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Journal

Journal of Plankton Research, 8(6)

ISSN

0142-7873

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Publication Date

1986

DOI

10.1093/plankt/8.6.1051

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Peer reviewed

Spatial and temporal distribution patterns of three trophic levels in a saline lake

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Abstract. Horizontal distribution patterns of three trophic levels were investigated at Mono Lake, California, USA during the autumns of 1980 and 1981. Coefficients of variation for *Artemia monica* and grebes peaked in October of both years, whereas coefficients of variation for phytoplankton declined from August to November. Stable population gradients were observed in the *Artemia* population. In contrast, grebes were very mobile and their distributional patterns changed between sampling dates. *Artemia* and phytoplankton were negatively correlated during 1980, but no significant correlations occurred in 1981. Grebes and *Artemia* were positively correlated in October 1980 and 1981, suggesting active prey tracking by the grebes. Interactions between trophic levels may have contributed to the creation and maintenance of patchiness, although these effects appeared to be intermittent.

Introduction

Spatial variation in plankton distributions has been attributed to a wide variety of physical and biotic factors, and the dynamics of the spatial distribution of populations are becoming better understood (e.g. George, 1974, 1981; Hamner and Hauri, 1981a,b; Malone and McQueen, 1983; Tessier, 1983). Relatively few studies, however, have attempted to compare spatial distributions of organisms at more than one trophic level during the same time interval (Lewis, 1980; Tessier, 1983; Howard and Lowe, 1984; Woodby, 1984), although such an approach holds a promise of understanding the contribution of processes, such as predation and grazing, to the patchiness of adjacent trophic levels.

In the present paper, we compare the spatial distributions of three trophic levels in Mono Lake, California. The three aims of our work were: (i) to describe temporal changes in the spatial heterogeneity of the primary producers, primary consumers and secondary consumers; (ii) to determine the amount of variation owing to date-to-date (temporal), station-to-station (fixed spatial), and station-by-date (ephemeral spatial) differences in abundances of organisms at these three trophic levels; and (iii) to examine correlations among the horizontal spatial distributions of organisms at these three trophic levels. In general, plankton are patchily distributed on spatial scales ranging from decimeters to kilometers (e.g. Hutchinson, 1967; Stavn, 1971; Hauri *et al.*, 1978; Abbott *et al.*, 1982; Jones and Francis, 1982) and, although small-scale patchiness is present in at least two of the trophic levels at our study site (Lenz, 1980; Winkler *et al.*,

1977), we limit our attention here to patchiness on scales of 1 km and greater. We examined distributions at this scale because we needed lakewide abundances for common organisms in order to estimate the effects of grazers on algae, and to estimate the effects of aquatic birds on grazers (Lenz, 1982; Cooper *et al.*, 1984).

Study site

Mono Lake is a large, deep, hypersaline lake lying in the North American Great Basin (Mason, 1967; Melack, 1983; Melack *et al.*, 1985). The phytoplankton population is dominated by a single green alga (tentatively named *Nannochloris* sp.). During summer and fall, the primary grazer is the brine shrimp, *Artemia monica* (Lenz, 1980, 1982), which is preyed upon by aquatic birds, primarily California gulls (*Larus californicus*) during the summer (Winkler, 1983) and eared grebes (*Podiceps nigricollis*) in the fall (Cooper *et al.*, 1984; Winkler and Cooper, 1986). In this study we analyze the temporal and spatial distribution of the phytoplankton, *Artemia* and grebes during the fall period, when grebe densities are high, and rapid changes in both *Artemia* and phytoplankton densities occur.

Methods

Twenty-nine stations were established, with a uniform spacing of 2 km between stations, and all stations were in water depths of 15 m or deeper (Figure 1). The three trophic levels were sampled at 3- to 4-week intervals from August to November in 1980 and 1981, and the number of stations sampled on each date varied between 10 and 29.

Transparency was measured at each station with a 20-cm white Secchi disk, and phytoplankton samples were taken at 9–17 stations. Water samples that integrated the euphotic zone were taken with a clear polyethylene tube 4 cm in diameter. Chlorophyll *a* concentrations were measured by the methods described in Strickland and Parsons (1972).

