

## ***In situ* predatory behavior of *Mysis relicta* in Lake Michigan\***

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### **Abstract**

Selectivity coefficients ( $W'$ ) and predation rates on Lake Michigan zooplankton were determined for *Mysis relicta* during spring through fall using an *in situ* method.  $W'$  values indicated the following ranked order of prey preference: Cladocera > copepod copepodites and copepod nauplii > adult diaptomids and cyclopoids. With few exceptions,  $W'$  values for different prey categories remained fairly constant despite greatly changing relative abundances of prey. Predation rates and prey selectivity were similar in most cases to those determined in laboratory studies. Ingestion rates (percent dry body weight  $\cdot$  day<sup>-1</sup>) were correlated to total prey biomass ( $r = 0.38$ ) and to effective prey biomass ( $r = 0.85$ ), where the weighting factors were overall mean selectivity coefficients for the different prey categories. This result suggested that seasonally varying composition of prey caused much of the variation in ingestion rates among experiments. Feeding trials performed at the same depth with daytime and nighttime assemblages of zooplankton indicated that Cladocera may escape heavy *Mysis* predation at night by migrating from the metalimnetic-hypolimnetic interface into the epilimnion.

### **Introduction**

Predacious zooplankton sometimes play an important dual role in the structuring and function of planktonic communities because of their selective feeding on zooplankton and as preferred prey to planktivorous fish. A good example of a zooplankton having this dual role is *Mysis relicta*, the opossum shrimp. Long recognized as an important fish food (Tattersal & Tattersal 1951; Larkin 1948; Rawson 1961), *Mysis* is one of few crustacean zooplankton stocked in lakes to enhance fish production (Gosho 1975). From these introductions we have learned of the importance of mysid predation on

community structure through the decline of cladoceran populations in these lakes (Zyblut 1970), most notably in Lake Tahoe (Richards *et al.* 1975; Goldman *et al.* 1979). Although *Mysis* is an omnivore (Lasenby & Langford 1973; Grossnickle 1978; Bowers & Grossnickle 1978), the above observations have recently stimulated investigations of mysid predatory behavior on zooplankton (Rybock 1978; Grossnickle 1978; Cooper & Goldman 1980). Coupled with supportive laboratory experiments, Rybock's (1978) study of mysid gut contents indirectly estimated feeding selectivity and predation rates on the natural prey assemblage in Lake Tahoe. Grossnickle's (1978) and Cooper & Goldman's (1980) laboratory efforts for Lake Michigan and Lake Tahoe prey respectively directly estimated prey selection and feeding rates on multispecies assemblages using concentrated prey. These predation studies indicated higher predation rates on

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cladoceran prey than on copepods. *Neomysis mercedis*, a slightly smaller mysid, behave similarly in Lake Washington (Murtaugh 1981a, b). These patterns were correlated to mysid hunger, prey density, prey escape behavior and prey size.

Our efforts focused on two goals. First, we wished to look at relationships of selectivity and predation rates as functions of a naturally changing zooplankton prey assemblage. With our method mysids were released into a totally natural prey environment circumventing problems encountered with laboratory experiments and gut contents analysis (see Vanderploeg *et al.* 1982). Our second goal was to assess the possible cladoceran benefits from their own diurnal vertical migration in avoiding *Mysis* predation. In Lake Michigan, during daylight hours *Mysis* remains well below the thermocline while Cladocera reside in metalimnetic and epilimnetic strata (Beeton 1960; Wells 1960). At night *Mysis* ascends into thermocline depths while significant numbers of cladocerans migrate into the epilimnion out of the reach of *Mysis*. Two daytime experiments were performed to provide initial observations regarding this idea.

### Materials and methods

All experiments were performed at a 60-m-deep sampling station 9.6 km west of the harbor entrance to Grand Haven, Michigan. The depth placement and feeding time duration of the night experiments were chosen to reflect the spatial and temporal pattern of feeding dictated by the diurnal vertical migration pattern of *Mysis* in Lake Michigan. A nocturnal migrator (Hutchinson 1967) during the summer, *Mysis* leave the lake bottom or deeper strata in very deep waters near sunset and ascend for about an hour to the meta-hypolimnetic interface (Beeton 1960; Bowers & Grossnickle 1978) at approximately 10–20 m where they remain until the morning descent, approximately an hour before sunrise. Each evening of an experiment a temperature profile was taken with an electronic bathythermograph to locate this meta-hypolimnetic interface. All the trials were performed for approximately 6 hours to approximate the time period *Mysis* remained at this depth (Bowers & Grossnickle 1978). One hour after sunset, 50 m vertical tows ( $0.5 \text{ m} \cdot \text{s}^{-1}$ ) with a 1.5 m diameter plankton net

(#000 mesh, 1050  $\mu\text{m}$  aperture) captured 10–30 of the vertically ascending mysids. The 2 l closed plankton bucket was larger than normally fitted to this net to reduce crowding. They were immediately diluted into an 8 l plastic tub containing fresh lake water from the hypolimnion screened through an 80  $\mu\text{m}$  Nitex net. Each nightly experiment consisted of two sets of traps each having one control and one experimental trap. Five fourth or fifth instar female *Mysis* approximately 14–17 mm in length (Morgan & Beeton 1978) were introduced into the 150 ml dispenser of the experimental trap; only screened water was introduced into the dispenser of the control trap.

