Zooplankton Distribution and Abundance in the Sacramento-San Joaquin Delta in Relation to Certain Environmental Factors

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ABSTRACT: The dominant members of the freshwater zooplankton in the Sacramento-San Joaquin delta were those typical of temperate zone rivers—*Bosmina* and *Cyclops* among the crustaceans and *Keratella, Polyarthra, Trichocerca* and *Synchaeta* among the rotifers. The estuarine or brackish component of the plankton was represented by the copepod *Eurytemora affinis* and the rotifer *Synchaeta bicornis*. Abundance of freshwater zooplankton was highest in the San Joaquin River near Stockton, the region with the highest chlorophyll *a* concentrations and highest temperatures. This was also the region least affected by water project operations, which alter the normal river flow patterns and bring large volumes of zooplankton-deficient Sacramento River water into the San Joaquin River and south delta channels. Over a seven-year period, abundance of most zooplankton genera was positively correlated with chlorophyll *a* concentrations and temperature but not with net flow velocity. Only *Bosmina* had a significant and negative correlation with abundance of a predacious shrimp, *Neomysis mercedis*. Extreme salinity intrusion in 1977 reduced freshwater zooplankton abundance throughout most of the delta to seven-year lows. All zooplankton groups showed a long-term abundance decline from 1972 to 1978. In the cases of rotifers and copepods, this decline was significantly correlated with a decline in chlorophyll *a*.

Introduction

The large inland delta of the Sacramento and San Joaquin rivers in central California is estuarine in that it is tidal, but salinity intrusion is usually limited to its western extension during periods of low river flow. High densities of freshwater crustaceans occur in some channels, but other channels have sparse populations in spite of negligible salinity levels (Turner 1966a). Turner attributed these population differences to variations in net flow velocity (a measure of net advective rate) and total dissolved solids (a measure of dissolved nutrients). We examined data from routine surveys of crustacean and rotiferan plankton in the delta from 1972 to 1978 to characterize the zooplankton of the important channels and to analyze the abundance of freshwater taxa in relation to the following environmental factors: chlorophyll *a*, temperature, net flow velocity, salinity, abundance of *Neomysis*

mercedis, a predacious shrimp (Siegfried and Kopache 1980), and the introduction of large volumes of Sacramento River water (relatively deficient in zooplankton according to Turner 1966a) into the San Joaquin River by the operation of the state and federal water project pumping plants in the south delta. The analysis ends in 1978 because of the introduction of two Asian copepods to the delta in that year and in 1979 (Orsi et al. 1983; Ferrari and Orsi 1984). The impact of this introduction and long-term trends in zooplankton abundance in the years after 1978 will be discussed in a subsequent paper.

Methods

Zooplankton was sampled twice monthly from April to October and monthly in March and November from 1972 to 1978 at 24 stations located in the main river channels (Fig. 1). A Clarke-Bumpus net with No. 10

mesh (154-μm openings) was used for large zooplankton. Organisms small enough to pass through a 154-μm mesh were collected using a small pump of 15 1 min^{-1} capacity. The Clarke-Bumpus net was mounted within a rectangular steel towing frame designed to protect the net from snags. Ten minute oblique bottom-to-surface tows were made, during which the frame was raised to the surface in several equal steps. At the end of each tow the pump intake was lowered to the bottom, the motor started, and the intake slowly raised to the surface. Pumped water was collected in a 20-1 carboy and approximately 1.7 l was decanted into a jug. All samples were preserved in a 5% formalin solution with Rose Bengal dye added to aid in distinguishing plankton from detritus. *Neomysis mercedis* was taken in a conical net 1.4 m long, 30 cm in mouth diameter, with 505-μm mesh, mounted on the towing frame below the Clarke-Bumpus net (Knutson and Orsi 1983).

Surface temperature and electrical conductivity were measured at every station. Electrical conductivity was converted to salinity by the following equation: $S\text{‰} = -100 \ Ln(1 - C_{25}/178.5)$, where C_{25} is electrical conductivity in millisiemens per cm at 25° C. Beginning in 1976, chlorophyll *a* was measured in water samples collected at a depth of 1 m at each station. For years prior to 1976, bimonthly chlorophyll *a* measurements were available for 15 of the stations from the U.S. Bureau of Reclamation and the California Department of Water Resources (USBR et al. 1977), although their samples were not usually taken on the same days as the zooplankton samples.

In the laboratory, Clarke-Bumpus samples were passed through a 154-μm mesh screen. Organisms retained on the mesh screen were washed into a volume of water which was then subsampled (after stirring) by removing a 1-ml aliquot with an automatic pipette. Additional aliquots were examined until a minimum of 200 organisms were counted. The volume of water collected by the pump was measured and then passed through 154-μm and 43-μm mesh screens. Organisms retained by the 43-μm mesh screens were identified and counted as with the Clarke-Bumpus samples. Prior to 1976 we identified all plankters to the
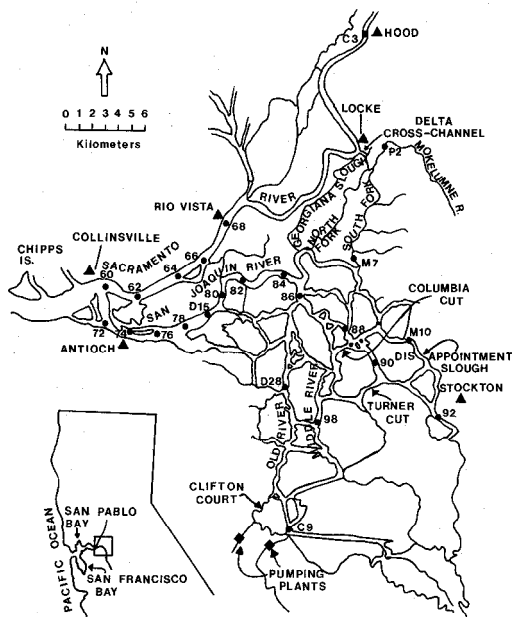

Fig. 1. Map of the Sacramento-San Joaquin delta showing sampling stations.

species level, but this eventually became impractical due to the large number of samples and the time required to make such determinations. Therefore, from 1976 to 1978 most identifications were limited to the genus level with the exception of important species or where a genus was represented by a single species. Copepod copepodids were identified as cyclopoid or calanoid. No attempt was made to categorize nauplii.

Because the delta is tidal, measurements of the rate of water movement are of net movement, that is, the algebraic sum of the landward and seaward dislocations. These net flow velocities were calculated from net flow volumes and channel cross sections estimated by the California Department of Water Resources (personal communication).

