

Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans

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Abstract

Analysis of zooplankton communities in over 1,100 water bodies spanning the Western Hemisphere (77°S, 81°N latitude) revealed latitudinal patterns in cladoceran body size and *Daphnia* seasonal dynamics. The mean body length of cladoceran species occurring at different latitudinal intervals was greatest in north temperate regions, declining in size toward the poles and equator. Thus, mean cladoceran size was greatest in regions where the mean annual surface temperatures of lakes ranged from 6 to 8°C in both the Northern and Southern Hemispheres. The date of maximum *Daphnia* abundance and the period of minimum *Daphnia* abundance in lakes of North America was positively, linearly related to the latitudinal position of the lakes. The date of maximum abundance increased with latitude such that *Daphnia* peaked during nearly all months of the year depending on latitude, but usually within the same, narrow temperature range (15–20°C). The period of minimum *Daphnia* abundance decreased linearly with latitude such that abundance generally was minimal when water temperatures exceeded 20°C.

Cladocerans are important to aquatic ecosystem function because they include the primary herbivores in lakes (*Daphnia*) and are important diet items for fishes (Dodson and Hanazato 1995). Attributes of cladoceran communities, including the mean body size and population dynamics of species, are often considered to be most influenced by biotic factors (e.g., competition, predation), largely on the basis of investigations of individual lakes in temperate regions. A comparison of cladoceran communities across lakes may provide a valuable new understanding of the factors influencing the mean body size and population dynamics of cladoceran communities by highlighting the role of abiotic factors operating at larger scales (e.g., climate). Specifically, a comparison of patterns in cladoceran communities in lakes across latitudes provides an opportunity to consider the relationship of temperature to the mean body size and population dynamics of cladocerans. Temperature has been shown to be critical to the survival, growth, and reproduction of cladocerans (Allan and Goulden 1980; Goss and Bunting 1983; Moore et al. 1996), yet it is seldom recognized as an important influence on the body size or population dynamics of cladoceran communities.

The presence of broad-scale patterns in cladoceran communities across lakes has rarely been recognized, or even explored, at regional scales (exceptions: Kratz et al. 1987; Wiseman 1996). Although within temperate lakes, a recurring seasonal pattern is widely recognized whereby *Daphnia* populations increase in spring, decline in midsummer, and increase again in the fall (Hutchinson 1967; Culver 1980; Threlkeld 1985). Here we evaluate whether patterns in cladoceran body size and population dynamics are present across latitudes. We begin with an analysis of published data to explore patterns in the mean body size of cladocerans

occurring at different latitudinal intervals spanning South, Central, and North America and the Caribbean. Next, we investigate patterns in the timing of the maximum and minimum abundance of *Daphnia* from published studies of individual water bodies of North America. We conclude with a brief comparison of patterns in cladoceran body size across latitudes to patterns in cladoceran population dynamics.

Materials and Methods

Patterns in the body size of cladocerans across latitudes—Zooplankton data were obtained from published studies and compendia for over 1,100 lakes, ponds, and reservoirs in the Americas and Caribbean (Haiti, Cuba, Dominican Republic) from 81°N to 77°S latitude (Table 1). The amount of data collected for each region reflects the availability of data for that region.

Most data have been collected and analyzed by zooplankton taxonomists since 1970 from water bodies that varied widely in their thermal structure, productivity, and biotic communities. The sampling of zooplankton spanned all 12 months of the year, except in regions where lakes freeze; in these regions, zooplankton were sampled only during the spring and/or summer months. We excluded from consideration lakes above 1,000 m in elevation because of the influence elevation has on water temperature. In the tropics, we included a small number of floodplain lakes. While the seasonal nature of floodplain lakes is different from that of other water bodies (Junk 1996), the zooplankton species found in these floodplain lakes were not different from those of other water bodies in the same region.

Latitudes were subdivided into intervals of 2.5°, except in cases where a lack of data required a greater range of latitude, or where all of the data acquired in a given region occurred over a narrower range of latitude. Water bodies were grouped into these 24 latitudinal intervals to obtain a sample of the limnetic, cladoceran species found within each interval. The mean body size of cladocerans for each interval was calculated by dividing the sum of the body lengths of

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Table 1. Published data used to describe patterns in cladoceran body size across latitudes in South, Central, and North America and the Caribbean. Studies are ordered from most southerly to most northerly.