Five mysids per experimental chamber were chosen to satisfy two conflicting requirements. Sufficient predators must be present to ensure measurable feeding, while concurrently minimizing concentration induced stress. Mysid densities range from  $30 \cdot \text{m}^{-3}$  (Grossnickle 1978) to  $140 \cdot \text{m}^{-3}$  (Beeton 1960) at thermocline depths in Lake Michigan. Five mysids, or  $166 \cdot \text{m}^{-3}$ , was the chosen compromise.

After a set was loaded, it was activated at the meta-hypolimnetic interface. The set was then suspended from plastic spherical floats and set free to drift. Marker buoys with flashing red lights marked the locations of the traps. Approximately 20 min elapsed between activating the two sets of traps. At the end of the feeding period, the traps' contents were drained through a catch bucket covered with 53  $\mu\text{m}$  Nitex screen and preserved in 10% buffered formalin.

Prey populations were divided into six categories: Cladocera, calanoid copepod adults, cyclopoid copepod adults, calanoid copepodites, cyclopoid copepodites, and copepod nauplii. Prey categories were usually not further divided for predation parameter estimates, since instar specific sample counts would have been too low for statistical evaluation. With the exception of the nauplii, all the groups were totally counted to eliminate subsampling error. Naupliar densities were estimated by reducing the sample to 25 ml and counting 5 ml subsamples until a total of 400 individuals were counted.

When sample counts were below 16 prey for a prey category in the control trap, predation parameters were not calculated. A count of 16 or less would imply a large error in predation parameters

(Vanderploeg 1981; Vanderploeg *et al.* 1982). Clearance ( $F_i$ ) and predation ( $P_i$ ) rates were estimated from Gauld's (1951) and Frost's (1972) equations respectively. The daily ration,  $R_i$  % predator body wt.  $\cdot$  day<sup>-1</sup>, was estimated by the product of  $P_i$  times the dry weight of the prey divided by the *Mysis* weight. Prey weights used were from Hawkins & Evans (1979); mysid weights were calculated from the length-weight relationship given by Morgan & Beeton (1978). The selectivity index,  $W'_i$ , was estimated from clearance rates by the equation given by Vanderploeg & Scavia (1979). Arguments for the use of this index are summarized in Vanderploeg (1981) and Vanderploeg *et al.* (1982).

During September, daytime experiments were initiated at 1200 hours solely to contrast *Mysis* prey selection on the daytime prey assemblage to the nighttime assemblage at the same depth. Approxi-

mately 20 mysids were captured in the early morning between 2400 and 0100 hours and held in the dark at 5 °C in three 20 l polyethylene carboys containing hypolimnetic water. Instead of performing these trials in the lake at ambient light intensities, a deck-top incubator was used. This chamber held both sets of traps in the dark at a controlled temperature. The traps were again activated at the meta-hypolimnetic interface where temperatures were 6° to 7 °C.

## Results

The experiments were performed during one week cruises in June, August and September, 1979 (Table 1). On the June cruise the prey assemblage was dominated by all stages of diaptomid copep-

Table 1. Mysid predation on the natural zooplankton assemblage in Lake Michigan on the June, August and September, 1979 cruises. All predation parameters are means of the mean results of N duplicate experiments ( $\pm$  SE, N = 3 June, N = 4 August and N = 2 September) where  $D_i$  = prey density (Number  $\cdot$  l<sup>-1</sup>);  $F_i$  = clearance rate (l  $\cdot$  mysid<sup>-1</sup>  $\cdot$  day<sup>-1</sup>);  $P_i$  = predation rate (prey eaten mysid<sup>-1</sup>  $\cdot$  day<sup>-1</sup>); and  $R_i$  = daily ration (% dry wt. of *Mysis*  $\cdot$  day<sup>-1</sup>). A dash for mean cruise estimates indicates prey group not present in sufficient numbers (16 per trap) to estimate predation. The  $W'_i$  values for mean of experiments were calculated from mean clearance rates.