Multiple correlations were calculated using March to November station means of zooplankton abundance (number per cubic meter) vs. station means of temperature, chlorophyll *a,* net velocity, electrical conductivity and numbers per cubic meter of *N. mercedis.* Separate correlations were run for the following taxa: *Diaptomus* spp., *Cyclops* spp., *Bosmina longirostris, Daphnia*
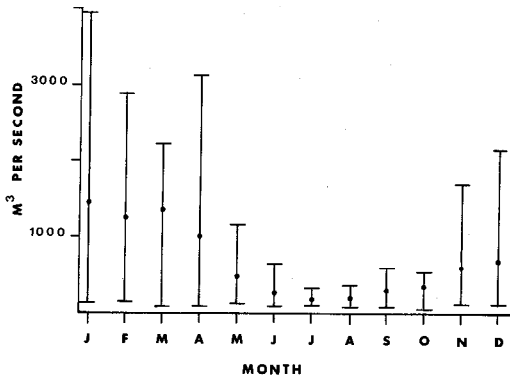
Fig. 2.   Monthly means and ranges (1972–1978) of river outflow measured at Chipps Island.

spp., *Diaphanosoma* spp., and all fresh-water rotifers. Two correlations were run, one for all variables and for the years 1972–1978 less 1975, and one without net velocity using all years because data for that parameter was lacking in 1975.

Environmental Description

HYDROLOGY: NORMAL, CROSS-DELTA AND REVERSE FLOW

The delta encompasses a triangular area of ~400 km² at the eastern end of the Suisun Bay, which connects with San Pablo and San Francisco bays and the Pacific Ocean (Fig. 1). Eighty percent of the inflow to the delta comes from the Sacramento River, 15% from the San Joaquin, and 5% from the Mokelumne River and minor streams. The Sacramento River is about 10 m deep in the ship channel downstream from Rio Vista and from 3 to 6 m deep upstream from it. The San Joaquin also averages 10 m in channel depth. Old and Middle rivers and Disappointment Slough generally are from 2.5 to 9 m deep.

Delta flow patterns are complex and are affected by the volume of river flow and the phenomena of cross-delta and reverse flow caused by the state and federal water project pumping plants that draw >100 m³ sec⁻¹ from Old River near Clifton Court in the south delta (Fig. 1). Tides also affect flow; water in delta channels oscillates as much as 13 km on a tidal cycle.

River flow is strongly seasonal, being lowest in summer and fall, highest during win-

ter rains and spring snowmelt in the Sierra Nevada Mountains (Fig. 2). During a typical winter, water exports are low relative to flow, direction of flow in all channels is seaward (Fig. 3A), and the San Joaquin River (60% of which diverts into Old River above Stockton) satisfies pumping demand. As river runoff declines during spring and the irrigation season begins, San Joaquin River flow becomes inadequate to supply the pumps. To meet pumping demand the gates of the delta Cross-Channel at Locke are opened and Sacramento River water is drawn down the forks of the Mokelumne River, across the San Joaquin River, into and up Old and Middle rivers to the pump intakes near Clifton Court. This is termed cross-delta flow. Flow direction in Old and Middle rivers is therefore reversed (Fig. 3B). Not all of the Sacramento River water flowing down the Mokelumne Forks enters Old and Middle rivers; some moves down the San Joaquin past Sherman Island and reenters the Sacramento channel at the junction of the two rivers. Essentially all of the San Joaquin River flow is pulled to the pumps either through Turner and Columbia Cuts or via Old River above Stockton. Since the volume of Mokelumne River flow is very small during summer, virtually all of the water in western and central delta channels at this time is of Sacramento River origin.

Frequently during summer and fall the pumping demand becomes so great and natural flows are so low that even the cross-delta flow cannot fill pumping demand. Under these conditions, Sacramento water also is drawn around the tip of Sherman Island into the San Joaquin channel, and then up Old River to the pumps, a condition known as reverse flow (Fig. 3C). As a result of these conditions, the net flow in the San Joaquin River switches from downstream to upstream because the duration of ebb tides is shortened and that of flood tides is lengthened. Some water of Sacramento origin continues on upstream past Stockton to the head of Old River. The only San Joaquin water remaining in the delta during reverse flows is in Old and Middle rivers upstream from the pumps.

During the March to November period of the years studied, cross-delta flows occurred in most months and flow reversals
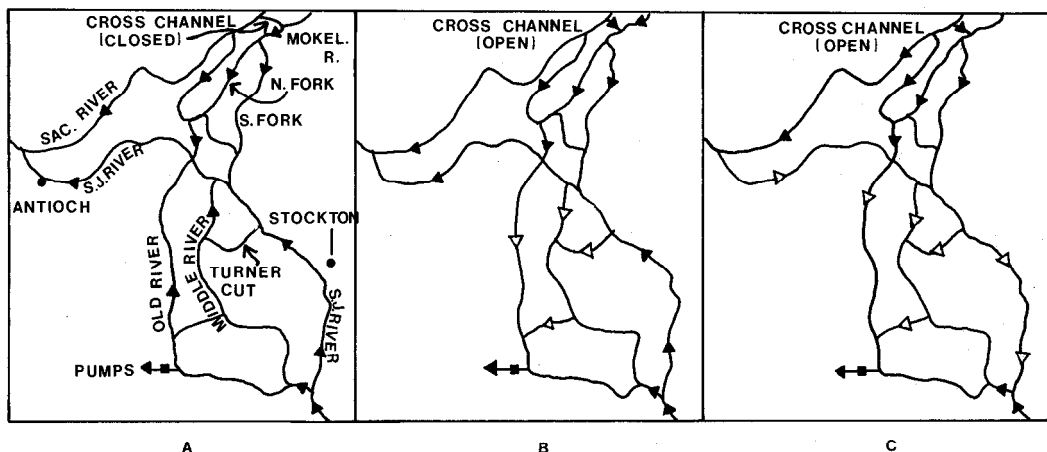
Fig. 3.   Net flow direction in important delta channels during A) normal downstream flow, B) cross-delta flow, and C) reverse flow.

in the San Joaquin River occurred in 30% of the months, mostly during summer.

Results
GEOGRAPHICAL PATTERNS OF ENVIRONMENTAL VARIABLES

To describe the patterns of the environmental variables in the delta, annual (March to November) means were calculated for each variable at each station in each year. Seven-year means and ranges were derived from these. The ranges are the maximum and minimum annual means.

