Trophic cascades and trophic trickles in pelagic food webs

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Prey-dependent models, with the predation rate (per predator) a function of prey numbers alone, predict the existence of a trophic cascade. In a trophic cascade, the addition of a top predator to a two-level food chain to make a three-level food chain will lead to increases in the population size of the primary producers, and the addition of nutrients to three level chains will lead to increases in the population numbers at only the first and third trophic levels. In contrast, ratio-dependent models, with the predation rate (per predator) dependent on the ratio of predator numbers to prey, predict that additions of top predators will not increase the population sizes of the primary producers, and that the addition of nutrients to a three level food chain will lead to increases in population numbers at all trophic levels. Surprisingly, recent meta-analyses show that freshwater pelagic food web patterns match neither prey-dependent models (in pelagic webs, 'prey' are phytoplankton, and 'predators' are zooplankton), nor ratio-dependent models. In this paper we use a modification of the prey-dependent model—incorporating strong interference within the zooplankton trophic level—that does yield patterns matching those found in nature. This zooplankton interference model corresponds to a more reticulate food web than in the linear, prey-dependent model, which lacks zooplankton interference. We thus reconcile data with a new model, and make the testable prediction that the strength of trophic cascades will depend on the degree of heterogeneity in the zooplankton level of the food chain.

Keywords: trophic cascade; predation; intratrophic interference; density dependence; omnivory; food chain model

1. INTRODUCTION

The simplest food webs are linear chains of interactions between successive trophic levels (Polis & Strong 1996). A primary question has been what determines the rate of predation per predator: does it depend only on the number of prey (as in Oksanen *et al.* 1981) or does it depend on the ratio of predators to prey (as in Arditi & Ginzburg 1989). The linear trophic chain model of Oksanen *et al.* (1981) with prey-dependence predicts that increases in primary productivity lead to a stepping series of increasing densities in the chain (see DeAngelis 1992; fig. 5.5). Although Oksanen's trophic cascade model was originally applied to terrestrial systems, it has been applied frequently to aquatic systems (e.g. Carpenter & Kitchell 1993). In the aquatic version of the model, as productivity exceeds the level sufficient to support a zooplankton herbivores, the herbivore grazing holds the density of the plant constant and all increases in productivity go to increases in density of the herbivore. A switch occurs as further increases in productivity exceed the level sufficient to support a carnivore (zooplanktivorous fish); now the feeding of the carnivore holds the density of the herbivore constant with increasing productivity. This generalizes to increases in biomass at odd trophic levels in chains of odd-numbered trophic levels, and likewise for biomass at

even levels for chains of even numbers of trophic levels. Although the aquatic trophic cascade is frequently strong in dimictic lakes, with planktivorous fish suppressing zooplankton and thereby indirectly releasing phytoplankton to flourish, it is not as strong as in the pure prey-dependent model (DeMelo *et al.* 1992; Strong 1992; Carpenter & Kitchell 1993) though the carnivore depresses the herbivore, increases in primary production lead to a continually increasing biomass for both plant and herbivore (Mazumder 1994).

Using meta-analysis Brett & Goldman (1996, 1997) found, contrary to trophic cascade predictions, that phytoplankton increased little, if any, in roughly two thirds of 54 different planktivorous fish addition experiments; these were more 'trophic trickles' than strong trophic cascades. Brett & Goldman (1997) identified two general patterns in these pelagic food webs: (i) in two-level systems of zooplankton and phytoplankton (without zooplanktivorous fish) nutrient addition experiments (i.e. increased phytoplankton productivity) caused large increases in phytoplankton with modest, if any, increases in zooplankton densities; (ii) phytoplankton densities in three-level systems (with zooplanktivorous fish) increased less than in two-level systems, with equivalent increases in nutrients.

