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Pelagic species size distributions in lakes: Are they discontinuous?

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Abstract

Aquatic ecologists have many models for size distributions of pelagic communities. However, few studies have looked for discontinuities (clumps of similarly sized species or gaps of sizes that contain no or relatively few species) in pelagic community size structure. We investigated size distribution characteristics in aquatic communities by calculating kernel density functions for plankton and fish in 11 lakes in Wisconsin. Size distributions in aquatic communities of these lakes were not smooth. Rather, multiple lump and gap regions were found within each functional group of phytoplankton, zooplankton, and fish. Simulations showed the gaps could not be explained by incomplete censuses of species or by systematic underestimation of intraspecific size variation. In an experimentally enriched lake, before and after comparisons showed lumps were not affected by large additions of P and N, even though biomass and production changed substantially. Lump regions in the two lakes with both food web manipulations and nutrient enrichment were substantially less similar pre- versus post-enrichment than the reference lake and the lake with only nutrients added, but lump number remained relatively unchanged. Lakes that differed widely in nutrient status, trophic structure, species diversity, and area had similar size distributions. Comparisons of functional groups showed that phytoplankton had more lumps than zooplankton. In these north temperate lakes, size distribution characteristics seem to be conservative properties shaped by common regional ecosystem processes and organism patterns and not by lake-specific factors.

The study of species body size, a simple integrative measure of organism niche, has a long history in ecology. A variety of research areas have been addressed using body size scaling, including species diversity, community structure and stability, interspecific competition, predator-prey interactions, production and energy transfer, biomass concentrations, fisheries yields, scaling discontinuities, species extinctions and invasions, and ecosystem perturbations (Hutchinson 1959; Sheldon et al. 1972; Peters 1983; Dickie et al. 1987; Sprules 1988; Holling 1992; Thiebaut and Dickie 1993; Allen et al. 1999).

In aquatic ecology, size distribution research has focused on the concentration of individuals or biomass in logarithmic size classes and the variation in concentrations among classes. Size-spectrum analysis has generally not dealt with individual species identities that comprise size classes (Duplisa et al. 1997) and thereby differs from the minimum and constant ratio theory, although both invoke scaling laws. Sheldon et al. (1972) concluded there are roughly equal concentrations of material at all logarithmic particle sizes from bacteria to whales in pelagic marine environments. Size-spectrum models generally predict a regular trend in amounts of biomass in all size classes, although trophic cascades may cause peaks and troughs between functional groups (Sprules 1988). Food web energy flows, though, can be calculated using body size distributions without specifying the trophic levels of organisms involved (Dickie et al. 1987). More recently, Vidondo et al. (1997) showed pelagic size distributions are better fit with the more flexible Pareto model, wide-

ly used in many disciplines to describe size distributions. They also note, though, there will always be sets of organism sizes that cannot be appropriately described by the Pareto nor by the normalized biomass size-spectrum model (e.g., multimodal distributions).

Holling (1992) combined cross-scale properties of ecosystems and individual species in the textural discontinuity hypothesis. It states that the interaction between characteristic scales of ecosystem processes and organisms' foraging patterns on the landscape will constrain the adult sizes of organisms and thereby create discontinuities in species adult body size distributions. Ranges of body sizes in which no species exist (gaps) will alternate with ranges of body sizes in which many species are found (lumps). Ranked size distributions of average adult body sizes of birds and mammalian carnivores, omnivores, and herbivores from 23 ecosystems showed a consistent pattern of body-mass clumping, with equal numbers of body-mass clumps and gaps occurring at the same size locations for different ecosystems.

The minimum and constant size ratio hypothesis suggests smoother size distributions within guilds as species are added to a community and fill previously unoccupied niches (Hutchinson 1959). A lumpy pattern in species size distributions is consistent with at least three alternate hypotheses to smoothness: Evolutionary Legacy (precluded evolution of certain sizes), Trophic Trough, and the Textural Discontinuity Hypothesis (Holling 1992). Although the textural discontinuity hypothesis was devised for terrestrial landscapes, if these arguments are a general and powerful explanation for community structure, we should expect to find similar patterns in aquatic environments. Lakes include dominant processes at different scales that shape the aquatic environment and affect organisms' interactions and fitness (Harris 1980). Physical scaling in lakes can result from factors that produce turbulence at a range of spatial extents and biogeochemical processes with a range of turnover times (Levin et al. 1993).

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If aquatic size distributions are discontinuous, is the pattern caused by local, lake-specific factors, regional factors, or generic factors common to all lakes? Lake size affects numerous physical and chemical properties of lakes as well as ecosystem process rates (Fee et al. 1994; Paterson et al. 1998). Nutrient status also has profound effects on aquatic communities (Schindler 1977). Different top predators (e.g., piscivore vs. planktivore) in lake food webs (Brooks and Dodson 1965; Carpenter and Kitchell 1993; Carpenter et al. in press) can cause pronounced differences in community structure. Alternatively, morphological constraints and evolutionary legacies that occur in the pelagic zones of all lakes may control lumps and gaps. Phytoplankton cells, for example, assume only a subset of the possible shapes that are theoretically available (Lewis 1976). We compared lakes with differing size, nutrient status, community dominants, and species composition to look for systematic differences in pelagic species size structure.

Many studies in terrestrial systems have shown smooth species size distributions across a small range of scales, and several authors have questioned the existence of lumps (Brown 1995; Manly 1996). The purpose of the present work was to establish whether lake ecosystem species size distributions are lumpy or smooth over a large range of sizes. Once a pattern has been established for aquatic communities, limnologists can then move forward to describe mechanisms that give rise to such a pattern. If pelagic species size distributions are lumpy, the variability of lumps and gaps among lakes can provide clues about the relative importance of generic factors common to all lakes versus lake-specific factors in controlling pelagic community size distributions. We compared size distributions for 11 lakes that spanned a range of lake size, trophic status, and food web structure to test for distribution discontinuities and the importance of lake-specific factors in species size patterns. Some lakes were experimentally manipulated, allowing us to test for effects of nutrient enrichment on size structure. In addition, we searched for similarities or differences in distribution patterns across functional groups (phytoplankton, zooplankton, and fish).

Methods

Size distribution estimation—Species size distributions for all lakes were calculated by kernel density estimation based on the average body size and its empirically estimated standard deviation for each species present in the phytoplankton, zooplankton, and fish functional groups (Silverman 1986; Efron and Tibshirani 1993). This allowed us to analyze distribution structure without using predetermined size classes or bins to calculate frequency. We used the kernel density estimator:

$$\hat{f}(t, h_i) = \frac{1}{nh_i} \sum_{i=1}^n \varphi\left(\frac{t - x_i}{h_i}\right)$$

where \hat{f} is the kernel density estimate, $\varphi(y)$ is the standard normal density $(1/\sqrt{2\pi}) \exp(-y^2/2)$; n is the number of spe-

cies, t represents evenly spaced points along the size axis at which density is estimated, x_i is the mean size of each species present during the sample years, and h_i is the sample standard deviation of each mean. Normal probability plots showed that normal distribution was the best choice to approximate each species' size for kernel density estimation. By treating each species distribution as normal, we could capture the largest range of size, maximize h_i , and yield the fewest number of lumps in the overall distribution across all species. The integral of each kernel density function is 1, so it is a proper probability function, and distributions among lakes are comparable.

