1990

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The Iowa Lakeside Laboratory

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The Cladocera of Lake West Okoboji, Iowa - Revisited

KENNETH L. LANG1
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Seven stations, established in 1968 to sample Cladocera, were sampled again, using the same methods, in 1988. Seven species, all of them in low abundance, are new records for Lake West Okoboji. In 1988, there was little difference in the ranking of the stations relative to abundance of cladocerans. 2) the distribution and abundance of the species by habitat-type, 3) the seasonality of the diversity of cladocerans is in some sense an indicator of the diversity of microhabitats that had been studied initially in 1959. They suggest open water. Because of apparent niche specialization, the diversity of cladocerans and other taxa in Lake West Okoboji is likely to be higher than in other lakes and serve as trophic intermediaries for the carnivores. Diverse in form, they have radiated from a benthic ancestor (Cannon 1933; Goulden 1968) to utilize a wide variety of microhabitats. Mostly filter-feeders, morphologies range from heavy-bodied benthic forms of the shallow, weed-choked littoral to light-bodied plankters of the open water. Because of apparent niche specialization, the diversity of cladocerans is in some sense an indicator of the diversity of microhabitats in a lake. For instance, within littoral habitats, relevant mosaic elements for cladocerans are weed beds and interspersed patches of open water (Pennak 1966; Lang 1970); within beds, the different species of plants (Quade 1969; Lang 1970); on plants, the vertical position (Lang 1970).

To examine the connection between cladoceran diversity and habitat heterogeneity in Lake West Okoboji was the goal of an earlier study (Lang 1970). Of the 30 species studied in those collections in 1968, 25 were largely confined to the complex littoral habitats and 5 to the relatively simple habitat of the open water.

Since 1968, routine limnological monitoring of the Lake West Okoboji (Bachmann and Jones 1974, Bachmann 1987) has been initiated to follow water quality in the face of increased recreational and residential pressure on the lake and watershed. Likewise, Bovbjerg, Dusil and Broer (1982) sampled the snail populations at 53 littoral stations that had been studied initially in 1959. They suggest that the snail fauna is stable, the number of species per unit area has increased throughout the lake and there is a decided shift in relative abundance toward the less pollution-tolerant species. These studies suggest that the quality of Lake West Okoboji as a freshwater habitat is not deteriorating.

In the spirit of continuing the limnological and biological study of this exceptional lake, this paper reports the results of sampling, during the spring, summer and fall of 1988, the Cladocera of the same 7 stations used in 1968. In particular, I compare the composition, abundance and seasonality of species comprising the assemblages of 7 habitats. Since Lake West Okoboji has great environmental heterogeneity relative to important mosaic elements for cladocerans, I also compare the richness of the species composition with those of other northern lakes where intensive sampling has been done. The work was done at the Iowa Lakeside Laboratory, Milford, Iowa.

LAKE WEST OKOBOJI AS A HABITAT
Lake West Okoboji is located in Dickinson County, Iowa, and is of Wisconsin drift origin (Figure 1). Its north-south axis has a length of 8.79 km, a maximum breadth of 4.57 km, an area of 15.4 ha and shoreline length of 50.0 km; it has a maximum depth of 42.7 m and a volume of $184 \times 10^3$ m$^3$ (Bachmann, Bovbjerg and Hall 1966). While a relatively deep lake, 50% of West Okoboji is 10 m or less in depth and approximately 17% is 3 m or less in depth. Thus, it has extensive littoral regions associated with the bays and the shallow north end.

West Okoboji is a dimictic, second-class lake in that it has two full circulation periods per year, a thermocline is nearly always established in the summer and the bottom waters are usually well above 4°C (Barclay 1955; Clampitt, Waffle and Bovbjerg 1960; Cooke 1963, 1966). Chemically the lake is considered a freshwater lake with high bicarbonate alkalinity occurring predominantly as Mg(HCO$_3$)$_2$ (Cooke 1966). Bovbjerg, Dusil and Broer (1982) describe West Okoboji as "naturally eutrophic, culturally augmented", with dense macrophytes in the bays and a rich algal flora including a diverse planktonic component as well as filamentous forms associated with plants and substrates. Relative to the needs of cladocerans, there is great habitat heterogeneity in the extensive littoral region, a true limnetic region, a favorable chemical environment and high productivity; high cladoceran diversity is possible.

THE SAMPLING STATIONS
To maximize the potential for a complete list of the Cladocera of the lake, habitats for sampling were chosen for variation in exposure to wave action, type and slope of the substratum and abundance of rooted vegetation. The sampling stations were located on the two-meter isobath in each habitat and if rooted vegetation was present, were sampled in both 1968 and 1988 (Figure 1).

