Selective predation by *Neomysis mercedis* in Lake Washington¹

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Abstract

Feeding experiments and examination of gut contents show that *Neomysis mercedis* is an effective predator on zooplankton in Lake Washington. *Daphnia* is consistently preferred to other prey; *Diaptomus* and *Cyclops* copepodids and nauplii are always underrepresented in mysid diets. This pattern of selectivity is consistent with the hypothesis that a large population of *Neomysis* formerly excluded *Daphnia* from the lake.

Because of their strong size selectivity and high feeding rates, vertebrate predators (especially visually feeding fish) are often considered the primary threat to freshwater zooplankton. The low feeding rates of the blindly foraging invertebrate planktivores led Hall et al. (1976) to doubt that invertebrate predation alone causes the extinction of populations of zooplankton. The invertebrates, however, are usually more abundant than fish, and there is growing appreciation of their potential significance to total predation pressure (Lane 1979).

Evidence is accumulating that freshwater mysids may be potent predators, with especially strong effects on cladoceran populations. Zyblut (1970) and Rieinan (1977) reported suppression of *Daphnia* coincident with the growth of introduced populations of *Mysis relicta* in Kootenay Lake and Lake Pend Oreille, and Goldman et al. (1979) believed that *Mysis* was at least partly responsible for the disappearance of *Daphnia* and *Bosmina* from Lake Tahoe. Several workers have shown that *Mysis* can prey effectively on zooplankton (Lasenby and Langford 1973; Grossnickle 1978; Rybock 1978).

In Lake Washington (Seattle), the recent success of *Daphnia* after decades of scarcity may be related to changes in mysid predation; various hypotheses to ex-

plain the long term change in abundance of *Daphnia* have been considered by Edmondson (1979). The abundance of *Neomysis mercedis* declined precipitously in the mid-1960s, and, with the increase in water transparency accompanying de-eutrophication, there has been a tendency for more of the mysids to stay in deep water by day (Fig. 1; see also Eggers et al. 1978). The reduction in *Neomysis*, probably caused by changes in fish predation, preceded the gradual re-establishment of *Daphnia* that began in the early 1970s (Edmondson 1979), but there is a lag of roughly 10 years between the mysid decline and the first appearance of dense populations of *Daphnia* in Lake Washington. Inhibitory effects of the blue-green alga *Oscillatoria* could possibly explain the suppression of *Daphnia* during this period (W. T. Edmondson pers. comm.).

Little information is available on the feeding of *Neomysis*, which is superficially similar to, although somewhat smaller than, *Mysis*. Examining gut contents of estuarine populations, Wilson (1951) found copepod and mysid remains along with other plant and animal material, and Kost and Knight (1975) reported mostly "detritus and diatoms," with occasional animal fragments. *Neomysis* in the Sacramento River estuary is omnivorous, but predation on rotifers and copepods accounts for most of the energy ingested (Siegfried and Kopache 1980). If the change in the Lake Washington zooplankton is to be explained by mysid predation, it is necessary to demonstrate that *Neomysis* is a capable planktivore and

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Fig. 1. Upper panel. Annual average abundance of *Neomysis mercedis* in Lake Washington. ●—Average densities for the 58-m water column calculated from daytime Clarke-Bumpus hauls taken by the staff of W. T. Edmondson. ○—Data from an entirely independent study using a midwater trawl in nocturnal sampling (Eggers et al. 1978). Lower panel. Daytime vertical distribution of *Neomysis* indicated by ratio of population density in top 20 m to that in deeper layer, from Clarke-Bumpus data.

that *Daphnia* is more vulnerable than the other zooplankters, whose abundances did not change with the mysid population. Here I examine food selection by *Neomysis*, using information from feeding experiments and analyses of gut contents.

