

Empirical evaluation of observation scale effects in community time series

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Natural communities are highly complex and dynamic over time, with populations structured by numerous abiotic and biotic forces acting through direct and indirect pathways. Multispecies Autoregressive (MAR) modeling can be used to partition effects of variables that are interrelated and temporally autocorrelated in time series from natural systems. Here we address two main questions in applying MAR models to community time series. First, what is the effect of observation scale on interpretation of community dynamics? We used a 10-year weekly planktonic time series from Lake Washington to construct multiple “biweekly” and “monthly” data sets, and compared resulting community interaction models. Direct abiotic effects and intraspecific autocorrelation were apparent using all data sets. Biotic interactions were more apparent using biweekly and monthly data, indicating that time lags longer than one week were necessary to detect numerical response to interspecific interactions. Second, we examined effects of dropping the winter months from our analyses to simulate the common practice of sampling only during the “growing season” in long-term ecological studies. We found that biotic interactions remained similarly characterized in models using only non-winter months, but that the importance of seasonal physical factors nearly disappeared in non-winter models. Exclusion of winter data in sampling designs may therefore allow us to characterize biotic interactions, although it may not help us understand populations’ relationships to seasonal abiotic variables. The models supported many previous findings from experimental and qualitative investigations of Lake Washington community interactions, implying that MARs provided plausible characterizations of community dynamics, but some previously unconsidered relationships did emerge, such as the importance of cryptomonads and picoplankton for zooplankton growth. We conclude that explicit consideration of time lags in biotic response is necessary to understand relative importance of abiotic and biotic factors, and that sampling regime can therefore strongly influence our interpretations of community dynamics.

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Abiotic factors and biotic interactions act in concert to affect species abundance and distribution (Connell 1972, Menge and Sutherland 1987). Simultaneous consideration of population responses to multiple abiotic variables and biotic relationships challenges ecologists at both a theoretical and practical level (Yodzis 1988). Traditionally, ecologists have advocated experimental manipula-

tion of ecological systems to explicitly determine causal relationships between presumed drivers and population dynamics (Paine 1994). Given the natural variety of potential abiotic and biotic drivers for any population, experimental designs that include all natural variables are impossibly complex, so researchers generally use a priori knowledge of systems to choose only a few

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interactors for study (Kareiva 1994). Obviously, such focused experimentation sacrifices the possibility for uncovering relationships among a larger, natural assemblage of interacting variables (Menge 1995), and logistics usually constrain experiments to temporal and spatial scales that may be inadequate for realistic characterization of relationships (Yodzis 1988, Levin 1992). While manipulation is the most direct method to assess the potential interaction strength for species and response to abiotic variation, it rarely allows researchers to discern whether that potential is actually reached in natural communities and environments.

Long-term ecological data sets are increasingly valued for the perspective they can provide on natural responses of communities to perturbations and interactions among species, against a naturally existing backdrop of environmental and community complexity (Edmondson 1993, Kratz et al. 2003). Comprehensive studies of single systems over many years can help define the range of environmental variation affecting the community, and provide the large number of data points necessary to differentiate pattern from noise in complex systems (Bjørnstad and Grenfell 2001, King et al. 2004). Additionally, some responses may exhibit long time lags that require longer study periods, such as population fluctuations of longer-lived organisms (Schindler et al. 1985) or biotic responses that manifest through more complex indirect pathways (Yodzis 1988).

Complex pathways are especially difficult to trace when a population response is treated as a univariate problem, with the population thought to respond to one or a few effectors having unidirectional effects (Ives 1995). Consideration of community dynamics as a multivariate problem is necessary for at least two reasons. First, where population responses to an important abiotic or biotic driver are moderated by other species (Peacor and Werner 2004), these indirect pathways may be misunderstood through simple visualization of the data or univariate tests (Wootton 1994). Second, feedbacks can occur over time as populations affect each other reciprocally, a phenomenon that may cause negative relationships at one time step and positive relationships at others (Carpenter and Kitchell 1987).

Multivariate autoregressive (MAR) modeling has been developed for analyzing long-term ecological data to quantify interactions among species and environmental drivers (Ives 1995, Ives et al. 1999, 2003). Rather than ignoring the biological and statistical non-independence of time-ordered data points, as would traditional statistical analyses in this application, autoregressive models explicitly use correlation between time steps to improve predictions. In ecological applications of MAR models, variance in population abundance is partitioned among potentially interacting components of a system, such that direct and indirect pathways through which environment and community members affect each population

can be discerned. The usefulness of MAR modeling has been effectively demonstrated with plankton community data from the North Temperate Lakes Long-Term Ecological Research program (Klug and Cottingham 2001, Beisner et al. 2003, Ives et al. 2003), and several fundamental ecological questions can and should now be addressed in its implementation.

First, what are the effects of the temporal resolution of data on our understanding of community relationships? It is known that observation scale affects our interpretation of species interactions in both experimental and observational data (Levin 1992). We can expect time lags in observable biotic response to species interactions and abiotic drivers (Carpenter et al. 1993), such that relationships may be obscured at short time scales, or that numerical evidence for interactions degrades at longer time scales. Additionally, different types of interactions may be best viewed at different time intervals, depending upon the nature of cause-effect relationships (e.g. guild responses to El Niño precipitation, reviewed by Jaksic 2001). For example, top-down forces may be evident at shorter time scales, since organisms are immediately removed from the system, while bottom-up processes take longer to result in observable numerical responses due to physiological constraints on growth and reproduction times.

Second, can community interactions be effectively characterized within the limited range of environmental conditions in which data are frequently available? Limnological data, and many other types of ecological data, are often collected only during the non-winter months of the year. Winter data are sometimes logistically difficult to collect, and their omission in food web studies could be reasonably justified on the basis that primary production may be decoupled from food web interactions during the winter due to a strong reliance on physical drivers (Carpenter and Kitchell 1987). Effects of limiting our view of communities to this restricted range of abiotic variation are mostly unknown.

In this study we examined the changes in interpretation of community interactions that occur when observation scale is restricted in two common ways: 1) data collection at increasingly coarse scale, here weekly data sets are compared to those at biweekly and monthly intervals, and 2) exclusion of data collected in winter months. We predicted that the importance of the autoregressive component (i.e. the influence of a species' abundance at the previous time step on its own abundance in the present time step) would deteriorate with increasing time intervals, but that most biotic interactions would be more evident at the longer observation intervals due to time lags in biotic response. We compared the emergence of bottom-up and top-down relationships at different time intervals, expecting that top-down interactions (i.e. grazing and predation) would appear at shorter time intervals than bottom-up

relationships which require time for growth. Regarding the importance of winter data, we predicted that food webs constructed using only non-winter months would include fewer biotic interactions than those using full annual data, the rationale being that the diversity of relationships among community members over the annual cycle is not fully represented when one third of the data is omitted. The resulting models provided a characterization of the Lake Washington food web that is largely consistent with historical conceptual models of the lake's community dynamics, increasing our confidence in using the models to make inferences about community structure across scales.

