

Algal defense, grazers, and their interactions in aquatic trophic cascades

Anurag A. Agrawal

Center for Population Biology, One Shields Avenue, University of California at Davis, Davis, CA 95616-8584, USA.
(fax: +1-530 752 1537; e-mail: aaagrawal@ucdavis.edu)

Received January 21, 1998; revised June 11, 1998; accepted June 15, 1998

Abstract – Freshwater phytoplankton exhibit a range of levels of resistance to grazing by zooplankton. Defense theory developed for algal-grazer interactions predicts that there should be a trade-off between resistance and growth. To test this aspect of the theory, the growth rates of several putatively resistant and edible algal species that are present in systems where aquatic trophic cascades are known to occur and where algal resistance is assumed to be minimal were compared. After demonstrating that there is an inverse relationship between resistance to grazing and growth rate, I reviewed the evidence concerning the role of resistant algae in aquatic trophic cascades. Both defense theory and aquatic trophic cascade theory suggest that resistant algae should be favored in an environment with heavy grazing, while edible algae should be favored in the absence of grazing. However, by definition, four- and two-level trophic cascades are characterized by runaway consumption resulting in near elimination of the primary producers. Data from the well-studied cascading freshwater systems seem to contradict some of the predictions of trophic cascade and defense theory; relatively resistant algae can bloom in the absence of heavy grazing and relatively edible algae can bloom after grazer pressure is increased. Based on these observations, I hypothesized that size-specific grazing by zooplankton may partially explain blooms of resistant algae in the absence of grazing and blooms of edible algae in the presence of heavy grazing. In spite of the complex interactions between phytoplankton and zooplankton, the strong top-down signal, which is the signature of the aquatic trophic cascade, often persists. © Elsevier, Paris

Aquatic trophic cascades / community dynamics / cost of defense / *Daphnia* / defense theory / food webs / grazing / top-down

1. INTRODUCTION

The study of aquatic trophic cascades (ATC) has generated insights in community ecology that extend beyond the freshwater systems where they occur. Such systems with strong top-down control have been at the center of discussions regarding the generality of food web theory and, especially, the importance of top-down and bottom-up forces in structuring ecological communities (*figure 1*) [7, 8, 23, 27, 30, 36, 39, 42–44]. Although powerful top-down signals have been documented in many freshwater systems [3, 8, 48], some of the secondary predictions of ATC theory regarding grazer-resistant phytoplankton and the attenuation of the cascade at lower trophic levels have not been thoroughly examined [41]. I will discuss the application of defense theory developed for plants and freshwater algae [10, 13, 16, 19, 22, 37, 45, 55] to cascading systems and ask whether algal populations in the examples of ATCs behave consistently with the predictions of defense theory.

An important component of defense theory is the general claim that defenses are costly and that there should be a trade-off between defense and growth.

Given this relationship, it is predicted that fast growing, edible algae should dominate the system when grazing is minimal, whereas resistant algae, which should grow more slowly as a result of investment in defenses, should bloom and dominate under heavy grazing regimes [5, 22, 37, 52]. However, testing this hypothesis is problematic because classifying algae as edible or resistant is not straightforward. In addition, rapid growth may be a form of defense, that is, highly grazable algae may persist because of high growth rates in nutrient rich environments. Numerous examples from the literature show that different grazer species vary in their ability to consume and assimilate the same algae (e.g. [38]). In fact, algae that are edible to one grazer may be resistant to grazing by another (reviewed by Demott [12]). This variation could be simply the result of grazing limited by size and shape or it could be a specialization by grazers to feeding on particular algae. The ATC literature in light of these differences in algal resistance was reviewed to see whether shifts in the composition of algal communities occur under different grazing regimes, whether shifts in the phytoplankton community are caused by higher trophic level manipulations,

