The effect of prey composition and abundance on the predation rate and selectivity of *Mysis relicta*

Carol L. Folt, [1,2] James T. Rybock, [3] & Charles R. Goldman [1]

[1] *Division of Environmental Studies, University of California, Davis, CA 95616, U.S.A.*

[2] *Present address: W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49606, U.S.A.*

[3] *Ertec Northwest, Inc., 4525 11th Ave., Seattle, WA 98105, U.S.A.*

Abstract

The predation rate and selection of specific prey by *Mysis relicta* in Lake Tahoe depends on both the total and the relative densities of prey classes. Functional responses of mysids to changes in the density of two species of calanoid copepod prey were curvilinear in laboratory experiments. In the field and in 2-prey treatments, preference was usually positive for *Epischura* and negative for *Diaptomus*. However, the preference for *Epischura* was greatest at the lowest combined densities of prey in the laboratory and decreased at densities >100 *Epischura* / m³ in the field. Several hypotheses to explain the inverse relationship between selectivity and prey density are discussed. Field assemblages of prey vary vertically, horizontally and seasonally. Potential effects of this heterogeneity on both predator and prey populations are examined.

Introduction

One way to evaluate the impact of a predator on the prey community is to measure predation rates and preferences for specific prey types. However, these parameters are affected by many factors that undergo changes in the field (e.g. relative and absolute abundances of prey classes; age and size of predators; hunger, experience and individual abilities to use each prey type). Consequently, the outcomes of predator-prey interactions are also likely to be variable, especially in heterogeneous systems.

The pelagic environment is particularly patchy, with biological and physical mechanisms creating ephemeral aggregations of animals in some areas and very low densities in others (Cassie 1959; Dagg 1977; Fasham 1978; Lewis 1978). As a result, the communities experienced by both predators and prey continually change. An understanding of the relations between absolute and relative prey densities and predator foraging behavior is critical to the construction of a general theory for the impact of aquatic predators on their prey. It is therefore very

surprising that so little data exist that compare the foraging behaviors of predaceous zooplankton at different absolute and relative densities of prey.

In this paper the effects of heterogeneity in the distributions and abundances of their zooplankton prey on several aspects of the foraging behavior of the pelagic predator, *Mysis relicta*, are examined. Three general questions were addressed. First, what is the relation between predation rate and prey density in the laboratory and field? Second, do predator preferences change as a function of relative prey density? Third, what are the effects of the changes in total prey densities on prey selection and predation rate?

The predation rates and prey preferences of *Mysis relicta* were measured experimentally over a range of prey densities and estimated from the gut contents of animals captured in Lake Tahoe, California-Nevada.

Three species dominate the pelagic crustacean community in Lake Tahoe. These are the predator *Mysis relicta* Loven, and two species of calanoid copepod, *Diaptomus tyrelli* and *Epischura neva-*

densis (Richerson 1969; Goldman 1981). Cooper & Goldman (1980, 1982) demonstrated that *Mysis* was both size (large predators took large prey) and species selective (*Mysis* preferred *Epischura* over *Diaptomus*). Although similar in size as juveniles, *Epischura* average 0.2 to 0.3 mm larger than *Diaptomus* as adults. *Diaptomus* however has a much more vigorous escape response. They suggested the preference for *Epischura* was due to the greater ease with which *Mysis* captured this prey. In contrast, Rybock (1978) measured positive preferences for *Diaptomus* on several occasions in the field. Based on our laboratory experiments and *in situ* measurements we demonstrate below that both the predation rates and the preferences of *Mysis* vary as a function of the absolute and relative density of prey. On this basis positive preferences for *Diaptomus* are predicted in some situations.

Methods

The temporal abundances of the zooplankton were determined from samples (three replicates on each date) collected as a part of the Lake Tahoe research program (Goldman 1981) at a central index station. Large scale horizontal distributions were inferred from additional samples (one tow at each station) collected throughout 1977-1981 at 20 stations around the lake (described in Morgan 1979) and at three stations in a protected embayment of Lake Tahoe (Emerald Bay). Samples were collected with an 80 μm mesh net, towed vertically from 150 m to the surface (volume of sample calculated from calibrated flow meter). These are the average densities of animals in a volume of approximately 50 000 l.

