A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada[1]

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Abstract

A comparison of the population dynamics of *Daphnia pulicaria* and *Daphnia rosea* in 1967–1969 and during their decline from Lake Tahoe in 1970 showed that the decline resulted from a combination of increased death rates and decreased birth rates. The remaining cladoceran, *Bosmina longirostris*, disappeared from the plankton in 1971. The elimination of cladocerans coincided with high densities of the opossum shrimp, *Mysis relicta*, and the kokanee salmon, *Oncorhynchus nerka*. Predation by these two introduced species is believed to have increased cladoceran death rates. Changes in the timing of the peaks of primary productivity are a possible cause for the decline in birth rates.

A brief resurgence of *Bosmina* in late 1974 was associated with a dramatic decline of the mysid population and the continued decline of kokanee which began in 1970. The mysids recovered by late 1975 but *Bosmina* again disappeared and has remained absent since. The failure of *Daphnia* to reappear suggests that factors in addition to predation by kokanee and *Mysis* exclude them from Lake Tahoe. Changes in the phytoplankton community composition may have altered the ability of the cladocerans to maintain birth rates sufficiently high to offset increased losses due to predation.

Goldman (1974) and Richards et al. (1975) documented the dramatic decline and disappearance of the three pelagic cladoceran species (*Daphnia pulicaria, Daphnia rosea,* and *Bosmina longirostris*) from Lake Tahoe in 1970 and 1971. Little direct evidence was available of a specific cause for this remarkable event, but several possibilities were discussed. These included predation by two introduced species, kokanee salmon (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*), changes in algal species composition and productivity due to cultural eutrophication, and the suggestion of a cladoceran pathogen.

We here re-examine the reasons for the decline of the Lake Tahoe cladocerans from two new perspectives. The first evolved from considerations raised by symposium participants when the Richards et al. (1975) report was presented and focuses on a comparison of cladoceran population dynamics before and during the period of decline. The second concerns ongoing changes in the limnetic community and centers on the question of why cladocerans have generally remained absent from the Lake Tahoe zooplankton. Although the decline of cladocerans in 1970 and 1971 may not have been from the same causes as their continued absence, we feel that examination of both points in concert sheds considerable light on processes structuring the present zooplankton community.

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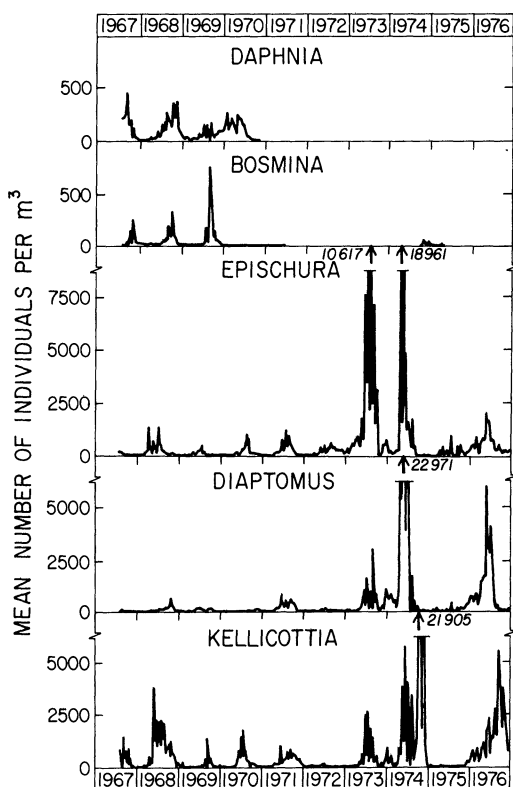
Fig. 1. Mean density of Lake Tahoe zooplankton for period 1967–1976. To prevent overlap among panels, curves have been cut off and maximum values indicated.