Size distributions were compared using simple numerical indicators that could be calculated in a consistent manner for each sample: lump number, lump regions, lump areas, gap number, gap regions, number of lumps per number of taxa, and a similarity index of lump and gap regions between lakes. Lump number of a size distribution was the number of modes (local maxima) in its kernel density function. The less clumped a size distribution, the smoother and closer to unimodality will be its kernel density estimate (Efron and Tibshirani 1993). Lump regions were defined as a mode bracketed by its nearest surrounding inflection points, analogous to a confidence interval of lump location (Fig. 1). Lump areas were defined as the integral of each lump region and reflected the proportion of density associated with each lump region. Gap number and gap regions were defined, respectively, as the number of local minima and these minima bracketed by their nearest surrounding inflection points. We note that lump regions are not necessarily the inverse of gap regions as we defined them. It is possible for multiple inflection points to exist between a zenith and a nadir, which means there potentially were areas on a kernel density curve that were classified neither as lump region nor gap region. Because we estimated probability density at many points along the body size axis and did not fit a polynomial function, there were a few cases where no inflection point existed between a zenith and a nadir. When this occurred, we used the zenith as a confidence bound for the gap location and the nadir as the confidence bound for the lump location. This means there can be overlap in the confidence bounds for lump location and gap locations—what we termed lump region and gap region. Number of lumps per number of taxa was simply the number of lumps divided by the number of taxa in a lake used to generate the density estimate. The number of lumps in each functional group was calculated by enumerating lumps that lay between the maximum and minimum species size for each functional group within each lake. The number of gaps was always one less than the number of lumps. Because of the overlap in size among several species of phytoplankton and zooplankton, their distributions were also calculated separately.

Lump and gap region similarity indices were calculated using the following formula:

$$2(\sum W_k) / (\sum X_i + \sum Y_j)$$

where X_i represents lengths of lump (gap) regions in Lake X ; Y_j represents lengths of lump (gap) regions in Lake Y ; and W_k represents the lengths of overlapping lump (gap) regions common to both Lakes X and Y . The similarity value

across all lakes was the average of the pairwise similarity indices. The similarity index could take on values from 0 (no overlap) to 1 (complete overlap). To compare the departure from unimodality of the kernel density functions, we calculated an index based on both the separation and area of lumps:

$$\Sigma(A_i \cdot d_i)/N$$

where A_i is the lump area of the i th mode, d_i is the absolute value of distance between the locations of the i th mode and the mode of the largest lump area in the distribution, and N is the number of modes in the distribution. This index is zero for a unimodal distribution, and it increases as more large lump areas are located further away from the largest lump area in the distribution.

A concern of any statistical analysis is whether the observed pattern is merely an artifact of nonrepresentative sampling and therefore does not reflect the true pattern of the population. Sampling inadequacy could create artificial lumps in two ways: underestimation of h and missed species. To test the sensitivity of the distributions to underestimating h , we increased the empirically derived standard deviation for each species by 10% and recalculated the distribution. This is a conservative test because it is unlikely that all standard deviations were underestimated (more likely, some were overestimated, and some were underestimated). Although the sampling regime that generated the size data was extensive, the effect of a few species that possibly were missed across all samples and years on the kernel density estimate was unknown. To evaluate this, we performed simulations that added "pseudospecies" to the size distribution and then recalculated the kernel density estimate. This process determined the number of pseudospecies that must be added to each density estimate to reduce the lump number by one, termed $\Delta\text{lump}/\Delta\text{taxa}$. Each pseudospecies was assigned a mean size equal to the location of the smallest gap and a standard deviation equal to the average coefficient of variation for all known species multiplied by the mean size of the pseudospecies. The smallest gap was defined as the gap that would require the least shift in kernel density to smooth. The artificial taxa then had the average standard deviation of known taxa and a mean size that placed it in a sensitive portion of the graph to gap filling. This test is more aggressive than randomly adding pseudospecies because it targeted gap regions that would likely fuse two lumps. Pseudospecies were assigned iteratively until the lump number dropped by one or until 500 pseudospecies had been added.

Comparisons of north temperate lakes—Trout Lake, Big Muskellunge Lake, Sparkling Lake, Crystal Lake, and Trout Bog ($89^{\circ}39'W \pm 3'$, $46^{\circ}01'N \pm 1'$) lie in a forested watershed of the Northern Highland Lake District, Wisconsin. Lake Mendota ($89^{\circ}24'W$, $43^{\circ}06'N$) is located in an agricultural watershed. Lake Wingra ($89^{\circ}25'W$, $43^{\circ}03'N$) is located in an urban watershed. Both Lake Mendota and Lake Wingra are located in southern Wisconsin in the Yahara River Lake District. All seven lakes are part of the Long Term Ecological Research program-Northern Temperate Lakes site of the University of Wisconsin-Madison (NTL-LTER, www.limnology.wisc.edu). These seven lakes represented a di-

verse range of north temperate lakes to evaluate our size distribution hypotheses (Table 1).

Fish were sampled in all lakes each year during a 1-month period from late July until late August (except Lake Mendota, which was sampled from late August until mid-September) by night seining; fyke, trammel, and gill nets; electroshocking; and minnow traps. The same sampling sites were used each year as marked by stakes, buoys, maps, and local landmarks. Sampling effort across lake size was constant. Three seine sites were hauled per day for a total of six seine sites (100 m of shoreline) on each lake. Each site was evenly subdivided into three seine hauls. Each fyke net was ≈ 12 m long and consisted of two rectangular steel frames, 90 cm wide by 75 cm high, and four steel hoops, all covered by 7-mm delta stretch mesh nylon netting. An 8-m-long by 1.25-m-deep leader net made of 7-mm delta stretch mesh nylon netting was attached to a center bar of the first rectangular frame (net mouth). The second rectangular frame had two 10-cm-wide by 70-cm-high openings, one on each side of the frame's center bar. The four hoops followed the second frame. Throats 10 cm in diameter were located between the second and third hoops. The net ended in a bag with a 20.4-cm opening at the end, which was tied shut while the net was fishing. Each fyke net was set in shallow water perpendicular to shore such that the net mouth was covered by ≈ 1 m of water when possible. Three fyke net sites were set per day, each with a single net, for a total of six fyke net sites per lake. Minnow traps were set in shallow water on both sides of the fyke net lead. These were baited with one slice of bread per trap. Thirty traps were set on each lake (covering six sites) and fished for ≈ 24 h each. Minnow traps used were galvanized steel two-piece traps, 44.5 cm long by 30.5 cm in maximum diameter with 2.5-cm-diameter openings at the ends and a mesh size of 6.4 mm on a side.

Seven monofilament vertical gill nets of mesh sizes 19, 25, 32, 38, 51, 64, and 89 mm were attached end to end and curtained surface to bottom for two 24-h periods at the deepest location in each lake. The trammel net used was 30.5 m long and 1.1 m deep. It consisted of two outer nets of 170-mm square 32-kg test mesh multifilament nylon with an inner panel of 51-mm stretch mesh 9-kg test multifilament nylon. The three nets were connected at the leaded foot line and the buoyed head rope. The trammel net was set on the bottom, along a line perpendicular to the shoreline and crossing the thermocline. The trammel net was set at two sites in each lake and fished for ≈ 24 h at each site. Four electroshock transects were done on each lake, and the same transects are used each year. Each transect consists of 30' of current output, with the boat moving parallel to shore in 2–3 m of water at a slow, steady speed. We used the direct current pulse system, with 240 volts and 3–5 amps. Two dippers in the bow of the boat dipped up all stunned fish and placed them in the live well for processing at the end of each transect. In Trout Bog, which was sampled with only fyke nets and minnow traps, there were no fixed sites: nets were placed equal distances apart around the entire circumference of the lake. Because of a small lake circumference, nets were in about the same locations each year (NTL-LTER, www.limnology.wisc.edu).