Latitude range	Mean latitude	Water bodies	Cladoceran spp.	<i>Daphnia</i> spp.	Reference
73.0–77.0 S	75.0 S	NA	0	0	Heywood (1983)
45.3–46.3 S	45.8 S	11	4	1	Soto and Zuniga (1991)
37.5–41.3 S	39.9 S	24	8	2	Ruiz and Bahamonde (1989)
					Soto and Zuniga (1991)
					Ruiz and Bahamonde (1989)
					Modenutti and Balseiro (1994)
					Zuniga (1988)
32.3–34.1 S	33.2 S	7	7	3	Ruiz and Bahamonde (1989)
19–23 S	21 S	10	7	2	Arcifa (1984)
4–10 S	7	30	7	1	Vasquez and Rey (1993)
					Zoppi and Vasquez (1991)
					Robertson and Hardy (1984)
					Saunders and Lewis (1988)
1–1.5	1.25	5	15	1	Bozelli (1992)
					Brandorff (1978)
					Robertson and Hardy (1984)
8–14	11	26	7	0	Collado et al. (1984)
18–23	20.5	70	7	0	Collado et al. (1984)
27.2–29.4	28	33	10	1	Brezonick et al. (1984)
					Blancher (1984)
					Dawes et al. (1987)
33.5–36.3	34.9	NA	9	5	Adams et al. (1992)
42–44	43	74	19	8	Torke (1979)
					Patalas et al. (1994)
44–46	45	116	19	9	Torke (1979)
					Patalas et al. (1994)
46–48.75	47.7	50	18	8	Patalas et al. (1994)
48.75–51.25	50	171	22	13	Patalas et al. (1994)
51.25–53.75	52.5	61	19	11	Patalas et al. (1994)
53.75–56.25	55	108	21	13	Patalas et al. (1994)
56.25–58.75	57.5	30	14	6	Patalas et al. (1994)
58.75–61.25	60	70	14	7	Patalas et al. (1994)
61.25–63.75	62.5	61	13	7	Patalas et al. (1994)
63.75–66.25	65	56	10	5	Patalas et al. (1994)
					Moore (1978)
66.25–68.75	67.5	108	10	4	Patalas et al. (1994)
68.75–71.25	70	71	7	4	Patalas et al. (1994)
					Kling et al. (1992)
71.25–76.25	73.75	25	5	2	Patalas et al. (1994)
76.25–81.25	78.75	10	4	1	Patalas et al. (1994)

all species (rare or abundant) found in each interval by the number of species in that interval. The sparse land mass and/or lack of data for water bodies south of 46°S latitude prohibited the inclusion of these regions in statistical analyses. Data were obtained for only four lakes (51°S latitude) near the southern tip of South America (54°S latitude), while in Antarctica (73–77°S) limnetic cladocerans do not occur (Heywood 1983).

We included only pelagic, herbivorous cladoceran species in our analyses because these communities are the simplest and most well studied of the zooplankton. As such, the following littoral cladoceran species were excluded from consideration: all Chydoridae species except *Chydorus sphaericus*, all Sididae except *Diaphanosoma* spp., all Macrothricidae, *Simocephalus* spp., *Polyphemus* spp., and

Moina spp. (Dodson 1992). Species size was defined as the mean total body length of adult females. The body sizes of North American species were generally obtained from general reference texts (Ward and Whipple 1966; Pennak 1978; Hebert 1995), except when body sizes were reported in the literature (Table 2). Body sizes for Central and South American species were obtained directly from the published studies, from previous studies by the authors of these studies, or from summary articles on tropical zooplankton (Fernando 1980; Dussart et al. 1984; Fernando et al. 1987). When two or more different body sizes were reported for a species, the mean size of all reported measurements was used. In cases where body sizes were not identified for species of the genera *Bosmina*, *Bosminopsis*, and *Eubosmina*, the mean body size was assumed to be 0.4 mm based on the sizes of other

Table 2. List of cladoceran species and corresponding body sizes from lakes in South, Central, and North America and the Caribbean.

