5-1987

Comparison of littoral and limnetic zooplankton communities of Lake Mead

Patrick Joseph Sollberger
University of Nevada, Las Vegas

Repository Citation

Sollberger, P. J. (1987). Comparison of littoral and limnetic zooplankton communities of Lake Mead.
Available at: https://digitalscholarship.unlv.edu/water_pubs/84

Comparison of Littoral and Limnetic Zooplankton Communities of Lake Mead

by

Patrick Joseph Sollberger

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

in

Biological Sciences

Department of Biological Sciences
University of Nevada, Las Vegas

May, 1987

The thesis of Patrick Joseph Sollberger for the degree of Master of Science in the Biological Sciences is approved.

Chairperson, Larry J. Paulson

Examining Committee Member, Peter L. Starkweather

Examining Committee Member, James E. Deacon

Graduate Faculty Representative, Stephen M. Rowland

Graduate Dean, Ronald W. Smith

University of Nevada
Las Vegas, Nevada
May, 1987

Table of Contents

Figure

List of Figures

List of Tables

Abstract

Microfaunal communities were studied in littoral (inshore) and limnetic (offshore) areas of the lower basin in Lake Mead to compare species composition and abundance between the two zones. Planktonic forms (zooplankton) dominated inshore and offshore habitats and the occurrence of littoral species was low. Therefore, high similarity in zooplankton species composition was found among all sampling stations. This was perhaps due to two main factors: (i) the physical and chemical environment among the stations were very similar and (ii) the lack of aquatic vegetation in the littoral zone reduced the occurrence of littoral species.

Although species composition did not vary a great deal, there were large differences in average zooplankton densities between sampling stations. This was most likely due to differences in the amount of algal biomass and fish predation. The more productive station in inner Las Vegas Bay showed a higher relative algal biomass and a higher average density of zooplankton (about $118 \cdot l^{-1}$) than other sampling stations. In middle Las Vegas Bay, average zooplankton densities ($44 \cdot l^{-1}$ in the limnetic zone and $80 \cdot l^{-1}$ in the littoral zone) and relative algal biomass were less than inner Las Vegas Bay. Boulder Basin had the

lowest relative algal biomass and, therefore, lowest average zooplankton densities (about $23 \cdot l^{-1}$ in the limnetic zone and $37 \cdot l^{-1}$ in the littoral zone) of any location.

Relative abundance of fish increased at sampling areas in late spring and summer when fishes migrated from deeper areas of the reservoir to the surface waters to spawn. Adult planktivorous fishes and newly hatched young then decimated zooplankton populations causing low summer zooplankton densities. Fish predation was more intense in inner Las Vegas Bay and middle Las Vegas Bay and less in Boulder Basin. Fish predation was also greater in littoral areas than limnetic areas.

Acknowledgements

I would like to acknowledge many people for their help during my thesis. A large thanks to my major advisor, Larry Paulson, for his friendship and support to get me through my thesis. Other thesis committee members, James Deacon and Peter Starkweather, provided helpful comments throughout my studies. Thanks also to Dave Culp for statistical assistance, Tim LeMaster for computer programming and Sandie Branca for assistance with the word processor. I am indept to Rich Axler and Jennifer Haley for their helpful editing comments. I also appreciate the excellent field help from Lisa Heki. Most of all, thanks to my parents for their love and support not only on this project, but of all things I have tried to achieve.

INTRODUCTION

Lake microfaunas are classified as either littoral (inshore) or limnetic (offshore) based on their horizontal distribution (Edmondson 1959, Wetzel 1975, Pennak 1978). Planktonic microcrustaceans generally avoid inland areas, perhaps by visually detecting differences in horizontal light intensities (Siebeck 1964, 1980). During the day, zooplankton orient themselves away from visually darkened shoreline areas and swim towards the limnetic zone. Some species of microcrustaceans strictly inhabit the littoral zone, never leaving the safety of aquatic macrophytes (Fairchild 1981, Lemly and Dimmick 1982a). Other species are found in both inshore and offshore areas. Their distribution depends on several factors including the abundance of prey (Lemly and Dimmick 1982a, Meyers 1984), wind generated water currents (George and Edwards 1976, Hart 1978, Threlkeld 1981, Byron et al. 1983), and the density of aquatic plant growth (Straskraba 1964, Pennak 1966, Vigerstad and Tilly 1977).

Zooplankton communities in limnetic area usually consists of one to several species of cladocerans, copepods and rotifers; normally one species in each group dominates at any one time (Pennak 1957, 1966 Colinvaux and Steinitz 1980). Cladoceran (Smyly 1952, Straskraba 1964, Lemly and

Dimmick 1982a, Vigerstad and Tilly 1977, Williams 1982) and rotifers (Pennak 1966) mainly doninate in littoral habitats. Calaniod copepods are generally absent and any cyclopoid copepods, if present, exist at very low numbers (Smyly 1952, Pennak 1953, 1966, Straskraba 1964, Gehrs 1974). Harpacticoid copepods may be found in littoral habitats, in both the water column and benthic areas (Pennak 1978).

The density of vegetation largely determines the diversity and abundance of littoral microfauna. In most instances, as the abundance of macrophytes increase, so does the diversity of the littoral microfauna (Smirnov 1963, Straskraba 1964, Pennak 1966, Lemly and Dimmick 1982a). These species are usually poorly represented in littoral areas lacking vegetation and in such areas the species composition and abundance of animals are similar to that of adjacent limnetic areas (Smyly 1952, Smirnov 1963, Straskraba 1964, Stolbunova and Stolbunov 1981, Lemly and Dimmick 1982a,b). Pennak (1966) found that in Colorado lakes the number of zooplankton species was greater in the littoral zone (between 1-3 more species) than the limnetic zone. However, the density of zooplankton was greater in the limnetic zone than the littoral zone.

Several zooplankton studies have been conducted in limnetic areas of Lake Mead, in Arizona and Nevada, in the past decade. Wilde (1984) noted that during this period, zooplankton densities have decreased 10-fold and are currently low throughout the reservoir. This suggests that low densities of zooplankton may result in poor recruitment of larval fish and therefore may be the cause for a serious decline in largemouth bass (Micropterus salmoides) fishing success (Paulson et al. 1980, Baker and Paulson 1983, Paulson and Baker 1983).

In contrast, the catch of other fish species in Lake Mead has increased during this period. Bluegill (Lepomis macrochirus) harvest has increased somewhat since 1967, black crappie (Pomoxis nigromaculatus) since 1972 and striped bass (Morone saxitilis) since 1969 (Nev. Dept. Wildl. 1982). Zooplankton appear to be important food for larval and juvenile stages of all fish species in Lake Mead (Allan and Roden 1978). Therefore, differences in the success of certain fish species may reflect utilization of different habitats and food resources by young fish. Even though limnetic microfauna densities are low it may be that littoral zooplankton densities are high enough and provide a better food base for fishes utilizing this area of the reservoir.

Few studies have simultaneously compared the microfauna in littoral verses adjacent limnetic areas. Sampling has usually been concentrated in either the littoral or the limnetic zone. Since each zone can be unique in species composition and abundance of microfauna, one should not assume that the two zones are similar.

The purpose of this study was to: (i) compare species composition and abundance of the microfauna (crustacean and rotifer) in limnetic and adjacent littoral areas in the lower basin of Lake Mead; and (ii) evaluate possible causes for such differences, or similarities, between the microfauna in these two zones of the reservoir.

STUDIES OF ZOOPLANKTON IN LAKE MEAD

Zooplankton studies have been conducted in Lake Mead since 1976 (Everett et al. 1976, Baker et al. 1977, Burke 1977, Paulson et al. 1980, Paulson and Baker 1983, Youngs 1983, Wilde 1984). With the exception of Youngs (1983), these studies have been conducted in limnetic areas of the reservoir. These results, nevertheless, provide useful background information for this study.

Zooplankton in Lake Mead show variation in vertical, horizontal and seasonal distribution patterns. During the summer months, zooplankton concentrate in the metalimnion (Baker 1974, Deacon 1975, Everett et al. 1976) at depths from about 10-25 m and were thought to be a prime contributor to the development of the metalimnion oxygen minimum that is characteristic of the reservoir (Burke 1977). Certain species like, <u>Keratella cochlearis</u>, Polyarthra sp. and Bosmina longirostris, undergo extreme vertical migrations (Staker 1974) while others, like Asplanchna priodonta, Syncheata and herbiverous crustaceans (i.e. some cladocerans and calanoid copepods) show specific depth affinities (Staker 1974, Baker et al. 1977, Burke 1977).

Zooplankton densities in the epilimnion are generally low ($<15 \cdot l^{-1}$) during the summer due to intense predation by threadfin shad (Dorosoma petenenese) (Wilde 1984). Densities are highest usually during late fall, winter and early spring (Paulson and Baker 1983, Wilde 1984).

Zooplankton are more abundant in the productive inflow areas near the Las Vegas Wash, the Virgin River and the Colorado River (Everett et al. 1976, Paulson et al. 1980, Paulson and Baker 1983, Wilde 1984). Paulson and Baker (1983) and Wilde (1984) have found that the spatial distribution and abundance of zooplankton in Lake Mead are closely related to levels of phytoplankton productivity and chlorophyll-a. In the productive inflow areas, rotifer densities may exceed $100 \cdot l^{-1}$ during the summer, while in the main basin areas they are usually less than $5 \cdot l^{-1}$. Cladocerans and copepods also have elevated densities in the inflow areas, sometimes as great as $150 \cdot l^{-1}$ and $70 \cdot l^{-1}$, respectively. Cladocerans and copepods rarely exceed $20 \cdot l^{-1}$ in most other areas of the reservoir (Paulson and Baker 1983, Wilde 1984).

Although most studies in Lake Mead have been conducted in limnetic zones, a few studies have been conducted in littoral zones. Allan and Romero (1975) found that during 1973 cladocerans comprised 70-80% of the zooplankton community in shallow coves. However, in 1974, copepods were the dominant zooplankton group in the same shallow coves. Morgensen and Padilla (1982) found no significant difference in zooplankton abundances in coves dominated by tamarisk (<u>Tamarix</u> sp.), brittlebush (<u>Encelia</u> <u>farinosa</u>), pondweed (<u>Potamogeton</u> sp.) or rocks. They did, however, find some variation in zooplankton abundances among coves manipulated with artificial structures such as tamarisk piles, plastic kelp and hay bales.

In studies by Allan and Romero (1975), Morgensen and Padilla (1982) and Youngs (1983), zooplankton were attracted to lights and collected with a motorized pump. Youngs (1983) noted that this method resulted in considerable variability in the number of zooplankton collected and might not be appropriate for comparisons. It was nevertheless, a useful method for evaluating species composition and relative abundances of animals in shallow inshore areas.

cov

was

100

lid

STUDY AREA

The littoral zone is generally described as the area close to shore which is characterized by aquatic vegetation growth (Hutchinson 1967, Wetzel 1975). It may vary considerably from lake to lake depending on the extent of growth of aquatic vegetation. In general, macrophytic growth diminishes below a 10 m shoreline contour due mostly to light limitation (Wetzel 1975).

In this study, the littoral zone was defined as the area from shore to a lake bottom contour of 10 m below the water line. This area consists of warmer epilimnetic water during stratification, and is usually well above 1% of the surface light transmittance. The limnetic zone is the open water area beyond the 10 m contour.

Littoral and limnetic sampling stations were located in Boulder Basin (BB), middle Las Vegas Bay (MLVB) and inner Las Vegas Bay (ILVB) (Fig. 1).

Boulder Basin

The littoral station in Boulder Basin was located in a large cove along Saddle Island. The corresponding offshore site was located slightly northeast of this at a depth of about 100 m. At the littoral site, substrate was composed of solid rock, and had a slope, from waters edge to the

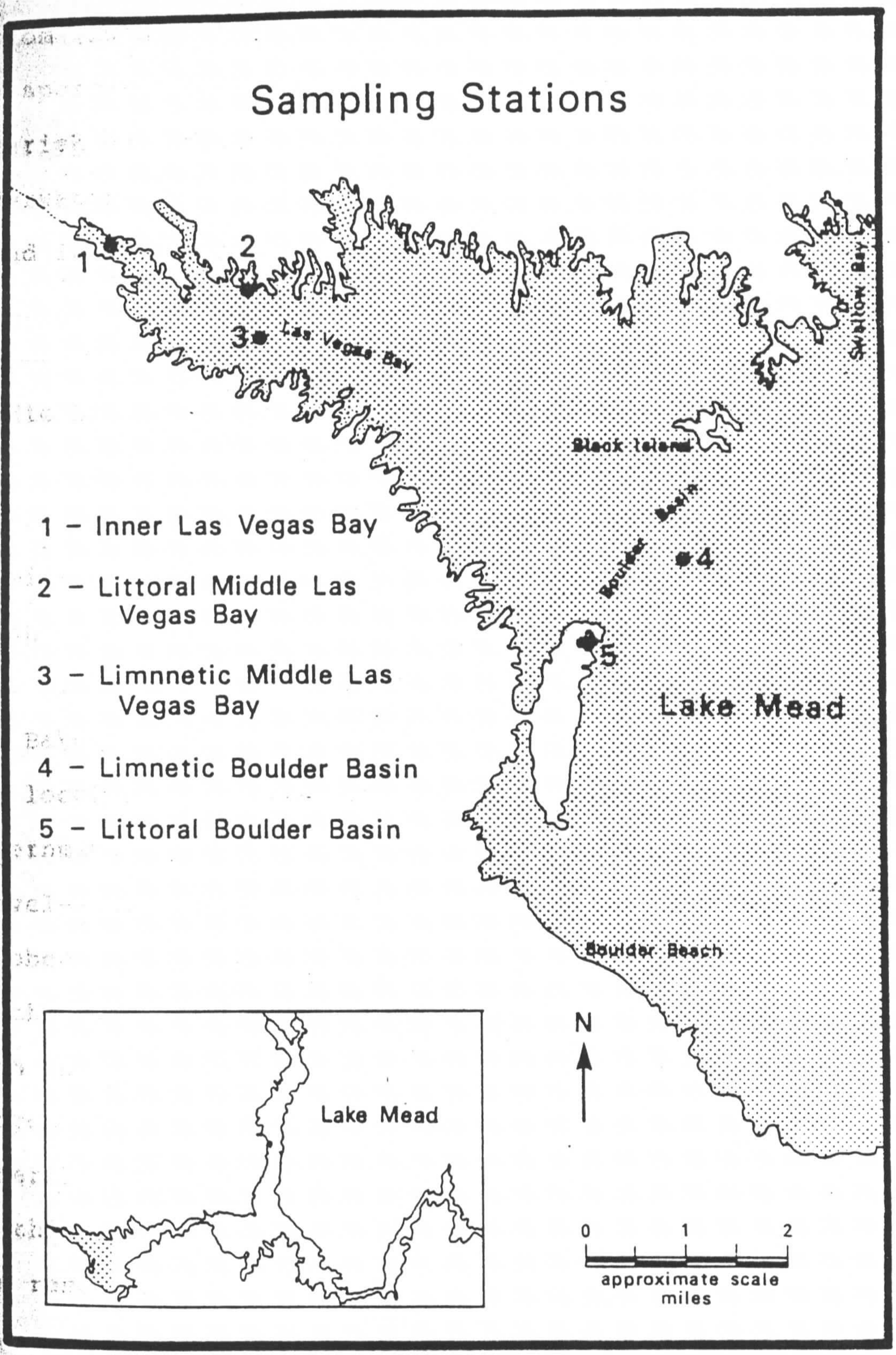

Figure 1. Map of Lake Mead showing littoral and limnetic sampling sites.

bottom (10 m), that averaged about 20 . Aquatic vegetation was sparce in the cove, although a few inundated, dead, tamarisk were found near the shoreline. This type of underwater cove environment is typical of many canyon areas found in Lake Mead.

Middle Las Vegas Bay

The middle Las Vegas Bay limnetic station was located in mid-channel at a depth of about 40 m, although this depth was subject to annual water level fluctuations (see Fig. 2). This site was used in previous studies by Paulson and Baker (1983) and Wilde (1984). The littoral station was located in an adjacent cove to the north between Government Wash and Gypsum Wash. The substrate was of gravel-sand sediments and the sides of the cove had slopes of about 14 . There was an average slope of 6 to the back of the cove. Inundated tamarisk were more abundant here than in the littoral cove of Boulder Basin, but no macrophytes could be seen growing on the bottom. The general terrain, slope, plant community and bottom sediment of this cove is typical of the many areas found throughout the reservoir.

Inner Las Vegas Bay

The inner Las Vegas Bay station was also located at the same site as used by Paulson and Baker (1983) and Wilde (1984) (Fig. 1). The entire region was littoral so there was no adjacent limnetic station for comparison. Its location was directly mid-channel in the Las Vegas Wash inflow and had a relatively flat bottom covered with silt and sand. The lateral banks leading directly to the back of the bay were nearly vertical and the bottom slope from the sampling site to the inflow was about 6 . Due to errosion, much of the latteral banks leading to the inflow had fallen in the lake. There was sparse aquatic vegetation, but inundated tamarisk was found along most of the bank.

Physical and Chemical Features

There is a gradient of nutrients and phytoplankton productivity that extends from the inner Las Vegas Bay to Boulder Basin (Baker and Paulson 1980). Wastewater inflows from Las Vegas Wash form a density current in Las Vegas Bay due to differences in temperature and salinity of wash and bay waters. This produces high nutrient concentrations resulting in high productivity in inner Las Vegas Bay that gradually decreases towards Boulder Basin (Baker and Paulson 1981, Paulson and Baker 1984). Higher phosphorus concentrations extend the farthest (approximately middle Las Vegas Bay) during winter than any other time (Baker and Paulson 1981). Therefore, the mixing effect and seasonal distribution of the density current influence the availability of nutrients for phytoplankton growth in Las Vegas Bay and the Boulder Basin area (Baker and Paulson 1981). The inner Las Vegas Bay is considered slightly eutrophic, the middle bay mesotrophic and Boulder Basin oligotrophic based on primary productivity (PPr), chlorophyll-a, water clarity (Secchi depth) and total phosphorus concentrations (Paulson et al. 1980).

Other regions of Lake Mead vary in productivity depending on their proximity to inflows and the amount of runoff (Paulson and Baker 1984). The Colorado River inflow into Lake Mead has moderate amounts of both nitrogen and orthophosphorus which increase phytoplankton standing crop (chlorophyll-a) in the upper portions of the reservoir (Paulson and Baker 1984). The Overton Arm receives some nutrients from the Muddy and Virgin Rivers but quantities are much lower than from the Colorado River and Las Vegas Wash (Paulson and Baker 1984). Major portions of the upper and lower basins are oligotrophic.

Basin areas of Lake Mead remain isothermal (11-12°C) from December to February. A distinct thermocline develops at 10 m in June and gradually drops to 15-18 m by September (Paulson and Baker 1984). During stratification, oxygen concentrations in the epilimnion are near saturation or slightly supersaturated and show a negative heterograde profile normally from June to January (Deacon and Tew 1973, Paulson et al. 1980). Oxygen concentrations are lowest in the metalimnion, dropping to about 1 $mg \cdot l^{-1}$ in Las Vegas Bay and between 2-3·$mg\ l^{-1}$ in Boulder Basin. An orthograde oxygen profile then develops during isothermal periods (Paulson et al. 1980, Paulson and Baker 1984).

The pH profile is similar to the oxygen profile and ranges from 7.5-9.0 with higher values in the epilimnion due to photosynthetic activity (Paulson et al. 1980). Conductivity is highest at the Las Vegas Wash inflow and averages around 3000 $\mu mhos \cdot cm^{-1}$ (Baker and Paulson 1981). As the density current reaches the middle Las Vegas Bay, mixing reduces conductivities to about 1000 $\mu mhos \cdot cm^{-1}$. Boulder Basin conductivities were typically between 800-900 $\mu mhos \cdot cm^{-1}$ (Paulson, unpub. data).

METHODS

Zooplankton samples were collected in littoral and limnetic sites at 1, 3, 5, 7, and 10 m, and at every 5m beyond this down to a maximum depth of 40 m in deeper stations. The littoral stations were fixed at 10 m and sometimes varied slightly in position each month due to water level fluctuations during the year (Fig. 2). Limnetic stations were located at permanent channel buoys. Sampling was performed from July 1984 to June 1985.

