model 2 and our previous model; Mougi and Nishimura 2007) (Fig. 3). As shown in Fig. 4, this coupling effect can decrease the density of the more profitable prey for a flexible predator, which actually uses the less profitable prey frequently, to a point below the critical threshold for the flexible predator, in contrast to KYM (Mougi and Nishimura 2007).

This common dynamics behavior is crucial for resolution of the paradox of enrichment. Here, we briefly explain why an inflexible and a flexible adaptive predator results in such dynamics behavior. For example, in a two predator–two prey system in which the more profitable prey is common to the predators, the inflexible predator can decrease the density of the more profitable prey of the flexible predator to a point below the critical threshold for the flexible predator, because the critical threshold for the inflexible predator is lower than that for the flexible predator (Mougi and Nishimura 2007). This mechanism also applies to model 2. In model 1, a flexible predator can decrease the density of its more profitable prey (which is also the inflexible predator) to a point below the critical threshold because the flexible predator uses not only its more profitable prey but also the prey of its more profitable prey. For brevity, we omit the explanations of the other models.

Briefly, the common dynamics behavior (Fig. 4) results from the potential stability of the flexible predator–two prey subsystem (shown by KYM) being destabilized by another, inflexible predator. In addition, in our general model, the less profitable prey of a flexible predator has higher density than the other prey species because of low predation pressure (black circles in Fig. 3), as is also true in KYM (as described above).

Stabilization mechanism

We emphasize two features of our model systems. First, our models show dynamics behavior in which the density of the more profitable prey of a flexible predator is reduced to a point below the critical threshold for the flexible predator by an inflexible predator. This is different from what occurs in KYM and is crucial for resolution of the paradox of enrichment. Second, and also important, as in KYM, the less profitable prey has a much higher density than the other prey species. These factors can explain the mechanism that allows resolution of the paradox of enrichment (Fig. 5). As

in KYM, the less profitable prey functions nicely as supplemental prey under higher enrichment. Thus, the degree of relaxation of predation pressure on the more profitable prey by a flexible predator while that predator continues to use both prey species is greater under higher enrichment. This raises the minimum density of the more profitable prey (note that this phenomenon does not occur in KYM), which increases the minimum density of the predator themselves resulting in the smaller amplitude of population density oscillations (Fig. 5, Mougi and Nishimura 2007). In fact, this stability mechanism can also work in KYM; however, the constant minimum density of the more profitable prey with enrichment precludes a pattern of stabilization with enrichment (above). In other words, the coupling of an unstable inflexible predator–prey subsystem with a stable flexible predator–prey subsystem can change the effect of increasing prey density caused by enrichment on system stability from one of destabilization to one of stabilization.

Limitations of the model

Our models are based on several assumptions. In order to focus on commonalities among food-web structures and to enable comparison with previous studies (Rosenzweig 1971, Genkai-Kato and Yamamura 1999, Mougi and Nishimura 2007), we ignored several realities, such as other types of adaptive behavior (Fryxell and Lundberg 1994, Ma et al. 2003), spatial structure (Jansen 1995), the dynamic energy value of prey according to intracellular nutrient content and stoichiometry (Anderson et al. 2004), and the possibility that prey responses vary with enrichment. The relaxation of these assumptions may influence our results. But we know that the error effect which prevents perfect optimal diet use (Fryxell and Lundberg 1994, Ma et al. 2003) and the effects of evolution of the foraging effort (Kondoh 2003) and the prey's defense (Yamauchi and Yamamura 2005) can lead to resolution of the paradox of enrichment (Mougi and Nishimura unpubl.).

At the least, our result holds for different food-web structures. In this study, we modeled food-web systems having no more than four trophic levels, four species, and two direct interaction links. Although in the natural world, there are usually fewer than four trophic levels (Pimm 1991), natural systems can obviously have many species and many direct interaction links. Nevertheless, a mechanism that does not depend on species number or food-web structure (Fig. 3) may be little affected by these differences. Future research will clarify whether the stabilization mechanism is applicable to more realistic complex food-web systems (Kondoh and Mougi unpubl.).

