in receptor interaction [for instance, the COOH-terminus, α4-β6 loop, and β6 (*7–10*)], if they were known to interact with βγ in the 3D structure of α_t (*5*), or if they were located on the surface of the 3D structure of α_t near either known or postulated rhodopsin- or βγ-interacting residues (*3–5*).
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14. That is, binding values for different mutants in the presence of GTP-γ-S were consistent and small enough not to confound the results. We failed to find a mutant α_t that could bind to rhodopsin but would not be susceptible to rhodopsin-catalyzed replacement of GDP by GTP-γ-S. A mutant rhodopsin with this phenotype has been described (O. P. Ernst, K. P. Hofmann, T. P. Sakmar, *ibid.*, p. 10580).
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16. The failure of individual mutants to be protected from trypsin by AlF_4^- could indicate improper folding of the protein or an inability of the α2 helix, in which the protected cleavage site is located, to take on the trypsin-resistant (active, GTP-bound) conformation. Of the 66 mutants tested in both assays, only four showed an I phenotype in both. It is likely that overexpression of recombinant α_t in COS cells and its translation in vitro affect folding in different ways.
17. Of the 23 residues identified (*5*) as interacting directly with βγ, we tested 22. By one or the other assay, mutational replacement of 14 of the 22 residues (in 10 mutants) produced an R phenotype, whereas six mutants were WT and two were indeterminable (*11*).
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19. This loop comprises residues 321 to 324 of α_t. Corresponding β6-α5 loops of other GTPases interact similarly with the guanine ring of bound GDP and GTP [H. R. Bourne, D. A. Sanders, F. McCormick, *Nature* **349**, 117 (1991)].
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24. An indirect effect of alanine substitution is especially likely for the few residues we tested whose side chains are directed toward the protein's hydrophobic core; these include two phenylalanine residues, colored cyan (F185) or red (F332) in Fig. 3, A through C. We considered four additional R residues (green in Fig. 3, A through C), scattered through the α_t molecule, as quite unlikely to interact directly with βγ or rhodopsin. Residues Gly^2 and Ser^6 are required for myristoylation of α_t, which in turn is necessary for efficient activation [P. J. Casey, *Curr. Opin. Cell Biol.* **6**, 219 (1994)]. Residues Thr^{323} and Asp^{324} are located very close to the guanine nucleotide–binding pocket (*3–5*), where they might be expected to alter regulation of GTP-GDP exchange.
25. We thank members of our laboratories for helpful discussions and reading of the manuscript, H. Czerwonka for preparing the manuscript, H. Hamm (University of Illinois at Chicago) for a sample of rod outer segment membranes, and B. K.-K. Fung (Jules Stein Eye Research Institute, Los Angeles, CA) for the TF15 monoclonal antibody used for α_t immunoblots. R.O. is a Helen Hay Whitney fellow, P.C. was supported by a grant from the Genentech Foundation, P.D.G. was supported in part by funds from Daiichi, and O.L. was supported by funds from the American Heart Association. Supported by NIH grants GM-27800 and CA-54427 (to H.R.B.).

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Consumer Versus Resource Control in Freshwater Pelagic Food Webs

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Models predict that food-web structure is regulated by both consumers and resources, and the strength of this control is dependent on trophic position and food-web length. To test these hypotheses, a meta-analysis was conducted of 11 fish (consumer)-by-nutrient (resource) factorial plankton community experiments. As predicted, zooplankton biomass was under strong consumer control but was weakly stimulated by nutrient additions; phytoplankton biomass was under strong resource control with moderate control by fish. However, the phytoplankton and zooplankton responses to nutrient additions did not follow theoretical predictions based on the number of trophic levels in the food web.