Methods and materials

Zooplankton samples were collected approximately weekly during summer and about every 10 days in winter from August 1967 through 1976 with a Clarke-Bumpus sampler equipped with an 80-μm-mesh net towed vertically from 150 m to the surface at an index station near the west shore. Zooplankton abundance and composition at this station is typical of the entire lake (Richerson 1969; Roth and Goldman unpubl.). Independent estimates of sample volume in 1972, 1975, and 1977 ranged from 0.9 to 1.5 m³ depending on the degree of net clogging (Goldman unpubl.). Since there were occasional mechanical failures of the impeller on the sampler during this study, we have assumed an average sample volume of 1.2 m³. Samples were preserved in 5% Formalin. The 1973–1976 data are based on single samples; before that, triplicate samples were counted.

All crustacean zooplankton were counted and identified at 30–40× magnification under a dissecting microscope. The morphologically similar *D. rosea* and *D. pulicaria* were counted as *Daphnia* spp. Detailed examination of June–December 1970 samples showed that >95% of these *Daphnia* were *D. pulicaria* (cf. Hrbáček 1959; Brandlova et al. 1972). Richerson (1969) found that *D. pulicaria* greatly outnumbered *D. rosea* during his 1967–1968 study. In our analyses of population dynamics, the two *Daphnia* species were pooled. Of the rotifers, only numbers of *Kellicottia longispina* are included; other species were seen only occasionally. Protozoans, the only other limnetic zooplankters in the lake, were not counted.

Both loose and attached eggs and embryos of *Daphnia* were counted for estimation of population egg ratios (Edmondson 1965). Instantaneous birth rates, *b*, were calculated from these egg ratios according to Paloheimo (1974) and the relationship between egg development time (*D*, in days) and water temperature (°C): $1/D = -0.0796 + 0.02439$ (°C) ($r^2 = 0.82$), based on published information on *Daphnia* egg development times for temperatures between 4° and 20°C (Esslová 1959; Green 1956; Hall 1964; Jacobs 1961; Korinek 1970; Kryuchkova 1973; Lei and Clifford 1974; Schindler 1972; Weglenska 1971). The temperatures used for these calculations were those at the surface and at 100 m, the range of depths over which *Daphnia* populations were normally distributed in Lake Tahoe (Richerson 1969; unpubl.). Because population birth rate is highly dependent on temperature, this technique permits the calculation of a range of birth rate values which must include the actual value, even though vertical migration activities and seasonal variation in the depth distribution of *Daphnia* make calculation of an exact population birth rate problem-

atic. Population growth rates, *r*, for *Daphnia* were based on least-squares parameter estimation of average growth rates for extended periods of sustained population increase or decrease. Instantaneous death rates, *d*, were obtained by subtraction, where $r = b - d$.

Population densities of *M. relicta* were estimated from daytime tows of an epibenthic sled equipped with a 1-m² mouth, 500-μm-mesh plankton net (Richards et al. 1975; Wickwire unpubl.) and nighttime vertical tows with a 0.75-m-diameter mouth, 500-μm-mesh plankton net, taken in November 1975 and regularly since October 1976. This information was supplemented by data on the contribution of *Mysis* to the stomach contents of angler-caught lake trout (Frantz 1970–1978). Kokanee densities were inferred from spawning run information for Taylor Creek, the primary spawning stream in Lake Tahoe, and the frequency of their occurrence in lake trout stomachs (Frantz 1970–1978; Wickwire unpubl.).

Results

Zooplankton population dynamics— Dramatic changes in the Lake Tahoe zooplankton began in 1970 and continued through 1976 (Fig. 1). The lake has remained essentially free of cladocerans since 1971, except for a brief reappearance of *Bosmina* in 1974–1975.