Little Miller's Bay (LMB) is a small embayment at the northwestern corner of Miller's Bay, enclosed along the southeastern margin by a sandpit, the bay is a shallow saucer scarcely over two meters in greatest depth. The concave profile and protection from the wind allows silt and organic debris to accumulate. In both summers, the predominant plant species, Myriophyllum ecallebos, Potamogeton waterforms, Ceratophyllum demersum and Potamogeton richardsonii formed dense, mixed beds interspersed with patches of open water. In addition, Ranunculus longirostris was abundant both years in late spring through early summer. Potamogeton crispus was not present in the lake in 1968 but formed dense patches along the western margin in 1988. The filamentous algae Rhizoclonium sp. and Spirogyra sp. were...
present most of both summers and eventually entangled the weed beds, forming solid walls of vegetation adjacent to the open water. 

Spirogyra sp. was particularly abundant in 1988.

The Miller's Bay station (MB) was 70 m from shore in the southwestern corner of the bay. Protected on three sides by hills, this station is exposed to wave action only when the wind is from the east. The bottom has a gentle slope, reaching a depth of 5 m, 340 m from shore. Potamogeton richardsonii, Potamogeton zosteriformis and Ceratophyllum demersum were the predominant species in 1968. In 1988, Myriophyllum exalbescens was an abundant addition to the beds.

Little Emerson's Bay (LEB) is very similar to Little Miller's Bay in that both are protected from wave action and are saucer-like, allowing silt and organic debris to accumulate. As in Little Miller's Bay, Ranunculus longirostris and Myriophyllum exalbescens formed the early beds in both years with Ceratophyllum demersum, Potamogeton pectinatus and Potamogeton zosteriformis appearing in abundance by mid-summer. By August, 1968, plants in both Little Miller's and Little Emerson's Bays had gelatinous coatings of the blue green alga Rivularia sp., the onset in Little Emerson's Bay preceding that in Little Miller's Bay by about two weeks. In 1988, Rivularia sp. was noticeable on most plants in Little Emerson's Bay by the end of June and was very abundant by mid-July. By contrast, the plants in Little Miller's Bay, covered most of the summer of 1988 by mats of Spirogyra sp., were mostly free of the blue-green.

The northern station (NORTH) was located 40 m from shore on the 2 m isobath. The bottom here has a gentle slope and is composed mainly of cobbles, sand and silt. The absence of any dense weed beds and exposure to wave action from the east and south results in reduced deposition of organic debris. The bulk of the sparse beds here in 1968 was made up by Potamogeton richardsonii, Potamogeton pectinatus, Vallisneria americana, Ceratophyllum demersum and Myriophyllum exalbescens. In 1988, these narrow beds were even more poorly developed and were covered by mats of Spirogyra sp. throughout the summer.

Fort Dodge Point (FDP), on the eastern shore, is subject to almost continual wave action. The substratum of boulders and cobbles slopes abruptly, the 2 meter isobath occurring no more than 10 m from shore. Vegetation was absent here in both years save for an occasional sprig of Potamogeton richardsonii or Ceratophyllum demersum.

Gull Point (GP) is a spit of sand, cobbles and boulders that extends from the western shore. The sampling station was located on the 2 m isobath, north of the spit, 20 m from shore. Here the substratum has a very gentle slope and is composed almost entirely of sand and cobbles. Wave action is significant only with winds from the northeast quadrant. Vegetation was absent in both summers until late summer when a low mat of Chara sp. developed. Potamogeton richardsonii, Potamogeton patens and Vallisneria americana appeared in 1968 but were widely spaced and not consolidated into beds; none of these rooted macrophytes appeared in 1988.

A limnetic station (LIM) along the main axis of the lake was sampled regularly for comparison with the six littoral stations.

In summary, the three bay stations resemble each other; they are shallow, protected, densely vegetated and have thick deposits of silt and organic debris. In sharp contrast, the point stations are buffeted by waves, devoid of vegetation and have no organic deposits. The north station is intermediate in habitat structure between those in bays and on points. As in other lakes of this type, the general circulation in the epilimnion tends to minimize physical and chemical differences of the water in these several stations. In 1968, measurements were made and minor differences in temperature, dissolved oxygen, turbidity, pH and alkalinity did occur among all stations but tended to be transient, occurring mainly during periods of calm weather. These parameters do not appear to be important in determining the dispersion and abundance of cladocerans in the lake. Except for temperature, these parameters were not measured in 1988. The lake was thermally stratified by the end of May in 1988 but in both years, the lake was well stratified by June 10; epilimnion temperatures were 20-21°C. The water level was 1.74 m lower in 1968 than in 1988. There was a substantial difference in the Secchi disc depths between the 2 years. Occasional measurements during the summer of 1968 put the Secchi depth between 2.8 and 3.5 m. This is close to the summer average of 3.2 m reported by Bachmann and Jones (1974) for the period 1971 to 1973. In 1988, the June mean Secchi depth was 6.5 m and the July mean, 5.3 m. These high values are likely related to the lack of runoff during the dry spring and summer of 1988. Subjectively, the water was very clear and phytoplankton was not evident until mid-July.