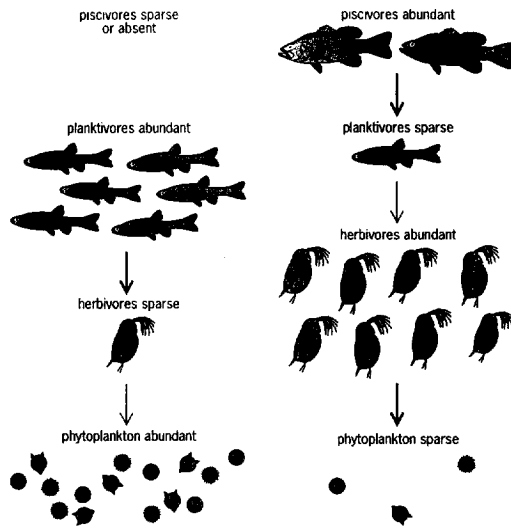


Figure 1. The classic three- and four-level aquatic trophic cascade. Where planktivores are abundant, grazing is limited and phytoplankton are released from grazing and they often bloom. Alternatively, when piscivores are present, algal blooms are suppressed because of the cascading effects of the top predator on the planktivores and herbivores. This figure is reproduced from Strong [57] with permission from the McGraw-Hill companies.

and how these changes relate to defense theory. In conclusion, although a strong top-down signal flows through ATCs, the current theory is inadequate to explain the diversity of algal responses to manipulations at higher trophic levels (e.g. [63]).

A further assumption of current ATC theory is that the dominant primary producers in systems that exhibit trophic cascades should be edible species of phytoplankton [19, 56]. The logic behind this assumption is that ATCs would not extend to primary producers if resistant algae achieved high biomass in systems with piscivores. Although resistant algae do not readily fit the theory, the labels of 'resistance' and 'edibility' are themselves ambiguous terms. In this paper, the terms 'edible' and 'resistant' will be used generically to indicate two ends of the spectrum of algal grazability by *Daphnia* spp. The characteristic defining edibility will be noted whenever possible. In reality, there probably exists a gradient for the grazing rate on an algae relative to other coexisting species. This continuous axis should be a sum of toxicity, repellence, size, shape, gelatinous shielding, and other factors, including those that are specific to particular biotic and abiotic environments (see also [36]).

In a discussion of trophic cascades in lakes, McQueen [41] suggests that understanding the problem of grazer resistant algae is of utmost importance towards developing a synthesis of lake community structure. Therefore, I attempted to reconcile ATC

theory and defense theory with experimental results from some well studied lakes that exhibit the trophic cascade. After examination, the predictions of defense theory based on algal resistance, growth rates, and compositional shifts suggest that size-specific grazing may explain some of the phytoplankton dynamics in ATCs.

2. NEGATIVE CORRELATION OF ALGAL GROWTH RATES AND RESISTANCE TO GRAZING

To test a primary assumption of the algal defense theory, that resistance is costly in terms of growth, growth rates of several putatively resistant and edible algae were compared. Resistance and edibility of algae was determined by experiments from the literature usually using grazability of algae by *Daphnia* spp. (table 1). If conflicting results were reported in various literature sources, the algae were not included. Data were only used if convincing tests of grazability were provided and growth rates in favorable conditions were available. The test was conducted using a one-tailed analysis of variance; my a priori hypothesis was that grazer resistant algae have lower growth rates than edible species. Alternative analyses were conducted in an attempt to maximize statistical power and robustness. For example, an analysis in which each study was considered a block, to remove variance associated with different experimental protocols used in different studies, was conducted. However, the reduction in power associated with this test outweighed the benefits of blocking. Therefore, because a total of 31 literature values for algal growth rates and resistance to grazing was found, statistical power was maximized by including all studies in a single factor analysis.

Literature values for the 31 species of freshwater algae reveal that grazer resistant species have significantly slower growth rates than edible species (table 1, $F_{1,29} = 3.637$, $P = 0.033$). On average, the growth rate (divisions per day) of resistant algae is one-third the growth rate of edible species (table 1). These findings corroborate the assumption of the defense theory that algal resistance to grazing and growth rates should be negatively associated among taxa.

