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# Littoral and limnetic zooplankton communities in Lake Mead, Nevada-Arizona, USA

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*Key words:* littoral, limnetic, species richness, zooplankton abundance, phytoplankton biomass, fish abundance

## Abstract

Zooplankton were collected from adjacent littoral and limnetic sites in Lake Mead, Nevada-Arizona, USA. Limnetic species dominated both littoral and limnetic zooplankton communities; littoral species rarely exceeded 2% of monthly total zooplankton densities. Low species richness of littoral taxa and high similarity in species composition between littoral and limnetic habitats appeared to result from uniform horizontal physical and chemical environments, due to horizontal mixing, and from the absence aquatic macrophytes.

Significant differences in spatial distribution occurred in phytoplankton biomass, total zooplankton density, and fish abundances; highest concentrations of these factors occurred nearest an inflow high in nutrients and progressively declined farther below the inflow. These factors generally showed no significant difference between adjacent littoral and limnetic sites. Large variation also occurred in seasonal zooplankton community structure among some sites.

## Introduction

Zooplankton are typically considered either littoral or limnetic (Edmondson, 1959; Hutchinson, 1967; Wetzel, 1983; Pennak, 1978). Limnetic communities are frequently dominated by cladocerans, copepods, and rotifers (Pennak, 1957, 1978; Hutchinson, 1967). Particular cladocerans (Smyly, 1952; Straskraba, 1964; Lemly & Dimmick, 1982a) and rotifers (Pennak, 1966) generally dominate littoral habitats where macrophytes are present. Calanoid copepods are less abundant among vegetation and Gerhs (1974) suggested that secretions or physical effects of *Potamogeten* inhibit survival and reproduction of *Diaptomus clavipes*. Straskraba (1964) and Pennak (1966) found that cyclopoid copepods generally occurred in low abundance in weedbeds. However, Cryer & Townsend (1988) found cyclopoid copepods had greater concentrations in littoral areas than in limnetic areas. The density of aquatic vegetation largely determines the diversity and abundance of littoral zooplankton (Straskraba, 1964; Pennak, 1966; Lemly & Dim-

mick, 1982a). Common littoral species are usually poorly represented in littoral areas lacking vegetation and in such areas species composition and abundances resemble that of adjacent limnetic areas (Smyly, 1952; Smirnov, 1963; Straskraba, 1964; Stolbunova & Stolbunov, 1981; Lemly & Dimmick, 1982a, b).

Variability in zooplankton horizontal distribution, however, may be greatly influenced by environmental conditions other than aquatic vegetation. Meyer (1984) reported equal numbers of *Daphnia pulex* in the limnetic zone and the littoral-limnetic interface during times of unlimited food availability. When phytoplankton became scarce, it was found grazing predominantly in outer margins of the littoral zone. *Chydorus sphaericus* followed a similar pattern, but ranged farther into the vegetation zone when food was scarce.

Advection by wind can concentrate plankton in down-wind areas along lake edges (George & Edwards, 1976). Hart (1976) noted that copepodite and adult *Pseudodiaptomus hessei* were benthic during the day and were generally undisturbed by wind-induced surface currents. During their migration upward at night, *P. hessei* was dispersed down-wind by surface currents. Naupliar stages that always lived near the surface were influenced by wind activated surface currents during the night and by slightly deeper counter currents during the day (Hart, 1976).

Effects of fish predation also can influence the distribution of zooplankton (Jakobsen & Johnsen, 1987; Cryer & Townsend, 1988). Cryer & Townsend (1988) found that limnetically associated taxa abundantly occupied the lake periphery as a result of large numbers of fish and the ability of fish to feed more efficiently in openwater than in stands of vegetation. During years having fewer fish, zooplankton showed a greater limnetic distribution (Cryer & Townsend, 1988). Siebeck (1980) suggested that limnetic species which become horizontally disoriented and wander inshore migrate back offshore during the day by optically distinguishing differences in light intensities between openwater and shoreline areas.

The objective of our study was to examine rotifer and microcrustacean zooplankton communities in littoral and limnetic areas of Lake Mead, Nevada and Arizona, a large desert impoundment with a littoral zone that is sparsely vegetated. We also discuss possible influences of physical and chemical limnological conditions, relative phytoplankton biomass, and relative fish abundance on zooplankton horizontal distribution and seasonal dynamics.