Material and methods

To examine the effects of restricted observation scales on food web analyses, we used MAR modeling to construct food webs using 10 years of weekly planktonic community data (Appendix 1) from Lake Washington (Seattle, WA). From the weekly data set, we extracted two "biweekly" and four "monthly" data sets. We compared food webs that were constructed from the MAR models based on weekly, biweekly, and monthly data, to understand the effects of altering the time intervals at which data are viewed. Similarly, we built a food web based only on our non-winter data and compared it to one based on the full annual data.

Lake Washington long-term data

Between 1971 and 1981, Lake Washington chemical, physical and planktonic data were collected at roughly weekly intervals, primarily to capture changes occurring in the lake following diversion of secondary sewage effluent (Edmondson 1994). Detailed methods for data collection can be found in Edmondson and Lehman (1981), Edmondson and Litt (1982), and Edmondson et al. (2003). While the Lake Washington data set includes vertical profiles from many different sampling sites, data from 20 m to the surface at the control station (Madison Park) provided the most continuous time series and only those data are analyzed here. We divided potentially interacting phyto- and zooplankton species into 14 taxonomic categories.

Because trophic interactions between zooplankton and phytoplankton were of primary interest to us, we chose to divide algae into categories based on nutrition and palatability to grazers: diatoms, green algae, cryptomonads, unicells, *Oscillatoria/Planktothrix* and other algae. Brett and Müller-Navarra (1997) summarized literature and experiments to describe diatoms, green algae and cryptomonads as being the mostly nutritionally valuable foods to zooplankton. The unicells group

was comprised of a variety of free-living phyto- and bacterioplanktonic cells from 1 to 10 μm in length that were too small and varied to have been routinely counted to higher taxonomic resolution over the entire Lake Washington study period. The size range of the unicells makes them widely available to zooplankton grazers. *Oscillatoria* was singled out in this study due to its high abundance during Lake Washington's eutrophied period, and suspected importance in controlling food web structure in Lake Washington (Infante and Abella 1985, Edmondson 1994), concordant with many literature accounts of strong *Oscillatoria* influence in freshwater communities (Hosper 1998). *Oscillatoria agardhii* is now classified as *Planktothrix agardhii*, but we retain the older nomenclature for ease of comparison with previous Lake Washington literature. Other algae includes both edible and inedible forms of algae, such that its effects on zooplankton are probably variable.

Zooplankton group definition was determined by taxon abundance and guild (Appendix 1). *Daphnia*, non-daphnid cladocerans, *Diaptomus*, the colonial rotifer *Conochilus* and non-colonial rotifers are grazers. In general, the two rotifer taxa are physically smaller and have shorter generation times than the three crustacean grazers. *Daphnia* was rarely observed in Lake Washington prior to 1976 (Edmondson 1994). While *Daphnia* species exhibit different seasonal dynamics, their long-term dynamics and ecological similarity as important grazers led us to group them together. The non-daphnid cladocerans were dominated by *Bosmina* and *Diaphanosoma*. The category *Diaptomus* is dominated by *Leptodiaptomus ashlandi*. While some diaptomid copepods can be omnivorous (Williamson and Vanderploeg 1988), gut content study of Lake Washington *Diaptomus* did not detect carnivory (Infante and Edmondson 1985). *Conochilus* was considered separately from other rotifers, due to the relatively large size of its colonies which should make it differently susceptible to mechanical interference from cladocerans (sensu Gilbert 1988) and invertebrate predation (Wallace 1987) than other rotifers. 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 considered to be an omnivore based on literature accounts (Arts et al. 1992). The invertebrate predators *Epischura* and *Leptodora* occur sporadically and in low abundance in Lake Washington.

Exogenous drivers considered here were temperature, as average temperature from 0 to 20 m, total phosphorus (TP) measured as $\mu\text{g l}^{-1}$, and maximum abundance of the invertebrate predator *Neomysis* (Appendix 1). *Neomysis* is thought to have been an important predator of *Daphnia* in Lake Washington, but was present in extremely low numbers in this time series, after the increase of longfin smelt in Lake Washington

(Edmondson 1994). *Neomysis* was classified as an exogenous rather than endogenous variable in these models, because we do not consider it to be controlled by factors within the plankton food web. This mysid is a relatively large crustacean that likely is primarily controlled by fish predation in Lake Washington (Chigbu and Sibley 1998). Following the methods of Ives et al. (2003), we also used week (week number of the year) and week² as exogenous factors accounting for seasonality in our models.

Data analysis

Where data were missing, we used linearly interpolated values. 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 non-linear relationships more effectively (Ives 1995). Finally, the data were standardized to dimensionless units (Z scores), by subtracting the mean for each taxon and dividing by its standard deviation, such that all effects in the resulting models were directly comparable.

MAR modeling can be loosely described as path analysis for time series, or even more simply, several multiple regression equations (one for each species) executed with time lagged data and solved simultaneously to arrive at the most parsimonious model overall. The MARs described here closely follow the methods described by Ives (1995) and Ives et al. (1999, 2003) in which a greater variety of possible implementations are explored. The Matlab (The Mathworks, Inc.) code has been made publicly available by Ives et al. (2003) through Ecological Archives. For each of the endogenous effects (i.e. each species), we fit the autoregressive model

$$x_i(t+1) = x_i(t) + c_i + \left[\sum_{j=1}^{14} b_{i,j} x_j(t) \right] + \left[\sum_{k=1}^5 a_{i,k} u_k(t) \right]$$

where x_i is the standard Z score of each taxonomic group at time t , $u_k(t)$ is the value of the exogenous variable k in units of standard deviation at time t , c_i is a species-specific constant, and $a_{i,k}$ and $b_{i,j}$ are regression coefficients that evaluate the effects of exogenous and endogenous interactions, respectively, for each species.

The 14 equations were fit simultaneously, using conditional least-squares estimation. Because the number of possible interactions is large, overparameterization of the models is a potential problem. Therefore, we used a priori knowledge of the Lake Washington plankton dynamics to restrict interactions to those that were biologically meaningful (Ives et al. 1999). Conceptually such a priori constraint is similar to that practiced in the use of structural equation modeling

(Wootton 1994, McCune and Grace 2002). We excluded interactions of the predators *Epischura*, *Leptodora* and *Neomysis* with primary producers, and direct effects of TP on all zooplankton. As suggested by Ives et al. (1999), we also constrained the signs of certain interactions to be biologically plausible. Specifically, we assumed that predators could not increase prey numbers, the filamentous cyanobacterium *Oscillatoria* could not increase abundance of grazers, and that TP could not negatively affect algal abundance. While indirect interactions could lead to the emergence of these excluded responses, we assumed that such effects would be comparatively minimal at the time intervals considered here.