Although estimates of grazer resistance and growth rates are independently plentiful, there are still a limited number of systems for which both have been measured. Hopefully, this initial comparison will stimulate more investigators to consider both factors simultaneously for specific species (e.g. [1, 14, 15, 35]). Because the level of algal resistance often varies with the grazer, only studies in which *Daphnia* spp. were dominant grazers were considered. The findings are consistent with the predictions of the theory sug-

Table I. Summary of algal growth rates, given in maximum divisions per day (DPD), and algal edibility, with the character used to define edibility. Each box contains the edibility of algae to a specific grazer. Grazability refers to algal mortality due to grazing. Divergent edibility ratings for *Asterionella formosa* are reported in references [15] and [35] and has therefore been omitted from the table and analyses.

Grazer	Algae (edible)	Character (defining edibility)	Growth rate (DPD)	Algae (resistant)	Character (defining edibility)	Growth rate (DPD)	Refs.
<i>Daphnia pulicaria</i>	<i>Scenedesmus</i> spp.	grazer performance	2.84	<i>Aphanizomenon</i> spp.	toxic and large size	0.98	17, 33, 34, 50
	<i>Synechococcus</i> spp.	consumption rate	7.97	<i>Microcystis aeruginosa</i>	toxic	1.1	
<i>Daphnia magna</i>	<i>Chlamydomonas</i> spp.	grazer performance	2.91	<i>Anabaena flos-aquae</i>	toxic, grazability	0.78	18, 47, 50, 52
<i>Daphnia pulex</i>	<i>Pseudopedinella erkensis</i>	grazability	2.1	<i>Uroglena americana</i>	grazability	1.5	18, 21, 35, 50, 52
	<i>Cryptomonad</i> spp.	grazability	0.83	<i>Quadragula chodatii</i>	grazability	0.6	
<i>Daphnia</i> spp.	<i>Selenastrum minutum</i>	grazability	0.4	<i>Gloeocystis gigas</i>	grazability	0.6	15, 21, 35, 46, 52
	<i>Glenodinium quadridens</i>	grazability	0.2	<i>Crucigenia</i> sp.	grazability	0.3	
	<i>Rhodomonas minuta</i>	grazability	1.0	<i>Sphaerocystis schroeteri</i>	grazability	0.71	M.T. Brett, pers. comm.
				<i>Dinobryon cylindricum</i>	grazability	0.2	
<i>Daphnia pulex</i>	<i>Chlamydomonas</i> spp.	grazability	2.91	<i>Cerasterias staurastroides</i>	grazability	0.7	1, 50
	<i>Cryptomonas</i> spp.	grazability	0.83	<i>Crucigenia quadrata</i>	grazability	0.4	
<i>Daphnia</i> spp.	<i>Gymnodinium limneticum</i>	grazability	0.15	<i>Cosmarium bioculatum</i>	grazability	0.15	14
	<i>Chroococcus limneticus</i>	grazability	0.08	<i>Anabaena circinalis</i>	grazability	0.25	
	<i>Aphanocapsa elcachista</i>	grazability	0.06				
	<i>Cyclotella glomerata</i>	grazability	0.05				
<i>Daphnia</i> spp.	<i>Chlorella</i> spp.	grazer performance, grazability	2.15				9, 11, 31, 50, 52
<i>Daphnia</i> spp.	<i>Fragilaria crotonensis</i>	grazer performance, grazability	1.37				11, 31, 50, 52, 66
<i>Daphnia</i> spp.				<i>Ceratium hirundinella</i>	architecture and size	0.25	26, 50
<i>Daphnia</i> spp.				<i>Peridinium</i> spp.	architecture, grazability	0.16	25, 50
			AVERAGE ± SE 1.58 ± 0.56				AVERAGE ± SE 0.55 ± 0.99

gesting that grazer resistance should be costly in terms of growth rate. The exact nature or mechanisms of these costs, however, are unknown. For example, under natural conditions, larger more resistant algae may have relatively lower growth rates because of higher sinking rates and longer periods of time spent under lower light conditions.

Even though growth rate is negatively associated with resistance to grazing, neither growth rate nor edibility necessarily predict which species will dominate under different grazing regimes. For example, variation among species in response to temperature, nutrient ratios, light and carbon dioxide availability, grazing, algal densities and pH are also important factors influencing growth rate and, hence, competitive ability in phytoplankton [9, 11, 19, 24, 31, 32, 50, 54, 60, 64]. Furthermore, different grazer size classes and species have been shown to have significantly different effects on the phytoplankton community composition due to differential consumption [2, 38, 64].