A gasoline driven pump with an average pumping velocity of 12.5 $l \cdot min^{-1}$ was used to collect zooplankton samples. The pump was attached to a hose 40 m in length (15.9 mm diameter) with a double plexiglas plate connected to the bottom of the hose. There was a 2.5 cm gap between the two plexiglas plates to collect an even draw of water from a depth. This method of collection has been used successfully in Lake Mead by Burke (1977) and is useful for collecting large numbers of samples from discrete depths.

The water from each depth was collected in a 20 l container and filtered through an 80 µm Wisconsin net. A volume of 7.9 l was needed to completely flush the hose, therefore, at least this amount was discarded before collecting the next sample. Animals were preserved in 4% formalin-sucrose solution (Haney and Hall 1973).

Chlorophyll fluorescence was measured simultaneously with a Turner Designs Fluorometer to estimate relative phytoplankton biomass. Temperature, conductivity, dissolved oxygen and pH were measured with a Hydrolab Model 8000. Light transmittance was measured using a LI-COR Quantum Photometer Model LI-185A equipped with a quantum sensor (400-700 nm sensitvity).

A Furuno Model FM-22A echo sounder was used to measure the relative abundance and depth distribution of fish at each station. Echo-grams were ranked using a procedure developed by Wilde (1984) which estimates relative fish abundance. In the absence of fish, a score of 1 was given. When one to a few traces were observed a score of 2 was assigned. Each higher score represented double the fish biomass of the score below it. Ranking proceeded to a top score of 5.

Lake Mead surface area of both littoral and limnetic areas was determined by planimetry. Measurements were made from 7.5 minute USGS topographical maps (1970) of the lower basin. An estimate was taken from between the 1160-1200 ft contours above mean sea level (MSL).

Generally an entire zooplankton sample was enumerated. For dense samples three 1 ml subsamples were counted and then averaged. Densities were expressed as number per liter. Most animals were identified to species using keys by Edmondson (1959), Pennak (1978) and Wilde (unpubl. key to the zooplankton species of Lake Mead).

Zooplankton collected from the upper 10 m at all stations were compared. Statistics were performed using Statistical Package for the Social Sciences (SPSS). Spearman's rank correlation was used to evaluate the relationship between animal densities and physical environmental factors (temperature, dissolved oxygen, conductivity, pH and light extinction coefficients) and biological factors (algal fluorescence and relative fish abundance. An One-Way Analysis of Variance (One-Way ANOVA) was performed to test the hypothesis that zooplankton densities were spatially similar. A Student Newman-Kuels (SNK) test was performed to show which sites had similar densities if the original hypothesis was incorrect.

RESULTS

RESERVOIR HYDROLOGY

Lake Mead Elevation

Water level in Lake Mead varied about 3 m during the course of this study (Fig. 2). On 19 July 1984, lake elevation was at approximately 369 m MSL and gradually declined during late summer, fall, winter and early spring to a minimum of about 367 m MSL. Lake elevation increased in late spring and early summer to a maximum of about 370 m MSL at the end of the project on 27 June 1985.

Lake Mead Surface Area

The total surface area (SA) of the lower basin study area averaged 132.51 km^2 (Table 1). Approximately 89% of this area is open water, particularly in Boulder Basin which is 91% limnetic (SA=111.1 km^2). The middle Las Vegas Bay had a more extensive littoral zone (26%, SA=2.52 km^2). Virtually all of ILVB was littoral.

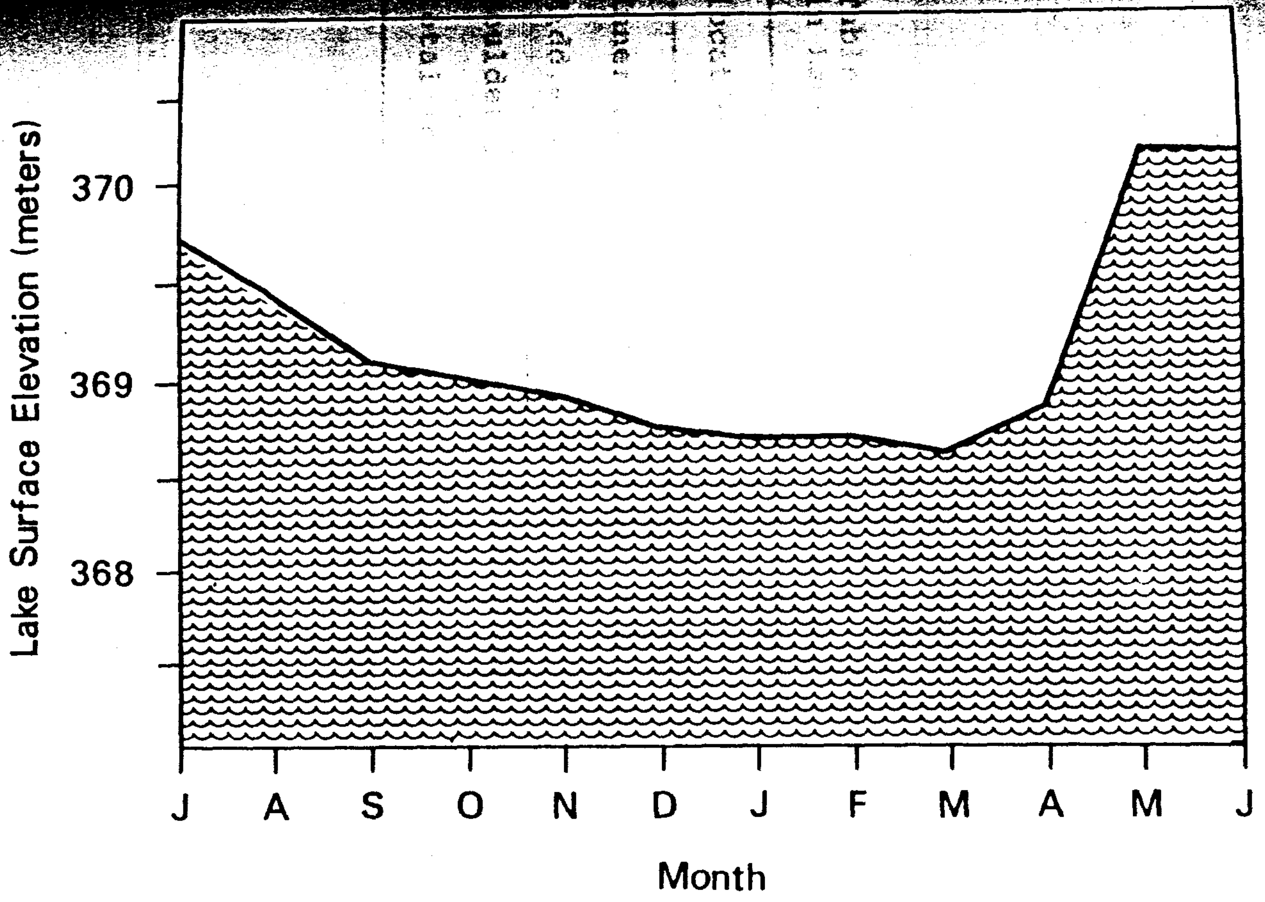

Figure 2. Lake Mead surface elevation from July 1984 to June 1985.

ble 1. Average surface area (SA) of sampling locations Lake Mead and the percentage of littoral area.

ocation	SA (km^2)	% littoral zone
ner Las Vegas Bay	0.91	100
dle Las Vegas Bay	9.60	26
lder Basin	122.09	9
l lower basin	132.60	11

Physical Factors

Temperature

Average epilimnetic temperatures varied considerably throughout the year at each station (Fig. 3). Temperatures normally ranged from a maximum of about 26-27°C during the summer and early fall to a low of around 12°C during the winter after the breakdown of thermal stratification. Generally each station followed a similar pattern seasonally. However, there were some temperature differences among adjacent limnetic and littoral habitats, and ILVB had a slightly higher temperature than other stations during summer. An average temperature of 38.1°C was reached in ILVB in September, 1984. The littoral MLVB station also had slightly higher summer and early fall temperatures than the corresponding limnetic area. No temperature differences were found between littoral and limnetic BB stations. During winter and spring, there was little difference between any of the stations.

Figure 3.

Average epilimnetic dissolved oxygen (DO)

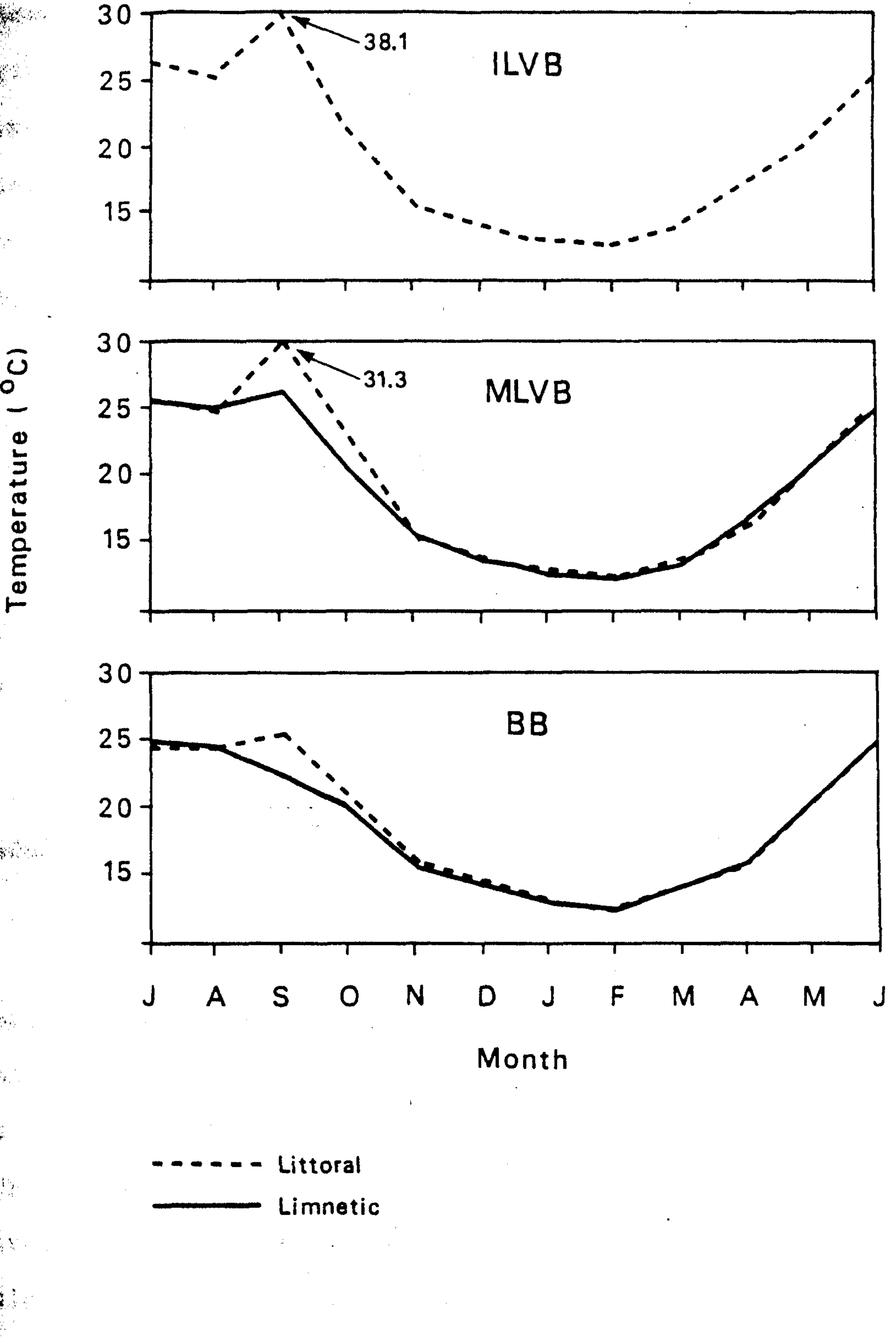

Figure 3. Average epilimnetic temperatures at littoral and limnetic sampling sites in Lake Mead.

concentrations ranged from 7.5-11.5 mg·l^{-1} at all stations during the study (Fig. 4). There were small differences between stations, generally less than 1 mg·l^{-1}. The littoral stations had slightly higher DO concentrations than did the limnetic stations and concentrations were slightly higher in ILVB and MLVB stations than in BB.

pH

Average epilimnetic pH ranged from a minimum of about 6.8 to a maximum of about 8.6 (Fig. 5). There were very few differences in pH values seasonally and among stations.

Conductivity

Epilimnetic conductivity (EC) was highest during the summer and early fall months and decreased throughout the remainder of fall, winter and early spring (Fig. 6). It was as high as 1300-1340 µmhos·cm^{-1} during the summer in ILVB but decreased to between 950-1175 µmhos·cm^{-1} in littoral and limnetic MLVB stations during the same period. Boulder Basin was spatially uniform and ranged from 900-[illegible]0 µmhos cm^{-1} during the summer. During the winter, EC remained slightly higher in ILVB and MLVB than in BB, but

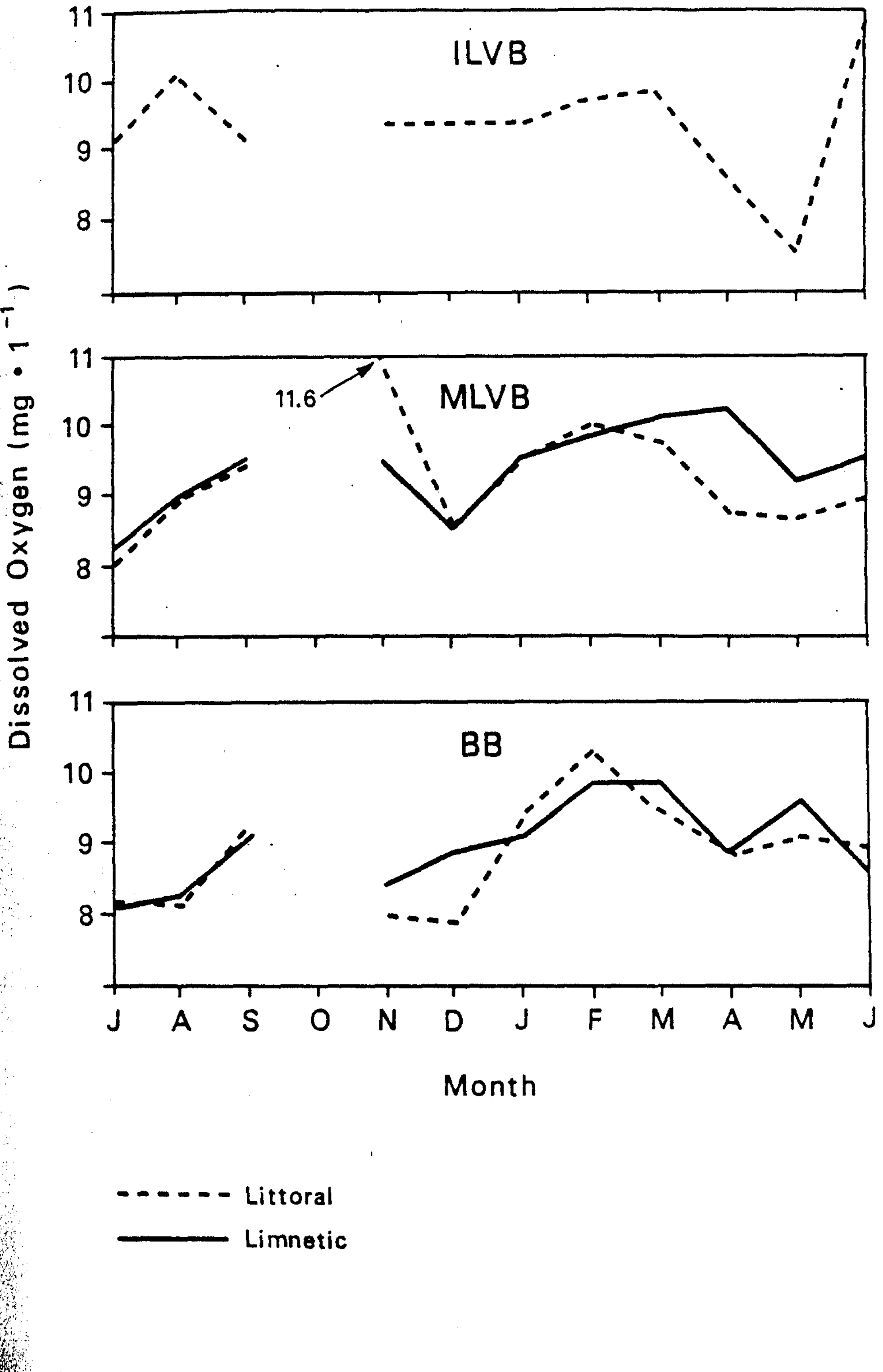

Figure 4. Average epilimnetic dissolved oxygen concentrations at littoral and limnetic sampling sites in Lake Mead.

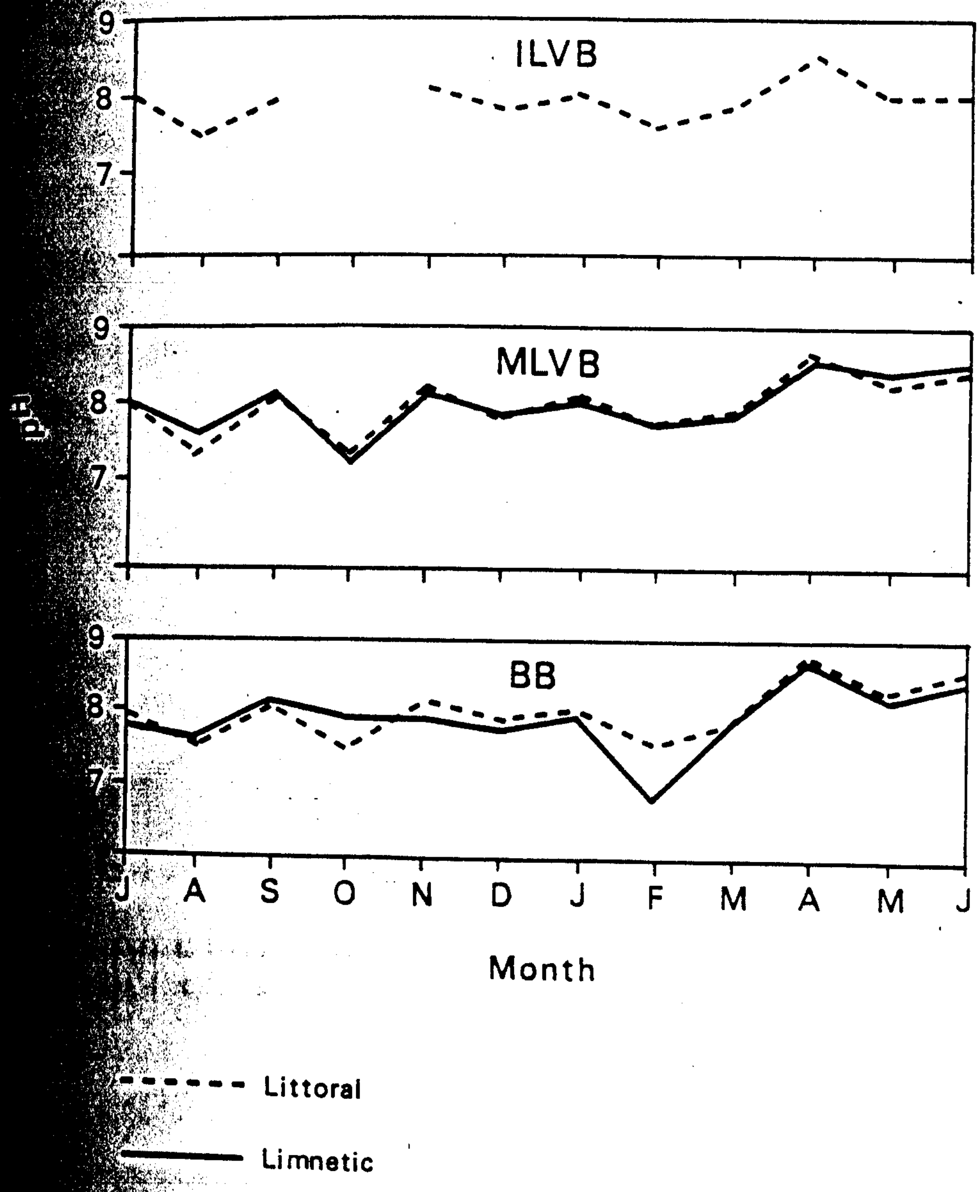

Figure 5. Average epilimnetic pH at littoral and limnetic sampling sites in Lake Mead.