At each station, a zooplankton net (150 μ m mesh, 30 cm diameter) was towed vertically through the water column from either 15 or 20 m depth. Throughout most of the study periods, this procedure effectively sampled the entire epilimnion; brine shrimp were absent from the anoxic hypolimnion. From 19 to 29 stations were sampled for *Artemia* in 1980, whereas 10 stations were sampled in 1981. Using the data acquired in 1980, we found that population means calculated from the 19–29 stations were similar to population means calculated from the subset of 10 stations sampled in 1981. Zooplankton samples were preserved in ~5% formalin until they were analyzed by volume displacement (Lenz, 1980, 1982) or counted under a dissecting microscope. Abundance estimates (adults m^{-2}) have been corrected for a net efficiency of 70% (Lenz, 1982). The *Artemia* population is almost entirely composed of adults in the autumn.

Grebes were counted by an observer in a motorboat en route between adjacent stations. The observer counted grebes on both sides within ~25 m of the boat's path. For comparison with other trophic levels, we calculated station estimates of grebe density by averaging grebe counts from the leg before and after the station. Although this

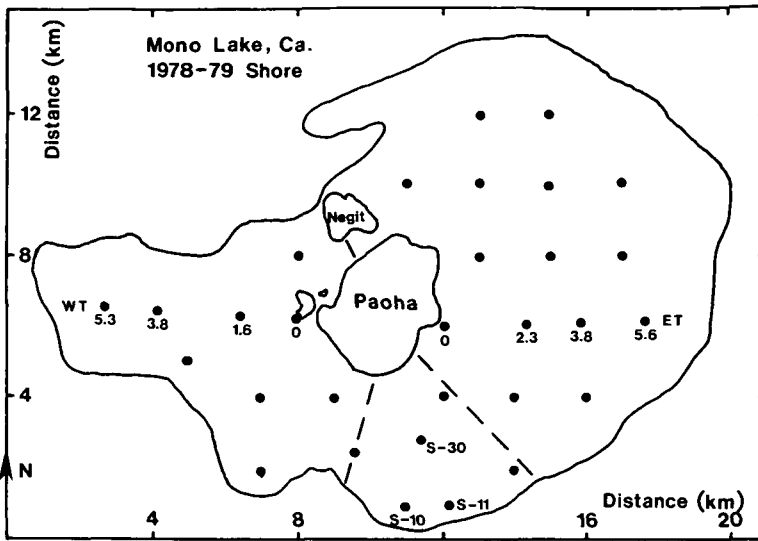


Fig. 1. Map of Mono Lake and sampling stations (closed circles). Stations used in 1981 are named. The y axis is aligned with true north. The dashed lines mark the boundaries of the eastern, western and southern sectors.

censusing method probably underestimates grebe abundances because some are under water, our results agree well with densities obtained by other methods (Cooper *et al.*, 1984).

We examined changes in the relative variability of samples for each trophic level by using the coefficient of variation (Zar, 1984). Various indices of dispersion, such as Lloyd's patchiness index, Morisita's I , the variance to mean ratio, k of the negative binomial, and b of Taylor's power law were not used because: (i) for phytoplankton, abundance estimates were based on measurements of chlorophyll a concentration instead of counts; and (ii) all of these indices are dependent on the number of replicate samples and the sample mean (Elliott, 1977; Downing, 1986; and J.A. Downing, personal communication). Because sample means varied among trophic levels and through time within a trophic level, it was inappropriate to use these indices of dispersion to compare differences in sample heterogeneity among trophic levels or dates. Values of dispersion indices also depend on the size of the sampling unit, emphasizing the importance of defining sample unit size (or the ambit, Lloyd, 1967). Conversion of numbers per sample to numbers per unit area or volume requires multiplication or division by a constant. Because the variance changes as the square of this constant, indices based on variance to mean relationships, including most of those listed above, will change depending on whether results are first standardized to a unit area or volume. On the other hand, the standard deviation changes in the same manner as the mean so the coefficient of variation is not changed by these scaling constants. Because of its standard use, we use the coefficient of variation to compare changes in sample heterogeneity through time within a trophic level. Caution should be exercised, however, when interpreting changes in coefficients of variation because the standard deviation generally scales as the mean to the 0.75 power (J.A. Downing, personal communication). Because

of the problems outlined above, we made no attempt to compare degrees of spatial heterogeneity among trophic levels.