The present study focused on non-equilibrium dynamics. Thus, our approach to a theoretical problem, the paradox of enrichment, is not valid for stable systems at relatively low values of K, but only for unstable systems at values of K much higher relatively (The systems are stable for lower values of K, and unstable for higher values of K). This implies that the paradox of enrichment occurs within a narrow range of low values of K but the pattern shifts suddenly to a resolution of the paradox at relatively higher values of K. In other words, our results do not show a true

resolution pattern in which the system stabilizes with enrichment monotonically if we consider the entire range of K. Theoretical studies that use a local stability analysis demonstrate a type of resolution of the paradox in equilibrium dynamics: a stable equilibrium that is not influenced by enrichment (Arditi and Ginzburg 1989, Abrams and Walters 1996, Arditi et al. 2004, Vos et al. 2004). The pattern demonstrated by these theoretical studies may be close to the pattern observed in the rare natural field study by McCauley and Murdoch (1990). However, not all natural populations exist in a stable equilibrium state. We show that a combination of inflexible and flexible food-web links can promote the persistence of enriched non-equilibrium communities.

Factors for resolution of the paradox of enrichment

Previous studies have proposed a number of theoretical mechanisms for resolving the paradox of enrichment. Some theories either directly or indirectly indicate the importance of predator-induced effects such as a ratio-dependent functional response, density-dependent predator mortality, and an inducible defense (Arditi and Ginzburg 1989, Gatto 1991, Vos et al. 2004). Others indicate the importance of spatial interaction (Jansen 1995, Petrovskii et al. 2004, Klepac et al. 2007). These are simple modifications of Rosenzweig's model of a one predator–one prey system and may be generally applicable in various simple ecosystems.

In addition, some theories assume the presence of an alternative prey such as an inedible, invulnerable, unpalatable, or toxic prey (Kretzschmar et al. 1993, Abrams and Walter 1996, Genkai-Kato and Yamamura 1999, Roy and Chattopadhyay 2007a). These models may be applicable to some specific ecosystems (Roy and Chattopadhyay 2007b). In short, previous theoretical studies have focused mainly on simple predator–prey systems (but see Rall et al. 2008), and it is unclear whether their findings are applicable to complex food-web systems.

In our study, we suggest a mechanism for resolution of the paradox of enrichment that is applicable to various complex food-web systems. In nature, however, different mechanisms may combine to cause stability in an ecosystem, and the mechanisms that operate in specific ecosystems may differ. Obviously, ecologists need to collect and compare appropriate empirical data and theoretical predictions until intuition, theory, and empirical observations are harmonized (Jensen and Ginzburg 2005) and the stability–productivity relationship is understood.

Paradoxes in community ecology

Theoretical studies on food-web stability have suggested that a weak interaction can strongly promote stability (McCann et al. 1998, McCann 2000, Neutel et al. 2002). Flexible interaction based on optimal foraging falls under the category of a weak interaction. Kondoh (2003) suggested that theoretically an adaptive forager resolves the 'paradox of diversity–stability,' which refers to the question of how complex ecological communities can persist (May

1972), leading to a positive complexity–stability relationship in a flexible food web.

In addition, Kondoh (2003) proposes that a stable food web must have a few strong and many weak links, as do food webs in the real world. Huisman and Weissing (1999) suggested that the intrinsic instability of a competitive system resolves the 'paradox of the plankton' (Hutchinson 1961), leading to cyclic or chaotic coexistence of many competing species (Huisman and Weissing 1999, but see Vos et al. 2001). This planktonic system (Huisman and Weissing 1999) can also be interpreted to involve irregular flexible weak and strong interactions through the non-linear dynamics of species densities. These studies consistently suggest that a balance of strong and weak interactions, which have stabilizing and destabilizing power, respectively, is crucial for stability of the entire food web.

The study of the paradox of enrichment is therefore an exciting topic in studies of food-web stability. In this regard, our results also suggest that a balance between strong (inflexible or specialist) and weak (flexible or generalist) interactions both is crucial for the stability of food webs and resolves the paradox of enrichment. In other words, there is a beautiful commonality regarding the stability mechanism of ecosystems that transcends specific topics and may thus portend a general rule of ecosystem stability.

