Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web

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Abstract

    Lake Washington is arguably the most famous case study of lake pollution and subsequent recovery, and the widely cited story implicates just a few major players in the lake's food web transformations. "The Lake Washington story" historically highlights key players that negatively affect other taxa—filamentous cyanobacteria, the influential grazer *Daphnia*, and its predator *Neomysis*. This food web model has been based variously on experiments, observation, and educated inference. Here we tested the robustness of that historical conceptual model in a single multivariate analysis of long-term data. Most aspects of the historical model are supported, but the analysis also suggests key roles for food resources not previously considered—the nutritious cryptomonads and ubiquitous picoplankton. This cohesive analysis helps align the historical model with recent studies emphasizing "bottom-up" controls in Lake Washington and similar systems, and demonstrates the usefulness of using long-term data analysis to validate results from traditional ecological approaches.

While biodiversity and complexity are viewed as important components of properly functioning ecosystems, ecologists recognize that some species are more important than others (Power et al. 1996; Kareiva and Levin 2002; Hooper et al. 2005). The population fluctuations or removal of keystone species (those that affect other species out of proportion to their own abundance) or numerically dominant species can trigger exceptionally large changes that are transmitted throughout communities. Ecologists struggle with identifying such key players in communities prior to losses or additions caused by human action. Traditionally, an experimental approach guided by natural history observation has been advocated to identify key species (e.g., Paine 1994; Power et al. 1996; Kareiva and Levin 2002), but both approaches can be limited in time and across space, raising questions about relevance to the scale at which ecological processes shape communities. Here we capitalized on an unusual opportunity to "ground truth" a famous historical conceptual model of food web dynamics, previously based on short-term experimental research and educated inference, by quantitatively analyz-

ing a taxonomically rich, 33-yr data set. Further, we tested whether food webs constructed using experimentation and observation of a few presumably key taxa are different than those constructed using statistical analysis of large observational data sets that include a wider range of taxa.

"*The Lake Washington story*"

    Lake Washington is perhaps the most famous case study of a lake's response to pollution and subsequent recovery, from both scientific and social perspectives (Edmondson 1991; Smith 1998; Williams 2002). "The Lake Washington story" (Edmondson 1994) has been derived largely from visual assessment of 10–30 yr of data, laboratory experimentation, and inferences from literature, but a cohesive analysis of the long-term data set is still lacking.

    Edmondson's (1994) historical conceptual model emphasizes the important roles of a very few key players with strong negative effects on other species, namely *Oscillatoria*, *Daphnia*, and its predator *Neomysis* (Fig. 1). Secondary sewage treatment plants delivered effluent to the lake beginning in 1941, with the maximum inputs occurring in 1962. Water clarity was reduced during the time of sewage inputs, relative to historical records, and blooms of the cyanobacterium *Oscillatoria* were conspicuous throughout the year. Edmondson (1970) famously demonstrated that sewage-related phosphorus inputs were responsible for nuisance algal growth. Diversion of the sewage began in 1963 and was completed in 1968. In 1971, maximum water transparency exceeded the historical maximum, and by 1972, Edmondson (1991) considered the lake recovered in a practical sense. Lake Washington's stakeholders were
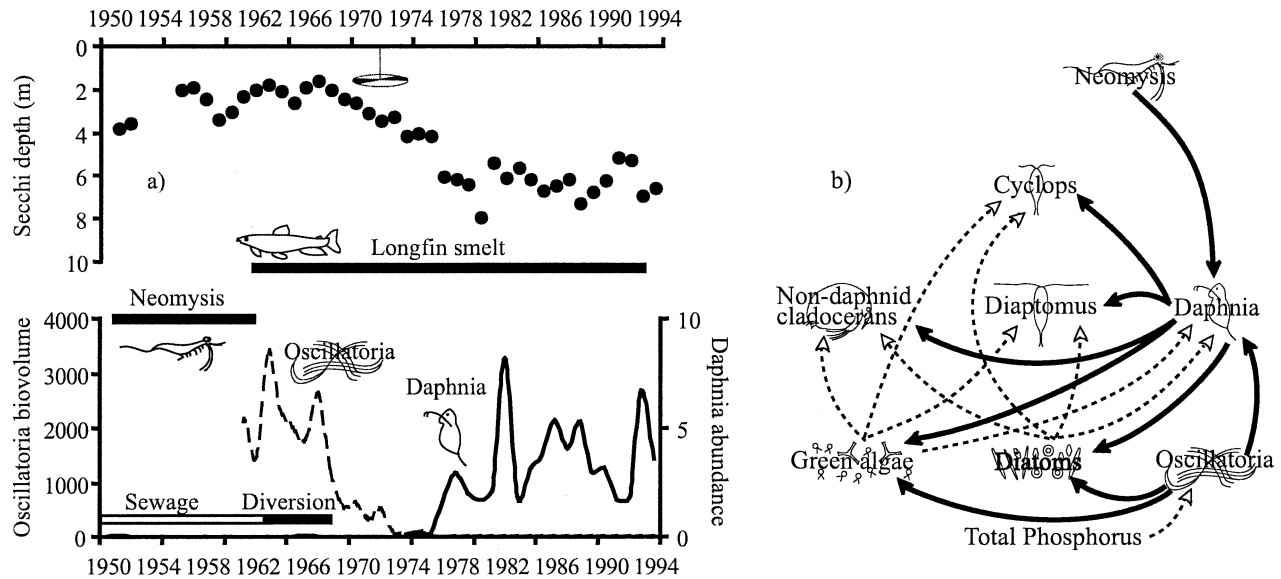
Fig. 1. Major relationships historically thought to affect water quality and food web structure in Lake Washington, based largely on the synthesis of Edmondson (1994). Edmondson's group observed (a) events in Lake Washington that, taken together, suggested (b) a conceptual model for planktonic food web interactions. See text in "The Lake Washington story" section for details. (a) Secondary sewage treatment plants delivered effluent to the lake from 1941 to 1968, and the filamentous cyanobacterium *Oscillatoria* dominated the algal community at levels regarded as a public nuisance. Sewage diversion proceeded from 1963 through 1968. The mean annual biovolume of *Oscillatoria* is expressed as mm^3 L^{-1}, with complete records beginning in 1961. Secchi disk symbol indicates the point after sewage diversion when maximum summer water clarity (expressed as Secchi depth in meters) exceeded prior maxima and Edmondson considered the lake recovered in a practical sense. In 1976, a further increase in Secchi depth was associated with *Daphnia* establishment (shown as average annual individuals L^{-1}), for the first time in record. *Daphnia*'s invertebrate predator *Neomysis* declined in the 1960s in concert with the dramatic increase of its predator, the longfin smelt. (b) The historical conceptual model emphasizes that *Daphnia*, well known as a superior grazer, strongly influenced both water clarity and competing zooplankton grazers through suppression of dominant phytoplankton. The roles of *Neomysis* and the cyanobacterium *Oscillatoria* were prominent in suppressing *Daphnia* and its food resources. Green algae and diatoms are the phytoplankton in Lake Washington that have historically drawn the most attention, based on their abundance, nutritional content, and presence in gut content analysis of the zooplankton (Infante and Edmondson 1985; Infante and Litt 1985). The crustacean grazers *Diaptomus*, *Cyclops*, and non-daphnid cladocerans codominate the zooplankton biomass, and their dynamics have been considered in more detail than those of the rotifers. Arrows point toward the response species. Solid lines are negative effects and dashed lines are positive effects.

