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Opossum Shrimp (*Mysis relicta*) Predation on Zooplankton

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COOPER, S. D., AND C. R. GOLDMAN. 1980. Opossum shrimp (*Mysis relicta*) predation on zooplankton. Can. J. Fish. Aquat. Sci. 37: 909-919.

Mysis relicta clearance rates were not affected by changes in prey and predator density in single-prey systems where *Epischura nevadensis* late instars were used as food. A comparison of the results obtained from single-, two-prey, and multiple-prey systems revealed that *Mysis* clearance rates of *E. nevadensis* late instars and *Diaptomus tyrrelli* males were significantly affected by the presence and abundance of alternative prey.

When offered natural prey assemblages, the smallest *Mysis* preyed preferentially on the smallest available prey (*Bosmina*, *Ceriodaphnia*, *Diaptomus* nauplii) while larger *Mysis* showed an increased preference for larger prey (*Epischura*, *Daphnia*). In general, *Mysis* preferred *Daphnia* over copepods; *Epischura*, *Ceriodaphnia*, *Bosmina*, and cyclopoid copepods over *Diaptomus* copepodites and adults; and *Diaptomus* males over *Diaptomus* females. Total consumption rates increased with increasing predator size and starvation duration. Food selectivity patterns exhibited by *Mysis* were attributed to the mechanical efficiency with which the predators captured and handled food particles of different sizes, to the vigor of prey escape responses, and to predator-prey encounter frequencies.

Key words: *Mysis relicta*, predation, zooplankton, feeding preferences, opossum shrimp

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Les taux d'élimination chez *Mysis relicta* ne sont pas affectés par des changements de densité des proies et des prédateurs dans des systèmes à un type de proies dans lesquels des stades larvaires avancés de *Epischura nevadensis* sont utilisés comme nourriture. Quand on compare les résultats obtenus avec des systèmes à un, deux ou plus de deux types de proies, on constate que les vitesses d'élimination chez les *Mysis* de larves avancées de *E. nevadensis* et de mâles de *Diaptomus tyrrelli* sont nettement affectées par la présence et l'abondance de la proie subsidiaire.

Devant un choix de groupes de proies naturels, les plus petits *Mysis* se nourrissent de préférence des plus petites proies disponibles (*Bosmina*, *Ceriodaphnia*, nauplii de *Diaptomus*),

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alors que les *Mysis* plus gros montrent une préférence croissante de proies plus grosses (*Epischura*, *Daphnia*). En général, les *Mysis* préfèrent *Daphnia* aux copépodes; *Epischura*, *Ceriodaphnia*, *Bosmina* et copépodes cyclopoïdes à *Diaptomus*, copépodites et adultes; et *Diaptomus* mâles à *Diaptomus* femelles. Les taux de consommation totale augmentent en fonction de la croissance accrue des prédateurs et de la durée du jeûne. Nous attribuons trois types de sélectivité de la nourriture chez *Mysis* à l'efficacité mécanique avec laquelle les prédateurs capturent et manipulent des particules de nourriture de différentes tailles, à la vigueur des réponses d'échappement des proies et enfin à la fréquence des rencontres prédateurs-proies.

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RECENT studies have shown that trophic interactions often determine the structure and composition of freshwater communities (Hrbáček et al. 1961; Zaret and Paine 1973). In particular, the effects of intensive size-selective vertebrate predation on zooplankton assemblages are well documented (Brooks and Dodson 1965; Dodson 1970). A number of recent studies have elucidated the effects of invertebrate predators on freshwater zooplankton assemblages (Dodson 1974; Kerfoot 1977; Fedorenko 1975). Unfortunately very little is known about the ecology of many invertebrate predators and, therefore, their influence on freshwater communities often remains obscure. A case in point is the effect of opossum shrimp (*Mysis relicta*) predation on zooplankton assemblages. In many montane lakes where *Mysis* have been introduced as fish food, cladoceran populations have declined or disappeared (Cybulut 1970; Goldman et al. 1979). However, the presence of planktivorous fish and changes in primary productivity (Northcote 1972; Richards et al. 1975) prevent the clear attribution of these trends to direct interactions between cladocerans and *Mysis*. An analysis of the role of *Mysis* predation in these systems is further hampered by our ignorance of *Mysis*' feeding biology. The studies of Cannon and Manton (1927) suggested predatory capabilities for the marine mysid, *Hemimysis lamornae*, and Forbes (1882) reported the presence of *Bosmina* in the stomachs of Lake Michigan *Mysis*. However, other investigators, such as Stalberg (1933) cast *Mysis* in a primarily herbivorous role. Omnivory was reported by Mauchline (1971a, b, c, d) for several marine mysids, by Wilson (1951) for the freshwater *Neomysis awatschensis*, and by Tattersall and Tattersall (1951), Lasenby and Langford (1973), and Grossnickle (1978) for *M. relicta*. Thus, any study evaluating the effects of *Mysis* introduction must consider possible *Mysis* predation on zooplankton assemblages. Such an analysis requires a knowledge of *Mysis* prey preferences. With the exception of Grossnickle (1978), however, there have been no studies on *Mysis* prey selectivity.

Because of its implications for questions concerning the introduction of exotic species, the importance of predation in structuring aquatic ecosystems, and the management of lake resources, a detailed study of *Mysis* predation was warranted. The following study deals with *M. relicta* predation on natural zooplankton assemblages.

Materials and Methods

Zooplankton samples were collected from Lake Tahoe, Prosser Reservoir, Martis Creek Reservoir, Tahoe Keys, and Stampede Reservoir, California, with 0.6 m, 60- μ m mesh or 0.75 m, 80- μ m mesh nylon plankton nets. *Mysis* were collected in July and August, 1977, with 0.5 m, 500- μ m mesh nylon nets towed at a depth of 20–60 m in Lake Tahoe at night. All experimental animals were held in the dark at 10°C in 3- to 34-L glass containers filled with filtered lake or spring water before experiments began. Unless otherwise stated *Mysis* individuals, at densities of 1–10 per litre, were starved for 18–24 h before experimentation.