Characteristic of the annual dynamics of both cladoceran populations before 1970 were long periods of sustained increase (up to 9 months in the case of *Daphnia*), followed by brief periods of decline. In 1970, both populations began to show changes in their patterns of population growth. *Daphnia* failed to show a substantial midwinter decline in 1969–1970, but *Bosmina* declined to subnormal densities. In mid-1970 the *Daphnia* population began its final decline at a time of year when it had previously exhibited growth, although the animals collected during this period were not obviously diseased and were free of epizoics and fungi (cf. Green 1974). *Bosmina* also failed to show late year increas-
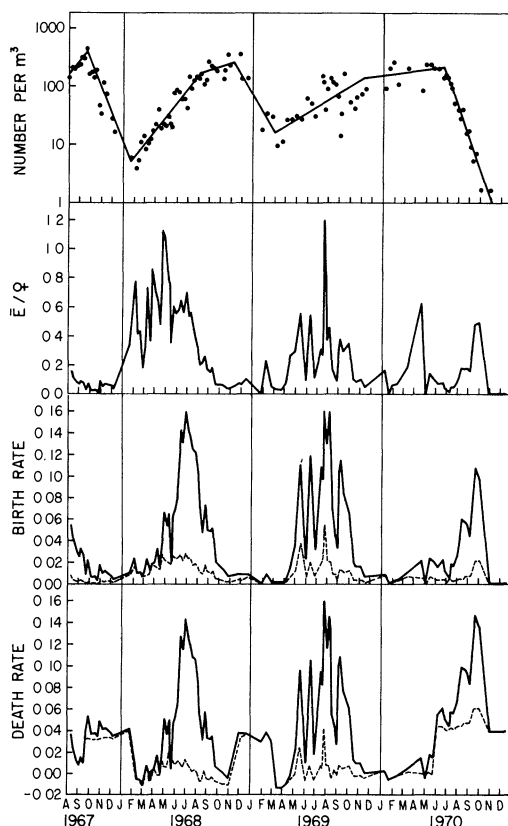
Fig. 2. Mean density (logarithmic scale), egg ratio, and instantaneous birth and death rates of *Daphnia* in Lake Tahoe, 1967–1970. Birth and death rates calculated on basis of surface temperatures (———) and temperatures at 100-m depth (------); *see text for explanation.*

es in 1970, and disappeared completely in early 1971. Since egg data were not recorded for *Bosmina* we are unable to speculate further on the dynamics of that population during its decline.

Several features of the population dynamics of *Daphnia* are noteworthy in relation to their disappearance. Egg ratios and birth and death rates in this system are extremely low (Fig. 2), as much as an order of magnitude less than in more productive systems (e.g. DeBernardi 1974; George and Edwards 1974; Hall 1964; Wright 1965). While such differences are to be expected in view of the ultraoligotrophic nature of Lake Tahoe and the

Table 1. Mean population growth rate (r), birth rate (b), and death rate (d) for *Daphnia* during time periods from 1967 to 1970.

		b		d	
	r	0 m	100 m	0 m	100 m
9 Aug–21 Sep '67	0.018	0.035	0.0046	0.017	−0.014
21 Sep '67–8 Feb '68	−0.031	0.009	0.003	0.040	0.034
8 Feb–26 Sep '68	0.016	0.063	0.018	0.047	0.002
26 Sep–1 Dec '68	0.013	0.014	0.004	0.001	−0.009
1 Dec '68–15 Mar '69	−0.029	0.006	0.004	0.035	0.033
15 Mar–28 Oct '69	0.007	0.067	0.014	0.060	0.007
28 Oct '69–4 Jun '70	0.004	0.011	0.005	0.007	0.001
4 Jun–22 Dec '70	−0.039	0.034	0.006	0.073	0.045

strict dependency of birth rates on food quality and quantity (Edmondson 1965; Hall et al. 1976), the vulnerability of such a precariously balanced population to slight increases in predation or decreases in birth rate must be recognized.

Another important feature is a shift in the timing of the peak of the mortality rate curve, which occurs later each succeeding year. This shift had considerable importance in influencing the rate and perhaps the extent of decline of the *Daphnia* population in 1970, when it affected the *Daphnia* population at a time of normally declining birth rates, making recovery more difficult. Less noticeable from Fig. 2 but summarized in Table 1 are substantial increases in death rate and decreases in birth rate from 1968 to 1970. In particular, the final decline of *Daphnia* in 1970 came at a time of year when the population normally increased, but birth rates were 49% lower and death rates 23% higher than in previous years at this time. The size structure of the population during this decline did not reveal any preferential loss of very large or very small classes that might have indicated the presence of size-selective predators. However, the age distribution of eggs being carried by the *Daphnia* population did shift as the population declined, becoming more dominated by younger developmental stages as the decline proceeded. This shift in egg age distribution is not expected in populations that decline solely as a result of declining birth rates (Edmondson 1968, 1977), but has been observed in populations whose de-