Zooplankton were sampled biweekly in February, May,

Table 1. Limnological characteristics of comparison north temperate lakes and of experimentally enriched lakes prior to manipulation.

	Lake Mendota	Lake Wingra	Big Muskellunge Lake	Crystal Lake	Sparkling Lake	Trout Lake	Trout Bog	East Long*	West Long*	Peter*	Paul*
Area (ha)	3,937.7	139.6	396.3	36.7	64.0	1,607.9	1.1	2.5	3.5	2.3	1.5
Mean depth (m)	12.8	2.7	7.5	10.4	10.9	14.6	5.6	4.9	4.4	6.0	3.9
Water temp (°C)	24.3	23.0	20.9	20.8	20.9	19.9	18.0	18.7	19.2	19.1	19.0
pH	8.2	9.4	7.3	6.0	7.3	7.6	4.8	5.0	5.1	6.1	5.5
Total P ($\mu\text{g} \cdot \text{L}^{-1}$)	118.0	331	22.5	8.6	15.2	16.9	40.0	14.2	9.5	9.6	12.2
Total N ($\mu\text{g} \cdot \text{L}^{-1}$)	1,080	2,000	489	207	375	235	873	492	401	345	376
Chlorophyll ($\mu\text{g} \cdot \text{L}^{-1}$)	7.4	—	3.0	1.8	2.2	3.3	14.0	2.7	2.4	3.4	3.6
Secchi depth (m)	3.4	0.7	6.7	7.3	6.1	4.6	1.2	2.4	4.3	4.4	4.2
No. fish taxa	28	26	28	17	20	30	1	—	—	—	1
No. zooplankton taxa	15	15	47	50	42	53	39	33	32	32	43
No. phytoplankton taxa	117	—	—	—	—	—	—	108	99	136	120

Notes: Water temperature 0–2 m, except *, which is average epilimnetic temperature June–August; Secchi from June to August; pH from the average of spring and fall mixis sampling, except *, which is average pH June–August; total P and N from spring mixis, except *, which is average epilimnetic total P and N June–August; chlorophyll (surface) from open-water season.

June, August, and November at no more than nine locations with Schindler traps and net hauls over the entire water column with an 80- μm mesh net. Traps were placed at sample depths of surface, bottom of epilimnion, entire metalimnion, and lake bottom during stratification and at target depths during mixis and winter (NTL-LTER, www.limnology.wisc.edu). Lake Mendota and Lake Wingra were sampled at least once a month year-round and once a week during the summer months at a central lake station over a 0–20-m haul in Mendota and a haul over the entire water column in Wingra with an 80- μm mesh net. Zooplankton samples were chilled, preserved, and enumerated and measured by species. Phytoplankton in Lake Mendota were sampled biweekly year-round with van Dorn casts at 25, 50, and 100% of surface irradiance. The samples from the three van Dorn casts were pooled, preserved, mounted, and enumerated and measured by species (St. Amand 1990).

The data used for the present analysis were individual lengths of zooplankton and fish, except for sample average of zooplankton length in Lake Wingra and sample average of greatest axial linear dimension for phytoplankton in Lake Mendota because individual lengths were unavailable. All individual lengths for a species across all samples within a lake were pooled to determine mean size and standard deviation for a species. When only average sample lengths were available, standard deviation for all individuals of a species was calculated by hierarchically pooling the standard deviation within samples and across samples based on counting protocols. If any species standard deviation was <0.05 , it was replaced by the average coefficient of variation for all the species multiplied by the average size for that species. This procedure prevented the creation of spurious lumps due to small sample sizes. Data were pooled across years to make comparisons as consistent as possible. The pooled years were 1991–1993, 1995 (Lake Mendota, Crystal, Sparkling, and Trout Lakes); 1993, 1995–1997 (Big Muskellunge Lake and Trout Bog); and 1996–1997 (Lake Wingra). A North Regional species pool was calculated by pooling all individual lengths for a species across all samples from lakes Trout, Big Muskellunge, Sparkling, Crystal, and Trout Bog and calculating mean size and standard deviation for each species present. Similarly a South Regional species pool was calculated by pooling data from Lake Mendota and Lake Wingra. From these data, North and South Regional species size distributions were constructed by kernel density estimation. Although the northern and southern lakes share many species, differences in species composition exist because they contain species at the southern and northern boundaries of habitat range, respectively.

Experimentally enriched lakes with contrasting food webs—Comparisons of Paul Lake, Peter Lake, East Long Lake, and West Long Lake assessed differences among lakes with contrasting food webs before and after nutrient enrichment. The lakes lie on the grounds of the University of Notre Dame Environmental Research Center (89°32'W, 46°13'N) in the Northern Highland Lake District. The four lakes lie within ~1 km of one another in a forested watershed. West Long and East Long lakes were created when Long Lake was divided into three basins with plastic curtains in May

1991 (Christensen et al. 1996). Prior to nutrient enrichment, limnological characteristics of the lakes were similar (Table 1).

Paul Lake served as an unmanipulated reference ecosystem for this study to distinguish regional and climatic variability from that caused by nutrient enrichment. The food web in Paul Lake was dominated by piscivorous largemouth bass (*Micropterus salmoides*), zooplanktivorous larvae of *Chaoborus* spp., relatively large cladoceran herbivores (*Daphnia pulex*, *D. rosea*, and *Holopedium gibberum*), and phytoplankton dominated by small gelatinous colonies, colonial chrysophytes, and unicells <20 μm in length (Carpenter and Kitchell 1993). Prior to and during nutrient enrichment, the food web of West Long Lake was dominated by piscivorous bass (*Micropterus salmoides* and *M. dolomieu*), large cladocerans, especially *Daphnia pulex*, and colonial chrysophytes, chlorophytes, cyanophytes, and unicells <20 μm in length. Average total biomass of phytoplankton in West Long Lake increased every year, including a brief 10-fold increase during the enrichment period when dominance shifted to very large taxa (Cottingham 1999). Both Paul and West Long Lakes were low-planktivory systems dominated by large to moderately large zooplankton and small phytoplankton.

The food webs of Peter and East Long Lakes were converted to dominance by planktivorous minnows in 1991 via the removal of piscivores by electroshocking, angling, and rotenone and subsequent stocking of golden shiners (*Notemigonus crysoleucas*). The result was a planktivore dominated food web and a zooplankton community dominated by rotifers and cyclopoid copepods, small to moderately small zooplankton. Nutrient enrichment caused significant increases in chlorophyll and crustacean biomass. Differently sized phytoplankton dominated during different years and months (Cottingham 1999). In mid-1994 in Peter Lake, the planktivore density radically decreased, which was followed by an increase in larger species of *Daphnia*, an increase in crustacean biomass and mean length, and chlorophyll decreased substantially (Carpenter et al. 1998, in press).

In Peter Lake, the golden shiner remained the top predator during the enrichment experiments, but unexpected changes in the lake chemistry of East Long Lake caused a fish kill in 1991. By 1993, DOC concentration and the mean light extinction coefficient had nearly doubled from the 1990 (pre-enrichment) levels and mean thermocline depth had dropped by 30%. The loss of planktivores and sporadic recolonization events resulted in a highly variable zooplankton assemblage (Carpenter et al. 1998, in press). Total biomass of phytoplankton increased from 1991 to 1993, then stabilized in 1994 and was much lower than in the other three lakes. Although the lack of planktivores increased grazing pressure on the phytoplankton, differently sized phytoplankton dominated during different years and months unlike the piscivore lakes with mostly small phytoplankton (Cottingham 1999).