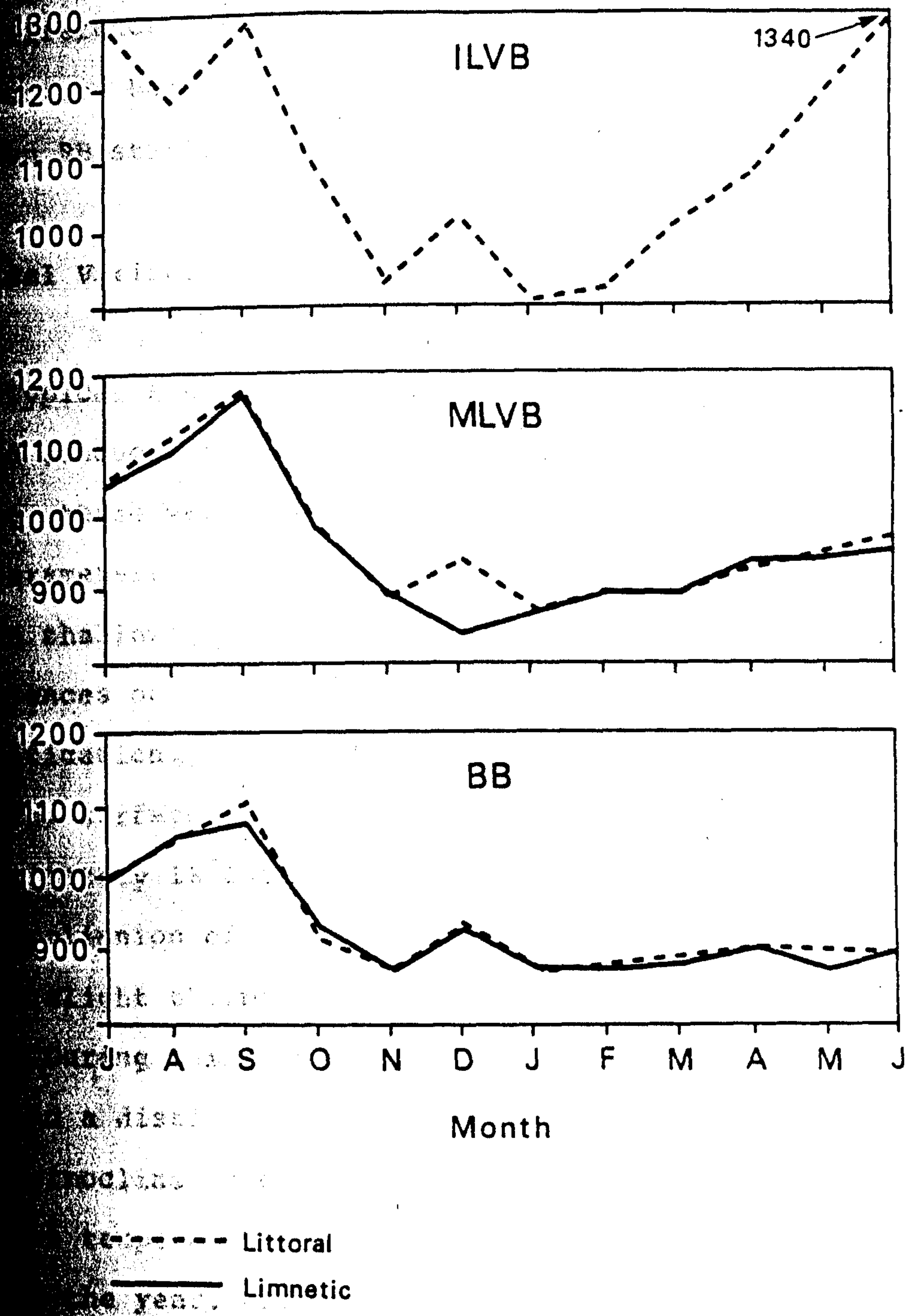

Figure 6. Average epilimnetic conductivities at littoral and limnetic sampling sites in Lake Mead.

the difference was less pronounced. Little difference in EC occurred between littoral and limnetic MLVB stations and between BB stations.

Vertical Variability in Physical Parameters

Typical seasonal vertical profiles of temperature, pH, DO and conductivity are plotted in Figure 7. During winter mixing, there were minimal vertical differences in any of the parameters at all sites. Differences were also minimal at the shallow BB station during spring, summer and fall. Differences occurred at other stations during stratification.

The surface temperature during spring was approximately 18°C and gradually decreased to about 12°C in the hypolimnion of the deeper MLVB and BB stations (Fig. 7). A slight thermocline developed at about 5 m at this time. During summer the surface waters warmed to about 25-27°C and a distinct thermocline developed at about 10 m. The thermocline gradually dropped to 15 m by fall. Vertical temperatures were uniform at shallow sites for most of the year. However, in late spring and early summer, littoral areas were cooler near the bottom.

Vertical DO concentration (Fig. 7) also varied seasonally. In the epilimnion during summer and early fall, DO was either near saturation or slightly above, from

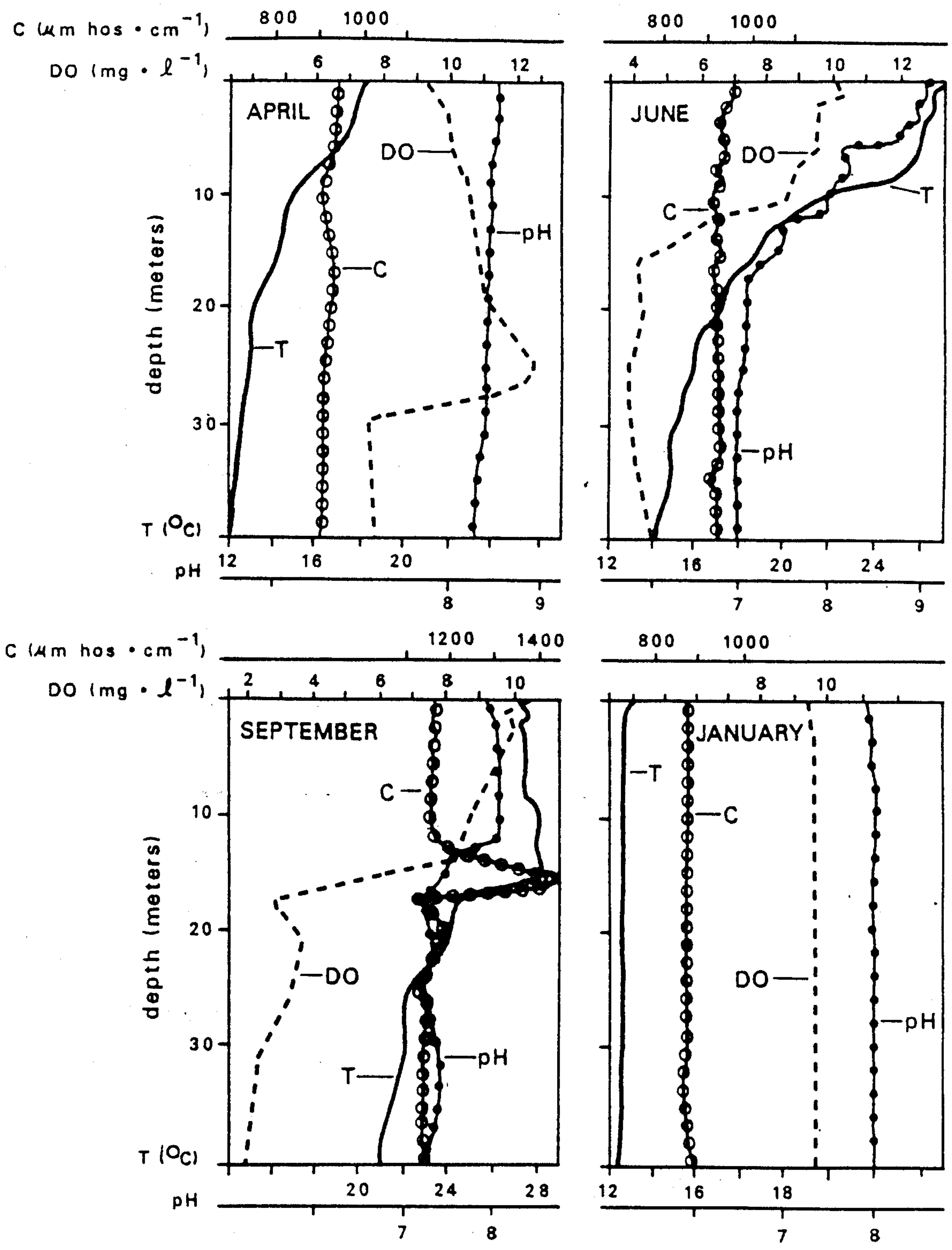

Figure 7. Seasonal vertical measurements of dissolved oxygen, temperature, conductivity and pH in middle Las Vegas Bay. 1984-1985.

about 8.5-15.0 $mg \cdot l^{-1}$. In the hypolimnion, DO ranged from 4-7 $mg\ l^{-1}$ in MLVB and from 7-8 $mg \cdot l^{-1}$ in BB. DO concentration near the bottom of shallow stations was generally lower in the summer, from 2-4 $mg \cdot l^{-1}$ in the ILVB and MLVB.

Vertical variation of pH occurred in the epilimnion (from about 7.8-9.0) with higher values near the surface, decreasing at the thermocline and becoming uniform (7-7.5) in the hypolimnion .

Conductivity was always highest in ILVB and the peak along the bottom was inluenced by the Las Vegas Wash density current. During stratification, conductivity was higher in the epilimnion than hypolimnion in limnetic stations and was highest in the metalimnion region in MLVB. Adjacent inshore and offshore areas had a similar vertical conductivity profile.

Light Extinction

Light extinction coefficients (LEC) for each station are presented in Table 2. LEC was always higher in ILVB than any other station and reached a maximum during summer due to higher phytoplankton biomass.

Both littoral and limnetic MLVB stations showed similar seasonal patterns, but the littoral had slightly

Table 2. Lake Mead light extinction coefficients at littoral and limnetic sampling stations.

Month	ILVB	LimnMLVB	LittMLVB	LimnBB	LittBB
J	1.47	0.41	0.43	0.21	0.29
A	0.62	0.55	0.63	0.29	0.28
S	1.18	0.42	0.52	0.25	0.18
O	0.77	0.45	0.47	0.29	0.31
N	0.48	0.36	0.40	0.27	0.37
D	0.64	0.29	0.33	0.28	0.32
J	-	-	-	-	-
F	0.40	0.28	0.33	0.29	0.30
M	0.50	0.29	0.32	0.24	0.27
A	0.66	0.29	0.33	0.24	0.28
M	1.23	0.73	0.73	0.44	0.58
J	1.29	0.53	0.53	0.37	0.35

higher LEC (less transparency) during the summer. In BB, there was little difference either seasonally or spatially.

ZOOPLANKTON DYNAMICS

Species Composition

A total of 42 zooplankton species was encountered during this study, 9 were copepods, 10 were cladocerans and 23 were rotifers (Table 3). Relatively few littoral species were found. Rotifers had the most diverse composition of littoral and planktonic species, although most species had a low occurence. The dominant rotifers were *Asplanchna priodonta*, *Polyarthra* spp., *Syncheata* sp. and the littoral species *Trichocerca cylindrica*. Cladocerans and copepods comprised most of the zooplankton community. The dominant species were the copepods *Diaptomus ashlandi*, and to a smaller degree *Cyclops bicuspidatus thomasi*, *D. reighardi*, *D. siciloides* and *Mesocyclops edax* and the dominant cladocerans were *Bosmina longirostris*, *Daphnia galeata mendotae* and *D. pulex*. Most all zooplankton species were found in both littoral and limnetic habitats and sampling sites showed a high similarity in species composition (Table 4).

Table 3. Species of zooplankton in Lake Mead, their natural habitat and relative commonness. For commonness, A is abundant, C is common, R is rare and ER is extremely rare.

Species	Littoral	Limnetic	Commonness
Copopoda			
Cyclops bicuspidatus thomasi	X	X	C
C. varicans rubellus*	X		ER
C. vernalis		X	ER
Diaptomus ashlandi	X	X	A
D. clavipes	X	X	R
D. reighardi	X	X	C
D. siciloides	X	X	C
Mesocyclops edax	X	X	C
Onychocamptus mohammed	X	X	ER
Cladocera			
Alona acutirostris*	X		ER
A. guttata*	X	X	ER
A. quadranularis*	X		ER
Bosmina longirostris	X	X	A
Ceriodaphnia lacustris	X		ER
Chydorus sphaericus*		X	ER
Daphnia galeata mendotae	X	X	A
D. pulex	X	X	A
Diaphanosoma brachyurum	X	X	C
Leptodora kindtii	X	X	ER

(continued)

(Table 3 cont.)

Rotifera			
Ascomorpha saltans	X	X	ER
Asplanchna priodonta	X	X	C
Brachionus calyciflorus	X	X	ER
B. patulus	X	X	ER
B. quadridentatus	X	X	ER
Filinia sp.	X	X	R
Hexarthra sp.	X	X	ER
Kellicottia longispina		X	ER
Keratell cochlearis	X	X	ER
K. earlinae	X	X	ER
Lecane (*Lecane*) *crepida**	X	X	ER
L. (*L.*) *luna**	X	X	ER
L. (*Monostyla*) *decipiens**	X	X	ER
L. (*M.*) *lunaris**	X	X	ER
*Lepadella acuminata**		X	ER
Macrocheatus sp.*		X	ER
*Platyias quadricornis**		X	ER
Pleosoma sp.	X	X	ER
Polyarthra spp.	X	X	A
Syncheata sp.	X	X	A
*Trichocerca cylindrica**	X	X	C
*T. multicrinis**	X	X	ER
Trichotria sp.*	X	X	ER

*=littoral species (according to Edmondson, 1959, and Pennak, 1978)

Table 4. Percent similarity in species composition among sampling stations in Lake Mead.

Station	Percent Similar*
ILVB x Limn MLVB	73
ILVB x Litt MLVB	85
ILVB x Limn BB	86
ILVB x litt BB	79
Limn MLVB x Litt MLVB	78
Limn MLVB x Limn BB	79
Limn MLVB x Litt BB	79
Litt MLVB x Limn BB	78
Litt MLVB x Litt BB	81
Limn BB x Litt BB	87

*, Sorensen Similarity Index which is $\frac{2C}{D + E}$ x 100, where C is the number of zooplankton species common to both stations, and D and E are the total number of species in each of the respective stations.

Relative Zooplankton Abundance

The average densities of zooplankton in Lake Mead from July 1984 to June 1985 are shown in Table 5. The yearly zooplankton density in the lower basin averaged $32.7 \cdot l^{-1}$ (Table 5). The density of zooplankton were influenced more by Boulder Basin because of its greater relative size. Adult and juvenile copepods dominated the community with a density of $21 \cdot l^{-1}$, more than twice the density of cladocerans ($9.9 \cdot l^{-1}$). The overall rotifer density was low during this study (Table 5). Most species averaged less than $2 \cdot l^{-1}$.

Dominance of zooplankton groups varied seasonally and spatially (Fig. 8). At ILVB, rotifers were the dominant group during part of the summer and fall. Copepods dominated during all other times of the year and at no time did cladocerans dominate.

In the offshore area of MLVB, copepods dominated the entire year (Fig. 8). In the littoral zone, cladocerans and rotifers were co-dominant (i.e., percent occurrence was similar for both groups) during September and rotifers and copepods were co-dominant in November (Fig. 8). Copepods were the dominant group during the summer, winter and spring.

Copepods also dominated in the littoral area of Boulder Basin during the entire year (Fig. 8). However, in

Table 5. Average density of zooplankton in the lower basin of Lake Mead from July 1984 to June 1985.

Species	Density (No.$\cdot l^{-1}$)
copepod nauplii	10.3
Cyclops copepodites	1.2
Diaptomus copepodites	3.6
Mesocyclops copepodites	2.3
Cyclops bicuspidatus thomasi	0.3
Diaptomus ashlandi	2.2
D. reighardi	0.3
D. siciloides	0.2
Mesocyclops edax	0.5
Bosmina longirostris	3.9
Daphnia galeata mendotae	4.6
D. pulex	1.4
total rotifers	1.8
total copepods	21.0
total cladocerans	9.9
total zooplankton	32.7

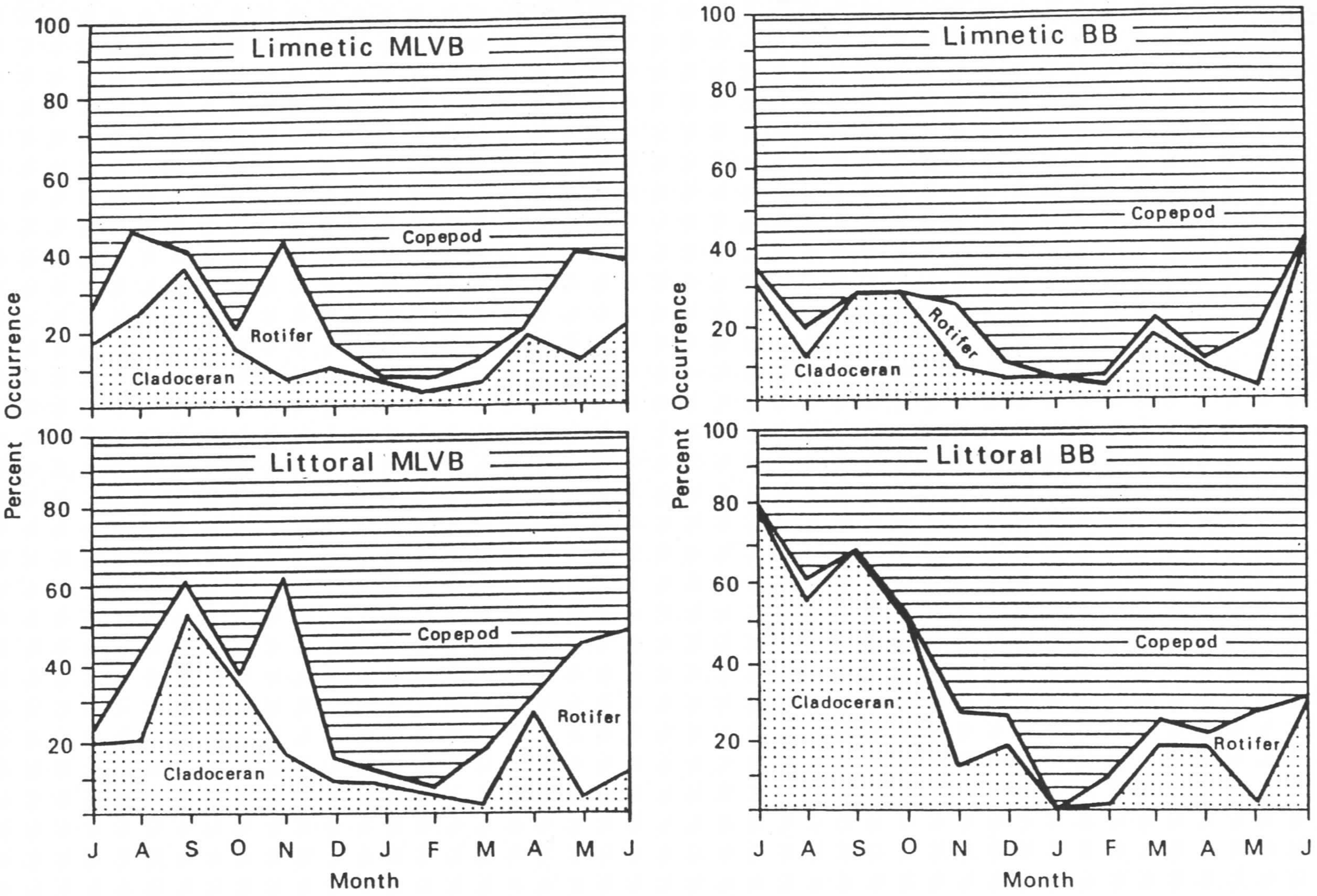

Figure 8. Seasonal percent occurrence of major zooplankton groups (cladoceran, copepod, rotifer) at littoral and limnetic sampling sites in Lake Mead.