clines were associated with severe predation on egg-bearing individuals (Threlkeld 1979). This is consistent with the observed increase in estimates of mortality rate in the declining population. Thus, it appears that the disappearance of *Daphnia* from Lake Tahoe in 1970 resulted from a combination of declining birth rates (for equivalent periods from year to year) and increased death rates.

Since the disappearance of *Daphnia* and *Bosmina* from Lake Tahoe in 1970–1971, the zooplankton have continued to change. Two years after the elimination of cladocerans, both copepods (*Epischura nevadensis* and *Diaptomus tyrelli*) showed order-of-magnitude increases in density (Fig. 1) which were sustained into 1974. The rotifer *K. longispina* also showed increases following the decline of cladocerans. Associated with a rapid decline of the copepods and rotifers in late 1974, *Bosmina* made a brief reappearance, but disappeared again in spring of 1975 as the copepods re-established pre-1973 densities. The reappearance of *Bosmina* coincides seasonally with its autumnal increases in 1967–1969 and with the lowest densities of copepods observed since 1971. The possibility of a predator-prey relationship between *Bosmina* and *Epischura* (Kerfoot 1975) should not be overlooked. In spite of the consistent inverse relationship between these two species throughout our study, the apparent balance of *Bosmina* and *Epischura* before 1970 argues that some additional factor was necessary to

cause the disappearance of *Bosmina* in 1971.

Other limnetic changes—After an accidental introduction of kokanee fry into Lake Tahoe in 1944, the Fish and Game Departments of Nevada and California tried to establish a fishery for this species in the lake (Cordone et al. 1971). Our estimates of kokanee density in the lake are indirect, coming from the size of spawning runs in Taylor Creek and the proportion of lake trout found to have eaten kokanee. These estimates are remarkably consistent with each other (for 1968–1976, $r = 0.70$, $P < 0.05$), both showing a continuing decline of kokanee since about 1970 (Fig. 3).

Only spawning data are available before 1968, but they show that until about 1970 this species was on the increase, its peak nearly coinciding with the decline of cladocerans. In view of the heavy dependence of kokanee on the Cladocera, primarily *Daphnia*, as food (Cordone et al. 1971), it remains possible that kokanee were largely responsible for the decline of *Daphnia* in 1970. However, if kokanee were solely responsible for the cladoceran decline, it is puzzling that *Daphnia* has not been able to recolonize Lake Tahoe with the reduction in kokanee numbers, since *Daphnia* is found in many surrounding lakes that drain into Lake Tahoe.

Although mysids were first introduced into Lake Tahoe in 1963 as forage for juvenile lake trout (Linn and Frantz 1965), it was not until 1969 that lake trout were found to be eating the shrimp (Frantz 1970; Fig. 4). In 1971 kokanee were found to be eating the shrimp (Frantz 1972), although they have never become a primary food source for this fish (Morgan et al. 1978). Benthic daytime trawls for *Mysis* from 1969 indicate its presence. Both fish stomachs and trawl data show dramatic increases in presence of mysids in the early 1970s, indicating that *Mysis* was well established at the time of the cladoceran decline. Although the trawl data do not permit precise estimates, comparison of trawl data from
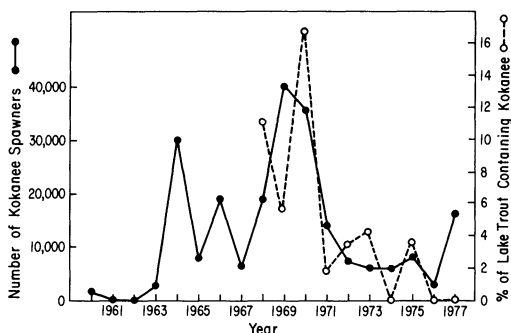

Fig. 3. Number of kokanee in annual spawning run in Taylor Creek and frequency of 38–50-cm lake trout caught by basin fishermen and found to contain kokanee remains.