## Study sites

Lake Mead, bordering Nevada and Arizona, USA, is a major reservoir along the Colorado River. It has a surface area of about 66096 ha, maximum depth of about 180 m, and mean depth of approximately 55 m (Hoffman & Jonez, 1973). Zooplankton were collected from five stations in three areas in the lower basin (Fig. 1). Samples were collected at inner Las Vegas Bay (ILVB), a site consisting of only littoral zone. ILVB had no close limnetic, similarly fertile habitat. Limnetic samples at middle Las Vegas Bay (MLVB) were collected mid-channel at a depth of approximately 40 m and littoral samples were collected in an adjacent nearby cove. Samples were collected at the offshore site at Boulder Basin (BB) having a depth of over 100 m and the adjacent littoral sampling station was located in a large cove on Saddle Island.

Aquatic macrophytes occurred sparsely throughout the reservoir (Haley *et al.*, 1987). In particular, ILVB was depauperate of rooted aquatic vegetation and in MLVB vegetation was very sparse and generally located less than 2 m deep (Haley *et al.*, 1987). Water clarity was greatest in Boulder Basin (summer Secchi depth ranged from 6 to 7 m) and no macrophytes were seen in the littoral area. Because very little vegetation existed in Lake Mead, and the distribution of rooted aquatic vegetation determines the extent of littoral zone (Wetzel, 1983), we identified the littoral zone as the area from shore to a depth of 10 m. Only about 11% of the total surface area of the lower basin then is considered as littoral zone.