The nature of the factors regulating food-web structure has been a very active area of ecological research (*1*, *2*) since the classic paper by Hairston, Smith, and Slobodkin (*3*) was published in 1960. In aquatic systems, food-web interactions strongly influence fisheries production, biogeochemical cycling, and ecosystem responses to anthropogenic eutrophication. A recent quantitative summary of the freshwater trophic cascade (*4*) literature showed that planktivorous fish treatments result in decreased herbivore (zooplankton) and increased primary producer (phytoplankton) biomass (*5*). In addition, phytoplankton response to the cascade is weakly dampened and highly variable, with weak responses in two-thirds of the experiments and very strong responses in the other experiments (*5*). Still, many questions regarding the dynamic nature of food-web interactions remain unresolved (*1*, *2*). In particular, what is the relative strength of consumer and resource control in pelagic food webs (*6*), and how do food webs respond to changes in system productivity under different food-web configurations (*7*)?

The debate over top-down (consumer) versus bottom-up (resource) control represents a synthesis of the known impact of nutrient regulation of primary producers (*8*) and higher trophic levels (*9*), and the more recent emphasis on consumer control of trophic levels through the cascade (*4*). In essence, the debate centers on whether herbivore and plant communities are regulated through predator control of herbivore abundance or through nutrient control of primary production. McQueen and colleagues (*6*) predicted bottom-up control is stronger at the base of the food web, and top-down control is stronger at higher trophic levels. For example, the zooplankton should be more strongly controlled by zooplanktivorous fish than by nutrients, whereas phytoplankton biomass should be primarily controlled by nutrient availability and to a lesser extent by higher trophic levels.

Oksanen *et al.* (*7*) developed a series of models to explore the theoretical relationship among ecosystem productivity, patterns of biomass accrual, and the number of trophic levels in that ecosystem. This predicted "a stepped pattern of biomass accrual" (*2*) across productivity gradients (*10*). In food webs with an odd number of trophic levels, increases in primary production should lead to increased biomass for odd-numbered trophic levels and no change in biomass for even-numbered trophic levels. Conversely, in food webs with an even number of trophic levels, increases in primary production should lead to increased biomass for even-numbered trophic levels and no change in biomass for odd-numbered trophic levels.

We assembled eight studies (*11*) that reported the results of 11 independent mesocosm experiments employing factorial nutrient addition and zooplanktivorous fish treatments. Simple criteria were used to decide which studies to include in our analysis (*12*). Six of the studies used simple fish-by-nutrient designs, and two used slight modifications of this design (*13*). In five studies, zooplankton community biomass values were obtained directly, and in three studies, zooplankton biomass was estimated using abundance and individual biomass data (*14*). All phytoplankton community biomass values were taken directly from the respective studies.

Mesocosms are classic experimental de-

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Table 1. The size of the experimental mesocosms, length of the experiments, samples averaged and source of the data for the 11 fish-by-nutrient experiments (*11*) summarized. Exp., experiment; Encl., enclosure.

Study	Exp.	Encl. size (m^3)	Exp. length (weeks)	Samples averaged	Measure of biomass (zooplankton)	Source	Measure of biomass (phytoplankton)	Source
Lynch and Shapiro	Exp. 2	1.4	6	3	Crustacean biomass	Fig. 6	Biovolume	Table 8
Vanni	1980	1	4	5	Crustacean biomass	Tables 1 & 2	Biovolume	Fig. 2
Vanni	1981	1	4	6	Crustacean biomass	Tables 1 & 2	Biovolume	Fig. 3
Drenner *et al.*	Exp. 1	5.5	3	4	Crustacean biomass	Fig. 2	Chlorophyll	Fig. 2
Faafeng *et al.*	Spring	7	3	3	Total biomass	Fig. 2	Chlorophyll	Fig. 1
Faafeng *et al.*	Summer	7	4	4	Total biomass	Fig. 2	Chlorophyll	Fig. 1
McQueen *et al.*	Exp. 1	700	15	9	Total biomass	Fig. 2	Chlorophyll	Fig. 2
Markosova and Jezek	Exp. 1	110	17	10	Large daphnid biomass	Fig. 5	Biovolume	Fig. 5
Qin and Culver	Exp. 1	0.6	4.5	5	Crustacean biomass	Fig. 1	Biovolume	Fig. 1
Proulx *et al.*	Shallow	150	10	6	Total biomass	Table 2	Biovolume	Fig. 2
Proulx *et al.*	Deep	600	10	6	Total biomass	Table 2	Biolvolume	Fig. 2