Month of experiment	Dates, Temperatures, depths	Prey category	$D_i$	$F_i$	$P_i$	$R_i$	$W'_i$
June	4, 5, 6 5.0°, 6.0°, 7.7 °C 10.0 m	Cladocera	0.00(0.00)	-	-	-	-
		Diaptomid adults	3.42(0.17)	2.05(0.74)	9.75(1.49)	0.75(0.17)	0.23
		Cyclopoid adults	0.13(0.08)	-	-	-	-
		Copepod nauplii	56.93(4.58)	2.83(0.16)	119.20(22.54)	0.73(0.16)	0.31
		Diaptomid copepodites	3.95(0.38)	9.02(0.01)	27.83(3.64)	1.15(0.16)	1.00
		Cyclopoid copepodites	0.70(0.07)	5.93(3.77)	3.57(2.31)	0.08(0.05)	0.66
		August	28, 29, 30, 31 7.5°, 7.0° 10.0°, 11.0° 20.0, 20.0, 20.0, 21.0 m	Cladocera	2.75(0.31)	20.88(2.10)	39.09(5.97)
Diaptomid adults	3.00(0.21)			0.96(0.66)	2.08(1.46)	0.76(0.20)	0.03
Cyclopoid adults	0.50(0.03)			0.00(0.00)	0.00(0.000)	0.00(0.00)	0.00
Copepod nauplii	29.79(1.19)			7.06(0.97)	172.13(24.64)	1.30(0.18)	0.25
Diaptomid copepodites	1.44(0.16)			2.72(1.79)	0.29(0.22)	0.01(0.01)	0.10
Cyclopoid copepodites	4.94(0.14)			8.14(1.12)	33.14(3.43)	0.79(0.08)	0.29
September 2400h EDT	27, 29 7.0°, 6.0 °C 20.0, 22.0 m			Cladocera	0.60(0.36)	29.35(9.75)	19.05(0.75)
		Diaptomid adults	14.50(2.12)	1.55(0.36)	19.80(3.14)	1.40(0.20)	0.05
		Cyclopoid adults	0.19(0.08)	-	-	-	-
		Copepod nauplii	30.85(5.75)	6.35(1.27)	163.68(39.50)	1.28(0.30)	0.21
		Diaptomid copepodites	3.30(0.88)	16.20(4.43)	31.80(3.82)	1.35(0.15)	0.55
		Cyclopoid copepodites	1.08(0.43)	12.65(5.95)	8.03(5.01)	0.20(0.12)	0.43
		September 1200h EDT	27, 29 7.0°, 6.0 °C 20.0, 22.0 m	Cladocera	5.45(0.85)	22.25(4.91)	74.38(9.16)
Diaptomid adults	1.13(0.14)			0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00
Cyclopoid adults	0.80(0.08)			2.56(1.64)	1.80(1.55)	0.08(0.11)	0.12
Copepod nauplii	9.95(0.78)			5.80(0.54)	50.30(2.88)	0.38(0.02)	0.26
Diaptomid copepodites	5.58(0.69)			4.13(1.43)	21.03(6.70)	0.88(0.28)	0.19
Cyclopoid copepodites	5.20(0.35)			5.03(1.17)	23.38(5.99)	0.60(0.15)	0.23

ods, naupliar instars in particular. The adult diaptomids were chiefly composed of *Diaptomus ashlandi* and *Diaptomus minutus*. Cladocera were absent, while adult cyclopoids (*Cyclops bicuspidatus thomasi*) were present only in very low numbers. Clearance rates and selectivity coefficients indicated the following order of preference: diaptomid copepodites, cyclopoid copepodites, nauplii and diaptomid adults. Predation rates were highest on diaptomid nauplii, mostly N1 and N2 states, mainly due to their abundances. Diaptomid copepodites, CIII and CIV stages, had the second highest selectivity coefficients. Only a few adults of *Diaptomus ashlandi* and *Diaptomus minutus* were consumed. Also during this period large numbers of filamentous diatoms, *Melosira*, *Fragilaria* and *Tabellaria*, were observed in the samples. Examination of fecal pellets from the experimental traps indicated that *Mysis* was consuming appreciable numbers of these phytoplankters.

In August all prey groups were present. Nauplii and cyclopoid copepodites were the most abundant prey. Clearance rates and selectivities were always highest on the Cladocera followed by cyclopoid copepodites or nauplii. Again *Mysis* consumed nauplii, N3 and N4 stages, at the highest rates. Cyclopoid copepodites and Cladocera had the second highest predation rates followed by adult diaptomids. Daily food rations were highest for nauplii and Cladocera. Approximately half of the cladoceran group was *Bosmina longirostris* with the rest divided between *Daphnia retrocurva*, *Daphnia galeata mendotae* and a few *Leptodora kindtii*. When counting the survivors in the experimental traps only large *Daphnia* and *Leptodora* remained indicating a greater vulnerability of *Bosmina* to mysid attacks. The mean clearance rate for *Bosmina* was  $32.10 \text{ l} \cdot \text{mysid}^{-1} \cdot \text{day}^{-1}$ , while the combined mean rate for *Daphnia retrocurva*, *Daphnia galeata mendotae* and *Leptodora kindtii* was  $13.42 \text{ l} \cdot \text{mysid}^{-1} \cdot \text{day}^{-1}$ . The mean selectivity coefficient for *Bosmina* was 0.71 and significantly greater than the 0.29 for the *Daphnia* and *Leptodora* (one tail t-test,  $N = 4$ ,  $P < 0.01$ ).

In September diaptomid adults and nauplii dominated the prey assemblage, while Cladocera were present on only one evening and even then at a low density. Clearance rates were highest on Cladocera with the same *Bosmina* and *Daphnia* species above being the major victims. Interestingly, clearance

rates for diaptomid copepodids were much higher on the night that Cladocera and cyclopoid copepodids were absent. Predation rates were highest on the nauplii and approximately equal for the other prey groups. Daily food rations were equally divided among the chosen prey. Selectivity coefficients for the cladocerans, *Daphnia* and *Bosmina*, were still highest.

The two daytime experiments in September make an interesting contrast to the two nighttime experiments. Performed at approximately the same depth as the nighttime trials, the purpose of the daytime trials was to observe the possible effects of diurnal vertical migration by both *Mysis* and prey relative to mysid feeding behavior. *Daphnia* are epilimnetic migrators in Lake Michigan. Scattered throughout the metalimnion and epilimnion during the day, these cladocerans concentrate in the upper surface strata at night in summer (Wells 1960). The previous studies cited earlier and our own August results indicated a mysid's preference for *Daphnia* and *Bosmina*. The daytime trials would therefore contrast daytime predation with their normal nighttime feeding pattern.