We assess these results from the standpoint of three models: the prey-dependent model of Oksanen *et al.* (1981), the ratio-dependent models of Arditi & Ginzburg

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(1989), and from a strongly density-dependent model (where density-dependence arises from intratrophic zooplankton interference). A general model of this tri-trophic pelagic system is

$$\begin{aligned}\frac{dP}{dt} &= rPG(P) - \tilde{Z}F_{\tilde{Z}}(P, \tilde{Z}) \\ \frac{d\tilde{Z}}{dt} &= -M_{\tilde{Z}}(\tilde{Z}) + \tilde{Z}F_{\tilde{Z}}(P, \tilde{Z}) - CF_C(\tilde{Z}, C) \\ \frac{dC}{dt} &= -M_C(C) + CF_C(\tilde{Z}, C)\end{aligned}\quad (1)$$

where P is phytoplankton density, $\tilde{Z}$ is zooplankton density, and C is the top consumer, zooplanktivorous fish, density. $G(P)$ is a density-dependent growth function of phytoplankton in the absence of predation; r is the per capita rate of increase of phytoplankton assumed dependent on the level of primary productivity; $F_I(\tilde{J}, I)$ is a saturating functional response of species I on its prey $\tilde{J}$; and $M_I(I)$ is the rate of decline of species I in the absence of consumption and predation. This model is general in that it can reflect either the prey-dependent, ratio-dependent or density-dependent (i.e. intratrophic interference) models, depending on the features included in the functional forms, as discussed below. We will follow DeAngelis (1992) in employing r as an index of primary production. Thus, we will consider the predictions of each model as primary productivity, r , increases. We rely on phaseplane techniques using nullclines. Specifically, we determine the equilibrium for system (1) from the intersections of the nullclines: $dP/dt=0$, $d\tilde{Z}/dt=0$, and $dC/dt=0$ of system (1). Graphical presentation of these nullclines allow us to illustrate each of the model's predictions (e.g. Hastings 1997).

2. THE PREY-DEPENDENT MODEL

In the prey-dependent model of Oksanen *et al.* (1981) the functional responses are Holling type 2 and dependent only on prey densities so they can be simplified to $F_{\tilde{Z}}(P)$ and $F_C(\tilde{Z})$. Additionally, the mortality functions, $M_{\tilde{Z}}(\tilde{Z})$ and $M_C(C)$ are assumed to be density-independent. Under these assumptions, the P -nullcline ($dP/dt=0$) is humped-shaped and the $\tilde{Z}$ -nullcline ($d\tilde{Z}/dt=0$) corresponds to a constant P -value (figure 1a). Increasing r shifts the P -nullcline up from the solid curve to the dashed curve in figure 1a (DeAngelis 1992).

Ignoring planktivorous fish temporarily, we see that the increase in productivity causes the system to go from the equilibrium, E_1 , to the equilibrium, E_2 , in figure 1a. Therefore, all productivity increases go directly to increasing the zooplankton, $\tilde{Z}$, densities (shown as $\Delta\tilde{Z}$ in figure 1a) while phytoplankton densities (P) do not change, consistent with the prey-dependent model and inconsistent with the findings (i) of Brett & Goldman (1996, 1997). In a three level prey-dependent model, with planktivorous fish, increases in primary productivity cause density increases in phytoplankton and planktivorous fish, but zooplankton densities remain constant. Since the prey-dependent model predicts productivity-related increases for phytoplankton in three-level systems but none in two-level systems, the prey-dependent model is inconsistent with pattern (ii).

Figure 1. Phaseplane depiction of the three models. The phytoplankton and zooplankton nullclines are identified by $dP/dt=0$ and $d\tilde{Z}/dt=0$, respectively. In all cases, nutrients increase and lift up the phytoplankton nullcline (solid to dashed curve) which shifts the system from equilibrium E_1 to equilibrium, E_2 (a) Depicts the prey-dependent model of Oksanen *et al.* (1981) in which all the nutrient increases go to zooplankton ($\Delta\tilde{Z}$). (b) Depicts the ratio-dependent model of Arditi & Ginzburg (1988) in which nutrient increases go to zooplankton ($\Delta\tilde{Z}$) and phytoplankton (ΔP); (c) Depicts the strong zooplankton intratrophic interference model, in which nearly all nutrient increases go to phytoplankton (ΔP). The quantity, $\Delta\tilde{Z}$, is approximately zero here.

3. THE RATIO-DEPENDENT MODEL

In the ratio-dependent model the functional responses, $F_I(\mathcal{Z}, I)$, are dependent on the ratio of prey densities to predator densities (i.e. $F_Z(P/\mathcal{Z})$ and $F_C(\mathcal{Z}/C)$). Predators interfere with each other but only in the sense that they directly influence their per capita feeding rates. As with the prey-dependent model, mortality, $M_Z(\mathcal{Z})$ and $M_C(C)$, are assumed to be density-independent. Under these assumptions, the P -nullcline ($dP/dt=0$) is humped-shaped and the $\mathcal{Z}$ -nullcline ($d\mathcal{Z}/dt=0$) has a positive slope originating from the origin in the $\mathcal{Z}$ - P phaseplane (figure 1b). As before, increasing r shifts the P -nullcline up (from the solid curve to the dashed curve in figure 1b).