The experimental regime duplicated summer conditions at Lake Tahoe. Predation trials were conducted in the dark at 9–10°C in glass containers filled to the 3-L mark with filtered (60 μ m) Lake Tahoe or spring water. While *Mysis* spend most of their time in cool hypolimnetic waters (5°C), they experience experimental temperatures when they enter the thermocline during their nightly upward migrations. In single and two-prey experiments, control jars contained only prey species at known densities while experimental jars contained both the prey species, at identical initial densities to those in the controls, and one *Mysis*. Because there was no mortality in the control jars, the difference between prey numbers in the experimental jars at the beginning and end of the standard 12-h (21:00–09:00) trial period was an estimate of the number of prey eaten per half day. In general the number of prey consumed was less than 35% of the initial number of prey present.

In the assemblage experiments, experimental and control jars were inoculated with equivalent aliquots of well-mixed plankton assemblages. *Mysis* were then added to the experimental jars. Where densities of a given prey were sufficiently high, i.e. greater than 8 per replicate (2.7/L), initial concentrations for each prey type in the trial replicates were nearly equivalent, the standard error being less than 10–15% of the mean. The mean number of replicates for each treatment was 5 (range = 2–6). The difference between experimental and control replicate means at experiment termination was an estimate of the number of prey eaten during the trial period. To control for mortality not due directly to mysid predation, experimental jars were periodically checked for prey corpses. With one exception (expt. 5) such mortality proved to be negligible. In this case a correction factor was calculated for small numbers of *Daphnia* and *Bosmina* caught in the surface film.

The consumption rate (number of prey eaten per predator per day), the predation coefficient or clearance rate (k), and, in the assemblage trials, the electivity index (E) for each prey type were calculated from these data. Because *Mysis* fragmented some of its prey in the single and two-prey trials, the

"consumption rate" was considered a mortality rate rather than ingestion rate. The predation coefficient or clearance rate was calculated

$$k = \frac{-\ln(P_T/P_I)}{XT}$$

where P_T is the final prey density, P_I is the initial prey density, X is the predator density (number per litre), and T is the time in days (Dodson 1975). The coefficient k is equivalent to Gaud's F (1951) and has been variously called the grazing rate, filtering rate, or clearance rate of the animal being investigated (Paffenhöfer and Harris 1976; Ikeda 1977; Frost 1975; Gundry 1978). In this case k represents the number of litres cleared of prey per predator per day. Means and standard errors for k were calculated from the independent, random replicates for each trial set in single and two-prey experiments. In the assemblage experiments the k value mean for each prey type was calculated by multiplying the difference between the means of the natural logs for experimental and control replicates

by $\frac{1}{P_T - \ln P_I}$ by $-\frac{1}{XT}$. Standard errors were calculated as

$$SE = \left(\sqrt{\frac{SP_T^2}{n_E} + \frac{SP_I^2}{n_C}} \right) \left(-\frac{1}{XT} \right)$$

where SP_T^2 is the variance of the natural logs of the experimental replicates (+ *Mysis*), SP_I^2 is the variance of the natural logs of the control replicates, n_E is the number of experimental replicates, and n_C is the number of control replicates. While this method of standard error calculation assumes log-normality of the data, it does provide a relative indication of data variability. Because further statistical analyses require assumptions of normality that might be inappropriate to these data, the standard errors were not used in direct statistical comparisons. Because of the variation caused by chance occurrences at low prey densities, results for species occurring at densities less than 8 per replicate in a given assemblage experiment were not reported.

Ivlev's (1961) electivity index was calculated for each prey type in each assemblage experiment. Electivity indices were not reported in detail, however, because they indicated the same feeding patterns as the clearance rates. "Preference" and "selection" are used here to indicate that clearance rates and electivity indices for one prey type were consistently greater than those for another prey type in the assemblage experiments.

For each experiment a random sample of 10–60 individuals of each common prey type were measured with a Hewlett-Packard 9100 B digitizer as shown in Fig. 1. *Mysis* lengths were measured from the tip of the rostrum to the tip of the telson with an ocular micrometer mounted in a Wild dissecting scope at 12 \times . Lengths and densities of zooplankton prey and *Mysis* used in the assemblage experiments are summarized in Table 1. Biomass consumption estimates were calculated by using the length-dry weight relationships in Dumont et al. (1975) for zooplankton, and Morgan (1976) for *Mysis*.

Consistent, significant trends in *Mysis* prey preferences were examined by applying the sign test to k value means for all pairs of prey types over all predator size-classes and all experimental sets (Conover 1971). Other statistical comparisons were made with the Wilcoxon Rank Sum test or the median test at the $P < 0.05$ level and Spearman's ρ was used as a measure of correlation (Wilcoxon and Wilcox

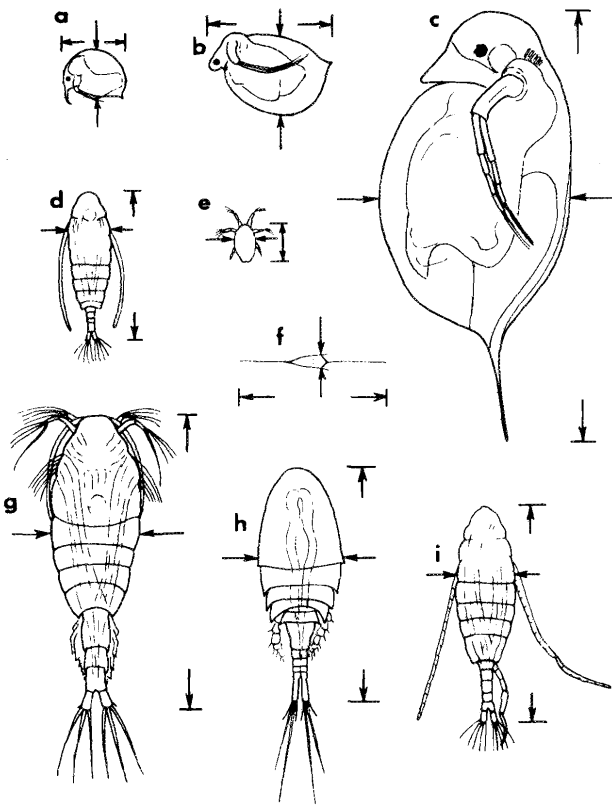


FIG. 1. Measurement of representative zooplankton. Length measurements included the shell spines of rotifers and cladocera (a–c, f) but not the caudal setae of copepods (d, g–i). Heights represent the widest dorsal dimensions of rotifers and copepods (d–i) and the maximum lateral carapace heights of cladocerans (a–c). a = *Bosmina longirostris*; b = *Ceriodaphnia laticaudata*; c = *Daphnia pulicaria*; d = *Diaptomus tyrrelli* copepodite; e = *D. tyrrelli* nauplius; f = *Kellicottia longispina*; g = *Epischura nevadensis* female; h = *Cyclops* sp. female; i = *Diaptomus tyrrelli* male. a–c = lateral view, d–i = dorsal view. 23 \times .