The daytime assemblage collected at the meta-hypolimnetic interface was very different from the nighttime assemblage. Relative to the nighttime assemblage, diaptomid adult and nauplii densities decreased whereas Cladocera and cyclopoid copepodids increased. Mysid clearance rates remained about the same for Cladocera and nauplii and decreased for diaptomid copepodids, cyclopoid copepodids, and diaptomid adults. As a result of the increased density of Cladocera in the daytime assemblage, Cladocera became the most important prey in the diet. Copepod nauplii decreased in importance in the diet because of their lower density. Diaptomid copepodites decreased in the daytime diet because of the lower clearance rates on them. Diaptomid adults were an important part of the diet in the nighttime assemblage but were not preyed upon at the lower densities in the daytime assemblage. The zero clearance rate, however, for the daytime assemblage could be a statistical artifact, caused by the low number of prey in the traps. These results from the daytime experiments illustrate how completely prey assemblage changes may alter mysid predation rates and prey selection.

It is only possible to directly compare selectivity coefficients of experiments which include the most

avored prey, since selectivity coefficients are clearance rates normalized to the clearance rates of the favored prey. In Table 2, we give mean  $W'_i$  values calculated from the means for the August and September cruises. We were also able to calculate overall mean  $W'_i$  values using the June data, which did not include Cladocera, by assuming the ratio of  $W'_i$  values for Cladocera and other prey groups calculated for the August and September data would also hold for the June data if Cladocera were present. These overall mean  $W'_i$  values changed little by including the June data. The resulting order of prey preference in Table 2 was cladocerans, juvenile copepods, nauplii and adult copepods. However, only three groups were statistically different from each other: Cladocera, diaptomid and cyclopoid adults and copepodites, and nauplii (Student-Newman-Keuls test,  $P < 0.05$ , Sokal & Rohlf 1969).

The standard errors (SEs) of the selection coefficients given in Table 2 are a useful approach to consider the invariance of prey selection. Each prey group is composed of a large and diverse spectrum of prey with each specific instar having its own defense capabilities which would account for much of the observed variance. Two prey categories, cyclopoid adults and diaptomid copepodites, have relatively larger SEs. The cyclopoid SE is equal to the mean values. Part of the variance here could have been related to the small number of adults captured in the traps. The diaptomid copepodites are a diverse group including copepodite stages of at least four species, *Diaptomus minutus*, *Diaptomus ashlandi*,

*Diaptomus oregonensis* and *Diaptomus sicilis*. This diversity no doubt contributes to their large SE.

We were interested in using our data to evaluate the effective food supply concept (Vanderploeg & Scavia 1979; Bartrum 1980). This concept holds that ingestion rates on all prey categories is a simple function of the weighted sum of the biomass of all prey categories, where the weights are the  $W'_i$  values. Our results with the natural prey assemblages are particularly suitable for this purpose because the *Mysis* used were about the same size and because temperature did not vary greatly. Ingestion rates (percent dry body weight  $\cdot$  day $^{-1}$ ) were plotted against total prey biomass ( $\Sigma B_i$ ) and total effective biomass ( $\Sigma W'_i \cdot B_i$ ) where the weighting factors were the overall mean selectivity coefficients for the different prey categories (Fig. 1). Weighting the total

Table 2. Overall mean  $W'_i$  values calculated from cruise mean  $W'_i$  values. Because of the absence of a  $W'_i$  value for Cladocera in June, the unmodified (unnormalized) June  $W'_i$  data could not be averaged with those of other cruises. Normalized June data were calculated assuming: 1) if Cladocera were present they would have a  $W'_i$  value of 1; 2) the ratio of  $W'_i$  of diaptomid copepodites to the  $W'_i$  of Cladocera would be the same as that ratio given by the  $W'_i$  values for the mean of the Aug. + Sept. data in table (0.28/1.00); 3) the ratio of  $W'_i$  of diaptomid copepodites to  $W'_i$ 's of other taxa would remain the same in the presence of Cladocera.

Prey category	$\bar{X} \pm SE$ for Aug. + Sept.	Normalized June	$\bar{X} \pm SE$ for normalized June + Aug. + Sept.
Cladocera	1.00 $\pm$ 0.00	1.00	1.00 $\pm$ 0.00
Diaptomid adults	0.03 $\pm$ 0.01	0.06	0.04 $\pm$ 0.01
Cyclopoid adults	0.06 $\pm$ 0.06	—	0.06 $\pm$ 0.06
Copepod nauplii	0.24 $\pm$ 0.02	0.09	0.20 $\pm$ 0.04
Diaptomid copepodites	0.28 $\pm$ 0.14	0.28	0.28 $\pm$ 0.10
Cyclopoid copepodites	0.32 $\pm$ 0.06	0.18	0.28 $\pm$ 0.05