METHODS

Since the littoral zone of Lake West Okoboji is a mosaic of habitats ranging from rocky points to vegetation-filled bays, the major problem was to devise a sampling method that could be used in all habitats. Unlike Pennak (1966), who wished to study only the "plankton" of the macrophyte zone but carefully avoid the plants in sampling or Goulden's (1971) study of the dynamics of benthic chydrid Cladocera, I wished to study the entire cladoceran assemblage, including both the planktonic forms and forms attached to plants. The method here described, to make comparisons among the existing types of littoral regions of West Okoboji, represents a compromise between rigorous replicate sampling and that of single, small samples.

All stations were sampled 13 times during 1968; eight times from mid-June to mid-August; three times from mid-August to mid-December; once in March through the ice; once in mid-April. In
1988, all stations were sampled 16 times; 12 times from mid-May to early-August and 4 more times between mid-August and late-November. All samples were obtained with a bolting-silk net (25 cm diameter, 0.88 um mesh size) towed obliquely from the bottom to the surface along a 6 m length. Three tows made up each sample which contained bottom materials as well as material dislodged from plants. The goal was to filter a large amount of water from the array of microhabitats typical of each station.

In Little Miller's Bay, Miller's Bay and Little Emerson's Bay, all samples were taken from dense weed beds with the boat swinging on its anchor. The three tows were never made along the same path. At the North station, samples were taken where the emergent vegetation was most dense. At Fort Dodge Point and Gull Point, where no emergent vegetation was present, samples were taken on the 2 m isobath at approximately the same place each sampling day. Samples from the Limnetic station consisted of three oblique tows in the upper 5 m. Since previous work in the limnetic zone of West Okoboji had shown that all species constituting the limnetic cladoceran assemblage were present within the upper 5 meters of the epilimnion (McDonald 1939; Cooke 1963; Lang 1966), this method provides a good estimate of the composition of the planktonic assemblage.

Each entire sample was preserved in 70% ethanol and concentrated to a final volume of 180 ml. Identification and counting of the species were done using a Sedgewick-Rafter cell; only cladocerans were counted. Counts of animals in the one milliliter aliquots from the stirred sample concentrate were accumulated until 100 animals had been identified. This was done three times. The relative abundance of species in the entire sample was calculated as the mean of the proportions in the three 100-animals draws. Total cladoceran abundance in the entire sample was expressed as the mean of the cladocerans in each one milliliter aliquot from the stirred sample. These means were converted to animals per cubic meter of sampled lake water.

**SPECIES LIST**

Thirty-two species of Cladocera appeared in the collections from 1968-69 and 1988. Many of them have been encountered in other studies and in this list, investigators previously reporting the species are named in parentheses. Species names* here follow the cladoceran taxonomies of Pennak (1989), Brooks (1957, 1959) and Goulden (1968).

*Echtonisico rosa* Lieven was collected in a preliminary sampling study in 1968 in Little Miller's Bay. It did not appear again in any of the routine samples in either year but is included here in the interest of completeness.

Seven species reported here are new records for Lake West Okoboji. In the list they are preceded by an asterisk.

**ORDER: Cladocera**

Suborder: Haplopodida Sars

Family: Leptodoridae Lilljeborg

Genus: Leptodora Lilljeborg 1860

1. *Leptodora kindtii* (Focke) 1844
   (= *Leptodora hyalina* of Ross 1895)
   (Stromsten 1920; McDonald 1939; Cooke 1963; Lang 1966, 1970)

Suborder: Eucladocera

Family: Sidae Baird

Genus: Diaphanosoma Fischer 1850

2. *Diaphanosoma bergei* Korinek

3. *Sida crystallina* (O.F. Muller) 1875
   (Stromsten 1917, 1920; Cooke 1963; Lang 1970)

Family: Daphniidae (Sars)

Genus: Daphnia O.F. Muller 1785

4. *Daphnia galeata* Sars 1864 mendobas Birge 1918
   (= *Daphnia hyalina* Leydig of Ross 1895 and Stromsten 1917; = *Daphnia longispina* var. *hyalina* Leydig 1860 of Birge and Juday 1920; = *Daphnia longispina* var. *hyalina* Leydig 1860 and *Daphnia longispina proper* (O.F. Muller) 1785 of Stromsten 1917, 1920 and McDonald 1939; Cooke 1963; Lang 1966, 1970)

5. *Daphnia reticulata* Forbes 1882
   (= *Daphnia kahlbergensis* var. *reticulata* of Ross 1895; = *Daphnia kahlbergiensis* of Ross 1895 and Stromsten 1917, 1920; = *Daphnia longispina* var. *hyalina* of McDonald 1939; Birge and Juday 1920; Cooke 1963; Lang 1966, 1970)

   (= *Daphnia pulex* var. *pulicaria* Forbes of Stromsten 1920; = *Daphnia pulex* of Birge and Juday 1920 and McDonald 1939; Cooke 1963; = *Daphnia shodleri* of Cooke 1965 and Lang 1966, 1970)