The best model structure was chosen using Akaike's information criterion (AIC). AIC awards parsimony in model structure, allowing selection of the model that best fits the data using the fewest parameters. Exhaustive search of potential models is impractical for most ecological applications of MARs. Therefore we rely on model selection procedures that maximize the possibility of finding the set of models with the lowest AIC values, and on several further levels of model evaluation.

To choose the most parsimonious model, we randomly constructed 100 model structures by including or excluding coefficients with equal probability, and chose the resulting model with the lowest AIC. The process was repeated 100 times, for a total of 10 000 random models, and resulted in a single model structure with the lowest AIC (sensu Ives et al. 1999).

We further evaluated the quality of each resulting model by examining bootstrapped coefficient values and R^2 values. We used bootstrapping ($n=500$) to obtain confidence limits for the coefficients retained in the best-fit model. We calculated a conditional R^2 value to assess model fit. The conditional R^2 reports the proportion of change in a factor from time t to $t+1$ that is explained by the model, and is considered the most appropriate way to assess fit of MAR models (Ives 1995).

Comparisons of data sets

Results from the weekly data set were compared to those of "biweekly" and "monthly" data sets. Two biweekly data sets were extracted from the weekly data set, using every other week of data starting at weeks one and then two. Four monthly data sets were constructed by using data from every fourth week, starting at weeks one, two, three and four. Mean bootstrapped coefficients and R^2 values from the biweekly and monthly data sets were then compared to weekly values.

In addition, two growing season data sets were constructed from and compared to the biweekly data sets. For the growing season data sets, the months of

November through February were excluded, to emulate a standard limnological sampling strategy, which is also likely to occur at biweekly intervals. For this analysis, correlations between the last (autumn) sample of each year and the first (spring) sample of the next year were excluded, so that only relationships between consecutive samples were considered (sensu Ives et al. 1999).

Results

Endogenous interactions across time intervals

The conditional R^2 , assessing the ability of the model to describe changes in abundance across time steps, increased with decreasing temporal resolution for all taxa (Fig. 1). The range of conditional R^2 values for models in this study was similar to those obtained in previous studies characterizing planktonic food web interactions using MARs (Ives et al. 1999, 2003). The autocorrelation of each taxon decreased substantially as time interval increased for all taxa except *Leptodora* (Fig. 2) which also always had the lowest autocorrelation in any model. In contrast, biotic interactions became more evident at longer time intervals. Bottom-up effects were more numerous and stronger than top-down effects overall (Fig. 3). While several relationships remained detectable across time intervals, the most numerous interactions appeared using biweekly data sets.

Bottom-up effects

The number and strength of bottom-up effects in the models increased substantially with time interval (Fig. 3). The algal taxon with the most numerous and consistent positive effects on grazers was the grouping of unicells between 1 and 10 μm in cell length (Fig. 2), a group that is presumably widely edible and of mixed nutritional value. Unicells and the relatively small and nutritious cryptomonads were the only algae that strongly affected abundance of the dominant grazer *Daphnia* (Fig. 2). Highly edible and nutritious diatoms positively affected only non-daphnid cladocerans and *Diaptomus* in the biweekly data sets (Fig. 2).

Effects of prey on the zooplanktivores were less numerous than other bottom-up effects, but tended to be strong (Fig. 2) and did not appear to increase over time (Fig. 3). *Cyclops* and *Conochilus* enhanced *Leptodora* numbers, but the effects were no longer apparent at the monthly time interval (Fig. 2). The effect of non-daphnid cladocerans was retained in the most parsimonious models for *Leptodora* at several time intervals, but differed significantly from zero only at the monthly time interval.

Top-down effects

Grazing effects increased modestly with time interval (Fig. 3), but were restricted to the grazers *Daphnia* and *Diaptomus* (Fig. 4). The inhibition of unicells by *Daphnia* was the only grazing interaction that appeared in all models.

Similarly, predator effects were more apparent with increasing time interval (Fig. 3). *Leptodora*'s negative effects on prey were evident only at the biweekly interval, impacting the colonial rotifer *Conochilus* and the other main predator *Epischura*. *Epischura* negatively affected the copepod *Cyclops* at both longer time intervals.

Interference and exploitative competition

Competition among the primary producers was not as evident as it was among zooplankton, and showed no strong pattern across time intervals (Fig. 3). Unicells and cryptomonads were the taxa most frequently inhibited by other phytoplankton (Fig. 4). The filamentous cyanobacterium *Oscillatoria* strongly impacted both unicells and cryptomonads in several models (Fig. 4), and diatoms consistently inhibited cryptomonad abundance across time intervals.

Among the zooplankton, competitive interactions were nearly exclusive to the three dominant taxa *Daphnia*, *Diaptomus* and *Cyclops* (Fig. 4). *Daphnia* was the dominant taxon in all competitive interactions, with an increasingly negative effect on *Cyclops* at longer intervals and relatively strong effects on *Diaptomus* in the weekly and biweekly models. Weaker, less consistent negative interactions were apparent between *Diaptomus* and *Cyclops* (Fig. 4).

Exogenous effects across time intervals

In general, when retained in models, the exogenous factors produced much higher coefficients than did the biotic interactions (Table 1). The strictly seasonal elements week and week² had more numerous, consistent and strong effects than any of the biotic interactions (Table 1). All phytoplankton and zooplankton responding to week and week² showed similar trends, corresponding to the generally lower abundance of plankton during the winter. At longer time intervals, temperature and the strictly seasonal factors were informative for fewer taxa, but where the seasonal elements were retained in the monthly models, the coefficients were extremely high (Table 1). Total phosphorus (TP) was only retained in the weekly model for cryptomonads ($a=0.13$), and no effects of the predator *Neomysis* were apparent in these models.