3. GRAZER-ALGAE INTERACTIONS IN AQUATIC TROPHIC CASCADES

The general development of algal defense theory in freshwater systems predicts that increased grazing should cause a decrease in the abundance of edible algae, which should be replaced by slower growing, more resistant algae [19, 32, 36, 46, 52]. Data from McCauley and Briand [40] support this idea; they concluded from a two-year study that reduction in grazing caused a significant decrease in the numbers of resistant species. They defined resistant algae as species larger than 50 μm and all cyanobacteria. Curiously, lowering grazer levels favored some putatively resistant algae such as *Synedra* sp., a large needle-like unicellular diatom [40, 52]. Conversely, examples of increased grazing resulting in dominance by inedible species are reviewed by Sterner [55]. Sterner also lists some exceptions to these patterns and suggests that nutrient dynamics may be important in these cases (see also [61]). These exceptions to the generally accepted theory, demonstrated early on by Reinertsen and Olson [49] and later by Van Donk [58], will be the focus of this discussion.

Carpenter et al. [9] review the studies demonstrating ATCs in Paul, Peter, and Tuesday lakes (USA). Replicated manipulations have been conducted in these lakes by Carpenter and colleagues for many years. These lakes include many chemically toxic algae (e.g. *Microcystis* spp. [33]), algae with protective gelatinous sheaths (e.g. *Sphaerocystis Schroeteri* [46]), and spiny chrysophytes (e.g. *ChrysoSphaerella longispina*), in addition to large (resistant) dinoflagellates (*Peridinium* spp.), and highly edible nanoplankton. The most abundant algae in the 4-level Paul Lake were the gelatinous

colonies [9], which are generally considered to be resistant to grazing [32]. Abundance of resistant algae in these four-level lake systems is in contradiction to Strong's suggestion [56] that cascades will only "occur when the plant community is composed entirely of plant-herbivore species combinations in the 'Edible' category". A broader assessment of a four-level trophic cascade may include relative dominance of the suppressed primary producers by resistant species.

In Peter Lake, when *Daphnia* spp. were depressed by the introduction of zooplanktivorous fish, the resistant algae, *Sphaerocystis Schroeteri*, had the biggest bloom. Porter [46] reported that these algae could survive gut passage and actually absorb nutrients from *Daphnia*. Carpenter et al. [9] attempted another manipulation to increase zooplanktivory and cause an algal bloom. The expected bloom occurred, but in the nutrient poor cyanobacteria, *Aphanocapsa elachista*, not the more edible algal species. The above observation and results deviate from the predictions of defense and ATC theory. Note that the overall 'cascading' effect did take place; in the three-level system, zooplankton decreased and algal biovolume was at a two-year high (including edible algae); however, resistant algae bloomed when grazer pressure was decreased.

In a contradiction to ATC theory [6], Carpenter et al. [9] found that zooplankton size was negatively correlated with algae size. ATC theory assumes that an increase in zooplankton biomass and/or body size reduces the number of small edible algae and should correlate with dominance by larger, more resistant algae [6, 8]. The finding of Carpenter et al. [9] also contradicts algal defense theory because they found that under increased grazing pressure, the smaller, more edible algae dominated the system (see also [19]).

In Tuesday Lake, where there were initially only three trophic levels (phytoplankton, zooplankton, and zooplanktivorous fish) and low grazing, the phytoplankton community was dominated by large and resistant algae. As predicted by ATC theory, the introduction of piscivorous fish resulted in a cascading effect in which algal populations were reduced. However, the algae remaining were the edible algae, while the resistant gelatinous colonies and chemically defended algae were totally gone [9]. This demonstrates that an increase in grazing can sometimes result in increased susceptibility for previously 'resistant' algae and relative resistance for smaller 'edible' species. Two years later, small and limited blooms of resistant algae occurred. These inconsistent findings are not isolated cases (for further examples see [53, 55]). Why do 'resistant' algae sometimes dominate in the absence of grazers and wane in the presence of heavy grazing?