1964; Conover 1971). Least-squares linear regression methods were taken from Draper and Smith (1966).

Results

PRELIMINARY EXPERIMENTS

The absolute densities and relative proportions of different prey types and predators vary a great deal in natural assemblages and may affect a predator's feeding rate on a given prey item. For this reason the question, "How does prey abundance, predator abundance, and the presence and relative abundance of alternative prey affect *Mysis* clearance rates (k s) on a given prey type?" was examined in a series of preliminary experiments. The clearance rate (k) is independent of prey density if the number of prey eaten per predator per

TABLE 1. Mean length (L -mm) and control density (D - No./rep.) for each prey type and mean lengths and experimental densities for *Mysis* used in experiments 1-5. Densities represent the mean densities of three to seven replicates. See the text for an explanation of *Mysis* size-classes in experiments 4-5.

	Expt. 1		Expt. 2		Expt. 3		Expt. 4		Expt. 5	
	L	D	L	D	L	D	L	D	L	D
<i>Daphnia pulicaria</i> ^a			1.94	14.8	—	1.5			1.39	38.6
<i>Ceriodaphnia</i> spp. ^b					0.76	17.0			0.56	51.8
<i>Bosmina longirostris</i>									0.33	33.6
<i>Chydorus sphaericus</i>					0.36	3.0				
Ostracods (unident.)									0.28	1.00
Cyclopoid adults and copepodites ^c					0.87	11.5			0.76	27.2
Cyclopoid nauplii					0.11	108.5				
<i>Epischura nevadensis</i> ♂	—	2.6	—	10.8	1.54	22.0	1.55	15.3	1.52	5.4
<i>E. nevadensis</i> ♀	—	0.4	—	2.5	1.67	6.5	1.67	10.7	1.67	2.8
<i>E. nevadensis</i> copepodites	—	14.6	1.02	46.2			1.06	22.8	1.07	61.6
<i>Diaptomus tyrrelli</i> ♂	1.22	14.6	—	13.0	1.22	6.5	1.23	39.8	1.21	16.8
<i>D. tyrrelli</i> ♀	1.32	16.8	—	7.2	1.30	1.5	1.29	49.5	1.30	14.6
<i>D. tyrrelli</i> ♀ w/eggs	—	3.6					1.30	4.0	—	2.0
<i>D. tyrrelli</i> copepodites	0.87	21.0	1.12	22.5	1.01	5.0	1.08	10.7	0.94	17.8
<i>D. tyrrelli</i> nauplii ^d	0.23	15.6					0.21	32.5	0.22	24.6
<i>Kellicottia longispina</i>	0.73	46.0					0.70	40.7	0.69	6.2
<i>Asplanchna</i> spp.									—	0.4
<i>Volvox</i> sp.									0.54	1.0
<i>Mysis relicta</i>	16.7	1.0	16.1	2.0	14.9	2.0	IV 16.4	2.0	IV N 15.5	1.7
							III 13.4	3.0	IV S 16.0	2.0
							II 10.8	5.3	III N 13.9	2.7
							I 6.6	3.7	III S 13.2	2.7
									II N 11.7	5.0
									II S 10.8	5.0
									I N 8.1	4.5

^aSee Brandlova et al. (1972) for a discussion of the *Daphnia pulex*-*D. pulicaria* problem.

^bIn experiment 3, a mixture of equivalent proportions of *Ceriodaphnia reticulata* and *C. laticaudata*. In experiment 6, primarily *C. laticaudata*.

^c*Diacyclops thomasi* in experiment 3. A mixture of *D. thomasi*, *Eucyclops serrulatus*, *Acanthocyclops vernalis*, and *Macrocyclops albidus* in experiment 6. Nomenclature after Dussart (1969) and Torke (1976).

^dThis category includes a few *Epischura* nauplii.

unit time is approximately a linear function of prey density (Frost 1975; Dodson 1975). When large *M. relicta* (\bar{x} length = 15.8 mm) were given late instar *Epischura nevadensis* (\bar{x} length = 1.60 mm) as prey, the predator's consumption rates increased linearly with increasing initial prey density over the range of 1-50 prey per litre (Fig. 2A). Because later experiments indicated that feeding rates were not constant throughout the trial period, initial rather than average prey densities were used on the abscissa in Fig. 2A (S. D. Cooper and C. R. Goldman in preparation). The slope of the regression line for the plot of k versus prey density did not differ significantly from 0 and there were no significant differences between the k values obtained at each density (Fig. 2B).

In another pair of experiments initial *Epischura* prey densities were kept constant while the density of large *Mysis* was varied. In the first experiment predator densities of 0.33, 0.67, and 1.00 per litre were compared while in the second, conducted in 17.7-L aquaria, predator densities of 0.11 and 0.28 per litre were tested.

In both experiments no significant differences in k were noted between experimental sets having different predator densities (Table 2). These data suggest that predation coefficients are constant over the predator density range tested, all other conditions remaining equal.

The effect of changes in the relative abundance of alternative prey on the grazing rates and selectivity of large *Mysis* (\bar{x} length = 15.0 mm, s_x = 0.90) was studied in a two-prey system where the ratio of *Epischura* late instars (\bar{x} length = 1.60 mm) to *Diaptomus tyrrelli* males (\bar{x} length = 1.24 mm) was varied from 10:50 to 50:10. In this experiment initial total prey density was kept constant at 20 per litre and five replicates were run at each prey ratio. The predators, which had been fed on equivalent densities of *Epischura* and *Diaptomus*, were starved for 48 h before experimentation.