vices for studies of planktonic ecosystems, which make it easier to replicate and control treatments (in particular fish abundance). Mesocosms do, however, place constraints on spatial and temporal scale and prevent some important processes such as sediment–lake water exchange of nutrients. Whole lake investigations have optimal spatial scale and ecological relevance, but they present problems with reproducibility, cost, and access to suitable study sites. The time scale of the experiments we summarized (1 to 4 months, Table 1) is comparable to the period of major events in the typical seasonal succession of temperate planktonic ecosystems (*15*) and is many times longer than typical doubling times for common planktonic organisms.

To our knowledge, we have included all studies examining zooplankton and phytoplankton community responses to zooplanktivorous fish and nutrient addition treatments which fit our simple criteria (*11, 12*). Each experiment was considered a single blocked set of observations for our analysis. For the purposes of graphic display and to calculate treatment means, the data were transformed by calculating the logarithmic ratio of the control (no fish, no nutrients) to the other treatments accordingly: response = log(treatment mean/control mean). For analysis of variance (ANOVA), the data from each experiment were transformed accordingly: $\text{response}_{\text{ANOVA}}$ = log(treatment mean/geometric mean), where geometric mean equals the geometric mean of all four treatments. This transformation was used for the ANOVA because ANOVA assumes similar variance in each cell (*16*) and the former transformation results in zero variance for the control treatment cell. To test the response of two trophic level food webs to increases in system productivity, we compared the control treatments to the nutrient treatments. To test the response of three trophic level food webs to increases in system productivity, we compared the fish treatments to the fish-plus-nutrient treatments.

Our analysis provided generally strong agreement with the top-down and bottom-up control hypothesis of McQueen and colleagues (*6*). We found top-down (fish) control had a much stronger impact on zooplankton biomass than did bottom-up (nutrient) control (Table 2 and Fig. 1). The zooplankton had a geometric mean decrease of 72% in biomass in the fish treatments and an increase of 24% in the nutrient treatments. Our analysis found both top-down and bottom-up control of phytoplankton community biomass. However, nutrient control of phytoplankton biomass was substantially stronger than top-down control (Table

Table 2. The results of an ANOVA for the 11 fish-by-nutrient experiments. The ANOVA design used was the classic randomized block design without within-block replication (*23*), with the separate experiments serving as randomized blocks. Because this design lacks within-block replication, the *F* statistic is calculated as $MS_{model}/MS_{interaction}$ (*23*), with $MS_{interaction}$ being the overall interaction term for fish × nutrients × experiment. Percent variance explained refers to the portion of sum of squares attributable to that model.

Source	df	Sum of squares	*F* test	*P* value	Variance (%)
		Zooplankton			
Fish	1	3.467	401.73	0.0000	52
Nutrients	1	0.086	9.96	0.0101	1
Fish × nutrient	1	0.000	0.02	0.9595	0
Experiment	10	0.000	0.00	1.0000	0
Fish × experiment	10	2.478	28.71	0.0000	37
Nutrient × experiment	10	0.521	6.04	0.0044	8
Fish × nutrient × experiment	10	0.086			1
		Phytoplankton			
Fish	1	0.345	12.30	0.0056	12
Nutrients	1	1.540	54.88	0.0000	54
Fish × nutrient	1	0.057	2.04	0.1844	2
Experiment	10	0.000	0.00	1.0000	0
Fish × experiment	10	0.321	1.14	0.4192	11
Nutrient × experiment	10	0.323	1.15	0.4139	11
Fish × nutrient × experiment	10	0.281			10

