

FOOD LIMITATION AS THE PROBABLE CAUSE OF A LONG-TERM DECLINE IN THE ABUNDANCE OF *NEOMYSIS MERCEDIS* THE OPOSSUM SHRIMP IN THE SACRAMENTO-SAN JOAQUIN ESTUARY

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Neomysis mercedis was sampled from 1968 to 1993 throughout Suisun Bay and the Delta. Adults alternated between large ones in winter and spring and small ones in summer and fall. Annual abundance tended to reach a maximum from May to July. A long-term downtrend in abundance occurred in spring, summer and fall after 1975. Abundance was lowest during the drought years 1987-1992 but did not rise when the drought ended in 1993. Females tended to be smaller in the years of lowest abundance and the percent of females carrying eggs was low in those years. Five hypotheses for the decline were investigated: (1) reduced concentration by estuarine gravitational flow and increased seaward loss to tidal pumping, (2) food limitation, (3) rice herbicides, (4) high temperature, (5) export pumping losses. Food limitation of juveniles in the form of reduced phytoplankton concentrations best explained the decline. Food appears to be permanently limited by the grazing of the introduced Asian clam, *Potamocorbula amurensis*. Competition for food by two introduced Asian mysid shrimps may also hamper the recovery of the native mysid population.

Neomysis mercedis is a member of the malacostracan order Mysidacea, a group of small, shrimp-like animals that are commonly known as opossum shrimp because of the ventral brood pouch in which they carry their developing young. Mysidaceans are found in a variety of habitats from deep oceans and coastal seas to estuaries, rivers and lakes. They are often found in shoals or schools numbering thousands of individuals (Clutter 1969).

In the Sacramento-San Joaquin Estuary there are eight species, of which one, *Acanthomysis aspera*, was introduced from Japan in 1992, presumably in ballast water, and another but undescribed *Acanthomysis* species was introduced from an unknown part of the Far East in the same year. *Neomysis mercedis* is located primarily in Suisun Bay and the Delta (Heubach 1969; Siegfried *et al.* 1979; Knutson & Orsi 1983) where it is by far the most abundant mysidacean. It is an important food for juvenile striped bass (Heubach *et al.* 1963; Stevens 1966a and b), and is also consumed by many other fish species (Radtke 1966; Stevens 1966b), and by the caridean shrimps, *Crangon franciscorum* and *Palaemon macrodactylus* (Sitts & Knight 1979).

Sampling for *N. mercedis* began in 1964 as part of the original Department of Fish and Game (CDFG) ecological studies (Turner & Heubach 1966). Sampling was suspended in 1967 and resumed in June 1968.

N. mercedis was found to be most abundant from freshwater to 2.0 ‰ chlorinity (3.6 ‰ surface salinity) (Heubach 1969) or from 1.2 to 5.6 ‰ salinity (Knutson & Orsi 1983). These salinities place it in what the literature on this estuary has

traditionally termed the entrainment zone. This is the section of the salinity gradient where particle settling and estuarine flow patterns concentrate particulate matter. It has been given an operational definition of 1.2-6.0 ‰ salinity (specific conductance 2-10 mS/cm (Arthur & Ball 1980; Kimmerer 1992). Turbidity tends to maximize in this area, making it roughly equivalent to the maximum turbidity zone identified in other estuaries.

Temperature $> 22^{\circ}\text{C}$ in combination with low dissolved oxygen concentration was associated with low mysid abundance (Heubach 1969) but temperature was not a factor affecting interannual abundance variations (Knutson & Orsi 1983). The upper lethal temperature was established as 24.2 to 25.5°C . in 48 hour bioassays (Hair 1971).

Regression analysis of 1968-1981 data indicated that annual July-October population size was significantly and negatively related to salinity intrusion and positively related to the abundance of the copepod *Eurytemora affinis*, a food item. Salinity intrusion is an indirect measure of the location of the entrainment zone and the location of this zone is associated with variations in mysid abundance. Highest abundance from 1972 to 1988 was associated with entrainment zone positions in Suisun Bay < 72 km from the Golden Gate and lowest abundance when the entrainment zone was at > 92 km and in the western Delta (Kimmerer 1992). The reason for the relationship between abundance and entrainment zone position has not been established.

Mysids migrate vertically. Adults tend to have a midwater location and the neonates are closer to surface than bottom in the turbid entrainment zone (Orsi 1986). In clearer water seaward from the entrainment zone, the adults were closer to bottom than to surface. The vertical migration pattern may interact with two-layered estuarine flow to concentrate the mysids in the entrainment zone and prevent their downstream loss from the estuary (Orsi 1986). Losses upstream to the Federal and State water export pumping plants in the south Delta might also occur (Knutson & Orsi 1983).

Food habits investigations showed that detritus and diatoms were the most abundant items in mysid gut contents (Baldo Kost & Knight 1971). But Siegfried & Kopache (1980) found that although diatoms were the most abundant prey identified, predation on rotifers and copepods accounted for $> 80\%$ of the energy consumed by adults. Mysids fed as herbivores when small, as carnivores when large (Siegfried & Kopache 1980).

Toxic chemicals may have adverse effects on *N. mercedis*. Sacramento Valley rice fields are treated with several herbicides and pesticides and the fields are drained from April through June into the Sutter Bypass, which enters the Sacramento River upstream from the city of Sacramento. The toxicity of some of these chemicals to *N. mercedis* has been determined in bioassays (Bailey 1985; Faggella *et al.* 1990).

The purpose of this paper is to present relevant life history information, to describe mysid abundance trends from 1968 to 1993, and to evaluate hypotheses to explain the trends. Several hypotheses can be constructed based on the above literature results. These are:

(1) Greater seaward loss of mysids when estuarine gravitational circulation is lessened during periods of low freshwater outflow. This hypothesis envisions an interaction between the predominant vertical positions of juvenile and adult mysids in the water column and the ebb-flood asymmetry in vertical velocity profiles that causes slightly greater seaward displacement of surface water on the ebb tide and slightly greater upstream displacement of bottom water on the flood over a tidal cycle (Pritchard 1956). Juvenile mysids are positioned above mid-depth (Orsi 1986) and should experience a net downstream movement over a tidal cycle. As they mature they drop into the bottom layer and experience a net upstream movement. The downstream movement of one life stage is thus balanced by the upstream movement of the other to minimize population loss from the entrapment zone. During periods of low freshwater outflow tidal circulation dominates over gravitational flow and tidal pumping may remove mysids from the estuary.

(2) Food limitation. Food limitation has been extensively investigated in copepods (Checkley 1980; Ambler 1986; Beckman & Peterson 1986) but no work has been done on mysidaceans. However, the biological effects of food limitation should be similar in mysids and copepods. At low food levels copepod egg production declines sharply and growth is reduced. These conditions will affect birth rate and hence, population size.

(3) Mortality from high temperature. In the laboratory, mysid mortality increased sharply at temperatures $> 22^{\circ}\text{C}$ (Hair 1971). Field abundance in 1965 and 1966 showed a decline at such temperatures (Heubach 1969). Obviously, temperature mortality will occur only in summer and possibly early fall.

(4) Mortality from rice herbicides. This would also be a seasonal phenomenon restricted to the months when such chemicals are in the river – April, May and June.

(5) Loss to the south Delta export pumping plants. These plants draw water out of Old River and send it to the San Joaquin Valley and southern California. In summer and fall the volume they extract is so large – a maximum of $> 300 \text{ m}^3\text{sec}^{-1}$ – that water to supply them is pulled out of the Sacramento River, down the Mokelumne River, across the San Joaquin River, and up Old and Middle rivers. Much of the water in the San Joaquin River up and downstream from the mouth of Old River flows to the pumps in summer and fall. When mysids are located in the Delta they can conceivably become entrained in these pumping flows and be exported from the estuary. Clearly, mysids would be most vulnerable to export when the entrapment zone is in the Delta.

METHODS

Field

Mysids were collected in a conical plankton net attached to a rectangular towing frame of steel pipe designed to protect the net from snags. Mesh size and net dimensions have varied over the years (Knutson & Orsi 1983). The most important change was from 1 mm mesh to 0.505 mm mesh in 1974 to reduce net escapement by juvenile mysids < 4 mm in total length. Because of this change, abundance calculations in this paper are for ≥ 4 mm mysids. Net mouth diameter has been 30

cm and net length 1.48 m since 1974. Ten minute oblique, stepwise, bottom to surface tows were made at a varying number of stations from San Pablo Bay throughout the Delta. Of these, 35 in Suisun Bay and the Delta have been sampled consistently since 1968 and are the ones used in this analysis (Fig. 1). Sampling was generally done once monthly from November to March and twice monthly the rest of the year. But no December to February sampling was done after 1983. Surface specific conductivity and surface temperature were measured and Secchi disk readings were taken at each station. Starting in 1976, chlorophyll *a* was measured by the acidification method from water collected at 1 m depth. For years prior to 1976 chlorophyll *a* data from the Department of Water Resources monitoring program was used. Starting in 1972, a Clarke-Bumpus net and a small pump were used to collect copepods, cladocerans and rotifers at the same stations. Field sampling and laboratory processing methods for *N. mercedis* are detailed in Knutson & Orsi (1983) and for zooplankton in Orsi & Mecum (1986).