Ignoring the planktivorous fish trophic level, we see that the increase in productivity causes the equilibrium to shift from E_1 to E_2 in figure 1b, increasing both zooplankton, $\mathcal{Z}$ ($\Delta\mathcal{Z}$ in figure 1b) and phytoplankton densities (ΔP in figure 1b). This, too, is inconsistent with the Brett & Goldman pattern (i) which is a much greater increase in P than $\mathcal{Z}$. It is worth noting that the ratio-dependent model can approximate pattern (i) if the slope governing the $\mathcal{Z}$ -nullcline is so small as to intersect the P -nullcline near zero densities of $\mathcal{Z}$. This is a severe restriction biologically, as it implies extraordinarily small densities of zooplankton, $\mathcal{Z}$, and it is reasonable to infer that the ratio-dependent model does not produce the Brett & Goldman pattern (i).

4. THE TROPHIC INTERFERENCE MODEL

Next we consider a form of trophic interference that is different from ratio-dependence: interference which affects zooplankton population growth rates but not their consumption rates (Yodzis 1994). The form of this model is similar to that invoked by Mittelbach *et al.* (1988) to examine food web influences of age structure in fish that feed upon invertebrates in lakes. However, we focus on interference within the zooplankton trophic structure that occurs as a result of zooplankton consuming other zooplankton (i.e. intratrophic predation), competition for space or emigration within or between zooplankton species. Many taxa of 'herbivorous' zooplankton consume phytoplankton and substantial amounts of animal matter, in particular microzooplankton such as rotifers and ciliates (Sprules & Bowerman 1988; Gilbert 1988; Adrian & Frost 1993; Burns & Gilbert 1993; Jack & Gilbert 1993; Brett *et al.* 1994) so interference related to intratrophic predation ought to be common in zooplankton. One example is cyclopoid copepods, zooplankton that are herbivorous as immatures and carnivorous as adults (Lampert & Sommer 1997).

As with the prey-dependent model, the strong intratrophic interference model assumes the functional responses, $F_I(\mathcal{Z}, I)$, are dependent only on prey densities so they can be simplified to $F_Z(P)$ and $F_C(\mathcal{Z})$. However, zooplankton mortality, $M_Z(\mathcal{Z})$, is assumed to be composed of a density-independent and a strongly density-dependent term (the zooplankton intratrophic interference term). An example of a zooplankton mortality function of this form is:

$$M_Z(\mathcal{Z}) = -k_1\mathcal{Z} - k_2\mathcal{Z}^2; \quad (2)$$

Figure 2. Depicts changes in equilibrium densities of phytoplankton under the two cases; (i) zooplankton-phytoplankton (solid curve); and (ii) fish-zooplankton-phytoplankton (dashed curve).

where the k_i are constants, the first term is density-independent and the second term is density-dependent. Under these assumptions, the P -nullcline ($dP/dt=0$) will still be humped-shaped and the $\mathcal{Z}$ -nullcline ($d\mathcal{Z}/dt=0$) will now start from a positive P -value and gradually decrease in slope until it reaches an asymptote in the $\mathcal{Z}$ - P phaseplane (figure 1c). As before, increasing r shifts the P -nullcline up (from the solid curve to the dashed curve in figure 1c).

Without planktivorous fish, we see that the increase in productivity causes the system to go from the equilibrium, E_1 , to the equilibrium, E_2 , in figure 1c. Productivity increases go to increasing phytoplankton densities (shown as ΔP in figure 1c). This matches pattern (i) detected by Brett & Goldman. Thus, while interference in the functional response (i.e. ratio-dependence) does not produce the Brett & Goldman pattern (i), interference that operates to reduce zooplankton population growth rates (via increased mortality) will reproduce the general phytoplankton-zooplankton patterns discovered by the meta-analysis of Brett & Goldman.