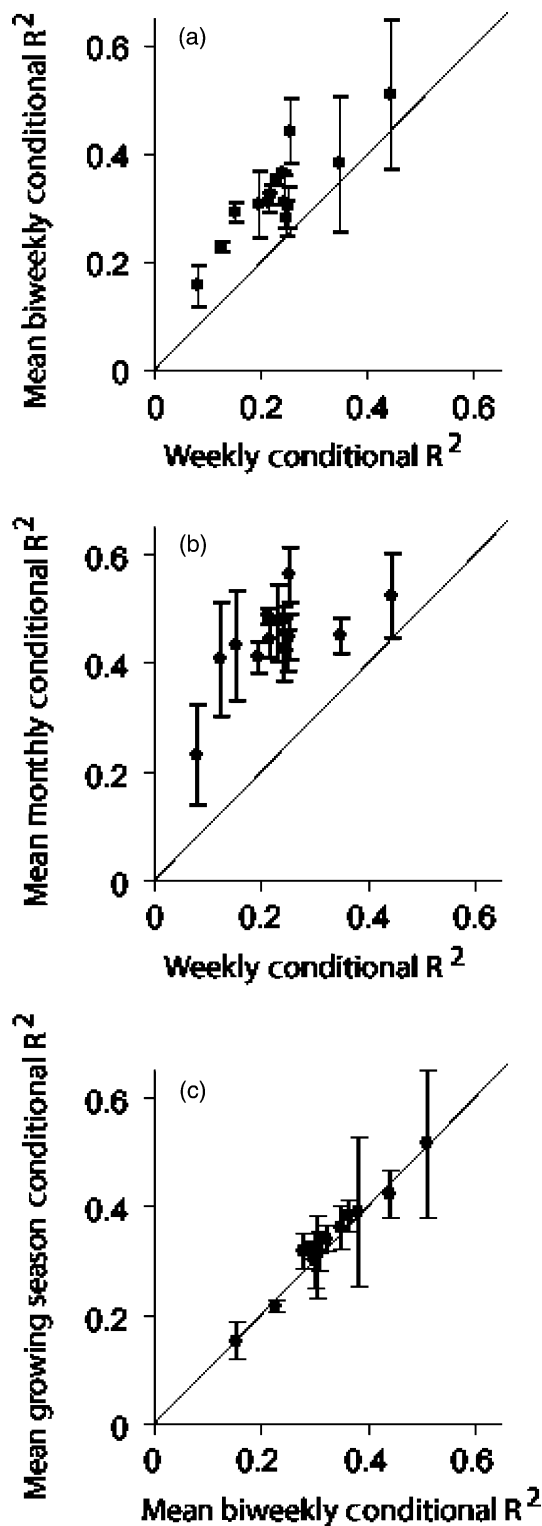


Fig. 1. Mean conditional R^2 values of (a) biweekly and (b) monthly models plotted against weekly model results, and (c) growing season models plotted against full annual biweekly models. Error bars indicate 95% confidence intervals. The solid line is a 1:1 line.

Annual vs “growing season” dynamics

Since growing season data sets were produced using biweekly data, the results were compared to the biweekly models. The growing season model R^2 fits were comparable to those of models built on annual data (Fig. 4), implying that increases of R^2 among the set of annual models (“Results, Endogenous interactions across time intervals”) were not simply an artifact of the changes in the number of input data. Autocorrelation for each taxon (Fig. 4, 5) was also remarkably consistent between growing season and annual biweekly models. The most serious effect of eliminating winter months from analyses was the substantially decreased importance of temperature and the seasonal elements week and week² (Table 1). In contrast, relatively few bottom-up, top-down, or competitive effects were lost by exclusion of the November–February data (Fig. 6). Rather than exhibiting general patterns in losses and gains common to trophic levels, changes were fairly taxon-specific.

More bottom-up effects were lost from non-winter models than were added (Fig. 6). Bottom-up effects of unicells on all rotifers and *Daphnia* disappeared, leaving the cryptomonad group as the only detectable benefactor of the dominant grazer *Daphnia* in the growing season (Fig. 5). The effect of diatom algae shifted away from herbivorous non-daphnid cladocerans to non-colonial rotifers and *Cyclops* (Fig. 5).

Although some top-down and competitive effects were lost in the growing season models, *Daphnia*’s negative interactions were more numerous when the winter months were dropped from analysis (Fig. 4, 5). *Daphnia*’s suppression of unicells and *Cyclops* remained apparent, and additional inhibition of the ecologically similar non-daphnid cladocerans and the tiny herbivorous non-colonial rotifers emerged. Competitive interactions between *Cyclops* and non-daphnid grazers were less evident in non-winter months. The filamentous cyanobacterium *Oscillatoria* negatively affected *Daphnia* in the growing season model, although its impact on cryptomonad algae disappeared.

Discussion

The exogenous seasonal factors had far stronger effects on plankton abundance than did biotic interactions in models that included complete annual dynamics, but their almost total disappearance from growing season models indicated that biotic interactions govern plankton dynamics in the non-winter months. While growing season data thus captured most of the strong biotic relationships present in annual models, sampling interval (weekly, biweekly or monthly) was comparatively