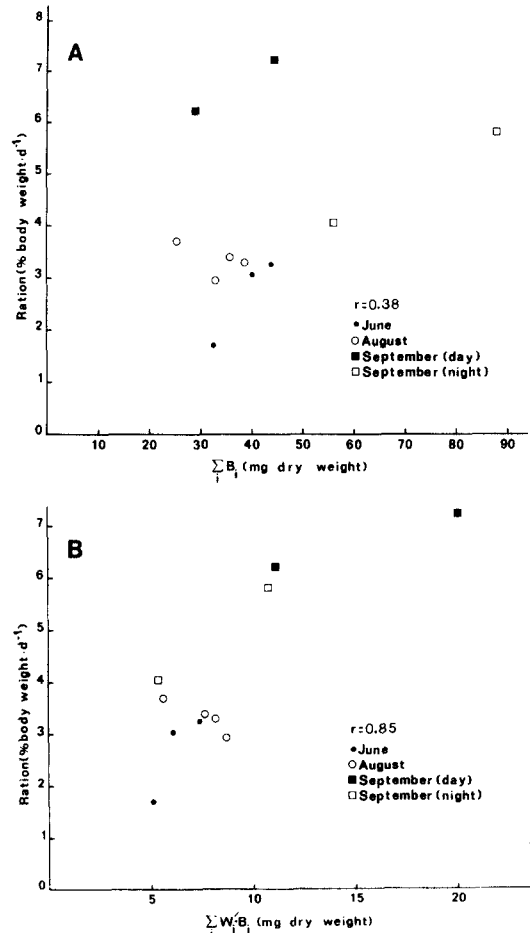


Fig. 1. A: The relationship between the daily ration ( $R_i$ ) of *Mysis relicta* and the total biomass of the prey assemblage. B: The relationship between the daily ration ( $R_i$ ) of *Mysis relicta* and the total effective biomass of the prey assemblage.

prey biomass resulted in a higher degree of association between food rations and food supply. The correlation coefficient increased from 0.38 (Fig. 1A) to 0.85 (Fig. 1B), suggesting that the concept of effective food supply is useful for, at least approximately quantifying the relationship between ingestion rate and food concentration. Variance in this relation is partially caused by time variance in the  $W'_i$ s and by the lack of consideration of algae as a food source.

On the assumption that total effective food concentration is below limiting concentration where rations reach a maximum level, we would expect plots of clearance rates for different prey categories as a function of their density to yield insight on possible changes in prey preference. That is, if there were no density-dependent effects on prey selection,

we would expect clearance rates to be constant. An obvious alternative possibility would be that clearance rates would increase for a prey category as its density increased. Figure 2 shows that clearance rates for Cladocera remained relatively invariant with increasing density, while the other prey categories surprisingly exhibited generally decreasing values of clearance with increasing prey concentration. This surprising result suggests that *Mysis* does not become more selective for a given prey when it is more abundant. Further insight comes from viewing the relationship between  $W'_i$  and relative abundance in August and September when all prey categories were present (Fig. 3). Our  $W'_i$  coefficients for Cladocera were always equal to 1. The other prey categories were quite variable over relative abundance, but no obvious trends are visible. Perhaps the best ex-

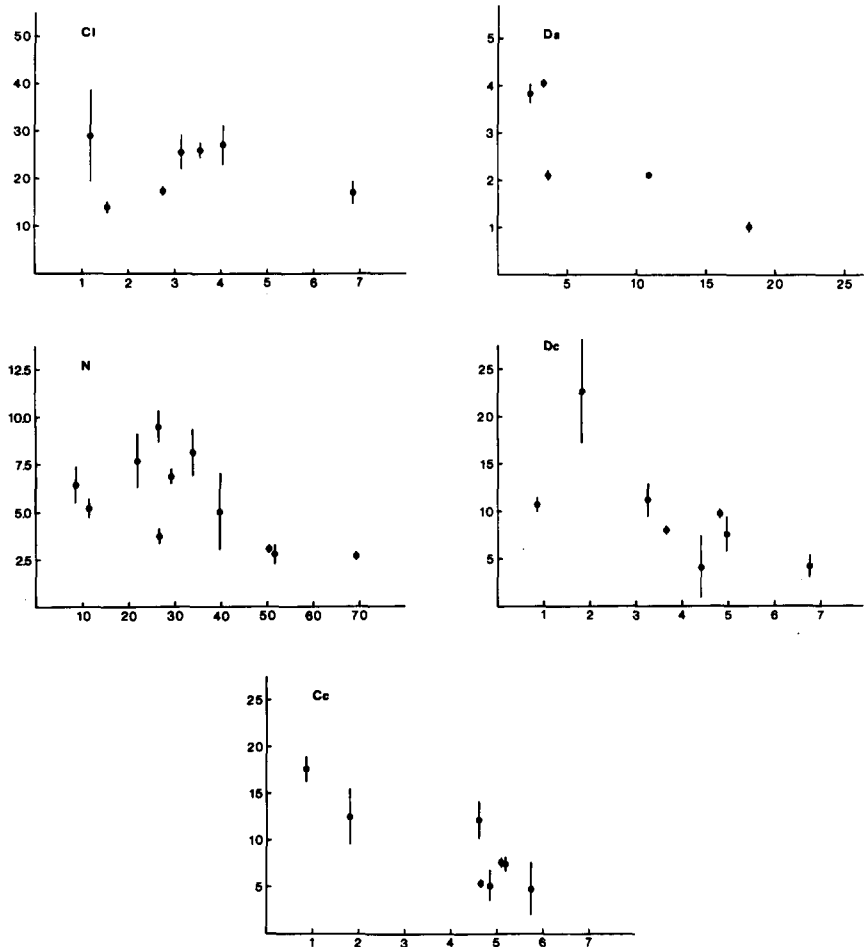


Fig. 2. The effect of prey density (abscissa, numbers  $\cdot l^{-1}$ ) on the clearance rate (ordinate,  $l \cdot mysid^{-1} \cdot day^{-1}$ ) of *Mysis relicta* where Cl = Cladocera, Da = diaptomid adults, N = nauplii, Dc = diaptomid copepodites and Cc = cyclopoid copepodites.