An opening-closing Tucker Trawl (similar to that described by Hopkins *et al.* 1973) was towed horizontally to capture animals from specific depths. The trawl netting was 80 μm Nitex mesh with a mouth area of 1 m² while under tow. Tow depth was estimated from standard 'wire length-wire angle'-conversions, and tow speed was measured with a digital flow meter. The density of animals per cubic meter was the average density in a volume of approximately 25 000 l. By counting the zooplankton from 10-15 depths (one tow each) from 150 m to the surface, the vertical distribution by age-class and species was determined.

Mysids were collected after sunset throughout the year by vertical tows (200 m to surface) using paired Bongo nets (0.75 m dia, 500 μm mesh). In the laboratory, similarly sized adults (16 to 18 mm, sorted visually) were placed individually into glass containers with 3 l of lake water, which had been filtered through a 60 μm mesh net to remove other zooplankton. Mysids were acclimated to laboratory conditions (one animal per 3 l, 8-10 °C, dark or red light) and starved for 12 to 24 h. Only those individuals which remained vigorous were used in the predation trials. Prey individuals were collected simultaneously and acclimated to laboratory conditions at higher densities at the same time. Males and females were used and randomly assigned to treatment jars on all experimental dates.

The following procedure was used in all the experiments. At the start of the experiment, the appropriate number of prey were pipetted into each jar. Only adult calanoids (visually sorted) of similar size and normal vigor were used. Each treatment was replicated 3 to 18 times, with a replicate being a jar containing one mysid and the treatment density of prey. After each feeding period of 3 to 24 h, the number of prey which had been eaten or killed was counted, and any fragments of dead, wounded, or non-vigorous prey removed. Prey density was restored to the original treatment density and the experiment repeated. The predation rate (more correctly a mortality rate) was taken as the number of prey killed by a single *Mysis* during each feeding period. The predation rates for each mysid over all repetitions of the experiment were measured separately, and means and standard errors calculated accordingly. There were no significant trends in predation rate over subsequent repetitions of the trials.

Controls (without *Mysis*) consisted of the highest treatment density of either *Diaptomus* of *Epischura*. Mortality in these controls was very low (less than 1% per 6 h) There was no difference between species in mortality in the controls. Adult *Epischura* are omnivorous in Lake Tahoe (Folt 1982). However, their predation rate on adult *Diaptomus* is extremely low. In fact, although we have seen an adult *Epischura* feeding on an adult *Diaptomus* in extremely crowded conditions, we have been unable to measure a significant predation rate on adults in any experiments. Hence, the mortality of *Diaptomus* due to predation in experiments with

Table 1. Experimental design for all of the laboratory experiments. E = *Epischura;* D = *Diaptomus.*

Expt.	Date	Feeding period (h)	# Mysids per treatment (a)	# Repetitions of each treatment (b)	N (axb)	No. of total prey per 3 l	Treatments (No. E/No. D)
A.	18 IX 80	6	5	4	20	5–40	0/5, 0/10, 0/20, 0/40
B.	26 X 80	6	9	1	9	8–16	0/8, 0/16
	26 X 80	6	18	1	18	8	0/8
	26 X 80	3	3	3	9	2–4	0/2, 0/4
	26 X 80	4	6	1	6	4–16	0/4, 0/8, 0/16
	26 X 80	2.5	6	1	6	4–16	0/4, 0/8, 0/16
C.	19 X 81	6	8	1	8	16	16/0, 0/16
	21 X 81	6	8	1	8	21–36	21/0, 36/0
D.	26 X 80	4	4	2	8	8	8/0, 0/8, 2/6, 4/4, 6/2
E.	26 X 80	3	3	3	9	8	2/6, 4/4, 6/2
F.	19 X 81	12	4	1	4	16	8/8
		14	8	1	8	16	8/8
G.	17 IX 80	6	4	3	12	40	5/35, 10/30, 20/20, 30/10, 35/5
H.	19 IX 80	24	5	2	10	40	5/35, 10/30, 20/20, 35/5
I.	25 VII 77	12	5	1	5	60	10/50, 20/40, 30/30, 40/20, 50
	25 VI 77	12	3	1	3	60–150	60/0, 90/0, 150/0
J.	9 VIII 80	12–18	4	3	12	40	0/40, 40/0, 20/20
		6–24	3	4	12	40	40/0