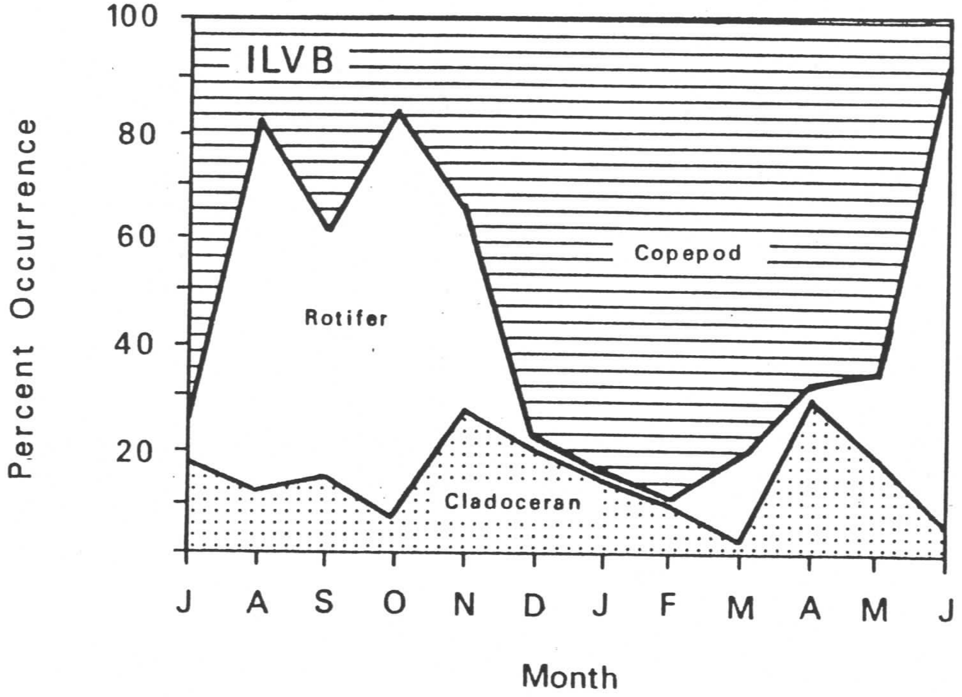

Figure 8. Continued

the littoral zone, cladocerans were the dominant zooplankton in summer and early fall and codominated with copepods in mid fall (Fig. 8).

The average density of each zooplankton group at each station is presented in Figure 9. The average number of cladocerans was similar in all inshore areas. Difference at limnetic sites, although lower than at littoral sites, were also minimal. Copepod densities were higher in ILVB and littoral MLVB and at both BB stations. Rotifer density was highest in ILVB, moderate in the littoral MLVB and low in Boulder Basin.

Seasonal and Spatial Heterogeneity in Zooplankton Abundances

Inner Las Vegas Bay

All major groups (cladoceran, copepod, rotifer) were typically higher in density in the inner Las Vegas Bay (Figs. 10-12). Cladoceran densities were lowest during the summer months, but increased sharply in fall and remained relatively high throughout the winter (Fig. 10). Cladocerans decreased again in March, but increased abruptly in April and May and then declined again at the

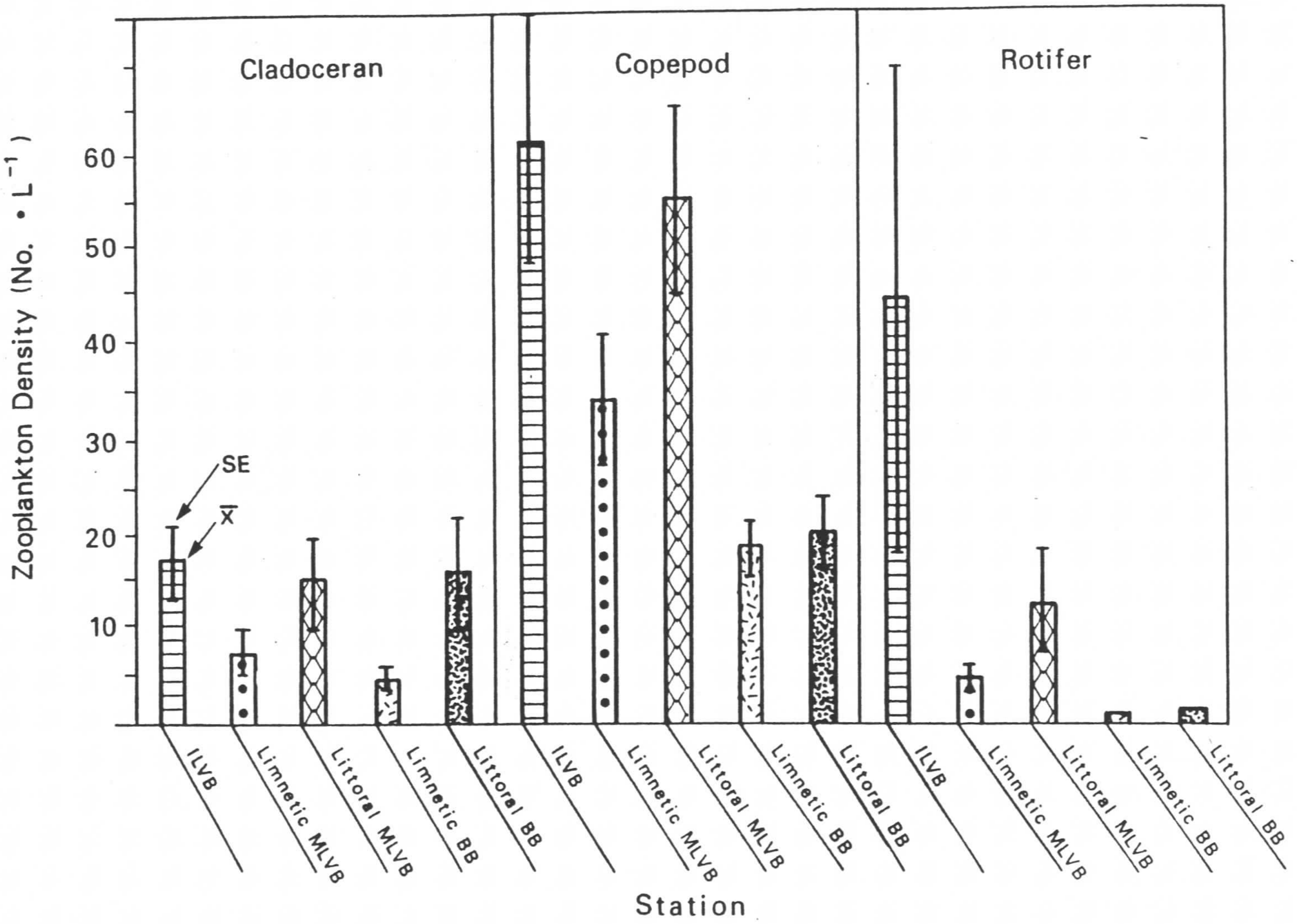

Figure 9. Average zooplankton density for each major group (cladoceran, copepod, rotifer) at littoral and limnetic sampling sites in Lake Mead.

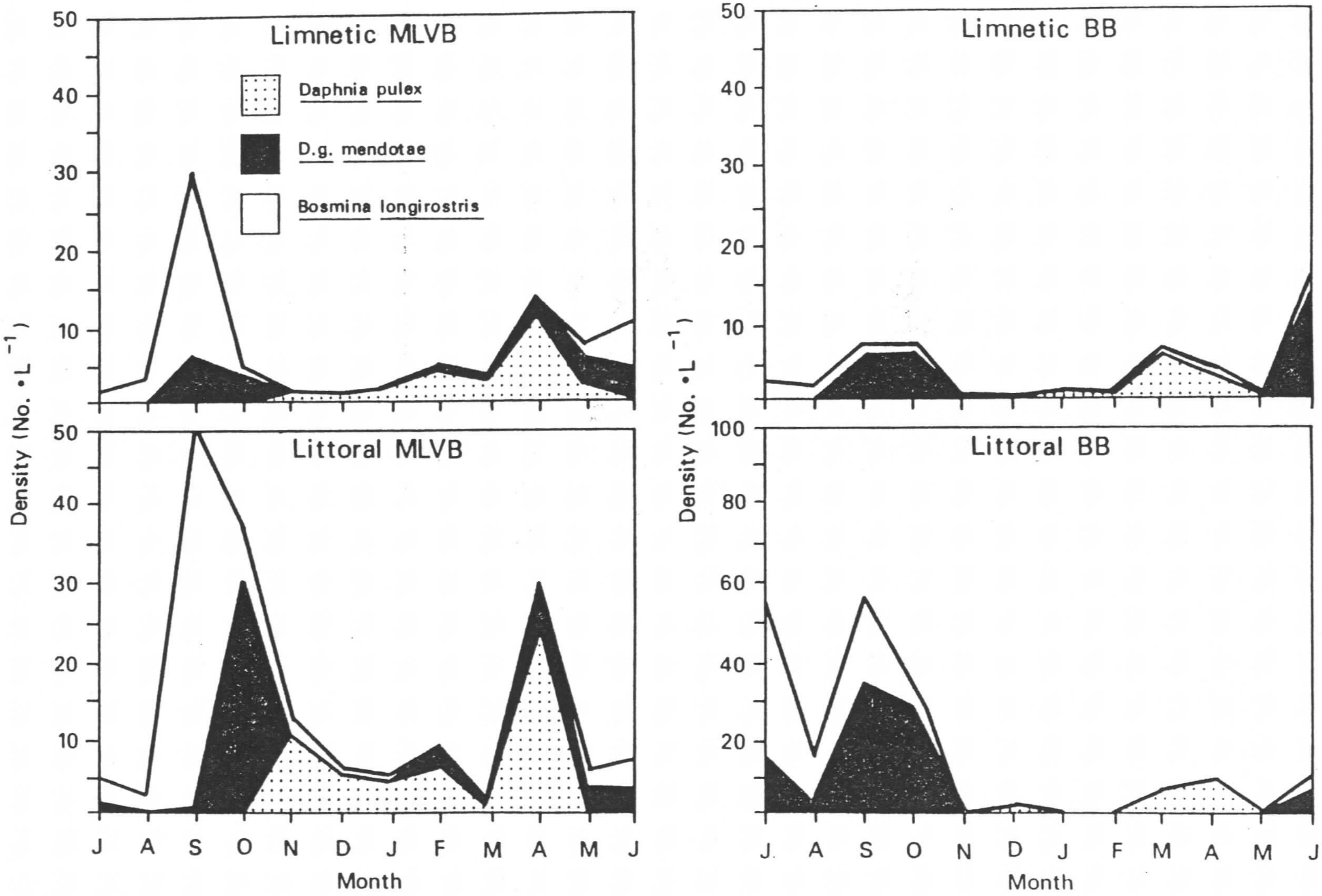

Figure 10. Seasonal densities of major cladoceran species at littoral and limnetic sampling sites in Lake Mead.

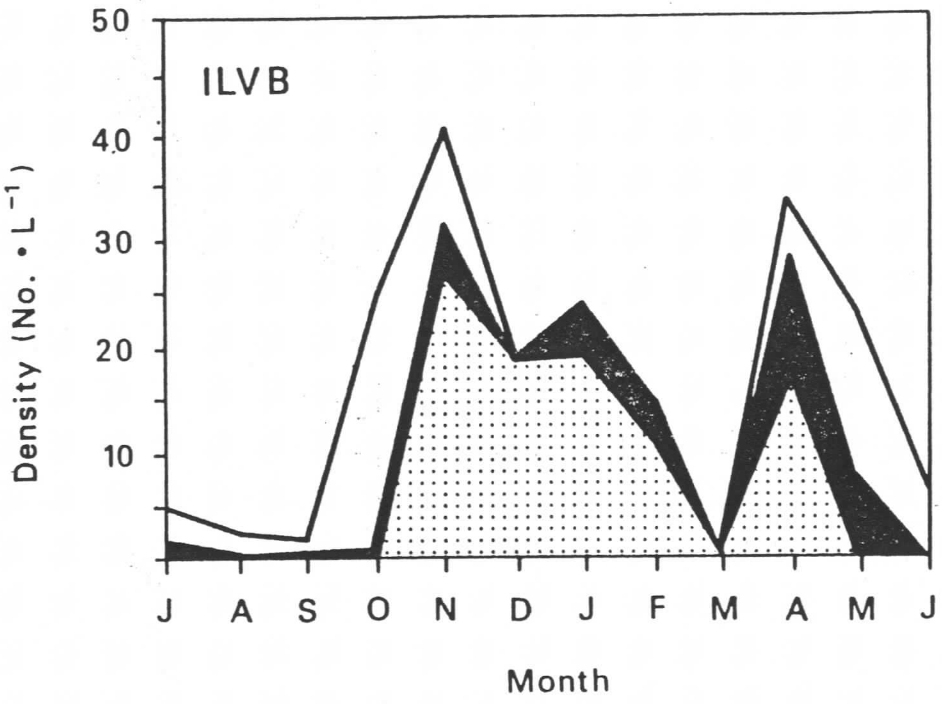

Figure 10. Continued

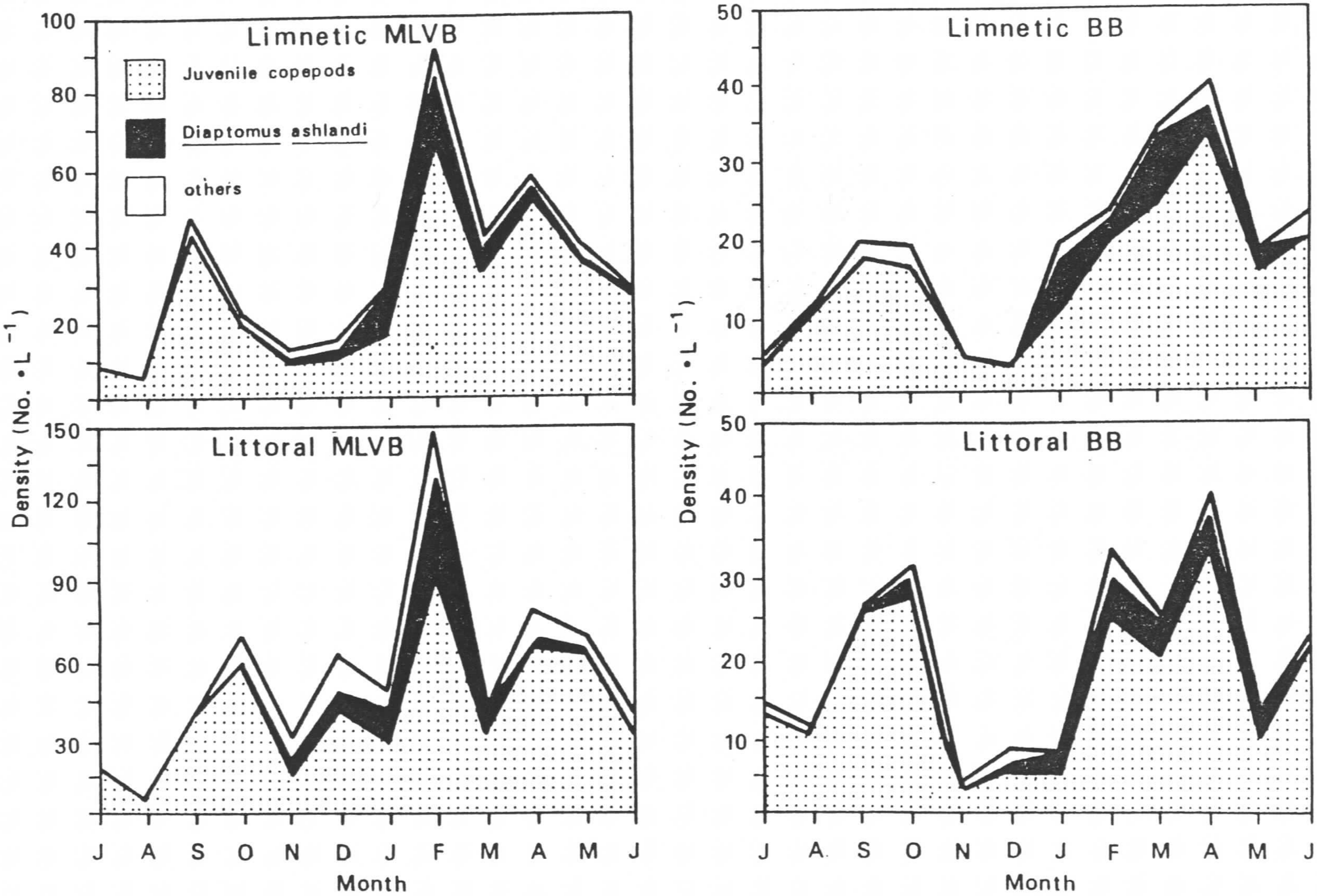

Figure 11. Seasonal densities of major copepods at littoral and limnetic sampling sites in Lake Mead.