Genus: Sinocephalus Schodler 1858

7. *Sinocephalus crenatum* (Koch) 1841 (Lang 1966)

8. *Sinocephalus versatilis* (Koch) 1841
   (Ross 1895; Stromsten 1917, 1920; McDonald 1939; Cooke 1963; Lang 1966, 1970)

9. *Sinocephalus vietnami Schodler 1858*
   (Stromsten 1917, 1920; Lang 1970)

Genus: Ceriodaphnia Dana 1853

10. *Ceriodaphnia lacustris* Birge 1893
    (Ross 1895; Cooke 1963; Lang 1970)

11. *Ceriodaphnia pulchella* Sars 1862
    (Cooke 1963; Lang 1966, 1970)

Genus: Scapholeberis Schodler 1858

12. *Scapholeberis marmorata* (O.F. Muller)
    (Stromsten, 1917, 1920; = *Scapholeberis kingi* Sars of Lang 1966, 1970)

Family: Bosminidae Sars

Genus: Bosmina Baird 1845

13. *Bosmina longirostris* (O.F. Muller) 1785
    (Stromsten 1917, 1920; McDonald 1939; = *Bosmina coregoni* of Cooke 1963; Lang 1966, 1970)

Family: Chydoridae Stebbing

Genus: Eury cercus Baird 1843

    (= *Eury cercus lamellatus* (Muller, 1776) Ross 1895 and Lang 1966, 1970)

Genus: Camptocercus Baird 1843

15. *Camptocercus mucronatus* (O.F. Muller)
    (= *Camptocercus rectirostris* Schodler 1862 of Ross 1895, McDonald 1939, Cooke 1963, and Lang 1970)

Genus: Acroperus Baird 1843

16. *Acroperus harpae* Baird 1843
    (= *Acroperus angustatus* of Stromsten 1920; McDonald 1939; Cooke 1963; Lang 1966, 1970)

Genus: Oxyurella Dybowski and Grochowski 1894

17. *Oxyurella brevispina* sp. nov. Frey

Genus: Leydigia Kurz 1874

18. *Leydigia leydigii* (Schodler)
    (= *Leydigia quadrangularis* (Leydig) 1860 of Stromsten

*My thanks to Dr. Stanley I. Dodson, Department of Zoology, University of Wisconsin, and Dr. Allen Tessier, Kellogg Biological Station, Michigan State University for assistance in identifying the species of Daphnia.
addition, a short note taken from recent taxonomic works describing
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Suborder: Eucladocera
Genus: Alona Baird 1850
19. Alona costata Sars 1862
   (Cooke 1963; Lang 1966, 1970)
20. Alona guttata Sars 1862
   (Lang 1970)
21. Alona quadrangularis (Leydig) 1860
   (Stromsten 1920; McDonald 1939; Lang 1970)
*22. Biaepiturna affinisi (Leydig)
*23. Alona rustica Scott
Genus: Graptoleberis Sars 1863
24. Graptoleberis testudinaria (Fischer) 1848
   (Stromsten 1920; Lang 1970)
Genus: Pleuroxus Baird 1843
25. Pleuroxus denticulatus Birge 1878
   (Ross 1895; Stromsten 1917, 1920; Cooke 1963; Lang
   1966, 1970)
26. Pleuroxus procursus Birge 1878
   (Stromsten 1920; = Pleuroxus procursus Birge 1878 of
   Stromsten 1917 and Lang 1970)
Genus: Chydorus Leach 1843
*27. Chydorus gibbus Lillieborg 1880
28. Pseudechydorus globoetus (Baird)
   (= Chydorus globoetus of Ross 1895, Stromsten 1920,
29. Chydorus sphaericus (O.F. Muller) 1785
   (Ross 1895; Stromsten 1920; McDonald 1939; Cooke
   1963; Lang 1966, 1970)
Genus: Alanopsis Sars 1862
*30. Alanopsis americana Kubensky
Family: Macrothricidae Norman and Brady
Genus: Macrothrix Baird 1843
*31. Echinisco hastatus Lieven
Genus: Ilyocryptus Sars 1861
*32. Ilyocryptus sordidus (Lievel) 1848

ADDITIONAL SPECIES REPORTED
The 7 species that follow appear in the lists of Stromsten (1917,
1920) and McDonald (1939). Three of these are accompanied by
specific notations that places them in Lake West Okoboji; these are
preceded by an asterisk in the list. The remaining 4 species appear
because the collection notes indicate a general kind of habitat that
does not exclude West Okoboji, e.g. "lakes". Following the name,
investigators reporting the species are given in parentheses. In
addition, a short note taken from recent taxonomic works describing
the distribution and/or habitat accompanies each species.
ORDER: Eucladocera
Suborder: Eucladocera
Family: Sididae Baird
Genus: Pseudosida Herrick 1884
1. Pseudosida blandae Herrick 1884
   (Stromsten 1920)
   Generally restricted to southern U.S. (Brooks 1959)
*2. Latanopsis occidentalis Birge 1891
   (Stromsten 1920; McDonald 1939)
   New England to Colorado and Texas (Brooks 1959)
Genus: Daphnia O.F. Muller 1785
*3. Daphnia longiremis Sars 1861
   (Stromsten 1920)
   Northern N.A. south to southern U.S. Confined to hy-
   polimnion of lakes during stratification (Brooks 1959).
   Stromsten (1920) collected this species in deep rows in
   Lake West Okoboji.