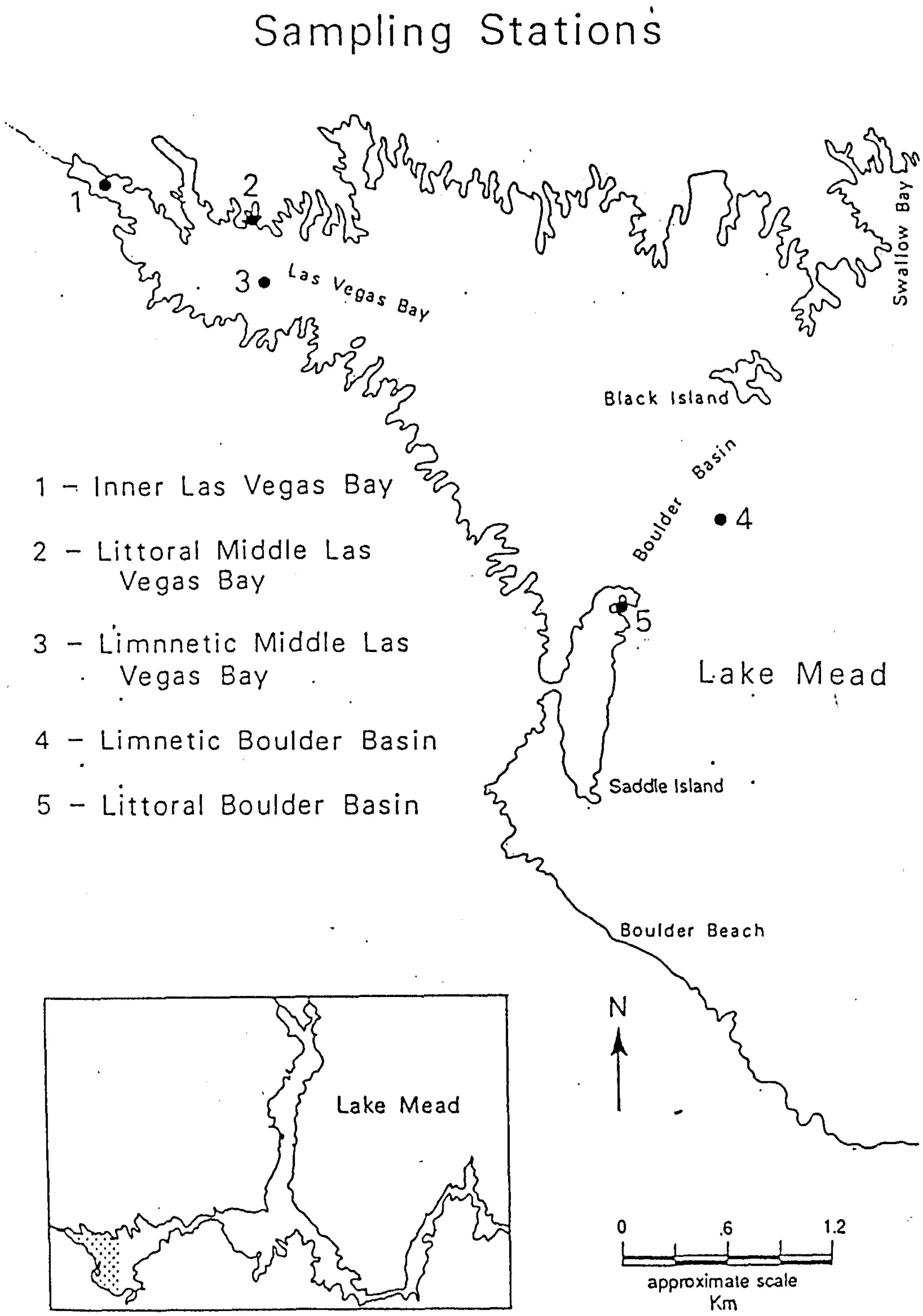


*Fig. 1.* Map of Lake Mead showing littoral and limnetic sampling stations in the lower basin.

## Methods

Littoral and limnetic zooplankton communities were collected at 1, 3, 5, 7, and 10 m. Littoral samples were collected where bottom depth was 10 m. Samples were collected using a pump sampler with a clearance rate of 20 l $min^{-1}$. One end of a hose (1.6 cm inner diameter) was attached to the pump and the opposite end had a double plexiglas plate with a 2.5 cm gap to collect an even draw of water. Twenty liters of water were filtered through an 80 $\mu$m mesh plankton net and zooplankton were preserved in 4% formalin-sucrose solution. Before samples from succeeding depths were collected, the first 20 l of water were discarded to flush the hose of organisms from the previous depth. Samples were collected monthly from July 1984 to June 1985 and between 0800 and 1300 hrs. Entire contents of each sample were counted except for particularly dense samples, where three separate 1 ml subsamples were counted and an average count was taken. Zooplankton communities were compared from water column averages (0 to 10 m).

Chlorophyll fluorescence was measured for each sample using a Turner Designs flow-through fluorometer to estimate relative phytoplankton biomass (see Heaney, 1978). Water temperature, dissolved oxygen, conductivity, and pH were measured with a Hydrolab Model 8000 Water Quality Analyser at each sampling depth. A Furuno Model FM-22A echolocator was used to record fish at each station. Echolocation transects of at least 500 m were run from adjacent limnetic to littoral sites at a constant boat velocity of about 8 km $h^{-1}$. Relative abundance of fish was then estimated from echograms following the procedure of Wilde & Paulson (1989) by scoring from 1 (no fish) to 5 (maximum relative fish abundance).

Friedman two-way ANOVA by ranked blocks (Zar, 1974) was used to evaluate monthly spatial differences among physical and chemical parameters, relative phytoplankton fluorescence, relative fish abundance, and zooplankton densities. Newman-Kuels multiple range test using standard errors appropriate for ranked blocks were used to compare conditions between adjacent littoral and limnetic sampling sites. Relationships of zooplankton density with limnological parameters, relative phytoplankton fluorescence, and relative fish abundance were determined using Spearmans rank correlation. A Sorensen Similarity Index was used to determine percent similarity in species composition among stations.

## Results

### *Physical and chemical conditions*

Average (0 to 10 m) temperature, dissolved oxygen, and pH showed no spatial heterogeneity ($P > 0.05$ for each parameter). Thermal stratification developed during summer with the thermocline between 7 and 12 m. Summer epilimnetic temperature averaged 25.2C $\pm$ 0.7 (SD) and pH averaged 7.9 $\pm$ 0.4 (SD). Dissolved oxygen averaged 8.9 mg $l^{-1}$ $\pm$ 0.9 (SD) and at no time did the upper 10 m become anoxic at any station. Almost complete vertical mixing occurred during winter. Temperature (0–10 m) averaged 12.9C $\pm$ 0.7 (SD) and dissolved oxygen and pH averaged 9.2 mg $l^{-1}$ $\pm$ 0.7 (SD) and 7.7 $\pm$ 0.3 (SD), respectively.