both prey is assumed to be due to *Mysis.*

Specific details for each experiment are listed in Table 1. The functional response curve for *Mysis* with *Diaptomus* as prey was constructed from the data collected in several experiments (Table 2). The predation rates were all corrected to 6 h rates; however, the treatments with low densities were terminated after 3 or 4 h before all prey were killed. Three values were collected in 2-prey trials in which the *Diaptomus* density was close to the total density (e.g. the predation rate at 6 prey per 3 l came from treatments with 6 *Diaptomus* (D) and 2 *Epischura* (E); 30 prey per 3 l from treatments with 30 D and 10E; 35 prey per 3 l came from treatments with 35 D and 5E). The mortalities (as the number of *Diaptomus* killed per number available) in these treatments were not significantly different from values measured in 1-prey treatments at similar densities.

The functional response curve for *Epischura* was also constructed from data collected in 1- and 2-prey trials (Table 2). The high density treatments (40, 60, 90, 150 prey·3 l⁻¹) lasted 6–24 h. The raw data from these experiments (and I, Table 1) were generously supplied by S. Cooper for our analyses. However, since a large proportion of the original prey remained after this period, we felt justified in including these points on the functional response curve. Nevertheless, they may have slightly under-

estimated the actual 6-h rate. As for *Diaptomus,* several 2-prey treatments with densities of *Epischura* near to the total density of prey were included (Table 2).

Preference was calculated using the formula:

$$C(E) = \frac{\#E \text{ killed}}{\#D \text{ killed}} \times \frac{\#D \text{ available}}{\#E \text{ available}}, \quad \text{Murdoch(1969)},$$

where C(E) is preference for *Epischura* (E) and 1/C(E) is the preference for *Diaptomus* (D). The value ranges from 0 to 1 for negative preference and 1 to ∞ for positive preference. The number of prey available is assumed to remain constant during the experiment. This assumption is appropriate when the prey are not significantly depleted, such as in the field or in the laboratory if prey densities are restored periodically. The C(E)'s in the laboratory experiments were thus calculated from the means of the treatments over all repeated trials. This measure was used in order to compare the laboratory preferences to those measured in the field. The use of the term 'preference' to describe the frequency of specific prey classes in the diet may be misleading. In this research, positive preference for *Epischura* simply means the number of *Epischura* killed was greater relative to the number available than the similar

Table 2. Specific treatments used to construct the functional response curves. N(i) = initial number of prey at the start of each trial; H = length of each trial in hours; E = 3^5 the experiment (Table 1); N = the number of mysids in each treatment multiplied by the number of times the trial was repeated;* indicates 2-prey treatments.

A. *Diaptomus*

N(i)	H	E	N
2	4	B	9
4	3,4	B	21
5	6	A	20
6	3,4	B	14
8	2,5–6	B,D	49
10	6	A	20
*10	6	G	12
16	6	B,C	22
20	6	A	20
*30	6	G	12
*35	6	G	12
40	6	A	20

B. *Epischura*

N(i)	H	E	N
*4	3,4	B	17
*6	3,4	B	17
8	4	D	7
16	6	C	8
21	6	C	8
*30	6	G	12
*35	6	G	12
36	6	C	8
40	6–24	J	12
60	12	I	3
90	12	I	2
150	12	I	4

ratio for *Diaptomus*. It does not imply that *Diaptomus* were rejected in favor of *Epischura*.

If preference for particular prey items by *Mysis* was affected by the length of the feeding trial, the use of different feeding periods in some of the experiments may have biased our results. We tested for the effect of the length of the feeding period on the preference (Table 3). The values of C(E) in all treatments at each total density and feeding period were pooled and the mean C(E) calculated for that density and time. The mean C(E) was then compared among experiments which lasted different lengths of time. There were no significant differences between C(E)'s measured in experiments which had the same number of prey but lasted different lengths of time (t-test p>.10). Hence, we concluded that the C(E)'s measured in our experiments were comparable.