Family: Moinidae Goulden 1968
Genus: Moina Baird 1850
4. Moina micrura Kurz 1874
   (= Moina brevicollis (Jurine) 1820 of Stromsten 1920)
   The most ubiquitous and probably the most variable of all
   species of Moina (Goulden 1968)
Family: Macrothricidae Norman and Brady
Genus: Macrothrix Baird 1843
5. Macrothrix laevis Sars
   (= Pleuroxus stramineus Birge of Stromsten 1918; of
   Stromsten 1920)
   Widely distributed, but nowhere very abundant (Brooks
   1959)
Family: Chydoridae
Genus: Kurzia Dybowski and Grochowski 1894
6. Kurzia latissima Kurz 1894
   (Stromsten 1920)
   Found in all regions of the continent among weeds in
   pools or lakes (Brooks 1959)
Genus: Pleuroxus Baird 1843
*7. Pleuroxus laevis Sars
   (= Pleuroxus stramineus Birge of Stromsten 1917;
   = Pleuroxus haitius Sars 1862 of Stromsten 1920)
   Common everywhere in vegetation (Pennak 1989).

This potential list of 7 species includes 5 species which have wide
distributions and if not present now could occur in the assemblage in
the future. One species, Daphnia longiremis, is especially worthy of
note. Though not present now, it may serve as an indicator of
ecological change in the lake since 1920. It was last reported from
deep tows made by Stromsten (1920) in the same year Birge and
Juday (1920) made a limnological study of Lake West Okoboji. At
the end of July, 1919, the thermocline stood at 12 meters and the
hypolimnion still retained measurable dissolved oxygen, e.g. 2.5
ppm at 20 m and 1.3 ppm at 30 m (Birge and Juday 1920). From my
own data of the first week in August, 1968, with the thermocline at
15 m, dissolved oxygen was 0.3 ppm at 20 m and undetectable at 30
m. Even though the water column was distinctly warmer in 1968 and
one would expect lower levels of dissolved oxygen, the percent
saturation values were also considerably lower, e.g. 3% compared to
23% in 1919 at 20 meters and 0% compared to 12% in 1919 at 30
m. This suggests that respiration in the hypolimnion had increased
over the interval of 39 years with longer and more intense periods of
anoxic conditions over a wider range of strata. Bachmann and Jones
(1974) attributed this decline in oxygen in the hypolimnion from the
period 1919 to 1928 to the period 1950 to 1973, to a 50% increase in
the yearly deposit of organic matter. Since Daphnia longiremis retreats
into the hypolimnion during warmer months in the extreme southern
part of its range, the increasingly anoxic conditions probably elimi-
nated the species shortly after 1920. McDonald (1939) did not report
collecting this species even though he collected at many depths over a
two-month period.

My assessment of this additional list is that most of these species
are not part of the present West Okoboji assemblage. However, some
may be present in very low densities and become evident only
occasionally when conditions are favorable.

THE CLADOCERAN ASSEMBLAGE, 1968 AND 1988
Rank orders of the stations in 1968 and 1988 in terms of seasonal
abundance are shown in Table 1. Rankings reflect the proportions of
total yearly samples in which the total cladoceran density at each
station ranked 1st, 2nd or 3rd among the seven stations. Where the
percentages for two stations are the same, position in the table was
decided by the number of times the cladoceran abundance at each
station was ranked 1st.
Table 1. Ranking of Station Habitats by Cladoceran Abundance

<table>
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<th>Rank</th>
<th>Station</th>
<th>1968 %</th>
<th>Station</th>
<th>1988</th>
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<td>1</td>
<td>MB</td>
<td>30</td>
<td>MB</td>
<td>26</td>
</tr>
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<td>9</td>
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<tr>
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<td>6</td>
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<td>FDP</td>
<td>0</td>
<td>GP</td>
<td>4</td>
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</table>

a- MB = Miller's Bay
LMB = Little Miller's Bay
LEB = Little Emerson's Bay
LIM = Limnetic
GP = Gulf Point
NOR = North Station
FDP = Fort Dodge Point

b- % = Proportion of sampling dates cladoceran density at the station ranked 1st, 2nd or 3rd in abundance among the seven stations.