The methods of nutrient enrichment and data collection have been extensively described elsewhere (Carpenter et al. 1998, in press), so only a brief description of those methods relevant to the current analysis are presented here. Similar amounts of liquid fertilizer containing phosphate, nitrate and ammonium with an N:P ratio of >17 by atoms were added

daily during the summer season from 1993 to 1997 to Peter, East Long, and West Long lakes. From mid-May to mid-September during summer stratification, each lake was sampled weekly at a central station. Fish were sampled in all lakes by angling, electroshocking, and seining. Phytoplankton were sampled with van Dorn casts at 25, 50, and 100% of surface irradiance and zooplankton were sampled with two vertical hauls of the entire water column with a calibrated 80- μm mesh net. Samples were processed the same as for the north temperate lakes described above. A total of 16 weekly sample averages of length and the empirically derived maximum standard deviation based on counting protocols for each species of zooplankton and of greatest axial linear dimension for each species of phytoplankton for each year 1991–1997 were the data used for the present analysis.

To evaluate enrichment effects, data were pooled by pre-nutrient enrichment (1991–1992) and postnutrient enrichment (1993–1997) for each of the four lakes. Average species size within each lake and group (pre- or postenrichment) was the grand average of weekly sample averages. Standard deviation of all individuals of each species was calculated by a hierarchical pooling of the standard deviation within samples and across samples based on counting protocols. If any species standard deviation was <0.05, it was replaced by the average size of the species multiplied by the average coefficient of variation for all the sample species. This procedure prevented the creation of spurious lumps due to small sample sizes. Although biomass and size of dominant phytoplankton and zooplankton varied within a summer season and among years (Carpenter et al. 1998, in press; Cottingham 1999), we determined there were not detectable annual trends in distribution structure that required a year-by-year analysis (1991–1998 analyzed). All samples from all four lakes and all years were combined to create a regional species pool.

Results

Discontinuities and lake-specific factors—Lumps and gaps were evident in the size distribution of zooplankton and fish from each lake (Fig. 2). There was a relatively large trough in each kernel density function that reflected the size break between the maximum size of zooplankton and the minimum size of fish. No lump contained both fish and zooplankton.

The number of lumps ranged from four lumps in Paul Lake (43 zooplankton species and 1 fish species) to 10 lumps in Lake Wingra (15 zooplankton and 26 fish species). The mean number of lumps over all lakes was six. The average number of lumps generated per zooplankton taxon was 0.09, or 11 zooplankton taxa per lump. Lakes with lower N and P concentrations tended to have a lower ratio of zooplankton lumps per taxon. For fish, the average number of taxa per lump was 2.6 (lumps per taxon = 0.39). Crystal Lake and Lake Mendota had the largest departures from unimodality based on the lump dispersion index.

The detection of lumps was not an artifact of incomplete censuses based on values for $\Delta\text{lump}/\Delta\text{taxon}$. Kernel density functions required at least 15 additional pseudospecies to

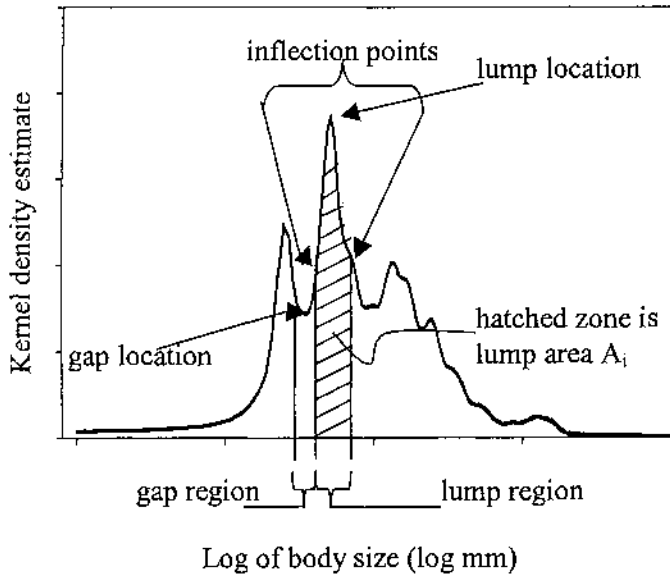


Fig. 1. Illustration of lump and gap definitions for kernel density estimates. A computer algorithm calculates point estimates of the lump, gap, and inflection point locations and sums of lump areas.

reduce the number of lumps by one, except for Crystal Lake, where $\Delta\text{lump}/\Delta\text{taxa}$ was one, but subsequent taxon additions increased the lump number. Thus, if species were omitted from the sample in Crystal Lake, then the number of lumps was underestimated. In general, the average number of taxa per lump was much lower than the number of pseudospecies required to reduce the number of lumps by one. Increasing the standard deviation for each species by 10% decreased

the lump number only by one for all lakes, except for Big Muskellunge, which remained unchanged.

Lump number did not correlate with the number of taxa used to generate the distribution ($r = 0.115, n = 8, P > 0.75$). Big Muskellunge Lake and Lake Mendota had 75 and 43 species, respectively. Both lakes had six lumps: zooplankton and fish each contributed three lumps. Trout Lake had the most species, 83, but it had neither the most nor the fewest number of lumps. The number of lumps created by fish and zooplankton were similar in many of the lakes, although the number of taxa per lump was lower for fish. Similarity indices that showed the overlap in lump regions between lakes and gap regions between lakes spanned a wide range of values, with a mean of 0.117 for lumps and 0.262 for gaps among all lakes (Table 2). Generally, the similarity index values for gap regions were several times higher than those for lump regions.

Lake Wingra and fish in Paul Lake did show notably different peak and trough patterns from the other lakes. Paul Lake had low lump region similarity values with all other lakes but high gap region similarity values. Lake Wingra had some high similarity values with other lakes but also had many small lump regions in the size range of fish. We hypothesized that the large number of smaller lump regions in Lake Wingra was an artifact of using only 2 yr of data in the kernel density estimate, as opposed to 4 yr of data in the other lakes. However, when we estimated kernel density using only 2 yr in the other lakes, we did not obtain a greater number of lumps at small fish body sizes. Therefore, the pattern in Lake Wingra cannot be explained as a result of only 2 yr of data.