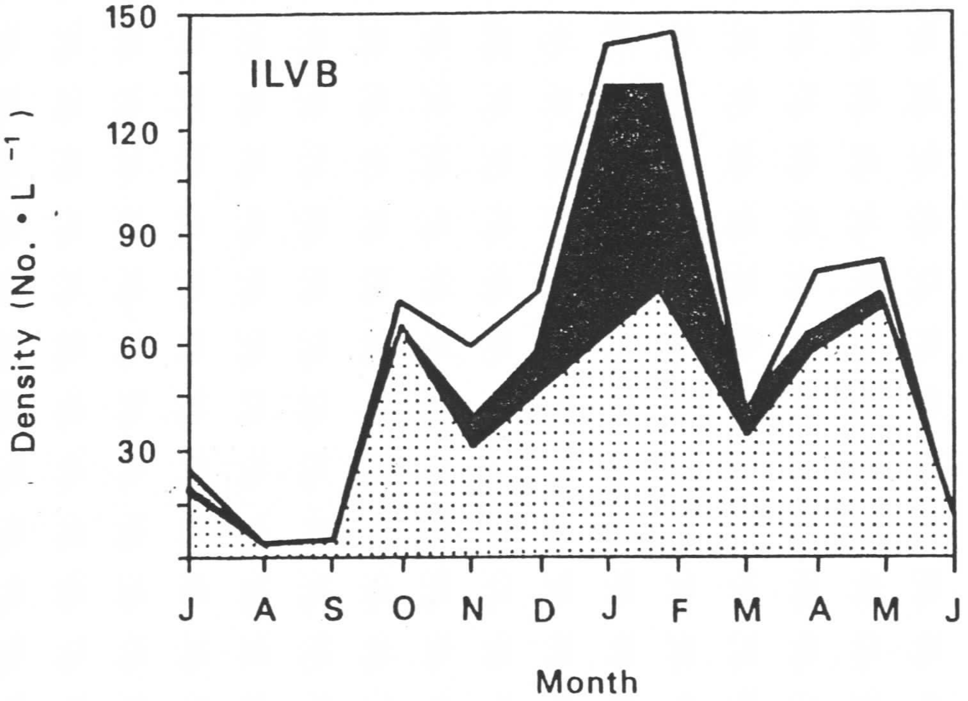

Figure 11. Continued

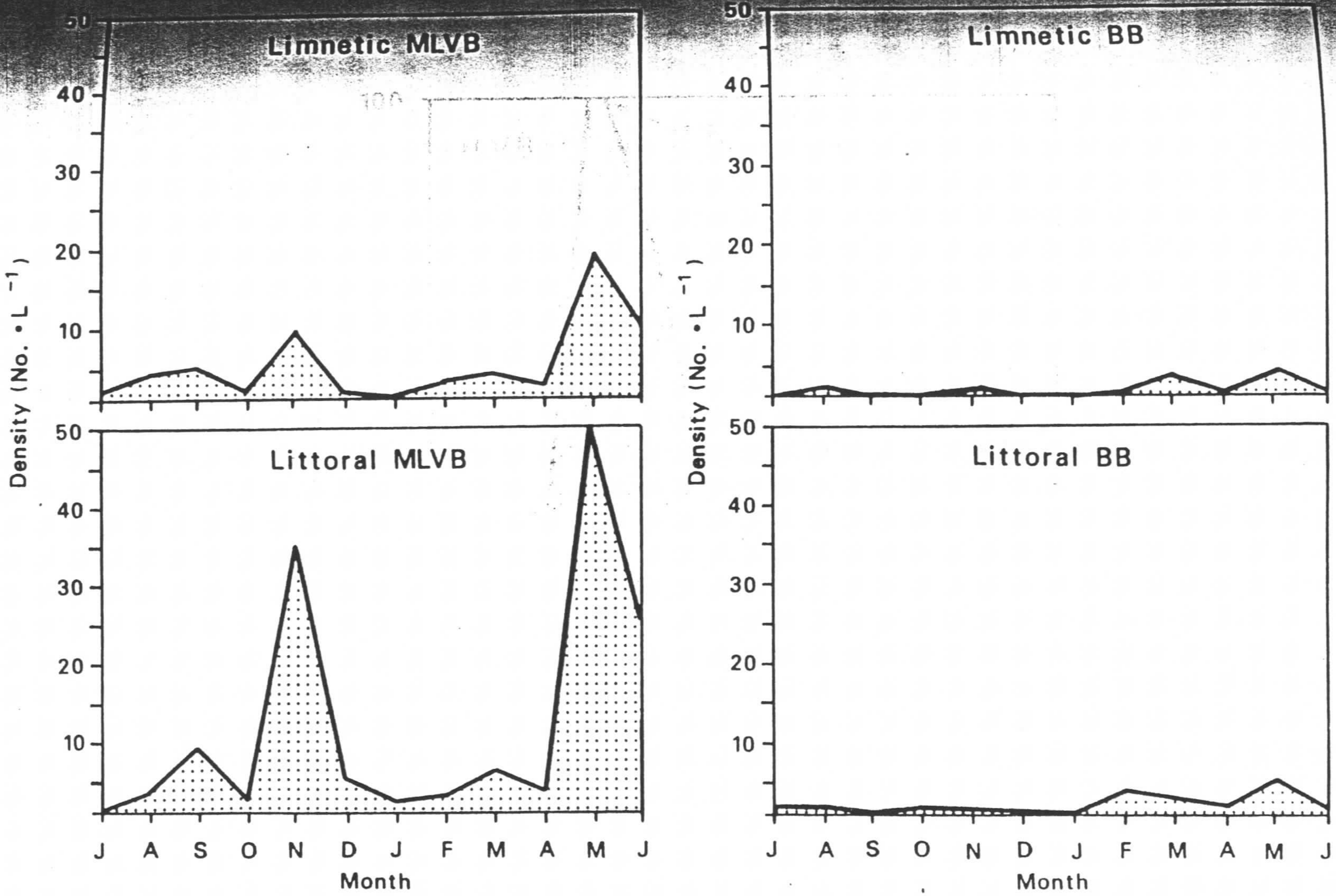

Figure 12. Seasonal rotifer densities at littoral and limnetic sampling sites in Lake Mead.

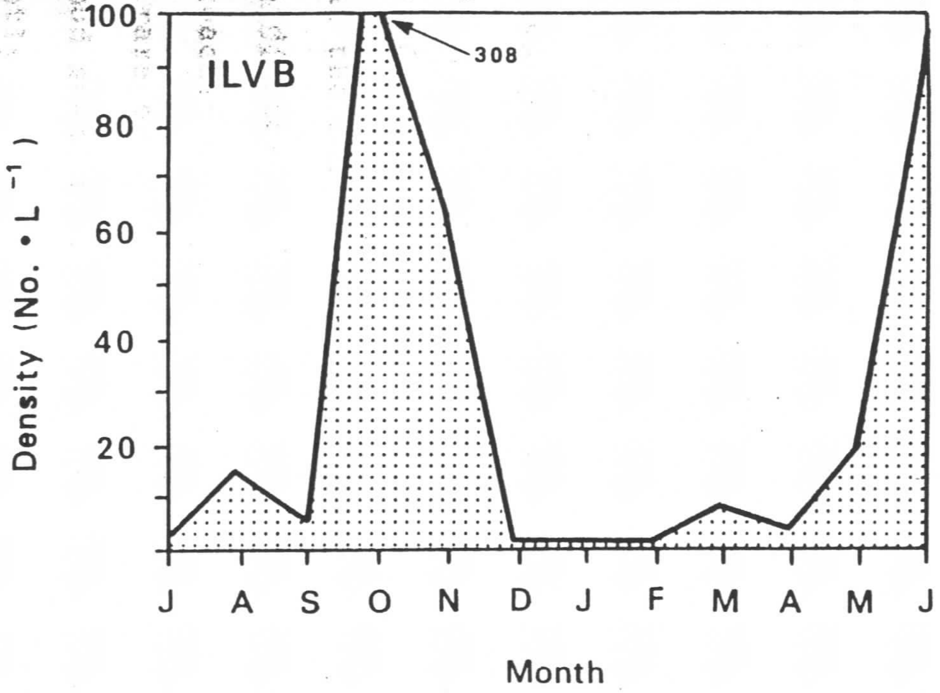

Figure 12. Continued

end of the study in June 1985.

All dominant zooplankton species showed clear seasonal patterns of abundance. Bosmina longirostris was the dominant species during the summer, although less than $5 \cdot l^{-1}$, and reached its maximum in the spring and fall (between $10\text{-}23 \cdot l^{-1}$ (Fig. 10). Daphnia pulex was not present during the summer, but it increased in winter and became the dominant cladoceran. D. pulex also peaked during April. D. galeata mendotae was present in low abundance throughout the year but showed a similar seasonal pattern to D. pulex (Fig. 10).

Copepods in ILVB were dominated by juveniles for most of the year (Fig. 11). Juvenile densities ranged from about $10 \cdot l^{-1}$ in the summer to an average of about $50 \cdot l^{-1}$ during the fall, winter and spring. Adult Diaptomus ashlandi increased in abundance during the winter months and reached densities of nearly $70 \cdot l^{-1}$ (Fig. 11). They were rare or absent for the rest of the year. All other copepod species were rare in ILVB and densities were slightly higher during the winter and spring.

Rotifer densities were also highest in the ILVB (Fig. 12). Densities increased dramatically during the fall when Polyarthra spp. and Syncheata sp. peaked. Polyarthra spp. was the dominant rotifer during winter and spring although its density was usually very low. In early summer, a large peak in rotifer density occurred due mostly to an increase in *Trichocerca cylindrica* and *Polyarthra* spp. *Asplanchna priodonta* became most abundant in late summer and remained abundant through the early winter.

Middle Las Vegas Bay

Successional patterns in MLVB and ILVB were generally similar (Fig. 10-12). However, actual densities were quite different and there were clear differences between littoral and limnetic zooplankton densities in MLVB.

During the summer, *B. longirostris* dominated the entire zooplankton community (Fig. 10) and its density was greater in the littoral zone. Peak abundance occurred during September, a month earlier than in ILVB.

D.g. mendotae peaked in the limnetic zone in September, but not until October in the littoral zone (Fig. 10). Its density at this time was much higher in the littoral zone. Numbers were typically lower in the winter and slightly higher during the spring and early summer in both inshore and offshore areas.

D. pulex was the dominant cladoceran in winter and remained dominant through spring in both habitats (Fig. 10). However, densities were higher in the littoral zone. The seasonal pattern for *D. pulex* in ILVB was similar to the pattern in the littoral of MLVB.

In MLVB, the copepod community was dominated by juveniles during the entire year (Fig. 11). Juvenile densities were typically lower in summer and then increased in fall. Copepod densities showed differences between littoral and limnetic sites during the fall. They were highest during winter in both habitats.

Diaptomus ashlandi was the dominant adult copepod at both MLVB stations during the winter and early spring (Fig. 11). In late winter, densities reached about $45 \cdot 1^{-1}$ in the littoral zone and about $25 \cdot 1^{-1}$ in the limnetic zone.

Peak rotifer abundance (Fig. 12) occurred in October in ILVB and a month later in MLVB. Another peak occurred in June in ILVB but in May in MLVB. Rotifer density was much lower during the winter, early spring and summer. In addition, a higher density was found in the littoral than the limnetic zone of MLVB.

Boulder Basin

Densities of all zooplankton were lowest in Boulder Basin (Fig. 10-12) where rotifers were virtually absent for the entire year (Fig. 12). Cladocerans were also sparce in BB (Fig. 10). At the limnetic station B. longirostris peaked in summer and fall, but was relatively rare the rest of the year (Fig. 10). Its density was much higher in the littoral zone during peaks and it was the dominant cladoceran during the summer. D.g. mendotae also peaked during summer and fall (Fig. 10). It was the dominant cladoceran during the fall and early summer at both stations (Fig. 10). D. pulex was the dominant cladoceran during the winter and peaked at a relatively low density during the spring (Fig. 10). The littoral station in BB had a much higher cladoceran density during the summer than did any other station.

Juveniles dominated the copepod community in BB, although densities were lower than in Las Vegas Bay (Fig. 11). Densities were bimodal with a peak in fall and again in late winter/ early spring. Littoral and limnetic numbers were generally similar in both areas of BB.

D. ashlandi was the dominant adult copepod in Boulder Basin. It occurred in late fall through winter and spring. The population peaked in winter and early spring, although its density was low ($>10 \cdot l^{-1}$). All other adult copepod densities were low throughout the year. Generally, copepod densities were similar in both inshore and offshore sites in Boulder Basin.

Relationships of Zooplankton to Environmental Factors

As seen in Table 6, correlation coefficients (r_s) of

Table 6. Spearman correlation of zooplankton density at littoral and limnetic stations with physical and biological measurements.

Sta	T	DO	Cond	pH	Light	Fluor	Fish
ILVB	-.212*	.001	-.247*	.039	.132*	-.149*	.085*
MLVB	-.002	.156*	.265	.136*	.056	.014	.007
LMLVB	-.041	.025	-.048	.056	.000	-.090*	.036
BB	.070	.031	.013	.167*	.067	-.046	.053
LBB	.246*	-.028	.295*	-.077	.029	-.191*	.048

*=P<0.05

environmental and biolgical factors to average zooplankton densities at each station were low and few were significant ($P<0.05$). No clear pattern was observed between zooplankton density and temperature, dissolved oxygen, conductivity, light extinction or relative fish abundance. A slightly positive and significant correlation was found for pH at all limnetic stations. Algal fluorescence showed a slightly negative and significant correlation with zooplankton density for all littoral stations.

Most physical and biological measurements did not correlate to zooplankton density (Table 7). Temperature and species density were frequently correlated, however, this was especially true for juvenile _Diaptomus_ and adult _D. ashlandi_. Several species showed a significant correlation to DO and conductivity. Light transmittance, pH and algal fluorescence were in general not significantly correlationed to species density. The correlation between relative fish abundance and zooplankton density was positive and significant for most species.

The One-Way ANOVA probability showed significant differences in zooplankton density between stations (Table 8). A SNK test showed that zooplankton densities in ILVB and littoral zone of MLVB were, however, statistically similar.

Table 7. Spearman correlation of zooplankton species density with physical and biological measurements.

Sp**	T	DO	Cond	pH	Light	Fluor	Fish
n	-.169*	.102	.022	.075	-.155*	.140*	.189*
c	-.246*	.096	-.049	.210*	.004	.136*	.099
m	.286*	-.246*	.284*	.159*	-.039	.024	.173*
d	-.612*	.400*	-.332*	-.011	-.027	.072	.089
Cbt	-.296*	.235*	.129	.153*	-.174*	.186*	.328*
Me	.109	-.002	.278*	.130	-.003	.169*	.396*
Da	-.618*	.463*	-.264	-.092	-.039	.003	.217*
Dr	-.004	.056	.174*	-.033	.090	-.096	.328*
Ds	-.205*	.204*	.151	-.046	.179*	.177*	.493*
Bl	.372*	-.102	.433*	-.100	-.126	-.155*	.150*
Dgm	.217*	-.213*	.252*	.109	.025	-.083	.216*
Dp	-.195*	.242*	.165*	.126	.007	-.019	.333*
r	.163	.281*	.226*	.142*	-.095	.250*	.236*

*, P>0.05

**, n=nauplii, c=_Cyclops_ copepodites, m=_Mesocyclops_ copepodites, d=_Diaptomus_ copepodites, Cbt=_Cyclops bicuspidatus thomasi_, Me=_Mesocyclops edax_, Da=_Diaptomus ashlandi_, Dr=_D_. _reighardi_, Ds=_D_. _siciloides_, Bl=_Bosmina longirostris_, Dgm=_Daphnia galeate mendotae_, Dp=_D_. _pulex_, r=rotifers

Table 8. One-way ANOVA comparing average zooplankton densities at each station in Lake Mead. A SNK test shows which stations have statistically similar zooplankton densities.

	DF	SS	MS	F ratio	F prob
ANOVA	4	12408.73	3102.18	9.694	.000

SNK - zooplankton density at ıLVB = littoral MLVB

ALGAL FLUORESCENCE

Average epilimnetic algal fluorescence was relatively higher during the summer (Fig. 13). The ILVB typically had much higher algal fluorescence than all other stations. Fluorescence peaked in July, declined during late summer, reached a minimum in winter and increased again in early spring in the inner Las Vegas Bay.

The littoral MLVB site had higher fluorescence than did the limnetic station during mid-summer, but at other times both stations were similar. Fluorescence was low at both BB sites and seasonal differences were small.

RELATIVE FISH ABUNDANCE

Relative fish abundance was highest in ILVB (Fig. 14) where fish were abundant to very abundant throughout most of the year. The limnetic MLVB ranked second highest although it was much lower than ILVB. Fish abundance in MLVB was high in the summer, declined in fall, was low in winter, and increased again in spring. Inshore and offshore sites in MLVB were similar (Fig. 14).

Littoral and limnetic zones of BB had the lowest relative fish abundances (Fig. 14). Some fishes occurred there in the summer and fall, but abundances were very low

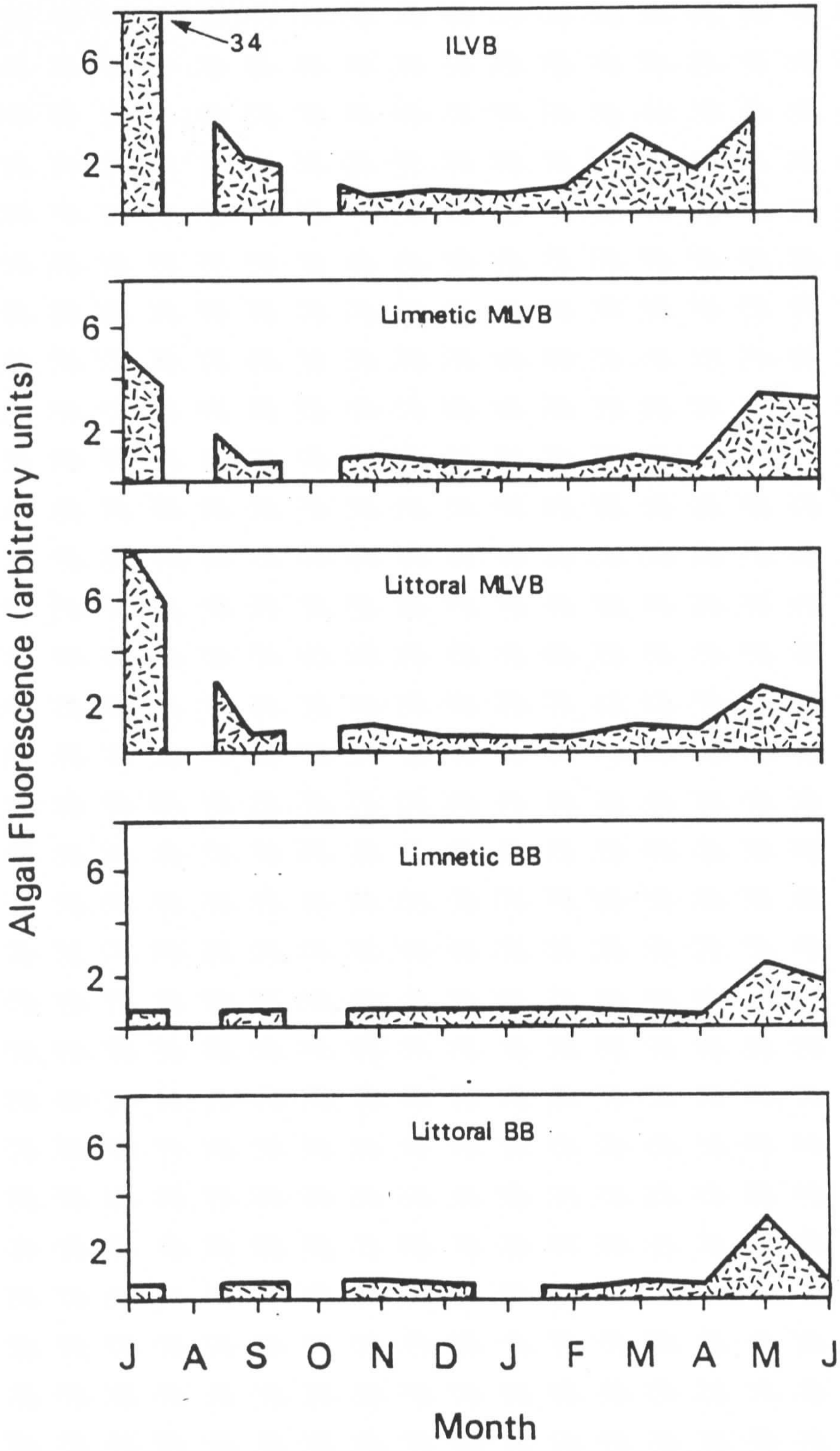

Figure 13. Relative algal fluorescence at littoral and limnetic sampling sites in Lake Mead.

