ORIGINAL ARTICLE

Implications of resting eggs of zooplankton for the paradox of enrichment

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Abstract In this study, we numerically investigated to
what extent introducing resting-egg dynamics would sta-
bilize simple *Daphnia*–algae consumer–resource models.
In the models, the density of viable resting eggs was
explicitly expressed, and we assumed that zooplankton
produced resting eggs seasonally or in response to food
deficiency and that resting eggs hatched seasonally. The
models predicted that, although the paradox of enrichment
was not completely resolved (i.e., the system was desta-
bilized by eutrophication), we found the following condi-
tions under which the stabilizing effects of resting eggs
would be significantly large: (1) resting eggs are produced
seasonally (rather than in response to food deficiency), (2)
the annual average allocation ratio to resting eggs is large,
and (3) the annual average hatching rate of resting eggs is
low. The results suggest that resting-egg dynamics can
significantly reduce the paradox of enrichment within the
biologically meaningful parameter space and contribute to
the stability of plankton community dynamics.

Introduction

In a simple consumer–resource model in which the resource
grows logistically and the consumer has a Holling's type II
functional response, increases in productivity are predicted
to destabilize the system (Rosenzweig and MacArthur
1963), increasing the amplitude and decreasing the mini-
mum density of population oscillations. This prediction
suggests that extinction risk due to stochasticity or envi-
ronmental fluctuations becomes higher under eutrophic
conditions. Cautioning against the danger of eutrophication
in lake ecosystems, Rosenzweig (1971) called this phe-
nomenon "the paradox of enrichment."

However, even under eutrophic conditions, such catas-
trophes are not always observed (e.g., McAllister et al.
1972; McCauley and Murdoch 1990), indicating that nat-
ural ecosystems potentially have stabilizing factors that
negate the destabilizing effects of eutrophication. The
elucidation of these stabilizing factors has been the subject
of intensive research efforts in ecology, and many
researchers have addressed this problem using empirical or
theoretical approaches (see "Discussion" for references).
The zooplankton-phytoplankton system is the most
extensively studied one.

In this study, we consider the situation where zoo-
plankton produce resting eggs (dormancy stage), which is
an alternative reproductive strategy widespread among
zooplankton (reviewed by Gyllström and Hansson 2004).
McCauley et al. (1999) experimentally observed that
Daphnia population dynamics became less stable in a

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Daphnia–algae microcosm system when *Daphnia* individuals having resting eggs were replaced by the same number of individuals having subitaneous eggs. Then, they suggested that resting-eggs "production" would be stabilizing. However, the data collected by McCauley et al. (1999) spanned less than 1 year, which implies that resting-egg "dynamics" and the long-term effect of egg banks were not evaluated. Motivated by this problem, Kuwamura et al. (2009) mathematically showed the possibility that consumer dormancy depending on resource availability would have stabilizing effects on a consumer–resource system.

In the present study, we extend the previous model (Kuwamura et al. 2009) to include the following considerations. Kuwamura et al. (2009) assumed that food deficiency induced dormancy, as McCauley et al. (1999) suggested. However, it is not the only major factor. We consider two major mechanisms underlying resting-egg production in zooplankton species living in permanent, temperate lakes (see the review by Gyllström and Hansson 2004). The first is seasonality; zooplankton produce resting eggs mainly in late autumn in response to short photoperiods or low water temperatures as portents indicating harsh environmental conditions in winter. According to a review by Gyllström and Hansson (2004), it seems that Cladocera and Copepoda have this tendency. The second trigger is food deficiency, as assumed by Kuwamura et al. (2009). In addition, we consider that the hatching of resting eggs also occurs seasonally, mainly in spring (Hairston et al. 2000), while it was assumed to be constant in the previous model (Kuwamura et al. 2009). The triggering stimuli are usually long photoperiods or high water temperatures. As a result, resting-egg production is thought to be an adaptive strategy for low food availability in winter (Gyllström and Hansson 2004). Although other factors are also known to influence resting-egg production (e.g., fish kairomones, Pijanowska and Stolpe 1996; Ślusarczyk et al. 2005; maternal effects or time delay, Alekseev and Lampert 2001; LaMontagne and McCauley 2001; crowding, Rose et al. 2002) or hatching (e.g., pH, Schönbrunner and Eder 2006), these factors seem to be minor (Gyllström and Hansson 2004), and therefore are not considered in this study (see "Discussion" for expected influences on dynamics).