Patterns in size structure for both zooplankton and fish in the other six lakes were similar to one another despite con-

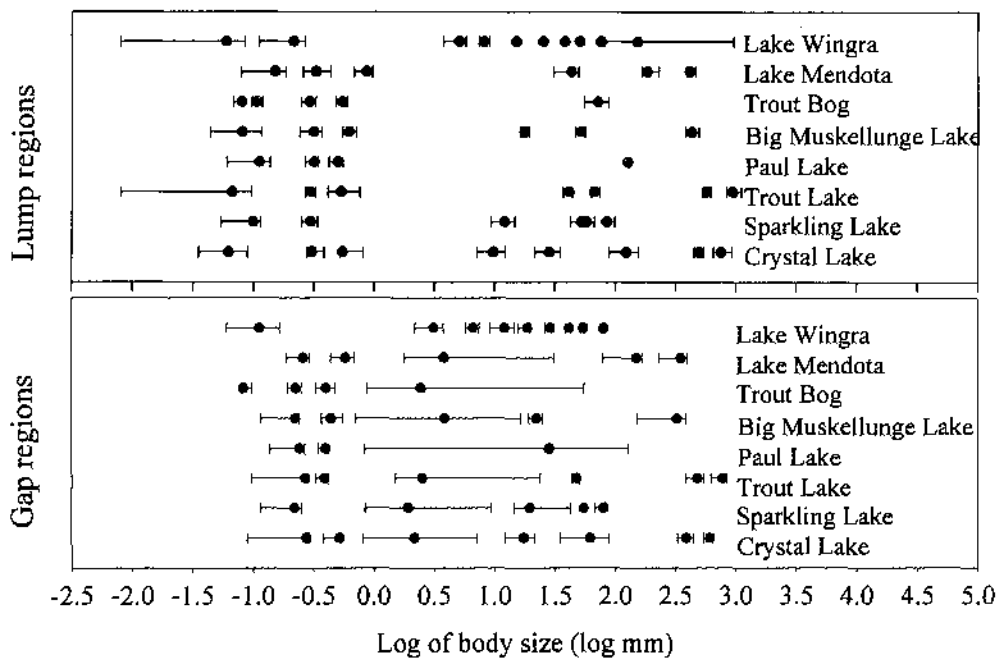


Fig. 2. Lump locations and gap locations for zooplankton and fish species lengths in eight northern temperate lakes (gap regions are not necessarily the inverse of lump regions, see Methods).

Table 2. Similarity matrix of lump and gap regions for zooplankton and fish in north temperate lakes. Lump region similarity values are below the unity; diagonal and gap region similarity values are above the unity diagonal.

	Big Muskellunge	Crystal	Paul	Mendota	Sparkling	Trout Bog	Trout	Wingra	North Regional species pool	South Regional species pool
Big Muskellunge	1	0.240	0.107	0.706	0.105	0.140	0.0600	0.0671	0.460	0.0870
Crystal	0.166	1	0.310	0.304	0.218	0.201	0.328	0.121	0.331	0.322
Paul	0.00219	0.00583	1	0.468	0.536	0.534	0.105	0.305	0.110	0.484
Mendota	0.535	0.0652	0.00190	1	0.164	0.175	0.00835	0.116	0.308	0.251
Sparkling	0.0808	0.0514	0.00567	0.0729	1	0.702	0.0748	0.486	0.0897	0.315
Trout Bog	0.0100	0.000577	0.00985	0.00100	0.429	1	0.127	0.568	0.103	0.245
Trout	0.00109	0.209	0.00120	0.0265	0.0285	0.0622	1	0.0573	0.473	0.446
Wingra	0.224	0.647	0.00277	0.260	0.0384	0.0177	0.328	1	0.0470	0.161
North Regional	0.0653	0.0108	0.00181	0.0227	0.111	0.0982	0.311	0.361	1	0.513
South Regional	0.000705	0.226	0.0156	0.0625	0.0209	0.00104	0.261	0.314	0.321	1

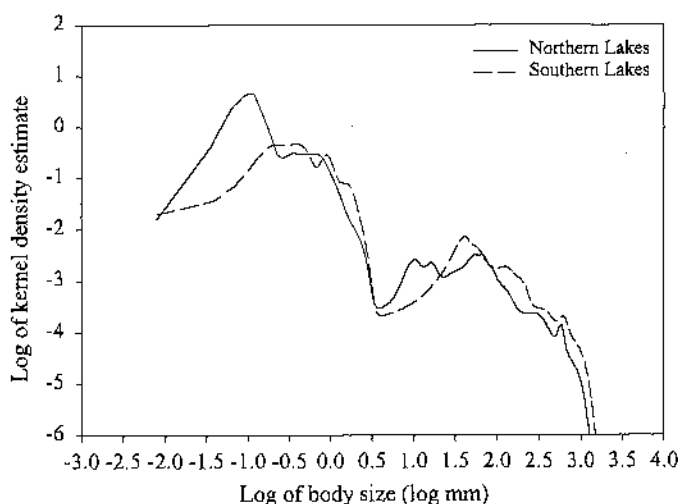


Fig. 3. North Regional species pool size distribution created from lakes Big Muskellunge, Crystal, Sparkling, Trout Bog, and Trout. South Regional species pool size distribution created from Lakes Mendota and Wingra. Logarithmic units are used for clarity of display.

siderable differences in other limnological properties. Many of the gap similarity values and several of the lump similarity values were quite high (Table 2). Differences and trends in limnological characteristics among lakes such as P concentration, area, and Secchi depth were not associated with differences in the characteristics of species size distributions. Big Muskellunge Lake and Lake Mendota had a lump similarity of 0.535 and a gap similarity of 0.706 but were quite different in many ecosystem properties. Big Muskellunge Lake has ~10% the area of Lake Mendota, much lower concentrations of P and N than Lake Mendota, and a Secchi depth approximately twice as deep as Lake Mendota. Crystal and Sparkling Lakes are similar in most limnological properties and had moderate similarity values of 0.0514 (lump regions) and 0.105 (gap regions). Most of the lakes had moderately high gap region similarity values with both the North and South Regional species size distributions. Both the North and South Regional species size distributions showed multiple lumps and gaps in the zooplankton and fish, indicating each individual lake subsample comes from discontinuous regional species pools (Fig. 3). The similarity index values between the North and South Regional distributions were 0.321 (lump regions) and 0.513 (gap regions). Lake-specific contrasts such as nutrient concentrations, areas and depths, and species diversity did not substantially change size distribution characteristics.

Effects of nutrient enrichment and food web contrasts on size structure—Multiple lump and gap regions were evident within the plankton size distributions of the experimental lakes both before and after nutrient manipulation (Fig. 4). Pre- and postmanipulation species size distributions for each lake were relatively similar, despite massive changes in community structure, nutrients, chlorophyll, primary production, bacterial production, and gas exchange with the atmosphere (Carpenter et al. in press). The similarity values of lump and

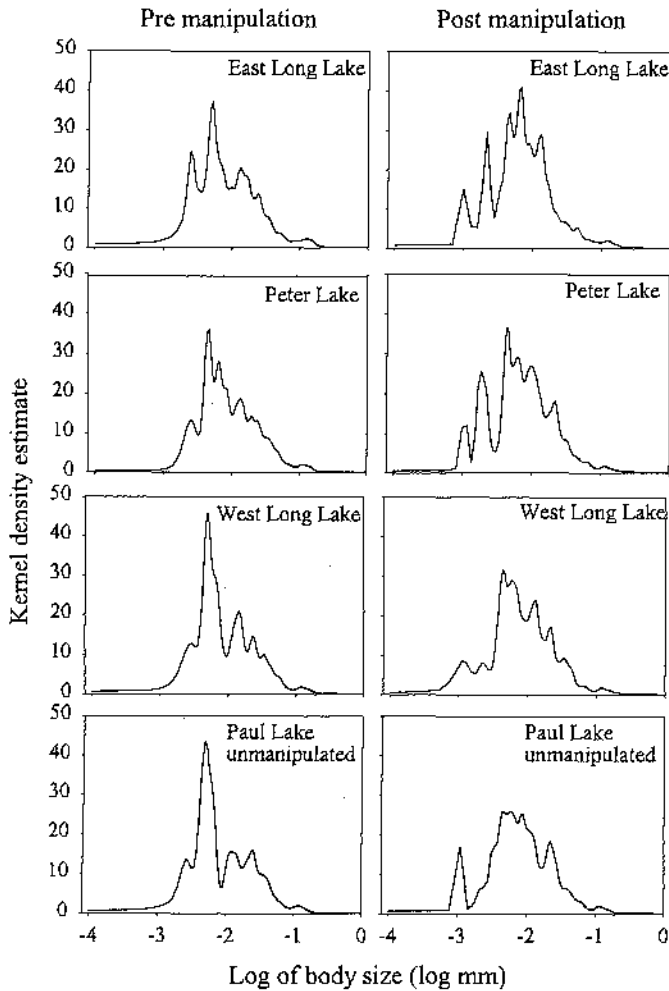


Fig. 4. Species size distributions for phytoplankton and zooplankton in the four experimental lakes. East Long, Peter, and West Long Lakes were enriched with a liquid fertilizer daily during the summer season from 1993 to 1997. Paul Lake was unmanipulated and served as a reference lake. All distributions were estimated using kernel density analysis from data pooled in two groups: 1991–1992 and 1993–1997.