Rank orders of the assemblages in Miller's Bay, Little Miller's Bay, Little Emerson's Bay and the Limnetic were the same in the two years. Rank orders of assemblages at Gull Point, Fort Dodge Point and the North station differed in the two years. The principal difference observed was that the assemblage densities at the North station and the Limnetic were generally higher more of the time in 1988 than 1968.

Table 2 summarizes the abundance categories and distributions of the 32 West Okoboji Cladocera among the three habitat types considered in these studies. The bays are considered to be weed beds, and points, together with the northern station, as open littoral. For each species there are three pairs of observations comparing distribution and abundance for the two years, a total of 96 pairs of observations for the 32 species.

In general, there is a good match between the two years. Twenty-five of the possible 96 pairs are identical when the species are present both years. If observations where species are absent in both years are included there is an exact match in 56 of the 96 pairs. Since rarity seems to be the rule for nearly half of the West Okoboji cladocerans, the 9 species which were found in only one or two of the habitats in one year are likely to still be in the lake. Adding these to the number of matches makes the total 63 of 96, nearly two thirds. Considering that the rest of the observations are different only in estimate of abundance, I find the degree of similarity to be remarkable.

With regard to the distribution pattern, 8 species were found in all three habitat types, none of them are considered rare and 4 of these are typically limnetic species. Thirty species were found in 2 habitat types; only 4 of these are considered rare. And 11 were found in only 1 habitat type; all but two of these are considered rare. While it is tempting to associate rarity with habitat specificity, the year to year uncertainty of finding them at all suggests it is more parsimonious to infer that if one would take more samples the rare species would be found in more places.

Twelve species were the most abundant forms somewhere in the lake at some season of the year (Table 3). The same species were the abundant forms in both years; there were no surprises. Each specific habitat studied had a unique assemblage and a unique shift of abundance in each year, but three persistent patterns can be seen.

1) In the bays and the northern station, the littoral species are the predominant forms from June to the end of October; the 1968 assemblage at the northern station was an exception where limnetic species were predominant after July. In both years, Chydorus sphaericus was the predominant species through July and Bosmina longirostris and Ceriodaphnia pulchella were predominant through September. In the bays, Chydorus sphaericus became abundant again in October.

2) Except for a brief period in early summer limnetic forms are the predominant species in the habitats of Gull and Fort Dodge Points. The assemblages in both years were predominate by Daphnia pulsata until mid-July, by Diaphanosoma bergii

Table 2. Distribution and Abundance of Lake West Okoboji Cladocera

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<td>C A - C -</td>
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<tr>
<td>S. obtusus</td>
<td>A A - C -</td>
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<tr>
<td>Ceriodaphnia pulchella</td>
<td>R R - R R</td>
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<tr>
<td>Sida crassicornis</td>
<td>C C - R -</td>
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</tr>
<tr>
<td>Saphothele macronota</td>
<td>C - C - R</td>
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<tr>
<td>Bosmina longirostris</td>
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<tr>
<td>Eurytemora affinis</td>
<td>A C C A A -</td>
<td></td>
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<tr>
<td>Camptocerus megarus</td>
<td>A C C C -</td>
<td></td>
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<tr>
<td>Alona americana</td>
<td>- - - R</td>
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</tr>
<tr>
<td>Alona costata</td>
<td>- C A R</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Alona guttata</td>
<td>- R R - R</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Alona quadangularis</td>
<td>- R C R - R</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaphanosoma bergii</td>
<td>- - - - -</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Pleuronema gibbonis</td>
<td>R R R R R</td>
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</tr>
<tr>
<td>Chydorus sphaericus</td>
<td>A A A R R</td>
<td></td>
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<tr>
<td>Ilyocypris sp.</td>
<td>- R - - R</td>
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<tr>
<td>Echinodorus rosea</td>
<td>R - - - -</td>
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</tbody>
</table>

- Limnetic is defined here as the region of open water generally beyond the five-meter contour. Open littoral is that region inside the five-meter contour, often supporting rooted, emergent vegetation, but if present, the vegetation is not concentrated into beds; Weed beds are generally found inside the three-meter contour and usually associated with protected embayments such as Little Millers and Litter Emerson's Bays; vegetation is generally very dense and any open water occurs as small 'holes' in the weed bed, usually one to two meters wide.

a Abundant - Found in relatively large numbers in almost all samples or in large numbers in a few samples.
b = Common - Found in relatively small numbers in many to almost all samples.
c = Rare - Found in very small numbers in only one to a few samples.
Table 3. Predominant Cladocerans by Station and Season.