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Methods

I sampled at a station 20 m deep on the west side of the Madison Park trench in

Lake Washington (inshore from the Madison Park station in fig. 1 of Shapiro et al. 1971). Mysids were collected with a small epibenthic dredge (similar to that pictured in Pennak 1978, p.771; 520-cm² mouth area, 900- μ m mesh) and were either preserved immediately in 10% Formalin or transported to the laboratory in jars ($\approx$ 4 liters) of surface water. Zooplankton collections were made with a 12.5-cm-diameter Clarke-Bumpus sampler with a 73- μ m-mesh net. The species of zooplankton referred to by genus below are the cladocerans *Daphnia thorata*, *Daphnia pulicaria*, *Diaphanosoma leuchtenbergianum*, and *Bosmina longirostris*; the copepods *Epischura nevadensis*, *Diaptomus ashlandi*, and *Cyclops bicuspidatus*; and the rotifer *Kellicottia longispina*.

Mysids and zooplankton were kept in filtered (Whatman GF/C) lake water for 1–2 days before feeding experiments. Feeding chambers were small glass jars (0.15–0.40 liter), each provided with one mysid and equal proportions of individually pipetted *Daphnia* and *Diaptomus*. (Pilot experiments showed that feeding rates increase with container size, but there was no discernible effect on electivities.) To minimize changes in prey availability during experiments, I used high prey densities (avg concn, 45–70·liter⁻¹) and short feeding periods (avg durations, 1.5–4.4 h). Control vessels lacking mysids were used to check on natural prey mortality; all containers were kept in complete darkness at 10°C. At the end of the trials the contents of the jars were poured through a 118- μ m-mesh screen and the animals washed into a Petri dish. Mysids were preserved in Formalin, and the prey remaining were examined and counted under a dissecting scope while still alive. Average sizes of prey used in the experiments were estimated by measuring specimens from controls: *Daphnia* from head to base of posterior spine and *Diaptomus* from head to end of caudal rami. Mysid sizes are expressed as total body lengths, measured from the apex of the rostrum to the apices of the telson.

Fig. 2. Remains of *Daphnia thorata* from a mysid stomach. Postabdomen, molar surfaces of the mandibles and parts of carapace and posterior spine are visible. Bar is 100 μ .

To account for depletion of prey during the feeding trials, I express the results as clearance rates (Gauld 1951):

$$F = \frac{v}{t}(\ln C_0 - \ln C_t)$$

where F is the clearance rate in liters per mysid per day, C_0 and C_t are the prey concentrations initially and at time t , and v is the volume of water per mysid.

The bulbous stomachs and straight intestines of preserved mysids were dissected out and teased apart in drops of glycerine; permanent mounts of the gut contents were examined under 100 $\times$. Found among clumps of material that might superficially be described as "detritus" were recognizable remains of prey organisms (Fig. 2). Characteristic fragments, identified to species by comparison with dissected specimens of Lake Washington zooplankton, were counted.

Two lines of evidence suggest that the prey remains I recognized in mysid stomachs accurately represent the actual diet. First, the efficiency of recovery of remains can be estimated by examining the gut contents of mysids used in short term feeding experiments. The ratio of prey consumption inferred from gut contents to actual consumption was lower for *Diaptomus* (median = 0.71) than for

Daphnia (median = 0.77), but the difference was not significant (Wilcoxon rank-sum, two-tailed $P > 0.4$). Second, if some prey are digested more rapidly than others, they would form a smaller proportion of the total remains found late in the digestive process (in the intestine) than early (in the stomach). A χ^2 -test comparing numbers of different prey (*Daphnia*, *Diaptomus*, *Cyclops*, rotifers) in the intestines and stomachs of a large sample of mysids showed no dependence between prey type and location in the digestive tract (56 mysids, 701 prey; $\chi^2 = 1.89$, 4 df, $P > 0.75$); none of the species was significantly underrepresented in the intestine. Thus, the available evidence on the representation of prey in gut contents fails to indicate any pronounced differences in recognizability or digestibility that would bias my evaluation of predator selectivity.

I calculated electivities by comparing gut contents to prey densities in the lake. The index I use is the standardized forage ratio (Chesson 1978). Selectivity for prey type i is given by

$$(r_i/p_i) / \sum_{i=1}^n (r_i/p_i)$$

where r_i is the relative occurrence of type i in the diet, p_i is the relative occurrence of i in the environment, and n is the total number of prey types. The index varies between 0 and 1 and provides a consistent assessment of preference over different regimes of prey availability, unlike some other commonly used electivity indices (Paloheimo 1979).