gap regions between pre- and postenrichment within the piscivore lakes were moderately high (Table 3). However, the similarity values were noticeably smaller in East Long and Peter, lakes in which both their food webs were manipulated and enriched with nutrients. $\Delta\text{lump}/\Delta\text{taxa}$ showed that at least seven species additions, and usually more than 30 species additions, were required to reduce by one the number of lumps in the distribution. In general, the average number of taxa per lump was much lower than the number of pseudospecies necessary to reduce the number of lumps by one. Increasing the standard deviation by 10% for each species did not reduce the lump number in four of the distributions and reduced the lump number only by one in the other four.

Lump number did not consistently decrease or increase in the postenrichment group (Table 3) and was relatively insensitive to nutrient addition, number of taxa used to compute the kernel density function, and years of data pooled. Lump and gap numbers in the enriched lakes were similar to the reference lake. Similarity index values for lump regions and gap regions between the experimentally enriched lakes and the reference lake were moderately high both pre- and postenrichment (Table 3). Postenrichment, each lake had its highest lump region similarity value with the reference lake. There were more species in the postenrichment group because 5 yr versus only 2 yr were combined for the postenrichment group. Paul Lake, the reference lake, increased by only one lump in the postenrichment years, even though the number of species increased from 152 to 233.

Food web contrasts were not a factor in lump number postenrichment, but the lakes with both a manipulated food web and nutrient enrichment were less similar postenrichment than the reference lake and West Long, whose dominant predator was never manipulated. East and West Long Lakes increased by three and four lumps, respectively, while Peter Lake decreased by one lump. East Long Lake (small and variable fish populations) and West Long Lake (dominated by piscivorous bass) both had 12 lumps postenrichment. Peter Lake, dominated by planktivorous golden shiners, had only one less lump than West Long and East Long postenrichment.

The spread of lump areas in the distributions, lump dispersion index, was similar between pre- and postnutrient en-

Table 3. Summary characteristics of species size distributions generated from phytoplankton and zooplankton lengths in the experimental lakes located in the Northern Highland Lake District of Wisconsin. Pre refers to the years 1991–1992, before East Long, Peter, and West Long Lakes were enriched with fertilizer daily in the summer season. Post refers to experimentally enriched years 1993–1997. Paul Lake served as an unmanipulated reference lake.

		Lump No.	Lump dispersion	Taxa No.	$\Delta\text{lump}/\Delta\text{taxa}^{-1}$	Lump similarity index	Gap similarity index
East Long Lake	Pre	9	0.003	141	1/31	0.114	0.173
	Post	12	0.004	177	1/7		
Peter Lake	Pre	12	0.004	168	2/9*	0.205	0.358
	Post	11	0.003	240	1/86		
West Long Lake	Pre	8	0.008	131	1/52	0.530	0.622
	Post	12	0.004	181	1/33		
Paul Lake	Pre	8	0.005	152	1/58	0.540	0.696
	Post	9	0.003	233	1/46		

* Adding nine pseudospecies dropped the kdf modality from 12 to 10.

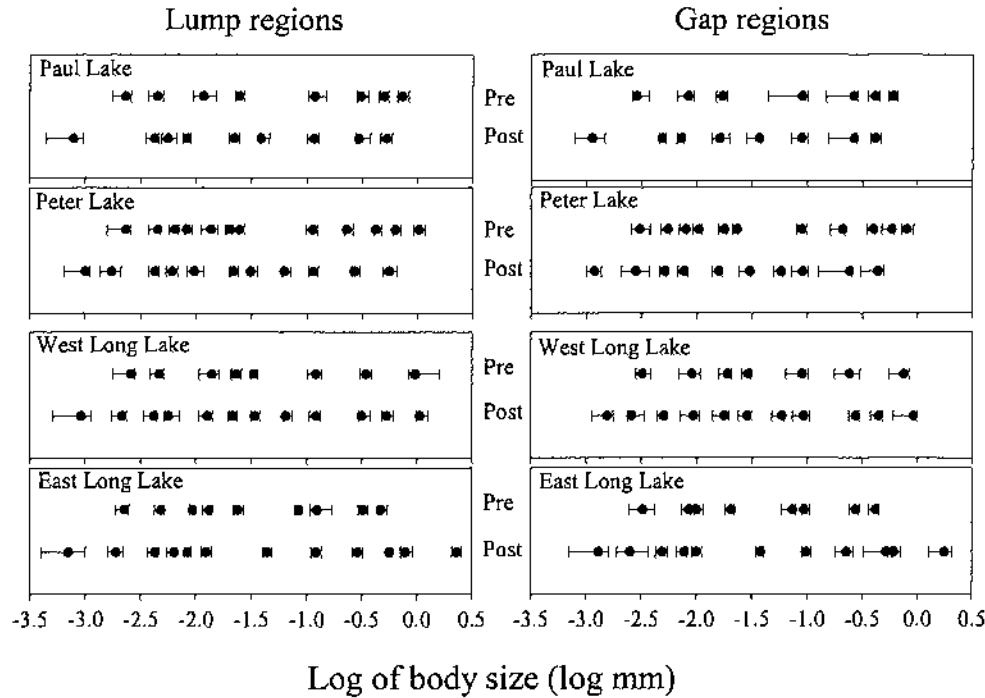


Fig. 5. Lump and gap locations for phytoplankton and zooplankton species lengths in the experimental lakes pre- and postnutrient enrichment. Paul Lake was unmanipulated and served as a reference lake.

richment and among lakes. The overall similarity among lakes for lump regions was 0.288 preenrichment and 0.360 postenrichment. For gap regions, it was 0.424 preenrichment and 0.381 postenrichment.

Comparison of phytoplankton and zooplankton—Phytoplankton and zooplankton showed differences in species size distributions when their kernel density functions were estimated separately (Fig. 6). Phytoplankton always had more lumps than zooplankton within a given lake ($P < 0.05$, Wilcoxon Ranked Sum test). The zooplankton all had a large lump caused by rotifers centered around 0.2 mm, followed by a few lumps with fewer species at larger body size. Phytoplankton distributions tended to have lumps that were more similar in size.

Phytoplankton distributions required more pseudospecies additions to reduce the number of lumps by one than zooplankton distributions. Lake Mendota, the most eutrophic of the five lakes, had the lumpiest phytoplankton distribution with 10 lumps, although it did not contain the most phytoplankton taxa. West Long Lake had the fewest phytoplankton taxa and had seven lumps. Lake Mendota also showed the most spread from unimodality in its distributions, both phytoplankton and zooplankton.