largely satisfied with the lake conditions, and Edmondson doubted additional oligotrophication could occur given the level of watershed activity (Edmondson 1991).

In 1976, a further increase in Secchi depth was associated with *Daphnia* establishment for the first time in record (Fig. 1). *Daphnia* are thought to have increased transparency by heavily grazing algae in summer (Edmondson and Litt 1982). Because historical and extant colonization routes were apparent, and *Daphnia* were occasionally observed in the plankton previously, it was unclear why *Daphnia* had not been previously established. Edmondson and Abella (1988) suggested that *Neomysis*, a native invertebrate predator specializing on *Daphnia* in Lake Washington (Murtaugh 1981), was very abundant and suppressed *Daphnia* early in the time series. However, in the early 1960s, Lake Washington's longfin smelt (*Spirinchus thaleichthys*) population increased, possibly due to unintentional improvements in its spawning habitat resulting from flood-control measures undertaken on the lake's main tributary (Edmondson and Abella 1988). Longfin smelt in Lake Washington specializes on eating *Neomysis* and is thought to control mysid populations in Lake Washington

(Chigbu and Sibley 1998). While predatory conditions with respect to *Neomysis* were therefore improved for *Daphnia* by the early 1960s, at this time the cyanobacterium *Oscillatoria* was extremely abundant. Infante and Abella (1985) demonstrated that *Oscillatoria* directly suppresses *Daphnia*, probably through mechanical interference with feeding, and also indirectly inhibits *Daphnia* by depressing certain food resources. *Oscillatoria* essentially disappeared from the plankton by 1976, the year in which *Daphnia* clearly came to dominate the summer plankton. In this description of Lake Washington's most dramatic events, there remains a puzzling lag between *Oscillatoria*'s decline and *Daphnia*'s establishment in the plankton (1972–1976).