I propose that heavy grazing does not always result in an increase of resistant algae because edibility and resistance are specific to the particular species of grazers involved in each system (for examples of differential algal resistance to alternate grazers determined by ecological factors see [28, 38, 59]). Consistent with the algal defense theory, resistance and growth rate may have a negative association when considering a limited number of algae consumed by *Daphnia* spp. (table I). However, the relationship between algal dominance and growth rate appears to be dependent on other factors and not tightly coupled. This conclusion challenges the implications of defense theory and ATC theory.

Rapid growth itself may function as a defense (sensu [10]). In nutrient rich environments, fast growing algae may be able to 'outrun' high herbivore pressure. For example, the bloom of edible algae under heavy grazing described for Tuesday lake may be a function of nutrient dynamics favoring a fast growing species (see reviews by Rosemond [51] and Vanni [62]). Consistent with the predictions of nutrient dynamics on algal blooms, Vanni and Layne [65] found that nutrient recycling can have a relatively greater effect on phytoplankton dynamics than herbivory per se (see [36] for a counter example).

Another possible explanation for some of the observed deviations from the algal defense theory examined above is that the 'resistant' algae in these cascading freshwater systems are edible to large *Daphnia* [36]. Phytoplankton up to 200 µm in length can be grazed by large *Daphnia* [35]. If seemingly resistant algae are consumed by large zooplankton and algal regeneration is limited by growth rate, resistant algae may not replace edible algae when grazing is increased (see also [36, 52]). Increased grazer size can increase filtration rate and consumption of larger 'resistant' algae [4]. This grazing of larger algae can effectively reduce the relative consumption of smaller,

more edible algae [29] and could promote a bloom of edible algae. This size-specific grazing may result in opposing outcome for phytoplankton blooms than traditional 'grazer pressure' based models predict (table II).

These opposing predictions of ATC theory and size-specific grazing could be untangled by testing the varying edibility of algae for varying sizes of a given *Daphnia* species. For example, the bloom of the grazer resistant *Sphaerocystis schoeteri* in Peter Lake followed an increase in zooplanktivory and a reduction in grazing by *Daphnia*. It has been well documented that grazer body size is strongly affected by levels of zooplanktivory (reviewed in Gliwicz and Pijanowska [20]) When zooplanktivory increases, average *Daphnia* body size plummets. If larger individual *Daphnia* consumed the resistant *S. schoeteri*, but smaller *Daphnia* could not, then grazer pressure on *S. schoeteri* was likely to have been minimized. Although overall grazing may have been reduced, *S. schoeteri* could have been freed from grazing (totally resistant) and favored to bloom. Conversely, if planktivore pressure is low and grazer size is increased, size-specific grazing predicts that larger (previously resistant) algae will be grazed and may not be able to regenerate because of their slow growth rate. This prediction is also consistent with data from Tuesday lake [9]. Increased consumption of larger food particles by zooplankton can decrease the relative consumption of smaller ones [29].

In future studies, whenever the third trophic level is manipulated or affected by changes in the fourth trophic level, investigators should consider the difference between an effect on zooplankton body size versus an effect on zooplankton population size, as it is relevant to the phytoplankton. Of course, size of the individuals and size of the population may both change, and we must therefore consider the relative effects on phytoplankton communities for each case.

Table II. Alternative theoretical outcomes of decreased planktivore pressure in aquatic trophic cascades.

Dominance of grazer size	Dominance of grazer pressure
Body size of zooplankton decreases	Population size of zooplankton decreases
↓	↓
Zooplankton consume only small and edible algae (freeing larger algae from any grazing)	Grazing of all algae decreases
↓	↓
Large (resistant) algae bloom	Edible algae bloom (because of high growth rates)

Acknowledgements

I gratefully acknowledge the thoughtful and patient input of Don Strong, Mike Brett, and Sharon Lawler. Jennifer Thaler, Rick Karban, Jim Grover, Mary Power, Matthew Leibold, Henry Wilbur, Ted Grosholz, Nelson Hairston Jr., Don McQueen, Crispin Jordan, Lynn Adler, Martha Hoopes, Michael Vanni, Arie van Noordwijk and anonymous reviewers who also commented and improved the manuscript. This study was financially supported by Phi Beta Kappa and the Center for Population Biology at University of California, Davis.