In general, the numbers of lumps were consistent among lakes in both the phytoplankton and zooplankton despite many ecosystem differences. Phytoplankton distributions both for West Long Lake (piscivore dominated) and East Long Lake (low and variable fish populations) had seven lumps. Paul Lake and West Long Lake were both dominated by piscivorous bass and had four lumps in the zooplankton.

Lake Mendota is much larger than either Paul or West Long Lakes and also had four lumps in the zooplankton.

Lump and gap locations were similar among the phytoplankton distributions and among the zooplankton distributions, with the exception of a lump at a large body length in both the phytoplankton and zooplankton of Lake Mendota (Fig. 7). Similarity values for lump regions and gap regions were, in general, moderately high in the phytoplankton and higher in the zooplankton. Lake Mendota, though, had consistently low similarity index values in the phytoplankton. The average similarity index values for phytoplankton were 0.292 (lump regions) and 0.156 (gap regions). For zooplankton, they were 0.325 (lump regions) and 0.435 (gap regions).

Discussion

Our statistical analysis of size distributions differs from some previous approaches (Holling 1992; Manly 1996; Allen et al. 1999). It is possible to postulate a smooth null model for the size distribution and to use this to draw inferences about the number of lumps and the kernel density smoothing parameter, h (Efron and Tibshirani 1993; Manly 1996). However, there is no agreement on the most appropriate null model for size distributions, and results are sensitive to this assumption (Efron and Tibshirani 1993; Manly 1996; Allen et al. 1999). An alternative is to compare censuses of species (not samples), as in Holling (1992) and this paper. In addition, we directly measured the kernel density smoothing parameter, h , by empirically measuring the variability in body size of each species. In the few cases where h could not be measured, we assumed a value that was con-

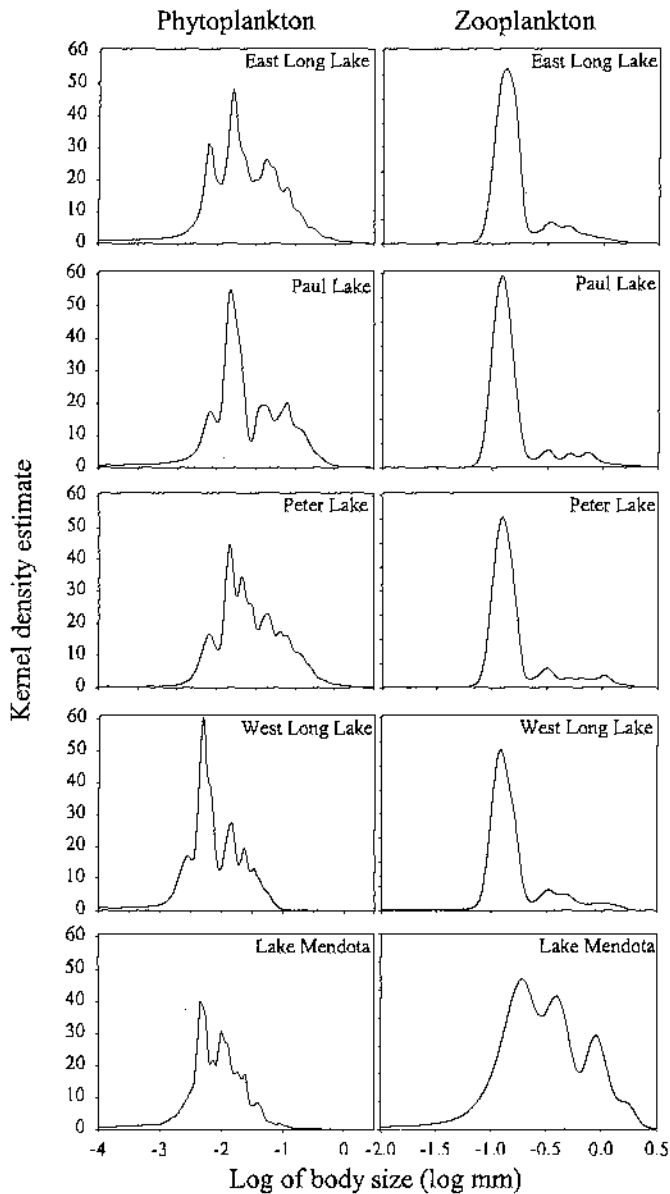


Fig. 6. Species size distributions from kernel density estimation for phytoplankton and zooplankton in the experimental lakes pre-nutrient enrichment and Lake Mendota. The two trophic groupings were calculated separately. Data are pooled from 1991 to 1992.

servative, in the sense that it would bias our analysis toward finding a more regular distribution with fewer lumps and gaps. An important criticism of our approach is that the number of lumps could be sensitive to rare species that were omitted from the census. To address this criticism, we added pseudospecies of a size that would be most likely to eliminate apparent lumps. In all cases, this exercise showed that the results were not sensitive to species that may have been omitted. To decrease the estimates of lump number, one would have to posit large numbers of missing species (in excess of the number in a typical lump) of just the right body size to eliminate the most sensitive lump. This is not plausible. Another potential criticism would contend that we underestimated the variability of size within a species and

undersmoothed the overall distribution. A severe increase of 10% in the empirically derived standard deviation did not decrease the lump number in 5 of 15 distributions and dropped the lump number by only one in the other 10. Increasing the uncertainty by 10% is aggressive and in the direction most likely to eliminate lumps: some standard deviations in the original h vector were likely overestimated, and some were underestimated. One could also argue for standard errors instead of standard deviations in kernel density estimation. We chose the latter, which favors smoother distributions. The existence of lumps and gaps in these size distributions is robust.

Ecosystem characteristics such as lake size, food web structure, and nutrient status explain variability in basic lake ecosystem properties such as total biomass, biomass per trophic level, production, and nutrient cycles (Vollenweider 1976; Schindler 1977; Carpenter and Kitchell 1993; Fee et al. 1994; Paterson et al. 1998). We expected that such different lakes would show significant differences in species size distributions. For example, larger lakes may have greater variability of available habitat, leading to greater diversity and smoother size distributions. Higher productivity may decrease diversity and favor a restricted range of large, bloom-forming phytoplankton (Dodson et al. 2000), thereby leading to size distributions with a few lumps. Trophic cascades may create gaps and lumps through size-selective predation (Carpenter and Kitchell 1993). However, none of these expected differences among lakes were supported by the data. All lakes show lumps and gaps, and many of these occur at similar size ranges across lakes, despite substantial differences in species composition and physical-chemical characteristics of the lakes.

These findings suggest that factors common to all north temperate lake ecosystems explain the similarities in pelagic community size structure. Factors that could be involved include, but are not limited to, similarities in the variance spectrum of physical forcing (Platt and Denman 1975; Levin et al. 1993), physical constraints on cell size and shape (Lewis 1976; Reynolds 1984), common allometry of physiological and demographic rates (Peters 1983), and constraints on body size imposed through predation or predator-avoidance mechanisms (Zaret 1980). We reject that species size distributions are smooth within and across guilds in favor of some other hypothesis with the mechanism yet to be determined. The lumpy size distributions we found are consistent with Holling's Textural Discontinuity Hypothesis but do not preclude other alternative hypotheses consistent with lumpiness, such as the Evolutionary Legacy and the Trophic Trough hypotheses.

We acknowledge that our lump results are scale-specific and that we are investigating a particular duration of a few years. Other scales, such as weekly or seasonal, merit investigation. This scale includes at least one generation of the longest lived species in the community and hundreds of generations of shorter lived species. It enabled us to aggregate many size measurements for each species and thereby yields more precise estimates of h .