Testing Edmondson's model

Here we ask whether quantitative evidence exists in the continuous long-term data set that supports Edmondson's (1994) conceptual model for the Lake Washington food web, which was based variously on experimentation and observation. We used multivariate autogressive models (MARs) (Ives 1995; Ives et al. 1999, 2003) to evaluate how
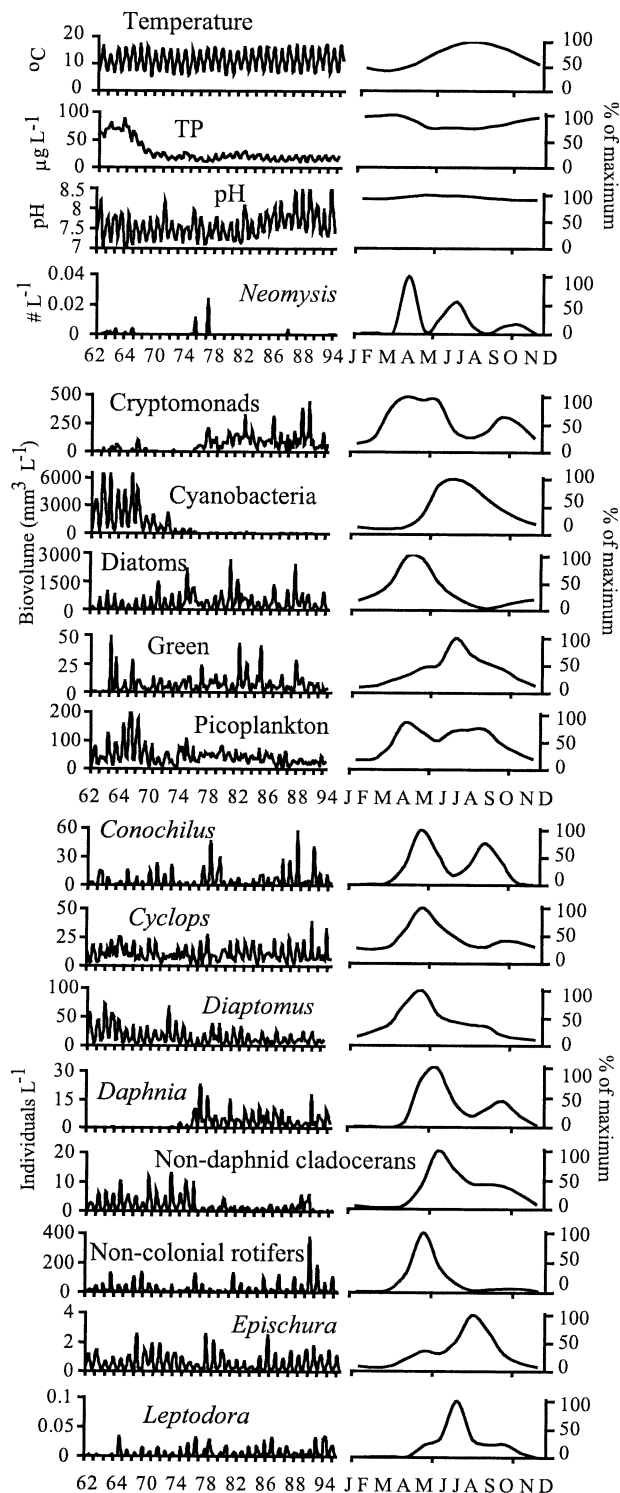
Fig. 2. Time series of all variables used in multispecies autoregressive (MAR) models for 1962 to 1994 in Lake Washington. For these figures the data are expressed as quarterly means (Quarter 1 = January, February, March; Quarter 2 = April, May, June; Quarter 3 = July, August, September; Quarter 4 = October, November, December) (left-hand column) and as proportion of each variable-specific maximum in each month to show patterns of seasonality (right-hand column). For cyanobacteria, these seasonality patterns in the right-hand column were

changes in the phytoplankton and zooplankton communities relate to biotic interactions and changes in exogenous drivers, such as water temperature and total phosphorus. MAR analysis may be interpreted as path analysis for time series data, or more simply as a set of multiple linear regressions (one for each taxon, here) solved simultaneously to achieve the greatest overall parsimony. Therefore, the cautions that apply to path analysis and multiple regressions generally apply to MARs; importantly, it is a method of establishing correlation between presumed drivers and responses, and limits on inference are set by the experimental or nonexperimental arena from which the data are collected. In the analysis of community time series, MARs have the advantage of highlighting potentially key players in communities through the elimination of species interactions that are too weak to predict and quantify interaction strengths.

Methods

Lake Washington long-term data—Since 1962, limnological data in Lake Washington have been collected every 1–4 weeks, and counts for taxa considered here are complete through 1994 (Fig. 2). Edmondson and Lehman (1981), Edmondson and Litt (1982), and Edmondson et al. (2003) provide details on data collection. The surface collections at the mid-lake station (Madison Park) provided the most continuous time series, and so we only analyzed those data in our study.

We aggregated the various interacting phytoplankton and zooplankton species into 13 taxonomic categories. Algae were categorized based on nutrition and palatability to grazers: diatoms, green algae, cryptomonads, picoplankton, and cyanobacteria. Brett and Müller-Navarra (1997) described diatoms, green algae, and cryptomonads as being the most nutritious foods for zooplankton. The picoplankton group is a variety of free-living phytoplanktonic and bacterioplanktonic cells from 1 to 10 μm in length that are too small and varied to have been routinely characterized at higher taxonomic resolution over the entire period. While the size range does span the nannoplankton, typical nannoplankton in Lake Washington are relatively easily recognized and assigned to other categories, such that this category is dominated by picoplankters such as *Synechococcus*. Cyanobacteria in Lake Washington's eutrophied period was mainly *Oscillatoria rubescens* (now classified as *Planktothrix*); in later years, *Oscillatoria* disappeared almost entirely, and cyanobacteria is primarily represented by *Anabaena* and *Aphanizomenon* (Edmondson et al. 2003).