Genus and species	Mean body length (mm)
<i>Bosmina affinis</i>	0.40
<i>Bosmina deitersi</i>	0.40
<i>Bosmina gessneri</i>	0.40
<i>Bosmina longirostris</i>	0.40
<i>Bosminopsis brandorff</i>	0.40
<i>Bosminopsis negrensis</i>	0.40
<i>Bosminopsis deitersi</i>	0.40
<i>Ceriodaphnia reticulata</i>	0.80
<i>Ceriodaphnia affinis</i>	1.00
<i>Ceriodaphnia cornuta</i>	0.45
<i>Ceriodaphnia dubia</i>	0.80
<i>Ceriodaphnia lacustris</i>	0.85
<i>Ceriodaphnia laticaudata</i>	0.85
<i>Ceriodaphnia pulchella</i>	0.55
<i>Ceriodaphnia quadrangula</i>	0.80
<i>Ceriodaphnia reticulata</i>	1.00
<i>Chydorus sphaericus</i>	0.40
<i>Daphnia ambigua</i>	0.88
<i>Daphnia catawba</i>	1.25
<i>Daphnia dubia</i>	1.50
<i>Daphnia galeata</i>	2.15
<i>Daphnia gessneri</i>	0.84
<i>Daphnia middendorffiana</i>	2.75
<i>Daphnia hyalina</i>	1.55
<i>Daphnia laevis</i>	1.30
<i>Daphnia longiremis</i>	1.00
<i>Daphnia longispina-hyalina</i>	0.84
<i>Daphnia parvula</i>	0.88
<i>Daphnia pulex</i>	1.75
<i>Daphnia pulicaria</i>	1.75
<i>Daphnia retrocurva</i>	1.20
<i>Daphnia rosea</i>	1.40
<i>Daphnia schoedleri</i>	1.60
<i>Daphnia similis</i>	2.80
<i>Daphnia thorata</i>	1.55
<i>Diaphanosoma chilense</i>	1.00
<i>Diaphanosoma birgei</i>	0.65
<i>Diaphanosoma brachyurum</i>	0.85
<i>Diaphanosoma brevirme</i>	0.88
<i>Diaphanosoma fluviatile</i>	0.85
<i>Diaphanosoma leuchtenbergianum</i>	1.05
<i>Diaphanosoma neotropicum</i>	0.99
<i>Diaphanosoma polypina</i>	0.72
<i>Diaphanosoma spinulosum</i>	0.99
<i>Eubosmina coregoni</i>	0.40
<i>Eubosmina hagmanni</i>	0.40
<i>Eubosmina longispina</i>	0.40
<i>Eubosmina tubicen</i>	0.40
<i>Neobosmina chilensis</i>	0.45

species from these genera. As body-size data from different regions were generally not available for individual species, we used a single size for all intervals in cases where species occurred in more than one latitudinal interval. The necessary use of a single body size for a species across latitudes prohibits consideration of the influence of intraspecific variation in body size on the interspecific patterns of body size presented here. However, the influence is probably minimal, as

relatively few species were broadly distributed across latitudes, of which most were small with a limited range of body sizes (e.g., *C. sphaericus*).

To relate latitudinal patterns in the mean body size of cladocerans to lake temperature, we predicted the mean annual surface temperatures of lakes at a given latitude from Straskraba's empirically based model (1985). Straskraba's model, based on data from 50 lakes distributed from 26°S to 74°N latitude, explains 85–95% of the variance in daily lake surface temperatures for temperate and subtropical lakes of various sizes. The model effectively predicts daily lake surface temperatures for lakes in the Southern Hemisphere as far south as 45° (Straskraba 1985). While Straskraba (1985) acknowledges that the model explains a lower (and undefined) percentage of the variability in surface lake temperatures in tropical and high latitude lakes, annual variability in surface temperatures for these lakes is relatively small. Thus, we use Straskraba's model to predict mean annual surface temperatures for lakes from 45°S to 73°N latitude, excluding lakes beyond this range.

Patterns in the mean body size of cladocerans with respect to lake temperature and latitudinal position were analyzed using least-squares polynomial regression. Polynomial models were fit using weighted least-squares regression to account for differences in variance at different latitudes. The appropriate order of polynomial model was selected using a forward selection procedure (Zar 1996).

Patterns in the seasonal dynamics of cladocerans across latitudes— We evaluated 27 published descriptions of zooplankton seasonal dynamics from 24 different lakes, ponds, and reservoirs in North America ranging from 28°N to 64°N latitude (Table 3). In each study, zooplankton were sampled at least once monthly, always across a range of depths. In water bodies that do not freeze, sampling occurred nearly year round; for all remaining water bodies, sampling generally occurred from early spring to late fall (the period of greatest zooplankton abundance). In 14 of these 24 water bodies, only a single species of *Daphnia* occurred during the year of the study, while two or three *Daphnia* species were present in the remaining water bodies. In water bodies with more than one *Daphnia* species, we included only the first species to peak in abundance in our analyses. We analyzed the first species to peak, rather than species peaking later in the season, because species occurring earlier in the season are more likely to be influenced by abiotic factors than by biotic processes (e.g., competition or predation) (Sommer et al. 1986).

The maximum abundance of *Daphnia* was defined as the date of maximum population density prior to midsummer decline. Minimum *Daphnia* abundance or midsummer decline was defined as the period of low or no *Daphnia* between the spring and fall maximums. For 20 of the 27 data records, surface-water temperature records were available and included in the analyses. For the remainder of the studies, surface temperatures at the date of maximum abundance were estimated using the model of Straskraba (1985). For studies in which abundances were only rendered graphically, minimum and maximum abundances were visually estimated from the fitted line. Least-squares linear regression was used to evaluate the relationships between the date of maximum