REFERENCES

- [1] Bergquist A.M., Carpenter S.R., Limnetic herbivory: effects on phytoplankton populations and primary productivity, *Ecology* 67 (1986) 1351–1630.
- [2] Bergquist A.M., Carpenter S.R., Latino J.C., Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages, *Limnol. Oceanogr.* 30 (1985) 1037–1045.
- [3] Brett M.T., Goldman C.R., A meta-analysis of the freshwater trophic cascade, *Proc. Natl. Acad. Sci. USA* 93 (1996) 7723–7726.
- [4] Burns C.W., The relationship between body size of filter-feeding Cladocera and the maximum size of particles ingested, *Limnol. Oceanogr.* 13 (1968) 675–678.
- [5] Carney H.J., A general hypothesis for the strength of food web interactions in relation to trophic state, *Int. Ver. Theor. Angew. Limnol. Verh.* 24 (1990) 487–492.
- [6] Carpenter S.R., Kitchell J.F., Plankton community structure and limnetic primary production, *Am. Nat.* 124 (1984) 59–172.
- [7] Carpenter S.R., Kitchell J.F., Consumer control of lake productivity, *BioScience* 38 (1988) 764–769.
- [8] Carpenter S.R., Kitchell J.F. (Eds.), *The trophic cascade in lakes*, Cambridge University Press, Cambridge, England, 1993.
- [9] Carpenter S.R., Morrice J.A., Elser J.J., Amand A.L.S., MacKay N.A., Phytoplankton community dynamics, in: Carpenter S.R., Kitchell J.F. (Eds.), *The trophic cascade in lakes*, Cambridge University Press, Cambridge, England, 1993, pp. 189–209.
- [10] Coley P.D., Bryant J.P., Chapin F.S., Resource availability and plant antiherbivore defense, *Science* 230 (1985) 895–899.
- [11] Dauta A., Devaux J., Piquemal F., Boumnic L., Growth rate of four freshwater algae in relation to light and temperature, *Hydrobiologia* 207 (1990) 221–226.
- [12] Demott W.R., The role of competition in zooplankton succession, in: Sommer U. (Ed.), *Plankton ecology: succession in plankton communities*, Springer-Verlag, Berlin, Germany, 1989, pp. 195–253.
- [13] Edwards P.J., Gillman M.P., Herbivores and plant succession, in: Gray A.J., Crawley M.J., Edwards P.J. (Eds.), *Colonization, succession and stability*, 26th Symposium of the British Ecological Society. Blackwell, Oxford, England, 1987, pp. 295–314.
- [14] Elser J.J., Goldman C.R., Zooplankton effects on phytoplankton in lakes of contrasting trophic status, *Limnol. Oceanogr.* 36 (1991) 64–90.
- [15] Elser J.J., Goff N.C., MacKay N.A., St Amand A.L., Elser M.A., Carpenter S.R., Species-specific algal responses to zooplankton: experimental and field observations in three nutrient-limited lakes, *J. Plankton Res.* 9 (1987) 699–717.
- [16] Fagerström T., Larsson S., Tenow O., On optimal defense in plants, *Funct. Ecol.* 1 (1987) 73–81.
- [17] Fulton R.S., Paerl H.W., Toxic and inhibitory effects of the blue-green alga *Microcystis aeruginosa* on herbivorous zooplankton, *J. Plankton Res.* 9 (1987) 837–855.