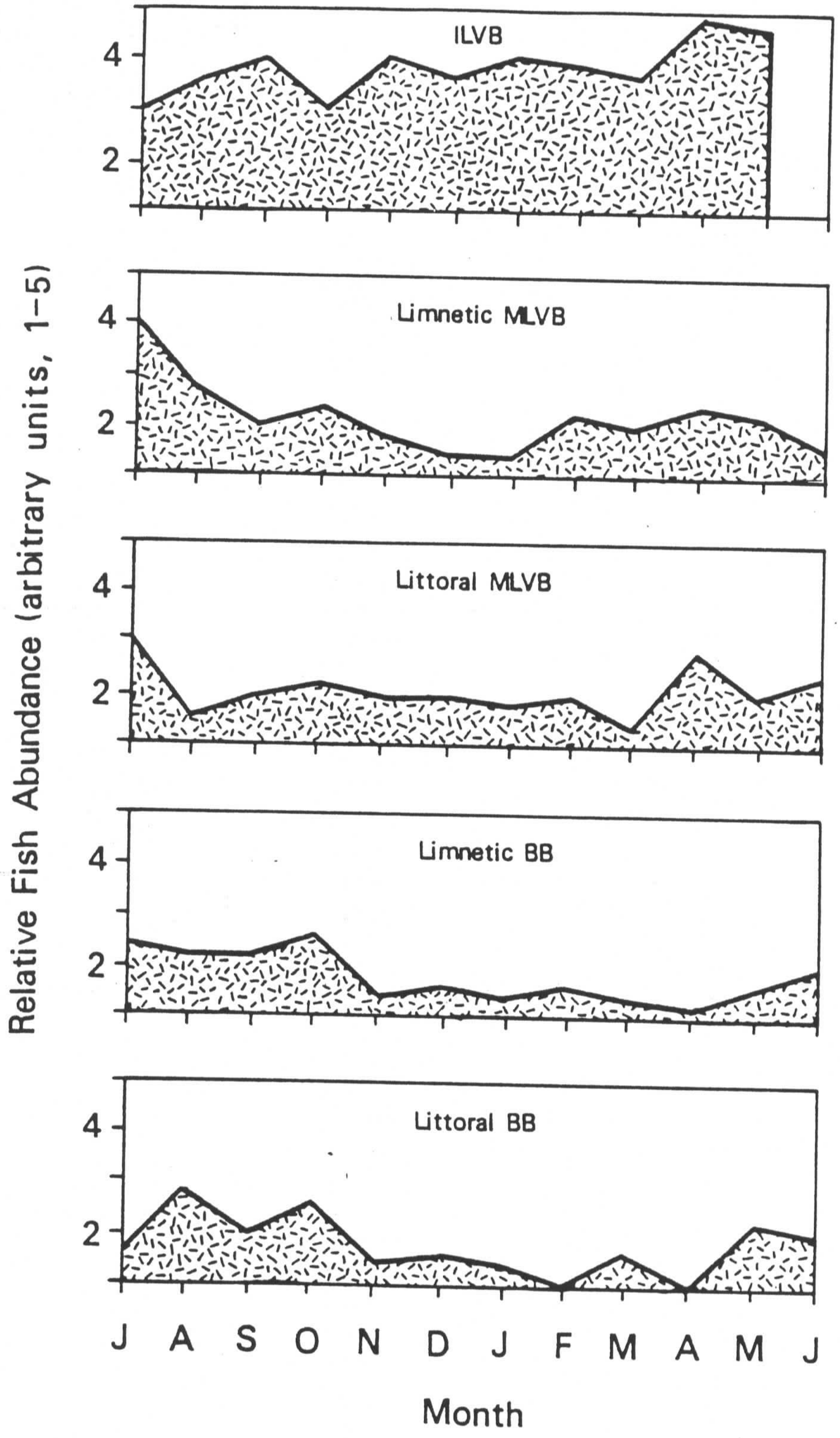

Figure 14. Relative abundance of fish at littoral and limnetic sites in Lake Mead.

in winter. Seasonal patterns were similar in both inshore and offshore areas.

DISCUSSION

SPECIES COMPOSITION - LITTORAL vs. LIMNETIC

A diverse community of microcrustaceans and rotifers were found in Lake Mead during the course of this study. Twenty-seven species were considered as true planktonic, or limnetic, and fifteen species of littoral organisms (Edmondson 1959, Pennak 1978) were also found, although their abundances were very low. Many of the littoral species were only found once and rotifers were the dominant littoral microfauna with regard to abundance and diversity. The most common microcrustacean and rotifer species found in the littoral zone of Lake Mead were planktonic which were also dominant in the limnetic zone.

Normally, zooplankton avoid inshore areas during the day (Seibeck 1964, 1980). This study indicates, however, that in Lake Mead the littoral zone is dominated entirely by zooplankton. Youngs (1983) also found that zooplankton dominated coves in the Virgin Basin in Lake Mead. The densities of littoral microfauna were low and similar between inshore and offshore areas. This suggests that the species described as littoral by the literature (see Edmondson 1959, Pennak 1978) may not be strict littoral inhabitants.

Zooplankton species diversity is usually associated with a combination of several factors. Sprules (1975) found that pH, the size and depth of a lake and the number of different types of predaceous fish accounted for most of the variation in zooplankton species diversity. Those lakes that were small, shallow and had a low pH had the least variability. Increased selective predation by different fishes increased the diversity of the plankton community.

Littoral zones tend to have more habitat heterogeneity than limnetic zones, creating a diversity of microfaunal niches associated with aquatic plant growth. Colinvaux and Steinitz (1980) noted that larger lakes generally had a greater diversity of microcrustaceans. The larger lakes had from 8-9 species as opposed to having only 2-3 species in smaller lakes. Lakes ranged in size from nearly 8.0 to 6.6×10^6 m^2 and maximum depths from 0.5 to 132 m. Pennak (1966) found, on average, 2.4 copepod species, 4.9 cladoceran species and 7.7 rotifer species in the vegetation during the summer. In each group, there was from one to several species less in open water areas. The amount of habitat heterogeneity is the most significant factor in determining species diversity, with a great number of species being found in very heterogeneous habitats (Smyly 1952, Smirnov 1963, Straskraba 1964, Pennak 1966, Whiteside and Harmswoth 1967, Vigerstad and Tilly 1977, Colinvaux and Steinitz 1980, Stolbunova and Stolbunov 1981, Lemly and Dimmick 1982a, Venglinskiy et al. 1985, Green 1986).

In contrast to this, Fryer (1985) found that some species were associated with larger lakes or smaller ponds regardless of habitat heterogeneity. Some lakes with extensive macrophytic growth had fewer littoral species (mostly chydorids) than smaller lakes with fewer plants. Fryer (1985) postulated that a heterogeneous habitat was not a neccessity for having a large diverse group of microfauna in many lakes. Other more likely causes of increasing species composition are the availability of different prey, habitat preference, dispersal of eggs, production of resting eggs, or the rate of which a species can colonization.

Smirnov (1963) found that in lakes having a small vegetated littoral zone, there were fewer numbers of species of littoral microcrustaceans. Many lakes that have a greater littoral species diversity have a larger, vegetation-filled littoral zone, ranging from 24% to nearly the entire lake (see Straskraba 1964, Pennak 1966, Vigerstad and Tilly 1977, Stolbunova and Stolbunov 1981, Lemly and Dimmick 1982a, Williams 1982). For example, Lake Itasca, Minnesota, has a maximum depth of 14 m, a mean depth of 5.2 m, a littoral zone comprising 55% of the lake and has 24 littoral chydorid species (Williams 1982). However, lakes with little or no vegetation in littoral areas have a microcrustacean community with species abundance similar to that in limnetic areas (Smirnov 1963, Straskraba 1964, Lemly and Dimmick 1982a).

In Lake Mead, there is an average depth of about 55 m and Las Vegas Bay and Boulder Basin consist of an average volume of 8.95 x 10^9 m^3 and a surface area of about 1.33 x 10^5 m^2. The lower basin of Lake Mead is very large and the littoral zone averages about 11% of the surface area. Because the reservoir is relatively steep sided (resulting in a small littoral zone), has temporal water level fluctustions, experiences high winds and is dominated by the limnetic zone, there is tremendous exchange between inshore and offshore areas. Physical and chemical conditions were generally uniform between adjacent areas. This, in turn, may effect the distribution of microorganisms and possibly explain why similarities were found between inshore and offshore areas.

Rotifers were the most diverse (10 species) and most abundant of littoral microfauna identified in this study. Trichocerca cylindrica was the most abundant littoral rotifer, and it became abundant during late June in ILVB (about $33 \cdot l^{-1}$) and at both littoral and limnetic sites of the MLVB (about $7 \cdot l^{-1}$). Other studies have found that rotifer abundance in the littoral zone is reduced when there is a dense amount of aquatic vegetation (Hasler and Jones 1949, Pennak 1966). Although rotifer densities are affected by vegetation, species composition becomes more diverse as the concentration of vegetation increases (Pennak 1966, Green 1986). Rotifer densities and species diversity in Lake Mead follow a similar pattern. Their densities were somewhat higher in inshore sites of the ILVB and MLVB. This may be due to the lack of aquatic vegetation. A recent cove survey (using SCUBA) of the lower basin in Lake Mead in 1986 indicates that most inshore areas were depauperate of aquatic vegetation in winter and if vegetation was found during summer and fall it was generally in small patches and no deeper than 5 m (Jennifer Haley, pers. comm.).

Even though the number of rotifer species was high in Lake Mead, species composition of rotifers was also very similar in both littoral and limnetic areas. The species composition of copepods and cladocerans were also similar between the two zones. This study indicates that species composition of littoral microfauna is lower than it otherwise would be if a large littoral zone with dense aquatic vegetation was present.

SEASONAL AND SPATIAL ZOOPLANKTON SPECIES ABUNDANCE

There are numerous factors regulating zooplankton poulations and community dynamics, including: changes in phytoplankton abundance and composition (Porter 1977, Gliwicz et al. 1981, Edmondson and Litt 1982, Infante and Litt 1985); effects of competitive interactions (Lynch 1978, Smith and Cooper 1982, DeMott 1983, Romanovsky and Feniova 1985, Vanni 1986); invertebrate and vertebrate predation (Dodson 1974, McNaught 1975, Gliwicz et al. 1981, Gilyarov 1982); and physical environmental conditions (Moore 1980, Seitz 1980).

Previous studies in Lake Mead have found that a positive relationship existed between phytoplankton biomass (chlorophyll-a) and average zooplankton density (Paulson and Baker 1983, Wilde 1984). This was also evident during my study. Densities of zooplankton were considerably higher in the more productive areas of the inner and middle Las Vegas Bay than farther out into Boulder Basin where phytoplankton biomass (fluorescence) was low. This type relationship has also been found in other lakes (Anderson and Green 1975, DeBernardi et al. 1985). McCauley and Kalff (1980) reported that zooplankton biomass was significantly correlated to total phytoplankton biomass. They found an even higher relationship between nannoplankton and zooplankton emphasizing the importance of the former to zooplankton.

Summer Decline in Zooplankton Density

During summer, water temperature was warmer and chlorophyll fluorscence was higher, but relatively few zooplankton were present. Although in winter and spring when the water temperature was considerably colder and algal biomass was lower, zooplankton densities were clearly higher. There may be several possibilities why animal abundance was low during the most productive time of the year. These include competitive interaction, changing phytoplankton community structure, and predation.

Part of the size-efficiency hypothesis predicts that large species of zooplankton persist and competitively displace smaller species (at least for cladocerans) in the absence of fish predation (Brooks and Dodson 1965). In most instances, larger cladocerans can outcompete small zooplankton (DeMott and Kerfoot 1982, Gilbert 1985, Vanni 1986), because they filter large amounts of food, due to a more efficient filtering apparatus (i.e., larger filtering area) (Egloff and Palmer 1971, Brendelberger and Geller 1985), they have faster filtering rates (Bogdan and McNaught 1975), and they are able to alter diurnal feeding times when certain prey sizes are spatially segregated or when the nutritional value of prey is highest (see Starkweather 1983).

During the summer, small zooplankton, i.e., rotifers, copepod nauplii and copepodites and Bosmina longirostris completely dominated the community, although densities were low. Gilbert (1985) showed that Daphnia could displace rotifers by reducing food densities and Vanni (1986) found that Daphnia could outcompete Bosmina and copepod nauplii in the same manner. Accordingly, large species should dominate during the summer in Lake Mead. It appears there must be other factors accounting for the low summer densities and the dominance of small species.

Most of the zooplankton species found in Lake Mead are herbivorous, with the exception of late copepodid and adult Mesocyclops edax and Cyclops bicuspidatus thomasi and Asplanchna priodonta, Pleosoma, Syncheata and Trichocerca cylindrica. The feeding behavior, type of feeding apparatus and prey selectivity separate the feeding niches of many species (Brendelberger and Geller 1985, Geller and Muller 1981, Vanderploeg and Paffenhofer 1985). This suggests that a species may lose dominance or die out not only from direct competitive interaction, but also as the composition of the phytoplankton community changes. A species may lose dominance because algae become too small or too large for it to consume (Geller and Muller 1981). A species of zooplankton may not gain enough nutrition at times when algae have protective coatings (Porter 1976, 1977), or it may not be able to collect enough prey because prey concentrations fall below its threshold feeding level (Gliwicz et al. 1981, Gilyarov 1982).

Cladocerans feed passively by fitering an abundance of prey. Particle collection may depend on the distance between setae and setules of filtering combs (Geller and Muller 1981, Gophen and Geller 1984, Hessen 1985, Brendelberger et al. 1986). However, smaller particles are retained than the smallest setule gap which may result from "piggybacking" (Porter et al. 1983) or surface charge attractions (Gerritsen and Porter 1982).

Calanoid copepods are suspension feeders and produce flow fields to chemically and physically detect prey in advance of capture (Strickler 1982). Particle capture may be active by grabbing prey individually, or passive (Koehl and Strickler 1981, Paffenhofer et al. 1982, Price et al. 1983, Vanderploeg and Paffenhofer 1985). Like cladoceran feeding, particle retention for copepods is still a function of setae and setule distances, although it is more important in passive feeding (Vanderploeg and Paffenhofer 1985). This feeding behavior allows calanoid copepods to be very selective and also handle prey that other zooplankton cannot capture or ingest (Price et al. 1983, Vanderploeg and Paffenhofer 1985).

Because of the non-selective prey capture of most passive feeding cladocerans, they appear to become very dominant in dense homogeneous environments of preferred prey (DeMott 1986, Vanni 1986). Therefore, as the frequency of quality prey in the environment decreases, the species that can invariably select preferred prey; e.g., by taste, size or nutritional value; dominates (Vanderploeg and Paffenhofer 1985, DeMott 1986).

Based on prey selection, Geller and Muller (1981) noticed that zooplankton were seasonally variable in lakes of different trophy. Calanoid copepods dominate in oligotrophic lakes that have many large and irregular shaped phytoplankton. In mesotrophic lakes, macrofiltering zooplankton, e.g., Holopedium gibberum and calanoid copepods dominate in the winter when prey is large or irregular in shape, and several species of Daphnia with medium size filters dominate during all other times of the year when algae become smaller. Bacteria is abundant in summer in eutrophic lakes, therefore species with fine mesh filtering apparatus, e.g., Diaphanosoma brachyurum and Chydorus sphaericus usually dominate and species feeding predominatly on nannoplankton such as Bosmina longirostris and some Daphnia species, are dominant in the spring and fall. Copepods dominate as prey becomes larger in winter (Geller and Muller 1981).

Janik (1984) studied lake wide phytoplankton communities in Lake Mead and found that nannoplankton dominanted during the summer, although filamentous bluegreen algae (Lingbya beirgei mostly) also peaked at this time (about 10% of the phytoplankton community). The presence of increasing L. beirgei may be the cause for the dominance of small zooplankton (see Geller and Muller 1981, Orccutt and Pace 1984), because larger cladocerans are physically inhibited by filaments during feeding (Porter 1977, Webster and Peters 1978). Infante and Abella (1985) found that Oscillatoria inhibited the feeding of several species of Daphnia and with increasing abundance of Oscillatoria, slower growth rates, lower fecundity and higher mortality occurred in Daphnia. Infante and Abella (1985) and Edmondson and Litt (1982) concluded that large abundances of filamentous bluegreen algae, especially Oscillitoria, was the cause for a serious decline in abundances of most large species of Daphnia in Lake Washington.

It is natural for smaller bacteria and nannoplankton feeding zooplankton to dominate when filamentous bluegreen algae is present. Orcutt and Pace (1984) found that rotifers become dominant because they can selectively feed on bacteria without interference from filamentous algae. Bosmina longirostris passively feeds on small particles and actively feeds on large particles (DeMott 1982, Bleiwas and Stokes 1985) and can chemically detect and select preferred prey (DeMott 1986). Therefore, it can effectively select prey in mixed suspensions of preferred and nonpreferred prey (DeMott 1982) and feed on nannoplankton when filamentous algae is abundant (Webster and Peters 1978, Geller and Muller 1981).

In Lake Constance, Knisely and Geller (1986) found that *Daphnia galeata* did not eat filamentous bluegreen algae when, at the same time, *D. hyalina* did. This suggests that *D. galeata* can be selective and can survive in the presence of filamentus bluegreen algae. In the Las Vegas Bay, however, *D. galeata mendotae* was either not present during summer, or it was very rare. It is also one of the larger cladocerans in Lake Mead measuring an average 1.05 mm (Sollberger, unpub. data). It has a large filtering area, comparable to *D. pulex* (Brendelberger and Geller 1985) and should have been able to displace small rotifers and cladocerans. Even if the survival of *Daphnia* is reduced with increasing densities of filamentous algae (Infante and Litt 1985), concentrations of filamentous bluegreen algae do not appear high enough to be the cause for the complete absence of larger zooplankton in the summer in Lake Mead.

Brooks and Dodson (1965), Hutchinson (1971), O'Brien (1979), Hurlbert and Mulla (1981), Gilyarov (1982), Hamrin (1983), Luecke and O'Brien (1983), Evans (1986), Arumugam and Geddes (1986), Konkle and Sprules (1986) and others have found that planktivorous fish predation is responsible for reducing the abundance of large zooplankton species. Jacobs (1977), Seitz (1980) and Dawidowicz and Pijanowska (1984) conclude that predation relaxes competitive interaction between microfauna species and those species that can escape predation dominate at times. There are several ways zooplankton reduce predation: reduce visibility (Zaret and Kerfoot 1975), rapid escape (Confer and Blades 1975, Drenner and McComas 1980, Kerfoot et al. 1980), predator detection by mechano- or chemo- receptors (Kerfoot et al. 1980, Strickler 1984), akinesis (playing dead) (Kerfoot 1978, Kerfoot et al. 1980), hiding in vegetation (Fairchild 1981) or in deep water (Rippingale and Hodgkin 1974, Zaret 1975, Zaret and Suffern 1976, Iwasa 1982, Luecke and O'Brien 1981), and reduction in size (Brooks and Dodson 1965, Dodson 1974, Zaret and Kerfoot 1975).

Particulate feeding planktivores visually cue on obvious zooplankton (Braum 1967, Werner 1974, Keast 1985). Retention of prey depends on prey size and inter-gill raker spacing (Wright et al. 1983). Therefore because of their effectiveness in locating prey and optimal choice of larger prey, particulate feeding planktivors generally have wide inter-gill raker spacing (O'Brien 1979, Wright et al. 1983).

Clupeid fishes typically are non-selective filter feeders (O'Brien 1979, Janssen 1982). However, they selectively feed (particulate feeding) when young and non-selectively feed (filter feeding, i.e., swimming with mouth open and sieving prey) when older (Janssen 1980). Janssen (1980) also found that filter feeding was favored when prey became dense and small in size, and when feeding at night. Because visual cues are less important for prey selection, filter feeding fish generally have narrow inter-gill raker spacing (O'Brien 1979). Mummert and Drenner (1986) found that inter-gill raker spacing widens with increasing size of gizzard shad (Dorosoma cepedianum). Therefore, plankton selectivity changes as fish grow. This seems to be common in other planktivorous fishes as well (see Mummert and Drenner 1986).

In Lake Mead, relative fish abundance increased in spring and summer. Nearly all species of fish spawn during this time (Jonez and Sumner 1954, Allan and Roden 1978). Littoral fish such as largemouth bass (Micropterus salmoides) spawn in March through June (Morgensen and Padilla 1982) and shortly after so do bluegill (Lepomis macrochirus) and green sunfish (L. cyanelles) (Allan and Roden 1978).

Wilde and Baker (1981) showed that zooplankton comprised the entire diet of largemouth bass fry, 4-19 mm. From 72-89% of the larger fry (up to 67 mm) consumed zooplankton for much of their diet. As yet, there have been no studies in Lake Mead to document bluegill and green sunfish prey selection or their impact on zooplankton communities. However, other studies show that they are size selective, chosing larger and more visible prey (usually cladocerans within a certain size range) (e.g., Werner 1974, Werner and Hall 1974, Janssen 1982).

Threadfin shad (Dorosoma petenense) spawn during May through June (Allan and Roden 1978) in the more productive littoral areas of Lake Mead (Deacon et al. 1972). The adults remain in littoral areas in summer while newly hatched larvae and juveniles occupy limnetic areas (Paulson and Espinosa 1975, Paulson and Baker 1983).

Striped bass (Morone saxatilis) spawn in the inflow areas in Lake Mead during April through May (Allan and Roden 1978). Larvae migrate to limnetic areas and return to littoral areas sometime during the summer (see Paulson and Baker 1983). Zooplankton are known to be an important part of larval striped bass diet (Martin et al. 1985). Albert and Baker (1982) also found that age class I (253-430 mm) and age class II (431-640 mm) striped bass in Lake Mead commonly utilize larger zooplankton (Daphnia) when fish prey was not availible.