Analysis

Abundance of an organism in the salt field of an estuary is partly a function of salinity. High freshwater outflow in spring can push most of the mysid population downstream from the sampling sites so the tail of the distribution is sampled and a biased estimate of abundance is obtained. Temperature also has a large influence on population size. To determine if changes in abundance over time have occurred due to other factors, the effects of salinity and temperature must be removed from

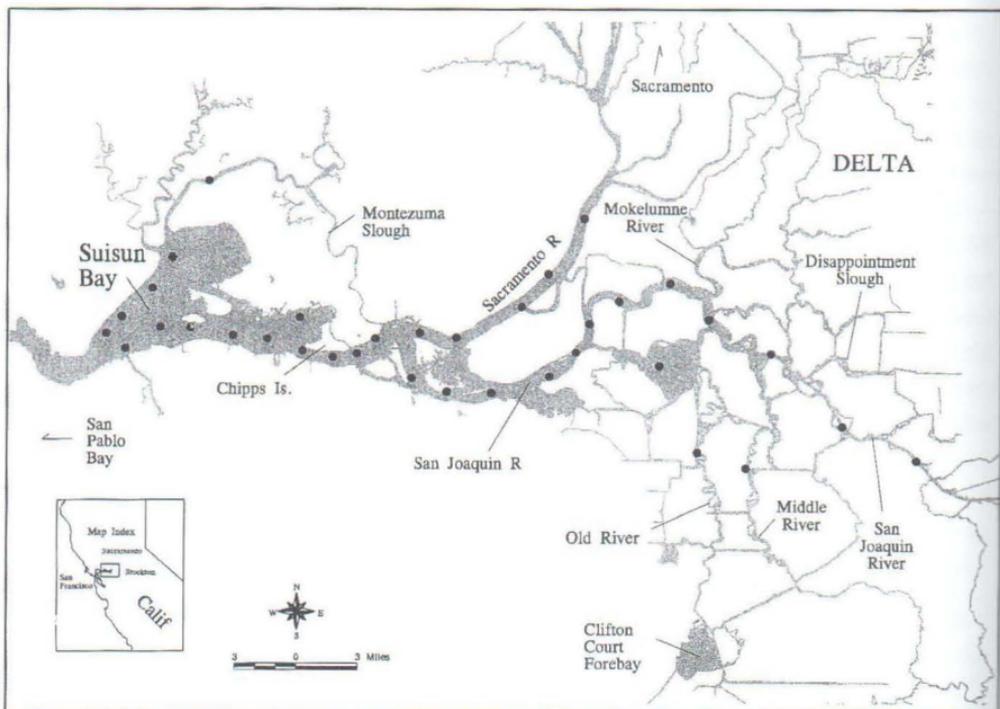


FIGURE 1. Map of Suisun Bay and the Delta, showing location of sampling stations.

the measurements of abundance. To do this, abundance calculations in numbers per cubic meter for all years were combined for all stations in Suisun Bay and the Delta and divided into 20 specific conductivity classes of nearly equal sample size (Table 1). Mean abundance was then calculated for each combination of specific conductivity class and month and each abundance value at each date and station was subtracted from the class and month mean to yield a corrected or anomaly value. The anomalies are expressed as unitless numbers positive or negative to the all-over mean. The anomalies are the abundance values actually subjected to statistical analysis.

RESULTS

Life History

Neonates are released from the brood pouch at a total length of 2 or 3 mm and grow to a maximum length of 16-18 mm for females and 14-16 mm for males. Adult length varies seasonally (Fig. 2). Females mature at ~10 mm and reach their maximum length in March. The largest females then begin to disappear and young females begin to mature at smaller sizes so that female length becomes progressively shorter until it ranges between 7-8 mm and 11-12 mm in July and August. Length begins to increase again in late October as water temperatures drop. The

TABLE 1. Mean salinity and specific conductance in each salinity class used in the abundance-salinity relationship.

<i>Salinity Class</i>	<i>Mean Salinity (%)</i>	<i>Mean Specific conductance (mS/cm)</i>
1	0.04	0.07
2	0.08	0.15
3	0.10	0.17
4	0.11	0.20
5	0.12	0.22
6	0.15	0.26
7	0.16	0.28
8	0.25	0.42
9	0.30	0.57
10	0.45	0.80
11	0.70	1.21
12	1.01	1.89
13	2.02	2.98
14	3.05	4.53
15	4.08	6.42
16	5.13	8.66
17	6.19	11.27
18	8.34	14.23
19	10.53	18.11
20	15.03	26.85

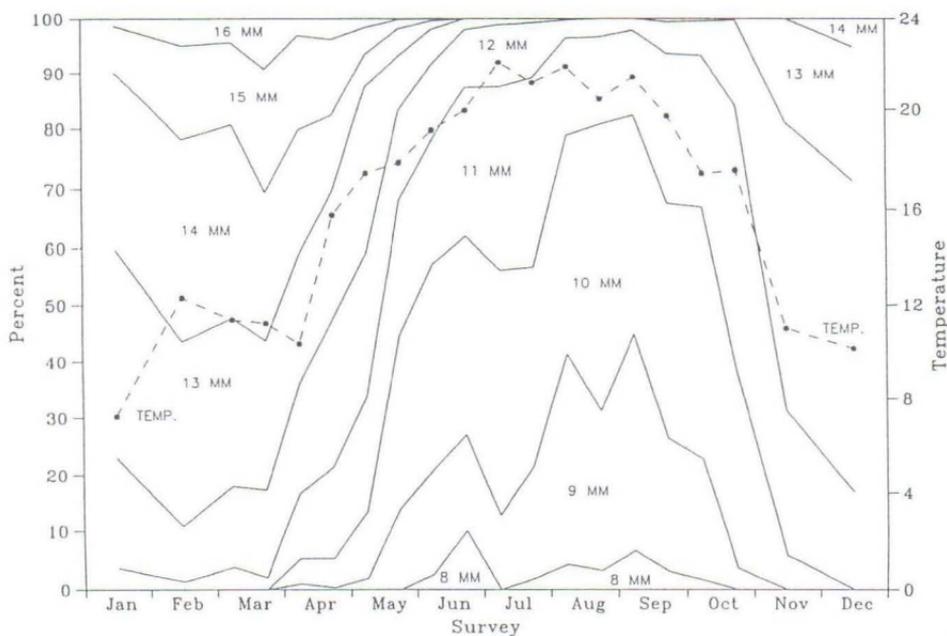


FIGURE 2. Female length frequency composition and mean temperature (C) on each 1982 sampling survey.

largest changes in length frequencies occur in April when temperature rises rapidly. The population thus cycles between large females in winter and small ones in summer. This also occurs in *N. mercedis* in the Fraser River, British Columbia (Johnston & Northcote 1988).

Because the number of young carried per female is a function of female size, fecundity varies with season (Figs. 3 and 4). The number of young per brood ranges from a mean of ~11 for 8 mm females to a mean of ~80 for 17 mm females. Population fecundity is highest in spring, declines rapidly to a summer low and increases slightly in fall. The number of developing young in the population depends not only on female size and abundance but on the percent of females gravid. This varies over time but has no apparent seasonal pattern (Fig. 5). Adult density may be a factor regulating percent gravid as samples with > 500 mysids usually have a higher percent gravid than those with < 500 mysids. The percent gravid was very low in 1976 and 1977 and from 1989 to 1993, years characterized by low mysid abundance (Fig. 7).

Prior to 1981 three cohorts of young appeared in most years, large ones in May to July and a small one in October (Fig. 6). The May cohort was presumably produced by overwintering females and young born during winter and early spring and maturing in May. Young from the May cohort should mature in about two months (H. C. Bailey, Univ. California, Davis, pers. commun.) and should produce the July cohort.

The length frequencies for adult females show that 13 to 15 mm females dominated from January to March but by the time the first cohort appeared, 10 to

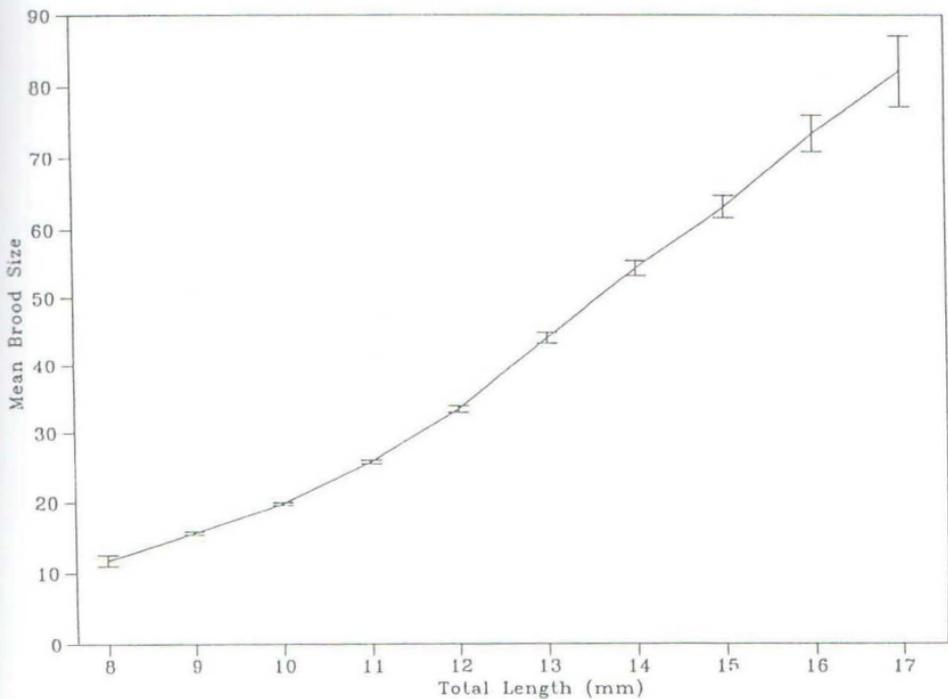


FIGURE 3. Female length-brood size relationship. Bars mark the 95% confidence intervals of the 1976-93 means for each length group.

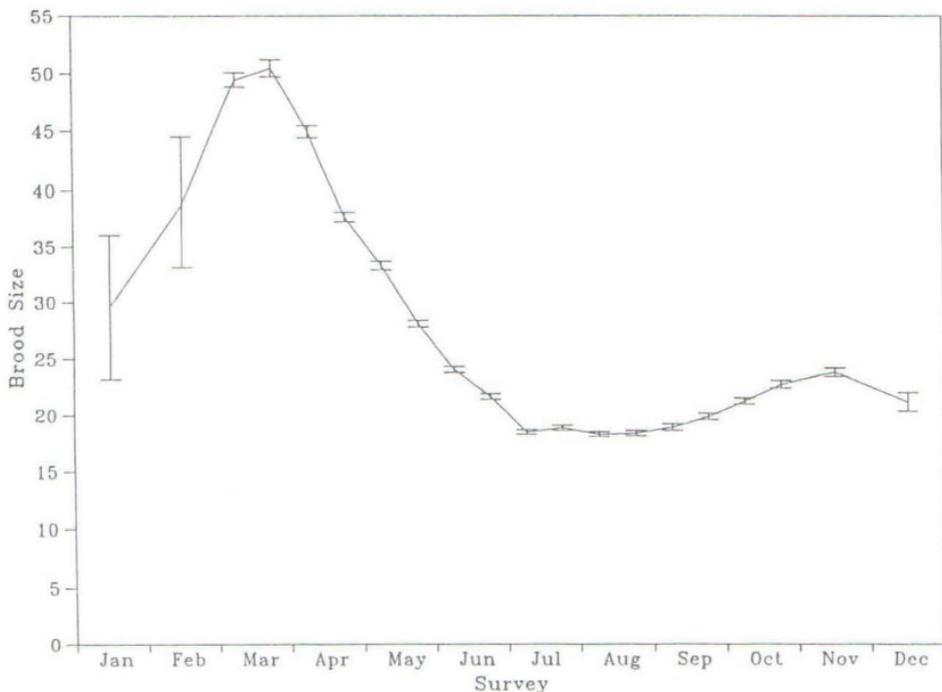


FIGURE 4. Mean brood size of all gravid females on each sampling survey from 1976 to 1993. Bars mark the 95% confidence intervals of the means.