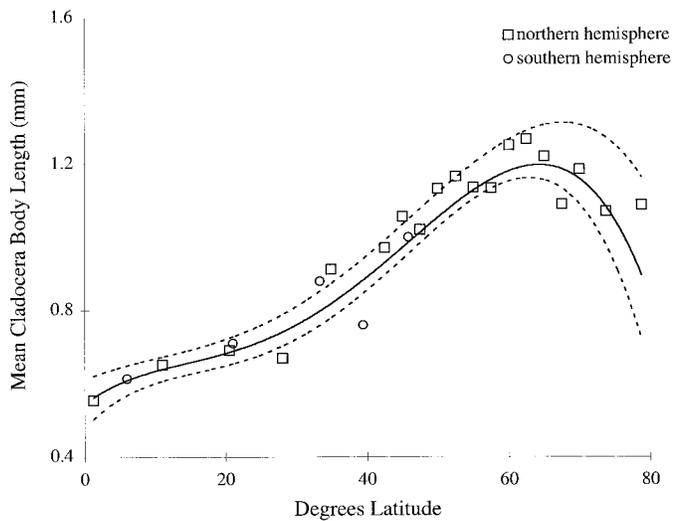


Fig. 1. Mean body size of cladocerans versus latitude in South, Central, and North America and the Caribbean. Each data point represents the mean total body length of all limnetic herbivorous cladocera reported for water bodies occurring within one latitudinal interval. Each interval is plotted as the mean latitude of that interval (Table 1). The 24 latitudinal intervals represent zooplankton data from more than 1,100 water bodies in the Southern and Northern Hemispheres (48°S to 81°N latitude). Data were obtained from published studies and compendia (Table 1). The solid line represents the polynomial model fit to these data (mean body size = $[2 \times 10^{-7}x^4] + [2 \times 10^{-5}x^3] - [0.0008x^2] + [0.0144x] + 0.543$; $r^2 = 0.95$). The perforated lines represent the 95% confidence intervals for the fitted line.

abundance and the period of minimum abundance, with latitude.

Results and Discussion

Patterns in the body size of cladocerans across latitudes—The mean body length of limnetic cladocerans was smallest in tropical regions, increasing to maximum size in temperate regions (50–60°) in both the Northern and Southern hemispheres (Fig. 1). Thus, the pattern of increasing body size from tropical to temperate regions was symmetric about the equator such that the mean body size of cladocerans at latitudes from 0 to 50° in the Southern Hemisphere was indistinguishable from that of cladocerans at these latitudes in the Northern Hemisphere.

Mean cladoceran body size declined from north temperate regions in the Northern Hemisphere to arctic regions (Fig. 1). Although the decline in size from temperate to arctic regions is less conspicuous than the decline toward tropical regions, the relatively small number of latitudinal intervals (six) in this region represents over 300 water bodies. Furthermore, while the decline in mean size from temperate to arctic regions appears small compared to the decline in size from temperate to tropical regions, the mean size of cladocerans in subarctic and arctic regions is significantly increased by a small number of large species (e.g., *Daphnia pulex*, *Daphnia middendorffiana*). In the Southern Hemisphere, the

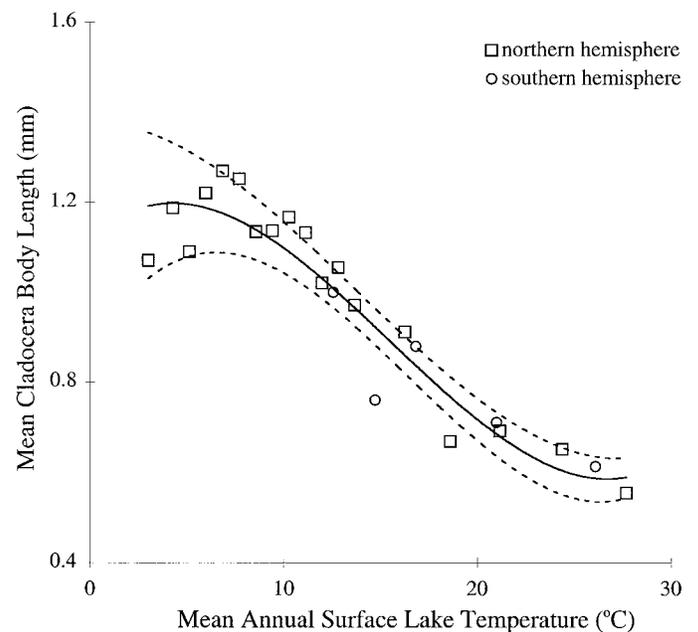


Fig. 2. Mean body size of cladocerans versus latitude in South, Central, and North America and the Caribbean. Each data point represents the mean total body length of all limnetic herbivorous cladocera reported for water bodies occurring within one latitudinal interval. Each interval is plotted as the mean annual surface temperature for lakes in that interval. (Table 1). The 24 latitudinal intervals represent zooplankton data from more than 1,100 water bodies in the Southern and Northern Hemispheres (48°S to 81°N latitude). Data were obtained from published studies and compendia (Table 1). Lake temperatures were estimated using Straskraba's empirically based model (1985). The solid line represents the polynomial line fit to these data ($y = [0.0001 \times x^3] + [0.0051x^2] + [0.0376x] + 1.12$; $r^2 = 0.93$). The perforated lines represent the 95% confidence intervals for the fitted line.