In this experiment individual *Mysis* showed a consistent, significant ($P < 0.001$, sign test) preference for *Epischura* late instars despite large fluctuations in

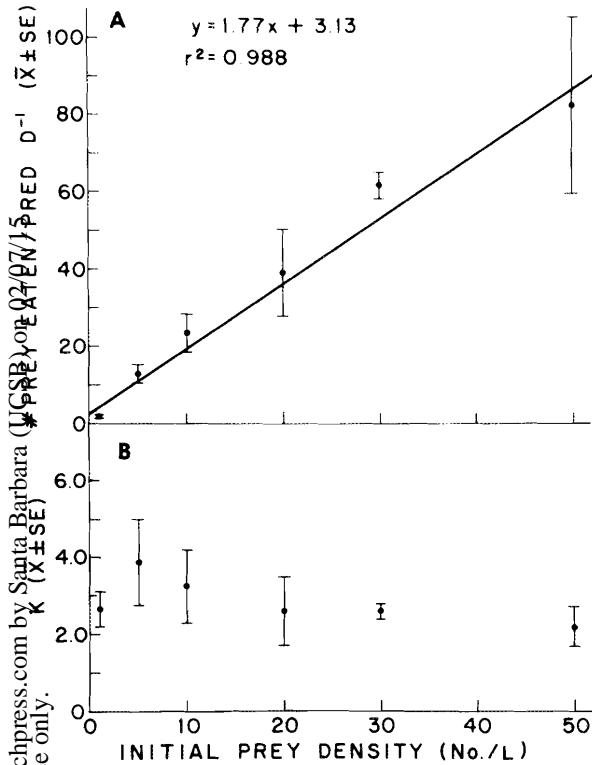


TABLE 2. Effects of predator density on *Mysis* clearance rates. None of the comparisons were significantly different. Prey density in experiment 1 was 16.7 *Epischura*/L, and in experiment 2 was 5.0 *Epischura*/L. *k* is the clearance rate, *n* the number of replicates per treatment.

Experiment	Container size (litres)	Predator density (no./L)	<i>n</i>	<i>k</i> ($\bar{x} \pm s_{\bar{x}}$)
1	3	0.33	6	4.52 ± 1.59
		0.67	5	6.43 ± 1.35
		1.00	4	4.66 ± 0.79
2	17.7	0.11	4	4.88 ± 1.22
		0.28	3	5.23 ± 1.95

($P < 0.05$; Wilcoxon rank sum test). The failure to find such differences in the *Epischura* data may have been an artifact of the high variability of the *Epischura* data or the asymmetry of Ivlev's electivity index. The maximum possible *E* value for a "preferred" prey decreases as its relative abundance increases, potentially masking any increasing preference for that item.

Finally, in an experiment designed to test the effect of alternative prey on *Mysis*' predation rates, individual *Mysis* were presented with single species cultures of *Epischura* late instars, a mixture of *Epischura* late instars and *Diaptomus* males, or the Lake Tahoe zooplankton assemblage (expt. 1 in the assemblage trials). The *Epischura* densities were 13.3 per litre in the single and two-prey systems and *Diaptomus* males were present at equivalent densities in the two-prey system. It was not possible to maintain these densities in the assemblage trials but the densities of these two prey types were about equal (5/L) in these trials.

The *k* values obtained from the single prey system ($\bar{x} = 3.54$, $s_{\bar{x}} = 0.38$) were significantly higher than the *k* values for *Epischura* obtained from the two-prey system ($\bar{x} = 2.46$, $s_{\bar{x}} = 0.26$). The *k* values obtained for *Epischura* from the assemblage trials were comparable ($k = 3.04$, $s_{\bar{x}} = 0.91$). For *Diaptomus* males the mean *k* value in the two-prey system was 0.70, $s_{\bar{x}} = 0.10$, while in the assemblage experiment *Diaptomus* males were not eaten ($k = 0.0$, $s_{\bar{x}} = 0.40$, Table 4, expt. 1).

In summary, for any given prey type, *k* values were not affected by changes in prey and predator density.

2. The effects of *Epischura* prey density on consumption rates (A) and clearance rates (B) of *Mysis*. The line fitted by least-squares linear regression methods.

ing coefficients (Table 3). The mean *k* value for all replicates obtained for *Epischura* was about twice that obtained for *Diaptomus* (1.45 versus 0.77). The values obtained for *Epischura* remained relatively constant over this range of prey ratios, there being no significant differences between the values obtained at any two ratios. On the other hand *k* values obtained for *Diaptomus* showed general declines with increasing *Epischura* density. *Diaptomus* *k* values at the 20:40 *Epischura*:*Diaptomus* ratio were significantly higher than those obtained at the 40:20 and 50:10 ratios. In addition, *E* values obtained for *Diaptomus* at the two lowest *Epischura*:*Diaptomus* ratios were significantly higher than those obtained at the two highest ratios

TABLE 3. Mean and range of *k* values for *Epischura* and *Diaptomus* and mean ratio of *k* values for these two prey at different *Epischura*:*Diaptomus* ratios.

Ratio of <i>Epischura</i> : <i>Diaptomus</i>	10:50	20:40	30:30	40:20	50:10
Mean <i>k</i> for <i>Epischura</i>	1.8	1.3	1.9	1.1	1.4
Range of <i>k</i> for <i>Epischura</i>	0-3.8	0.6-2.0	0.5-3.1	0.5-1.8	1.1-2.0
Mean <i>k</i> for <i>Diaptomus</i>	1.1	0.9	0.9	0.5	0.4
Range of <i>k</i> for <i>Diaptomus</i>	0.5-1.8	0.5-1.2	0.4-2.0	0-0.9	0-0.6
Ratio of <i>Epischura</i> <i>k</i> : <i>Diaptomus</i> <i>k</i> (\bar{x})	2.16	1.44	2.89	2.08	3.24

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TABLE 4. Clearance rates (k) for prey used in experiments 1-3. Predators were starved for 24 h in experiment 1, 80 h in experiment 2, and 19 h in experiment 3.