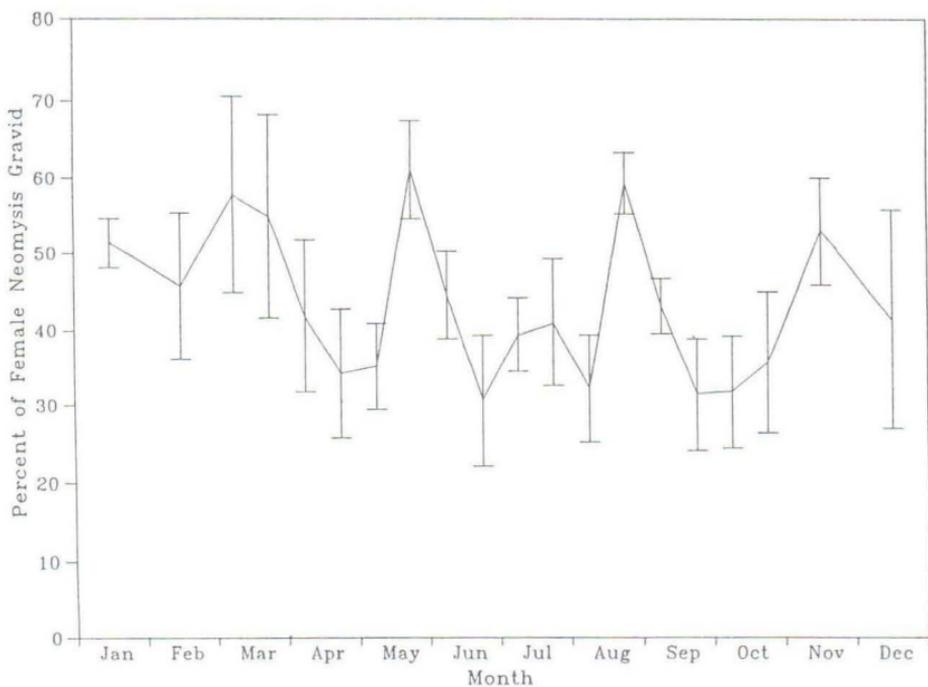


FIGURE 5. Percent of females gravid on each sampling survey of 1982.

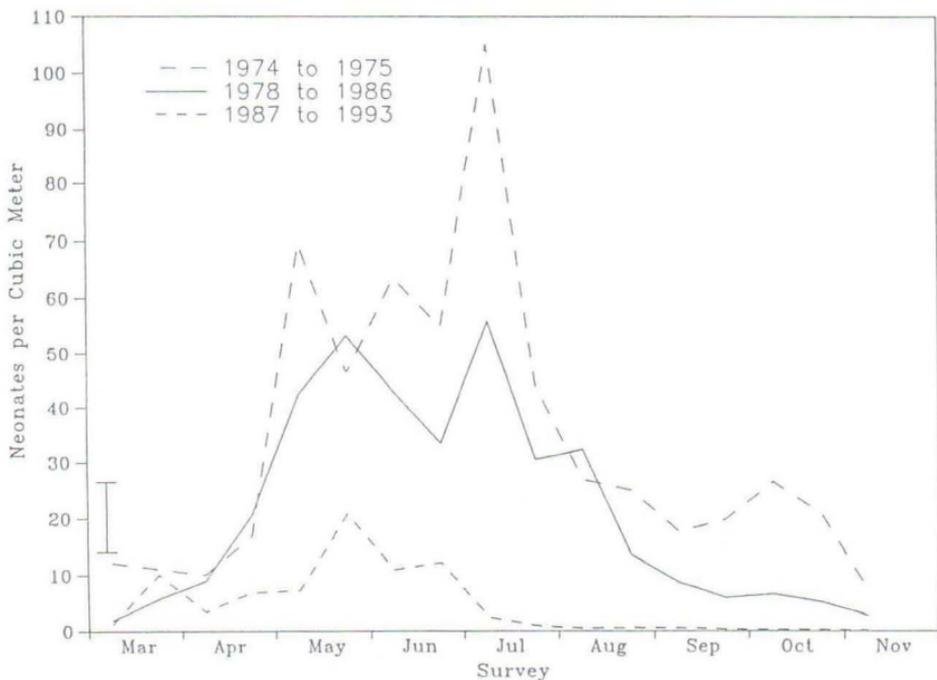


FIGURE 6. Mean abundance of neonates (2-3 mm mysids) on each March to November sampling survey in 3 groups of years, 1974-1975, 1978-1986 and 1987-1993. Bar at the lower left is the mean of the 95% confidence intervals for all points in the figure.

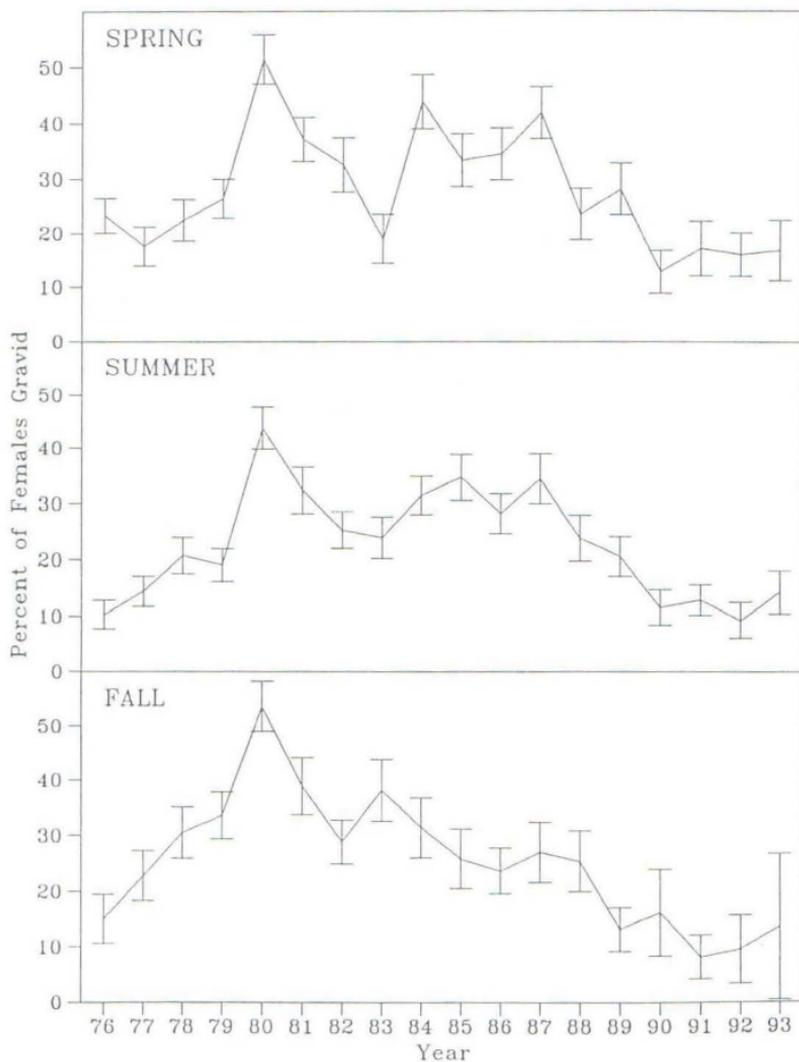


FIGURE 7. Mean percent of females gravid in spring, summer and fall of each year, 1976-1993. Bars mark the confidence intervals.

11 mm females were dominant (Fig. 2). The large females died off sequentially in spring and early summer, the largest and hence, presumably, the oldest, first. The October cohort should be produced by the females maturing from the July cohort. The small size of the October cohort and its absence after 1980 suggests that the young born in July experience high mortality during the summer.

Maximum adult length rarely exceeds 12 mm during summer (Fig. 2), presumably because life span is shorter at high temperatures and mysids die before they can reach greater lengths (Asttorsson & Ralph 1984; Toda *et al.* 1983), or because their growth slows at temperatures > 20°C (Toda *et al.* 1987).

Distribution and Abundance

As previously reported, mysids are concentrated in the entrapment zone, although they extend seaward of the entrapment zone and well downstream from it

(Fig. 8). Because the entrainment zone oscillates up and downstream with tide and freshwater outflow, the location of the mysid population also shifts between Suisun Bay and the Delta and during very high outflow events is located in Carquinez Strait and San Pablo Bay.

Mysid abundance is usually highest during May to July and lowest during winter (Fig. 9). Fall abundance was high from 1968 to 1975 but low in most years thereafter.