While the similarities of lump and gap regions across lakes are striking, some differences exist. The most notable of these is Lake Wingra, which has more gaps and smaller

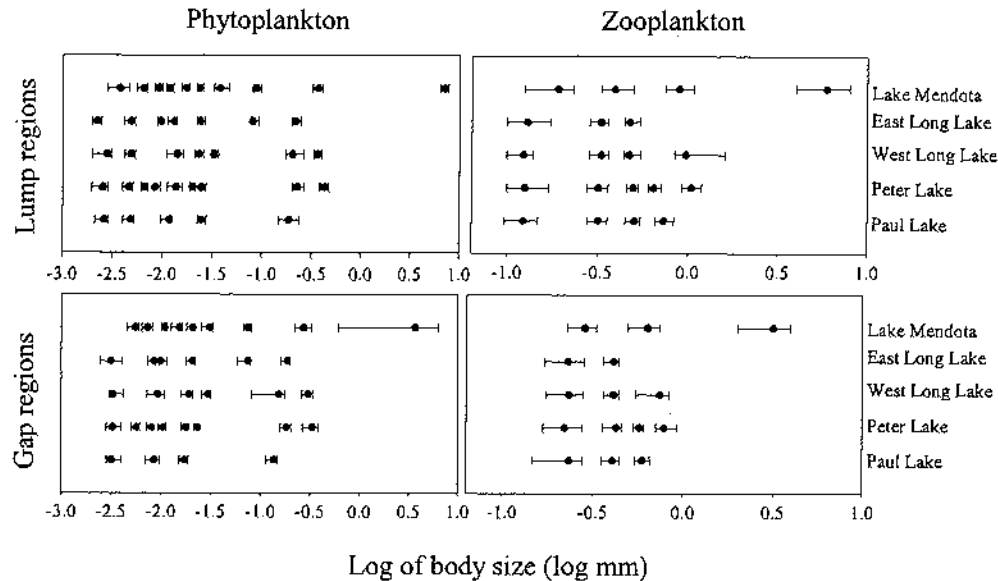


Fig. 7. Lump and gap locations of phytoplankton and zooplankton in the experimental lakes prenutrient enrichment and Lake Mendota. Data are pooled from 1991 to 1992.

lump regions in the fish size region than the other lakes. The most obvious limnological difference between Lake Wingra and the other lakes is lack of stratification. Lake Wingra fish display a lump at large body size associated with hybrid muskellunge \times northern pike (*Esox masquinongy* \times *lucius*), an introduced sport fish that is regularly stocked in the lake but does not naturally reproduce. In addition, there are several lumps with smaller body size associated with diverse littoral zone fish species. In Lake Wingra, there is no thermal refuge for zooplankton, which are subject to intense planktivory by high populations of bluegills and other littoral fish (Baumann et al. 1974). This may account for the distinctive fish lumps found in Lake Wingra. Paul Lake's fish size distribution also differs from that of the other lakes. Paul Lake has only one fish species. It was more diverse before 1951, when A. D. Hasler separated it from Peter Lake for experiments (Carpenter and Kitchell 1993). While we can only speculate about the location of missing lumps in Paul Lake, they were likely associated with yellow perch and small-bodied littoral zone fish.

Increased species richness could change lump and gap patterns if new species exploit gap regions and thereby increase or decrease the number of lumps. In the experimental lakes, more species were present after manipulation because the number of years pooled was larger. Nevertheless, number of lumps did not consistently increase or decrease postmanipulation, and the lump and gap patterns were similar despite the increase in species number. In the comparison of unmanipulated lakes, lakes with higher species number did not consistently have fewer or greater numbers of lumps than lakes with fewer species. Although species with body sizes in gap regions may have more resources available because of reduced competition, species-rich and species-poor lakes have similar lump and gap patterns. Thus, if body size is a guide to competitive interactions, the arena for competition seems to be determined by factors that establish similar gap

size regions across a wide range of lake types forcing species into lump regions. Similarity overlap was generally larger for gap regions than for lump regions.

N and P enrichment caused many changes in ecosystem processes of the experimental lakes (Carpenter et al. 1998, in press). Releasing nutrient constraints could potentially allow species of sizes that were formerly excluded to invade and persist. Thus, species would be more evenly spaced and create a smoother size distribution postmanipulation. Alternatively, increased nutrient concentrations could impose new size constraints and result in a more clumped distribution postmanipulation. The observed changes in species dominance could also cause a shift of lump and gap locations based on food web structure without change in the number of lumps and gaps. Although lump number remained relatively unchanged postenrichment, the lakes with manipulated food webs were much less similar pre- versus postenrichment than the others. It seems that a combination of large perturbations may alter an otherwise conservative pattern.

Comparison between phytoplankton and zooplankton size distributions showed that phytoplankton have more lumps per taxon than zooplankton and that zooplankton and fish have roughly equal numbers of lumps per taxon. Increased lumps per taxon in phytoplankton could reflect a greater number of viable sizes for phytoplankton than for zooplankton or fish. More lumps could also result simply because phytoplankton span a larger range of sizes than zooplankton or fish. Or, it is possible that the species criterion for aggregation is inappropriate for phytoplankton size distributions and that a larger grouping, such as family, would be more relevant. Increasing the aggregation size will yield fewer kernel points with larger standard deviations (smoothing parameters) and therefore fewer lumps. We adhered to the species level because species are the unit of comparison for the minimum and constant size ratio theory and the textural discontinuity hypothesis.

Hutchinson (1961) proposed the solution to the paradox of plankton (how there can be so many similar types of plankton species) was disequilibrium, because of high species turnover rates, and thus the end result of competitive exclusion is not seen in nature. The coherent pattern of lump and gap structure across lakes suggests an expansion of this interpretation. The broad pattern of lumps and gaps appears to be established by a set of cross-scale interactions common to all lakes we examined. This sets the template for phytoplankton diversity and, regardless of notions of equilibrium, offers a solution to the paradox of the plankton. If a species is of a body size that is in a lump region, then that species succeeds as a member of the community. Species composition of the plankton community changes day to day because of variable recruitment and encystment cycles in response to environmental cues, competition, and predation, and many species have relatively short life cycles (Hansson 1996; Reynolds 1997; Rengefors et al. 1998). There can be so many species of phytoplankton, even though they are competing for relatively few types of resources, because there is species replacement through and redundancy within multiple lump regions. Increased diversity, overlapping function, and redundant species within and across scales confer resilience on the community with respect to ecosystem function (Walker et al. 1999).

That species size distributions are generally conservative to experimental perturbations and differences among lakes corroborates recent results obtained on intertidal marine sediment assemblages (Raffaelli et al. 2000). It is not yet known whether size distribution patterns are conserved across latitudinal gradients or from lakes to the oceans. Comparisons across systems more diverse than in the study presented here could determine the universality of species size distribution patterns in aquatic systems and help elucidate critical processes and features that shape the pattern. Surface area to volume ratios for individual phytoplankton taxa underlie the similar successional sequences seen in tropical and temperate lakes. Tropical lakes have seasonal patterns, and the biological effects of this seasonality are similar to those seen in temperate lakes, whereas critical differences exist between tropical and temperate lakes in the nature and biological effects of nonseasonal variation (Lewis 1979). Moreover, if species size distributions prove to be a conservative property of terrestrial communities (Holling 1992; Allen et al. 1999) as well as aquatic ones, this invites discovery of new unifying principles for ecology.

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