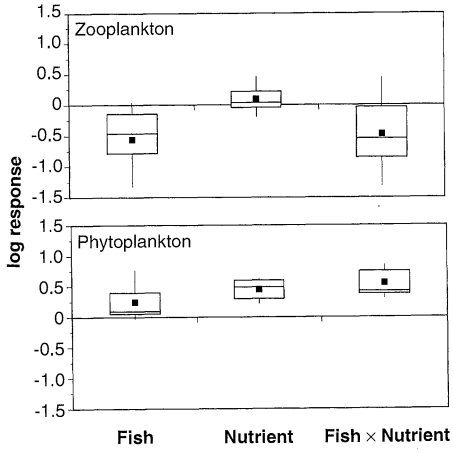

Fig. 1. The response of the zooplankton and phytoplankton community biomass to the fish and nutrient treatments. The values plotted were calculated as the $\log_{10}$-transformed ratio of the mean treatment biomass divided by the mean control biomass. The line through the middle of the box shows the median, and the dot shows the mean of the distribution. The outer edges of the box correspond to the 25th and 75th percentiles, and the "whiskers" to the 10th and 90th percentiles.

2 and Fig. 1). Phytoplankton biomass had a geometric mean increase of 179% in the nutrient treatments and a 77% increase in the fish treatments.

There were generally weak statistical associations between the spatial and temporal scale of the experiments and the strength of the zooplankton and phytoplankton responses to the fish and nutrient treatments (*17*). One potential explanation for the lack of a strong positive zooplankton biomass response to the nutrient treatments is that the experiments we summarized were simply too short for the zooplankton to respond to the increased phytoplankton supply. However, the zooplankton actually had somewhat stronger biomass responses in the shorter experiments (*17*), and common zooplankton are capable of at least nine population doublings during a 21-day experiment (assuming $r = 0.30$). Furthermore, Elliott and colleagues found, in simple food-chain experiments, that zooplankton can achieve equilibrium values well within the temporal scale of the experiments summarized in our analysis (*18*). This suggests that the lack of a strong positive zooplankton biomass response to the nutrient treatments was not due to life history constraints on zooplankton growth. We believe the nutrient treatments failed to markedly stimulate zooplankton biomass, because the phytoplankton stimulated by these treatments may have been difficult to ingest, digest, or were nutritionally inadequate, or a combination of these factors (*19*).

Our analysis did not support the predictions of Oksanen and colleagues (*7*) for how food webs of different lengths should respond to increases in system productivity. They predicted that in a two trophic level food web, increases in primary production would result in increased zooplankton biomass and no change in phytoplankton biomass. We found adding nutrients to two level pelagic food webs resulted in greatly increased phytoplankton biomass and little change in zooplankton biomass. For three trophic level food webs, they predicted increases in the system primary production would result in increased phytoplankton biomass and no change in zooplankton biomass. These responses were to some extent observed in the present analysis. However, the increase in phytoplankton biomass in the two trophic level food web (at 179%) was larger than the increase in phytoplankton biomass seen in the three trophic level food web (at 101%). These data suggest the response of phytoplankton and zooplankton biomass to nutrient additions was unrelated to the number of trophic levels in the food web.

The results of our analysis contrast with the experimental results of Wootton and Power (*20*) who found generally good agreement with the predictions of Oksanen *et al.* in a three trophic level food web. However, Leibold and Wilbur (*21*) showed that the biomass responses of two trophic level food webs was dependent on the dominant herbivore species in the system. The lack of a general relationship between ecosystem primary production and food-web length in planktonic food webs can be further emphasized by considering some of the world's least productive aquatic food webs. Whereas the model of Oksanen and colleagues predicts that ecosystems with low primary production will only have one or two trophic levels, ultraoligotrophic lakes and open oceans have between three and five functional trophic levels (*22*). Our results suggest that, under certain conditions, increased primary production due to nutrient inputs may not be efficiently transferred to herbivorous zooplankton biomass. To gain a better understanding of food-web interactions, it is important to determine which factors regulate the efficiency at which primary production is converted to herbivore biomass.