For temperature, a pattern of relatively low values existed in the Sacramento and Mokelumne rivers and higher ones in the San Joaquin River, Old River and Disappointment Slough (Fig. 4). The seven-year means averaged 18.0–18.5 °C along the Sacramento River, with minimum and maximum values of 16.5 and 19.9 °C, both of which were recorded at Hood (station C3). The San Joaquin River means followed a sinusoidal pattern, with the low point of 18.7 °C at the farthest downstream station and the high point of 20.9 °C at Stockton. The Disappointment Slough (station M10) mean temperature was slightly lower than at Stockton. Temperatures in the Mokelumne River (stations P2 and M7) were similar to those in the Sacramento River and showed the widest range. South delta stations (D28 and C9) had temperatures higher than at all San Joaquin River stations except

those near Stockton and immediately downstream from there.

Similarities existed between the temperature and chlorophyll *a* patterns (Fig. 4). Chlorophyll *a* was lower at most Sacramento River stations than at San Joaquin ones, and decreased moving upstream to Hood. Chlorophyll *a* also was low in the Mokelumne River. The highest chlorophyll *a* concentrations and the widest range in the means occurred in the San Joaquin River at Stockton. The influence of cross-delta flow
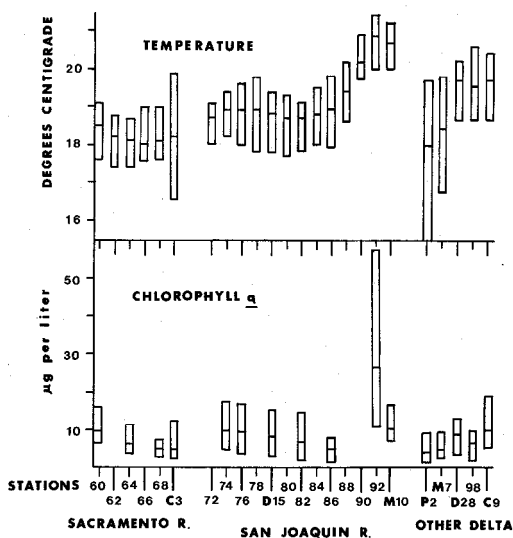

Fig. 4.   Seven-year means and ranges of temperatures and chlorophyll *a* at each sampling station for which data are available.
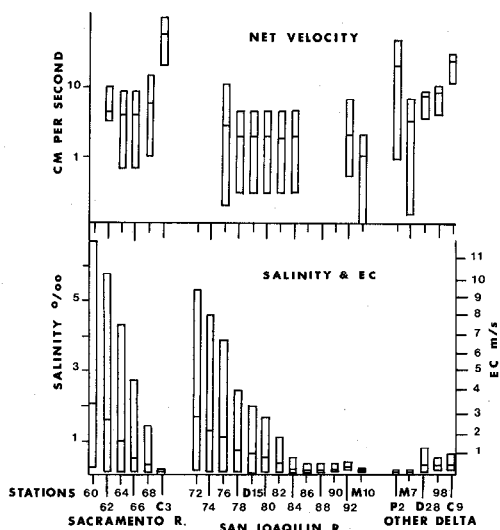
Fig. 5. Seven-year means and ranges of net velocity and salinity-electrical conductivity (EC) at each sampling station for which data are available.

tions. In the San Joaquin River, stations located upstream from the mouth of the Mokelumne River contained freshwater in all years as did stations in the Sacramento River upstream from Rio Vista.

RELATIVE ABUNDANCE OF ZOOPLANKTON TAXA

Cyclopoids constituted 70–80% of all freshwater copepods sampled over the seven years (Fig. 6). The remainder were diaptomids, with trace numbers of *Epischura nevadensis* and *Osphranticum labronectum* at some north delta stations. *Acanthocyclops vernalis* was the most abundant cyclopoid species. *Cyclops bicuspidatus thomasi* and *C. scutifer* were the most common of the minor cyclopoids. *Diaptomus novamexicanus* accounted for 40–60% of the diaptomids, followed by *D. pallidus* and *D. siciloides*. During early spring, *D. franciscanus* was present in low abundance.

Seven genera of planktonic cladocerans were present, but only three genera accounted for >90% of the total each year (Fig. 6). *Bosmina longirostris* was dominant in all years, constituting 61–82% of the annual mean numbers per cubic meter. *Daphnia*, of which *D. pulex* and *D. rosea* were the most abundant species, accounted for up to 25% of the cladocerans. Next was *Disphanosoma* with a relative abundance of 4 to 14%. Other planktonic genera were *Ceriodaphnia, Moina, Chydorus,* and *Leptodora*.

Keratella cochlearis was usually the dominant rotifer, although its abundance declined from 42 to 20% of all rotifers between 1972 and 1976 and did not increase significantly in the next two years (Fig. 6). *Polyarthra* (two unidentified species), *Trichocerca cyclindrica* and *T. similis* were the next most abundant with 20–30% of the mean numbers per cubic meter. *Synchaeta* and *Brachionus*, of which there were several species in each genus, were 4th and 5th most abundant. The abundance of *Synchaeta* increased after 1974. It was the most abundant genus in 1977, comprising 35% of the rotifer population in that year, and was second most abundant in 1978. Other genera only constituted 7% of the rotifers at the most.
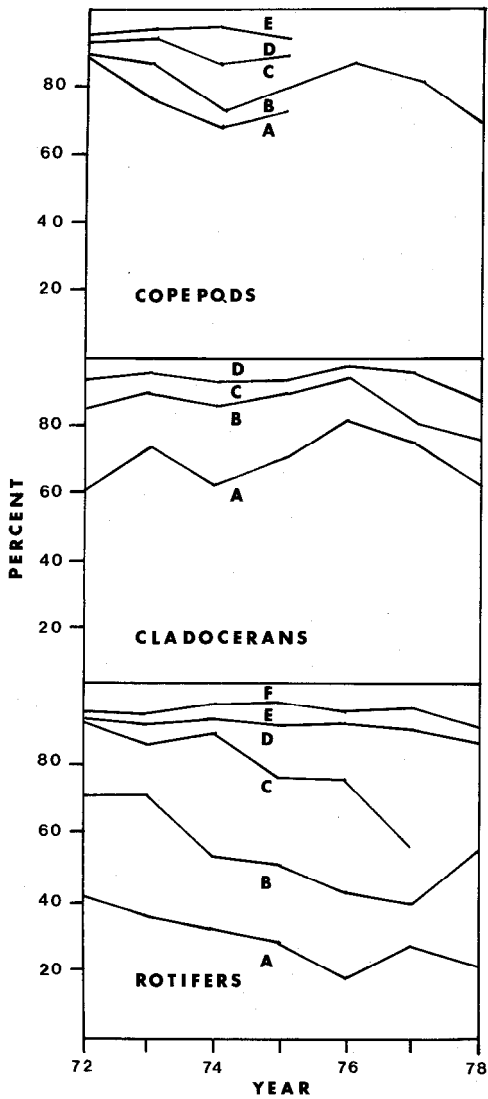
The freshwater zooplankton was thus

could be seen in the depressed concentrations in the San Joaquin River at the mouth of the Mokelumne River, where Sacramento River water first enters the San Joaquin (station 86). Chlorophyll *a* concentrations in Old River were similar to those at the farthest downstream San Joaquin River stations.