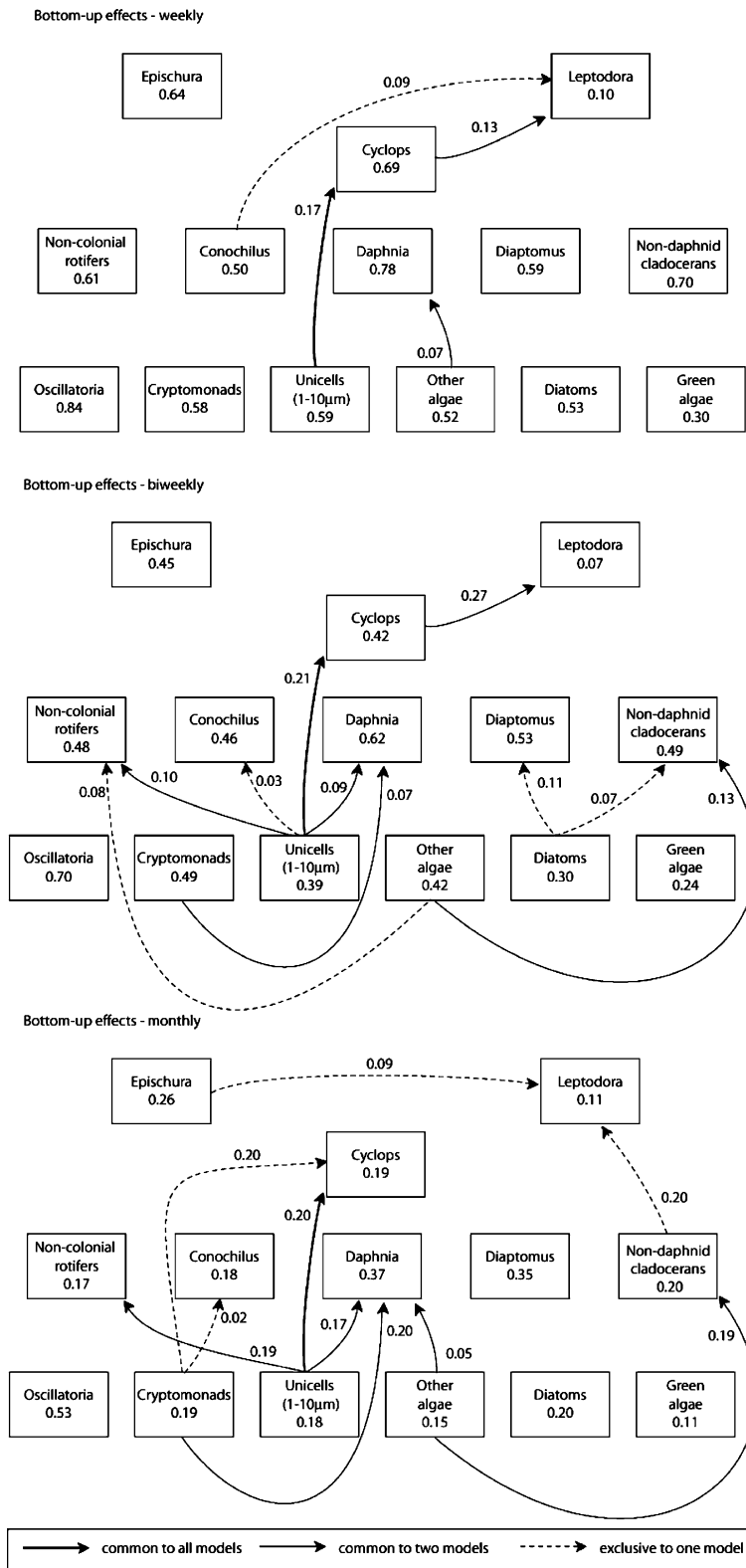
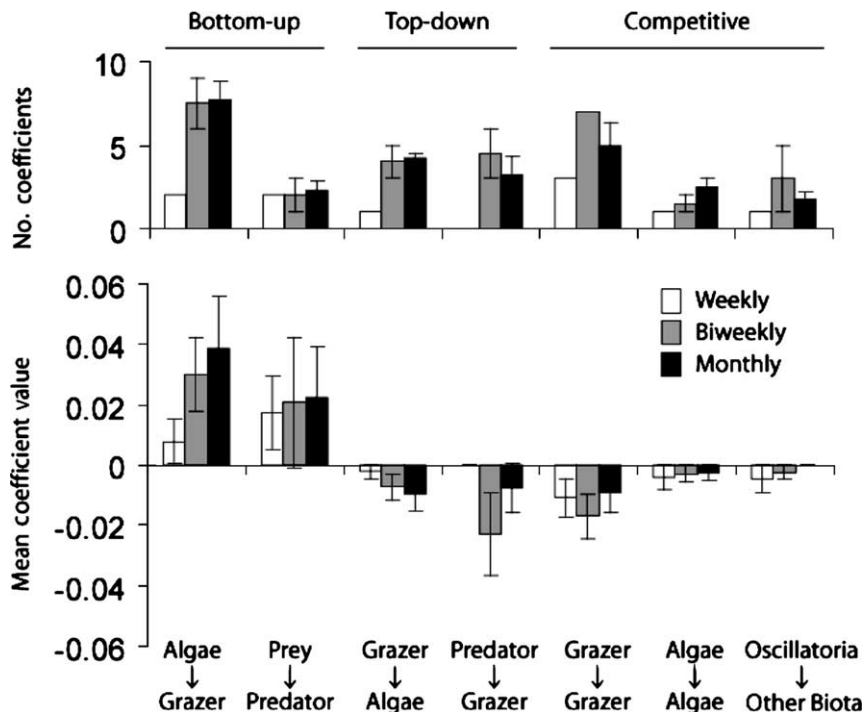


Fig. 2. Food webs showing bottom-up interactions as indicated by weekly, biweekly and monthly models. Numbers next to interaction lines are the coefficients that represent interaction strength. Only those interactions retained by the best fit models, and with coefficients significantly different from zero, are shown as arrows. Numbers in taxon boxes are autocorrelation coefficients for that species.

Fig. 3. Number of coefficients retained within each grouping of interaction type, and mean coefficient values (± 1 SE) of each interaction type for weekly, biweekly and monthly models. For some interactions, signs were constrained during model selection, as described in Methods. Mean coefficient values include zeroes (potential interactions lacking arrows in Fig. 2, 4).



important in determining which relationships emerged as important in analyses. First, we discuss these general conclusions regarding the influence of observation scale on our interpretations of the Lake Washington food web, and then evaluate the MAR models' characterization of specific aspects of the food web in comparison to historical conceptual models of the Lake Washington system.

The importance of time intervals between observations

As we predicted, a population's own abundance at time t became less useful for predicting abundance at time $t+1$ as the time interval increased, but examination of model changes from weekly to monthly time intervals strongly suggested that time lags longer than one week were necessary to capture interspecific biotic interactions, supported by two main attributes of these models. First, conditional R^2 values increased for all taxa in models using biweekly and monthly data. Second, both number and strength of coefficients describing biotic interactions were greater in the biweekly and monthly models. Many interspecific relationships retained in models for biweekly and monthly data sets did not emerge at the relatively close time intervals of the weekly data set, indicating that some biotic effects require more time to manifest to detectable levels. This result is concordant with the findings of Carpenter and Kitchell (1987), who determined through food web simulations that relation-

ships between primary productivity and zooplankton biomass were best observed at sampling intervals greater than six days.

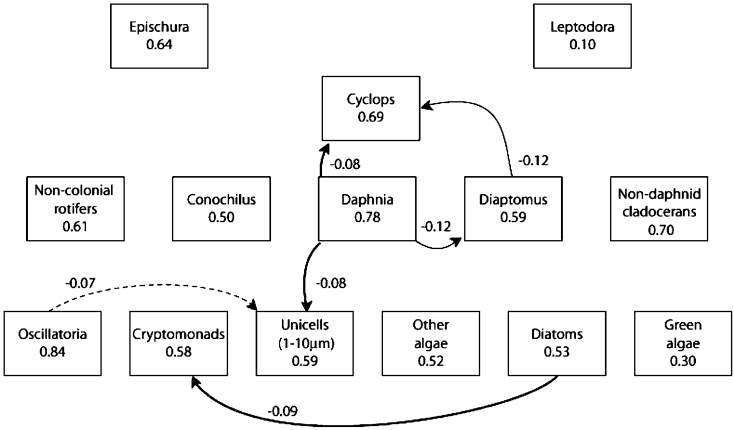
In bottom-up interactions, time lags in observing numerical response to trophic activity likely are necessary due to physiological constraints on the transformation of food into reproductive output at a level we can detect. The rotifers and possibly *Daphnia* can exhibit generation times under a week at summer temperatures (Gillooly 2000), such that response within a week is possible at certain but not most times of year.