Because *Neomysis* stays on or near the lake bottom at 20 m during the day but migrates up at night into relatively plankton-rich strata, the assessment of prey availability is complicated. Two approaches to estimating electivities from gut contents were taken. In the first, I compared gut contents of mysids collected on the lake bottom in the morning to whole-water-column estimates of prey availability based on plankton hauls. In the second, I compared gut contents of mysids collected at night, off the bottom,

Table 1. Results of *Neomysis* feeding experiments. Prey are Lake Washington zooplankton, except for *Daphnia pulex* from Hall Lake. Median clearance rates (liters per mysid per day) are compared with a one-tailed Wilcoxon rank-sum test; probability of the aggregate of the four tests occurring by chance is <0.02 .

Mysid sizes (mm)	Prey	Avg prey size (mm)	Median <i>F</i>	<i>P</i>
10.9–12.3 (<i>n</i> = 6)	<i>Daphnia thorata</i> <i>Diaptomus ashlandi</i>	1.45 1.10	2.31 0.62	0.021
11.5–13.8 (<i>n</i> = 4)	<i>D. thorata</i> <i>D. ashlandi</i>	1.46 1.06	1.22 0.64	0.243
6.2–13.3 (<i>n</i> = 7)	<i>Daphnia pulex</i> <i>D. ashlandi</i>	1.40 0.96	0.93 0.53	0.16 < <i>P</i> < 0.19
9.4–12.7 (<i>n</i> = 9)	<i>Daphnia pulicaria</i> <i>D. ashlandi</i>	2.21 0.97	0.87 0.35	0.081

with prey densities in their immediate vicinity. The variability of the electivity indices derived from the nighttime collections was estimated with a Monte Carlo simulation (*see results*).

Results

Feeding experiments—Table 1 shows the results of four experiments in which *Neomysis* was given a choice between *Daphnia* and *Diaptomus*. The ranges of average ingestion rates were 0.4–1.1 *Diaptomus* and 0.8–3.1 *Daphnia* per mysid per hour; these rates, measured under artificial experimental conditions, should not be taken as estimates of natural feeding rates in the lake. Because of high variability in individual feeding behavior, a significant difference between prey-specific clearance rates was obtained in only one of the Table 1 trials. If the probabilities from these four independent tests are combined according to the method of Fisher (1970, p.99), we can reject the hypothesis of no discrimination between prey types ($\chi^2 = 19.57$, 8 df, $P < 0.02$).

Gut contents—Table 2 shows electivities calculated by comparing the gut contents of mysids collected on the lake bottom in the morning to prey densities estimated for the 20-m water column. Rybock (1978) found that copepod mandibles may persist in the stomachs of *M. relicta* for more than 10 h after cessation of feeding. Thus, the gut contents of mysids collected in the morning may well be a reasonable representation of the re-

sults of the previous night's foraging. Average prey densities for the 20-m water column are only a rough approximation to the actual prey densities encountered by the mysids, however; the extent and duration of the mysids' vertical migration the preceding night are obviously not known.

Daphnia is the most preferred item on all five dates (Table 2). *Diaptomus* and *Cyclops* copepodids are uniformly underrepresented in the diet, and copepod nauplii are almost never taken. If the "selection" between *Daphnia* and the other prey on the different dates is viewed as a series of independent Bernoulli trials, the binomial probability that *Daphnia* would be preferred on all five dates allows us to reject the hypothesis of indiscriminate predation (one-tailed $P = 0.031$).

I also estimated electivity by comparing the pooled gut contents of mysids collected at midnight about 2.5 m off the bottom with prey densities calculated for the 10–20-m layer (Table 3). Variability in individuals' feeding behavior and in the densities of plankton encountered contributes to variability in electivity indices derived from these collections. Both components of variability can be assessed (by examining individual guts and replicate plankton hauls), but they cannot be combined analytically to yield an estimate of the variance of the electivity index. I therefore used a distribution-sampling application of the Monte Carlo

Table 2. Standardized forage ratios for zooplankton prey, based on gut contents of morning-collected mysids and whole-water-column average prey densities. Mysid lengths and sample sizes indicated below dates. Dashes indicate prey type rare (<0.5 org·liter⁻¹) or absent.