For reach sampling date, spatial correlations between trophic levels were tested with the Spearman rank correlation coefficient (Siegel, 1956). Variances due to date, station and their interaction were partitioned using a two-way analysis of variance (ANOVA), random-effects model (Sokal and Rohlf, 1969; Lewis, 1978). The relative magnitude of these components, as expressed by their coefficients of determination (r^2 , Sokal and Rohlf, 1969), estimates the variability due to seasonal effects, and fixed and ephemeral spatial patchiness (Lewis, 1978). A large temporal effect indicates large date-to-date differences in abundance across all stations. Spatial variation is divided into fixed variation, i.e. that due to predictable differences among stations independent of date, and ephemeral variation, that due to spatial differences in abundance which vary from date to date. Because we did not take replicate samples from each station, the ephemeral variation (i.e. the interaction term) is an overestimate, and includes both within and between station variation. Additional sampling, however, revealed that within station variability is small, at least for the algae and *Artemia*. Duplicate and triplicate samples were taken from each *Artemia* sampling station in the falls of 1982 and 1983 respectively. On each date an ANOVA was run to examine the contribution of within and between station variation to the total variance. On all dates, within station variation accounted for very little of the total (<7%). Similarly, within station variation was much smaller than between station variation for phytoplankton on dates when replicate samples were taken. Our method of calculating grebe abundance at a station (see above) results in autocorrelation of adjacent grebe stations; however, the ANOVAs should still indicate the relative importance of spatial versus temporal components of spatial variation. This autocorrelation, however, will affect our analyses of the scale of spatial variation, i.e. the relative contributions of between station versus between sector variation to total variation (see below).

In a second analysis, stations were categorized into sectors delineated by geomorphological and meteorological features of the lake (Figure 1). Large islands in the center of the lake divided it into western and eastern basins, separated by a transition zone we call the southern sector. Persistent winds tend to come from the southwest and wind patterns differ between the eastern and western portions. Freshwater springs and streams enter only in the west. The variance for each trophic level was partitioned into date, sector and station, and their interactions tested in a nested two-way ANOVA. This further partitioning of variance allowed us to assess how much of the variability could be attributed to consistent differences among sections versus consistent differences among stations within sectors. Because of our unbalanced design, we used the General Linear Models (GLM) procedure from the SAS statistical package (Helwig and Council, 1979) to compute the appropriate sums of squares. East and west sector means for each trophic level were compared statistically for each date using a Mann-Whitney *U* test (Siegel, 1956).

Results

Demographic patterns

The period from August to November was marked by large changes in phytoplankton and *Artemia* abundances (Figure 2). Chlorophyll *a* concentrations increased from low

Distribution patterns of three trophic levels

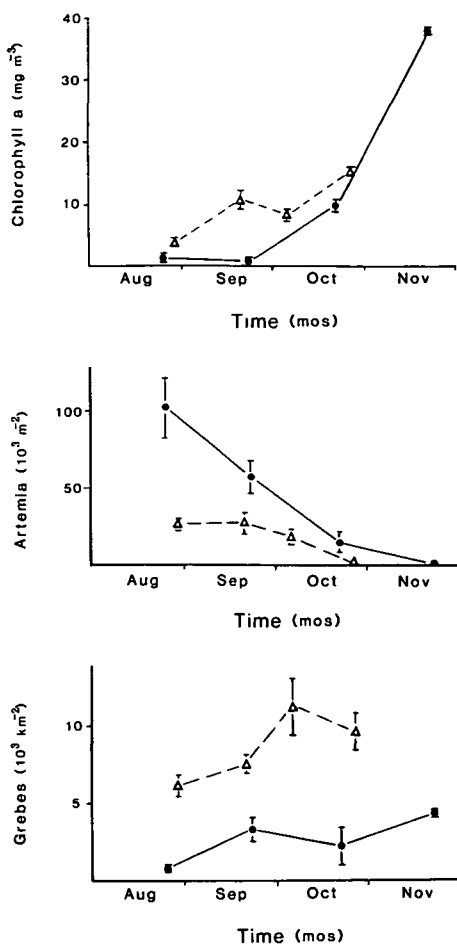


Fig. 2. Chlorophyll *a* concentrations, *Artemia* abundances, and grebe densities (means \pm standard errors) for 1980 (Δ) and 1981 (\bullet). *Artemia* abundances and grebe densities redrawn from Cooper *et al.* (1984).