For top-down effects, time lags longer than a week are less intuitive, since prey are instantly removed from the system. In Wisconsin lakes, similarly long time lags were required to observe effects of fish predation on zooplankton body size (Soranno et al. 1993) and grazing effects on many aspects of the phytoplankton communities (Carpenter et al. 1993). For the Lake Washington invertebrate predators, a fairly long period of interaction with prey seemed necessary to observe predatory effects. *Leptodora* and *Epischura* occur in low numbers in Lake Washington, meaning that predation rate is likely low overall and that our sampling for them is less effective, and both factors reduce our ability to observe interaction.

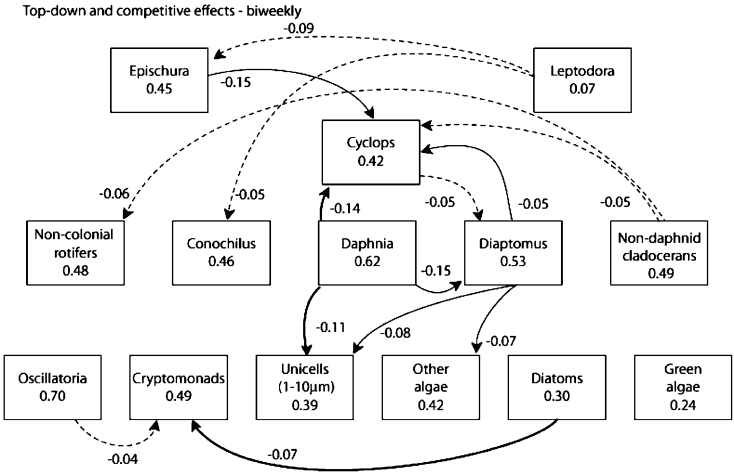
Annual vs growing season dynamics

The exogenous seasonal factors almost completely lost descriptive power when winter months were excluded from analyses, indicating that for most

Top-down and competitive effects - weekly



Top-down and competitive effects - biweekly



Top-down and competitive effects - monthly

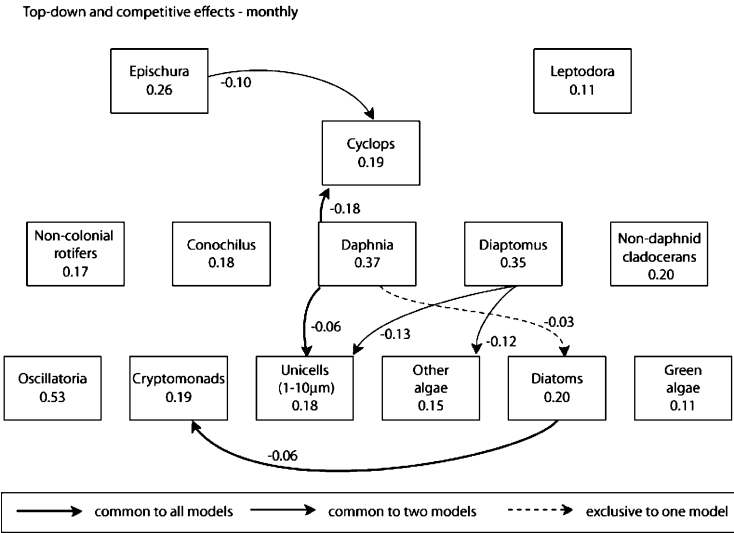


Fig. 4. Food webs showing top-down and competitive interactions as indicated by weekly, biweekly and monthly models. Numbers next to interaction lines are the coefficients that represent interaction strength. Only those interactions retained by the best fit models, and with coefficients significantly different from zero, are shown as arrows. Numbers in taxon boxes are autocorrelation coefficients for that species.

taxa, abundance could be adequately described by exogenous coefficients from the growing season models, R^2 fits were very similar to those of annual fits. In spite of the loss of many high exogenous coefficients from the growing season models, R^2 fits were very similar to those of annual fits. It appeared that biotic interactions were

Table 1. Mean coefficients for exogenous variables from MAR models using weekly, biweekly (growing season biweekly), and monthly data sets. Missing values indicate that the variables were not retained in the most parsimonious models, as selected using AIC's. Zeroes indicate that retained coefficients were not significantly different from zero, as judged by confidence intervals obtained from bootstrapping. Growing season biweekly values are shown in parentheses. TP was retained in only the weekly model for cryptomonads ($\alpha = 0.13$), and *Neomysis* was never retained in any model.

	Week			Week ²			Temperature		
	Weekly	Biweekly (summer)	Monthly	Weekly	Biweekly (summer)	Monthly	Weekly	Biweekly (summer)	Monthly
Cryptomonads	—	— (0)	—	—	— (0)	—	—	— (0)	—
Diatoms	0.85	1.6 (—)	—	—0.87	—1.35 (—)	0	—0.22	—0.35 (—)	—
Green algae	0.60	— (—)	—	—0.66	— (—)	—	—	— (—)	—
<i>Oscillatoria</i>	—	— (—)	—	—	— (—)	—	—	— (—)	—
Other algae	0.67	1.64 (—)	0	—0.71	—1.62 (0)	—2.31	—	0 (—)	0
Unicells	0.87	1.49 (0)	0	—0.88	—1.53 (—)	—1.57	—	0 (—)	—
Non-colonial rotifers	0.30	— (—)	—	—0.36	— (—)	—	—	— (—)	—0.19
<i>Conochilus</i>	—	— (—)	0.16	—	— (—)	—0.18	—	— (—)	—
Non-daphnid cladocerans	0.38	0.45 (0)	0.62	—0.41	—0.47 (—2.37)	—0.70	—	— (—)	—
<i>Cyclops</i>	1.23	1.71 (0)	0	—1.20	—1.69 (0)	0	—0.29	—0.29 (0)	—0.53
<i>Diaptomus</i>	1.25	1.71 (—)	0	—1.28	—1.63 (—)	—	—0.28	—0.37 (—0.26)	—0.53
<i>Daphnia</i>	—	— (—)	0	—0.28	— (—0.09)	—0.70	—	0 (—)	—
<i>Epischura</i>	0	0 (0.90)	1.12	—0.34	—0.61 (—1.09)	—1.41	0.18	0.27 (0.23)	0
<i>Leptodora</i>	—	0.33 (0.70)	—	—	—0.33 (—0.67)	—0.14	—	— (—)	—

sufficiently decoupled during the harshest months that no important relationships were missed through exclusion of winter data. This finding suggests that the many long-term limnological studies excluding winter months provide adequate data for characterizing most planktonic food web interactions.