1971 with those of 1975, when nighttime vertical net tows were also taken, suggests that *Mysis* densities in 1971 were probably of the order of $300 \cdot m^{-2}$ (Fig. 4). These densities are equal to or greater than those in the Great Lakes (Carpenter et al. 1974; Morgan and Beeton 1978), which are considerably more productive than Lake Tahoe.

The establishment of *Mysis* may have influenced the resident cladoceran populations through competition for shared resources or through predation by *Mysis* on the cladocerans (Morgan et al. 1978). Although competition for algae between *Mysis* and *Daphnia* has been proposed (Zyblut 1970), the amount of overlap of their food sizes is probably low. *Mysis* primarily consumes algae >50 μ in diameter (Bowers and Grossnickle 1978), while *Daphnia* typically consumes algae <15–20 μ (Burns 1968; Infante 1973). *Mysis* may however exert considerable predation pressure on cladocerans. Lasenby and Langford (1973) have shown that *Mysis* preys on *Daphnia* and *Bosmina*, and we have confirmed this. Stomach contents of *Mysis* recently collected from Lake Tahoe contain *Epischura* and *Diaptomus* mandibles and *Kellicottia* loricas. Mysids collected during the 1974–1975 reappearance of *Bosmina* were found to be eating these cladocerans (Rybock unpubl.).
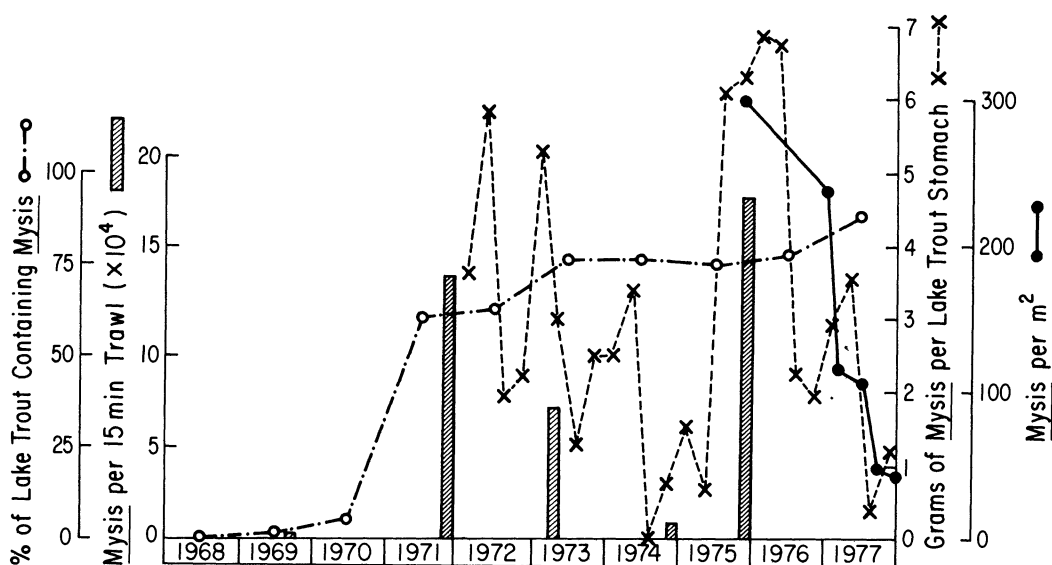
Although we have no quantitative es-

Fig. 4. Four estimates of relative *Mysis* density in Lake Tahoe: frequency of 38–50-cm lake trout caught by basin fishermen and containing *Mysis* (annual averages: data from Frantz 1970–1978); *Mysis* collected per 15-min daytime benthic trawl (Richards et al. 1975; Wickwire unpubl.); grams of *Mysis* per lake trout stomach containing *Mysis* (seasonal averages: data from Frantz 1975–1978 and unpubl.); mean number of *Mysis* per square meter as estimated from nighttime vertical net tows.