Prey type	16 Jun 78 10.3–13.7 mm (n=11)	29 Aug 78 10.9–12.6 mm (n=10)	20 Sep 78 10.7–12.7 mm (n=12)	3 Nov 78 11.2–13.6 mm (n=13)	22 May 79 13.3–14.7 mm (n=13)
<i>Daphnia</i>	0.596	0.809	0.812	0.469	0.638
<i>Bosmina</i>	—	—	—	0.230	—
<i>Diaphanosoma</i>	—	—	0.051	—	—
<i>Epischura</i>	—	0.154	—	—	—
<i>Diaptomus</i>	0.113	0.024	0.010	0.098	0.034
<i>Cyclops</i>	0.291	0.013	0.010	0.008	0.091
nauplii	0	0	0	0.009	0
<i>Kellicottia</i>	0	—	0.117	0.187	0.238

method (Kleijnen 1974, p.10) to generate confidence intervals about the observed indices.

The input for the Monte Carlo simulation was derived from replicate plankton hauls and mysid guts from the nighttime collections. Ranges of prey densities from six plankton hauls over a 14-h period spanning the midnight mysid collections and ranges of numbers of prey found in individual guts for each date are shown in Table 3. Hypothetical underlying distributions of these quantities were constructed by estimating percentiles from the ordered observations (Snedecor and Cochran 1967, p.125) and extending the observed ranges of values by two (gut contents) or three (plankton hauls) standard deviations. Thus, the hypothetical distributions were on average 1.3 (gut contents) or 1.9 (plankton hauls) times as wide as the observed ranges. From these distributions a computer program randomly selected prey densities encountered and individual diets for appropriately sized mysid samples and calculated electivity indices for each prey type. I selected 5th and 95th percentiles of distributions generated by 500 iterations of this program as bounds for confidence intervals about the observed indices.

The observed standardized forage ratios with confidence intervals generated by the simulation are shown in Fig. 3. On both dates *Daphnia* is strongly preferred, although there is overlap with the confidence interval for *Bosmina* on 14 September. The ratios for *Cyclops* and *Diap-*

tomus copepodids are close to zero; copepod nauplii were not found in any of the guts, although they were numerically dominant in the plankton (Table 3). (It

Table 3. Densities of prey in the 10–20-m layer and numbers of prey in mysid guts for two midnight trips. The 22 May mysids were 13.3–14.7 mm long ($n = 17$); the 14 September mysids, 10.8–12.7 mm ($n = 16$).

Prey type	Mean density and range (org·liter ⁻¹)	Mean No. per mysid gut and range
22 May 79		
<i>Daphnia</i>	3.47 (2.52–4.65)	12.29 (4–29)
<i>Diaptomus</i>	10.98 (7.59–14.19)	0.94 (0–4)
<i>Cyclops</i>	4.81 (3.85–6.11)	0.54 (0–3)
nauplii	39.49 (32.58–42.98)	0 (0–0)
<i>Kellicottia</i>	4.71 (4.24–7.63)	1.23 (0–4)
14 Sep 79		
<i>Daphnia</i>	0.056 (0.039–0.087)	1.94 (0–5)
<i>Bosmina</i>	0.084 (0.046–0.233)	0.69 (0–3)
<i>Epischura</i>	1.09 (0.32–1.97)	2.13 (0–4)
<i>Diaptomus</i>	10.33 (9.85–15.65)	2.38 (0–7)
<i>Cyclops</i>	1.82 (1.40–2.97)	0.25 (0–3)
nauplii	32.49 (29.14–36.17)	0 (0–0)
<i>Kellicottia</i>	0.53 (0.41–0.90)	0.69 (0–3)

Fig. 3. Standardized forage ratios calculated from pooled gut contents of midnight-collected mysids and prey densities in the 10–20-m layer (Table 3 data). Error bars are 95% confidence intervals generated by computer simulation (see text).

might be argued that nauplii should be excluded from this analysis. Unlike other indices, however, the standardized forage ratios are not affected by inclusion of a common but uneaten prey; the value of the ratio indicating nonselective procurement of prey is all that is changed.)