Table I. Coefficients of variation for three trophic levels.

Date	Phytoplankton	<i>Artemia</i>	Grebes
28 Aug. 80	0.53 ^a	0.84 ^a	0.58 ^a
20 Sep. 80	0.63 ^b	1.37 ^b	0.41 ^b
5 Oct. 80	0.41 ^a	1.46 ^b	0.79 ^a
25 Oct. 80	0.11 ^c	1.12 ^a	0.49 ^b
23 Aug. 81	0.90 ^a	0.54 ^a	0.81 ^a
22 Sep. 81	0.86 ^{a,b}	0.71 ^a	0.74 ^a
20 Oct. 81	0.26 ^b	1.50 ^b	1.39 ^a
23 Nov. 81	0.05 ^c	0.47 ^a	0.24 ^b

Within a trophic level and year, coefficients of variation with the same superscript letter are not significantly different ($P > 0.05$, *F* test, Zar, 1984).

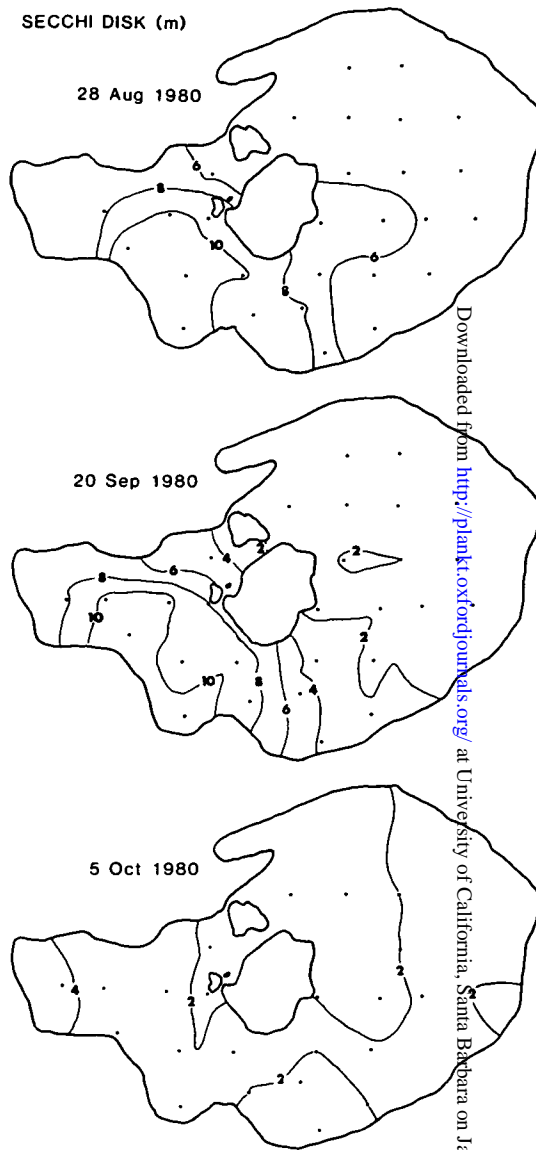


Fig. 3. Lakewide Secchi depths (m) for 28–29 August, 20–22 September and 5 October 1980.

summer levels ($<3 \text{ mg m}^{-3}$) to 15 mg m^{-3} by the end of October 1980 and nearly 40 mg m^{-3} by November 1981. In contrast, *Artemia* densities declined in both 1980 and 1981 and by the last sampling date population densities were below 1000 m^{-2} . Grebe densities remained high during both autumns, with higher abundances occurring in 1980 as compared to 1981 (Figure 2).

Coefficients of variation for *Artemia* and grebes tended to increase from August to October then declined on the last sampling date in both years (Table I). Coefficients

Distribution patterns of three trophic levels

Table II. Coefficients of determination for temporal and spatial components of variation for three trophic levels in two years.

Coefficient of determination (r^2)	1980			1981		
	Chla	Artemia	Grebes	Chla	Artemia	Grebes
Source						
Date	0.48	0.65	0.06	0.99	0.72	0.23
Station	0.31	0.25	0.11	0.003	0.06	0.34
Interaction (date \times station)						
plus error	0.21	0.10	0.83	0.007	0.22	0.42

Table III. Coefficients of determination for temporal and spatial components of variation where spatial effects are further divided by sector.