size and abundance of cladocerans similarly appears to decline and then disappear from north temperate regions to the Antarctic, although robust comparisons to the Northern Hemisphere are not possible. Soto and Zuniga (1991) found only one small zooplankton species (*Neobosmina chilensis*) in four lakes at 51°S latitude, whereas Heywood (1983) found no limnetic cladoceran species in Antarctica after extensive sampling.

Across all latitudes, the minimum body size of cladocerans was consistent (0.3–0.5 mm) because most regions contained *C. sphaericus*, or species of the genera *Bosmina*, *Eubosmina*, and *Bosminopsis*. Large cladoceran species, with the exception of *D. middendorffiana*, were most common in north temperate zones (Table 1). Both the size of individual species and total species richness declined from north temperate zones toward the poles and equator for three major genera of larger cladocerans (*Daphnia*, *Ceriodaphnia*, and *Diaphanosoma*).

When the body-size pattern was considered in terms of water-body temperatures, the mean body size of cladocerans was largest in water bodies with a mean annual surface temperatures of 6–8°C and smaller in cooler and warmer lakes toward the North Pole and equator, respectively (Fig. 2).

However, the use of mean annual surface temperatures does not account for possible effects of thermal stratification on the body-size pattern. Summer thermal stratification, particularly in temperate lakes, often provides a cold-water refuge that is important to the survival of large-bodied cladocerans (Tessier and Welser 1991). If data were available to incorporate the deeper, colder water layers of stratified water bodies into our mean annual temperature estimates, annual estimates would slightly decrease in tropical and arctic regions where the temperature difference between stratified water layers is small, and decrease more in temperate regions where the temperature difference between water layers is relatively large (Lewis 1995). These changes to the mean annual temperature estimates in Fig. 2 would move the curve slightly to the left (colder), and make the middle (temperate region) portion of the curve steeper.

It is also important to consider how differences in sampling intensity (number of lakes/latitudinal interval) across latitudinal intervals may have affected the patterns in adult body size presented here. Sparse available data in some regions resulted in a sampling bias whereby latitudinal intervals in temperate and arctic regions were comprised of more lakes than intervals in tropical regions. Conversely, the seasonal frequency of sampling in tropical regions was often greater than in temperate or arctic regions. The greater intensity of sampling in temperate regions may have facilitated the detection of the occasional rare, large-bodied species, thereby increasing the mean body size at these latitudes. Yet, there simply are not large-bodied species in the subtropics (Brezonik et al. 1984), tropics (Fernando et al. 1987; Lewis 1995), subarctic (Bertillon et al. 1995), and arctic regions (O'Brien et al. 1979) to be missed by small sample size.

The range in cladoceran sizes we have observed in tropical, temperate, subarctic, and arctic regions in the Western Hemisphere is also consistent with studies that describe the zooplankton found in these climatic zones on other continents, including Australia, Asia, Europe, India, and Greenland (Fernando 1980; Dussart et al. 1984; Fernando et al. 1987; Hrbáček 1987; Timms 1988). Moreover, the size pattern across latitudes whereby cladoceran species increase in size toward temperate regions is consistent with size patterns observed within individual species of zooplankton across latitudes. For example, Fernando et al. (1987) concluded the maximum length of *Daphnia laevis* and *Daphnia lumholtzi* is 1.3 mm in the tropics, while Hebert (1995) determined the maximum length of these species in temperate North America to be 1.8 and 2.6 mm, respectively. From temperate to arctic regions, *D. pulex* also declines in size (Hrbáček 1987). While among copepods, *Boeckella gracilipes* increases linearly in size from subarctic to temperate zones in Chile (Villalobos and Zuniga 1991), and the copepod *Scottolona canadensis* increases linearly in size from subtropical to temperate zones in the United States (Lonsdale and Levinton 1985). In each of these cases, the size pattern observed within individual species of *Daphnia* and copepods across latitudes parallels the pattern we observed across species.