timates of *Mysis* densities before 1975, variation in the contribution of *Mysis* to lake trout food suggests that these populations have undergone considerable fluctuation since 1972 (Frantz 1975–1978). In particular, the weight of *Mysis* consumed by lake trout declined steadily from 1972 through early 1975 (Fig. 4). The reliability of using information on lake trout feeding habits as estimators of relative *Mysis* densities is supported by the current coincidence of declining *Mysis* densities and declining contribution to lake trout forage. In addition, trawl catches dropped to very low levels in December 1974, substantially lower than in March 1973 ($P < 0.05$) and December 1975 ($P < 0.005$). Thus, the reappearance of *Bosmina* in late 1974 may have resulted, in part, from reduced predation pressure by *Mysis*.

The primary productivity of Lake Tahoe has been steadily increasing through cultural eutrophication; however, its pelagic zone can still be classified as ultraoligotrophic (Goldman 1974). Primary productivity in the euphotic zone varies from 0.5 to 2.6 mg $C \cdot m^{-3} \cdot d^{-1}$. This low level of plant production must keep the herbivore population in Lake Tahoe at close to subsistence levels during much of the year, as evidenced by the extremely low *Daphnia* birth rates. As a result, these animals may have a very limited ability to withstand even slight increases in death rate.

Considerable annual variation in the timing of primary production in Lake Tahoe could have a major influence on zooplankton dynamics and on the decline of cladocerans. Goldman (1974) reported that the peak of primary production in Lake Tahoe came at a later time in successive years before the disappearance of *Daphnia,* from March and April in 1968 to May and June in 1970. Although this shift has not been explained, it may have contributed to the reduced birth rates and egg production in *Daphnia* during these years. However, this relationship is confused since the peak in total phytoplankton biomass has not shifted similarly (Goldman unpubl.).

Although the magnitude and timing of

primary production have shown considerable variation since 1970 (Goldman 1974; Goldman and de Amezaga 1975), *Bosmina* and *Daphnia* may also have remained absent because of changes in phytoplankton species composition. The 1969–1970 phytoplankton was dominated by three large diatoms: *Fragilaria crotonensis* (510 μ^3), *Melosira crenulata* (1,209 μ^3), and *Cyclotella bodanica* (4,778 μ^3) (Holm-Hansen et al. 1976). Replacing this assemblage by 1974 was one dominated by *F. crotonensis* and several smaller species: *Cyclotella ocellata* (157 μ^3), *Cyclotella stelligera* (77 μ^3), and *Asterionella formosa* (480 μ^3) (Tilzer et al. 1977; Vincent 1977). However, this trend toward the increased importance of smaller forms has not been strictly observed in the other major group of phytoplankton, the chrysophytes. While *Mallomonas* sp. (21,236 μ^3), which was abundant in pre-1970 samples, has virtually disappeared from recent samples, *Dinobryon* sp. (1,900 μ^3) has increased in abundance. The green algae have never been important in the Lake Tahoe phytoplankton and have shown no major changes over the years (Goldman unpubl.). There has been a marked increase in the importance of very small green flagellates since 1970, but the significance of this observation is slightly clouded by changes in counting methodology (longer settling times) for the later samples.

Whether these changes have resulted from increased grazing activities of *Mysis*, reduced grazing by *Daphnia,* or physical and chemical effects associated with cultural eutrophication remains uncertain. However, they may be adequate to prevent the reappearance of cladocerans by slightly altering their ability to maintain birth rates adequate to balance losses related to predation. The phytoplankton during the 1974–1975 resurgence of *Bosmina* showed no reversion to pre-1971 conditions (Tilzer et al. 1977). However, the question still remains whether a reappearance by *Daphnia* is inhibited by the structure of the present algal community.