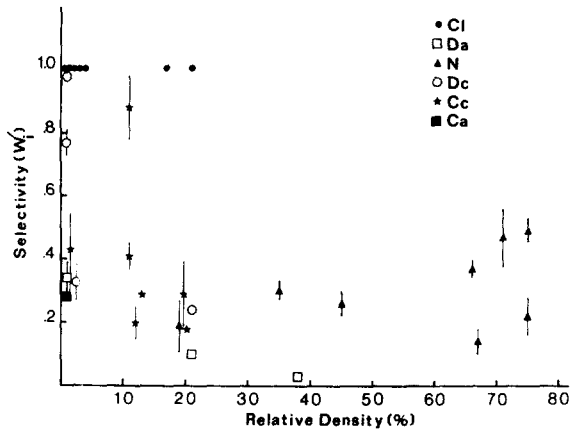


Fig. 3. The relationship between mysid selectivity coefficients ( $W'_i$ ) and relative prey density where Cl = Cladocera, Da = diaptomid adults, N = nauplii, Dc = diaptomid copepodites, Cc = cyclopoid copepodites and Ca = cyclopoid adults. Vertical bars represent standard errors ( $n = 2$ ).

ample is copepod nauplii which were present over a wide range of relative densities but mysid selection remained stable.

A comparison of the mean prey group rations for each cruise indicated how selectivity and prey field changes affect a mysid's daily ration (Table 3). In June, when most of the prey biomass ( $B_i$ ) was adult diaptomids and nauplii, effective biomass ( $\sum W'_i \cdot B_i$ )

was concentrated in the naupliar and diaptomid copepod stages which dominated the daily ration. As zooplankton succession proceeded to the Cladocera in August, cladoceran effective biomass became dominant. Along with nauplii, Cladocera formed the larger portion of the mysid's daily ration. The September experiments emphasized how changing prey assemblages alters *Mysis* feeding behavior over short time scales. During the normal nighttime feeding period all diaptomid instars were important regarding effective biomass and the ration. During the daytime Cladocera provided most of the ration.

## Discussion

Two important observations on *Mysis* predation stand out in this study. First, predation rates responded to the presence and absence of Cladocera. Second, calanoid and cyclopoid nauplii formed a significant and consistent portion of the *Mysis* diet. Though not the most preferred prey group, *Mysis* ate nauplii at significant rates due to their consistently high abundances. This result differs from *Mysis* in Lake Tahoe where copepod nauplii are not an important food item. Based on gut contents, Rybock (1978) rarely found naupliar mandibles in mysid

Table 3. A comparison of cruise means ( $\pm$ SE) for prey group daily ration ( $R_i$ ), biomass ( $B_i$ ) and effective biomass ( $W'_i \cdot B_i$ ). A dash indicates prey parameters were not estimated due to insufficient numbers ( $<16 \cdot l^{-1}$ ) in the control chambers.

	June			August		
	$R_i$	$B_i$	$W'_i \cdot B_i$	$R_i$	$B_i$	$W'_i \cdot B_i$
Cladocera	–	–	–	1.37(0.15)	2.52(0.31)	2.52(0.31)
Diaptomid adults	0.75(0.17)	13.8(0.85)	0.55(0.03)	0.76(0.20)	11.46(1.96)	0.46(0.08)
Cyclopoid adults	–	–	–	–	1.36(0.05)	0.08(0.01)
Nauplii	0.73(0.16)	16.98(2.28)	3.40(0.46)	1.30(0.18)	9.78(0.48)	1.96(0.09)
Diaptomid copepodites	1.15(0.16)	7.00(1.27)	1.96(0.36)	0.01(0.01)	3.21(0.50)	0.90(0.14)
Cyclopoid copepodites	0.08(0.08)	0.74(0.05)	0.21(0.02)	0.79(0.08)	4.99(0.24)	1.39(0.07)
Sum	2.67(0.49)	38.86(3.31)	6.20(0.65)	3.34(0.15)	33.32(2.87)	7.51(0.60)
	September (Day)			September (Night)		
	$R_i$	$B_i$	$W'_i \cdot B_i$	$R_i$	$B_i$	$W'_i \cdot B_i$
Cladocera	4.78(0.41)	10.84(4.37)	10.84(4.37)	0.70(0.41)	3.72(0.00)	3.72(0.00)
Diaptomid adults	0.00(0.00)	4.35(0.46)	0.18(0.02)	1.40(0.20)	52.09(13.63)	2.86(0.23)
Cyclopoid adults	0.08(0.11)	1.61(0.70)	0.10(0.05)	–	0.43(0.34)	0.03(0.02)
Nauplii	0.38(0.02)	3.53(0.53)	0.71(0.11)	1.28(0.30)	11.12(3.78)	2.23(0.76)
Diaptomid copepodites	0.88(0.28)	11.20(2.49)	3.14(0.70)	1.35(0.15)	5.60(3.16)	1.57(0.88)
Cyclopoid copepodites	0.60(0.15)	5.45(0.71)	1.53(0.20)	0.20(0.12)	0.97(0.55)	0.28(0.16)
Sum	6.70(0.50)	36.97(7.86)	15.62(4.48)	4.93(0.88)	72.02(15.82)	8.04(2.72)