Because of prey selection and increased production of larvae, centrarchid predation accounts, in part, for the decline in densities of larger zooplankton species (adult Daphnia and Diaptomus), especially in littoral habitats. However, the decline of zooplankton not only takes place in the littoral zone, but also in the limnetic zone, normally outside the habitat of sunfish.

Although identification of individual fish species is not possible from echo-grams, Paulson and Baker (1983) and Wilde (1984) concluded that threadfin shad and striped bass were the predominant fishes in the more productive areas of Lake Mead. They speculated that threadfin shad and larval striped bass accounted for the majority of the zooplankton predation. Von Geldern (1971) found that threadfin shad were very competitive in the littoral zone, being able to severely reduce the abundance of zooplankton. Others have shown that threadfin shad can effectively crop zooplankton densities in limnetic areas (Baker and Schmitz 1971, Kilambi and Barger 1975).

The abrupt decline of _D_. _pulex_ in both inshore and offshore areas during the spring coincided with the spawning of threadfin shad and striped bass. Because threadfin shad and larval striped bass can crop the larger zooplankton (Paulson and Baker 1983), smaller zooplankton species dominate during the summer. Hurlbert and Mulla (1981) and Dawidowicz and Pijanowska (1984) found that under intensive fish predation, zooplankton communities were dominated by rotifers. Green (1985) also found that due to fish predation small zooplankton such as _Bosmina longirostris_, copepod nauplii and rotifers, dominated in the main body of the lake. Larger crustaceans were found in the smaller creek arms where predaceous fish were less abundant. In Lake Mead, it is more likely that predation is the major factor in the spring and summer succession from larger to smaller zooplankton species. Smaller species may become less susceptible to predation by having reduced selective predation for them, or perhaps they can compensate for predation by high fecundity and reproductive rates (Allan 1976, Gilyarov 1982).

It is typical in Lake Mead that *Daphnia galeata mentotae* replace *D. pulex* (Paulson and Baker 1983, Wilde 1984). Fish, perhaps, selectively crop *D. pulex* because of their large size. Competitive interaction then might be relaxed between the two cladocerans allowing *D.g. mendotae* to increase in numbers. Fish then reduce *D.g. mendotae* populations.

D.g. mendotae produces a helmet in the spring and summer. This helps reduce attacks from vertebrate predators, but more importantly invertebrate predators (Hutchinson 1967, Dodson 1974, Zaret 1975, Kerfoot 1977, Krueger and Dodson 1981). Increasing abundance of *D.g. mendotae* coincides with increasing abundance of the predaceous copepods, *Cyclops bicuspidatus thomasi* and *Mesocyclops edax*. It is unlikely that predaceous copepods were the cause of the decline in *D.g. mendotae* populations in late spring and early summer because copepod densities were already extremely low. It is also unlikely that they were responsible for maintaining low zooplankton densities during summer, because the abundance of copepods also was low in summer. Gilyarov (1982) notes that invertebrate predation typically does not control zooplankton populations, because large invertabrate predators, the ones needed to reduce zooplankton populations, have either low densities due to fish predation; low phytoplankton concentrations during their juvenile stages; or possibly from zooplankton prey having evolved better defenses.

Wilde (1984) stated that the spring succession from the larger _D_. _pulex_ to the smaller _D_._g_. _mendotae_ was temperature related. During my study, _D_. _pulex_ was abundant at temperatures below 20 C and _D_._g_. _mendotae_ was generally found at temperatures above this. Perhaps the effect of temperature is real, because during stratification _D_. _pulex_ was found in the hypolimnion at equivalent temperatures. However, relating cladoceran succession with temperature changes may be misleading, because the number of juvenile fish and, therefore, predation increases as surface waters begin to warm. The hypolimnion then may be a refuge for larger zooplankton species during the summer.

In summary, only the littoral zone showed a significant slightly negative relationship between zooplankton density and algal biomass. Algal biomass was slightly higher in the littoral zone in the summer, although zooplankton densities were about the same between corresponding littoral and limnetic areas. Zooplankton densities were also higher in littoral areas than in linmetic areas during the winter and early spring. This suggests that predation was more intense in inshore areas than offshore areas during the summer.

Temporal and Spatial Heterogeneity in Zooplankton Communities During Fall and Winter

Fall, in Lake Mead is typically a time when zooplankton increase in numbers (see also Paulson and Baker 1983, Wilde 1984). The density of copepod nauplii was low during September (similar to the summer density) at the ILVB, but began to increase or peaked at other stations. The only obvious environmental difference was that the average epilimnetic temperature was much higher in ILVB (38° C). It was nearly 10°C warmer than at other stations, and perhaps responsible for lower zooplankton densities in ILVB. The density of copepod nauplii was higher in the littoral MLVB site during October than September, suggesting that the higher temperature (about 32°C) experienced there also had an effect.

During October at the inner Las Vegas Bay and littoral middle Las Vegas Bay, temperatures decreased to about 21°C.

The density of copepod nauplii increased and they dominanted at this time. It is possible that copepod nauplii emerged from diapause in October at the ILVB because the temperature was too high in September. They were able to emerge in September at the other stations because temperatures were more favorable (from 26-27°C). Hutchinson (1967) indicated that temperature was important for the emergence of diapausing copepod nauplii.

Temporal rotifer densities were also variabile between stations. They were very dense and peaked during October in the ILVB, whereas numbers did not increase and peak until November in MLVB. Burke (1977) speculated that the abundance of rotifers, especially _Syncheata_ which increased in September and October in Lake Mead, was from the resuspension of eggs during fall mixing. However, the inner Las Vegas Bay is usually completely mixed year round but did not show an increase of rotifers until fall. Temperature is also important for the emergence of diapausing rotifers (Hutchinson 1967). However, there were minimal temperature differences between stations. The high temperature during September should not have affected rotifer densities in October and November. Therefore, it appears that the decline in rotifer densities was, perhaps, due to competitive interaction with cladocerans. Rotifers peaked in October before cladoceran densities increased, and significantly decreased in November when the number of cladocerans were higher.

The successional pattern between cladocerans and rotifers was reversed in MLVB. When cladoceran densities significantly decreased in November the number of rotifers significantly increased. However, it seems unlikely that the decline in the cladoceran population was due to competitive displacement by rotifers, because rotifer densities were not high.

Relative fish abundance was high in the ILVB during September, perhaps cropping the cladoceran populations. When the abundance of fish decreased in October the number of cladocerans increased. The decrease in relative fish abundance may represent the time when threadfin shad migrate from the inner Las Vegas Bay to deeper limnetic areas (Deacon et al. 1972, Allan and Roden 1978). The abundance of fish increased slightly in MLVB, possibly shad en route to deeper water. In MLVB, the number of planktivorous fish was low during early fall when there were greater densities of cladocerans. When fish abundance increased in late fall cladoceran densities immediately declined.

Janik (1984) found that the percentage of nannoplankton biomass in the community increased from 20% to nearly 70% from summer to fall. This, perhaps, is why densities of small zooplankton, whether rotifers, copepod nauplii or small cladocerans, reached such high seasonal densities in the fall.

Larger zooplankton species became abundant in late fall and dominated the community. Sommer et al. (1986) also found that large zooplankton increased 2-10 fold during the fall cooling period. In Lake Mead, this is probably due to reduced fish predation. Echo-grams did not show an appreciable decrease in relative fish abundance, especially in ILVB, however, by then many littoral juvenile fishes have grown enough to switch to a diet dominated by insects and fish (Wilde and Baker 1981).

Cladocerans increased in density during late fall and most of the winter in the inner Las Vegas Bay. Numbers were lower at other sites. Paulson and Baker (1983) indicated that food was limiting for _D_. _pulex_ in areas beyond the middle Las Vegas Bay. This, perhaps, is why cladoceran densities were low in BB and MLVB.

Comita and Anderson (1959) found that _D_. _ashlandi_ was monocyclic, taking from 5-6 months to develop. In Lake Mead, _D_. _ashlandi_ was dominat during most of winter and peaked in February, 5-6 months after the observed fall increase in nauplii. In winter, algal biomass was low, however, copepods are effective in locating prey in dilute prey environments (Paffenhofer et al. 1982, Strickler 1982), have superior filtering capacities and high ingestion rates in dilute prey environments (McNaught 1975), and are better able to capture a wider range of prey sizes (Allan 1976, Vanderploeg and Paffenhofer 1985) favoring them at this time.

Predaceous copepods, C.b. thomasi and M. edax, increased in density, although values were still low, during late fall and winter. These animals eat a variety of zooplankton, although small species of zooplankton and juvenile zooplankton are at greater risk (McQueen 1968, Confer 1971). Brandle and Fernando (1979) found that M. edax consumed mostly rotifers and copepodites of their own and of other species. It was found that greater numbers of predaceous copepods coincided with greater copepodite and rotifer densities in Lake Mead.

Seasonal and Spatial Differences in Boulder Basin

Zooplankton densities and the dominance of certain species showed more variation in Boulder Basin than other stations. This area typically has a low phytoplankton standing crop, which limits the number of zooplankton (Paulson and Baker 1983). The littoral BB station had greater average microfauna densities and lower algal biomass than that of the limnetic station. Zooplankton grazing can reduce the standing crop of algae, especially in oligotrophic waters (Porter 1976). Therefore, algal production may be higher in the littoral zone, even though biomass was low due to grazing. I did not measure phytoplankton production, however, Wilde (1984) found that zooplankton abundance positively correlated with phytoplankton primary productivity at times when algal standing crop was low. This suggests that zooplankton grazing can depress the standing crop of algae.

The littoral BB station showed greater numbers of cladocerans during the summer and fall. _B_. _longrostris_ and _D_._g_. _mendotae_ were dominant and densities higher than any other station during these times. This suggests that fish predation was much lower in Boulder Basin than in Las Vegas Bay. Echo-grams showed that relative fish abundance was extremely low throughout Boulder Basin.

Rotifer densities were much lower in BB, perhaps due to competitive displacement by cladocerans. Although, the number of rotifers was similar in both littoral and limnetic sites. The number of large cladocerans (_D_._g_. _mendotae_) was low offshore and there would have been no real competitors for rotifers. Low phytoplankton biomass is the likely explaination for low rotifer densities. Wilde (1984) found that rotifer densities increased only in productive inflow areas throughout Lake Mead.

LITTORAL AND LIMNETIC ZOOPLANKTON DENSITIES IN RELATION TO LARVAL FISH SURVIVAL

Historically in Lake Mead, catch rates of largemouth bass have decreased considerably following the construction of Glenn Canyon Dam in 1963. Prentki et al. (1981) concluded that low largemouth bass production was the result of decreased lakewide fertility resulting in decreased zooplankton densities and reducing larval largemouth bass survival. Wilde (1984) found that zooplankton densities decreased nearly 90% from 1971-1980 and suggested a consequent low survival of young largemouth bass.

The survival of larval fishes greatly depends on the abundance of prey. Eldridge et al. (1981), Li and Mathias (1982) and Martin et al. (1985) found that at least 100 zooplankton per liter was required for optimal survival of larval fishes. Generally, larvae must continually feed if many of them are to survive (Smith 1976). When they begin exogenous feeding only small prey can be ingested. Even though consumption is low they are inexperienced at capturing prey, have low swimming endurance and slow swimming velocities. Therefore, prey densities must still remain high for fish to capture enough to survive (Braum 1967, Laurence 1972).

It is not known how long optimal growth and survival will be sustained as fish grow if zooplankton densities remain at 100 per liter. Wilde and Baker (1981) found that zooplankton is still a major prey for larger largemouth bass larvae (40-67 mm) in Lake Mead. Between 200-300 zooplankton were found in stomachs of fish this size. Fingerlings (>67 mm) then switch mostly to larger prey (insects and fish). Zooplankton densities in Lake Mead may be too low to support these larger fish.

Juvenile and adult largemouth bass primarily ocupy the littoral coves (Jonez and Sumner 1954, Allan and Roden 1978). It is inappropriate to utilize data collected in limnetic areas when studing the feeding ecology of largemouth bass or other littoral fishes (Limly and Dimmik 1982b). Yet, all studies concerning juvenile largemouth bass in Lake Mead make assumptions based on numbers of zooplankton in limnetic areas (Prentki et al. 1981, Wilde 1984).

Average littoral zooplankton densities in Lake Mead were greater than the limnetic values for most of the year. Wilde (1984) thought that increased relative zooplankton abundances in littoral coves (from data collected by Youngs 1983) was perhaps due to continual southwestern winds. Although this is possible (see George and Edwards 1976, Hart 1978, Byron et al. 1983) algal biomass was greater in the littoral zone and, as already found, zooplankton densities correlate to phytoplankton biomass. However, one must not overlook that algal cells also can be transported by wind generated currents (George and Edwards 1976). In Las Vegas Bay, it may be that nutrients loaded from Las Vegas Wash are trapped, at least vertically, and recirculated in the surface waters in shallow inshore areas and not lost into the hypolimnion as in deeper areas (Paulson, pers. comm). This may act to increase littoral algal biomass at higher levels than in the limnetic zone. On the other hand, the lower algal biomass in the littoral zone of BB may indicate that increased zooplankton densities are a function of wind generated water currents, at least in coves of the less productive areas in the reservoir.

Average densities rarely approached $100 \cdot l^{-1}$ in littoral areas and if they did it was because of either abundant rotifer populations or increased numbers of copepods during the winter, especially in the more productive areas. During the peak largemouth bass spawning season (March-June, Allan and Roden 1978, Morgensen and Padilla 1982) average zooplankton densities began declining. Densities were low throughout the summer, too low for optimal growth and survival of juvenile fishes. However, more fish than expected do appear to survive throughout the year (Morgensen 1983) on, what appears to be, a limited food supply. This may be a result of several factors: 1) fish or zooplankton populations have been inadequately sampled; 2) larval largemouth bass may have a lower feeding threshold than previously thought; 3) dense zooplankton patches may occur and fish feed in them; or 4) secondary production rates are high enough to support a large abundance of fish. The first two possiblities cannot be addressed from the available data and may require further sampling or experiments to be conclusive. The last two possibilities are discussed below.

Statistical tests (ANOVA) showed that yearly zooplankton densities did not vary significantly with depth ($P>>0.05$). However, spring and summer vertical profiles showed that zooplankton concentrate slightly more at certain depths during the day in littoral areas. Inshore sites of BB and MLVB typically had greater densities at 7-10 m. Densities sometimes exceeded $100 \cdot l^{-1}$ at these depths. At the ILVB, zooplankton densities were usually higher between 5-7 m and sometimes reached densities greater than $200 \cdot l^{-1}$. Bottom samples usually had fewer animals, perhaps due to currents from the Las Vegas Wash.

Zooplankton may concentrate in deeper water, possibly to meet thermal preferences (McLaren 1974) and, in Lake Mead, the cooler water of the upper metalimnion sometimes reached into the shallow stations in late spring and early summer. Zooplankton may also concentrate along the bottom to avoid predation (Threlkeld and Dirnberger 1986). Whatever the cause, zooplankton densities in Lake Mead still remained higher along the bottom in littoral areas during the summer suggesting that not all fish utilized these patches. However, it is possible that some larval fish find these dense patches, increasing their survival rate higher than those suggested by average zooplankton densities suggest.

During the summer, there were greater concentrations of zooplankton in the metalimnion, usually near the thermocline (from 10-15 m). Fish abundance was also greater at these depths (mostly at 10 m and occasoinally at 15 m). Limnetic fish, too, may increase survival rates by feeding in these dense zooplankton patches.

As for factor four, it has already been noted that smaller zooplankton generally have higher fecundity and reproductive rates than larger ones. This may help compensate for predation loses. Higher predation rates may account for low summer zooplankton numbers, but the high secondary production of small zooplankton species may in turn increase larval fish survival.

Zooplankton densities are low throughout most of Lake Mead and limnetic densities are very similar to those in Boulder Basin (Paulson and Baker 1983, Wilde 1984). The relative abundances of threadfin shad and largemouth bass have decreased considerably in the past decade or so, since a lakewide decline in primary production (Prentki et al. 1981, Baker and Paulson 1983, Paulson and Baker 1983, Wilde

1984). If lakewide littoral zooplankton densities are representive of those found in the littoral zone of Boulder Basin, then spring zooplankton densities are extremely low and possibly regulate the survival of fish larvae.

REFERENCES

Albert, E. and J.R. Baker. 1983. Food habits of sub-adult striped bass (<u>Morone saxatilis</u>) in Lake Mead, 1981-1982. Final Rept. to Nev. Dept. Wildl. 13 pp.

Allan, J.D. 1976. Life history patterns in Zooplankton. Am. Nat. 110:165-180.

Allan, R.C. and D.L. Roden. 1978. Fish of lakes Mead and Mohave. Nev. Dept. Wildl. Biol. Bull. No. 7. 105 pp.

Allan, R.C. and J. Romero. 1975. Underwater observations of largemouth bass spawning and survival in Lake Mead. pp. 104-112. <u>In</u>: R.H. Stroud and C. Clepper (eds.), Biology and Management of Centrarchid Basses. Sport Fishing Inst. Washington, D.C.

Anderson, R.S. and R.B. Green. 1975. Zooplankton and phytoplankton studies in the Waterton lakes, Alberta, Canada. Verh. Internat. Verein. Limnol. 19:571-579.

Arumugam, P.T. and M.C. Geddes. 1986. An enclosure for experimental field studies with fish and zooplankton communities. Hydrobiol. 135:215-221.

Baker, C.D. and E.H. Schmitz. 1971. Food habits of adult gizzard and threadfin shad in two Ozark reservoirs. Reservoir Fish. and Limnol., Special Pub. No. 8. Am. Fish. Soc. pp. 3-11.

Baker, J.R., J.E. Deacon, T.A. Burke, S.S. Egdorf, L.J.

Paulson and R.W. Tew. 1977. Limnological aspects of Lake Mead, Nevada-Arizona. Final Rept. to U.S. Dept. Int. Bureau Rec. 83 pp.

_____ and L.J. Paulson. 1981. Influence of Las Vegas Wash density current on nutrient availibility and phytoplankton growth in Lake Mead. pp. 1639-1647. In: H.G. Stefan (ed.), Symposium on Surface Water Impoundments ASCE. June 2-5, 1980. Minneapolis, MN.

__________. 1983. The effects of limited food availibility on the striped bass fishery in Lake Mead. pp. 551-561. In: V.D. Adams and V.A. Lamarra (eds.), Aquatic Resource Management of the Colorado River Ecosystem. Ann Arber Science Publ., Ann Arber, Michigan.

Bleiwas, A.H. and P.M. Stokes. 1985. Collection of large and small food particles by Bosmina. Limnol. Oceanogr. 30:1090-1092.

Bogdan, K.G. and D.C. McNaught. 1975. Selective feeding by Diaptomus and Daphnia. Verh. Internat. Verein. Limnol. 19:2935-2942.

Brandle, Z. and C.H. Fernando. 1979. The impact of predation by the copepod Mesocyclops edax (Forbes) on zooplankton in three lakes in Ontario, Canada. Can. J. Zoology 57:940-942.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply. pp. 113-131. In: S.D. Gerking (ed.), The Biological Basis of Freshwater Fish Production. Wiley. New York, NY.

Brendelberger, H. and W. Geller. 1985. Variability of filtering structures in eight Daphnia species: mesh sizes and filtering areas. J. Plankton Res. 7:473-486.

_____., M. Herbeck, H. Lang and W. Lampert. 1986. Daphnia's filters are not solid walls. Arch. Hydrobiol. 107:197-202.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size and composition of plankton. Science 150:552-564.

Bryon, E.R., P.T. Whitman and C.R. Goldman. 1983. Observations of copepod swarms in Lake Tahoe. Limnol. Oceanogr. 28:378-382.

Burke, T.A. 1977. The limnetic zooplankton community of Boulder Basin, Lake Mead in relation to the metalimnetic oxygen minimum. M.S. thesis. Univ. Nev., Las Vegas. 95 pp.

Colinvaux, P. and M. Steinitz. 1980. Species richness and area in Galapagos and Andean lakes: equilibrium phytoplankton communities and a paradox of the zooplankton. pp. 697-711. In: W.C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover.