We also address another problem. Although Kuwamura et al. (2009) evaluated the stabilizing effects of resting eggs in a qualitative manner, using a simple analytical model, it is still uncertain to what extent introducing resting-egg dynamics effectively resolves the paradox of enrichment. Therefore, in the present study, we attempt to evaluate qualitatively the potential stabilizing effects of resting eggs based on the original simple (i.e., Rosenzweig–MacArthur) model. Note that our aim is neither to reproduce plankton community dynamics in natural or experimental systems nor

to compare them virtually with and without resting eggs. We are not interested in developing realistic models including all known factors affecting population dynamics such as age/size structure, spatial structure, and trophic interactions with other species. Rather, the present study is specifically aimed at re-examining the potential for resolving the paradox of enrichment by introducing resting-egg dynamics within the biologically meaningful parameter space. We also aim to compare the stabilizing effects of resting eggs induced by seasonality and food deficiency. For these purposes, we develop two types of minimal consumer–resource models in which we independently assume two triggers inducing resting-egg production: seasonality and food deficiency. In both cases, we assume the seasonality of resting-egg hatching.

Models

We use a simple consumer–resource model that takes into account resting-egg dynamics.

$$\frac{dP}{dt} = r\left(1 - \frac{P}{K}\right)P - f(t)Z_1 \tag{1a}$$

$$\frac{dZ_1}{dt} = g(t)cf(t)Z_1 - d_1Z_1 + h(t)Z_2 \tag{1b}$$

$$\frac{dZ_2}{dt} = \{1 - g(t)\}cf(t)Z_1 - d_2Z_2 - h(t)Z_2, \tag{1c}$$

where

$$f(t) = \frac{aP(t)}{b + P(t)}, \tag{1d}$$

P, Z_1, and Z_2 are the densities of phytoplankton, active zooplankton, and viable resting eggs of zooplankton, respectively. For simplicity, we consider neither the gender of the zooplankton nor differences in the quality of offspring from subitaneous and resting eggs (but see Arbačiauskas and Lampert 2003). r and K are the intrinsic growth rate and carrying capacity of the phytoplankton, respectively. In this model, we define that increasing K values indicate eutrophication. The per-individual foraging rate is a Holling's type II functional response (Eq. 1d) in which a and b represent the maximum foraging rate and the half saturation constant, respectively. $h(t)$ is the seasonally changing hatching rate of resting eggs. The most accepted, although simple, way of modeling seasonality is to use a sinusoidal function (e.g., Rinaldi et al. 1993; Scheffer et al. 1997; Takimoto et al. 2002):

$$h(t) = h_a\left\{1 + h_s \sin\left(\frac{2\pi}{T}t\right)\right\}, \tag{1e}$$

where h_a, h_s, and T are the average hatching rate, the degree of seasonality, and the period of the seasonal cycle,

respectively. We assume that the hatching rate of resting eggs peaks in spring (Hairston et al. 2000). The per-individual foraging gain for zooplankton $f(t)$ is converted to reproductive energy with the efficiency c, and allocated to subitaneous and resting eggs with a ratio of $g(t):[1 - g(t)]$. Note here that the model is formulated at population level; i.e., $g(t)$ expresses the frequency of resting-egg-producing individuals in the population. d_1 and d_2 are the death (or loss) rates of the active zooplankton and resting eggs, respectively. Resting eggs are lost through sedimentation or predation by benthic animals (Parker et al. 1996). Other parameters may also change seasonally. However, we do not consider these because we focus on potential stabilizing effects of resting-egg dynamics (see Rinaldi et al. 1993 for influences of seasonality of other parameters).

We deal with two cases of the allocation ratio of reproductive energy $g(t)$, depending on the triggers inducing resting-egg production.

Seasonality

First, we assume that zooplankton produce resting eggs seasonally.

$$g(t) = g_a \left\{ 1 + g_s \sin\left(\frac{2\pi}{T} t\right) \right\}, \tag{2}$$

where g_a is the average proportion of reproductive energy allocated to subitaneous eggs and g_s is the degree of seasonality. Equation 2 explains that reproductive energy allocated to subitaneous eggs is reduced in autumn (Gyllström and Hansson 2004). If $(g_a, g_s) = (1, 0)$, then $g(t) = 1$ and the zooplankton do not produce resting eggs, resulting in a conventional two-variable model. Note also that $g(t)$ should range between zero and one.

Food deficiency

Next, we assume that zooplankton produce resting eggs in response to food deficiency. We model a shift in zooplankton's reproductive investment from subitaneous to resting eggs when the foraging gain $f(t)$ declines below a certain threshold, using the switching function in the same manner as described by Kuwamura et al. (2009).

$$g(t) = \frac{1}{2}\left[1 + \tanh\left\{\frac{f(t) - x}{y}\right\}\right]$$
$$= \frac{1}{1 + \exp[-2\{f(t) - x\}/y]}. \tag{3}$$

For small y, $g(t)$ converges to one (or zero) asymptotically with increasing (or decreasing) $f(t)$. In fact, such a switch response has been reported in empirical works (e.g., Carvalho and Hughes 1983). Here, x is the threshold of the foraging gain for producing resting eggs, and y captures the

smoothness of the switching (the curve is steep when y is small). When $x = 0$ and y converges to zero, we obtain a two-variable model without resting-egg dynamics.