Our model can also reproduce pattern (ii); with zooplankton grazing, phytoplankton densities have a larger numerical response (i.e. larger ΔP) to nutrient increases in the absence of zooplanktivorous fish (figure 2 solid line) than with them (figure 2, dashed line). We illustrate the mechanism behind this result using a two-dimensional nullcline representation of the three-link system. Figure 3 depicts the nullclines of the three-link system sliced at $C=0$. McCann & Yodzis (1994) have shown that this two-dimensional graphical representation accurately portrays the phytoplankton (P) and zooplankton ($\mathcal{Z}$) equilibrium densities for the two-link and three-link systems. The two-link equilibrium densities of P and $\mathcal{Z}$ occur where the $dP/dt=0$ nullcline intersects the $d\mathcal{Z}/dt=0$ nullcline. Thus, increasing productivity (r) yields a change in phytoplankton density for the two-link system equal to ΔP_2 (figure 3). The three-link equilibrium densities of P and $\mathcal{Z}$ occur where the $dP/dt=0$ nullcline intersects the $dC/dt=0$ nullcline. Thus, increasing productivity, r , yields a change in phytoplankton density for the three-link system equal to ΔP_3 (figure 3).

Figure 3. The nullclines for the three-link system are represented in reduced form on the P - Z phaseplane (that is, where $C=0$). The phytoplankton, zooplankton and zooplanktivorous fish nullclines are identified by $dP/dt=0$, $dZ/dt=0$ and $dC/dt=0$, respectively. As in figure 1, nutrients increase lift up the phytoplankton nullcline (solid to dashed curve) which shifts the system's equilibrium. McCann & Yodzis (1994) have shown that exact values for equilibrium densities of phytoplankton (P) and zooplankton (Z) for the two-link and three-link system can be determined from this reduced phaseplane. The two-link equilibrium densities of P and Z occur where $dP/dt=0$ intersects $dZ/dt=0$ (hence, changes in phytoplankton densities equal ΔP_2); while, the three-link equilibrium densities of P and Z occur where $dP/dt=0$ intersects $dC/dt=0$ (hence, changes in phytoplankton densities equal ΔP_3). Note, that the $dC/dt=0$ nullcline must lie below the $dZ/dt=0$ nullcline otherwise zooplanktivorous fish cannot persist. Hence, ΔP_2 is constrained to be greater than ΔP_3 .

This pattern (i.e. $\Delta P_2 > \Delta P_3$) is driven by the assumption that phytoplankton become nutrient limited at high densities combined with the fact that zooplanktivorous fish (C) can only persist in this system if the $dC/dt=0$ nullcline lies below the $dZ/dt=0$ nullcline in figure 3. Hence, in the presence of zooplanktivorous fish (C), zooplankton are suppressed in density releasing phytoplankton to attain a density close to the carrying capacity (K). Thus, with an increase in productivity, phytoplankton densities can only increase marginally (ΔP_3 in figure 3). On the other hand, without fish, zooplankton are capable of reducing phytoplankton to densities well below the carrying capacity, K . Hence, given the assumption of strong zooplankton interference, increases in productivity translate to proportionally larger increases in phytoplankton densities (ΔP_2 in figure 3) but not higher equilibrium densities of phytoplankton.

5. CONCLUSION

Our hypothesis is that Brett & Goldman's patterns can be explained with a specific form of interference in zooplankton: interference that hinders zooplankton population growth rates not their consumption rates. In this

model, the interference results not from a single population of a given species, but through interaction among a set of zooplankton populations and a set of zooplankton species. The mechanism for strong intratrophic interference may be related to zooplankton community structure such that behaviours like intratrophic predation (i.e. life-history omnivory and intraguild predation) act to dampen the numerical responses of the zooplankton trophic level (Strong 1992). Along similar lines of research, Polis & Holt (1992) have found that intraguild predation can act as a powerful hindrance to trophic cascades. The strong intratrophic interference model implies that trophic differentiation of the zooplankton compartment accounts for the empirical findings of weaker trophic cascades in pelagic food webs. A corollary is that stronger trophic cascades should be characterized by less antagonistic zooplankton community relationships.

Our model generates a prediction that can be tested experimentally: trophic cascades, at the phytoplankton level, become weaker as the zooplankton community becomes characterized by increased antagonisms in the zooplankton trophic level (i.e. intratrophic predation). The success of our model illustrates the importance of using interaction terms that correspond directly to biological interactions between predator and prey, rather than terms that are developed for mathematical convenience. The results presented here suggest that the application of prey-dependent and ratio-dependent models to aquatic systems may be unreasonable in many cases. This paper uncovers a simple plausible mechanism which accounts for weak pelagic trophic cascades found in natural systems (Brett & Goldman 1996, 1997). We caution that our results do not allow us to estimate the importance of this mechanism relative to alternative mechanisms. For example, McCauley *et al.* (1988) have proposed a compelling argument that the increasing proportion of inedible algae which tends to accompany increases in productivity can also account for poor zooplankton population responses. It is interesting to note that both the intratrophic predation mechanism and the inedible algae mechanism may not be mutually exclusive. For example, Polis *et al.* (1989) have found that intraguild predation increases with decreased supplies of alternative resources. Similarly, increasing proportions of inedible algae are likely to promote increased intratrophic zooplankton predation.