The Fig. 3 confidence intervals should be regarded as rough indices of variability rather than as grounds for rigorous statistical comparison between prey species, since the standardized forage ratios are not independent. An index whose values for the various prey types will be mutually independent can be obtained by dividing the mean number of prey type i in the gut by the mean density of type i in the 10–20-m layer. Table 4 shows the behavior of this index in the same simulation used to generate the Fig. 3 confidence intervals. The strong disparity between *Daphnia* and the other prey persists; it is not an artifact of the interdependence of the forage ratios.

To examine the effects of predator size on prey selection, I analyzed the gut contents of a broad size range of *Neomysis* collected on 3 November 1978 and calculated electivities using a single, whole-

Table 4. Ratio of mean number of prey per gut to mean density in 10–20-m layer for prey species in nighttime collections [$(\text{org} \cdot \text{gut}^{-1}) : (\text{org} \cdot \text{liter}^{-1}) = (\text{liters} \cdot \text{gut}^{-1})$]. Confidence intervals were generated by simulation.

Prey type	Observed ratio (liters · gut ⁻¹)	95% confidence interval
22 May 79		
<i>Daphnia</i>	3.54	2.08–6.43
<i>Diaptomus</i>	0.09	0.04–0.19
<i>Cyclops</i>	0.11	0.05–0.22
nauplii	0	0–0
<i>Kellicottia</i>	0.26	0.11–0.61
14 Sep 79		
<i>Daphnia</i>	34.64	17.35–108.2
<i>Bosmina</i>	8.21	2.68–42.69
<i>Epischura</i>	1.95	0.85–11.63
<i>Diaptomus</i>	0.23	0.13–0.49
<i>Cyclops</i>	0.14	0–0.52
nauplii	0	0–0
<i>Kellicottia</i>	1.31	0.54–3.46

water-column assessment of prey availability (Table 5). With this division of the mysids into three arbitrary size groups, there is a significant dependence of the nature of the diet on predator size (*Cyclops* and nauplii data lumped to satisfy the criteria for expected cell counts of Snedecor and Cochran 1967, p. 241; $\chi^2 = 20.87$, $df = 8$, $P < 0.01$). In spite of this heterogeneity, *Daphnia* is still “preferred” by all sizes of *Neomysis*. Further influences of predator size on the diet are considered in a detailed examination of size selection on *Daphnia* by *Neomysis* (Murtaugh in press).

Discussion

The assessment of preference from gut contents depends critically on the accuracy of the estimate of available prey. The difference between the 22 May 1979 electivity estimates based on midnight collections and local (10–20 m) prey densities (Fig. 3) and those derived from morning samples and whole-water-column averages (Table 2) illustrates this dependence: because *Daphnia* was concentrated in the top 10 m, the midnight index for *Daphnia* is higher, and the indices for the other prey are lower, than the corresponding morning indices.

Table 5. Numbers of prey in pooled mysid stomachs (top number) and standardized forage ratios (bottom number) for three size groups of mysids collected on morning of 3 November 1978. Whole-water-column estimates of prey densities were used in calculating electivities, with rare prey types ($<0.5 \text{ org} \cdot \text{liter}^{-1}$) excluded.

Prey type	Mysid size class*		
	Small (n=31)	Medium (n=16)	Large (n=13)
<i>Daphnia</i>	41 0.413	47 0.459	70 0.469
<i>Bosmina</i>	5 0.093	4 0.072	18 0.230
<i>Diaptomus</i>	7 0.174	4 0.096	6 0.098
<i>Cyclops</i>	1 0.004	4 0.016	3 0.008
nauplii	0 0	0 0	3 0.009
<i>Kellicottia</i>	48 0.316	56 0.358	42 0.187

* Small, 3.4–6.9 mm; medium, 7.4–10.7 mm; large, 11.2–13.6 mm.