stomachs even when captured at depth strata where naupliar densities were quite high. Further laboratory studies by Cooper & Goldman (1980) with the natural prey were conflicting. In some experiments *Mysis* fed on diaptomid nauplii and in others cyclopoid nauplii were not eaten. Since cladoceran predation rates were proportional to abundance (Fig. 4), significant increases in their proportion of the total predation rates occurred as in the daytime experiments of September. Total predation rates on all prey groups ranged from 118 to 289 prey · day<sup>-1</sup>. Equally sized mysids from Lake Tahoe (Cooper & Goldman 1980) all exceeded 100 prey · day<sup>-1</sup> at similar prey densities. However, Rybock's (1978) predation rates estimated from gut analysis were an order of magnitude lower. The maximum mean

predation rates at a mean prey density of approximately 550 m<sup>-3</sup> in Lake Tahoe was 24 prey · day<sup>-1</sup>. These mean predation rates were positively correlated to prey density (Rybock 1978). However, such comparisons must take into account that large size variations occur between the prey groups from these two lakes and that estimates of mean prey density ignore the patchiness of prey distributions.

Several relationships between density and clearance or predation rates have been reported for limnetic zooplankton (see Scavia 1979 for recent review). These relationships are important since they allow the development of modeling constructs for predictive capabilities. Results from single prey laboratory experiments with *Mysis* indicate that clearance rates gradually decrease with increasing

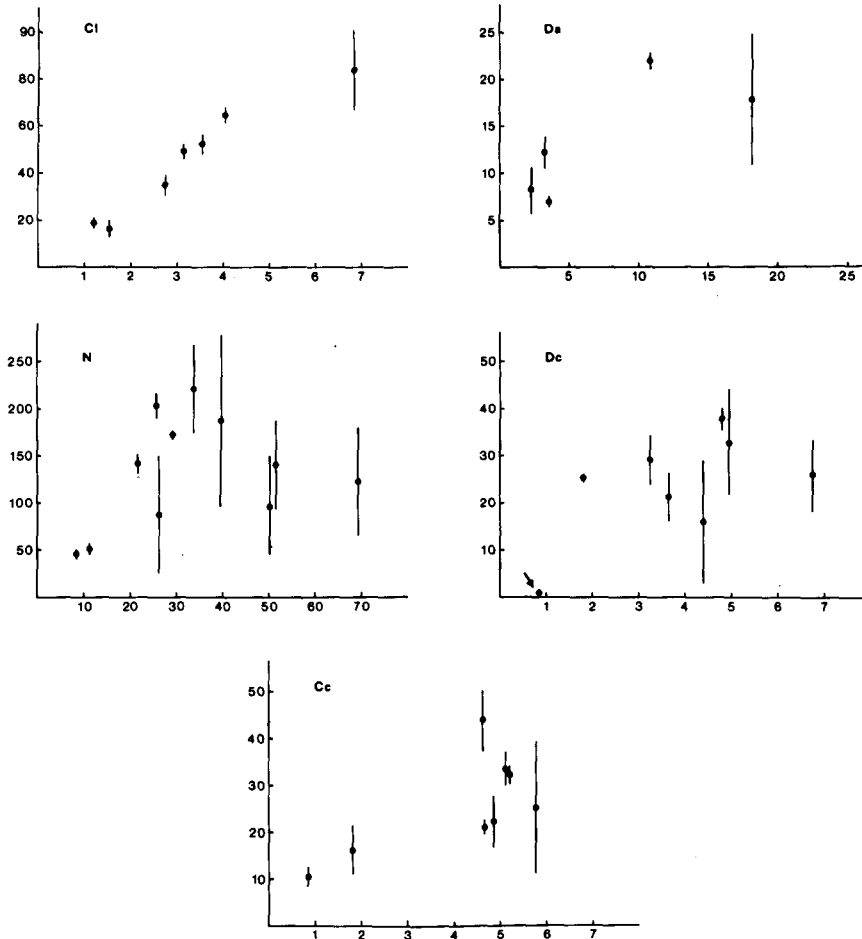


Fig. 4. The effect of prey density (abscissa, numbers · l<sup>-1</sup>) upon the predation rate (ordinate, number of prey · mysid<sup>-1</sup> · day<sup>-1</sup>) of *Mysis relicta* where Cl = Cladocera, Da = diaptomid adults, N = nauplii, Dc = diaptomid copepodites and Cc = cyclopoid copepodites.



prey densities while predation rates increase either in a linear or curvilinear fashion (Grossnickle 1979; Cooper & Goldman 1980). Only this study and Rybock's (1978) permit the investigation of these relationships using natural prey. Rybock's (1978) mean predation rates were directly proportional to density and appeared to reach a maximum at  $1300 \text{ m}^{-3}$ . In contrast the clearance rates in our study gradually decreased over density. Cladoceran rates however remained constant over density. Predation rates versus density curves were specific for each prey category (Fig. 4). None of the above results suggested that *Mysis* had reached maximum feeding rates. This conclusion is supported by Grossnickle's (1978) single-prey experiments where much higher predation rates were observed at artificially high densities. For example, at  $100 \text{ Daphnia} \cdot \text{l}^{-1}$ , *Mysis* had a consumption rate of approximately  $480 \text{ daphnids} \cdot \text{day}^{-1}$  whereas the highest rate on similarly sized daphnids at a Lake Michigan density of  $6.85 \cdot \text{l}^{-1}$  was  $84.10 \cdot \text{day}^{-1}$ .