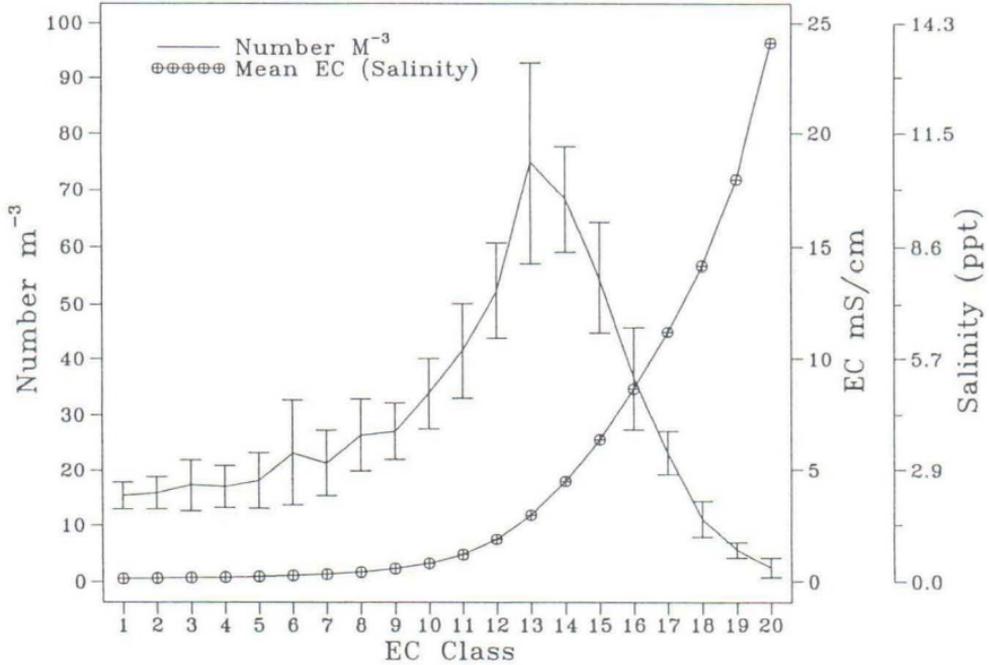


FIGURE 8. Mean abundance of mysids ≥ 4 mm in each specific conductivity class, 1968-1993. Bars mark the 95% confidence intervals of the means. Also shown is the mean specific conductivity and salinity in each class.

Long-term Trends in Abundance

Numbers per cubic meter as well as abundance anomalies were calculated for each season and for the March-November period for comparison (Fig. 10). The two measures of abundance were in good agreement, especially for March-November but long-term downtrends in spring and fall were apparent only in the anomalies. Mean densities ranged from $> 100 m^{-1}$ to $< 1 m^{-1}$.

The March to November abundance anomalies show that abundance was highest and rather stable from 1968 to 1975 (Fig. 10). Abundance fell very low in the drought year, 1977, rose in 1978 but not to previous levels and oscillated without a trend from 1978 to 1986. The drought years, 1987-1992, were characterized by very low and generally decreasing anomalies. Abundance did not increase in 1993, a wet year. The seasonal patterns were similar to the annual results with some variations.

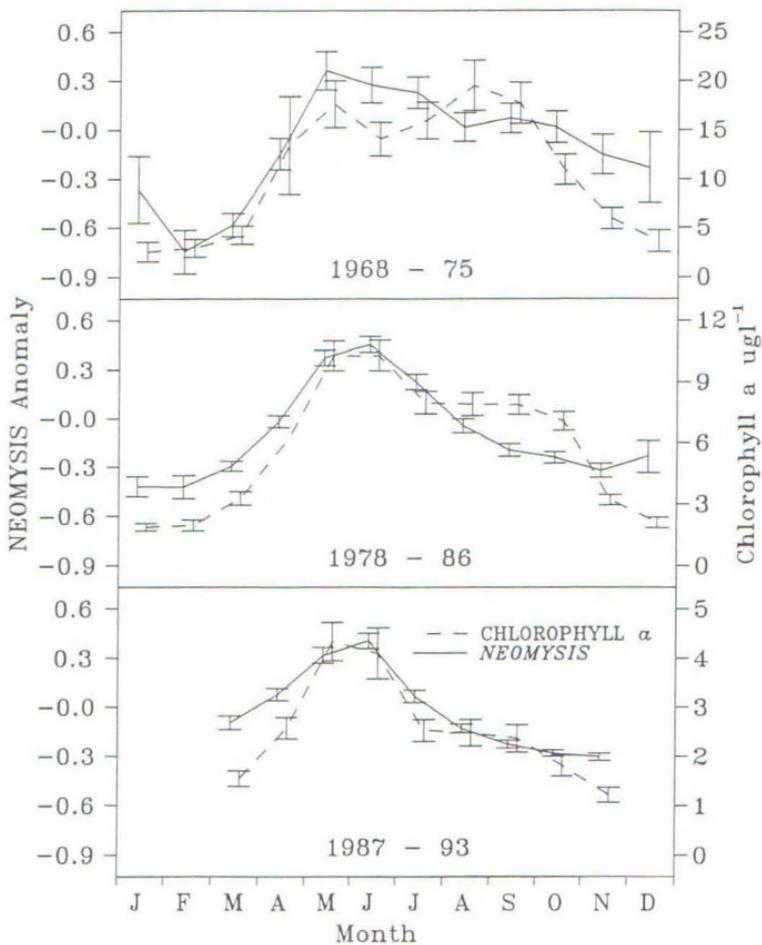


FIGURE 9. Mean abundance anomalies of mysids ≥ 4 mm and mean chlorophyll *a* concentration for each month in three groups of years: 1968-1975, 1976-1986, 1987-1993. Bars mark the 95% confidence intervals of the means.

Abundance Anomalies and Delta Outflow

The anomalies appear to be flow related because they are lowest in drought years. The outflow-abundance relationship can be explored by correlating the anomalies with the log of Delta outflow at Chipps Island in each season (Fig. 11). The variance in the anomalies accounted for by the correlations (R^2) ranges from 53.2% in summer to 56.1% in fall. The relationship is curvilinear due to low anomalies in the very high outflow years 1982 and 1983. By summer of 1983, outflow had dropped enough for the entrapment zone to enter Suisun Bay but the anomaly value was still low. Outflow explains a substantial portion of the variance but not enough to be the only factor affecting abundance.

Multiple Regression

A stepwise multiple regression analysis was done to apportion the variance in anomalies to factors related to the hypotheses. These factors are: Delta outflow,

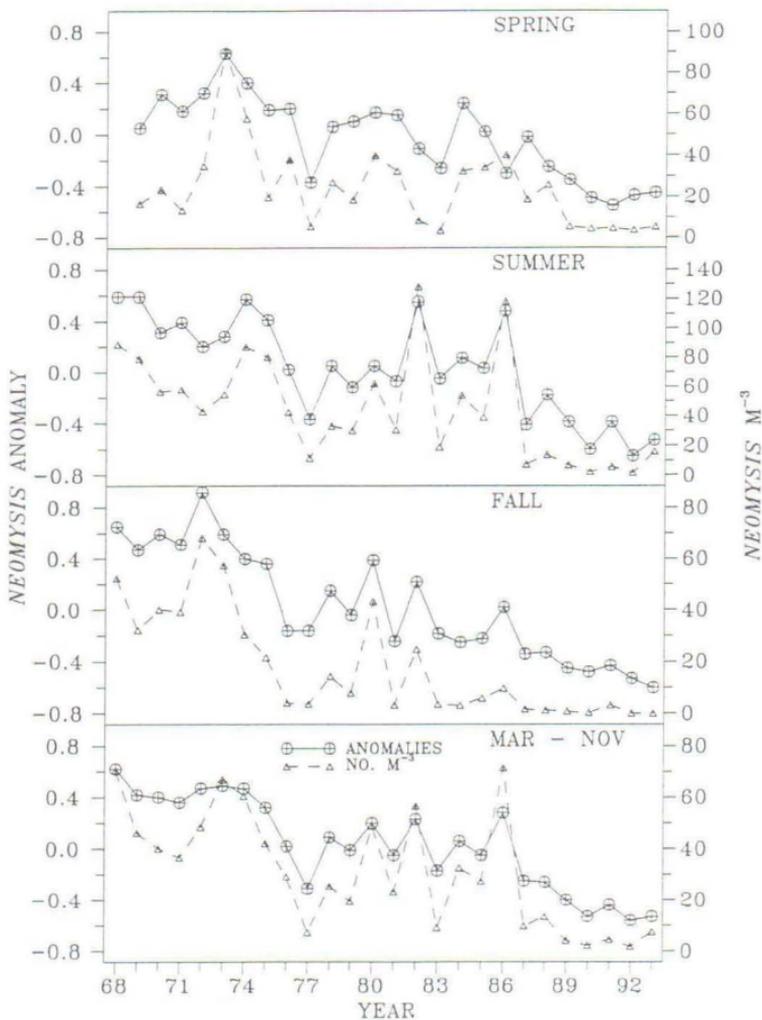


FIGURE 10. Abundance anomalies and numbers m^{-3} for mysids ≥ 4 mm for March to November and for spring, summer and fall of each year, 1968-1993. There was no sampling in spring 1968.

temperature, the rice herbicide molinate, and indices of food abundance – chlorophyll *a* and logs of copepod and rotifer densities. Cladocerans were excluded from the analysis because they are usually abundant upstream from *N. mercedis*. The analysis was restricted to April, May and June when the rice fields were drained and molinate was in the river. The years are those for which a complete data sequence was available, 1973-1992.

Chlorophyll *a* was the single most important variable and explained 77.6% of the variance (Table 2). Molinate was not significant. The best two variable model contained chlorophyll *a* and copepods and accounted for only a small additional amount of the variance, 1.2%. The best 3-variable model contained chlorophyll *a*, outflow and outflow squared and increased the variance explained to 87.7%. Addition of more variables to the model added little to its explanatory power.