We compare system stability between the cases where $g(t) = 1$ and $g(t)$ is defined by Eq. 2 or 3 using numerical simulations to investigate to what extent the system would be more stable in the latter cases. A consumer–resource model that includes seasonality can predict complex behaviors such as chaos (e.g., Rinaldi et al. 1993; Scheffer et al. 1997). However, we do not examine the details of such behaviors, because our models generally exhibited clear annual cycles, although with some noise (see below). In addition, we are confronted with the paradox of enrichment (i.e., extinction risk due to large population oscillations under eutrophic conditions). As such, we evaluate the variability and persistence along a eutrophication gradient K, calculating the oscillation amplitudes (i.e., the difference between the maximum and minimum densities) and the minimum densities of the phytoplankton and zooplankton population dynamics for the last 10 years of 30-year (T) simulations.
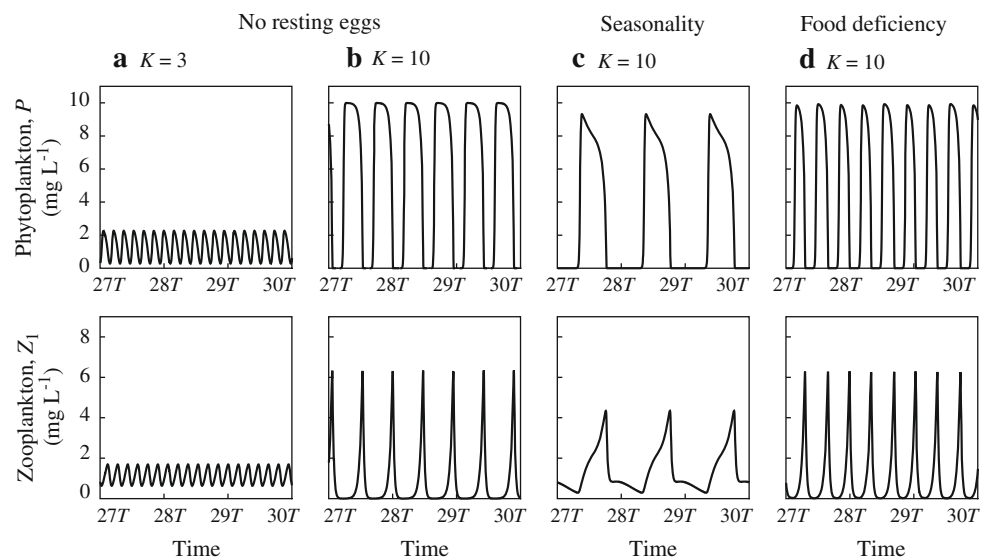
Parameterization

Some parameters describing standard zooplankton–phytoplankton dynamics are chosen from a previous study of the paradox of enrichment in a *Daphnia*–algae system (Scheffer and De Boer 1995; Table 1). Meanwhile, it is difficult to parameterize the resting-egg dynamics because of limited data. First, we set $d_2 = 5.0 \times 10^{-5}$ as default based on the small amount of research that estimated about 1% egg mortality rate per year (Hairston et al. 1995). However Hairston et al. (1995) studied copepod resting eggs. In addition, because they measured resting-egg density in sediments, their estimation may not include loss of viable resting eggs due to sedimentation. Thus, we vary d_2 by up to 10 times (i.e., $d_2 = 5.0 \times 10^{-4}$, which corresponds to about 15% loss per year). The hatching rate in natural ecosystems is also unknown, but some experiments observed that 10–50% of resting eggs hatched during several months (e.g., Hairston et al. 1995; Cáceres and Tessier 2003). So, we set $h_a = 0.005$, which is also increased up to 10 times (i.e., $h_a = 0.05$). We allow two parameters (g_a, g_s) or (x, y) to be variable to investigate demographic effects of resting-egg production. We can roughly estimate the order of x. If about half of zooplankton individuals produce resting eggs when food content is about 0.2 mg L^{-1}, then the foraging gain threshold is calculated as $x = 0.1$ from Eq. 1d. We set $T = 365$ and $h_s = 0.5$ for simplicity. Because the parameter space is very large and most parameters should take different values depending on species and systems, it is impossible to cover all possible situations. So, in this study