Comita, G.W. and G.C. Anderson. 1959. The seasonal development of a population of Diaptomus ashlandi Marsh, and related phytoplankton cycles in Lake Washington. Limnol. Oceanogr. 4:37-52.

Confer, J.L. 1971. Intraplankton predation by _Mesocyclops edax_ at natural prey densities. Limnol. Oceanogr. 16:663-666.

_____ and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20:571-579.

Dawidowicz, P. and J. Pijanowska. 1984. Population dynamics in cladoceran zooplankton in the presence and absence of fishes. J. Plankton Res. 6:953-959.

Deacon, J.E. 1975. Lake Mead monitoring program, University of Nevada, Las Vegas. Final Rept. to Clark Co. Wastewater Manag. Agen. 207 pp.

_____, L.J. Paulson and C.O. Minckley. 1971. Effects of Las Vegas Wash effluent upon bass and other gamefish reproduction and success. Final Rept. to Nev. Dept. Fish and Game. 22 pp.

_____ and R.W. Tew. 1973. Interrelationships between chemical, physical and biological conditions of the waters of Las Vegas Bay of Lake Mead. Final Rept. to Las Vegas Valley Water Dist. 185 pp.

DeBernardi, R., G. Giussani, E.L. Pedretti and T. Ruffoni. 1985. Population dynamics of pelagic cladocerans in three lakes with different trophy. Verh. Internat. Verein. Limnol. 22:3035-3039.

DeMott, W.R. 1982. Feeding selectivities and relative ingestion rates of _Daphnia_ and _Bosmina_. Limnol. Oceanogr. 27:515-527.

_____. 1983. Seasonal succession in a natural Daphnia assemblage. Eclog. Monogr. 53:321-340.

_____. 1986. The role of taste in food selection by freshwater zooplankton. Oecologia 69:334-340.

_____ and W.C. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. Ecology 63:1949-1966.

Dodson, S.I. 1974. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19:721-729.

Drenner, R.W. and S.R. McComas. 1980. The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impacts of planktivorous fish. pp 587-593. In: W.C. Kerffot (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover.

Edmondson, W.T (ed.) 1959. Ward and Whippel's Fresh Water Biology (2nd. edition). Wiley. New York, NY. 1248 pp.

_____ and A.H. Litt. 1982. Daphnia in Lake Washington. Limnol. Oceanogr. 27:272-293.

Eldridge, M.B., J.A. Whipple, D. Eng, M.T. Browers and B.M. Jarvis. 1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Trans. Am. Fish. Soc. 110:111-120.

Elgloff, D.A. and D.S. Palmer. 1971. Size relations of filtering area of two Daphnia species. Limnol. Oceanogr. 16:900-905.

Evans, M.S. 1986. Recent major declines in zooplankton populations in the inshore region of Lake Michigan: probable causes and implications. Can. J. Fish. Aquat. Sci. 43:154-159.

Everett, L.G., R.D. Staker and R.W. Hoshaw. 1976. Plankton transect analysis as an indicator of pollution levels. Am. Midl. Nat. 96:214-221.

Fairchild, G.W. 1981. Movement and microdistribution of Sida crystallina and other microcrustacea. Ecology 62:1341-1352.

Fryer, G. 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. Freshwater Biol. 15:347-361.

Gehrs, C.W. 1974. Horizontal distribution and abundance of Diaptomus clavipes Schacht in relation to Potamogeton foliosus in a pond and under experimental conditions. Limnol. Oceanogr. 19:100-104.

Geller, W. and H. Muller. 1981. The filtering apparatus of cladocerans: filter mesh-sizes and their implications on food selectivity. Oecologia 49:316-321.

George, D.G. and R.W. Edwards. 1976. The effects of wind on the distribution of chlorophyll A on crustacean plankton in a shallow eutrophic reservoir. J. Appl. Ecol. 13:667-690.

Gerritsen, J. and K.G. Porter. 1982. The role of surface chemistry in filter feeding by zooplankton. Science 216:1225-1227.

Gilbert, J.J. 1985. Competition between rotifers and *Daphnia*. Ecology 66:1943-1950.

Gilyarov, A.M. 1982. Factors regulating the numbers in populations of fresh-water planktonic crustaceans. Hydrobiol. J. 18:21-33.

Gliwicz, Z.M., A. Ghilarov and J. Pijanowska. 1981. Food and predation as major factors limiting two natural populations of *Daphnia cucullata* Sars. Hydrobiol. 80:205-218.

Gophen, M. and W. Geller. 1984. Filter mesh size and food particle uptake by *Daphnia*. Oecologia 64:408-412.

Green, J. 1985. Horizontal variations in association of zooplankton in Lake Kariba. J. Zool., Lond. 206:225-239.

______. 1986. Associations of zooplankton in six crater lakes in Arizona, Mexico and New Mexico. J. Zool., Lond. 208:135-159.

Hamrin, S.F. 1983. The food preference of vendace (*Coregonus albula*) in South Swedish forest lakes including the predation effects on zooplankton populations. Hydrobiol. 101:121-128.

Haney, J.F. and D.J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnol.

Oceanogr. 9:331-333.

Hart, R.C. 1978. Horizontal distribution of the copepod *Pseudodiaptomus hessi* in subtropical Lake Sibaya. Freshwater Biol. 8:415-421.

Hasler, A.D. and E. Jones. 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30:359-364.

Hessen, D.O. 1985. Filtering structures and particle size selection in coexisting Cladocera. Oecologia 66:368-372.

Horton, P.A., M. Rowan, K.E. Webster and R.H. Peters. 1979. Browsing and grazing by cladoceran filter feeders. Can. J. Zool. 57:206-212.

Hurlbert, S.H. and M.S. Mulla 1981. Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. Hydrobiol. 83:125-151.

Hutchinson, B.P. 1971. the effects of fish predation on the zooplankton of ten Adirondack lakes, with particular reference to the alewife, *Alosa pseudoharengus*. Trans. Am. Fish. Soc. 2:325-335.

Hutchinson, G.E. 1967. A Treatise on Limnology. Vol. II. Introduction to Lake Biology and the Limnoplankton. Wiley, New York, NY.

Infante, A. and S.E.B. Abella. 1985. Inhibition of *Daphnia* by *Oscillatoria* in Lake Washington. Limnol. Oceanogr. 30:1046-1052.

_____ and A.H. Litt. 1985. Difference between two species of Daphnia in the use of 10 species of algae in Lake Washington. Limnol. Oceanogr. 30:1053-1059.

Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. Am. Nat. 120:171-180.

Jacobs, J. 1977. Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. II. Field data analysis of Daphnia. Oecologia 30:313-329.

Janik, J.J. 1984. Role of nannoplankton in the phytoplankton dynamics of four Colorado River reservoirs (lakes Powell, Mead, Mohave and Havasu). M.S. Thesis. Univ. Nev., Las Vegas. 133 pp.

Janssen, J. 1980. Alwives (Alosa psudoharengus) and ciscoes (Coregonus artedii) as selective and non-selective planktivores. pp. 580-586. In: W.C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover.

_____. 1982. Comparison of searching behavior for zooplanton in an obligate planktivore, blueback herring (Alosa aestivalis) and a facultative planktivore, bluegill (Lepomis machrochirus). Can. J. Fish. Aquat. Sci. 39:1649-1654.

Jonez, A. and R.C. Sumner. 1954. Lakes Lead and Mohave investigations. Nev. Fish and Game Comm. Final Report.

D-J Proj. F-1-R. 186 pp.

Keast, A. 1985. Planktivory in a littoral-dwelling lake fish association: prey selection and seasonality. Can. J. Fish. Aquat. Sci. 42:1114-1126.

Kerfoot, W.C. 1977. Competition in cladoceran communities: the cost of evolving defenses against copepod predation. Ecology 58:303-313.

_____. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura and Bosmina. Limnol. Oceanogr. 23:1089-1103.

_____, D.L. Kellogg, Jr. and J.R. Strickler. 1980. Visual observation of live zooplankters: evasion, secape, and chemical defenses. pp. 10-27. In: W.C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover.

Kilambi, R.V. and L.E. Barger. 1975. Dynamics of feeding ecology of larval shad, Dorosoma, in Beaver Reservoir, Arkansas. Final Rept. to U.S. Dept. Int. Fish Wildl. Serv. 62 p.

Knisely, K. and W. Geller. 1986. Selective feeding of four zooplankton species on natural lake phytoplankton. Oecologia 49:316-321.

Koehl, M.A.R. and J.R. Strickler. 1981. Copepod feeding currents: food capture at low reynolds numbers. Limnol. Oceanogr. 26:1062-1073.

Konkle, B.R. and W.G. Sprules. 1986. Planktivory by stunted lake trout in an Ontario lake. Trans. Am. Fish. Soc. 115:515-521.

Krueger, D.A. and S.I. Dodson. 1981. Embryological induction and prey ecology in _Daphnia pulex_. Limnol. Oceanogr. 26:219-223.

Laurence, G.C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (_Micropterus salmoides_). J. Fish Biol. 4:73-78.

Lemly, A.D. and J.F. Dimmick. 1982a. Structure and dynamics of zooplankton communities in the littoral zone of some North Carolina lakes. Hydrobiol. 88:299-307.

____________. 1982b. Growth of young-of-the-year and yearling centrarchids in relation to zooplankton in the littoral zone of lakes. Copeia 1982:305-321.

Li, S. and J.A. Mathias. 1982. Causes of high mortality among littoral larval walleyes. Trans. Am. Fish. Soc. 111:710-721.

Luecke, C. and W.J. O'Brien. 1983. The effects of _Heterocope_ predation on zooplankton communities in arctic ponds. limnol. Oceanogr. 28:367-377.

Lynch, M. 1978. Complex interactions between natural coexploiters - _Daphnia_ and _Ceriodaphnia_. Ecology 59:552-564.

Martin, F.D., D.A. Wright, J.C. Means and E.M. Seltzer-Hamilton. 1985. Importance of food supply to nutritional state of larval striped bass in the

Potomac estuary. Trans. Am. Fish. Soc. 114:137-145.

McCauley, E. and J. Kalff. 1980. Emperical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. 38:458-463.

McLaren, I.A. 1974. Demographic strategy of vertical migration by a marine copepod. Am. Nat. 108:95-97.

McNaught, D.C. 1975. A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. verh. Internat. Verein. Limnol. 19:1484-1489.

McQueen, D.J. 1968. Reduction of zooplankton standing stocks by predaceous _Cyclops_ _bicuspidatus_ _thomasi_ in Marion Lake, British Columbia. J. Fish. Res. Bd. Can. 26:663-666.

Meyers, D.G. 1984. Habitat shifting, feeding mode versatility, and alternate resource exploitation by herbivorous cladoceran zooplankton in a montane lake. pp. 309-345. _In_: D.G. Meyers and J.R. Strickler (eds.), Trophic Interactions within Aquatic Ecosystems. Westview Press. Boulder, CO.

Moore, J.W. 1980. Zooplankton, and related phytoplankton cycles, in a eutrophic lake. Hydrobiol. 74:99-104.

Morgensen, S.A. 1983. Factors affecting the production and recruitment of largemouth bass, _Micropterus_ _salmoides_. M.S. Thesis. Univ. Nev., Las Vegas. 64 pp.

_____ and C.O. Padilla. 1982. The status of the black bass fishery in Lake Mead and a program towards restoration and enhancement. Final Rept. to U.S. Dept. Inter. Bur. Rec. 114 p.

Mummert, J.R. and R.W. Drenner. 1986. Effect of fish size on the filtering efficiency and selective particle ingestion of a filter-feeding clupeid. Trans. Am. Fish. Soc. 115:522-528.

Nevada Department of wildlife. 1982. Job progress report for Lake Mead, 1982. Proj. No. F-20-18. 198 pp.

O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67:572-581.

Orcutt, J.D., Jr. and M.L. Pace. 1984. Seasonal dynamics of rotifer and crustacean zooplankton populations in an eutrophic, monomictic lake with a note on rotifer sampling techniques. Hydrobiol. 119:73-80.

Paffenhofer, G.-A., J.R. Strickler and M. Alcaraz. 1982. Suspension feeding by herbivorous calanoid copepods: a cinematographic study. Mar. Biol. 67:193-199.

Paulson, L.J. and J.R. Baker. 1983. Interrelationships among nutients, plankton and striped bass in Lake Mead. Lake Mead Limnol. Res. Cent., Univ. Nev., Las Vegas. Tech. Rept. No. 10. 93 pp.

__________. 1984. The limnology in Reservoirs on the Colorado River. Lake Mead Limnol. Res. Cent., Univ. Nev., Las Vegas. Tech. Rept. No. 11. 276 pp.

__________ and J.E. Deacon. 1980. The limnological status of Lake Mead and Lake Mohave under present and future power plant operations of Hoover Dam. Lake Mead Limnol. Res. Cent., Univ. Nev., Las Vegas. Tech. Rept. No. 1. 229 pp.

Paulson, L.J. and F.A. Espinosa. 1975. Fish trapping: a new method of evaluating fish species composition in limnetic areas of a reservoir. Calif. Fish and Game 61:209-214.

Pennak, R.W. 1957. Species composition of limnetic zooplankton communities. Limnol. Oceanogr. 2:222-232.

_____. 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. Amer. Microsc. Soc. 85:329-349.

_____. 1978. Fresh-Water Invertebrates of the United States. Wiley. New York, NY. 803 pp.

Porter, K.G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. Science 192:1332-1334.

_____. 1977. The plant-animal interface in freshwater ecosystems. Am. Sci. 65:159-170.

_____, Y.S. Feig and E.F. Vetter. 1983. Morphology, flow regiems and filtering rates of Daphnia, Ceriodaphnia and Bosmina fed natural bacteria. Oecologia 58:156-163.

Prentki, R.T., L.J. Paulson and J.R. Baker. 1981. Chemical and biological structure of Lake Mead sediments. Lake

Mead Limnol. Res. Cent., Univ. Nev., Las Vegas. Tech. Rept. 6. 89 pp.

Price, H.J., G.-A. Paffenhofer and J.R. Strickler. 1983. Modes of cell capture in calanoid copepods. Limnol. Oceanogr. 28:116-123.

Rippingale, R.J. and E.P. Hodgkin. 1974. Predation effects on the distribution of a copepod. Aust. J. Mar. Freshwat. Res. 25:81-91.

Romanovsky, Y.E. and I.Y. Feniova. 1985. Competition among cladocerans: effects of different levels of food supply. Oikos 44:243-252.

Seitz, A. 1980. The coexistence of three species of Daphnia in the Klosteree. II. The stabilizing effect of selective mortality and conclusions for the stability of the system. Oecologia 47:333-339.

Siebeck, O. 1964. Researches on the behavior of planktonic crustaceans in the littoral. Verh. Internat. Verein. Limnol. 15:746-751.

_____. 1980. Optical orientation of pelagic crustaceans and its consequence in the pelagic and littoral zone. pp. 28-38. In: W.C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover.

Smirnov, N.N. 1963. On inshore Cladocera of the Volga Water reservoirs. Hydrobiol. 21:166-176.

Smith, D.W. and S.D. Cooper. Competition among Cladocera.

Ecology 63:1004-1015.

Smith, W.E. 1976. Larval feeding and rapid maturation of bluegill in the laboratory. Prog. Fish-Cult. 38:95-97.

Smyly, W.J.P. 1952. The entomostraca of the weeds of a moorland pond. J. Anim. Ecol. 2:11-11.

Sommer, U., Z.M. Gliwicz, W. Lampert and A. Duncan. 1986. The PEG-model of seasonal succession of planktonic events in freshwater. Arch. Hydrobiol. 106:433-471.

Sprules, W.G. 1975. Factors affecting the structure of limnetic crustacean zooplankton communities in central Ontario lakes. Verh. Internat. Verein. Limnol. 19:635-643.

Staker, R.D. 1974. A diurnal zooplankton migration study in Lake Mead. J. AZ. Acad. Sci. 9:85-88.

Starkweather, P.L. 1983. Daily patterns of feeding behavior in Daphnia and related microcrustacea: implications for cladoceran autecology and the zooplankton community. Hydrobiol. 100:203-221.

Stolbunova, V.N. and A.K. Stolbunov. 1981. The natural life of the littoral zone of a reservoir and its effect on the pelagic zone (with reference to the bacterioplankton and zooplankton of Ivan'Kovo Reservoir). Hydrobiol. J. 16:1-6.

Straskraba, M. 1964. Contributions to the productivity of the littoral region of pools and ponds. I. Quantitative study of the littoral zooplankton of rich vegetation of the backwater Labicko. Hydrobiol. 26:421-443.

Strickler, J.R. 1982. Calanoid copepods, feeding currents, and the role of gravity. Science 218:158-160.

_____. 1984. Sticky water: a selective force in copepod evolution. pp. 187-239. *In*: D.G. Meyers and J.R. Strickler (eds.), Trophic Interactions within Aquatic Ecosystems. Westview Press. Boulder, CO.

Threlkeld, S.T. 1981. The recolinization of Lake Tahoe by *Bosmina longirostris*: evaluating the importance of reduced *Mysis relicta* populations. Limnol. Oceanogr. 26:433-444.

_____ and J.M. Dirnberger. 1986. Benthic distributions of planktonic copepods, especially *Mesocyclops edax*. pp. 481-486. *In*: G. Schriever, H.K. Schiminke and C.-t. Shih (eds.), Preceedings of the Second Internatinal Conference on Copepods. Ottawa, Canada.

Vanderploeg, H.A. and G.-A. Paffenhofer. 1985. Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection. Limnol. Oceanogr. 30:871-885.

Vanni, M.J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnol. Oceanogr. 31:1039-1056.

Venglinskiy, D.L., V.A. Sokolova and M.M. Tyaptirgyonov. 1985. Zooplankton of lakes of Northwest Yakutia.

Hydrobiol. J. 21:68-73.

Vigerstad, T.J. and L.J. Tilly. 1977. Hyperthermal effluent effects on heleoplanktonic Cladocera and the influence of submerged macrophytes. Hydrobiol. 55:81-85.)

VonGeldern, C.E., Jr. 1971. Abundance and distribution of fingerling largemouth bass, _Micropterus_ _salmoides_, as determined by electrofishing, at Lake Nacimiento, California. Cal. Fish and Game 57:228-245.

Webster, K.E. and R.H. Peters. 1978. Some size-dependant inhibitions of larger cladoceran filters in filamentus suspensions. Limnol. Oceanogr. 23:1238-1245.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Can. 31:1531-1536.

_____ and D.J. Hall. 1974. Optimal foraging and size selection of prey by bluegill sunfish (_Lepomis macrochirus_). Ecology 55:1042-1052.

Wetzel, R.G. 1975. Limnology. Saunders. Philadelphia, Penn. 743 pp.

Whiteside, M.C. and R.V. Harmsworth. 1967. Species diversity in chydorid (Cladocera) communities. Ecology 48:664-667.

Wilde, G.R. 1984. Seasonal and spatial heterogeneity in the limnetic zooplankton community of Lake Mead. M.S. Thesis. Univ. Nev., Las Vegas. 95 pp.

_____ and J. Baker. 1981. Food habitis of fry and fingerling largemouth bass from lakes Mead and Mohave, 1979. Final Rept. to Nev. Dept. Wildl. 16 pp.

Williams, J.B. 1982. Temporal and spatial patterns of abundance of the Chydoridae (Cladocera) in Lake Itasca, Minnesota. Ecology 63:345-353.

Wright, D.I., W.J. O'Brien and C. Luecke. 1983. A new estimate of zooplankton retention by gill rakers and its ecological significance. Trans. Am. Fish. Soc. 112:638-646.

Youngs, D.L. 1983. The zooplankton of four Lake Mead study coves, 1980-1981. Final Rept. to Nev. Dept. Wildl. 62 pp.

Zaret, T.M. 1975. Strategies for zooplankton prey in homogeneous environments. Verh. Internat. Verein. Limnol. 19:1484-1489.

_____ and W.C. Kerfoot. 1975. Fish predation on *Bosmina longirostris*: body size selection versus visibility selection.. Ecology 56:232-237.

_____ and J.S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804-813.