Table 3. Comparison of preference by *Mysis* in experiments lasting different lengths of time. N = number of measurements of predation rate used in the calculation of preference; C_E = preference for *Epischura*; significance of difference between C_E's.

Total density (# per liter)	N	Feeding period (h)	$C_E \pm$ stnd error	Sig. of difference
13.3	60	6	1.615 ± 0.173	> NS
13.3	40	24	1.658 ± 0.179	
20.0	25	12	1.924 ± 0.280	> NS
2.7	36	3	4.28 ± 1.029	> NS
2.7	24	4	4.77 ± 0.993	

The field predation rate of *Mysis* was estimated as the average number of prey taken per *Mysis* during the night (see Rybock 1978 for details). Nocturnal feeding was quantified by counting the prey parts in the stomachs of 20 mysids captured as they began their upward migration (at sunset) and in 20 others as they moved downward at sunrise. Animals were collected at the Index Station using paired Bongo nets towed vertically from depth to the surface. They were preserved with formalin immediately after capture. Twenty individuals (when available) were selected for analysis of stomach contents. Stomachs from all 20 animals were placed into one petri dish. Each stomach was torn open with forceps, rinsed until all contents were free and the contents preserved with formalin and Rose Bengal.

The stomach contents (of the 20 mysids per tow) were pooled and suctioned through 0.45 μm Millipore filters at 35 cm Hg vacuum. After clearing the filter with 25% gluteraldehyde the entire filter was examined under a phase microscope.

Analyses of stomach contents were used to obtain counts of prey remains in the stomachs of the 'mean' or average *Mysis* captured in the vertical Bongo tows on nine dates from October 1977 to October 1978. Predation rates were calculated as

$$PR = \frac{(A-B)CF}{HRS} + \frac{SLR}{X},$$

where Pr = number of prey eaten $\cdot$ $Mysis^{-1}$ $\cdot$ h^{-1}; A,B = prey parts in stomach after (A) nocturnal and before (B) nocturnal feeding; CF = correction factor, or # prey eaten $\cdot$ # prey parts in gut^{-1}; HRS = time in hours before and after sampling (corrected for time it takes *Mysis* to reach upper waters);

SLR = stomach loss rate (prey parts lost from stomach · h^{-1}); X = number of prey parts · prey^{-1}.

Measurement of B was necessary because, during upward migration, *Mysis* stomachs contain a portion of prey remains from the previous night. The correction factor (CF) considers number of prey parts per prey and, more critically, the fact that remains in *Mysis* stomachs may be lost between the times of stomach removal and examination of contents. In addition, parts could be macerated beyond recognition during ingestion or missed in counting because they were obscured on the filter by debris or by occasional air pockets. CF also considers incomplete ingestion of prey, where the prey part is ingested but most of the prey is not, or vice versa. Stomach loss rate (SLR) considers maceration while in the stomach, excretion and any other loss of prey parts from the *Mysis* stomach over time. A common mistake with analysis of gut contents is the failure to consider such losses for each of the food items, usually referred to as differential digestion rates. Both CF and SLR were measured in laboratory studies where *Mysis* were fed a known number of prey (Rybock 1978).

The species of prey in the gut were distinguished by examining the prey remains (see Rybock 1978 for complete description of the method). The mysid stomachs contained recognizable remains of all the Lake Tahoe zooplankton, as well as some diatoms, other algae, pollen and detritus. However, only the mandibles of the crustaceans were used in the calculation of predation rates and selectivity because: 1) they were identifiable to species and preserved intact after feeding, and 2) number of prey parts was a known function of number of prey.