An inverse relationship existed between net flow velocity and temperature patterns (Fig. 5). The highest velocities were found at Hood, the next highest were in the Mokelumne River above its forks (station P2) and in Old River at the pumping plant intake (station C9). The lowest net velocities occurred in Disappointment Slough; velocities were only slightly higher and quite uniform along the entire San Joaquin River.

Salinity was highest at the junction of the Sacramento and San Joaquin rivers where they empty into Suisun Bay at stations 60 and 72 (Fig. 5). Salinity declined steadily going upstream in both rivers. Seven-year mean salinities were 2.1‰ in the Sacramento River at station 60 and 1.7‰ at station 72 in the San Joaquin River. Considerable annual variation occurred, reflecting the large variations in river inflow to the delta. In some years the entire delta was freshwater. In other years the salinities averaged >5‰ at the farthest downstream sta-

Fig. 6. Percent composition of each major group of zooplankton in each year. Copepods: A) *Acanthocyclops vernalis,* B) other cyclopoids, C) *Diaptomus novamexicanus,* D) *D. pallidus,* E) *D. siciloides.* Cladocerans: A) *Bosmina,* B) *Daphnia,* C) *Diaphonosoma,* D) other genera. Rotifers: A) *Keratella,* B) *Polyarthra,* C) *Trichocerca,* D) *Synchaeta,* E) *Brachionus,* F) other genera.

dominated by one copepod, *Acanthocyclops vernalis,* one cladoceran, *Bosmina longirostris,* and three or four rotifer genera, *Keratella, Polyarthra, Trichocerca* and *Synchaeta.*

Four brackish water species were found in the delta. Three, *Eurytemora affinis, Acartia californicus,* and *A. clausi* sensu lato (Ambler et al. 1985), were copepods and one, *Synchaeta bicornis,* was a rotifer. *Eury-*

temora affinis is an estuarine species. *Acartia clausi* s.l. appears to be a coastal species that enters estuaries, and *A. californensis* has its center of abundance in south San Francisco Bay (Ambler et al. 1985).

The *Acartia* species entered the delta only in the two driest years, 1976 and 1977, and were found only at the most seaward stations. *Eurytemora affinis* was found throughout most of the delta in all years. It became progressively less abundant moving upstream. *Synchaeta bicornis* was also present throughout the delta in all years and even reached Hood in small numbers. Its abundance increased slightly in the San Joaquin River upstream from the mouth of the Mokelumne River (Fig. 7).

Over the seven-year period the brackish water copepods (mainly *E. affinis*) averaged >90% of the total copepods at the most seaward stations and even at Rio Vista >50% of the copepods were brackish species (Fig. 8). In the San Joaquin River, brackish species dominated the copepod fauna up to
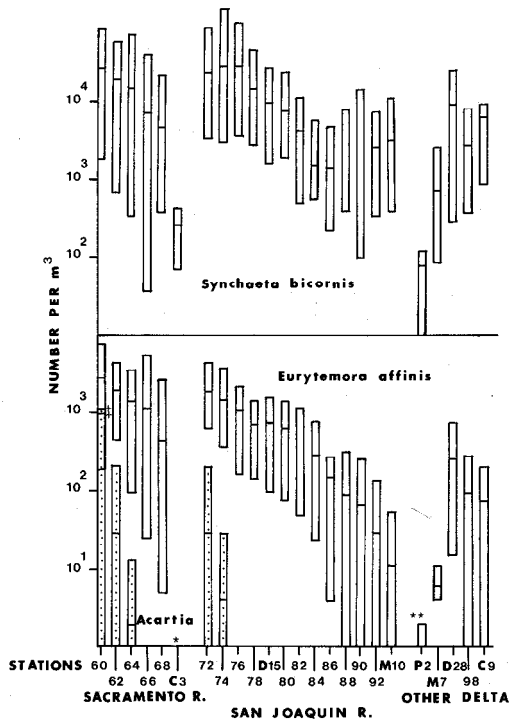

Fig. 7. Seven-year means and ranges of *E. affinis* and *S. bicornis* at each sampling station. * None found, ** mean is 1, minimum is zero, ‡ overlap between *Acartia* and *E. affinis.*

station 80, 20 km from Collinsville. On the other hand, *S. bicornis* did not dominate the rotifer fauna. Its highest average abundance was ~30%. It was more abundant in the Sacramento River than in the San Joaquin (Fig. 9).

There was a strong relationship between the percent abundance of brackish water species and the extent of salinity intrusion as measured at Collinsville. The percent of *E. affinis* changed little between 0.8 and 6.3‰ but below 0.8‰ it dropped sharply (Fig. 10). The relationship between the percent of *S. bicornis* in the rotifer population and salinity appeared to be a straight-line function, but the plot can also be interpreted to suggest a sharp decline at <1‰ (Fig. 10).

FRESHWATER ZOOPLANKTON ABUNDANCE PATTERNS

Rotifers were the most abundant group with densities of 10^4–10^5 m^{-3}. Cladocerans were next most abundant at 10^2–10^4 m^{-3} and adult copepods were least abundant with densities generally <10^3 m^{-3} (Fig. 11).