Coefficient of determination (r^2)	1980			1981		
	Chla	Artemia	Grebes	Chla	Artemia	Grebes
Source						
Date	0.50	0.66	0.06	0.99	0.47	0.21
Sector	0.23	0.19	0.003	0.001	0.01	0.19
Sta (sector)	0.04	0.05	0.12	0.001	0.09	0.16
Interaction (date \times sector)	0.17	0.03	0.53	0.003	0.23	0.32
Interaction [date \times sta (sector)]						
plus error	0.05	0.06	0.29	0.005	0.19	0.11

of variation for chlorophyll *a* concentrations declined throughout the autumns of both years (Table I).

Distribution patterns

Because of the large number of stations sampled in 1980, lakewide distribution patterns can be mapped for transparency, *Artemia* and grebes (Figure 3, 4 and 5). For 1981, we describe general patterns of distribution, and for both years we partition total variation into temporal and spatial components.

Phytoplankton. Secchi depth isopleths are presented in Figure 3 instead of chlorophyll *a* concentrations, because of the greater amount of data available for Secchi depths. The ANOVAs, however, were performed on actual chlorophyll *a* values. Secchi depth and chlorophyll *a* are inversely related in Mono Lake (Lenz, 1982), and increasing Secchi transparencies from east to west (Figure 3) indicate decreasing algal concentrations. Secchi transparencies decreased between August and October, and by the last sampling date in 1980 they ranged between 1 and 2 m.

In 1980 all sources contributed to variation in chlorophyll *a* (Table II). When divided by date, sector, station and their interactions, temporal changes accounted for half of the variation in chlorophyll *a*, whereas sector and the two interaction components of variance contributed approximately equally to the remaining variation (Table III). In 1981 variation in chlorophyll *a* was due almost entirely to temporal changes. Chlorophyll *a* concentrations were significantly different in the east and west sectors

Table IV. East (E) and west (W) mean abundances for three trophic levels (sample size for each sector on each date is given in parentheses).

		1980				1981			
		28 Aug.	20 Sep.	5 Oct.	25 Oct.	23 Aug.	22 Sep.	20 Oct.	23 Nov.
Chlorophyll <i>a</i> (mg m ⁻³)	W	1.1 (4)	2.3 (6)	5.3 (5)	16.3 (4)	0.1 (4)	0.6 (4)	10.7 (4)	39.0 (4)
	E	4.1 (8)	14.9 (8)	9.5 (7)	14.4 (4)	1.2 (4)	0.6 (4)	7.9 (4)	36.6 (4)
	P	0.004	<0.001	0.03	0.14 < P 0.20	0.028	0.88	0.114	0.114 < P < 0.2
<i>Artemia</i> (10 ³ m ⁻³)	W	54.6 (9)	68.4 (9)	40.5 (8)	0.7 (8)	158.5 (4)	56.5 (4)	0.1 (4)	0.3 (4)
	E	10.8 (15)	6.4 (14)	3.0 (9)	0.2 (7)	69.4 (4)	42.7 (4)	36.5 (4)	0.6 (4)
	P	<0.002	<0.002	<0.002	0.054 < P < 0.072	0.486	0.200	0.028	0.200
Grebes (10 ³ km ⁻²)	W	2.1 (9)	7.7 (9)	20.6 (9)	12.6 (8)	1.2 (4)	1.1 (4)	0.3 (4)	4.8 (4)
	E	8.6 (15)	6.6 (14)	3.0 (9)	8.4 (7)	0.6 (4)	5.5 (4)	7.8 (4)	4.0 (4)
	P	<0.002	>0.10	<0.002	0.102	0.20 < P < 0.342	0.028	0.028	0.20

East and west densities were compared statistically with a two-tailed Mann-Whitney U test.