Conductivity, however, varied significantly among stations ($P < 0.001$). ILVB had the highest summer conductivity averaging 1275 $\mu$mhos $cm^{-1}$ $\pm$ 79 (SD). Littoral and limnetic MLVB stations, however, showed no statistical difference ($P > 0.20$) and summer values averaged 1043 $\mu$mhos $cm^{-1}$ $\pm$ 64 (SD). Conductivity was uniform between littoral and limnetic BB sites ($P > 0.50$) and during summer averaged 985 $\mu$mhos $cm^{-1}$ $\pm$ 71 (SD). During winter, conductivity was low at all sites and averaged 906 $\mu$mhos $cm^{-1}$ $\pm$ 44 (SD).

### *Relative phytoplankton biomass and fish abundance*

Phytoplankton fluorescence showed significant variation among sites ($P < 0.001$). Fluorescence was highest at ILVB and progressively declined

at MLVB sites and BB sites. However, adjacent littoral and limnetic sites at MLVB ($P>0.20$) and at BB ($P>0.20$) sites had similar values. Seasonal fluorescence varied with maxima occurring during late spring and summer (Table 1).

Relative fish abundance also showed significant spatial differences ($P<0.001$). Adjacent littoral and limnetic MLVB ($P>0.20$) and BB ($P>0.50$) sites showed no difference. Fish were more abundant at ILVB and progressively declined at MLVB stations and BB stations (Table 2).

*Zooplankton species composition*

A diverse zooplankton community existed in Lake Mead. Species richness was greater for limnetic associated taxa (27 species) (Edmondson, 1959; Pennak, 1978) than littoral associated taxa (15 species). Littoral species comprised 2% or less of the total zooplankton density and occurred in about equal abundance between adjacent littoral and limnetic sites. Only during June did littoral zooplankton, primarily the rotifer *Trichocerca cylindrica*, increase; littoral taxa accounted for 40% of the total zooplankton density at ILVB and 10% and 11% at limnetic and littoral MLVB, respectively. No littoral species were found at BB sites during June.

Species composition generally was similar among all littoral and limnetic sites (Table 3). The most common were the copepods *Diacyclops bicuspidatus thomasi*, *Diaptomus ashlandi*, and *Mesocyclops edax*; the cladocerans *Bosmina longirostris*, *Daphnia galeata mendotae*, and *D. pulex*; and the rotifers *Polyarthra* and *Synchaeta*.

*Table 1.* Relative phytoplankton fluorescence among littoral and limnetic sampling stations in Lake Mead. Values are actual fluorescence measurements in arbitrary units.

| Month | ILVB | Litt MLVB | Limn MLVB | Litt BB | Limn BB |
|---|---|---|---|---|---|
| Jul. | 34.2 | 8.0 | 5.0 | 0.5 | 0.7 |
| Sept. | 2.2 | 0.8 | 0.7 | 0.6 | 0.8 |
| Nov. | 0.9 | 1.1 | 1.0 | 0.9 | 1.0 |
| Dec. | 1.0 | 0.8 | 0.8 | 0.6 | 0.7 |
| Jan. | 0.9 | 0.8 | 0.7 | 0.7 | 0.8 |
| Feb. | 1.1 | 0.8 | 0.6 | 0.5 | 0.8 |
| Mar. | 3.0 | 1.2 | 1.0 | 0.8 | 0.7 |
| Apr. | 1.7 | 1.0 | 0.7 | 0.6 | 0.6 |
| May | 4.0 | 2.8 | 3.4 | 3.1 | 2.4 |
| Jun. | – | 1.9 | 3.0 | 0.8 | 1.7 |

*Table 2.* Relative fish abundance among littoral and limnetic sampling stations in Lake Mead. A one indicates no fish present and a 5 indicates the maximum relative abundance of fish recorded.