<table>
<thead>
<tr>
<th>Station</th>
<th>Year</th>
<th>Mid-May</th>
<th>Early-June</th>
<th>Mid-June</th>
<th>Early-July</th>
<th>Mid-July</th>
<th>Early-August</th>
<th>Mid-August</th>
<th>Early-Sept</th>
<th>Late-October</th>
<th>Late-Nov</th>
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<tbody>
<tr>
<td>LMB*</td>
<td>1968</td>
<td>-</td>
<td>-</td>
<td>Chyb</td>
<td>Chy</td>
<td>Chy</td>
<td>Cerio</td>
<td>Bos</td>
<td>Cerio</td>
<td>Chy</td>
<td>Chyb</td>
</tr>
<tr>
<td>MB</td>
<td>1988</td>
<td>D. pul</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Cerio</td>
<td>Bos</td>
<td>Bos</td>
<td>D. gal</td>
<td>Chy</td>
</tr>
<tr>
<td>LEB</td>
<td>1968</td>
<td>-</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Bos</td>
<td>Bos</td>
<td>Bos</td>
<td>Chy</td>
<td>D. gal</td>
</tr>
<tr>
<td>NOR</td>
<td>1988</td>
<td>D. pul</td>
<td>Chy</td>
<td>Pleur</td>
<td>Bos</td>
<td>Bos</td>
<td>Bos</td>
<td>Bos</td>
<td>Chy</td>
<td>D. gal</td>
<td>Chyb</td>
</tr>
<tr>
<td>GP</td>
<td>1988</td>
<td>D. pul</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Chy</td>
<td>Cerio</td>
<td>Acrop</td>
<td>Diaph</td>
<td>Diaph</td>
<td>D. gal</td>
</tr>
<tr>
<td>FDP</td>
<td>1968</td>
<td>-</td>
<td>Chy</td>
<td>D. pul</td>
<td>D. pul</td>
<td>Diaph</td>
<td>Diaph</td>
<td>Diaph</td>
<td>Diaph</td>
<td>D. gal</td>
<td>Diaph</td>
</tr>
<tr>
<td>LIM</td>
<td>1988</td>
<td>D. pul</td>
<td>D. pul</td>
<td>D. pul</td>
<td>D. pul</td>
<td>Diaph</td>
<td>Diaph</td>
<td>Diaph</td>
<td>Diaph</td>
<td>Diaph</td>
<td>D. gal</td>
</tr>
</tbody>
</table>

1) Through July, bays in 1988 had more species than in 1968 (Figures 2a,b,c). 2) Points in 1988 had few species (Figure 2e,f). 3) The limnetic had fewer species throughout the summer in 1988 than in 1968 (Figure 2g). A 4th, and easily the greatest difference observed in the cladoceran assemblages between the two years was in the large predominance of Daphnia pulicaria in the limnetic through mid-July in 1988 (Figure 4a,b). In most other ways, the temporal patterns of species abundance in the 2 limnetic assemblages were identical. In both years:

1) Daphnia pulicaria was predominant into late July. During June, intestines of these animals were mostly half-filled and few mature females carried more than one egg.
2) Diaphanosoma bergii became the predominant species in early August.
3) Daphnia galeata mendotae become the predominant species in October.
4) The changes in the predominant species occurred in almost precisely the same weeks.

During 1968, Daphnia galeata mendotae and Daphnia retrocurva were significant components of the limnetic assemblage throughout the summer; in 1988, they became abundant only in the fall.

DISCUSSION

There is reason to be cautious when making comparisons of species assemblage characteristics in consecutive years and when the years of interest are 20 years apart caution is no less valid. Year to year variation in presence and absence and abundance of species comprising assemblages will reflect fluctuating conditions within the lake and certainly stochastic properties inherent in the population dynamics of the member species. Unless dramatic alterations have occurred in the lake environment, assemblage differences 20 years apart may reflect only natural variation expected from year to year in a rather stable state. There is ample evidence that the limnological conditions of Lake West Okoboji have changed little in recent years (Bachmann 1987) and compelling evidence that, as a habitat, the lake has...
stabilized or even recovered from the earlier, rapid rate of eutrophication (Bovbjerg, et al. 1982). Findings reported here suggest the cladoceran fauna is also stable.

The current species list contains no new species that are at all abundant. Additions and omissions since 1968 are almost certainly the result of minor booms and busts of species that are always in low abundance; their appearance or disappearance from such lists is more a function of sampling intensity than colonization and extinction.

Fig. 2. Monthly means of the number of cladoceran species collected at the 7 sampling stations in 1968 and 1988. No samples were taken in May 1968.

Fig. 3. Monthly means of the number of cladocerans per cubic meter at the 7 sampling stations in 1968 and 1988. No samples were taken in May 1968.
Occasionally a species such as *Daphnia longiremis* disappears from a list when environmental conditions are no longer supportive. Mostly, though, we know little of the specific requirements of these species and cannot associate changes in the list with specific environmental change.