We grouped zooplankton based on similarities in feeding and susceptibility to predation. *Daphnia*, non-daphnid cladocerans, *Diaptomus*, the colonial rotifer *Conochilus*,

←

calculated for pre-1976 years, because cyanobacteria were relatively scarce after this time. Similarly, seasonality patterns in the right-hand column are shown only using post-1976 years for *Daphnia* and cryptomonads because they were relatively scarce prior to 1976. For all variables, note that *y*-axis differs.

and non-colonial rotifers are grazers. *Daphnia* was rarely observed in Lake Washington prior to 1976. This category is composed mainly of *D. pulicaria, D. thorata*, and *D. galeata*. The non-daphnid cladocerans were dominated by *Bosmina* and *Diaphanosoma*. The category *Diaptomus* was dominated by *Leptodiaptomus ashlandi*. While some diaptomid copepods can be omnivorous (Williamson and Vanderploeg 1988), carnivory has not been detected in Lake Washington *L. ashlandi* (Infante and Edmondson 1985). We considered *Conochilus* separately from other rotifers because its colonial habit should make it differently susceptible to mechanical interference from cladocerans and invertebrate predation than other rotifers (Wallace 1987). The category non-colonial rotifers includes only herbivorous rotifers, mainly *Keratella, Kellicottia*, and *Polyarthra*. The cyclopoid copepod *Cyclops bicuspidatus thomasi*, one of the most abundant Lake Washington zooplankton, was classified as an omnivore based on literature accounts (e.g., Arts et al. 1992). The invertebrate predators *Epischura* and *Leptodora* occurred episodically and at low abundance.

Exogenous drivers considered here were temperature (average 0 to 20 m), total phosphorus (TP), and the invertebrate predator *Neomysis*. *Neomysis* is thought to have been an important predator of *Daphnia* (Edmondson 1994) in Lake Washington but was rare in these samples, as the long-term data set used here began after the time when *Neomysis* was especially abundant in Lake Washington. *Neomysis* was classified as an exogenous variable because we did not consider it to be controlled by factors within the plankton food web, but rather by fish predation in Lake Washington (Chigbu and Sibley 1998). We also used month of the year as an exogenous factor to account for seasonality in our models (sensu Ives et al. 1999). Unfortunately, data for longfin smelt or any other fish were not available at sufficient temporal resolution to incorporate in the MAR models.

Data analysis—We aggregated all data into monthly time steps. We used linearly interpolated values for missing data, resulting in interpolation for phytoplankton on 3 dates and zooplankton on 7 dates, out of a total of 396 dates. We replaced zeroes with random values between zero and half the lowest observed value for that time series. The data series were log-transformed, such that the models could characterize nonlinear relationships more effectively (Ives 1995). Finally, we standardized the data to a dimensionless unit interval [0,1] by subtracting the minimum value and dividing by the range according to

$$x' = \frac{(x - x_{\min})}{(x_{\max} - x_{\min})}.$$

This way, model parameters were directly comparable among taxa.

The MAR models have been described in detail in Ives (1995), Ives et al. (1999), and Ives et al. (2003), and the associated Matlab code is available through Ecological Archives (Ives et al. 2003). In MAR analysis, a multiple regression equation is fit to each taxon using the abundance of other taxa and levels of environmental variables from the previous time step as predictor variables. For each of the planktonic taxonomic groups *i*, we fit the following autoregressive model

$$x_{i, t+1} = x_{i, t} + c_i + \left[\sum_{j=1}^{13} b_{i,j} x_{j,t} \right] + \left[\sum_{k=1}^{5} a_{i,k} u_{k,t} \right],$$

where the abundance of taxon *i* at the next time step $x_{i,t+1}$ is a function of its abundance in this time step ($x_{i,t}$), a taxon-specific intercept (c_i), abundance of all of the other taxa ($x_{j,t}$), and levels of the exogenous drivers ($u_{k,t}$). The $b_{i,j}$ and $a_{i,k}$ parameters are regression coefficients that indicate the effects of endogenous and exogenous interactions, respectively, for each species.

The equations corresponding to each taxon in the model were fit simultaneously, with parameters $b_{i,j}$ and $a_{i,k}$ estimated using conditional least-squares. To reduce the probability of overparameterization of the model, we restricted interactions in several ways. We used a priori knowledge of plankton dynamics to confine interactions to those that were biologically meaningful (sensu Ives et al. 1999). We excluded interactions of the predators *Epischura*, *Leptodora*, and *Neomysis* with primary producers, and direct effects of TP on all animals. We also constrained the signs of certain interactions to be biologically plausible. Specifically, we assumed that predators could not increase prey numbers, the filamentous cyanobacteria could not increase abundance of grazers, and that TP could not negatively affect algal abundance. While indirect interactions could lead to such excluded results, we assumed that such effects would be comparatively minimal at the time intervals considered here.

We used Akaike's information criterion (AIC) to select the most parsimonious model from a field of randomly generated models that variously included interactions between species and environmental drivers. To arrive at the best model structure, we randomly constructed 100 models by including or excluding coefficients with equal probability, and chose the resulting model with the lowest AIC. The process was repeated 100 times (sensu Ives et al. 1999), resulting in a single model structure with the lowest AIC (out of 10,000 random models). This number of iterations has proven robust (Ives et al. 1999; S. E. Hampton unpubl. data), and the model selection procedure compares favorably to more computationally intensive model runs, such as forward or backward stepwise regression (S. E. Hampton unpubl. data). Coefficients that were retained in less than 15% of the models were dropped (sensu Ives et al. 1999). We then used bootstrapping (*n* = 500) of the final model to obtain 95% confidence intervals for the coefficients in the best-fit model. Coefficients with confidence intervals that overlapped zero were eliminated from the final best-fit model. Finally, we calculated the conditional R^2 for each taxon, which evaluates the ability of the model to predict the change in abundance of each taxon from one time step to the next (Ives et al. 1999).