Prey	k ($\bar{x} \pm s\bar{x}$)
Experiment 1 — Tahoe assemblage	
<i>Epischura</i> copepodites and adults	3.04 ± 0.81
<i>Diaptomus</i> copepodites	2.10 ± 0.87
<i>Diaptomus</i> nauplii	2.21 ± 0.76
<i>Diaptomus</i> ♀	0.50 ± 0.83
<i>Kellicottia</i>	0.00 ± 0.36
<i>Diaptomus</i> ♂	0.00 ± 0.89
Experiment 2 — Tahoe assemblage + <i>Daphnia</i>	
<i>Daphnia pulicaria</i>	> 11.38 ± 0.08
<i>Epischura</i> copepodites	5.53 ± 1.05
<i>Epischura</i> adults	4.23 ± 0.90
<i>Diaptomus</i> copepodites	1.77 ± 0.34
<i>Diaptomus</i> adults	1.30 ± 0.57
Experiment 3 — Prosser assemblage + Tahoe assemblage	
<i>Ceriodaphnia</i> sp.	> 7.56 ± 1.41
<i>Epischura</i> adults	3.88 ± 1.16
<i>Diaptomus</i> adults and copepodites	2.55 ± 0.63
<i>Cyclops</i> adults and copepodites	2.10 ± 1.46
<i>Cyclops</i> nauplii	0.00 ± 0.44

However, k values were significantly affected by the presence and abundance of alternative prey.

ASSEMBLAGE TRIALS

The assemblage trials were designed to answer the questions, "What prey sizes and types does *Mysis* prefer when offered natural prey assemblages?" and "How are these feeding patterns affected by changes in predator size and prior starvation duration?" The results of the first three experiments are summarized in Table 4. In experiment 1 *Epischura* copepodites and adults and *Diaptomus* juveniles were eaten at substantially higher rates than *Diaptomus* adults and *Kellicottia* while in experiment 2 *Daphnia* was preferred over *Epischura* and *Epischura* was preferred over *Diaptomus*. *Ceriodaphnia* was eaten at higher rates than copepods and cyclopoid copepod nauplii were eaten at lower rates than other prey types in experiment 3. Furthermore, the k values calculated for *Daphnia* and *Ceriodaphnia* in experiments 2 and 3 were underestimates because these cladoceran species were eliminated from one or more experimental replicates. In general, then, cladocerans were preferred to copepods and cyclopoid copepod nauplii and *Kellicottia* were not eaten.

In experiment 4, four size-classes of *Mysis* starved for 20 h were offered the Lake Tahoe zooplankton assemblage, while in experiment 5 four size-classes of *Mysis* starved for 18 h ("unstarved" "N" *Mysis*) and three *Mysis* size-classes starved for 9 d, 22 h ("starved" "S" *Mysis*), were given a mixture of zooplankton

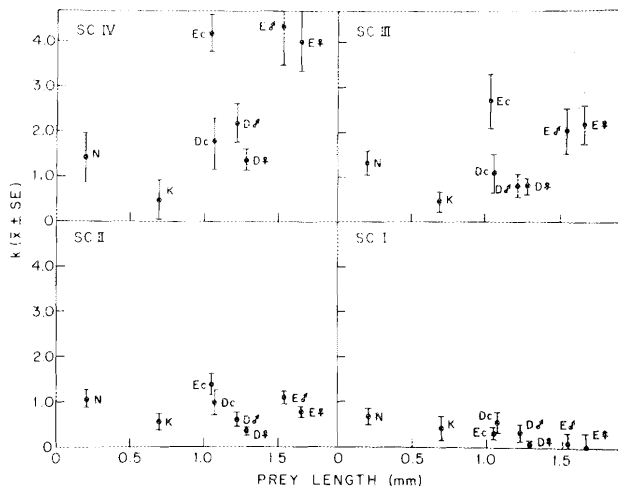


FIG. 3. The relationship between prey length and clearance rate (k) for each *Mysis* size-class in experiment 4. See Tables 1 and 5 for a description of each *Mysis* size-class. Prey code: N = *Diaptomus* nauplii, K = *Kellicottia*, Dc = *Diaptomus* copepodites, D♂ = *Diaptomus* males, D♀ = *Diaptomus* females, Ec = *Epischura* copepodites, E♂ = *Epischura* males, E♀ = *Epischura* females.

species collected from Lake Tahoe, Tahoe Keys, Stampede Reservoir, and Martis Creek Reservoir, California (Table 1). Spearman rank correlation analysis revealed significant negative correlations between predation coefficients and prey length for the smallest *Mysis* size-class in both experiments (Fig. 3 and 4).

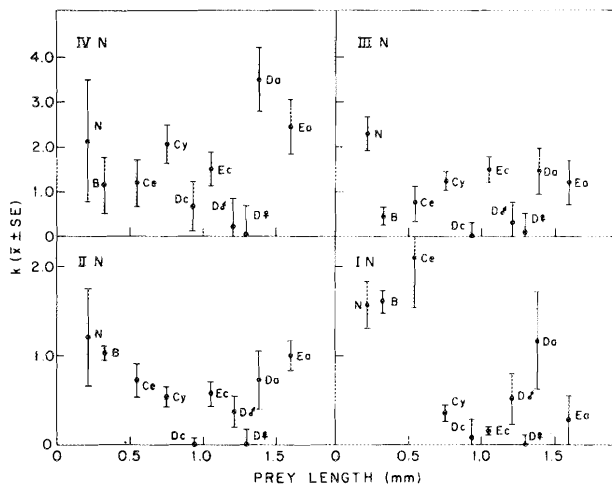


FIG. 4. The relationship between prey length and clearance rate (k) for *Mysis* size-classes I N-IV N in experiment 5. See the text for an explanation of the *Mysis* size-classes. Prey codes: Da = *Daphnia*, Ea = *Epischura* adults, Ec = *Epischura* copepodites, Cy = *Cyclops* adults and copepodites, Ce = *Ceriodaphnia*, B = *Bosmina*, N = *Diaptomus* nauplius, Dc = *Diaptomus* copepodites, D♀ = *Diaptomus* females, D♂ = *Diaptomus* males.