Lake Washington trophic dynamics

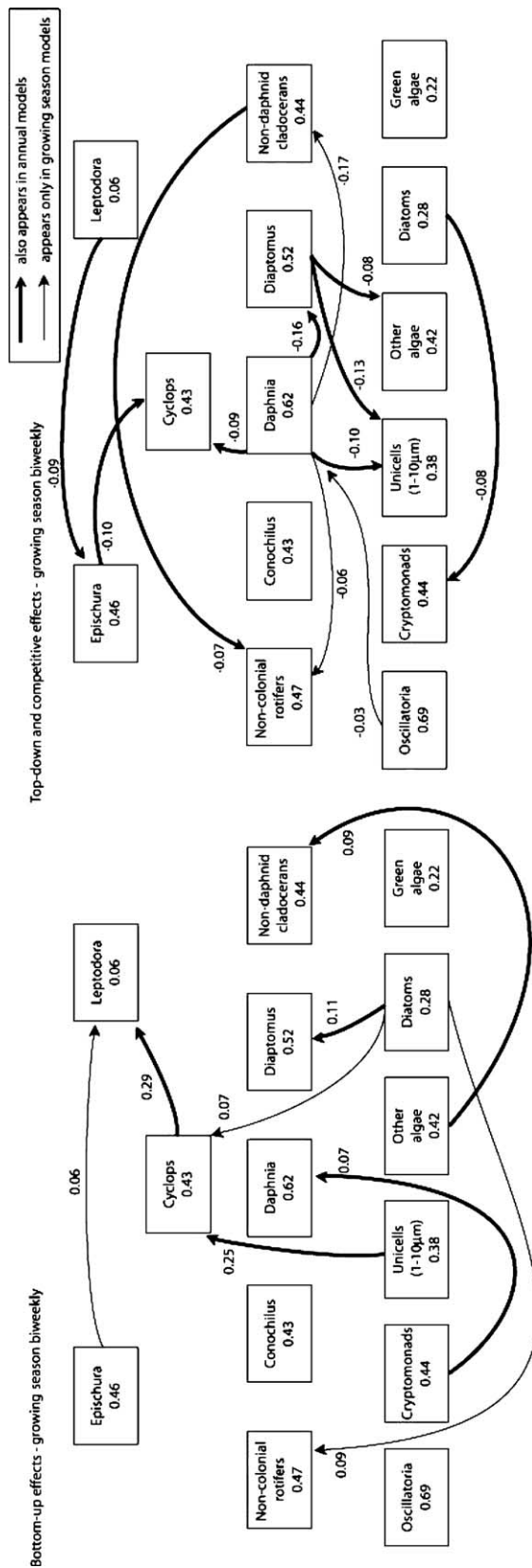
Our results generally supported previous characterizations of the Lake Washington food web that were based on experimental results and visual inspection of the time series, but also suggested the presence of several previously uninvestigated relationships among community members.

Grazer-phytoplankton relationships in Lake Washington

Bottom-up forces were more apparent in the Lake Washington planktonic food web than were top-down effects. This result is consistent with the findings of Arhonditsis et al. (2003) who focused on primary production in Lake Washington and determined that phytoplankton were controlled by abiotic processes through most of the year, and only modestly suppressed by grazers during the warm months.

Separation of the algae into taxonomic groups allowed us to discern subtle differences in relationships between specific grazers and resources that would not have been possible had we lumped primary producers into one group (e.g. algal biomass, chlorophyll a). While previous studies focused mainly on the role of diatoms in the Lake Washington community (Infante and Edmondson 1985), due to their high nutritional content (Brett and Müller-Navarra 1997) and abundance (Infante and Edmondson 1985), this study deemphasized their role in the food web. Instead, the algae that had the strongest and most consistent positive relationships with grazer abundance were the mixed category of widely edible but nutritionally variable unicells and the highly edible and nutritious cryptomonads.

While picoplankton such as those that dominate our unicells have been shown to be crucial primary producers in oligotrophic freshwater and marine environments (Li et al. 1983, Stockner 1991), their importance as a resource to secondary producers in non-oligotrophic lakes is relatively rarely explored. The small size of picoplanktonic cells makes them edible to nearly all planktonic grazers – possibly even difficult to avoid ingesting for filter feeders – and recent studies show that *Daphnia* can strongly suppress numbers of bacterioplankton and autotrophic picoplankton (Jürgens 1994, Weisse and MacIsaac 2000, Modenutti et al. 2003, Sommer et al. 2003). Pico- and nanoplankton are clearly ingested in high numbers by a variety of consumers such that these omnipresent small cells may be a much more



commonly important food resource than generally appreciated.

The importance of cryptomonads as a food resource for zooplankton has been increasingly recognized in the past decade, particularly as the crucial role of essential fatty acids is examined in zooplankton nutrition (Brett and Müller-Navarra 1997). Lake Washington *Daphnia*, like various other planktonic grazers (Arts et al. 1992, Santer 1994, Müller and Schlegel 1999, Bec et al. 2003), reproduce and grow at remarkably higher rates on *Cryptomonas* than on diatoms and green algae (Infante and Litt 1985). Prior to recent vigorous discussions of algal nutritional content for zooplankton (Gulati and DeMott 1997), the potential role of *Cryptomonas* in Lake Washington's *Daphnia* dynamics had been dismissed because it seemed unlikely for a single species to change the dynamics of the most important grazer (Edmondson and Litt 1982). The results in this study, and the growing literature on cryptomonads' importance in zooplankton nutrition, suggest that the concurrent increases in *Daphnia* and *Cryptomonas erosa* in 1976 were not merely coincidental but that *Cryptomonas* may have played a role in the increase of *Daphnia*. Cryptomonads have been suggested to be a critical food for *Daphnia* in other similarly diatom-dominated systems (George and Hewitt 1999, Talling 2003).

Predator-prey relationships in Lake Washington

A predatory relationship of *Leptodora* with *Conochilus* was implied by the reciprocal effects between them, a result that is concordant with previous Lake Washington investigations. *Leptodora* has previously been proposed to be an important predator of *Conochilus* in Lake Washington, based on examination of time series dynamics and preliminary gut content analyses (Edmondson and Litt 1987), and its predation on *Conochilus* has been demonstrated elsewhere (Branstrator and Lehman 1991).