Because *Eurytemora affinis* enters the delta, the early life stages of copepods (the nauplii and copepodids) could not be included in the total number of freshwater copepods. This biased copepod abundance relative to the other groups of zooplankton for which juveniles as well as adults were counted. To clarify the abundance of copepods relative to other zooplankton, abundance of early life stages at Stockton and Hood (where *E. affinis* was never or rarely found) was calculated for each year. At both stations the
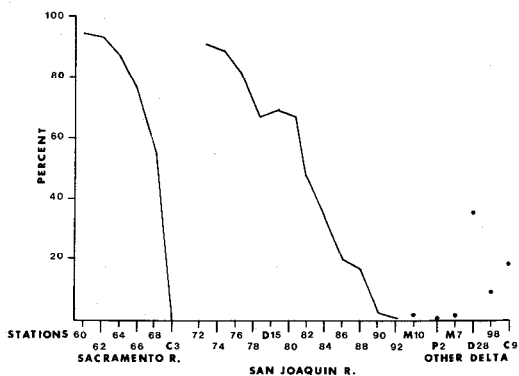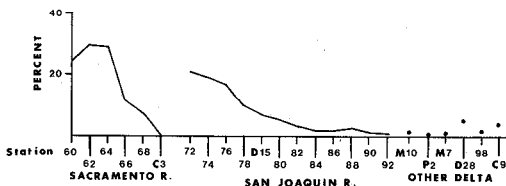
Fig. 9.   Seven-year mean percent of *Synchaeta bicornis* in the total rotiferan fauna at each station.

total abundance of all life stages of copepods was greater than cladoceran abundance and lower than rotifer abundance (Table 1). It is reasonable to infer that this relationship held true over the entire delta.

Seven-year means and ranges of zooplankton densities at each sampling station showed that all three zooplankton groups, copepods, cladocerans and rotifers, had a common abundance pattern. Densities were highest in the Stockton area of the San Joaquin River, decreased at San Joaquin stations in the path of cross-delta flow (stations 84–88), and then either remained fairly constant to the junction of the San Joaquin and Sacramento rivers in the case of rotifers, or declined irregularly to the rivers' junction in the case of crustaceans (Fig. 11). Abundance of all groups was slightly higher in the San Joaquin River downstream from Old
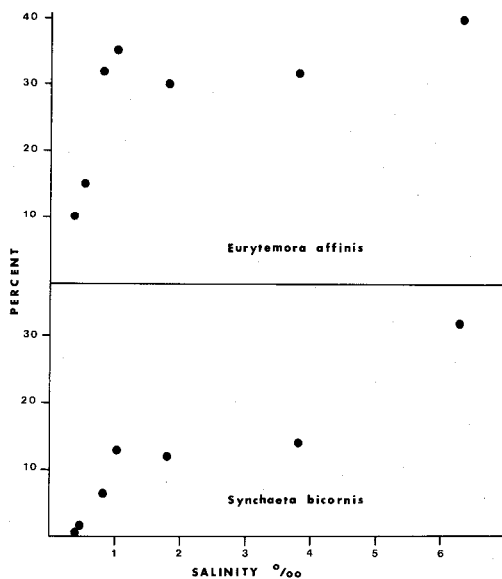
Fig. 8.   Seven-year mean percent of brackish water copepods in the total copepod fauna at each station.

Fig. 10.   Mean annual percent abundance of *Eurytemora affinis* and *Synchaeta bicornis* at all stations in relation to salinity at Collinsville.
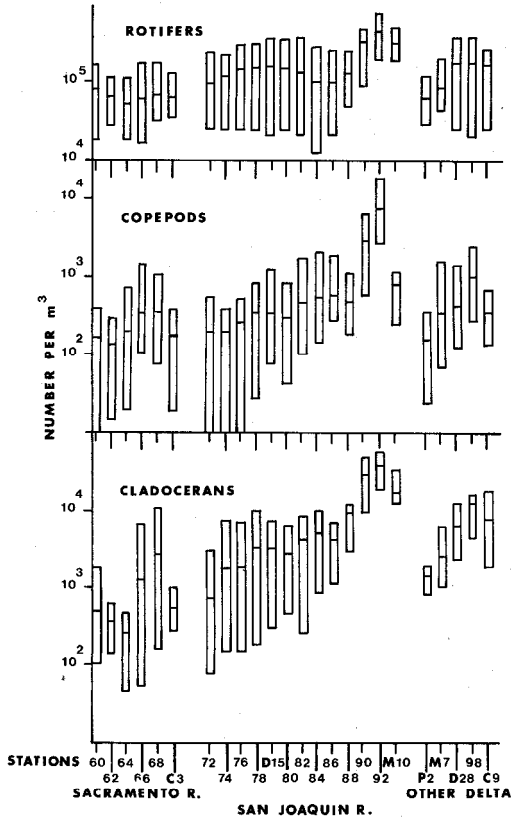
Fig. 11.   Seven-year means and ranges of each major zooplankton group at each sampling station.
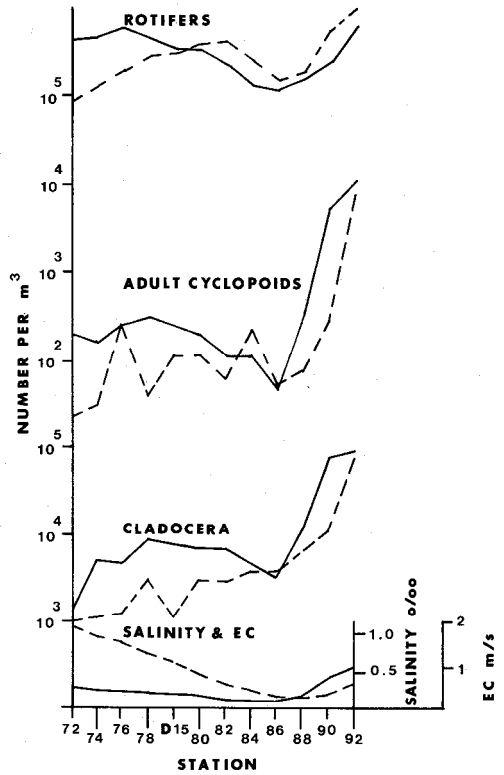

Fig. 12.   Abundance of major zooplankton groups in the San Joaquin River during cross-delta downstream flow, June and September average (——), and during cross-delta reverse flow, July and August average (– – –), 1974. Salinity and electrical conductivity (EC) given for each period.

TABLE 1.   Abundance of early life stages of copepods and total copepod abundance vs. cladoceran and rotifer abundance at stations beyond the range of *Eurytemora affinis*. Values are mean annual numbers per cubic meter. Hood was not sampled in 1972.