While the scope of this study was restricted to low-elevation lakes in the Western Hemisphere, a number of studies in other areas have reported results that appear exceptional to the latitudinal patterns of body size reported here. For

example, larger bodied cladocerans, as are typically found in temperate lakes, can also be found in high-elevation lakes in tropical South America and Africa (Fernando et al. 1987; Green 1995). Similarly, cladoceran species found in high-elevation lakes in temperate regions often closely resemble those found in lakes in subarctic and arctic regions (Anderson 1974). Yet, the thermal regimes of these high-elevation lakes are also more similar to those of lakes at a higher latitude than to those at lower elevations at the same latitude. Furthermore, larger bodied cladocerans (i.e., *Daphnia*) have been reported in certain low-elevation tropical lakes in the Eastern Hemisphere (Green 1967; Kalk 1979; Venkataraman 1981; DuMont 1994). Yet, these lakes are unlike most lowland tropical lakes in that they exhibit broad, seasonal fluctuations in lake temperature and cold-water refuges in the hypolimnion (Tessier and Welser 1991). Moreover, *Daphnia* in these lakes are usually observed at intermediate temperatures, consistent with the findings presented here. In a tropical pond in India, Venkataraman (1981) found significant numbers of *Daphnia carinata* in early spring at intermediate temperatures, but the population then declined to very low abundances during the remainder of the year when water temperatures exceeded 22°C. Similarly, in two African lakes where *Daphnia* have been reported, they were generally present only when temperatures fell below 20°C (Kalk 1979; DuMont 1994).

The presence or absence of cladocerans in different regions of the world has been attributed to biotic factors, which have been shown to influence the seasonal dynamics of zooplankton communities in individual lakes (e.g., competition and predation) (Brooks and Dodson 1965; DuMont 1994). However, there is little evidence that biotic factors play a dominant role in controlling cladoceran distribution at a regional scale (Fernando et al. 1987; Lewis 1995). The latitudinal patterns in cladoceran body size described here are also inconsistent with latitudinal patterns in primary production, nutrient regeneration, and oxygen availability in lakes across latitudes (Lewis 1995). Still, the strong correlations of body size with lake temperatures across latitudes could result from direct (e.g., physiological) or indirect (e.g., increased predation) effects of temperature.

One possible explanation for the paucity of larger cladocerans in tropical regions is that larger cladocerans have a lower upper thermal tolerance (Moore et al. 1996). In subarctic and arctic regions, the constraints of cold water and short growing seasons on population growth rates appear to exclude large-bodied zooplankton, with long generation times, from these regions (Brooks 1957; Gillooly 1999). Large-bodied species that do persist in these colder regions (e.g., *D. middendorffiana*, *D. pulex*) have a special ability to produce resting eggs parthenogenetically, an ability that drastically reduces the generation time of these species (Brooks 1957; Frey 1982).

Patterns in the seasonal dynamics of cladocerans across latitudes—The date of maximum *Daphnia* abundance within lakes varied regularly across latitudes from the subtropics to the arctic (Fig. 3). The date of maximum abundance (day of year) within a lake was positively correlated to the latitudinal position of each lake ($p < 0.0001$, $r^2 = 0.70$, $n = 27$). Thus, the month of the year when *Daphnia* were in greatest abun-

Table 3. Published data used in analyses of *Daphnia* seasonal dynamics across latitudes. Water body temperatures listed here represent surface temperatures that were empirically determined or estimated (italics) using Straskraba's (1985) model.