Results

The absolute and relative abundances of the zooplankton species varied over several scales of time and space (Richerson 1969; Morgan 1979; Goldman 1981; Folt 1982). Temporal variations in abundance were measured among and within years. The average copepod abundance (from 0 to 150 m) varied 1 to 2 orders of magnitude during the spring blooms and autumnal crashes (Goldman 1981). Day- and nighttime distributions of the copepods also differed, since both species moved into surface waters at night (Goldman, unpublished data). Ver-

tically migrating mysids moved from as deep as 450 m to the surface after sunset. Deep-living adults spent 12 to 13 h migrating and 5 to 9 h feeding. The bulk of the migrators on one date (Rybock 1978) spent 4 to 5 h from 20 to 60 m, and less than 3 h from 60 to 150 m. Some mysids of all age classes were routinely captured from 0 to 20 m, hence they penetrated the thermocline.

The vertical distributions of the copepods were stratified, particularly during months of the year when a strong thermocline existed (Richerson 1969; Rybock 1978). For example (Fig. 1) in June 1980, most of the adult population was located in a narrow band 20 m deep around the thermocline. Richerson (1969) found that most of the zooplankton were just below the top of the thermocline during the summer, and more evenly distributed (0-60 m) in the winter. Therefore, the average density (as copepods per liter) underestimated the density experienced by zooplankton at specific depths significantly. Comparisons between the zooplankton densities measured at depths of peak abundance with the mean density, indicated the peak density was up to 13 times greater than the mean density of adults and copepodids (Table 4).

On any given date, variability in zooplankton abundances within or among sites was substantial. In 1978, the average standard error for three replicate tows was 20% of the mean. Frequently, the difference between high and low tows was 100%. Large differences in densities were also measured among the 20 stations around the lake sampled on the same dates (Table 5).

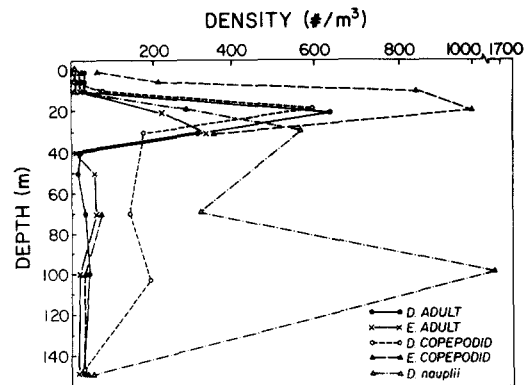The ratio of *Epischura* to *Diaptomus* also varied. *Epischura* declined prior to *Diaptomus* in 1978

Fig. 1. The vertical distribution of calanoid copepods in Lake Tahoe in June 1980. D = *Diaptomus;* E = *Epischura.*

Table 4. The difference between the density experienced by 90% of the copepods, and the average density of copepods in a vertical tow, Lake Tahoe. DA = Adult *Diaptomus;* EA = adult *Epischura*; A + C = adults plus copepodites of both D and E; Density is the number per m³; X = multiplication factor for the differences.

Date	Tow depth (m)	Density			Difference*		
		DA	EA	A + C	DA	EA	A + C
	Vertical[1]						
29 June 77	0–150	263	54	570	–	–	–
	Horizontal[2]						
28 June 77	0	506	314	6830	2X	6X	12X
28 June 77	10	485	302	7202	2X	6X	13X
28 June 77	20	192	28	5233	1X	0.5X	10X
28 June 77	30	1140	686	2638	4X	13X	5X
	Vertical[1]						
30 June 80	0–150	110	74	943	–	–	–
	Horizontal[2]						
30 June 80	0	1071	429	4961	10X	6X	5X
30 June 80	10	518	455	4435	5X	6X	5X
					$\bar{X}$ (DA + EA) = 5X		$\bar{X}$ (A + C) = 8X

*Difference between the average density measured in the vertical tow at that site and the horizontal tows at the depths where approximately 90% of the adults were aggregated.
[1]Averages of three tows.
[2]One tow.

(Table 6), the ratio went from 5.5 to 0.2 in 3 weeks. Certain samples contained such a high ratio of either species that there was effectively a one-species assemblage of prey at that time.

These data demonstrated several important points: 1. Densities much greater than the average densities throughout the water column were en-

Table 5. The abundance (no. animals · ℓ^{-1}) of adults (A) and adults plus copepodites (A + C) of *Diaptomus* and *Epischura;* at 20 stations around Lake Tahoe. Reported are the means of the 20 stations ± standard errors for each date; the range of each value before and after they were correted for vertical stratification, using the correction factors from Table 4.