One of the goals of the original study (Lang 1970) was to assess the richness of cladoceran fauna relative to the considerable environmental heterogeneity of Lake West Okoboji. Twenty-four species were reported then. Eight additional species are reported here. I suggest that the 32 species now listed is a comparatively rich fauna for a single lake. Records for single lakes where the sampling intensity is similar to the present study are few. Regional studies, while more likely to include animals from a variety of habitats, are difficult to compare directly with West Okoboji because the results from the individual lakes are seldom reported. For example, Brandlova, et al. (1972), list 70 species from 244 lakes and 33 ponds in Ontario. My intuitive sense is that, judged against this total regional list, the diversity of the Okoboji Cladocera (32 species) is quite high for a single lake. However, they report no results for single lakes. The same is true for Smyly (1958), who lists 53 species from 144 tarns in the English lake district.

But perhaps we lose sight of the important effect of the environmental mosaic when we simply compare lakes or regions. Anderson (1971) lists only 17 Cladocera from 146 alpine and subalpine lakes and ponds in western Canada. Except for a few at the lower elevations, these small lakes lack rooted vegetation. This lack of heterogeneity, in addition to limiting conditions of high elevations and perhaps low accessibility, must contribute to the lower diversity.

While it is tempting to associate diverse assemblages of cladocerans with rooted vegetation and the resulting three-dimensional heterogeneity, Lewis and Clarke Lake, a reservoir with virtually no rooted vegetation, in southeastern South Dakota, supports 22 species of Cladocera (15 of them littoral forms) (Tash, et al. 1966). Quiet, stable areas along the sides of what must be considered a slow-moving river are apparently enough to allow many species to utilize the heterogeneity that is offered by the benthos.

However, when stability and the three-dimensional heterogeneity of large weed beds are present, as in Lake West Okoboji, the supportive conditions are in place for a high diversity of cladocerans. Whiteside, et al (1974, 1978), sampling littoral areas in Lake Itasca and Elk Lake that are carpeted with *Chara* and rooted vegetation, found 23 species of chydorid Cladocera in each lake. There are 17 species of chydorids in West Okoboji. Had he added net samples to his repertoire of sampling methods he could have added several, more-planktonic species of other cladoceran families. In any case, these Minnesota lakes and Lake West Okoboji compare favorably in the richness of their cladoceran fauna.

The weekly ranking of cladoceran abundance at the seven sampling stations remained mostly unchanged in 20 years. The abundance of animals in the protected bays remained high and the rank order little different. The limnetic assemblage retained its intermediate position. The assemblages exposed to, and yet a product of, the habitat instability of the points and the northern station, remained low in abundance but were shuffled relative to one another. These latter assemblages are missing the stabilizing effect of rooted vegetation; their positions along the axis of the lake exposes them to changing currents that bring species together as an assemblage of drifters (Lang 1970).

The distribution and seasonal abundance patterns of the species among the seven sampling stations have also changed little in 20 years. I judge that the majority of the differences represent a degree of variation one could expect in yearly comparisons.

The higher numbers of species in the bays through August in 1988, results, I believe, from the early warming of the lake compared to 1868. In 1988, bay temperatures in the last week of May were the same as they were in the middle of June in 1968. As a correlate, the rooted vegetation in the bays in 1988, was nearly a meter high at the beginning of June, a height reached only in the middle of July in 1968.

The number of species in the assemblages at the points and in the limnetic were lower in 1988 through early summer. A correlate here is that after a windy May, the summer of 1988 was mostly calm compared to a relatively windy summer in 1968. Without the transport of animals caused by wind induced currents, the assemblages of the points and limnetic, far removed from the weed beds, did not receive representatives of the littoral fauna in large enough numbers to show up in the samples.

Easily the greatest difference observed in the cladoceran assemblages of the two years is in the large predominance of *Daphnia pulicaria* in the limnetic in 1988. The difference is striking. Low egg production and empty intestines coincident with exceptionally deep Secchi disc depths suggest a food-limited population; only in July with Seechi disc depths near 4 m and noticeable algal phytoplankton did the intestines appear full again and egg production increase. My inference is that *Daphnia pulicaria*, the early dominant in both years, entered the limnetic when early algal production had begun. Because the early stratification restricted nutrient availability that was already low because of the dry spring, the algal production was minimal and was largely grazed by the *Daphnia pulicaria*. If the assemblage as a whole was limited, then *Diaphanosoma bergei* was restricted and remained so until *Daphnia pulicaria* declined in early August. Similarly, *Daphnia galeata mendotae* and *Daphnia retrocurva* were restricted until *Diaphanosoma bergei* declined in October. It is tempting to evoke competition to explain the progression of predominant species; 1968 differs only in the abruptness of the changes in species predominance. Perhaps the observations in 1988 lend some weight to the inference. This limnetic assemblage should be studied quantitatively during the next years. If, indeed, the productivity is
being affected by the dry years, baseline data on the dynamics of these four species relative to food under limiting conditions could be established in preparation for a subsequent return to more productive conditions.

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But special and profound thanks go to Professor Richard V. Bovbjerg, valued friend, gifted scientist and teacher, who squirted some plankton in a dish under my microscope and changed my life forever.

REFERENCES