| Month | ILVB | Litt MLVB | Limn MLVB | Litt BB | Limn BB |
|---|---|---|---|---|---|
| Jul. | 4 | 4 | 5 | 2 | 2 |
| Aug. | 4 | 3 | 3 | 3 | 2 |
| Sept. | 4 | 3 | 2 | 2 | 2 |
| Oct. | 3 | 3 | 3 | 2 | 2 |
| Nov. | 5 | 3 | 1 | 2 | 2 |
| Dec. | 5 | 2 | 1 | 2 | 2 |
| Jan. | 5 | 2 | 2 | 2 | 2 |
| Feb. | 4 | 3 | 2 | 2 | 2 |
| Mar. | 4 | 2 | 3 | 2 | 2 |
| Apr. | 5 | 3 | 3 | 2 | 1 |
| May | 5 | 3 | 3 | 3 | 2 |
| Jun. | – | 3 | 3 | 3 | 2 |

*Zooplankton abundance*

Total average zooplankton densities throughout the water column are presented in Fig. 2. Seasonal patterns were, for the most part, similar between littoral and limnetic stations; peaks occurred during autumn and late winter and de-

*Table 3.* Sorensen Similarity Index showing the percent similarity in species composition among littoral and limnetic sampling stations in Lake Mead.

| | ILVB | Limn MLVB | Litt MLVB | Limn BB | Litt BB |
|---|---|---|---|---|---|
| ILVB | 100 | 73 | 85 | 86 | 79 |
| Limn MLVB | | 100 | 78 | 79 | 79 |
| Litt MLVB | | | 100 | 78 | 81 |
| Limn BB | | | | 100 | 87 |
| Litt BB | | | | | 100 |

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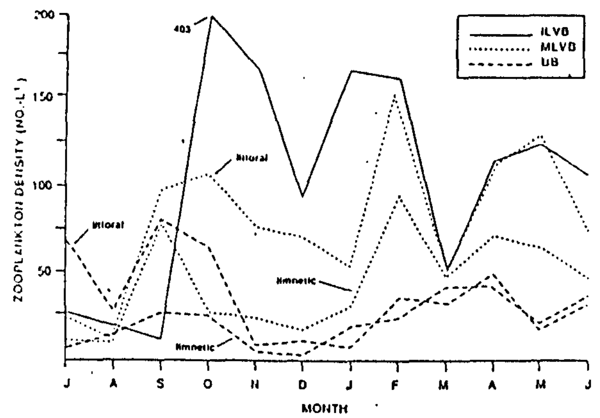


*Fig. 2.* Monthly total weighted-average zooplankton density among littoral and limnetic sampling stations in Lake Mead.

clined in late spring and summer. Densities were greatest at ILVB. Adjacent littoral and limnetic MLVB stations significantly differed ($P < 0.05$) in total zooplankton density, however, both BB sites had a similar total zooplankton density ($P > 0.20$).

Table 3 shows results from Spearmans correlation of zooplankton species with biological, physical, and chemical factors. Few species correlated with phytoplankton fluorescence and fish abundance, however, more species significantly correlated with physical and chemical factors.

Most species showed significant differences in density among sampling stations ($P < 0.05$). Rotifers (mainly *Synchaeta* spp., *Polyarthra* spp., and, at times, *T. cylindrica*) accounted for a large portion of the zooplankton community during late summer and autumn at ILVB (Fig. 3). Rotifers were far less important at MLVB and BB and reached similar community dominance in adjacent littoral and limnetic sites. Copepods (mainly nauplii, copepodites, and to a lesser extent adult *Diaptomus ashlandi*) dominated during winter and most of spring at ILVB and throughout the year at littoral and limnetic MLVB and limnetic BB (Fig. 3). Cladocerans dominated only at littoral BB when *Bosmina longirostris* and *Daphnia galeata mendotae* increased in abundance during summer and early autumn (Fig. 3). However, densities of *Mesocyclops edax* ($P > 0.10$), *Diaptomus ashlandi* ($P > 0.995$), *D. reighardi* ($P > 0.25$), *Daphnia pulex* ($P > 0.10$), and *D. galeata mendotae* ($P > 0.90$) showed no significant difference among stations.

Figure 4 summarizes relative phytoplankton fluorescence, relative fish abundance, and total zooplankton densities averaged during the study. These factors were greatest at ILVB and progressively declined at MLVB and even further at BB.