Table 1 Parameter definitions and default values

	Definition	Value (units)
Variables		
$P(t)$	Phytoplankton density	(mg L^{-1})
$Z_1(t)$	Zooplankton density	(mg L^{-1})
$Z_2(t)$	Resting-egg density	(mg L^{-1})
Functions		
$f(t)$	Foraging gain	(mg L^{-1} day^{-1})
$h(t)$	Hatching rate of resting eggs	(day^{-1})
$g(t)$	Allocation ratio to subitaneous eggs	(dimensionless)
Parameters		
r	Intrinsic growth rate of phytoplankton	0.5 (day^{-1})
K	Carrying capacity of phytoplankton	Variable (mg L^{-1})
a	Maximum foraging rate	0.4 (day^{-1})
c	Energy conversion efficiency	0.6
b	Half saturation constant	0.6 (mg L^{-1})
d_1	Death rate of zooplankton	0.15 (day^{-1})
d_2	Death rate of resting eggs	5×10^{-5} to 5×10^{-4} (day^{-1})
T	Period of seasonal cycle	365 (days)
h_a	Annual average of $h(t)$	0.005–0.05 (day^{-1})
h_s	Seasonal degree of $h(t)$	0.5 (dimensionless)
g_a	Annual average of $g(t)$	Variable (dimensionless)
g_s	Seasonal degree of $g(t)$	Variable (dimensionless)
x	Foraging gain threshold in switching function $g(t)$	Variable (mg L^{-1} day^{-1})
y	Smoothness of switching function $g(t)$	Variable (dimensionless)

Fig. 1 Population dynamics of the phytoplankton P and zooplankton Z_1: **a** $K = 3$ and zooplankton produce only subitaneous eggs; **b** $K = 10$ and zooplankton produce only subitaneous eggs; **c** $K = 10$ and zooplankton produce resting eggs seasonally; and **d** $K = 10$ and zooplankton produce resting eggs in response to food deficiency. $(g_a, g_s) = (0.7, 0.1)$ and $(x, y) = (0.1, 0.1)$


we concentrate our investigations on varying the functional form of the reproductive allocation ratio to subitaneous eggs $g(t)$, the hatching rate h_a, and the loss rate d_2 of resting eggs, holding the other parameters fixed at the values given above. Nevertheless, we consider that our model predictions will provide useful quantitative insights into the ecological consequences of resting eggs of zooplankton as a possible solution to the paradox of enrichment.

Results

We first plotted the trajectory of the population dynamics of the phytoplankton P and the active zooplankton Z_1 for the last 10 years of 30-year (T) simulations (Fig. 1). As previously predicted, an increase in productivity K destabilized the system in the absence of resting eggs, promoting fluctuations and reducing the minimum density

Fig. 2 Amplitudes and minimum densities of phytoplankton and zooplankton population dynamics for various functional forms of allocation ratio to subitaneous eggs in the seasonality case. The value of either the annual average g_a or the seasonal degree g_s is varied, with the other being constant. The *grey line* denotes the result without resting eggs. **a** The *dotted*, *broken*, and *solid lines* are for $g_a = 0.9$, 0.8, and 0.7, respectively, and $g_s = 0.1$. **b** The *dotted*, *broken*, and *solid lines* are for $g_s = 0.1$, 0.2, and 0.4, respectively, and $g_a = 0.7$. Other parameter conditions are provided in Table 1. The functional forms of $g(t)$ are shown in the *lowest panels* for the corresponding parameter settings
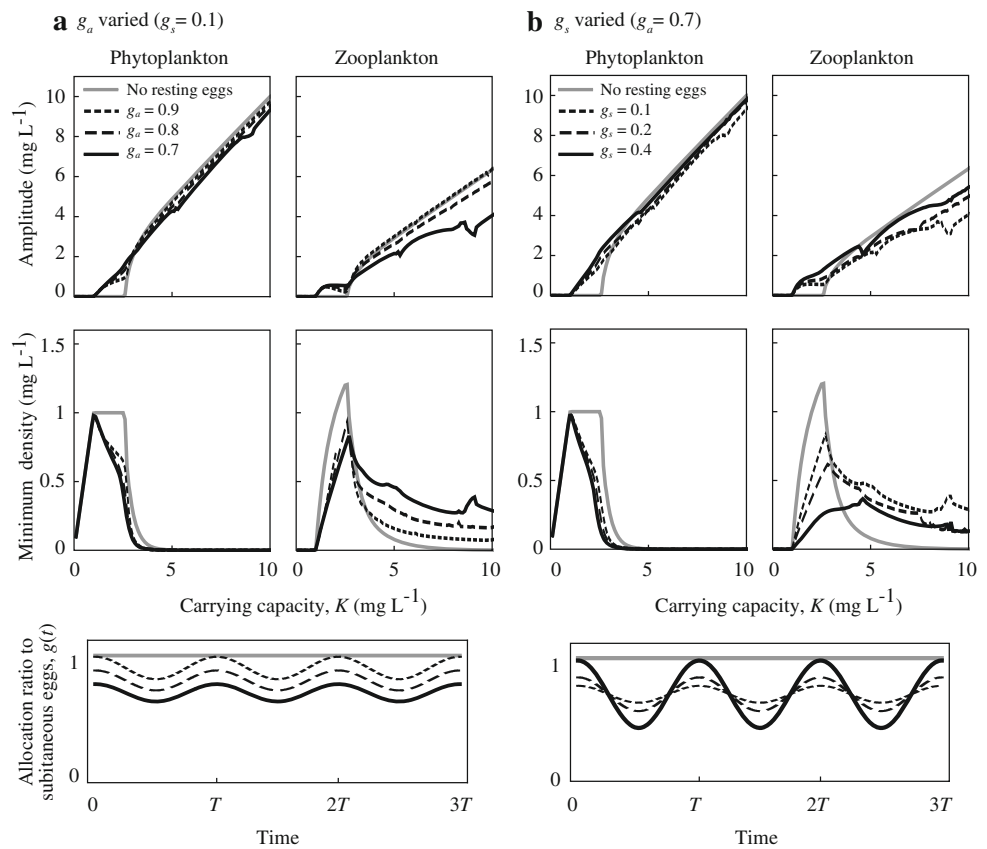
(Fig. 1a versus b). Figure 1c and d provides examples where resting-egg dynamics are introduced under a eutrophic condition ($K = 10$). In the seasonality case, the system clearly became less variable and the minimum densities of the zooplankton population increased significantly (Fig. 1b versus c). In the food deficiency case, however, these effects were not so clear, although slightly positive (see below). These results indicate that introducing resting-egg dynamics can have stabilizing effects, at least within some parameter space. Next, we show how system stability (variability and persistence) changes with the functional form of $g(t)$ and other resting-egg parameters (h_0 and d_2).