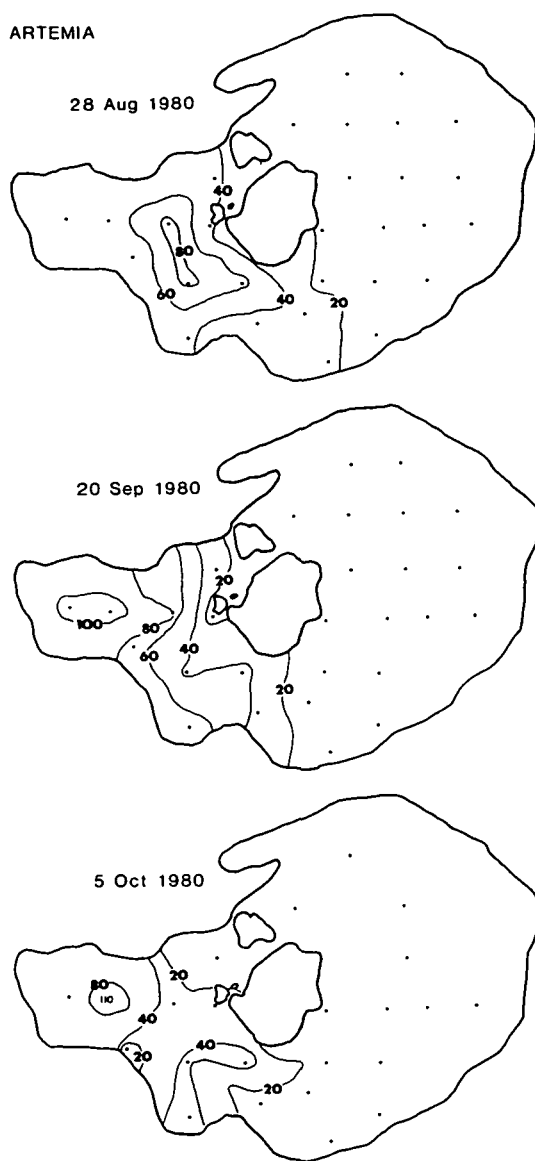


Fig. 4. Lakewide *Artemia* (10^3 m^{-2}) patterns for dates as in Figure 3.

on four dates: August 1980 and 1981, and September and early October 1980 (Table IV). On all four dates algal concentrations were greater in the east than in the west.

Artemia. In 1980 *Artemia* abundances increased from east to west (Figure 4), and this pattern was observed on all dates. The east and west sectors had significantly different *Artemia* densities on three of the four dates (Table IV). Variation in *Artemia* densities was primarily due to seasonal changes in 1980; temporal changes accounted for over 60% of the total variance (Tables II and III). This is not surprising, since mean den-

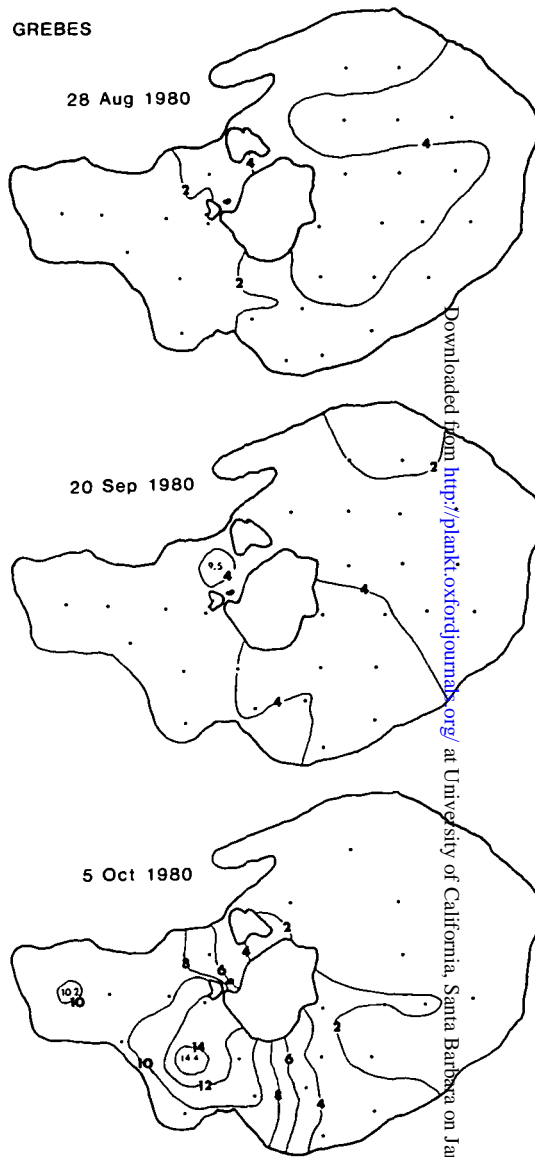


Fig. 5. Lakewide grebe (10^2 km^{-1} of transect) patterns for dates as in Figure 3.

sities decreased from over 26 000 to 400 individuals m^{-2} between August and October. Fixed patchiness exceeded the ephemeral component in *Artemia*. The station component in 1980 was smaller than the sector component, indicating consistent differences among sectors through time, but not between stations within a sector (Table III).