## Discussion

Zooplankton species composition in littoral and limnetic areas in Lake Mead was similar with few littoral taxa in either. Similar horizontal species distribution might result from several factors. The area of littoral zone is relatively small with little structural complexity and wind-generated currents can easily mix water between inshore and offshore areas. This may result in homogeneous physical and chemical environments and aid in the transport and mixing of zooplankton (George & Edwards, 1976; Hart, 1976; Kairesalo, 1980). The absence of rooted aquatic vegetation, however, appears to be a major contributor in reducing the number of littoral zooplankton species (Straskraba, 1964; Stolbunova & Stolbunov, 1981; Lemly & Dimmick, 1982a, b). Green (1986) suggested that vegetation is more important in increasing species diversity than merely location (i.e., inshore or offshore areas) because of greater habitat complexity than openwater. Williams (1982) found 24 littoral chydorid species in a lake dominated by littoral vegetation, and Quade (1969) found over 20 littoral cladoceran species amongst vegetation in each of several lakes. Lakes with extensively vegetated littoral zones have greater habitat heterogeneity contributing to greater species richness than lakes that lack vegetation (Pennak, 1966; Stolbunova & Stolbunov, 1981; Lemly & Dimmick, 1982a). Large, dense macrophyte stands also reduce horizontal water mixing and transport of plankton between littoral and limnetic zones (Kairesalo, 1980).

Although zooplankton species composition was horizontally similar, there was considerable variation among other environmental conditions. Significant difference in phytoplankton biomass