Water body, location, and year	<i>Daphnia</i> spp.	Latitude (°N)	Min. abundance (period of days)	Max. abundance (day of year)	Temper- ature (°C)	Reference
Pond, Ontario 1973	<i>ambigua</i>	46.00	38	191	21.0	Kwik and Carter (1975)
Roi Lake, Alberta 1982	<i>pulicaria</i>	53.35	0	172	21.0	Murtaugh (1985)
Waldsea Lake, Saskatchewan 1974	<i>similis</i>	52.17	81	195	21.4	Swift and Hammer (1979)
Lake Mathews, British Columbia 1976	<i>longiremis</i>	64.00	0	196	14.0	Moore (1978)
Nebish Lake, Wisconsin 1981	<i>unknown</i>	46.04	61	172	17.0	unpubl. data, DNR, Wisconsin (1990)
Lake Aleknagik, Alaska 1990	<i>longiremis</i>	59.50	0	273	12.4	D. Rogers, Univ. Washington unpubl. data (1995)
Lakes 122, Ontario 1971	<i>catawba</i>	49.35	0	211	21.4	Schindler and Noven (1971)
Lake 132, Ontario 1971	<i>longiremis</i>	49.35	36	190	22.0	Schindler and Noven (1971)
Frairs Lake, Michigan 1971	<i>ambigua</i>	42.50	—	140	18.0	Allan (1977)
Lake Mendota, Wisconsin 1987	<i>retrocurva</i>	43.25	—	125	15.5	Luecke et al. (1990)
Lake Mitchell, Vermont 1978	<i>rosea</i>	43.44	52	166	17.0	Demott (1983)
Lake Mitchell, Vermont 1979	<i>rosea</i>	43.44	75	181	20.0	Demott (1983)
Lake Erie, Ohio 1989	<i>galeata</i>	41.33	—	172	18.8	Wu (1991)
Pond (+ fish), Michigan 1989	<i>pulex</i>	42.19	—	104	16.5	Geedey (1990)
Pond (− fish), Michigan 1989	<i>pulex</i>	42.19	—	118	16.5	Geedey (1990)
Richter Lake, Wisconsin 1968	<i>galeata</i>	45.11	—	164	21.0	Stewart and Stewart (1983)
Richter Lake, Wisconsin 1969	<i>galeata</i>	45.11	64	162	21.0	Gannon et al. (1984)
Lake Washington, Washington 1981	<i>pulicaria</i>	43.37	120	166	15.0	Edmondson <i>in</i> Wiseman (1996)
Lake Washington, Washington 1982	<i>pulicaria</i>	43.37	118	168	16.8	Edmondson <i>in</i> Wiseman (1996)
Lake Reading, Kansas 1982	<i>ambigua</i>	38.25	—	136	17.5	Bruner (1983)
Lake Fort Smith, Arkansas 1972	<i>unknown</i>	35.38	122	141	16.0	Carter and Hoffman (1974)
Rainbow Bay Pond, South Carolina 1984	<i>laevis</i>	33.10	60	106	25.0	Taylor and Mahoney (1990)
Lake Oglethorpe, Georgia 1979	<i>parvula</i>	33.51	157	121	25.0	Pace et al. (1984)
Pond, Denton, Texas 1974	<i>pulex</i>	33.12	120	91	16.5	Smith et al. (1979)
King Pond, Florida 1985	<i>laevis</i>	29.39	98	98.5	20.0	Foran (1986)
Fairy Lake, Florida 1980	<i>ambigua</i>	28.05	210	91	17.1	Young (1978); Dawes et al. (1987)
Lake Oneida, New York 1975	<i>pulex</i>	43.12	0	151	16.5	Mills et al. (1978)

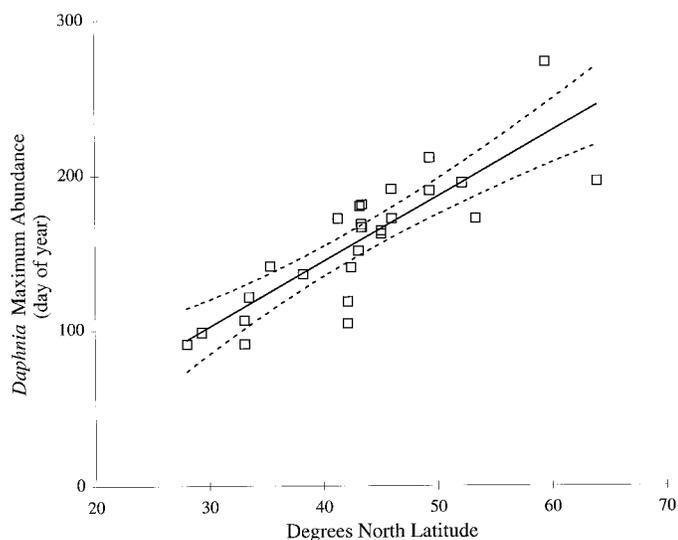


Fig. 3. Date of maximum *Daphnia* abundance (day of year) versus latitude in 24 individual lakes, ponds, and reservoirs in North America (date of maximum abundance = $(4.2x) - 24.8$; $r^2 = 0.70$). Data were obtained from published studies (Table 3).

dance ranged from February in Florida to September in Alaska. Yet, the water temperature at which maximum abundance occurred in individual lakes varied little across latitudes. The mean lake temperature at the date of maximum abundance for lakes from Florida to Alaska was 18.5°C ($\text{SD} = \pm 3.1$, $n = 27$).

The period of minimum *Daphnia* abundance (d) also was linearly related to latitude. The duration of the period increased from temperate to subtropical regions. That is, the period of minimum abundance was negatively correlated to degrees north latitude ($p = 0.007$, $r^2 = 0.44$, $n = 15$; Fig. 4). The period of minimum abundance occurred in individual lakes at nearly all months of the year depending on latitude. In subtropical lakes, *Daphnia* peaked in early spring and declined or disappeared for the next 98–210 d. In temperate lakes, *Daphnia* peaked in early summer and declined in mid-summer for 30–100 d. The period of minimum abundance often corresponded to the period when lake water temperatures were above 20°C . Thus, the period decreased from south to north until north temperate latitudes were reached where declines did not occur because *Daphnia* peaked only once in the fall. Therefore, lakes where *Daphnia* peaked only once were not included in the regression analysis of minimum *Daphnia* abundance, but are represented in Fig. 4 as experiencing zero days of decline to illustrate the relative latitudinal position of these lakes.