Year	Nauplii and Copepodids	Adult Copepods	Total Copepods	Cladocerans	Rotifers
			Hood (C3)		
1972	—	—	—	—	—
1973	6,110	30	6,140	360	98,670
1974	7,590	200	7,790	660	124,470
1975	6,040	40	6,080	270	50,970
1976	3,430	150	3,580	580	39,650
1977	13,280	370	13,650	1,240	220,550
1978	5,200	120	5,320	450	43,820
			Stockton (92)		
1972	127,470	12,970	140,440	41,640	735,190
1973	175,380	8,150	183,530	45,340	572,190
1974	134,800	7,300	142,100	54,670	741,560
1975	65,320	4,820	70,140	52,720	405,780
1976	76,020	8,680	84,700	54,720	240,100
1977	74,810	6,360	81,170	20,740	204,360
1978	41,600	2,740	44,340	18,980	270,270

TABLE 2. Partial and multiple correlation coefficients for zooplankton taxa vs. environmental variables, and *N. mercedis* abundance for a) 1972–1978, 112 df; and b) for 1972–1978 less 1975, with net velocity as an additional variable, 72 df (* p < 0.05, ** p < 0.01).

| Taxon	Temperature	Chlorophyll *a*	Water Conductivity	Net Velocity	*Neomysis mercedis*	R
		1972–1978 less 1975				
Cyclops spp.	0.127	14.489**	−0.105	0.389	−0.165	0.894**
Diaptomus spp.	2.519*	8.952**	−0.841	0.357	−0.864	0.790**
Bosmina longirostris	5.334**	8.671**	−1.814	0.378	−2.003*	0.867**
Daphnia spp.	2.476*	7.243**	−0.910	0.546	−1.215	0.772**
Diaphanosoma spp.	5.019**	0.468	−1.381	−0.671	−0.660	0.639**
Rotifers	3.342**	9.701**	−2.265*	−0.324	−0.086	0.859**
		1972–1978				
Cyclops spp.	1.485	14.420**	−1.826	—	−1.636	0.849**
Diaptomus spp.	3.424**	10.027**	−2.052*	—	−1.168	0.789**
Bosmina longirostris	5.570**	6.994**	−2.850*	—	−2.032*	0.767**
Daphnia spp.	2.994**	7.186**	−1.858	—	−1.463	0.697**
Diaphanosoma spp.	6.501**	1.056	−2.795*	—	−0.921	0.635**
Rotifers	3.680**	11.467**	−4.114**	—	−0.550	0.831**
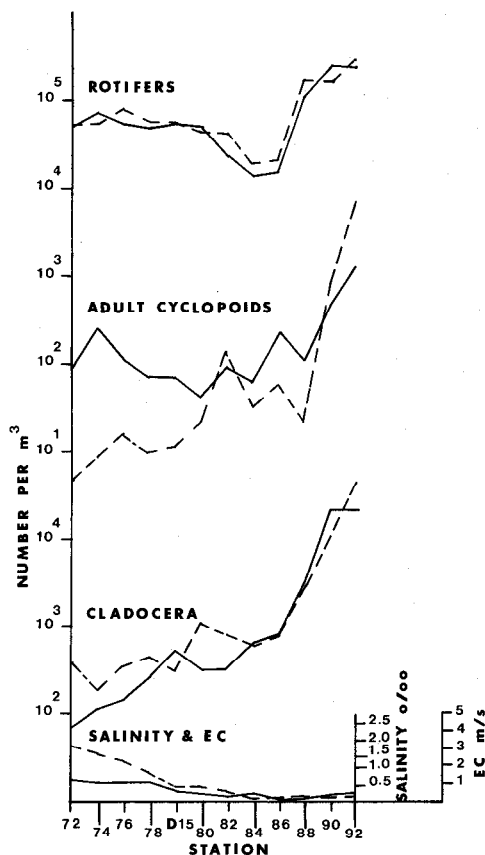
Fig. 13. Abundance of major zooplankton groups in the San Joaquin River during cross-delta downstream flow, June and September average (——), and during cross-delta reverse flow, July and August average (– – –), 1978. Salinity and electrical conductivity (EC) given for each period.

River mouth than in the Sacramento River below Rio Vista (station 68). Copepod and cladoceran densities exhibited a sinusoidal pattern in the Sacramento River, with highest abundance at Decker Island (station 66) and Rio Vista. Rotifer densities did not vary much along the Sacramento but were highest at the most seaward station.

MULTIPLE CORRELATIONS

For all of the zooplankton taxa tested, multiple correlations between their densities and chlorophyll *a*, temperature, electrical conductivity, net velocity and *Neomysis mercedis* were statistically significant (Table 2). Partial correlations were significant between 1) all zooplankton taxa, except *Diaphanosoma*, and chlorophyll *a*; and 2) all taxa, except *Cyclops*, and temperature. On the other hand no taxon was significantly related to net velocity; and only one, *Bosmina*, was significantly related to *N. mercedis*. Results with electrical conductivity were mixed depending on whether 1975, the year without net velocity data, was used.

REVERSE FLOW CONDITIONS

It is difficult to make meaningful comparisons of zooplankton abundance in the San Joaquin River between downstream and reverse flows because 1) salinity intrusion is typically higher at times of reverse flow than during normal flow, and 2) reverse flow usually occurs in summer and downstream flow the rest of the year. Nevertheless, an

TABLE 3.   March–November means of the three major zooplankton groups and environmental variables at Hood on the Sacramento River and Stockton on the San Joaquin River in 1974 and 1977. Copepods include all life stages. Zooplankton abundance is expressed in numbers per cubic meter.

Variable	Hood		Stockton	
	1974	1977	1974	1977
Chlorophyll a (μg l^{-1})	2.8	12.4	35.2	10.6
Temperature (°C)	17.5	20.0	21.0	21.5
Net velocity (cm s^{-1})	79.2	19.8	2.2	0.5
Rotifers	124,470	220,550	741,560	204,360
Cladocerans	660	1,240	54,670	20,740
Copepods	7,790	13,650	142,100	81,170

analysis was attempted by examining the abundance of the major zooplankton groups at each San Joaquin River station during July and August 1974 and 1978 (reverse flow periods) and June and September of the same years (downstream flow periods) (Figs. 12 and 13). In other years, reverse flows either lasted too long or not long enough for comparisons.

At the most seaward group of stations (72–82) all zooplankton groups had lower densities during the reverse flow months of 1974, but this was not true in 1978 in spite of high salinities during reverse flows of that year. At the middle groups of stations (84–88), where cross-delta flow occurs, zooplankton were not consistently more abundant during either type of flow. This was also true at the most upstream stations, 90 and 92. In general, during reverse flows, zooplankton abundance, with the exception of rotifers in 1978, increased moving upstream into fresher water. During downstream flow months of 1974, all types of zooplankton had higher abundance at stations 74–78 than at station 86 in the path of cross-delta flow. But, in 1978 this was true only for rotifers.