We simulated the amplitudes and the minimum densities of the phytoplankton and active zooplankton population dynamics between ($20T$, $30T$) along a eutrophication gradient K in both seasonality and food deficiency cases. Qualitatively similar patterns were predicted for various functional forms of $g(t)$ (Figs. 2, 3, 4, 5); when K was reduced below a certain threshold (the feasibility boundary), the zooplankton became extinct. When K was increased above a threshold (the bifurcation boundary), the amplitude of the population oscillations rapidly increased and the minimum densities decreased with increasing K.

In the seasonality case, we first changed the average allocation ratio g_a, with the seasonal degree being fixed at $g_s = 0.1$. When g_a was small, destabilization due to

eutrophication was well inhibited for larger values of K, resulting in a decrease in the amplitude and increase in the minimum density, in particular of the zooplankton population dynamics (Fig. 2a). This prediction implies that greater reproductive allocation to resting eggs would reduce the variability of the population oscillations and improve the persistence of the system. Next, we changed the degree of seasonality g_s, with the average allocation ratio being fixed at $g_a = 0.7$. In general, the system became less stable with increasing g_s, with increased amplitude and decreased minimum density (Fig. 2b), which is consistent with the prediction that seasonality normally destabilizes systems (Rinaldi et al. 1993). Next, we examined the sensitivity of the system to the hatching rate h_a and death rate d_2 of resting eggs. It was predicted that, in the seasonality case, the stabilizing effects of resting eggs were larger when h_a was smaller (i.e., the dormancy period was longer) under eutrophic conditions (Fig. 3a), while the influence of d_2 seemed relatively minor (Fig. 3b). In general, the phytoplankton density was very low, and the stability of the phytoplankton population dynamics did not significantly change with resting-egg parameter values under eutrophic conditions (Figs. 2, 3).

We conducted the same numerical simulations for the food deficiency case. The results showed that, although slightly positive (see Kuwamura et al. 2009), the stabilizing