- [18] Gensemer R.W., Kilham S.S., Growth rates of five freshwater algae in well-buffered acid media, *Can. J. Fish. Aquat. Sci.* 41 (1984) 240–243.
- [19] Gliwicz Z.M., Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201 (1990) 83–97.
- [20] Gliwicz Z.M., Pijanowska J., The role of predation in zooplankton succession, in: Sommer U. (Ed.), *Phytoplankton Ecology: Succession in plankton communities*, Springer-Verlag, Berlin, 1989, pp. 253–296.
- [21] Grover J.P., Phosphorus-dependent growth kinetics of 11 species of freshwater algae, *Limnol. Oceanogr.* 34 (1989) 341–348.
- [22] Grover J.P., Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants, *Am. Nat.* 145 (1995) 746–774.
- [23] Hairston Jr. N.G., Hairston Sr. N.G., Cause-effect relationships in energy flow, trophic structure and interspecific interactions, *Am. Nat.* 142 (1993) 379–411.
- [24] Hansson L.-A., Carpenter S.R., Relative importance of nutrient availability and food chain for size and community composition in phytoplankton, *Oikos* 67 (1993) 257–263.
- [25] Havens K., DeCosta J., An analysis of selective herbivory in an acid lake and its importance in controlling phytoplankton community structure, *J. Plankton Res.* 7 (1985) 207–222.
- [26] Heaney S.I., Talling J.F., *Ceratium hirundinella* - ecology of a complex, mobile, and successful plant, *Rep. Freshw. Biol. Assoc.* 48 (1980) 27–40.
- [27] Herendeen R.O., A unified approach to trophic cascade and bottom-up: top-down hypotheses, *J. Theor. Biol.* 176 (1995) 13–26.
- [28] Hessen D.O., Van Donk E., Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*, *Arch. Hydrobiol.* 127 (1993) 129–140.
- [29] Holm N.P., Ganf G.G., Shapiro J., Feeding assimilation rates of *Daphnia pulex* fed *Aphanizomenon flos-aquae*, *Limnol. Oceanogr.* 28 (1983) 677–687.
- [30] Hunter M.D. (Ed.), Special Feature: The relative contributions of top-down and bottom-up forces in population and community ecology, *Ecology* 69 (1992) 723–765.
- [31] Infante A., Litt A.H., Differences between two species of *Daphnia* in the use of 10 species of algae in Lake Washington, *Limnol. Oceanogr.* 30 (1985) 1053–1059.
- [32] Kerfoot W.C., Levitan C., DeMott W.R., *Daphnia*-phytoplankton interactions: density-dependent shifts in resource quality, *Ecology* 69 (1988) 1806–1825.
- [33] Lampert W., Inhibitory and toxic effects of blue-green algae on *Daphnia*, *Int. Rev. Gesamten Hydrobiol.* 66 (1981) 285–298.
- [34] Lampert W., Further studies on the inhibitory effect of the toxic blue-green *Microcystis aeruginosa* on the filtering rate of zooplankton, *Arch. Hydrobiol.* 95 (1982) 207–220.
- [35] Lehman J.T., Sandgren C.D., Species-specific rates of growth and grazing loss among freshwater algae, *Limnol. Oceanogr.* 30 (1985) 34–46.
- [36] Leibold M.A., Resource edibility and the effects of predators and productivity on the outcome of trophic interactions, *Am. Nat.* 134 (1989) 922–949.