We compared two MAR models: a simple model including only those taxa and environmental variables previously thought to be important to Lake Washington

Table 1. Coefficients retained and estimated in the best-fit multivariate autogressive (MAR) model, which used a simplified set of variables corresponding to the historical conceptual model in Fig. 1b. Taxa for this analysis were chosen based on the emphasis that has historically been placed on their importance in Lake Washington's food web dynamics. The conditional R^2 describes how well the model predicts change in densities from one time step to the next. Italics indicate autocorrelation within each taxon. *Neomysis* was not retained in any best-fit model, and is not shown here.

Response	Predictors										
	Diatom	Green	Cyano	Cyclops	*Daph*	*Diapt*	N-D clad	Month	Temp	TP	R^2
Diatoms	*0.52*		−0.06					0.07	−0.35		0.38
Green		*0.44*									0.31
Cyanobacteria			*0.92*							0.11	0.04
Cyclops				*0.66*	−0.16		−0.12	0.11	−0.12		0.31
Daphnia	0.23		−0.11		*0.57*				0.11		0.23
Diaptomus	0.09				−0.22	*0.64*	−0.14	−0.09			0.38
Non-daphnid cladocerans	0.23				−0.27		*0.54*		0.25		0.31

TP, total phosphorus.

food web functioning, based largely on Edmondson (1994), and a richer model that included all 13 plankton groups and 3 exogenous drivers. Taxa included in the simple model were diatoms, green algae, cyanobacteria, *Cyclops*, *Daphnia*, *Diaptomus*, and non-daphnid cladocerans (Fig. 1b).

Results

Both the simple model (Table 1; Fig. 3) and the larger community-wide analysis (Table 2; Fig. 4) produced similar views on the plankton community that largely reflected Edmondson's (1994) historical conceptual model for Lake Washington. Identity and magnitude of the variables retained in the two MAR models were almost identical to each other; correspondence between parameter values was high ($r^2 = 0.88$, $p < 0.001$). Conditional R^2 values were somewhat higher in the community-wide model (Tables 1, 2). The most outstanding difference between the two models was in their characterization of zooplankton-phytoplankton relationships. The simple model indicated strong interactions between diatoms and grazers (Table 1; Fig. 3); however, when the full suite of phytoplankton were considered in the larger model, picoplankton and crypto-phytes had the most numerous and strongest effects on zooplankton, and diatoms had greatly diminished importance (Table 2; Fig. 4). Additionally, the direct negative effect of cyanobacteria on *Daphnia* in the simple models was replaced by negative effects of cyanobacteria on *Daphnia*'s food source cryptomonads in the community-wide model.

As predicted, cyanobacteria and *Daphnia* played the most influential roles in Lake Washington's plankton (Fig. 4). Cyanobacteria was the only group that was significantly correlated with phosphorus (Table 2; Fig. 4), corresponding to its proliferation during the eutrophic period. Cyanobacteria had negative effects on almost all other algal taxa, and its effects on algae were greater than those for any other alga or grazer (Table 2). *Daphnia* had negative relationships with almost all other grazers (Table 2; Fig. 4).

Non-daphnid cladocerans appear to have influenced the Lake Washington plankton, as negative relationships with other grazers were fairly widespread, if weak relative to *Daphnia*'s effects (Table 2). Consistent with their modern decline, the non-daphnid cladocerans did not appear to negatively affect *Daphnia*, whereas the negative effect of *Daphnia* on them was strong during recent years when *Daphnia* came to dominate the community.

The picoplankton and cryptomonads were unexpectedly influential in the full-community model. Picoplankton had positive relationships with nearly all grazers, and these positive coefficients were much higher than taxa generally considered more nutritious, such as diatoms or cryptomonads (Table 2). In contrast, cryptomonads had few direct connections within the community, but these links were with the two most influential taxa: cyanobacteria and *Daphnia*. Therefore, a change in cryptomonads that would affect cyanobacteria and *Daphnia* in one month would be expected to affect nine more community members in the following month through connections with these powerful players.

The role of invertebrate predation in community dynamics did not strongly emerge in this analysis, although *Leptodora* interacted in an apparently predatory role with several other species, such as a fellow predator *Epischura* and the colonial rotifer *Conochilus* (Table 2; Fig. 4). *Neomysis* was not retained in any of the models.

Most taxa showed relationships with temperature (Table 2), reflecting seasonality and implying a potential for climate change to impact phenology, particularly as a fixed value for month of the year was retained as a seasonal factor for fewer taxa. The zooplankton also generally retained relatively high coefficients for pH effects (Table 2).