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REFERENCES

- Adrian, R. & Frost, T. M. 1993 Omnivory in cyclopoid copepods: comparison of algae and invertebrates as food for three, differently sized species. *J. Plankton Res.* **15**, 643–658.
- Arditi, R. & Ginzburg, L. R. 1989 Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* **139**, 311–326.
- Brett, M. T., Wiackowski, K., Lubnow, F., Mueller-Solger, A., Elser, J. & Goldman, C. 1994 Species-dependent effects of

- zooplankton on planktonic ecosystem processes in Castle Lake, California. *Ecology* **75**, 2243–2254.
- Brett, M. T. & Goldman, C. R. 1996 A meta-analysis of the freshwater trophic cascade. *Proc. Natl. Acad. Sci. USA* **93**, 7723–7726.
- Brett, M.T. & Goldman, C.R. 1997 Consumers versus resource control in freshwater pelagic food webs. *Science, Wash.* **275**, 384–386.
- Burns, C. W. & Gilbert, J. J. 1993 Predation on ciliates by freshwater calanoid copepods: rates of predation and relative vulnerabilities of prey. *Freshw. Biol.* **30**, 377–393.
- Carpenter, S. R. & Kitchell, J. F. 1993 *The trophic cascade in lakes*. New York: Cambridge University Press.
- DeAngelis, D. 1992 *Dynamics of nutrient cycling and food webs*. New York: Chapman & Hall.
- DeMelo, R., France, R. & McQueen, D. J. 1992 Biomanipulations: hit or myth? *Limnol. and Oceanogr.* **37**, 192–207.
- Gilbert, J. J. 1988 Suppression of rotifer populations by daphnia: a review of the evidence, the mechanisms, and the affects on zooplankton community structure. *Limnol. and Oceanogr.* **33**, 1286–1303.
- Hastings, A. 1997 *Population biology: concepts and models*. New York: Springer-Verlag.
- Jack, J. D. & Gilbert, J. J. 1993 Susceptibilities of different-sized ciliates to direct suppression by small and large cladocerans. *Freshw. Biol.* **29**, 19–29.
- Lampert, W. & Sommer, U. 1997 *Limnoecology: The ecology of lakes and streams*. New York: Oxford University Press.
- Mazumder, A. 1994 Patterns of algal biomass in dominant odd-versus even-link lake ecosystems. *Ecology* **75**, 1141–1149.
- McCann, K. & Yodzis, P. 1994 Bifurcation structure of a three-species food chain model. *Theor. Popul. Biol.* **48**, 93–125.
- McCauley, E. 1988 Simple models and variation in plankton densities among lakes. *Am. Nat.* **132**, 383–403.
- Mittelbach, G. G., Osenberg, C. W. & Liebold, M. A. 1988 In *Size-structured populations* (ed. B. Ebenman & L. Persson), pp. New York: Springer.
- Oksanen, L., Fretwell, S. D., Arruda, A. & Niemela, P. 1981 Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* **118**, 240.
- Polis, G. A., Myers, C. A. & Holt, R. D. 1989 The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**, 297–330.
- Polis, G. A. & Holt, R. D. 1992 Intraguild predation—the dynamics of complex trophic interactions. *Trends Ecol. Evol.* **7**, 151–154.
- Polis, G. A. & Strong, D. R. 1996 Food web complexity and community dynamics. *Am. Nat.* **147**, 813–846.
- Strong, D. 1992 Are trophic cascades all wet? the redundant differentiation in trophic architecture of high diversity ecosystems. *Ecology* **73**, 747–754.
- Sprules, W. G. & Bowerman, J. E. 1988 Omnivory and food chain length in zooplankton food webs. *Ecology* **69**, 418–426.
- Yodzis, P. 1994 Predator-prey theory and the management of multispecies fisheries. *Ecol. Applic.* **4**, 51–58.