- [37] Lubchenco J., Gaines S.D., A unified approach to marine plant-herbivore interactions. I. Populations and communities, *Annu. Rev. Ecol. Syst.* 12 (1981) 405–437.
- [38] Lundstedt L., Brett M.T., Differential growth rate of three cladoceran species in response to mono- and mixed-algal cultures, *Limnol. Oceanogr.* 36 (1991) 159–165.
- [39] Matveev V., The dynamics and relative strength of bottom-up vs. top-down impacts in a community of subtropical lake plankton, *Oikos* 73 (1995) 104–108.
- [40] McCauley E., Briand F., Zooplankton grazing and phytoplankton species richness: field tests of the predation hypothesis, *Limnol. Oceanogr.* 24 (1979) 243–252.
- [41] McQueen D.J., Manipulating lake community structure: where do we go from here? *Freshw. Biol.* 23 (1990) 613–620.
- [42] Morin P.J., Lawler S.P., Food web architecture and population dynamics: theory and empirical evidence, *Annu. Rev. Ecol. Syst.* 26 (1995) 505–529.
- [43] Polis G.A., Food webs, trophic cascades and community structure, *Aust. J. Ecol.* 19 (1994) 121–136.
- [44] Polis G.A., Strong D.R., Food web complexity and community dynamics, *Am. Nat.* 147 (1996) 813–846.
- [45] Porter K.G., Selective grazing and differential digestion of algae by zooplankton, *Nature* 244 (1973) 179–180.
- [46] Porter K.G., The plant-animal interface in freshwater ecosystems, *Am. Sci.* 65 (1977) 159–170.
- [47] Porter K.G., Orcutt J.D., Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for *Daphnia*, in: Kerfoot W.C. (Ed.), *Evolution and ecology of zooplankton communities*, University Press of New England, Hanover, New Hampshire, USA, 1980, pp. 268–281.
- [48] Power M.E., Effects of fish in river food webs, *Science* 250 (1990) 811–814.
- [49] Reinertsen H., Olson Y., Effects of fish elimination on the phytoplankton community of a eutrophic lake, *Int. Ver. Theor. Angew. Limnol. Verh.* 22 (1984) 649–657.
- [50] Reynolds C.S., *The ecology of freshwater phytoplankton*, Cambridge University Press, Cambridge, England, 1984.
- [51] Rosemond A.D., Indirect effects of herbivores modify predicted effects of resources and consumption on plant biomass, in: Polis G.A., Winemiller K.O. (Eds.), *Food Webs: Integration Of Patterns And Dynamics*, Chapman and Hall, New York, New York, 1996, pp. 149–159.
- [52] Samelle O., Herbivore effects on phytoplankton succession in a eutrophic lake, *Ecol. Monogr.* 63 (1993) 129–149.
- [53] Shapiro J., Wright D.I., Lake restoration by biomanipulation: Round Lake- Minnesota- the first two years, *Freshw. Biol.* 14 (1984) 371–383.
- [54] Sterner R.W., Herbivores' direct and indirect effects on algal populations, *Science* 231 (1986) 605–607.
- [55] Sterner R.W., The role of grazers in phytoplankton succession, in: Sommer U. (Ed.), *Phytoplankton Ecology: Succession in Plankton Communities*, Springer-Verlag, Berlin, 1989, pp. 107–170.
- [56] Strong D.R., Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems, *Ecology* 73 (1992) 747–754.
- [57] Strong D.R., *Population and community ecology*, McGraw-Hill Yearbook of Science and Technology, 1995, pp. 319–321.
- [58] Van Donk E., Changes in community structure and growth limitation of phytoplankton due to top-down food-web manipulations, *Int. Ver. Theor. Angew. Limnol. Verh.* 24 (1991) 773–778.
- [59] Van Donk E., Hessen D.O., Grazing resistance in nutrient-stressed phytoplankton, *Oecologia (Berlin)* 93 (1993) 508–513.
- [60] Van Donk E., Gulati R.D., Iedema A., Meulemans J.T., Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake, *Hydrobiologia* 251 (1993) 19–26.
- [61] Van Donk E., Gylstra R., Gulati R.D., A multivariate analysis of phytoplankton and food web changes in a shallow biomanipulated lake, *Freshw. Biol.* 36 (1996) 683–696.
- [62] Vanni M.J., Nutrient transport and recycling by consumers in lake food webs: implications for algal communities, in: Polis G.A., Winemiller K.O. (Eds.), *Food Webs: Integration of Patterns And Dynamics*, Chapman And Hall, New York, New York, 1996, pp. 81–95.
- [63] Vanni M.J., Findlay D.L., Trophic cascades and phytoplankton community structure, *Ecology* 71 (1990) 921–927.
- [64] Vanni M.J., Lampert W., Food quality effects on life history traits and fitness in the generalist herbivore *Daphnia*, *Oecologia (Berlin)* 92 (1992) 48–57.
- [65] Vanni M.J., Layne C.D., Nutrient recycling and herbivory as mechanisms in the 'top-down' effect of fish on algae in lakes, *Ecology* 78 (1997) 21–40.
- [66] Vanni M.J., Temte J., Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake, *Limnol. Oceanogr.* 35 (1990) 697–709.