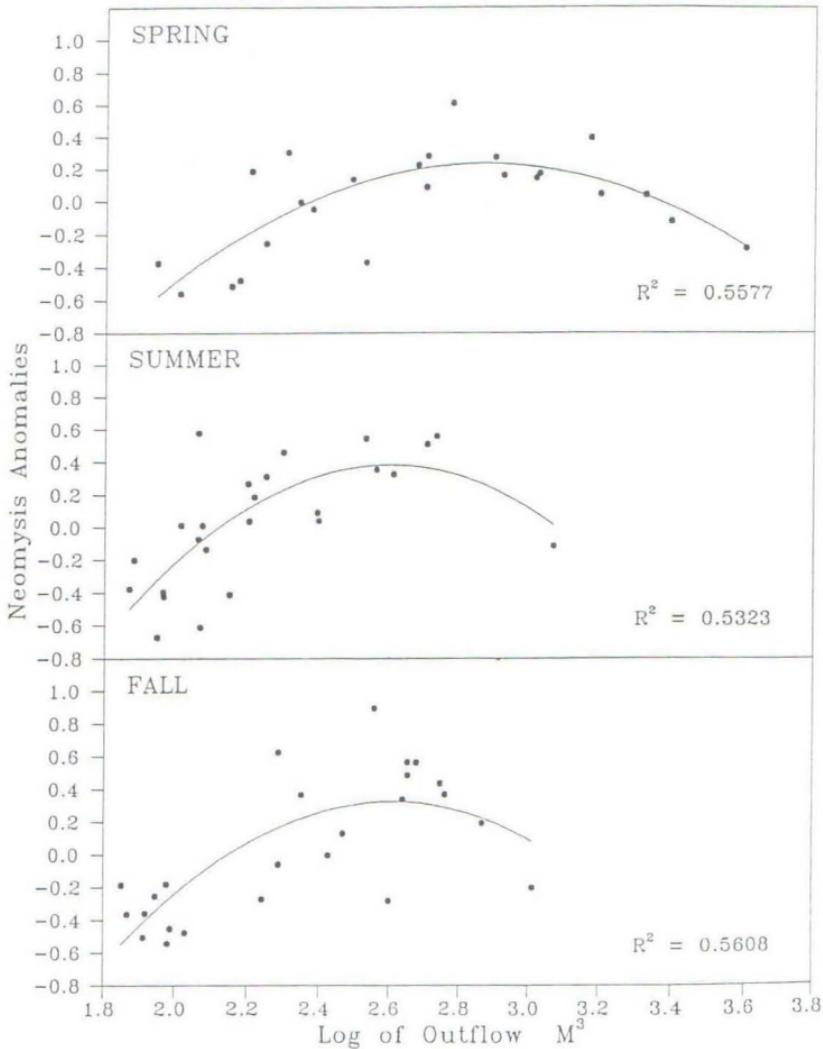


FIGURE 11. Abundance anomalies for mysids ≥ 4 mm vs. Delta outflow at Chipps Island in spring, summer and fall, 1968-1993. Each point represents a year.

Additional regression analyses were run for spring, summer and fall to determine if seasonal changes would occur in the significant variables. These regressions were run for small (4-7 mm) and large (> 8 mm) mysids because literature results indicate that phytoplankton is an important food source for small mysids and zooplankton for large mysids (Baldo-Kost & Knight 1971; Siegfried & Kopache 1980). Molinate was excluded from these analyses because it was not significant during the months when its in-river concentrations were highest.

The regression results were similar for both size groups and all seasons (Table 3). For both sizes in spring and summer, chlorophyll *a* was the most important variable, followed by outflow. In fall, chlorophyll *a* and rotifers were the most important variables for both sizes. Addition of more than two variables only slightly increased the variance explained except in spring when outflow squared increased

TABLE 2. *R*-square analysis results for mysids ≥ 4 mm vs. chlorophyll *a*, Molinate, outflow squared, temperature, log rotifers m^{-3} , log copepods m^{-3} in April, May and June 1973-1992

<i>Variables in Model</i> ¹	<i>R-squared Values</i>
chl	0.776
chl, copes	0.788
OF, OF2, chl	0.877
OF, OF2, chl, copes	0.888
Molinate, OF, OF2, chl, copes	0.891
Molinate, OF, OF2, temp, chl, copes	0.893
All	0.894
<i>Single Variables</i>	
chlorophyll a	0.776
rotifers	0.363
molinate	0.100
copepods	0.041
outflow	0.018
temperature	0.002
outflow squared	0.002

¹ chl = chlorophyll *a*; OF = outflow; OF2 = outflow squared; temp = temperature; copes = copepods

it significantly for both small and large mysids. The percent of the variance explained rose from spring to fall.

Mysid abundance actually had a curvilinear relationship with chlorophyll *a* in spring and summer and a linear relationship in fall (Fig. 12). Since both small and large mysids had similar *R*-square values in the regressions, they were combined in Fig. 12. Data points for 1968-1971 were added to this figure because chlorophyll *a* data was available for those years but copepod and rotifer sampling did not begin until 1972. The percent of the variance explained by these correlations was higher than in the *R*-square analysis.

Rotifer abundance experienced a long-term decline but copepod abundance did not (Figs. 13 and 14). Copepod abundance actually increased during the falls of 1987-93 relative to earlier years due to the presence of introduced exotic species.

Temperature was not a significant variable even in summer. To investigate temperature further, mysid abundance in the San Joaquin River at Stockton, where the highest temperatures in the sampling area are recorded, was compared with temperature for the years of record (Fig. 15). Abundance peaked at 21°C but was generally higher at temperatures $> 21^{\circ}\text{C}$ than at temperatures $< 21^{\circ}\text{C}$. Temperature did not show a long-term rise in summer and fall but did so in spring (Fig. 16).

Export Pumping

The significant correlation with outflow may indicate a concentration effect as hypothesized by Orsi (1986) or it may mean that when the population is located in

TABLE 3. *R*-squared analysis results for small (4-7 mm) mysids and large (≥ 8 mm) mysids vs. chlorophyll *a*, outflow, outflow squared, temperature, log rotifers m^{-3} , copepods m^{-3} during Spring, Summer and Fall, 1972-1992

Variables	SPRING	
	<i>R</i> -squared Values	
	Small Mysids	Large Mysids
chl	0.444	0.536
OF, chl	0.530	0.638
OF, OF2, chl	0.795	0.842
OF, OF2, chl, copes	0.797	0.849
OF, OF2, chl, temp, copes	0.798	0.852
All	0.798	0.852
	SUMMER	
	Small Mysids	Large Mysids
chl	0.740	0.813
OF, chl	0.798	0.846
OF, OF2, chl	0.820	0.864
OF, OF2, chl, rots	0.836	0.889
OF, OF2, chl, rots, temp	0.852	0.897
All	0.860	0.897
	FALL	
	Small Mysids	Large Mysids
chl	0.802	0.811
chl, rots	0.832	0.841
chl, copes, rots	0.874	0.878
OF, chl, copes, rots	0.905	0.902
OF, chl, copes, rots, temp	0.906	0.904
All	0.907	0.905

¹ chl = chlorophyll *a*; OF = outflow; OF2 = outflow squared; temp = temperature; rots = rotifers; copes = copepods

Suisun Bay it is too far downstream to be vulnerable to export pumping. To test the effects of export pumping from the south Delta pumping plants, an analysis was done using data from CDFG monitoring at two stations in the south Delta in Old and Middle rivers from 1972 to 1988 and from Department of Water Resources samples taken at the same locations during the spring and summer of 1989 with a Clarke-Bumpus net. Population size was calculated by multiplying the monthly abundance at each station by the water volume each station was considered to represent. Export loss rates were then calculated for each month by multiplying the mean of the abundance values at the two stations and the export flow rate for the

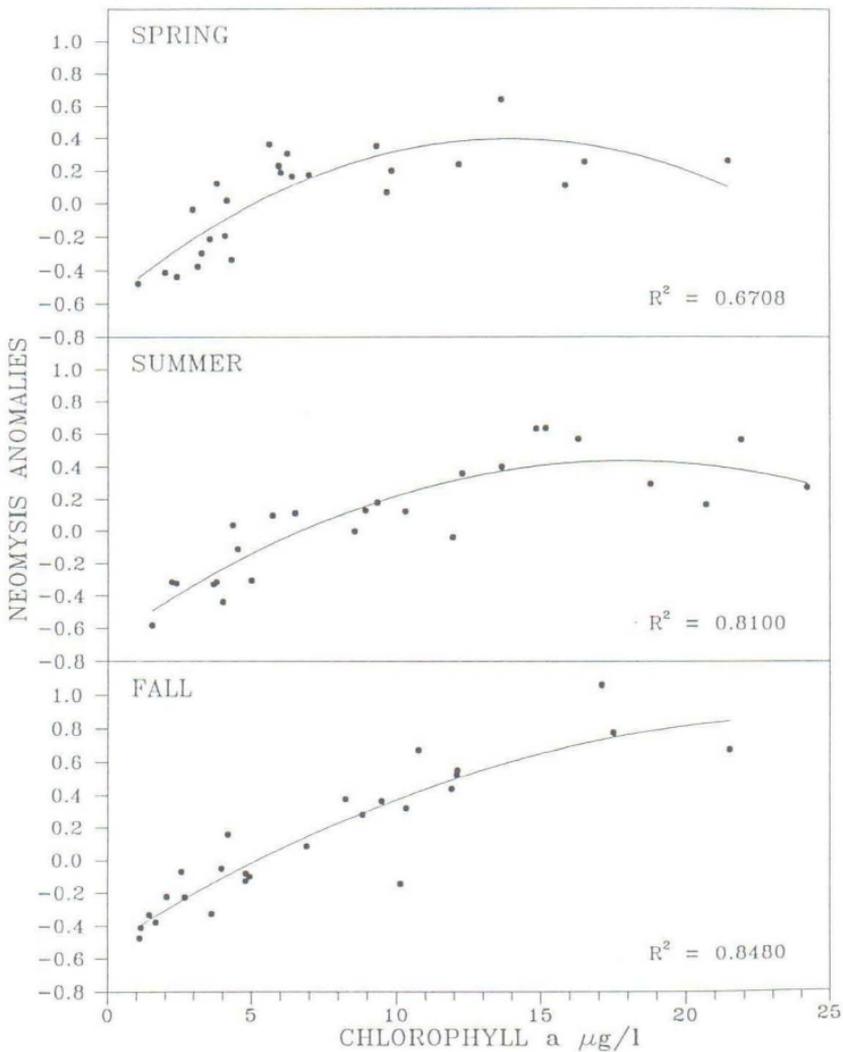


FIGURE 12. Abundance anomalies for mysids ≥ 4 mm vs. mean chlorophyll *a* concentrations in spring, summer and fall, 1968-1993. Each point represents a year.

same month. The proportion of the population exported was then determined by dividing the export loss rate by the population size. The resulting median daily loss rates were $0.01\% \text{ day}^{-1}$. The means were somewhat larger but only a few values exceeded $1\% \text{ day}^{-1}$ (Table 4) (W. Kimmerer, pers. commun.).