In August and September 1981 brine shrimp densities were higher in the west than the east, whereas in October and November the opposite occurred. In 1981 the variance components were dominated by temporal effects, followed by ephemeral spatial effects (Tables II and III). Fixed patchiness was less important in 1981.

Table V. Correlations between trophic levels for 1980 and 1981.

Date	<i>Chla</i> versus <i>Artemia</i>		<i>Artemia</i> versus Grebe	
	<i>n</i>	<i>r_s</i>	<i>n</i>	<i>r_s</i>
28 Aug. 80	13	-0.85*	29	-0.66*
20 Sep. 80	17	-0.82*	28	+0.06
5 Oct. 80	13	-0.28	23	+0.80*
25 Oct. 80	9	+0.51	18	+0.26
23 Aug. 81	10	+0.07	9	-0.10
22 Sep. 81	10	+0.04	10	-0.54
22 Oct. 81	10	+0.41	10	+0.94*
20 Nov. 81	10	+0.18	10	-0.42

* $P < 0.001$; n = sample size; r_s = Spearman rank coefficient.

Grebes. Variable distribution patterns were observed in the grebe population (Figure 5). In August and September 1980, grebe densities were lowest in the west, peak abundances occurring in the south and around the islands. In early October grebe densities increased from east to west, roughly paralleling the *Artemia* distribution. In contrast to both *Artemia* and phytoplankton, the variability in grebe numbers was dominated by ephemeral patchiness. In 1980 only 17% of the variance was caused by temporal changes and fixed patchiness (Tables II and III). In 1981, however, both temporal and fixed spatial components contributed significantly to the variance (Tables II and III). Grebes showed significant density differences between the east and west sectors on four dates: 28–29 August and 5 October in 1980, and September and October 1981 (Table IV).

Spatial correlations

Chlorophyll *a* and *Artemia* were negatively correlated in August and September in 1980 but not in 1981 (Table V). In late October 1980 and 1981 and November 1981 there was a positive, but not significant, correlation between *Artemia* and chlorophyll *a*.

Artemia and grebes showed both significant negative and positive correlations. In August 1980 grebes were negatively correlated with *Artemia* abundance. In 1981 there were no significant correlations between *Artemia* and grebe abundances in August and September. A significant positive correlation was observed on the third sampling date in both years; i.e. at the beginning of October 1980 and late October 1981. In both years *Artemia* and grebes were uncorrelated on the last sampling date (Table V).

Discussion

Our investigations revealed several different spatial distributions of organisms among the three trophic levels. Coefficients of variation for phytoplankton declined from August to November, whereas coefficients of variation for *Artemia* and grebes peaked in October. Both *Artemia* and phytoplankton populations showed large changes during the autumns of both years; consequently temporal variation was an important component of the total variation in their abundances. Consistent differences in the abundances of *Artemia* and phytoplankton were observed between sections of the lake in 1980, but not in 1981. Ephemeral spatial patchiness was the dominant component of variation

in grebe abundance in both years, and was an important component of variation in *Artemia* abundance in 1981 and phytoplankton density in 1980. At times there were significant spatial correlations between the abundances of adjacent trophic levels. *Artemia* densities and chlorophyll *a* concentrations were negatively correlated in August and September 1980, and *Artemia* and grebe densities were negatively correlated in August 1980. *Artemia* and grebe densities were positively correlated in October of both years.

How do we account for these patterns in distribution and correlations among trophic levels? Because this study was designed to describe lakewide patterns of distribution for these organisms, we can only speculate as to the mechanisms responsible for these patterns. No measurements of advection within the lake or of wind velocities over the lake are available for our study period. Comparisons of distribution among trophic levels, and additional data on trophic interactions (Cooper *et al.*, 1984; Lenz, 1982), however, allow us to formulate hypotheses to account for the observed distributional patterns.