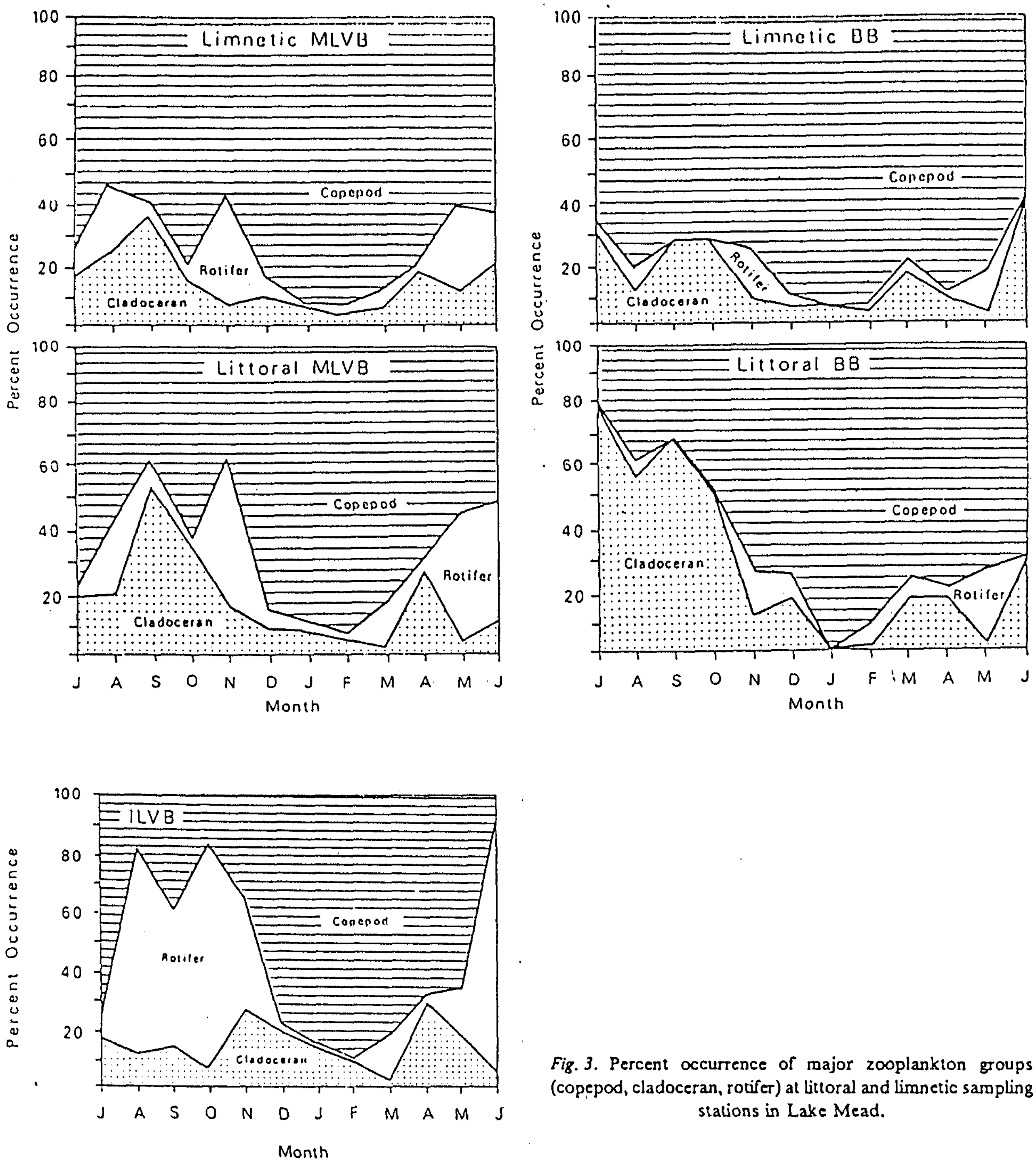


*Fig. 3.* Percent occurrence of major zooplankton groups (copepod, cladoceran, rotifer) at littoral and limnetic sampling stations in Lake Mead.

occurred horizontally from ILVB to BB, however, no difference was found between adjacent littoral and limnetic zones. ILVB was located near Las Vegas Wash inflow containing treated wastewater high in phosphorus that enhances phytoplankton biomass and growth (Baker & Paulson, 1981; Paulson & Baker, 1984). Diffusion of nutrients primarily due to a deep-water density current reduces growth and standing stock of algae in middle Las Vegas Bay and Boulder Basin (Baker & Paulson, 1981). Zooplankton abundances also were greater at ILVB and spatially

*Table 4.* Spearman's correlation coefficients of common zooplankton species abundance in Lake Mead with phytoplankton biomass, fish abundance, dissolved oxygen, temperature, pH, and conductivity. An asteric indicates a significant difference ($P < 0.05$).

| Species[s] | Phytopl | Fish | DO | Temp | pH | Conduct |
|---|---|---|---|---|---|---|
| naup | 0.098 | 0.317* | 0.274* | −0.146 | 0.279* | 0.053 |
| C cop | 0.080 | 0.133 | 0.233 | −0.361* | 0.290* | −0.181 |
| M cop | 0.341* | 0.341* | −0.299* | 0.472* | 0.506* | 0.401* |
| D cop | −0.261 | −0.114 | 0.354* | −0.797* | −0.048 | −0.580* |
| Dbt | −0.054 | 0.077 | 0.269* | −0.729* | 0.061 | −0.452* |
| Me | 0.229 | 0.201 | −0.093 | −0.131 | 0.392* | −0.064 |
| Da | −0.169 | −0.061 | 0.366* | −0.859* | −0.031 | −0.671* |
| Dr | −0.148 | −0.014 | 0.030 | −0.413* | 0.072 | −0.288* |
| Ds | 0.107 | 0.018 | 0.216 | −0.668* | 0.105 | −0.545* |
| Bl | 0.347* | 0.321* | −0.361* | 0.779* | 0.196 | 0.694* |
| Dgm | 0.166 | 0.272* | 0.023 | 0.277* | 0.423* | 0.255* |
| Dp | −0.078 | 0.017 | 0.230 | −0.737* | 0.207 | −0.550* |
| Rot | 0.491* | 0.409* | 0.357* | 0.153 | 0.167 | 0.239 |
| Total | 0.049 | 0.366* | 0.329* | −0.105 | 0.263* | 0.128 |

[s] naup = nuaplii; C cop = *Diacyclops* copepodites: M cop = *Mesocyclops* copepodites; D cop = *Diaptomus* copepodites; Dbt = *Diacyclops bicuspidatus thomasi*; Me = *Mesocyclops edax*; Da = *Diaptomus ashlandi*; Dr = *D. reighardi*, Ds = *D. siciloides*; Bl = *Bosmina longirostris*; Dgm = *Daphnia galeata mendotae*; Dp = *D. pulex*; Rot = rotifers; Total = total zooplankton abundance.

paralleled phytoplankton fluorescence (see Fig. 4). However, monthly values did not significantly correlate suggesting the uncoupling of links between grazers and phytoplankton indicating other factors showing stronger interactions to affect zooplankton dynamics. Wilde (1984), though, found a positive correlation in zooplankton abundance and phytoplankton biomass (measured as chlorophyll-*a*).