Roughly 72% of the 22 May mysid population and 99% of the 14 September population were below 10 m during the midnight sampling, so the 10–20-m layer seemed a reasonable delineation of the mysids' food environment. Yet, since the gut-content specimens were caught at 17.5 m, it might be argued that a more restricted domain should be assumed. Finer scale plankton sampling on 14 September revealed *Daphnia* densities that seemed too low to account for the numbers of *Daphnia* found in mysid stomachs. When calculated on the basis of densities at 15–20 m, the standardized forage ratio for *Daphnia* would have been 600 times larger than the *Diaptomus* index (instead of 150 times in the 10–20-m computation) and the average number of *Daphnia* found in the mysid stomachs would represent the contents of 140 liters of lake water (instead of 35). Perhaps, as Pearre (1973) proposed for his population of chaetognaths, the mysids are taking short feeding excursions into the upper waters, returning to deep water when satiated. The problems of assessing the exact food availability for

such a migrator would be formidable. Without information on the extent and timing of the mysids' vertical migration, it is impossible to know the accuracy of the various electivity estimates, yet the consistency of results from two methods based on different assumptions (Table 2, Fig. 3) suggests that the observed preference hierarchies are meaningful.

Differences in recognizability or digestibility of remains have not been ruled out for all the prey species considered in the gut-content analyses. Of particular interest is the apparent scarcity of nauplii in mysid diets; if real, it would imply a considerable refuge from predation for the copepods. Rybock (1978) and Siegfried and Kopache (1980) also rarely found naupliar remains in mysid stomachs, and, significantly, Rybock had "little success" feeding nauplii to *Mysis* in the laboratory.

The apparent ranking of prey by *Neomysis* in Lake Washington can be compared to that reported for *M. relicta* in other lakes. Grossnickle (1978) found in laboratory feeding experiments that Lake Michigan *Mysis* select *Daphnia* over both *Cyclops* and *Diaptomus*. Rybock (1978), examining gut contents of *Mysis* from Lake Tahoe, concluded that *Epischura* is strongly preferred to *Diaptomus* and that *Bosmina* is probably selected over both copepods. These findings are similar to the trends for *Neomysis* (Table 2, Fig. 3), but conclusive comparisons among the noncladoceran prey await the analysis of samples for which *Daphnia* does not so dominate the electivity calculations.

My laboratory observations suggest that the feeding mechanism of *Neomysis* is similar to that described in great detail for the marine *Hemimysis* by Cannon and Manton (1927). Small particles may be filtered from currents produced by the thoracic limbs, and large food masses are grasped by the thoracic endopodites and mandibular palps. The susceptibility of different prey to mysid predation is not simply a function of size; for example, the rotifer *Kellicottia* (probably obtained by filter-feeding) and the small cladoceran

Bosmina seem to be preferred to the much larger copepods, *Diaptomus* and *Cyclops*.

The overwhelming "preference" for *Daphnia* probably does not involve active choice by the mysid but can be explained by strictly mechanical considerations of the predator's feeding method and the prey's behavior. Pastorok (1978) found that *D. pulicaria* swims about twice as fast as *Diaptomus franciscanus* of the same size; the resultant difference in encounter rates with a predator could cause "selection" for the cladoceran. Gerritsen and Strickler (1977), however, argued that, for a predator that moves rapidly relative to its prey, as does *Neomysis*, differences in prey swimming speed will have little effect on encounter probabilities. Several workers have tested the ability of different kinds of zooplankton to escape currents produced by suction-intake tubes; Drenner et al. (1978), for example, found that *Diaptomus* and *Cyclops* were entrained significantly less often than *Daphnia*. Perhaps the effectiveness of the prey escape response is the most important factor affecting susceptibility to mysid predation.

Whatever the explanation for the "preference," it is clear that *Daphnia* is more vulnerable than the other Lake Washington zooplankton to predation by *Neomysis*. The exact role of *Neomysis* in the long term changes in abundance of *Daphnia* in Lake Washington remains to be determined, but the pattern of prey selection reported here is consistent with the hypothesis that intense predation by mysids formerly excluded the cladocerans from the lake. When combined with circumstantial evidence on the effects of introductions of the similar *M. relicta* into other lakes, the information on *Neomysis* in Lake Washington suggests that freshwater mysids may be potent plankton predators and that populations of *Daphnia* are especially susceptible to their control.

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