Fig. 3 Influences of annual average hatching rate h_a and death rate d_2 of resting eggs on amplitudes and minimum densities of phytoplankton and zooplankton population dynamics in the seasonality case. The *grey line* denotes the result without resting eggs. **a** The *dotted*, *broken*, and *solid lines* are for $h_a = 0.005$, 0.025, and 0.05, respectively. **b** The *dotted*, *broken*, and *solid lines* are for $d_2 = 5.0 \times 10^{-5}$, 2.5×10^{-4}, and 5.0×10^{-4}, respectively; $g_a = 0.7$ and $g_s = 0.1$. Other parameter conditions are provided in Table 1
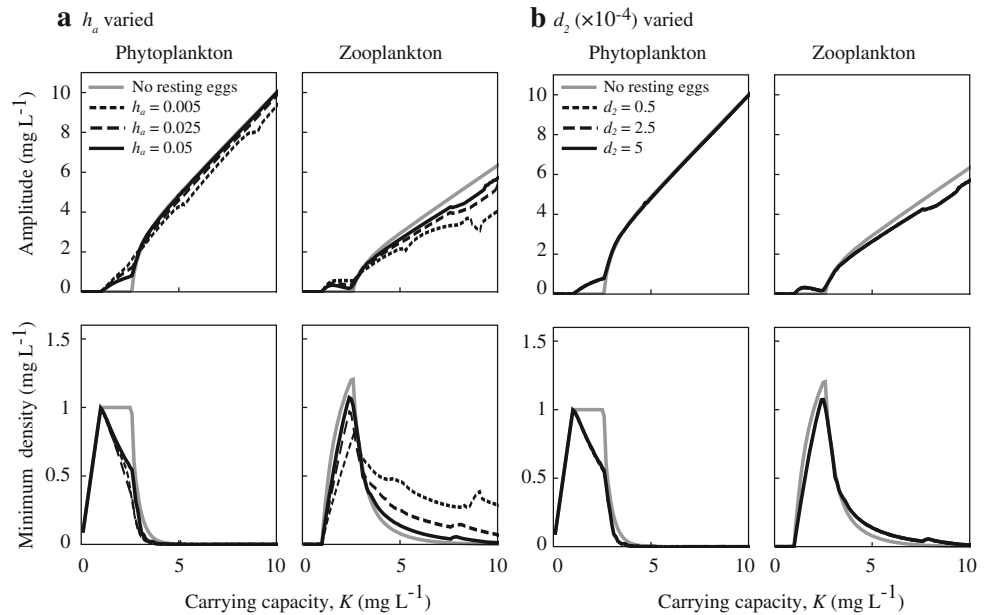
Fig. 4 Amplitudes and minimum densities of phytoplankton and zooplankton population dynamics for various functional forms of allocation ratio to subitaneous eggs in the food deficiency case. The value of either the threshold x or the smoothness y is varied, with the other being constant. The *grey line* denotes the result without resting eggs. **a** The *dotted*, *broken*, and *solid lines* are for $x = 0.05$, 0.1, and 0.15, respectively, and $y = 0.1$. **b** The *dotted*, *broken*, and *solid lines* are for $y = 0.05$, 0.1, and 0.15, respectively, and $x = 0.1$. Other parameter conditions are provided in Table 1. The functional forms of $g(f)$ are shown in the *lowest panels* for the corresponding parameter settings
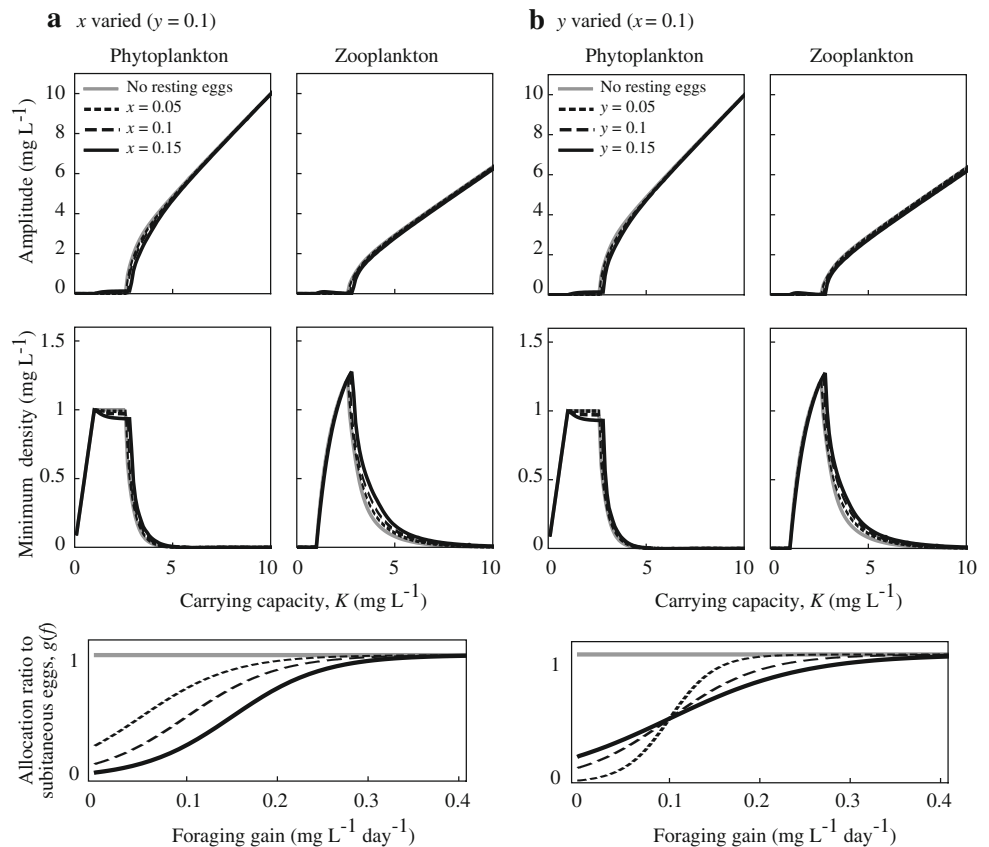

effects were generally much smaller than those predicted in the seasonality case. The stability of both phytoplankton and zooplankton population dynamics did not significantly change with x or y (Fig. 4). We also found that varying h_a and d_2 rarely affected the stability in the food deficiency case (Fig. 5).

Discussion

Previous researchers have rarely considered resting eggs of zooplankton in population and community ecological studies. Therefore, although it has recently become clear that their effect can be stabilizing (see McCauley et al.