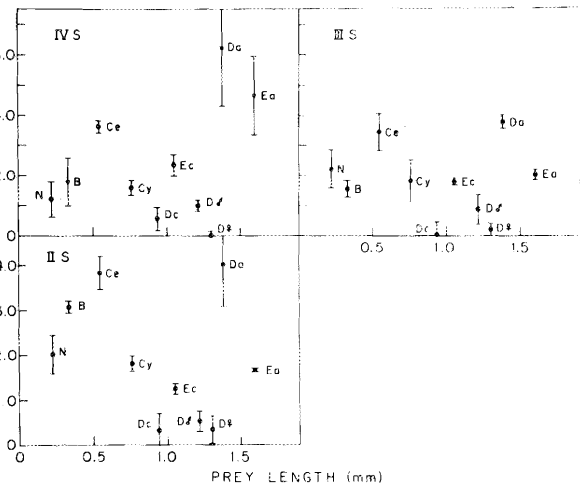


FIG. 5. The relationship between prey length and clearance rate (k) for *Mysis* size-classes II S-IV S in experiment 5. See the text for an explanation of *Mysis* size-classes. Prey code: as in Fig. 4.

In addition, Spearman's ρ , for correlations between k values and prey lengths, became increasingly positive with increasing predator size in both experiments. Because the electivity index rank and clearance rate rank were equivalent for each prey type and predator size-class, correlation analysis of E against prey size produced the same results. These trends were further clarified by plotting k against predator size for each prey class. Large prey exhibited greater, more consistent increases in k when compared to smaller prey as predator size increased (Fig. 6). These results suggest that *Mysis* show an increasing preference for larger prey as they increase in size. It should be noted that k values for

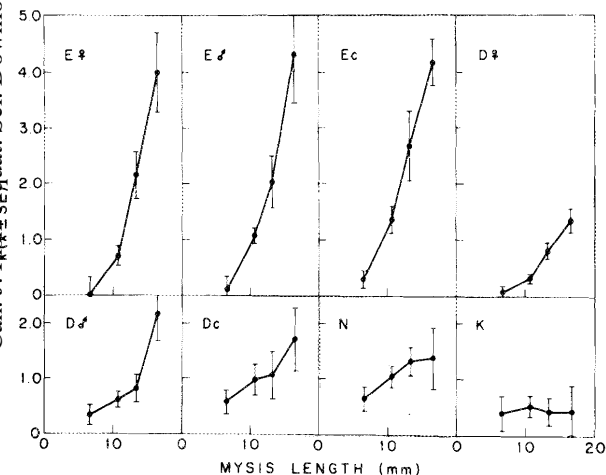


FIG. 6. The relationship between predator length and clearance rate (k) for each prey type in experiment 4. Prey codes as in Fig. 3.

the smallest prey obtained in the trials involving large *Mysis* may have been underestimated as preferential *Mysis* predation on adult and subadult *Epischura* and *Cyclops* may have released small prey from mortality they experienced in controls due to copepod predation (Main 1962; Kerfoot 1977; McQueen 1969; Anderson 1970; Brandl and Fernando 1975). An analysis of the importance of copepod predation in these experiments involved the calculation of naupliar and rotifer mortalities by comparing initial and final control densities of these prey as well as calculation of copepod consumption rates using Dodson's (1975) k values and control predator-prey densities. These analyses revealed that copepod predation was unimportant at these low temperatures over these short trial periods and could be ignored in the analysis of results.

For the three largest *Mysis* size-classes, pair wise comparisons of prey k value means over all experimental sets revealed that *Daphnia* was consistently preferred to copepods, and *Bosmina*, *Ceriodaphnia*, *Epischura*, and cyclopoid copepods were preferred to *Diaptomus* copepodites and adults ($P < 0.05$, sign test, Table 4, and Fig. 3-5). The relative rank of k values for *Diaptomus* nauplii showed less consistent patterns but were usually higher than those for *Diaptomus* adults and copepodites. The largest *Mysis* consumed *Kellicottia* at lower rates than those for other prey types in experiment 4 (Fig. 3). The relative k value ranks of *Epischura*, diaptomid nauplii, *Bosmina*, and *Ceriodaphnia* were dependent on predator size (see previous paragraph) or prior starvation duration (discussed later) (Fig. 3-5). Examination of standard errors for k value means in experiments 1-5 generally corroborated these patterns though *Daphnia* and *Epischura* error bars in 6 of 14 cases overlapped. In addition, *Daphnia* k value means were more than two standard errors higher than those for *Ceriodaphnia* for the largest "unstarved" *Mysis* size-class and more than two standard errors higher than those for *Bosmina* for *Mysis* size-classes III and IV.

It is apparent that this hierarchy of *Mysis* prey preferences was not entirely related to prey size. For example, the mean *Epischura* copepodite length was less than the mean lengths of *Diaptomus* males and females, yet its k values were consistently higher than those of the latter prey types for the three largest *Mysis* size-classes. Despite their similar lengths, k values for *Daphnia* were always greater than k values for *Diaptomus* adults for all predator sizes tested (expt. 2 and 5). In 10 out of 12 treatments (expt. 1, 4, and 5) k values for *Diaptomus* males were higher than those for *Diaptomus* females ($P \approx 0.02$, sign test), exceeding a difference of two standard errors in five of those cases.

There was also some indication that predator starvation duration affected the k value ranks for some prey types. Predation coefficient ranks for *Ceriodaphnia* were consistently higher for starved than for unstarved *Mysis* while those for nauplii were consistently lower.

TABLE 5. Length ranges and consumption rates of *Mysis* size-classes (SC) used in experiments 4 and 5.