Exploitative and interference competition in Lake Washington

Oscillatoria has been implicated in the suppression of *Daphnia* and some phytoplankton taxa during Lake Washington's eutrophied phase (Edmondson 1994). *Oscillatoria* is filamentous, allowing it to effectively shade other algae (Scheffer et al. 1997) and reducing its vulnerability to grazers (Gulati et al. 2001). Additionally, such filamentous cyanobacteria can directly harm grazers because filaments mechanically interfere

Fig. 5. Food webs showing bottom-up, top-down and competitive interactions as indicated by growing season models, which should be compared to biweekly results in Fig. 2 and 4. Numbers next to interaction lines are the coefficients that represent interaction strength. Only those interactions retained by the best fit models, and with coefficients significantly different from zero, are shown as arrows. Numbers in taxon boxes are autocorrelation coefficients for that species.

with feeding and increase metabolic costs to grazers (Porter and McDonough 1984). *Oscillatoria*'s effects were difficult to observe in these analyses, possibly because its presence was limited to only 5 years of the time series. Interestingly, the only algae that *Oscillatoria* negatively affected, although inconsistently, were those that provided benefits to *Daphnia*, the cryptomonads and unicells, suggesting that *Oscillatoria* can harm *Daphnia* by suppressing important food resources. During the growing season, modest negative effects on *Daphnia* were also apparent. This negative interaction could indicate direct toxic effects or mechanical interference to *Daphnia*, but it also may result from faster generation times in warmer months obscuring the indirect pathway involving *Daphnia*'s food resources such as cryptomonads. Overall our results strongly supported Infante and Abella's (1985) laboratory demonstration, using Lake Washington populations, that *Oscillatoria* suppressed *Daphnia* through not only direct effects on *Daphnia* but also inhibition of its culture food, *Cryptomonas*.

The main competitive interaction among the algae in these analyses was the inhibitory effect of diatoms on the cryptomonads. Diatoms are generally highly effective competitors under well-mixed, relatively high nutrient conditions (Willen 1991), and diatom suppression of cryptomonads has been suggested elsewhere (George and Hewitt 1999).

Consistent with Edmondson's long-time assertion (Edmondson and Litt 1982, Edmondson 1994) that

Daphnia appeared to have caused enormous changes in the Lake Washington food web upon its establishment in 1976, *Daphnia*'s superior competitive effects on the copepods was evident in our models. *Daphnia* was never the loser in competitive interactions with the copepods, and had especially consistent strong effects on the presumed omnivore *Cyclops*. A gut content study suggested that *Daphnia* in Lake Washington may out-compete the copepod *Diaptomus* by using a wider range of algae than *Diaptomus* (Infante and Edmondson 1985), but in that study visual inspection of population dynamics for *Daphnia* and *Diaptomus* was insufficient to provide evidence for competitive suppression (Edmondson 1985). The more sophisticated multivariate approach used here to analyze the time series does provide support for the resource competition between *Diaptomus* and *Daphnia* that had been suggested by gut content analysis (Infante and Edmondson 1985) but never before revealed in the time series data.

Conclusions

Time lags in biotic response to bottom-up, top-down, and competitive dynamics reduced the number of observable biotic interactions at the shortest time interval. Typically, biotic responses appeared to require more than a week to manifest to detectable levels, which is concordant with the modeling results of Carpenter and Kitchell (1987). This study reinforces the need to

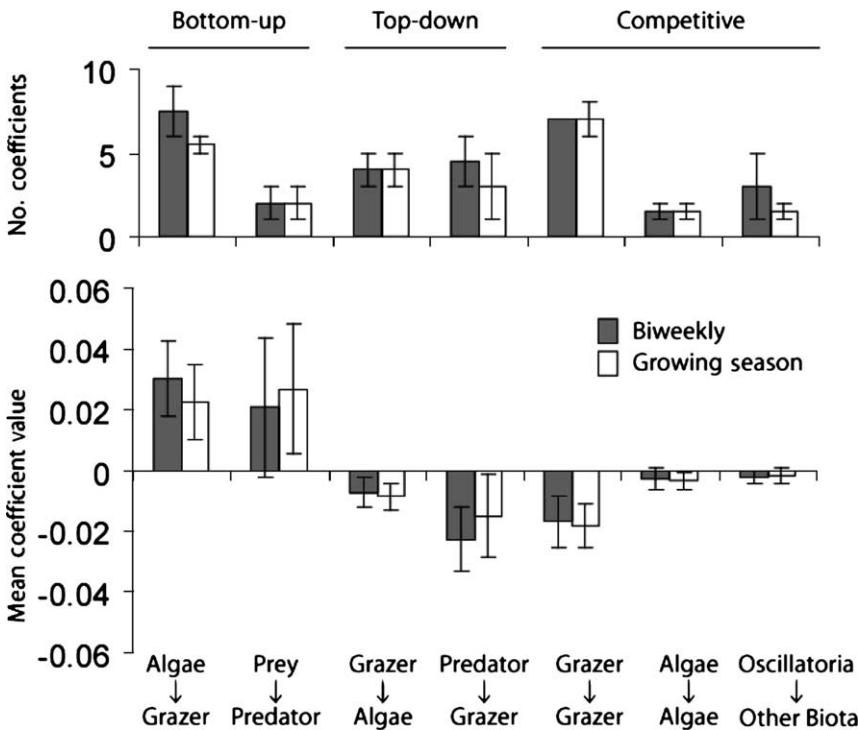


Fig. 6. Number of coefficients retained within each grouping of interaction type, and mean coefficient values (± 1 SE) of each interaction type for weekly, biweekly and monthly models. For some interactions, signs were constrained during model selection, as described in Methods. Mean coefficient values include zeroes (potential interactions lacking arrows in Fig. 5).

explicitly consider system-specific time lags in examination of food web linkages.

During non-winter months, biotic interactions overrode the otherwise strong effects of seasonal physical changes in structuring communities. Nearly all of the biotic relationships identified through use of the annual data set were also identified when the winter months were excluded from analyses, which bodes well for the ability of other long-term limnological data sets to provide insights on community dynamics without winter data.

The MAR models provided a biologically plausible characterization of the Lake Washington food web, confirming importance of many relationships that had been suggested by previous mechanistic studies and visual inspection of the time series, while also offering new insights. Bottom-up processes dominated the planktonic food web, with modest top-down effects of grazing by the two taxa known to be the dominant grazers in the lake. However, the primary producers picoplankton and cryptomonads, with which zooplankton had the strongest links, were previously little studied in Lake Washington. Taken together, these results confirm the utility of the MAR approach for estimating interaction strengths among taxa in relatively diverse communities.

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Appendix 1

Lake Washington data used in the MAR analyses. Graphs on the left show weekly dynamics through the entire time series, while the graphs on the right show the mean annual dynamics for each group. Vertical lines on graphs to the right show where winter and non-winter data split. Algal abundance is expressed as mean biovolume ($\mu\text{m}^3 \text{ l}^{-1}$). For cryptomonads and *Oscillatoria*, monthly means for this figure were only calculated for 1976 to 1981 and 1971 to 1976 respectively, since

cryptomonads were virtually absent before 1976 and *Oscillatoria* declined after 1976.

Zooplankton abundance is expressed as mean density (individuals l^{-1}). For *Daphnia*, monthly means for this figure were calculated for 1976 to 1981 only, since it was virtually absent before 1976. The exogenous variables were *Neomysis* (individuals l^{-1}), TP (mg P l^{-1}), and average water column temperature from 20 to 0 m ($^{\circ}\text{C}$).