Effects of Large Changes in River Flow

The year of highest salinity intrusion and lowest river flow was 1977. In that year, salinity averaged > 5‰ at the most seaward stations of both rivers and was detectable (0.5‰) in the San Joaquin River upstream to the mouth of Old River, where cross-delta flow provided a barrier to further intrusion. In the Sacramento River detectable oceanic salinity extended past Rio Vista but did not reach Hood. Large reductions of all

freshwater zooplankton occurred in the area affected by salinity intrusion and even upstream from it. The low points of the seven-year abundance ranges at all stations except Hood were set in this year. Conversely, the greatest freshwater flows occurred in 1974. Salinity intrusion in that year touched only the four most seaward stations in the San Joaquin River and only the two most seaward ones in the Sacramento River. Freshwater zooplankton was largely unaffected by salinity in that year.

These two years provided an opportunity to compare zooplankton abundance at Hood and Stockton where ocean salts did not reach but where the other environmental parameters varied greatly in response to river flows.

At Hood, the small water volumes moving down the Sacramento River in 1977 resulted in lower net velocity, higher temperature and much higher chlorophyll a concentrations compared to 1974 (Table 3). At Stockton the primary difference between the two years was much lower chlorophyll a concentrations in 1977. Zooplankton abundance appeared to respond to the change in chlorophyll a more than to any other variable. All zooplankton groups were approximately twice as abundant at Hood in 1977 as compared to 1974 and half or less than half as abundant at Stockton in 1977. The copepods were overwhelmingly cyclopoids in both years at Hood: 97% in 1974 and 75% in 1977. Cyclopoids also were dominant at Stockton but the percentages were lower: 75% in 1974 and 69% in 1977. This indicates that diaptomids were more adversely affected by 1974 conditions at Hood than were cyclopoids. The percentages at Stockton may be too close to reach the same conclusion there.
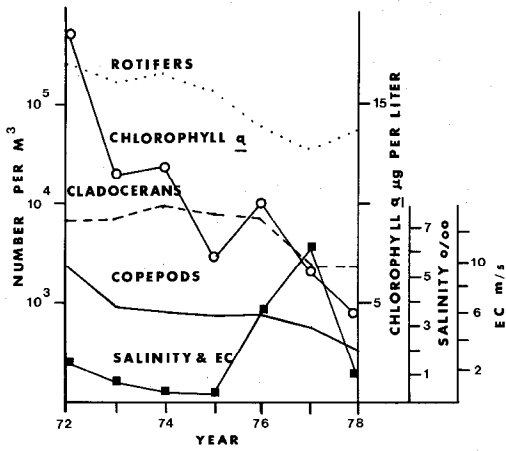
Fig. 14. Mean annual abundance of each major zooplankton group in the delta and annual values of chlorophyll *a* and salinity-electrical conductivity.
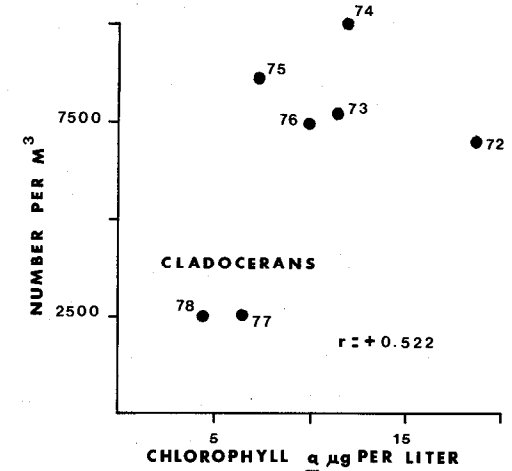

Fig. 16. Mean annual abundance of cladocerans vs. mean annual chlorophyll *a* at all delta stations from 1972 to 1978. Numbers next to the points signify the years.

ZOOPLANKTON ABUNDANCE TRENDS

Large variation in annual population size (annual mean numbers per cubic meter at all stations sampled) occurred in all three zooplankton groups (Fig. 14). A major downtrend in rotifer abundance took place between 1972 and 1977, with mean annual density declining from 260,000 to 37,000 m^{-3}. A slight recovery in 1978 brought mean

density up to 58,000 m^{-3}. The cladoceran population was almost stable from 1972 to 1976, declined sharply in 1977, and remained low in 1978. Copepods showed a steep decline between 1972 and 1973 from 2,270 to 970 m^{-3}, then stabilized until 1977, and decreased further in 1978 to a low of 335 m^{-3}.
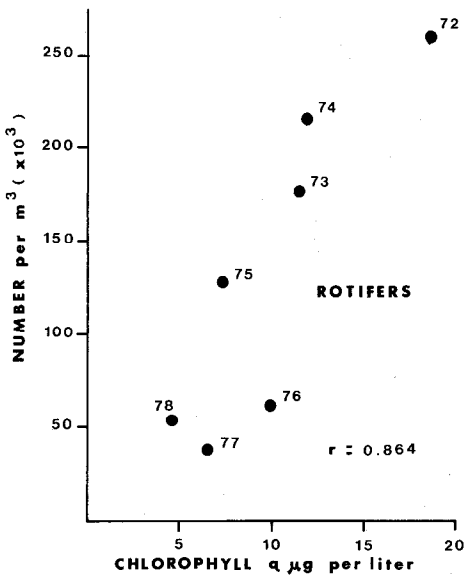

Fig. 15. Mean annual abundance of freshwater rotifers vs. mean annual chlorophyll *a* at all delta stations from 1972 to 1978. Numbers next to the points signify the years.
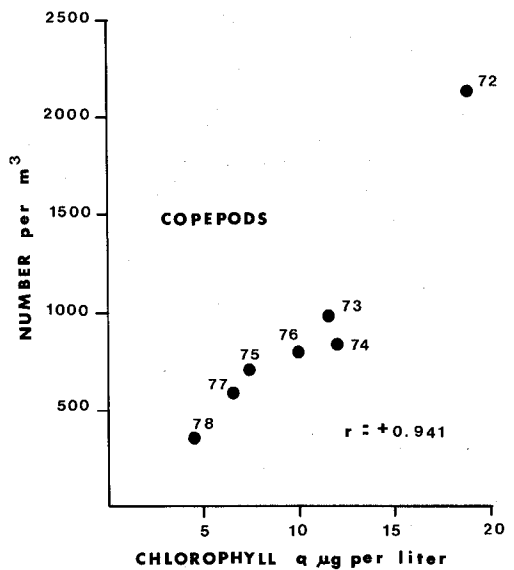

Fig. 17. Mean annual abundance of freshwater copepods vs. mean annual chlorophyll *a* at all delta stations from 1972 to 1978. Numbers next to the points signify the years.