Expt.	SC	Total length range (mm)	No. prey eaten/ predator · d ⁻¹	Dry wt prey eaten/ predator · d ⁻¹ (mg)	Ingestion rate as % predator body wt · d ⁻¹
4	I	5.0-8.3	18.8	0.09	28
	II	9.0-12.2	35.2	0.36	18
	III	12.0-15.0	55.7	0.68	15
	IV	14.8-18.3	89.9	1.22	12
5	I N	6.4-9.5	56.4	0.26	39
	II N	10.4-15.3	48.4	0.32	11
	III N	12.8-15.0	77.4	0.57	11
	IV N	15.0-16.2	117.0	0.92	12
	II S	9.7-12.0	87.9	0.56	29
	III S	11.7-15.2	122.9	0.85	20
	IV S	15.4-17.3	155.0	1.21	14

As might be expected, starved *Mysis* fed at consistently higher rates than "unstarved" *Mysis* and total consumption rates increased with increasing predator size (Table 5). However, there was often a decline in biomass consumption rates expressed as a proportion of the predator's body weight with increasing predator size. The starvation results were corroborated by an experiment in which late instar *Epischura* were fed to instar IV *Mysis* (\bar{x} length = 15.6 mm, $s_{\bar{x}} = 0.3$) that had been starved for 0, 10.75, 30.75, and 66.25 h. In this experiment there was a general, significant increase in k with increasing prior predator starvation duration, the plot of k versus starvation duration approximating the straight line, $y = 0.07x + 0.02$ ($r^2 = 0.93$), where y was the clearance rate and x the starvation duration in hours. Because few prey fragments were found in the assemblage experiments, these consumption rates probably approximated actual consumption rates but were still overestimated due to the loss of prey fluids when *Mysis* macerated their prey. Why there were more prey fragments in the single prey experiments as compared to the assemblage experiments is not known. In terms of impact on prey populations, the largest *Mysis* would have a greater individual effect on prey numbers because of their higher total consumption values.

In summary *Mysis* selected both specific prey sizes and types. The largest *Mysis* preferred the largest prey while the smallest *Mysis* preyed preferentially on the smallest available prey. In addition *Mysis* showed a consistent preference for *Daphnia* over copepods and for *Epischura*, *Bosmina*, *Ceriodaphnia*, and cyclopoid copepods over *Diaptomus*. Total prey consumption increased with increasing predator size and starvation duration.

Discussion

PRELIMINARY TRIALS

The results of the preliminary experiments suggest that k for a given prey type can be significantly affected by the presence and relative abundance of alternative prey. However, the relative rank of k for each prey

type remains the same as one moves from single to multiple-prey systems. In these experiments *Mysis* always exhibited a marked preference for *Epischura* late instars over *Diaptomus* males. Grossnickle (1978) found that the rank of *Mysis*' preference for each of four prey species in two-prey systems was the same as that predicted by k values obtained from single-prey trials; consequently, predator preferences but not absolute predation rates can be determined from single-prey systems.

Predation rates may decline for a given prey species when another prey species becomes available because of the time spent capturing and handling the alternative prey. The relative predation rates for a given prey species would be therefore dependent on the susceptibility to predation of the alternative prey. Furthermore, many theories of optimal diet predict changes in breadth of diet with changes in total prey density (Pyke et al. 1977). It is significant that the most "preferred" prey in experiment 1 were *Epischura* late instars while *Diaptomus* males were among the least preferred prey (Table 4). This may account for the comparability of *Epischura* k values obtained from single- or two-prey systems versus multiple-prey systems and the decline in *Diaptomus* k values from the two-prey to the multiple-prey systems. *Epischura* values may have remained comparable because it is a preferred prey but *Diaptomus* k 's declined because of the increased abundance of preferred prey items. The discrepancies in the results obtained for *Ceriodaphnia* in experiments 3 and 5 and the lower k values obtained for *Diaptomus* in experiment 5 relative to experiment 4 can also be explained in terms of the increased abundance of alternative preferred prey.

Whatever the reasons for these patterns, it is apparent that k values may be significantly affected by the presence of alternative prey, the extent of the effect being dependent upon the abundance and susceptibility to predation of the alternative prey. The rank of k values for each prey type, however, remains the same in single-, two-prey, and multiple-prey systems.

ASSEMBLAGE EXPERIMENTS

The assemblage experiments revealed that small *Mysis* (<9 mm) prefer small prey (*Diaptomus* nauplii, *Bosmina*, *Ceriodaphnia*) while larger *Mysis* show an increasing preference for larger prey (especially *Epischura*). In addition, *Daphnia* was consistently preferred over copepods and *Diaptomus* adults and copepodites and *Kellicottia* were eaten at lower rates than other prey items.

Some of the prey size selectivity noted in these experiments may have been due to the efficiency with which the feeding appendages retained particles of different size (Frost 1977; Neill 1975). Our observations indicate that *Mysis* capture large prey (*Epischura* or *Diaptomus* adults) by folding their extended thoracic endopodites latero-ventrally over prey items which had been swept into the thoracic region by natatory currents or that had fortuitously bumped into the thoracic areas of the rapidly moving predators. It is also clear, however, that mysids can filter smaller, less active food particles from the surrounding water with filtering combs on their second maxillae (inter-setule distance in adult female *Mysis* = 4–5 μm) or first thoracic endopodites (inter-setae distance in adult female *Mysis* = 29–36 μm) (Cannon and Manton 1927; Grossnickle 1978). In these experiments *Mysis* may have used a filter-feeding mode to capture small prey items and a raptorial feeding mode to seize larger prey (Sambler and Frost 1974). Grossnickle's (1978) measurements of sieve aperture size and our examination of prey held by the thoracic endopodites indicate that the largest mysids should have been able to retain the smallest prey items, particularly prey as spiny as *Kellicottia*, regardless of the feeding mode used. The minimum dimensions (heights or diameters) of diaptomid nauplii and *Kellicottia* were 99 μm and 62 μm . The particle retention efficiency of the filtering sieve may determine the size of algae taken by *Mysis* (Grossnickle 1978), but probably plays little role in determining the size of zooplankton prey taken.

It is also possible that the smallest prey did not elicit capture responses in the largest predators. The largest *Mysis*, however, exhibited significant predation rates on the smallest prey in experiments 4 and 5. Apparent changes in *Mysis* size selectivity with increasing mysid size were primarily due to large increases in predation rates on large prey, particularly *Epischura*. Predation rates on small prey increased at slower rates or remained relatively constant with increasing predator size. Changes in predator size selectivity with increasing mysid size can most readily be explained by an increasing predator ability to capture and handle large, mobile prey, rather than by a decreased ability to take small prey. Evidently, the smallest *Mysis* were unable to handle the largest prey or their feeding currents were too weak to entrain large, mobile organisms like *Epischura*.