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12. The experiments must employ simultaneous factorial planktivorous fish and nutrient addition treatments. The nutrient treatments must include both phosphorus and nitrogen additions. The studies must present data describing the quantitative response of the zooplankton and phytoplankton communities to these treatments. The treatment and response variables cannot be confounded. For example, Leibold (*10*) added dense cultures of the alga *Ankistrodesmus falcatus* to nutrient treatments, but did not add algae to non-nutrient treatments. The experiments must also last several weeks.
13. We used the treatments of Lynch and Shapiro (*11*) accordingly: L − No Fish = Control; L + Fish = Fish; M and H − No Fish = Nutrient; and M and H + Fish = Fish + Nutrient, and the treatments of Drenner and colleagues (*11*) accordingly: 0, NF = Control; 0, F = Fish; 45:1, NF = Nutrient; 45:1, F = Fish + Nutrient.
14. Lynch and Shapiro's (*11*) zooplankton species-specific dry weights were estimated using the mean lengths at first reproduction reported by Lynch [M. Lynch, *Limnol. Oceanogr.* **24**, 253 (1979)] and calculating dry weights with standard zooplankton length-to-weight regressions [E. McCaully, in *Secondary Productivity in Freshwaters*, J. A. Downing and F. H. Rigler, Eds. (Blackwell Scientific Publications, Oxford, 1984), pp. 228–238]. For Vanni (*11*), zooplankton species dry weights were calculated by taking the mean values reported for all dates and treatments reported in his table 2. For Drenner and colleagues (*11*), cladoceran and copepod dry weight were assumed to be 3 and 1 μg per individual, respectively. Zooplankton community biomass was calculated by multiplying species weight by abundance and totaling.
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17. The respective relationships between the response of the plankton to the size of the mesocosms are: zooplankton response to the fish treatments versus log(mesocosm size), $r = -0.10$, $P = 0.67$, $n = 22$; zooplankton response to the nutrient treatments, $r = -0.30$, $P = 0.18$; phytoplankton response to fish, $r = 0.34$, $P = 0.12$; phytoplankton response to nutrients, $r = 0.13$, $P = 0.56$. The respective correlations for the length of the experiments are: zooplankton response to fish treatments versus length of experiment, $r = -0.22$, $P = 0.34$, $n = 22$; zooplankton response to nutrient treatments, $r = -0.39$, $P = 0.07$; phytoplankton response to fish, $r = 0.50$, $P = 0.02$; phytoplankton response to nutrients, $r = -0.08$, $P = 0.71$.
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22. For example, Lake Tahoe, a large ultraoligotrophic lake in California and Nevada, has four to five functional trophic levels including phytoplankton, herbivorous zooplankton, mysid shrimp, kokanee salmon, and lake trout [C. R. Goldman *et al.*, *Limnol. Oceanogr.* **24**, 289 (1979); D. A. Beauchamp *et al.*, *N. Am. J. Fish. Manage.* **12**, 442 (1992); D. A. Beauchamp *et al.*, *Great Basin Nat.* **54**, 130 (1994); H. J. Carney and C. R. Goldman, unpublished data]. Crater Lake, a large ultraoligotrophic lake in Oregon, has three functional trophic levels including phytoplankton, herbivorous zooplankton, and kokanee salmon [special issue on Crater Lake, G. L. Larson, Ed., *Lake Reservoir Manage.* **12** (July 1996)]. Similarly, Pauly and Christensen [D. Pauly and V. Christensen, *Nature* **374**, 255 (1995)] concluded the ultraoligotrophic open oceans have 4.2 functional trophic levels.
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