Food Limitation

If phytoplankton is limiting *N. mercedis*, abundance patterns within years should be related to chlorophyll *a* concentrations. To test for this the years were divided into 3 groups based on abundance: 1968-1975, 1976-1986, and 1987-1993. Abundance anomalies were then calculated for each month of these periods, correcting the anomalies only for salinity. The anomalies were then plotted against mean monthly chlorophyll *a* concentrations. The plots showed that in all 3 year groups in spring, both abundance and chlorophyll *a* rose rapidly from winter lows to a peak

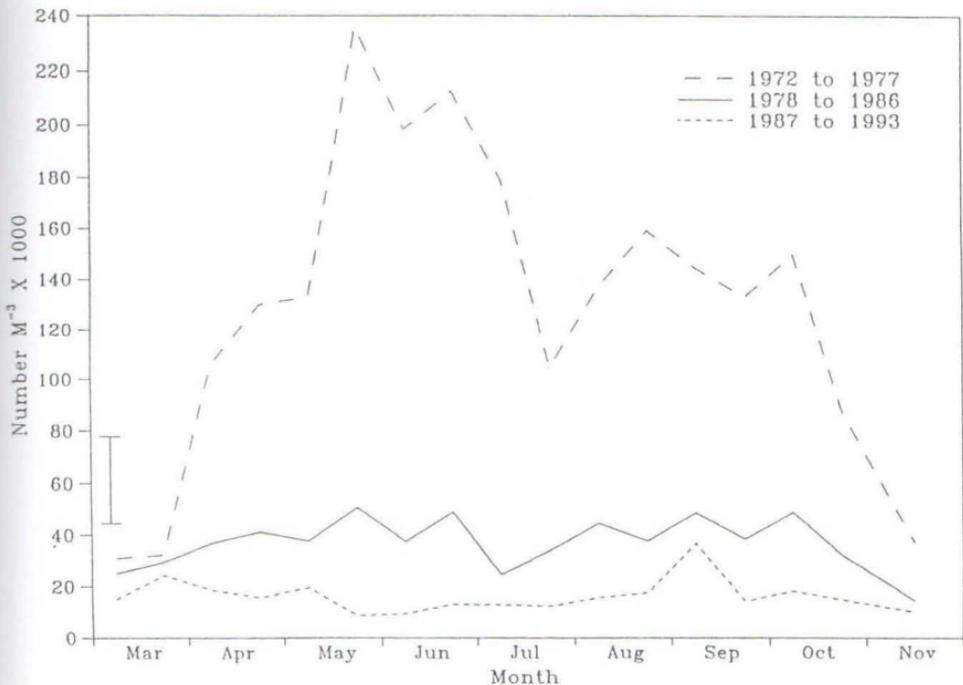


FIGURE 13. Mean rotifer abundance (in thousands per cubic meter) on each sampling survey for three periods: 1972-1977, 1978-1986 and 1987-1993. Bar at lower left marks the mean 95% confidence interval of all points on the figure.

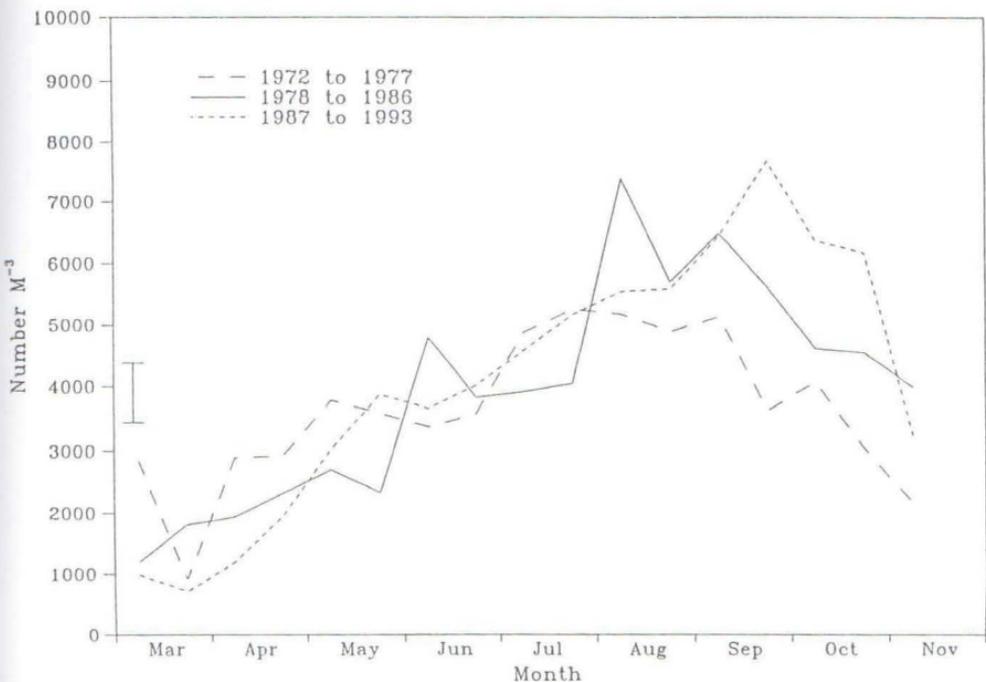


FIGURE 14. Mean copepod abundance (number per cubic meter) on each sampling survey for three periods: 1972-1977, 1978-1986 and 1987-1993. Bar at left marks the mean 95% confidence interval of all points on the figure.

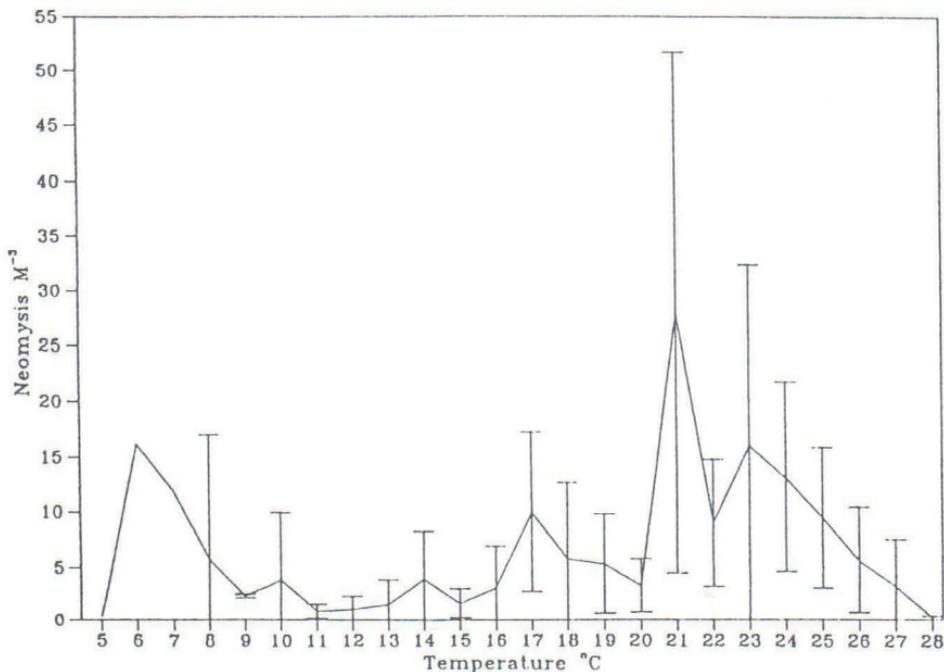


FIGURE 15. Mean abundance of mysids ≥ 4 mm in each degree Celsius temperature class. Data are for 1968-1993. Bars mark the 95% confidence intervals of the means.

in May or June and then declined (Fig. 9). But in the first group of years a second and higher chlorophyll *a* mode occurred in August and a second but small abundance mode appeared in September. In the second group of years, chlorophyll *a* leveled off in August and September but abundance declined steadily during summer and fall. In the last group of years, abundance and chlorophyll *a* were in good agreement from March to November.

If mysids are food limited, their abundance should be related to chlorophyll *a* concentrations under low flow conditions when gravitational circulation is weak

TABLE 4. Frequency table of the percent daily mortality rate due to export pumping on *Neomysis mercedis*.

Daily Percent Loss	Percent Frequency
0.00	41.4
0.005	9.2
0.01	10.7
0.02	17.9
0.05	6.4
0.10	7.1
0.20	5.3
0.50	1.0
1.00	1.0

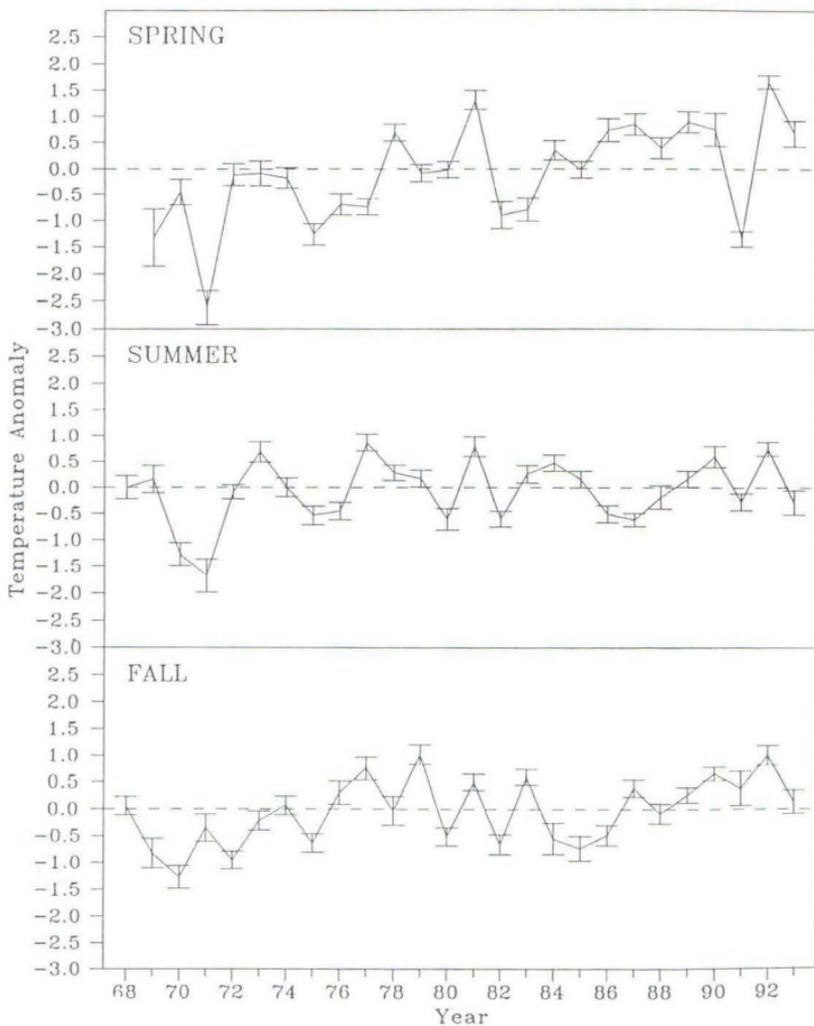


FIGURE 16. Temperature anomalies (corrected for salinity) in spring, summer and fall from 1968 to 1993. There was no sampling in spring 1968. Bars mark the 95% confidence intervals of the annual means.

or non-existent. To test for this, log mysid abundance in the entrapment zone (1-5.6‰ surface salinity) was plotted against chlorophyll *a* concentrations for sampling surveys when Delta outflow was $< 170 \text{ m}^3\text{sec}^{-1}$. The years were divided into three groups: 1968-1975, 1976-1986, and 1987-1993, corresponding to the abundance trends in Fig. 10. Abundance in the entrapment zone showed a significant correlation with chlorophyll *a* under low flow conditions (Fig. 17). Even at higher flows ($\geq 170 \text{ m}^3\text{sec}^{-1}$) the relationship between abundance and chlorophyll *a* was significant (Fig. 18).