Lasenby and Langford (1973) found that *Mysis* less than 5–6 mm long fed only on algae and detritus while

larger *Mysis* commonly preyed on *Daphnia* in Stony Lake, Ontario. McWilliams (1970, cited in Grossnickle 1978) found that late instar *Mysis* guts contained larger diatom frustules and more microcrustacean remains than the guts of smaller *Mysis*. In the euphausiids increased carnivory with increasing predator size has often been reported (Mauchline 1960, 1966; Fisher and Goldie 1959). Increased carnivory with increasing predator size is a reflection of the ability of larger predators to capture and handle large, mobile, food particles. This ability may or may not be associated with increased use of a raptorial feeding mode.

In addition, these experiments showed consistent selectivity for specific prey types out of proportion to their abundance or size. Despite its intermediate size and relatively high abundance, *Diaptomus* was consistently eaten at lower rates than other prey types. In addition, *Daphnia* was eaten at greater rates than copepods for most predator size-classes (expt. 2 and 5). Because prey responded to disturbances created by a pipette and an approaching *Mysis* in similar ways, a subjective evaluation of prey escape response efficiency was made based on hundreds of zooplankton captures with a pipette. Cladocerans were more easily captured than copepods and *Epischura* had a less vigorous escape response than *Diaptomus*. These differences in prey avoidance responses, which agree with results reported by Drenner et al. (1978) and Confer and Blades (1975), may account for many of the observed selectivity patterns. From a series of single and two-prey feeding trials Grossnickle (1978) found that the order of *Mysis*' preference for four prey types was *Daphnia pulex* > *Cyclops bicuspidatus thomasi* > *Diaptomus* spp. > *Limnocalanus macrurus* which agrees, in general, with our results. He also emphasized the importance of differences in prey escape mobility in producing the observed *Mysis* feeding patterns. Because large *Mysis* were often observed carrying and feeding on dead fish larvae (length = 7.5–10.3 mm), efficient prey escape responses were also probably responsible for a lack of mysid predation on similarly sized live fish larvae (S. D. Cooper and C. R. Goldman unpublished data). Although *Kellicottia* and *Bosmina* were easily captured with a pipette, large *Mysis* did not feed on them at high rates. Perhaps the "dead-man" escape response (of *Bosmina*), spines (of *Kellicottia*), small size, or hard integument of these prey items reduced the efficiency with which they were captured, handled, and ingested by *Mysis* (Kerfoot 1977; Li and Li 1979).

The importance of prey availability should also be considered. The differences in feeding habits reported for *Mysis* collected from different lakes were probably a reflection of the plastic, opportunistic nature of *Mysis*' feeding, and the availability of different types of food (Lasenby and Langford 1973; Bowers and Grossnickle 1978; Stalberg 1933; Grossnickle 1978; J. Rybock, Fugro Inc., Seattle, WA, personal communication). For example, Bowers and Grossnickle (1978) emphasized the importance of filamentous diatoms in the

diet of Lake Michigan *Mysis* while J. Rybock (personal communication) found that copepod remains were the most common item in Lake Tahoe *Mysis* guts. Filamentous diatoms are quite abundant in Lake Michigan but virtually absent in Lake Tahoe (N. E. Grossnickle personal communication; W. Vincent, Department of Scientific and Industrial Research, Freshwater Sect.-Ecology Div., Taupo, New Zealand, personal communication); consequently copepods may be the only appropriately sized food available to Lake Tahoe *Mysis*. The differences in the diets of *Mysis* collected from Stony Lake, Ontario, and Char Lake, N.W.T., can be attributed to the relative availability of different types of food (Lasenby and Langford 1973). Diel and seasonal feeding patterns in Clupeoids and mysids can also be explained in terms of food availability (Lasenby and Langford 1973; Fisher and Goldie 1959; Mauchline 1960, 1966; Ponomareva 1955, 1971; Hu 1978).

The explanations of predator selectivity cited here were mainly concerned with components affecting predator capture efficiency; however, encounter frequencies are undoubtedly quite important in dilute natural environments (Gerritsen and Strickler 1977). The large prey size selectivity of the largest predators may have been a product of higher swimming speeds of the larger prey which resulted in higher predator-encounter frequencies (Swift and Fedorenko 1975). In addition the preference for *Diatomus* males over *Diatomus* females may have been due to higher swimming speeds of the *Diatomus* males (Maly 1970). The changes in prey selectivity for starved versus unstarved *Mysis* may have been a function of differential activity patterns for starved versus unstarved predators. The more active starved *Mysis* spent more time swimming in the water column and the less active "unstarved" *Mysis* spent more time sitting on the container bottom. It was possible that the microdistribution of prey types in the experimental containers relative to the activity patterns of the predators could account for the patterns observed for starved versus unstarved *Mysis*. The increase in total consumption rates with increasing predator size and starvation saturation may have been due to concomitant increases in predator swimming speeds.

It should be noted that *Mysis* in Lake Tahoe migrate into strata containing zooplankton for only about 6-8 h each night (M. Morgan, Port Aransas Marine Lab., Port Aransas, TX, personal communication; see also Beeton 1960). Consequently while consumption and clearance rates are reported here as units "per day," *Mysis* feeding rates in the natural environment do not approach these values. Also, these diel migration patterns of *Mysis* make considerations of the vertical diel distributions of prey species extremely important. Because the thermocline acts as a barrier to the nightly upward migration of *Mysis* in Lake Tahoe, epilimnetic zooplankton species, such as *Epischura*, may occupy a warmwater refuge from mysid predation in the summer months (M. Morgan personal communication; Richerson 1969).

In summary, the prey selectivity patterns of *Mysis* are largely a function of prey availability, prey size, prey mobility, and prey escape response efficiency. The relative importance of each of these characteristics varies from prey to prey type and from situation to situation. Total consumption rates, on the other hand, are positively correlated with predator size and prior starvation duration.

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