When present, *Daphnia* and *Bosmina* were selected over all other prey. Based on the selectivity indices from all of the feeding trials (Table 2), the following ranking of mysid prey preference was: Cladocera > copepod copepodites and nauplii > adult diaptomids and cyclopoids. This order of preference is similar to previous observations (Grossnickle 1978; Rybock 1978; Cooper & Goldman 1980). Grossnickle (1978) proposed that his selection ranking was directly dependent upon prey escape behavior. His order of prey preference was *Daphnia pulex* > *Cyclops bicuspidatus thomasi* > *Diaptomus* spp. > *Limnocalanus macrurus*. Although Cladocera were the preferred prey category in our study, selection within this group possibly occurred due to size and body shape differences. *Bosmina* were relatively more vulnerable than *Daphnia galeatae mendotae* and *Daphnia retrocurva*. *Bosmina* is much smaller than either daphnid. Also, those cyclomorphotic daphnids remaining were large adults possessing long tail spines and large helmets which could present handling problems for many invertebrate predators (Dodson 1974). This strong preference for cladocerans was immune to changes in relative abundance (Fig. 3). Although the standard errors from the overall mean  $W'_i$ s indicated some variance in mysid preference, prey group  $W'_i$ s were relatively constant over relative abundance changes. Diaptomid copepodites are a good example. Cooper &

Goldman (1980) also reported this behavior when offering *Mysis* a choice between *Epischura* late instars and *Diaptomus tyrelli* males. Changes in their proportion of the prey field did not alter selection. Only detailed behavioral observations of *Mysis* and its prey will provide an adequate understanding of this interesting feature of mysid prey selection. Undoubtedly knowledge of predator-prey contact frequencies, prey swimming speeds, prey swimming escape behavior, mysid capture success and prey handling times will further this understanding.

The above selectivity patterns also had an important influence upon the daily food ration ( $R_i$ ) of *Mysis*, since the ration was correlated to selectivity coefficients. The use of selectivity coefficients to define an effective food supply (Vanderploeg & Scavia 1979) is a promising approach for predictive purposes. Once selectivity coefficients and prey specific biomasses have been estimated, one may then predict the relative proportion of each prey group in the predator's diet.

For the same size class of mysids the rations estimated from our experiments were lower than those that Cooper & Goldman (1980) reported for Lake Tahoe prey. While their values all exceeded  $10\% \text{ mysid dry weight} \cdot \text{day}^{-1}$ , the Lake Michigan estimates ranged from 2 to 6%. Several factors may account for this difference. First, prey densities in the Lake Tahoe experiments, specifically larger prey, were higher than in Lake Michigan. Neither study directly measured prey weights which significantly reduces the accuracy and precision of such estimates. Two prey groups were not included in our study, phytoplankton and rotifers, both potentially important prey. Finally, daily rations assumed a 100% ingestion efficiency which leads to an overestimation of the ration.

Temporal changes over two time scales in the prey assemblage had a considerable impact on prey specific rations. Diaptomid copepodites formed the largest proportion of the June ration, while cladocerans and copepod nauplii were the major contributors to the mysid diet in August. On shorter diel time scales migrations by Cladocera limited them to 14% of the mysid diet. During the artificial daytime conditions cladocerans constituted over 70% of the daily ration.

The four day-night experiments performed in September suggest that diurnal vertical migration by *Mysis* and cladoceran prey could have pronounced effects in regulating mysid prey selection

and cladoceran mortality rates in Lake Michigan. The data emphasize the general importance of vertical migration for predator-prey interactions in limnetic communities. In Lake Michigan, Cladocera are the preferred prey group, but mysids and these prey do not precisely coincide in time and space. Therefore, cladoceran mortality is reduced and *Mysis* cannot fully exercise this preference. This condition may be analogous to Lake Tahoe where the preferred prey *Epischura* primarily inhabits epilimnetic waters, above the mysid population (Richerson 1969). Although vertical migration by other invertebrate predators such as *Chaoborus* (Lewis 1977) and *Cyclops* (McQueen 1969) affects prey selection and mortality rates, our results further imply that prey migration patterns may result in reduced prey mortality. Thus Cladocera, besides having morphological (Dodson 1974) and swimming escape (Kerfoot 1978) defenses, may also benefit from their migratory habits as an effective escape mechanism from both visually oriented planktivorous fish and in this case an invertebrate predator.

This suggested escape mechanism in time and space also may partially explain the coexistence of *Mysis* and *Daphnia* populations. Noting the special mechanical susceptibility of daphnids to mysid predation and the ability of *Neomysis* to consume all but the very largest *Daphnia*, Murtaugh (1981b) proposed that mysids might eliminate any size refuge for middle sized *Daphnia* against the more commonly size-restricted invertebrate predators such as cyclopoids. This limitation thus suggests coexistence may sometimes be impossible. In Lake Michigan, *Daphnia* migration patterns may be an evolutionary refugium from *Mysis* that minimizes contact with the mysid population.

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