Fig. 5 Influence of annual average hatching rate h_a and death rate d_2 of resting eggs on amplitudes and minimum densities of phytoplankton and zooplankton population dynamics in the food deficiency case; $x = 0.1$ and $y = 0.1$. The notations are the same as in Fig. 3. **a** h_a varied. **b** d_2 ($\times 10^{-4}$) varied
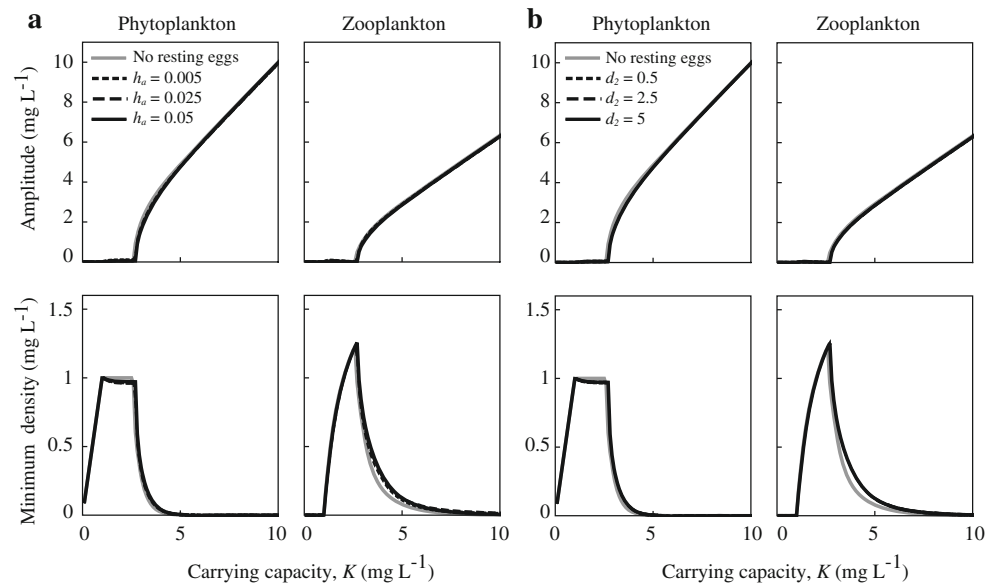
1999; Kuwamura et al. 2009), it has been unclear to what extent this effectively resolves the paradox of enrichment. In this study, we quantitatively explored Rosenzweig–MacArthur *Daphnia*–algae models including resting-egg dynamics. Then, we specified the biologically relevant conditions under which the potential stabilizing effects of resting eggs would be significantly large, which were found to be: that resting eggs are produced seasonally (rather than in response to food deficiency), that the annual average allocation ratio to resting eggs is large, and that the annual average hatching rate of resting eggs is low (Figs. 2, 3, 4, 5). Phytoplankton dynamics were relatively insensitive to changes in resting-egg parameter values. Nevertheless, our results suggest that resting-egg dynamics can significantly reduce the paradox of enrichment within the biologically meaningful parameter space and contribute to the stability of plankton (in particular, zooplankton) community dynamics.

First, we briefly explain the mechanism underlying the stabilizing effects of resting eggs (see also Kuwamura et al. 2009). In the food deficiency case, resting-egg production is enhanced (or reduced) when food availability is low (or high), and the apparent growth rate of the zooplankton population is reduced (or increased). This in turn suppresses (or enhances) grazing on phytoplankton, which exerts negative feedback regulation on the phytoplankton–zooplankton interactions. Meanwhile, in the seasonality case, the apparent growth rate of the zooplankton population is more directly regulated. Therefore, although we assumed that different mechanisms triggered resting-egg production in the two cases, we obtained qualitatively similar results (Figs. 2, 3, 4, 5). These phenomena are

related to a well-known fact in consumer–resource interactions: if the population growth rate of the consumer is reduced, then the equilibrium resource density increases and the dynamics are more likely to be stable (Murdoch et al. 2003; Nakazawa et al. 2009). As a consequence, in the presence of resting-egg dynamics, higher levels of eutrophication are required for the system to be destabilized.

Notably, resting eggs had larger stabilizing effects when produced seasonally than in response to food deficiency (Figs. 2, 3 versus 4, 5). This trend seemed to be robust to reasonable changes in other model parameters (not shown). It is difficult to explain the reason, but this result probably depends on the parameter values used. Therefore, more quantitative evaluation may still be needed. However, our results help explain why natural plankton communities are widely observed to be stable, considering that many zooplankton species, especially in Cladocera and Copepoda, tend to use seasonal cues for resting-egg production (Gyllström and Hansson 2004).