When food is limiting, egg production in copepods and cladocerans is reduced (Checkley 1980; Ambler 1986; Beckman & Peterson 1986; Urabe 1991). To see if *N. mercedis* egg production declined when chlorophyll *a* did, fecundity anomalies, corrected for female length, were calculated for each season, spring, summer

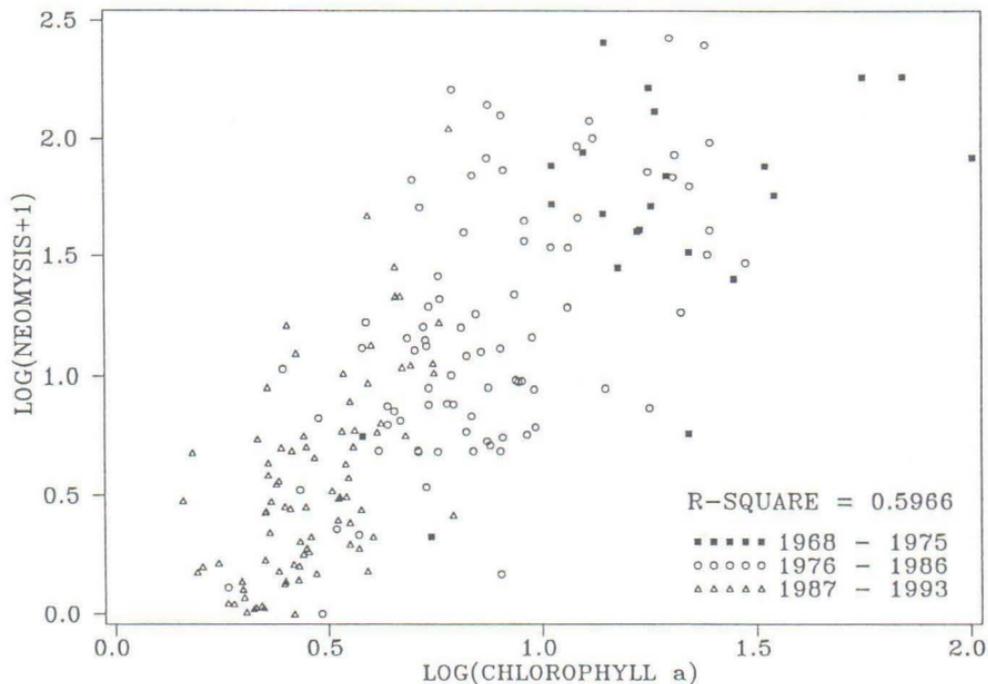


FIGURE 17. Log abundance of ≥ 4 mm mysids vs chlorophyll *a* concentrations in the entrainment zone on surveys when Delta outflow was $< 70 \text{ m}^3 \text{ sec}^{-1}$. Points represent three groups of years.

and fall for each year for which data was available, 1976-1993 (Fig. 19). The anomalies were then correlated with mean chlorophyll *a* in each season. None of the seasonal correlation coefficients were significant at the 5% level.

Another test for food limitation is reduced adult size. In copepods and cladocerans growth rates were lower or adults were smaller when food was limiting (Checkley 1980; Urabe 1991; Durbin *et al.* 1992). To see if this happened in *N. mercedis* the mean percent of females > 11 mm in July and August when adults reach their minimum size (Fig. 2), was calculated for each year, 1968-1993. The percent > 11 mm was very variable from 1968 to 1984 with a low point in 1979 (Figs. 20 and 21). After 1984, the percent of large mysids declined and was very low from 1988 to 1993. This could not have been a temperature effect because temperature showed no upward trend over this time period. Correlations with chlorophyll *a* were not run because they would obviously not be significant.

Birth rates can be used to detect declines in reproduction between groups of years. Because accurate birth rates could not be calculated from the data collected by the study, neonate abundance was used as a proxy. Neonates grow out of the 2-3 mm length class within a day or two (H. C. Bailey, Univ. California, Davis, pers. commun.) and hence are unlikely to suffer high mortality between birth and sampling times. Mean neonate abundance was calculated for each survey during the March to November period for the following groups of years: 1974-1975, 1978-1986, and 1987-1993 (Fig. 6). (Mysids < 4 mm were not caught efficiently

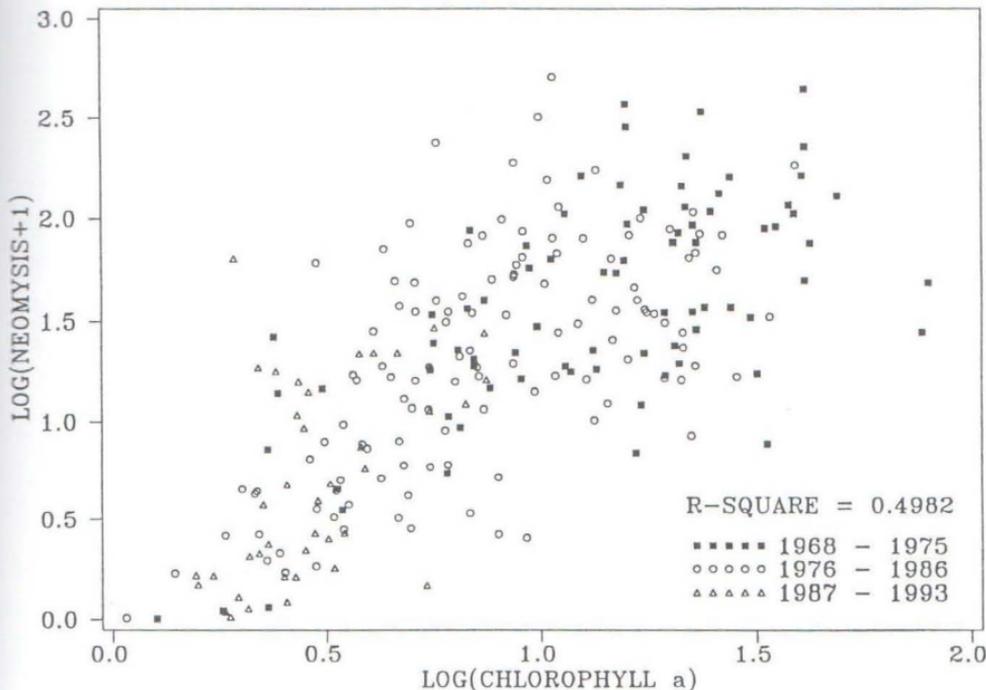


FIGURE 18. Log abundance of ≥ 4 mm mysids vs chlorophyll *a* concentrations in the entrapment zone on surveys when Delta outflow was $\geq 170 \text{ m}^3 \text{ sec}^{-1}$. Points represent three groups of years.

prior to 1974). Neonate abundance was highest for 1974-1975 and showed several large modes from May to July and a small one in October that mark the cohorts. Neonate abundance dropped sharply after July. In the 1978-1986 period cohorts were present in May and July but were smaller than in 1974-1975. Abundance decreased in August and the fall cohort was scarcely detectable. In the 1987-1993 period, abundance was greatly reduced. A May cohort was present, abundance decreased in July and no fall cohort appeared. In all three periods neonate abundance declined in summer. In the last group of years no significant reproduction occurred after June.

DISCUSSION

Neomysis mercedis abundance underwent a long-term downtrend with the greatest decline occurring in fall and in the years 1987-1993 (Fig. 10). These years encompass a long drought but also a high outflow year, 1993. Downtrends also occurred in some food organisms important to *N. mercedis*: phytoplankton and rotifers. But another type of food, copepods, did not decline and actually showed an increase in the fall of the years 1987-1993.

Five hypotheses to explain the *N. mercedis* decline were proposed and examined. The evidence to support three of them appears weak. These are the toxics, export pumping and temperature hypotheses. The stepwise regression analysis showed that the herbicide molinate did not explain a significant amount of the

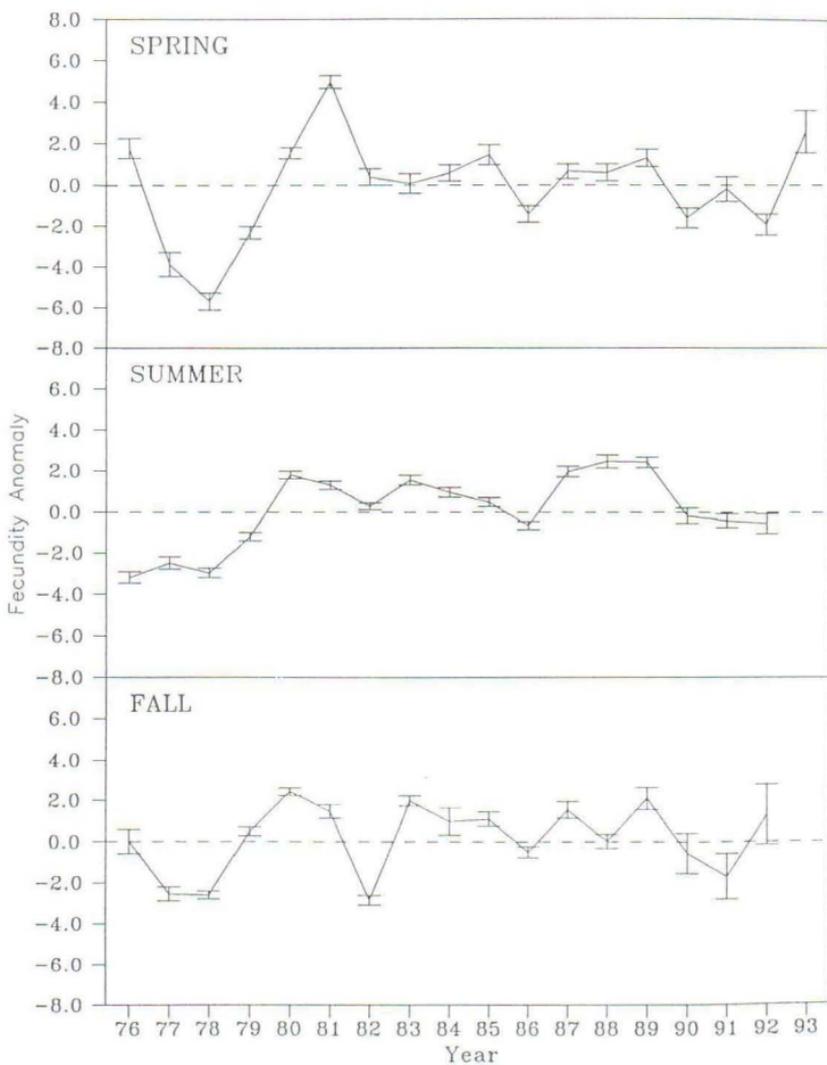


FIGURE 19. Fecundity anomalies corrected for female length in spring, summer and fall, 1976-1993. Not enough females were taken in summer and fall 1993 for calculation. Bars mark the 95% confidence intervals of the annual means.