Stability paradoxes in ecology can be linked and need to be resolved by a common mechanism. In fact, the destabilizing effects of connectance and enrichment can be inverted into stabilizing effects in more realistic food-web models (Rall et al. 2008). Our inflexible–flexible interaction mechanism may thus contribute to the resolution of the classical paradoxes in ecology (Kondoh and Mougi unpubl.).

Concluding remarks

Our results suggest that, as a theoretical exercise, a balance of inflexible and flexible interactions can be one factor that allows resolution of the paradox of enrichment. Until now, many studies have suggested factors that might contribute to resolution of the paradox of enrichment (Gilpin 1975, Arditi and Ginzburg 1989, Kretzschmar et al. 1993, Jansen 1995, Abrams and Walters 1996, Murdoch et al. 1998, Vos et al. 2004, Abrams and Quince 2005). We do not know if our proposed factor allowing resolution operates in the natural planktonic community system which is often the subject of empirical studies. However, future empirical studies will confirm the general applicability of flexible changes of food-web links depending on adaptive change in morphology and behavior (Kondoh 2003, Vos et al. 2004). At the least, our results contribute one factor that can lead to resolution of the theoretical problem 'the paradox of enrichment'. In particular, our study is important because of the rarity of theoretical research on the paradox of enrichment that is based on multi-species predator–prey systems and non-equilibrium dynamics (but see Rall et al. 2008).

Finally, our findings have relevance with regard to conservation efforts. Since a food-web structure that balances inflexible and flexible interactions, each of which

is potentially stabilizing or destabilizing, can be robust in the face of enrichment, the loss of a single species interaction from a food web, even one that is potentially destabilizing, may crucially affect the food web's robustness in a changing environment, such as one experiencing an increase in productivity.

References

Abrams, P. A. and Roth, J. D. 1994. The effect of enrichment of three-species food chains with nonlinear functional responses. – Ecology 75: 1118–1130.

Abrams, P. A. and Walters, C. J. 1996. Invulnerable prey and the paradox of enrichment. – Ecology 77: 1125–1133.

Abrams, P. A. and Quince, C. 2005. The impact of mortality on predator population size and stability in systems with stage-structured prey. – Theor. Popul. Biol. 68: 253–266.

Anderson, T. et al. 2004. Stoichiometry and population dynamics. – Ecol. Lett. 7: 884–900.

Arditi, R. and Ginzburg, L. R. 1989. Coupling in predator–prey dynamics: ratio-dependence. – J. Theor. Biol. 139: 311–326.

Arditi, R. et al. 2004. Does mutual interference always stabilize predator–prey dynamics? A comparison of models. – Compt. Rend. Biologies 327: 1037–1057.

Fryxell, J. M. and Lundberg, P. 1994. Diet choice and predator–prey dynamics. – Evol. Ecol. 8: 407–421.

Gatto, M. 1991. Some remarks on models of plankton densities in lakes. – Am. Nat. 137: 264–267.

Genkai-Kato, M. and Yamamura, N. 1999. Unpalatable prey resolves the paradox of enrichment. – Proc. R. Soc. Lond. B 266: 1215–1219.

Gilpin, M. E. 1972. Enriched predator–prey systems: theoretical stability. – Science 177: 902–904.

Gilpin, M. E. 1975 Group selection in predator–prey communities. – Princeton Univ. Press.

Grover, J. P. 1995. Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants. – Am. Nat. 145: 746–774.

Holyoak, M. 2000. Effects of nutrient enrichment on predator–prey metapopulation dynamics. – J. Animal. Ecol. 69: 985–997.

Huffaker, C. B. et al. 1963. Experimental studies on predation: complex dispersion and levels of food in an acarine predator–prey interaction. – Hilgardia 34: 305–330.

Huisman, J. and Weissing, F. J. 1999. Biodiversity of plankton by species oscillations and chaos. – Nature 401: 407–410.

Hutchinson, G. E. 1961. The paradox of the plankton. – Am. Nat. 95: 137–145.