It was predicted that the system became more stable with decreasing hatching rate, especially in the seasonality case (Fig. 3a), which suggests that a longer resting period would lead to higher stability. Therefore, if the hatching rate were smaller than we assumed (e.g., $h_a = 0$), the systems would be more stable. This may partly support the experimental results of McCauley et al. (1999), who showed that resting-egg production stabilized *Daphnia* population dynamics in a situation where hatching was almost absent, although other stabilizing mechanisms such as stage structure (McCauley et al. 2008) may also have been operating in their system. In contrast, as the hatching

rate increased, the stability decreased, which is also a quite reasonable result, because extremely high hatching rates (e.g., $h_a = \infty$) approximately correspond to no resting period. Varying resting-egg loss rates had minimal effects on the dynamics in both the seasonality and food deficiency cases (Figs. 3b, 5b). This should be because the absolute level was very low.

Our numerical results showed that introducing resting eggs would not completely resolve the paradox of enrichment, implying that other stabilizing factors need to be considered for the system to be robustly stable. So far, many researchers have explored stabilizing mechanisms of consumer–resource (or predator–prey) dynamics from various biological viewpoints. There is an enormous amount of work on this matter. At least, spatial structure (Jansen 1995; Holyoak 2000; Petrovskii et al. 2004), invulnerable resource (Scheffer and De Boer 1995; Abrams and Walters 1996), unpalatable resource (Genkai-Kato and Yamamura 1999, 2000; Genkai-Kato 2004), and inducible defense by resource (Verschoor et al. 2004; Vos et al. 2004) have been proposed to resolve the paradox of enrichment in the zooplankton–phytoplankton system. In those studies, the resource population was structured. Structure within the resource population can stabilize the system by reducing the effective carrying capacity of the resource (Persson et al. 2001), which Murdoch et al. (1998) called a "sponge." In contrast, we showed that structure only in the consumer population could also be stabilizing, by assuming resting eggs, which functioned as a refuge to escape food deficiency (see also McCauley et al. 1999, 2008; Kuwamura et al. 2009). That is, resting-egg production regulates the zooplankton apparent population growth rate but not the phytoplankton carrying capacity. Therefore, the stabilizing effect we showed differs mechanistically from the "sponge" effect. More recently, Morozov et al. (2007) showed theoretically that vertical migration of zooplankton would also be stabilizing, although the effect was not sufficiently quantitatively evaluated along a eutrophication gradient. It should also be remarked that the relative contribution of each above-mentioned mechanism is still unclear in natural ecosystems because of limited data on parameter values.

In this study, we evaluated the potential stabilizing effects of resting eggs as a possible solution to the paradox of enrichment. Therefore, our model includes several simplifications and must be modified or extended in various ways for more quantitative understanding of demographic effects of resting eggs. For example, we assumed in the simplest way that resting-egg production and hatching peak in autumn and spring, respectively (i.e., the peak lag was just half a year). Even if the production timing was shifted forward or backward by 1 month, however, we found almost the same level of stability at the

steady state (not shown). Nutrient and fish dynamics may be considered in more complex seasonal models (e.g., see Sommer et al. 1986 for Plankton Ecology Group Model). Age/size structure, spatial structure, environmental fluctuations, individual variation, and time delay may also be considered. Furthermore, we note that we modeled resting-egg dynamics phenomenologically. This is based on the assumption that the timescale of evolutionary dynamics was much greater than that of population dynamics. However, it will be important to scrutinize how our predictions change by introducing adaptive zooplankton reproductive strategy (cf. Hairston et al. 2005). In a simple model such as ours, resting-egg production cannot be an evolutionarily stable strategy, because it will be excluded by more productive strains that produce only subitaneous eggs. Therefore, the predicted stabilizing effects of resting eggs will be gradually lost unless its fitness aspects are explicitly considered, such as starvation avoidance and genetic recombination (Brendonck et al. 1998; Ellner et al. 1999).

Finally, we emphasize that what is most needed now is to accumulate empirical information on resting-egg dynamics in natural ecosystems or seminatural experiments. Production, survival, and hatching rates of resting eggs and also their seasonal variations are still subject to empirical evaluation (Gyllström and Hansson 2004). Consequently, the extent to which resting-egg dynamics contributes to stability of plankton communities and its prevalence in nature need more detailed quantitative investigation. Furthermore, it was recently suggested that resting eggs would have large effects on the genetic composition of zooplankton populations (reviewed by Hairston and Kearns 2002; Brendonck and de Meester 2003) and that genetic diversity can influence zooplankton–phytoplankton consumer–resource dynamics (cf. Yoshida et al. 2003). Therefore, resting eggs may also influence plankton community dynamics through the evolutionary effect of egg banks. The information presented herein will contribute to the development of more sophisticated models and further understanding of plankton community dynamics. In future studies, more focus on resting-egg dynamics is required in the study of population and community dynamics of aquatic ecosystems, which can yield additional and interesting insights into how plankton community stability is maintained following environment changes. The present study provides an important basis for this future theoretical and empirical research to link resting-egg dynamics and plankton community dynamics.

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