variance in the abundance anomalies during the months when it was in the system. In addition, the CDFG tolerance criteria for molinate do not ever appear to have been exceeded in the area where *N. mercedis* is abundant. Criteria for molinate have been set at $26 \mu\text{g l}^{-1}$ when present alone and $13 \mu\text{g l}^{-1}$ in the presence of thiobencarb, another rice herbicide that is usually present with molinate (Harrington 1990). The highest recorded in-river concentrations for molinate were $27 \mu\text{g l}^{-1}$ in the Sacramento River upstream from the city of Sacramento in 1983 (Harrington & Lew 1989). Since 1986, molinate concentrations have not exceeded $11 \mu\text{g l}^{-1}$ in this section of the Sacramento River, which is well upstream from where *N. mercedis* is found. Dilution of molinate would occur downriver in the

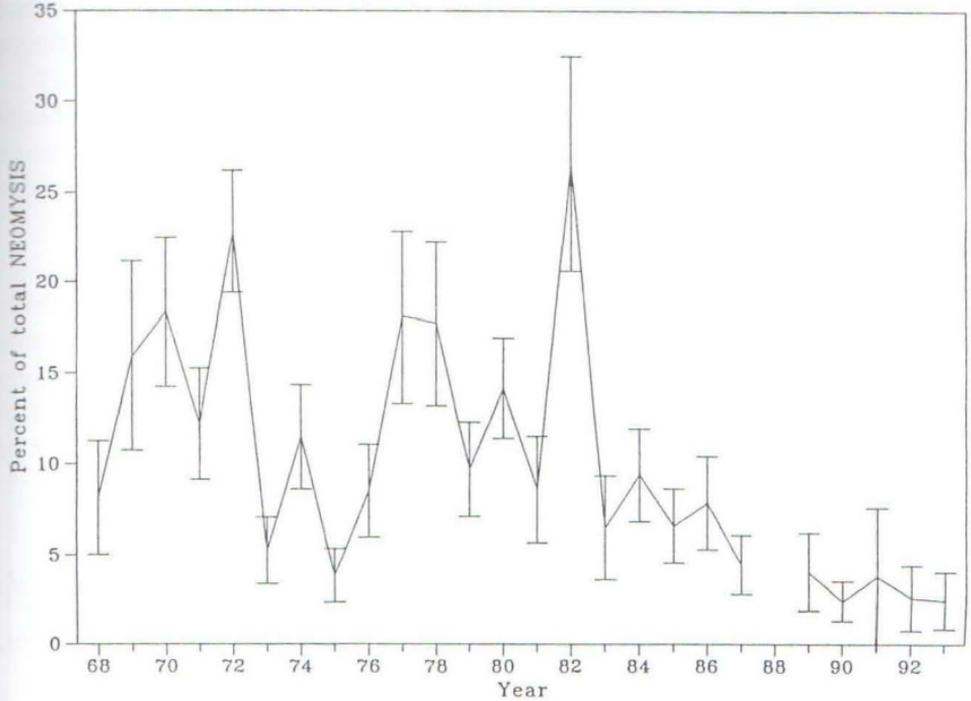


FIGURE 20. Mean percent of adult mysids >11 mm in length in July of each year, 1968-1993. Bars mark the 95% confidence intervals of the means. There was no sampling in July 1988.

Delta and Suisun Bay. This should have reduced molinate concentrations well below the criteria levels even in 1983.

Temperature also failed to explain a significant amount of the variance in the abundance anomalies. Temperature did rise somewhat from 1968 to 1993 but not in summer when high temperatures should impact survival. Additionally, the data from the San Joaquin River at Stockton did not show a strong decrease in abundance at temperatures $\geq 22^{\circ}\text{C}$.

Export pumping losses from the south Delta are simply not high enough to remove much of the population. Even at very low rates of population increase the calculated median daily loss rates of $0.01\% \text{ day}^{-1}$ are too small to explain the population decline. Losses to another type of export, agricultural pumping, which removes water from Delta channels to irrigate the farming islands cannot be evaluated because of a lack of data. However, it is unlikely that irrigation pumping increased during the study years. Hence, while some mysids must undoubtedly be lost to these pumps, it is unlikely that this source of mortality can explain the downtrend in mysid abundance.

Of the two hypotheses remaining, the food limitation one seems to be the strongest. The evidence for food limitation is (a) smaller adult size in July and August of recent drought years when chlorophyll *a* was low, (b) a significant correlation between abundance in the entrapment zone and chlorophyll *a* at both low and high outflows, (c) the good agreement between seasonal trends in abun-

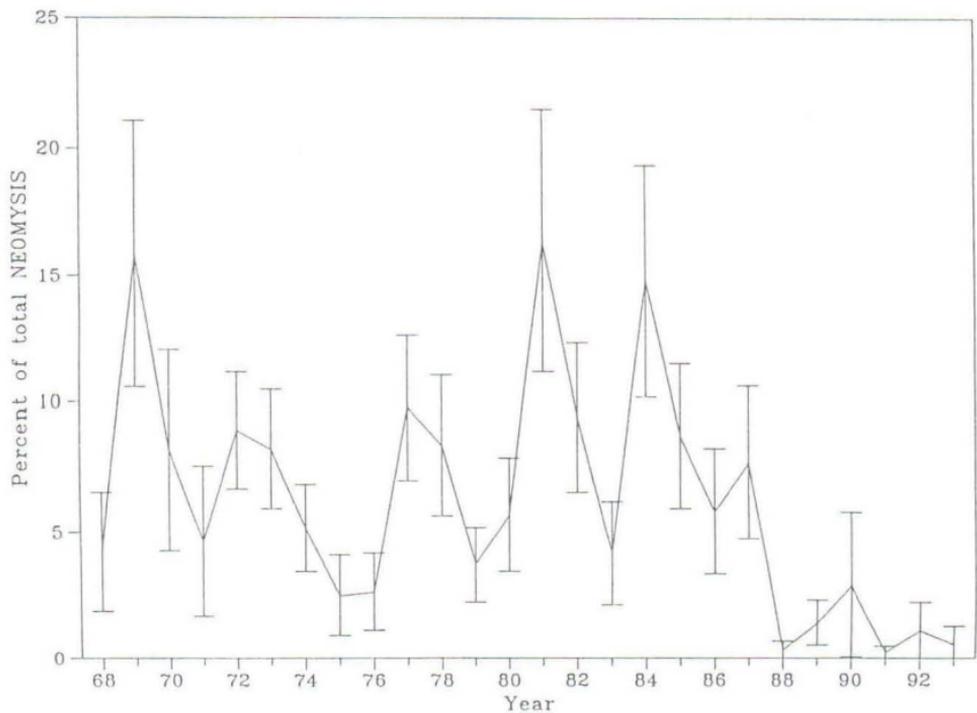


FIGURE 21. Mean percent of adult mysids >11 mm in length in August of each year, 1968-1993. Bars mark the 95% confidence intervals of the mean.

dance anomalies and chlorophyll *a*, (d) the correlations between abundance anomalies and chlorophyll *a* in all seasons.

Brood size was not reduced but this can be explained if adults are not food limited because they feed primarily on zooplankton (Siegfried & Kopache 1980) and copepod abundance did not decline Fig. 14). Only two other investigators have tried to find a relationship between mysid fecundity and productivity at lower trophic levels. The results were not conclusive. In Lake Washington, Seattle, the fecundity of *N. mercedis* was found to be unrelated to differences in copepod abundance between 1979 and 1980 (Murtaugh 1989). In Lake Tahoe, California, the number of eggs per brood of *Mysis relicta* was significantly higher in the more productive water of Emerald Bay compared to the main lake, but the number of stage 5 (the last stage) embryos was similar in both areas (Morgan 1980).

If food limitation of juveniles was the primary factor behind the long-term downtrend in mysid abundance, mysid population size is likely to be controlled by survival of young rather than by reproduction of adults.

The primary factor now affecting phytoplankton abundance where *N. mercedis* is most abundant is grazing by the introduced Asian clam, *Potamocorbula amurensis* (Kimmerer *et al.* 1994). So long as *P. amurensis* remains abundant in Suisun Bay, the abundance of *N. mercedis* should also remain low. Additionally, the introduction of two Asian mysids in 1992 should provide competition for *N. mercedis*. Neither of these species has become abundant and perhaps both are also food limited but if the food resource was already limiting *N. mercedis* then the

added competition for that resource can only have further negative effects on its population size.

Estuarine circulation could have important but secondary effects on mysid abundance. For a better understanding of how the complex hydrodynamics of the estuary interact with mysids, specific studies involving *in situ* measurements of vertical velocity profiles and mysid vertical distribution need to be done.

ACKNOWLEDGEMENTS

Many people contributed to this study in many ways over the many years of its existence. We express gratitude to all of them. G. Schmidt deserves special recognition for braving the waters in fair weather and foul, year after year to bring back many hundreds of crates containing thousands of jars and millions of mysids for S. Skelton to count and measure. Of such routine tasks is science made.

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