Spatial patchiness in plankton populations on scales of 1 km or greater has been attributed to a variety of factors, many of which are stochastic—vectorial (Stavn, 1971) in that they consist of a gradient in a physical factor overlain by turbulent mixing. When mixing is relatively low, patchiness can arise in response to local differences in temperature (e.g. Watson, 1976) or nutrients (e.g. Abbott *et al.*, 1982), but this patchiness can be superseded by larger-scale differences due to wind (e.g. Therriault and Platt, 1981) or river inflows (e.g. Patalas, 1969; Davis, 1969; Magadza, 1980). All these factors interact with basin morphometry (e.g. Davis 1969) and among-plankton interactions (e.g. Malone and McQueen, 1983; Threlkeld, 1983) to produce patterns of plankton patchiness at a single trophic level. A full understanding of plankton patchiness, however, must also integrate the effects of trophic levels above the plankton, perhaps with predator—prey or foraging approaches (e.g. Krebs *et al.*, 1983).

The distribution of phytoplankton observed in September 1980 (Table IV) is likely due to intense and patchy *Artemia* grazing. In 1980, *Artemia* and chlorophyll *a* were negatively correlated in August and September (Table V), and the difference in estimated grazing pressure between east and west basins increased from 2 to 20 times greater in the west during this period (Lenz, 1982). The more even distributions of phytoplankton in October of both years occurred shortly after overturn when chlorophyll *a* concentrations were uniformly high throughout the lake.

The *Artemia* population was always patchily distributed, both between basins and within each basin. Between basin differences in the *Artemia* population have been observed consistently from 1979 to 1982 (Lenz, 1982; present study; Lenz and Dana, unpublished data). In 1980 these basin differences were particularly pronounced (Figure 4). No data are available on the circulation patterns in Momo Lake, but it appears that the *Artemia* populations in the eastern and western sectors of the lake comprise largely independent populations. The boundary between these sectors remained virtually unchanged throughout the autumn in 1980 (Figure 4), and populations in the two sectors have distinct and stable sex ratios (Lenz, 1982). Although grebe predation can be intense, the grebes are highly mobile in their foraging (Figure 5, Winkler and Cooper, 1986), and it is unlikely that grebe predation could be responsible for the maintenance of temporally stable spatial patchiness in *Artemia* (Table IV). Temperature is not likely to be causing *Artemia* patchiness, at least at the level of between-basin differences (cf. Patalas, 1969), since no major temperature differences between basins have been observ-

ed (G.Dana and P.Lenz, unpublished data; R.Jellison, personal communication).

Grebe distributions probably have a behavioral component. The rapid and long-distance movements made by the grebes are reflected in the dominance of ephemeral patchiness among all variance components (Tables II and III, Winkler and Cooper, 1986). In October of both 1980 and 1981, grebe feeding rates were high (Cooper *et al.*, 1984) and *Artemia* densities were low and patchy (Figure 2, Table I). At these times, densities of grebes and *Artemia* were positively correlated (Table V); grebes appeared to be aggregating near rich pockets of their principal prey (cf. Woodby, 1984). Earlier in the season, the patchy distributions of the grebes (Figure 5) had no obvious relation to lower trophic levels, and it seems safest to assume that *Artemia* at these times were superabundant and that the patterns of distribution of the grebes were due to other physical or social factors. Also, later in the season there was no relation between grebe and *Artemia* abundance probably because *Artemia* densities were uniformly very low throughout the lake. Energetic or behavioral constraints may limit the ability of grebes to actively detect and track subtle differences in prey density at very low prey levels. The grebes left the lake en masse shortly after *Artemia* densities had decreased to low levels (Cooper *et al.*, 1984).

Our data suggest that interactions between trophic levels can have important but intermittent effects in creating and maintaining patchiness, both through the spatially variable consumption of prey and through predator aggregation. Teasing apart the contributions of each of the many factors affecting plankton distribution throughout an entire annual cycle and over the variation imposed by yearly differences in physical factors remains an important research challenge.

Acknowledgements

We thank Dan Hartline and Gayle Dana for field assistance, Ed McCauley, John Downing and Jim Bence for reviewing this manuscript, W.Woodard, J.Downing and R.Moody for statistical help, and the National Geographic Society and UCSB's Academic Senate for financial support.

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Received April 1985; accepted August 1986