The date of maximum *Daphnia* abundance and the period of minimum abundance were linearly related to latitude for lakes of all types across all climate zones. The pattern is strong despite enormous differences in food resources, predator communities, thermal regimes, and water-body morphologies among these water bodies. These relationships indicate that *Daphnia* seasonal dynamics operate at regional scales and may be driven by influences such as climate. The timing of *Daphnia* maximum and minimum abundance occurred in virtually all months of the year depending on the

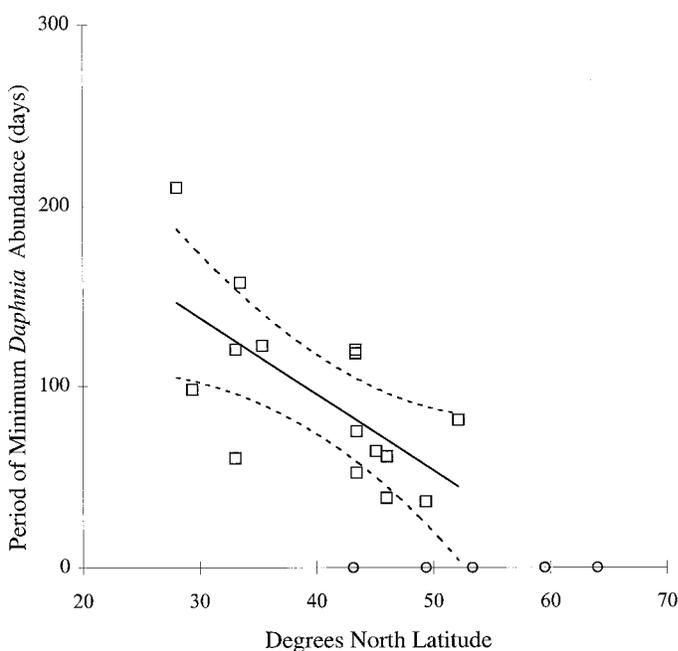


Fig. 4. Period of minimum *Daphnia* abundance (d) versus latitude for 15 lakes in North America (period of decline = $[-4.2x] + 264$; $r^2 = 0.44$). Circles represent those lakes that did not exhibit a seasonal decline and were not included in the regression analysis. Data were obtained from published studies (Table 3).

latitudinal position of the lake, yet most often these events took place within a narrow temperature range. The date of maximum *Daphnia* abundance occurred on average at 18.5°C for lakes from Florida to Alaska, whereas the period of minimum abundance often occurred at temperatures greater than 20°C . Our observations regarding the period of minimum abundance are consistent with Wiseman's result (1996) showing a negative correlation between the mean summer abundance of larger bodied *Daphnia* (e.g., *pulex*, *pulicaria* and *galeata mendotae*) to maximum surface temperature in water bodies of the United States ($r = -0.75$, $p < 0.0001$, $n = 26$). Wiseman (1996) found no such relationship for smaller bodied *Daphnia* spp. (e.g., *parvula*, *ambigua*).

The latitudinal patterns in *Daphnia* seasonal dynamics require a reconsideration of the current interpretations of the factors influencing the dynamics of zooplankton communities. Models used to describe zooplankton community dynamics most often do not include temperature as a factor influencing zooplankton community dynamics. For example, the plankton ecology group (PEG) model, derived from observations of temperate lakes, describes the dynamics of zooplankton communities in the context of seasonal events such as spring turnover and biotic interactions such as competition and predation (Sommer et al. 1986). The results presented here suggest that the timing of maximum and minimum abundance for *Daphnia* is more a temperature phenomenon than a seasonal one. The peaks and declines of *Daphnia* were not associated with a particular season, but rather a particular range of temperatures.

Conclusions—Both the pattern in cladoceran body size across latitudes and the pattern in cladoceran body size in temperate lakes through time are related to temperature. Across latitudes, the mean body size of cladocerans is largest at mean annual water-body temperatures of 6–8°C and smaller in colder and warmer temperatures. In temperate lakes, the mean body size of cladocerans is largest at intermediate temperatures (15–20°C) (spring and fall) and smaller in colder and warmer water temperatures (winter, summer) (Culver 1980; Threlkeld 1985).

Furthermore, the pattern in the abundance of *Daphnia* in temperate lakes with respect to temperature is similar to the pattern of *Daphnia* abundance in individual lakes across latitudes. *Daphnia* are greatest in abundance at intermediate temperatures (15–20°C) in lakes from Florida to Alaska, much as they are in temperate lakes (Hutchinson 1967; Threlkeld 1985; Sommer et al. 1986). Together, these patterns illustrate that cladoceran dynamics occur regularly across space and time depending on temperature. Thus, it may be more appropriate to speak of *Daphnia* thermal dynamics rather than *Daphnia* seasonal dynamics.

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