The decline in overall zooplankton abundance from 1972 to 1978 was roughly paralleled by a decrease in the mean chlorophyll a concentration from 18.5 μg l^{-1} in 1972 to 4.5 μm l^{-1} in 1978. Simple linear correlation coefficients between zooplankton density and chlorophyll a concentrations for 1972–1978 were 0.864 (p < 0.05) for rotifers, 0.522 (not significant) for cladocerans, and 0.941 (p < 0.01) for copepods (Figs. 15, 16, and 17). There appeared to be no relationship between abundance of any of the zooplankton groups and salinity intrusion.

Discussion

The delta's zooplankton fauna bears strong similarities to that of the upper Columbia River estuary (Haertel and Osterberg 1967). Dominant species in the fresh and brackish waters of both estuaries were *A. vernalis, Bosmina, Diaphanosoma,* and *E. affinis* (*E. hirundoides*). Major differences in abundance occurred, however, for *E. affinis* which rarely exceeded 20,000 m^{-3} in the delta but went as high as 108,000 m^{-3} in the Columbia, and for freshwater forms which peaked at only 17,000–26,000 m^{-3} in the Columbia vs. more than 100,000 m^{-3} in the delta.

All types of freshwater zooplankton were most abundant in the area of the delta with the highest temperatures and chlorophyll a concentrations and low net velocities—the San Joaquin River at Stockton. Turner (1966a) also found zooplankton to be highest near this location. Zooplankton abundance was lowest in the Sacramento River at Hood and in the Mokelumne River, regions of low chlorophyll a concentrations and temperatures and high net flow velocities.

Although no zooplankton taxon was significantly correlated with net velocity, rate of water movement is a fundamental factor affecting zooplankton density in all lotic habitats. Ketchum (1954) developed general equations describing the relationship between zooplankton reproduction and the net seaward movement of water in estuaries. These equations demonstrate that if population size is to increase, the reproductive rate of zooplankton must exceed the advective rate of the water. Perhaps the most

meaningful way of measuring advective rate is to consider the "age" of the water, that is, how long it has been moving down a channel. The utility of this concept was demonstrated in a field study in the Sacramento River, in which phytoplankton populations increased with distance downstream from Keswick Dam to the delta, a traverse of 499 km (Greenberg 1964). However, a statistically significant correlation between cell counts and stream velocity did not exist because velocity may have been as high or higher near the delta as at Keswick Dam.

Hence, in the delta, zooplankton population size may fail to correlate with net velocity because this parameter is an inadequate measure of water age. In addition, the significance of the correlations was affected by the wide variations in zooplankton abundance along the San Joaquin River where net velocities were quite uniform (Figs. 5 and 11). These zooplankton variations appear to be partly the effect of the entrance of zooplankton-deficient Sacramento River water from the Hood region into the San Joaquin as a result of cross-delta flow.

The effects of reverse flow are difficult to elucidate. Reverse flow brings Sacramento River water around Sherman Island into the San Joaquin River. If zooplankton density in the Sacramento River water that is pulled into the San Joaquin is lower than that in the latter river, the result should obviously be a reduction in zooplankton abundance in the affected area, as occurs further up the San Joaquin at the mouth of the Mokelumne River.

It is, however, difficult to determine if the low zooplankton densities in the San Joaquin River from its confluence with the Sacramento River to Jersey Island are caused by the entrance of Sacramento River water or simply by high salinities which would exist even in the absence of reverse flow. If reverse flow draws a greater volume of saline water into the San Joaquin River than would enter during downstream flow conditions, then reverse flow should have a negative effect on freshwater zooplankton. The available data are inadequate to determine if this actually happens.

The statistically significant correlation

between zooplankton densities and chlorophyll *a* concentrations agree with the result of laboratory experiments demonstrating that phytoplankton availability regulates zooplankton growth and reproduction (Weglenska 1971; Zurlini et al. 1978; Chi-Hsiang and Armitage 1980; Robertson and Salt 1980; Kankaala and Wulff 1981), and field studies in which zooplankton abundance or biomass was positively correlated with phytoplankton biomass or chlorophyll *a* (McCauley and Kalff 1981; Canfield and Watkins 1984).

The significant correlations between zooplankton and temperature are also reasonable in the light of literature results showing that temperature regulates egg development and post-embryonic growth of crustacean plankton (Elster 1954; Winberg 1956; Eichhorn 1959; Chi-Hsiang and Armitage 1980; Kankaala and Wulff 1981). Patalas and Salki (1984) calculated that a 3 °C drop in temperature would lower crustacean plankton growth rates by 25%. A temperature difference of this magnitude existed between Stockton and most of the Sacramento River and should have contributed to the higher zooplankton abundance at Stockton.

The change in rotifer abundance between 1974 and 1977 at Hood and Stockton definitely can be considered a response to the changes in the measured environmental variables. Cladocerans and copepods, however, were far less abundant at Hood in 1977 than they were at Stockton in 1974 at similar chlorophyll *a* concentrations and temperatures. At a mean rate of 19.8 cm s^{-1} in 1977, water movement may still have been too high in the Sacramento River to permit a stronger rise in the abundance of those organisms possessing low rates of increase.

Mysid shrimp are known predators on zooplankton (Siegfried and Kopache 1980; Bremer and Vijverberg 1982). However, only *Bosmina* had a significant and negative partial correlation with *N. mercedis* abundance. It is possible that *N. mercedis* had a preference for *Bosmina*; a similar mysid species, *N. integer,* is known to feed heavily on *Bosmina* in a freshwater Netherlands lake (Bremer and Vijverberg 1982). Other predators, whose effects on zooplankton cannot be easily tested due to a lack of data on their

abundance or because of seasonality of occurrence, are the young of various fishes, such as striped bass, black crappie and white catfish, and adult threadfin and American shad (Stevens 1966a, 1966b; Turner 1966b, 1966c).

The long-term downtrend in zooplankton densities from 1972 to 1978 is cause for concern, because many delta fishes depend on zooplankton at some point in their life cycles. Abundance of young-of-the-year striped bass, which feed on zooplankton after yolk sac absorption, has been depressed since 1977 (Stevens et al. 1985). The marked reduction in phytoplankton and zooplankton over the years suggests that a fundamental alteration in the trophic status of the delta and its ability to support fish has occurred. A reduction in the organic waste loading to the delta as a result of improved waste treatment has been mentioned as a possible cause of the phytoplankton decline. An alternative explanation is increased pumping rates at the south delta pumping plants (Stevens et al. 1985). Shutdowns of the state pumps for repairs in May 1981 and June 1982 were followed by phytoplankton blooms in the San Joaquin River and south delta channels. Possibly both mechanisms have contributed to the phytoplankton decline.

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