Discussion

Many aspects of the historical conceptual model were corroborated by this analysis, suggesting that a few key players in the plankton have greatly controlled food web
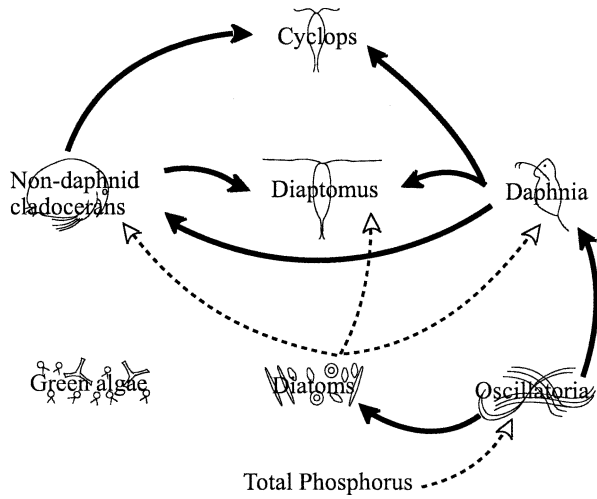
Fig. 3. Food web interactions suggested by the simple best-fit MAR model that was suggested by the historical conceptual model of food web functioning in Lake Washington. Line thickness reflects coefficient size, with values shown in Table 1. Arrows point toward the response species. Solid lines are negative effects, and dashed lines are positive effects.

structure over time. Such agreement between the historical model and the present analysis is important for at least two reasons. First, it provides coalescence for the widely cited "Lake Washington story" that was built variously on experimental work, visual inspection of the time series, and educated inference. Second, when novel interactions emerge in a biologically plausible model that otherwise reflects the historical conceptual model, it suggests that those interactions may be "real" and warrant further exploration. In this case, we can identify two more potentially influential groups in Lake Washington—the inconspicuous picoplankton and cryptomonads. The emergence of these effects is particularly notable because the importance of bottom-up forces in Lake Washington has been recently indicated (Scheuerell et al. 2002; Arhonditsis et al. 2003), but not yet adequately integrated in the conceptual model of the Lake Washington ecosystem (e.g., Edmondson 1991, 1994).

The Lake Washington Story—We found evidence that cyanobacteria was fueled by phosphorus inputs and that this group may have had dramatic effects on the other plankton. While all algae are likely to correlate positively with TP in a phosphorus-limited system, here only cyanobacteria retained the TP coefficient as predictive. Edmondson (1994) has previously made the point that proliferation of *Oscillatoria* was the main biotic response to sewage, rather than an overall increase in phytoplankton. Other algae thus appeared to benefit little from the TP increase during eutrophication, and instead only experienced the negative effects of cyanobacteria dominance, such as light limitation or toxicity (Infante and Abella 1985). However, some interactions among the phytoplankton and elsewhere in the model may be masked by the length of the time step; extremely rapid generation times for plankton could prevent detection of effects when viewed at the monthly interval (Hampton and Schindler 2006).

Table 2. Coefficients retained and estimated in the best-fit multivariate autoregressive (MAR) model for the full set of interacting phytoplankton and zooplankton taxa in Lake Washington. The conditional R^2 describes how well the model predicts change in densities from one time step to the next. Italics indicate autocorrelation within each taxon. *Neomysis* was not retained as a significant predictor in any model, and is not shown here.

| Response	Predictors																	
	Crypto	Diatom	Green	Cyano	Pico	Cono	Cyclops	Daph	Diapt	Epi	Lepto	N-D clad	N-C rot	Month	Temp	TP	pH	R^2
Cryptomonads	*0.56*			−0.36								−0.20						0.24
Diatoms		*0.53*		−0.16										0.10	−0.32		−0.06	0.38
Green			*0.45*	−0.22														0.32
Cyanobacteria	−0.12			*0.46*											0.13	0.18		0.28
Picoplankton			−0.05		*0.64*													0.26
Conochilus				−0.17	0.14	*0.45*		−0.27			−0.14	−0.32					0.47	0.46
Cyclops					0.26		*0.62*	−0.15				−0.12		0.13	−0.17			0.34
Daphnia					0.29			*0.62*						−0.04			0.34	0.32
Diaptomus						−0.09		−0.22	*0.63*			−0.11			−0.12		0.27	0.41
Epischura										*0.38*		0.17	0.09		0.25		0.19	0.35
Leptodora							0.10	0.24		0.24	*0.13*	0.52		−0.12	−0.11			0.52
Non-daphnid cladocerans		0.09			0.15			−0.26			−0.13				0.19		0.34	0.40
Non-colonial rotifers					0.31							−0.09	*0.52*	0.17	−0.35			0.39