Jansen, V. A. A. 1995. Regulation of predator–prey systems through spatial interactions: a possible solution to the paradox of enrichment. – Oikos 74: 384–390.

Jensen, C. X. J. and Ginzburg, L. R. 2005. Paradoxes or theoretical failures? The jury is still out. – Ecol. Modell. 188: 3–14.

Kirk, K. L. 1998. Enrichment can stabilize population dynamics: autotoxins and density dependence. – Ecology 79: 2456–2462.

Klepac, et al. 2007. Dispersal delays, predator–prey stability, and the paradox of enrichment. – Theor. Popul. Biol. 71: 436–444.

Kondoh, M. 2003. Foraging adaptation and the relationship between food web complexity and stability. – Science 299: 1388–1391.

Kretzschmar, M. et al. 1993. A predator–prey model for zooplankton grazing on competing algal populations. – Theor. Popul. Biol. 44: 32–66.

Luckinbill, L. S. 1974. The effect of space and enrichment on a predator–prey system. – Ecology 55: 1142–1147.

Ma, B. O. et al. 2003. Dynamic versus instantaneous models of diet choice. – Am. Nat. 162: 668–684.

May, R. M. 1972. Will a large complex system be stable? – Nature 238: 413–414.

McAllister, C. D. et al. 1972. Stability of enriched aquatic ecosystems. – Science 175: 562–564.

McCann, K. S. 2000. The diversity–stability debate. – Nature 405: 228–233.

McCann, K. S. et al. 1998. Weak trophic interactions and the balance of nature. – Nature 395: 794–798.

McCauley, E. and Murdoch, W. W. 1990. Predator–prey dynamics in environments rich and poor in nutrients. – Nature 343: 455–457.

McCauley, E. et al. 1999. Large-amplitude cycles of *Daphnia* and its algal prey in enriched environment. – Nature 402: 653–656.

Mougi, A. and Nishimura, K. 2007. A resolution of the paradox of enrichment. – J. Theor. Biol. 248: 194–201.

Murdoch, W. W. et al. 1998. Plankton abundance and dynamics across nutrient levels: tests of hypotheses. – Ecology 79: 1339–1356.

Neutel, A. M. et al. 2002. Stability in real food web: weak links in long loops. – Science 296: 1120–1123.

Persson, A. et al. 2001. Effects of enrichment on simple aquatic food webs. – Am. Nat. 157: 654–669.

Petrovskii, et al. 2004. Transition to spatiotemporal chaos can resolve the paradox of enrichment. – Ecol. Complex. 1: 37–47.

Pimm, S. L. 1991. The balance of Nature? – Univ. of Chicago Press.

Prigogine, I. and Stengers, I. 1984. Science and Change. – Bantam Books.

Rall, B. C. et al. 2008. Food-web connectance and predator interference dampen the paradox of enrichment. – Oikos 117: 202–213.

Riebesell, J. F. 1974. Paradox of enrichment in competitive systems. – Ecology 55: 183–187.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. – Science 29: 385–387.

Roy, S. and Chattopadhyay, J. 2007a. Enrichment and ecosystem stability: effect of toxic food. – Biosystems 90: 151–160.

Roy, S. and Chattopadhyay, J. 2007b. The stability of ecosystems: a brief overview of the paradox of enrichment. – J. Biosci. 32: 421–428.

Steiner, C. F. et al. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. – Ecol. Lett. 8: 819–828.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press.

Vandermeer, J. 2006. Oscillating populations and biodiversity maintenance. – BioScience 56: 967–975.

Verschoor, A. M. et al. 2004. Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. – Ecol. Lett. 7: 1143–1148.

Vos, M. et al. 2001. Does 'supersaturated coexistence' resolve the 'paradox of the plankton'? – Ecol. Lett. 4: 404–407.

Vos, M. et al. 2004. Inducible defences and paradox of enrichment. – Oikos 105: 471–480.

Yamauchi, A. and Yamamura, N. 2005. Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. – Ecology 86: 2513–2524.

Yodzis, P. and Innes, S. 1992. Body size and consumer–resource dynamics. – Am. Nat. 139: 1151–1175.