The dominant open-water planktivorous fish in Lake Mead is threadfin shad (*Dorosoma petenense*) (Allan & Roden, 1978). Planktivores in the littoral zone include bluegill sunfish (*Lepomis macrochirus*), green sunfish (*L. cyanellus*) and many other larval and juvenile fishes that become abundant in spring and summer (Allan & Roden, 1978). During our study, fish abundance paralleled total zooplankton abundance. Fish such as threadfin shad migrate from deep-water areas to Las Vegas Bay to spawn in spring and summer (Paulson & Espinosa, 1975; Allan & Roden, 1978). This suggests that these fish utilize areas of high food abundances that can support more fish and increase larval survival.

Zooplankton community structure differed monthly among sites indicating variability in factors influencing these patterns. For example, cladocerans dominated the littoral zone of BB in summer and autumn. *Bosmina longirostris* and *Daphnia galeata mendotae* densities totaled nearly 60 $l^{-1}$ in the littoral zone and less than 10 $l^{-1}$ in the limnetic zone (Sollberger, 1987). It is possible that greater food resources and production occurred in the littoral zone. Porter (1977) noted

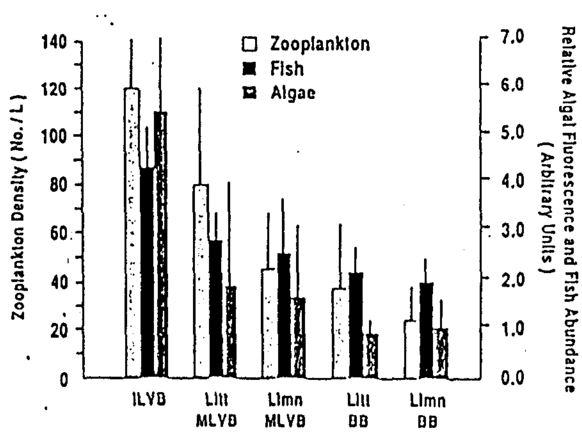


*Fig. 4.* Annual average zooplankton density, relative phytoplankton fluorescence, and relative fish abundance among littoral and limnetic sampling stations in Lake Mead. Vertical lines represent standard deviation.

that in oligotrophic lakes phytoplankton production may be high enough to support a greater number of zooplankton than suggested by phytoplankton biomass. Wind-induced water currents also can transport zooplankton from offshore to inshore areas (George & Edwards, 1976). Kairesalo & Penttila (1990) found that *Bosmina longispina* has relatively low resistance to wind-induced water currents which may control its horizontal distribution.

Rotifers, which positively correlated with phytoplankton biomass, were most abundant at ILVB and dominated the zooplankton community during summer and autumn. Wilde (1984) also found that rotifer spatial pattern paralleled those of chlorophyll-*a* concentrations throughout Lake mead. Pace (1986) and Zankai (1989) reported that rotifer abundances corresponded to algal biomass and production rates and were most abundant in eutrophic areas of lakes with variable degrees of fertility. Since fish were more abundant at ILVB than other sites, selective predation may have eliminated large competitive zooplankton (such as *Daphnia*) lending to the dominance of rotifers (Brooks & Dodson, 1965; Hurlbert & Mulla, 1981; MacIsaac & Gilbert, 1989). Rotifer abundances, however, never greatly increased until October and November when densities reached about $308\,l^{-1}$ and $63\,l^{-1}$, respectively (Sollberger, 1987). This increase might have resulted from a shift in larval fish diets to larger prey items (Wilde & Paulson, 1988) or from more favorable conditions occurring for rotifer production to offset predation losses (Hutchinson, 1967; Orcutt & Pace, 1984).

Many zooplankton species significantly correlated with temperature, DO, conductivity, and pH. Physical and chemical environments can influence zooplankton seasonal abundances (Hutchinson, 1967), but from this study it is difficult to determine the extent these factors constrain species abundances.

In summary, most zooplankton species showed differences in horizontal distribution between littoral and limnetic habitats. The lack of littoral vegetation and similar limnological conditions probably resulted in the dominance of limnetic zooplankton in littoral areas and low species richness of littoral taxa. If the littoral zone contained dense weedbeds, then perhaps zooplankton species richness would be greater in Lake Mead. Our data suggests that other factors, particularly relative abundance of fish, greatly influence zooplankton horizontal abundances and percent species composition.

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