TP, total phosphorus.
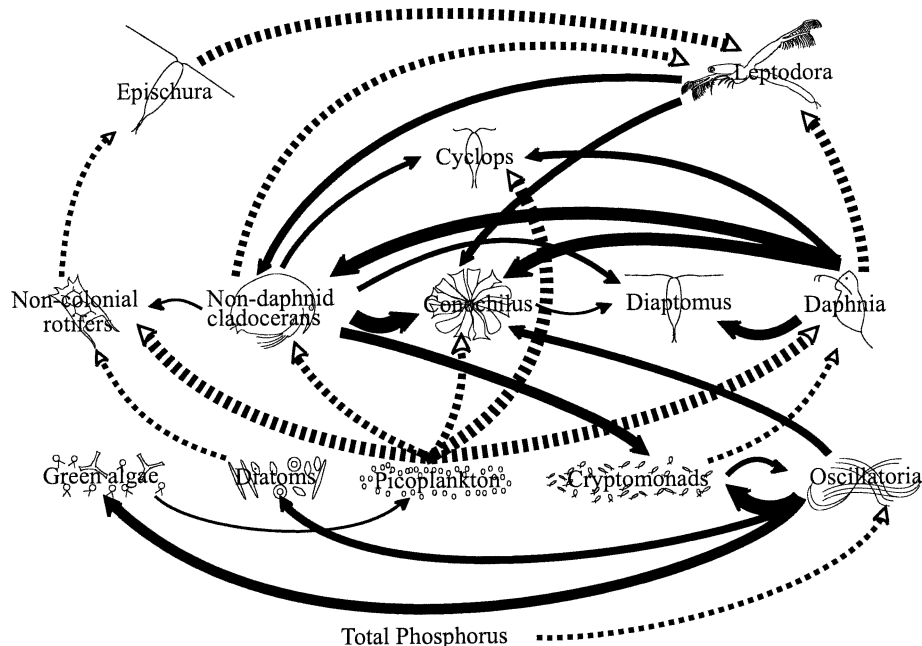
Fig. 4. Food web interactions suggested by the community-wide best-fit MAR model, shown in Table 2. Line thickness reflects coefficient size, with values shown in Table 2. Arrows point toward the response species. Solid lines are negative effects, and dashed lines are positive effects.

The algae suppressed by *Oscillatoria* were those that, in turn, supported growth of the common grazers—in particular, the nutritionally important diatoms that affected non-daphnid cladocerans, and the cryptomonads that benefited *Daphnia*. Indeed, laboratory experiments designed to estimate the direct negative effects of *Oscillatoria* on *Daphnia* unexpectedly found extraordinarily strong effects on its food resources in the laboratory (Infante and Abella 1985). Those researchers were simply unable to encourage enough diatom growth in the presence of *Oscillatoria* to support *Daphnia* in their experiments, and so abandoning the diatoms as a resource, they instead used *Cryptomonas*, which was heavily suppressed by *Oscillatoria* but resistant enough to support *Daphnia*'s growth for the duration of the experiments. Infante and Abella (1985) further found that *Oscillatoria* directly suppressed *Daphnia* growth through mechanical interference. While the simple conceptual model used here suggested such a direct negative interaction between *Oscillatoria* and *Daphnia*, the more complex model eliminated this link in favor of including the negative effects of *Oscillatoria* on *Daphnia*'s food resources. Thus, the present analysis would suggest that *Oscillatoria*'s strongest effects on zooplankton were through suppression of phytoplankton in Lake Washington.

When *Daphnia* rapidly came to dominate the plankton in 1976 and beyond, summertime water clarity was greatly increased, presumably at least partially due to *Daphnia*'s grazing effects (Edmondson and Litt 1982). Although Edmondson expected that this increased herbivory should have resulted in changes in *Daphnia*'s competitors (Edmondson and Litt 1982), he did not vigorously pursue this direction in future research (but see Edmondson 1985). In

the present analysis, we showed that by placing these competitors into the context of the multivariate community in which they are embedded, negative effects of *Daphnia* may be readily seen. In particular, *Daphnia*'s negative effect on non-daphnid cladocerans in this model was concordant with a visually apparent reduction (Fig. 2) of non-daphnid cladocerans as *Daphnia* increased in the 1970s. In addition, *Daphnia*'s negative effect on *Conochilus* in this model concurs with recent analyses showing that *Conochilus* no longer grows in months when *Daphnia* now dominates and presumably suppresses algal resources (Hampton 2005), particularly picoplankton (Hampton and Schindler 2006).

Picoplankton and cryptomonads in Lake Washington have been studied relatively little, but the present analysis suggests a role for them that may be more far-reaching than previously thought. Until very recently (Hampton 2005; Hampton and Schindler 2006), the role of picoplankton in the Lake Washington food web had not been examined. Other work shows that where picoplankton-zooplankton relationships are studied, picoplankton interactions with grazers are substantial across lakes of widely varying trophic status (e.g., Stockner and Shortreed 1994; Burns and Schallenberg 2001; Sommer et al. 2003). Therefore, we should not be surprised if these ubiquitous edible cells augment the nutrition provided by the traditional algal foci of our food web analyses, such as diatoms and green algae. Indeed, in the simplified model that included only diatoms and green algae as resources, diatoms seemed to have been retained primarily because of their usefulness as a proxy for the abundance of other phytoplankton that fluctuate with similar timing (Fig. 2), namely the picoplankton and

cryptophytes that replaced diatoms as the dominant food resources in the community-wide analysis.

Our analysis suggests that *Cryptomonas* played a role in *Daphnia*'s initial increase in the mid-1970s. When considering the historical conceptual model of Lake Washington dynamics (Fig. 1), there has always been an unexplained temporal gap between *Oscillatoria*'s disappearance and *Daphnia*'s rise to dominance. Unfortunately we also were unable to conclusively determine what factor(s) prevented *Daphnia*'s establishment between 1972 and 1976, but conspicuously, *Cryptomonas* was not a measurable component of the plankton until the same year that *Daphnia* finally increased. Naturally, Edmondson and Litt (1982) were aware of this concurrent emergence, but at the time thought it unlikely that a single taxon could so strongly affect *Daphnia* growth. In the intervening years, much more has been learned of the importance of algal nutrition for zooplankton growth; cryptomonads have been described as unusually nutritious, especially with regard to highly unsaturated fat content (Brett and Müller-Navarra 1997), and they also are seemingly universally edible to zooplankton in terms of shape and size. Such literature recognition of cryptomonads' nutritional value complements its favorable reputation among zooplankton culturists (e.g., Stemberger 1981).