Discussion

We have already seen that the decline of *Daphnia* in 1970 was associated with a decrease in birth rates coupled with increased death rates. In view of the ability of *Bosmina* to reappear in 1974–1975 under altered food conditions, we think that increases in death rate were largely responsible for its decline as well. These events were associated with the establishment of, or peak densities of, two introduced predators and with shifts in the timing and magnitude of primary productivity. Although it is impossible to say what particular dynamics governed the disappearance of *Bosmina* and its reappearance in 1974–1975, factors different from those regulating *Daphnia* may have been involved. This is suggested by both the different timing of its disappearance and by its brief reappearance without *Daphnia*.

It is worth considering in what way the combination of factors considered might affect the complete array of zooplankton species in Lake Tahoe, to see if our interpretation is consistent with the behavior of populations of other species. In particular, we must ask why the impact of kokanee and mysids and shifts in primary productivity was so adverse to *Daphnia* and *Bosmina*, but not to copepods or to *K. longispina*. As far as kokanee predation is concerned, selection of the slow-moving, large-bodied *Daphnia* has already been documented (Cordone et al. 1971). We suggest that predation by *Mysis* (and *Epischura*) falls most heavily on smaller-bodied, slow-moving forms. The ability of the small-bodied *K. longispina* to persist after *Bosmina* was eliminated may be due to the shorter development time of its eggs (Edmondson 1965; Hutchinson 1967)—a major influence on population growth rate (Hall et al. 1976).

The ability of *Epischura* and *Diaptomus* to persist in spite of ongoing predation by *Mysis* (Rybock unpubl.) and kokanee (Frantz 1977) reflects a different balance of birth rates and loss to predators. Whether this difference arises from more efficient escape from *Mysis* and ko-

kanee by the copepods than by *Daphnia* or from their higher birth rates is unknown. Before the elimination of cladocerans, copepods were found in only 25% of kokanee stomachs, afterward in between 70 and 80%. However, since kokanee densities have declined since 1970, the net predation impact may be lower and be insufficient to eliminate either copepod, even though earlier it may have been a factor in the elimination of *Daphnia*.

The greater capacity of copepods than of cladocerans to grow and reproduce in oligotrophic systems has been discussed by Allan (1976) and McNaught (1975). While there is no definitive evidence of a greater reproductive rate among copepods in Lake Tahoe than cladocerans, such a possibility would also give these copepod species a resiliency to predation that *Daphnia* and *Bosmina* did not exhibit.

Evidence that the balance of predation and birth rate is of paramount importance in determining the fate of cladocerans in Lake Tahoe comes from Emerald Bay, a shallow and more productive embayment of Lake Tahoe (Goldman and de Amezaga 1975). Here, *Bosmina* coexists with higher densities of *Mysis* (December 1977: *Mysis* $\simeq 200 \cdot \mathrm{m}^{-2}$) than occur in the lake itself (December 1977: *Mysis* $\simeq 40 \cdot \mathrm{m}^{-2}$). We propose that the ability of *Bosmina* to survive in Emerald Bay depends on its ability to offset losses to *Mysis* predation by having higher birth rates there than are possible in the more oligotrophic waters. Suggestions of higher birth rates in Emerald Bay come from higher egg ratios ($\bar{E}$) of *Bosmina* (in December 1977, $\bar{E} \simeq 1.0$) than in Lake Tahoe in a similar period in 1969 ($\bar{E} \simeq 0.1$). An additional test of the influence of *Mysis* predation on *Bosmina* may soon be at hand: *Mysis* densities in Lake Tahoe have been dropping steadily over the last 2 years, and *Bosmina* may reappear as it did in 1974–1975.

The conditions necessary for the reappearance of *Daphnia* would also seem to be present, and yet no such recurrence is evident. The present greater dominance of small diatoms should favor its reproduction. Although *Daphnia* did not produce males and resting eggs between 1967 and 1970, it seems unlikely that it does not reappear because it is not being introduced. This is especially true in view of the lake's enormous volume and considerations raised by Hutchinson (1965) about the actual size of plankton populations, however rare, in large systems. However, the possibility that *Daphnia* could not survive under current food conditions even if it were introduced remains; we are examining this by testing the population growth of isolated populations of *Daphnia* in Lake Tahoe water.

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