That the present analysis indicates a larger role for food resources in food web functioning, in addition to the more dramatic effects of grazing and interference that were emphasized in the classic telling of the Lake Washington story (Edmondson 1991, 1994), helps to reconcile the historical conceptual model with other accounts of Lake Washington as a community responding to bottom-up forces. Scheuerell et al. (2002) found that *Daphnia* population dynamics were relatively well-predicted by the overall nutritional quality of the phytoplankton. As discussed above, the cryptomonads highlighted in the present analysis would reasonably constitute an exceptionally nutritious food source (Brett and Müller-Navarra 1997). Additionally, in Arhonditsis et al.'s (2003) detailed analyses of limnological data from 12 stations in 1995–2000, the only grazing effects detected were those of *Daphnia* during a few months in summer, when grazing acted in concert with declining nutrients to produce a clearwater phase.

In this study, *Daphnia*'s impact on the food web through grazing may be inferred from its negative effects on competitors. Ideally, MAR analysis would indicate the negative effects *Daphnia* had on particular phytoplankton that in turn affected *Daphnia*'s competitors; unfortunately, in this case, *Daphnia*'s strong effects on competitors emerged directly, without identifying the phytoplankton that were presumably depressed by its grazing. As a generalist feeder, *Daphnia*'s grazing effects may be dispersed over a wide variety of vulnerable taxa. Lehman et al.'s (2004) comprehensive examination of Lake Washington's phytoplankton community suggested that the general lack of detectable grazing effects in this and other studies may be due to highly species-specific responses of phytoplankton to herbivory, which are swamped when taxa are considered in aggregate. Another possibility is that the temporal resolution of the study is too coarse to capture grazing-imposed decreases in phytoplankton within each category before other taxa respond positively to the reduction in algal competition and to nutrient recycling by zooplankton. The preceding suggestions are necessarily speculative, but they present testable hypotheses that might be addressed experimentally in the future.

Although *Neomysis* can reasonably be implicated in *Daphnia* suppression with other circumstantial evidence (Edmondson 1994), we could find no such effects in the analysis of the long-term data. However, we are aware that the historical sampling methods for the long-term Lake Washington program were not designed to adequately sample mysids, and so our understanding of their dynamics is not as complete as that for zooplankton and phytoplankton. Additionally, the data set used in the present analysis began at a time when *Neomysis* had declined in Lake Washington from historically higher levels.

The strong seasonality of plankton dynamics is generally well known (Sommer et al. 1986); thus, it is unsurprising that temperature was retained as a predictive value in the models for most taxa. Interestingly, a stronger relationship with temperature, as opposed to month of the year, is concordant with flexibility in the timing of plankton dynamics that has been suggested by previous work, i.e., that plankton have already responded to environmental warming with phenological changes in Lake Washington (Winder and Schindler 2004; Hampton 2005; M. González Sagrario unpubl. data) and aquatic systems worldwide (e.g., Straile 2002; Hays et al. 2005). Phenological responses to warming among the plankton may have increasingly apparent food web effects as climate continues to change.

While Edmondson (1994) speculated that the long-term increases in lake pH could shift phytoplankton back toward greater cyanobacteria abundance (sensu Shapiro 1990), positive associations between pH and cyanobacteria, or any algae, were not evident. Instead, correlations between zooplankton and pH in this analysis appeared to mainly reflect the seasonality of algal growth and temperature.

We had an unusual opportunity to construct a quantitative food web model built solely on long-term observational data and assess its concordance with a historical conceptual model that is well-documented and, by now, legendary in ecology. We corroborated the long-standing assertion that cyanobacteria and *Daphnia* are exceptionally influential members of the Lake Washington community through suppressive effects on other taxa, but our analyses also suggested potentially strong supporting roles for food resources—the ubiquitous picoplankton, and cryptomonads that may support *Daphnia* and other zooplankton. The model coalesces aspects of the Lake Washington story in a single analysis, and the "new" role it suggests for picoplankton and cryptomonads helps to reconcile the historical conceptual model with other more recent accounts of Lake Washington as a lake controlled from the bottom up. The analysis also highlighted the strong influence of temperature on plankton dynamics, corroborating recent research that indicates plankton phenology has responded to long-term environmental warming.

As more long-term data sets emerge worldwide, the tools needed to appropriately analyze multivariate time series have also begun to prove their usefulness and tractability. Accordingly, we suspect that many opportunities exist for using large observational data sets alongside more traditional experimental approaches. Recognizing that correlation is not causation, such that we must appropriately bound interpretations of results, the analysis of long-term observational data can act in synergy with experimentation and modeling to advance knowledge of ecosystems. The rigorous quantitative analyses of large observational data sets can provide ground truth at relevant scales for hypotheses derived in the laboratory and computational models, and may further focus mechanistic research on patterns not previously recognized.

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