	19 May 77	14 Aug. 78	12 Dec. 78
A X ± SE	0.24± 0.13	0.56± 0.19	0.05 ± 0.03
A + C X ± SE	0.91± 0.58	3.00± 1.34	0.44 ± 0.27
A Range	0.04– 2.82	0.20– 4.03	0.004– 0.63
A + C Range	0.10–12.20	0.92– 28.59	0.04 – 5.72
A Range ×5	0.18–14.08	0.98– 20.15	0.02 – 3.14
A + C Range ×8	0.80–97.60	7.36–229	0.32 –45.76

countered by mysids that migrated into the epilimnion and fed there. 2. Mysids separated spatially or temporally were likely to have encountered different absolute and relative densities of the two prey species. 3. Individual mysids that fed at several depths during the night or moved about horizontally would experience patchiness in the prey community.

Total prey density in our predation experiments ranged from 0.67 to 20 copepods per liter (except for calculations of the *Mysis* functional response to

Table 6. The ratio of adults (A) and copepodites (C) of *Epischura* (E) to *Diaptomus* (D) on seven dates 1978. The numbers in parentheses are the actual numbers of E over D per m³ measured in vertical tows (0–150 m).

Date	Ratio adult – E/D	Ratio adult + copepodids – E/D
11 Jan.	4.5 (192/43)	3.1 (227/74)
21 Mar.	1.2 (323/278)	0.7 (470/676)
27 Apr.	0.8 (166/195)	1.3 (731/571)
25 Jun.	0.1 (49/572)	0.7 (936/1420)
9 Aug.	5.5 (46/8.3)	5.7 (316/55)
28 Aug.	0.2 (1/5)	0.6 (22/36)
28 Sep.	0.1 (1/12)	0.8 (48/62)
29 Dec.	2.1 (11/5)	0.7 (19/29)

Epischura density). During 1977–1978 the average density of copepods at the index station (adults plus copepodites) ranged from 4 prey per liter during the summer to 0.02 prey per liter in December. Using the rough correction factors (Table 4) for vertical stratification, the density of adults and copepodids, above 30 m, ranged from 0.16 to 32 per liter. Referring to Table 5, it is apparent that much greater densities of animals were measured at other stations (up to 20 adults per liter). Hence, the densities chosen for this study were within the range experienced by the prey and predator populations, on at least some occasions.

Using the field data on *Mysis* predation rate and the average density of *Epischura* collected at the same time as the mysids, the functional response of *Mysis* to changes in *Epischura* density was estimated (Fig. 2). There was an increase in predation rate as *Epischura* density increased; however, the shape of the curve could not be determined. There were too few points at high densities, and the precise density of prey each mysid experienced was unknown. *Diaptomus* density related to mean predation rates similarly, but variability was greater. Seasonal changes in the mean predation rates of *Mysis* were primarily correlated with the density of *Epischura* ($r^2 = 0.803$, Figure 3). Other factors (e.g. changes in *Mysis* size, water temperature, *Mysis* density or the ratio of adult to copepodite prey) did not individually produce correlation coefficients greater than 0.300. Based on the field data, we simply concluded that the mean predation rates in the field increased with prey density. The shape of the curves describing this relationship for both prey
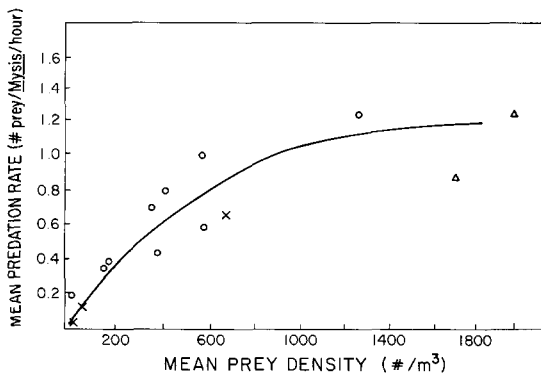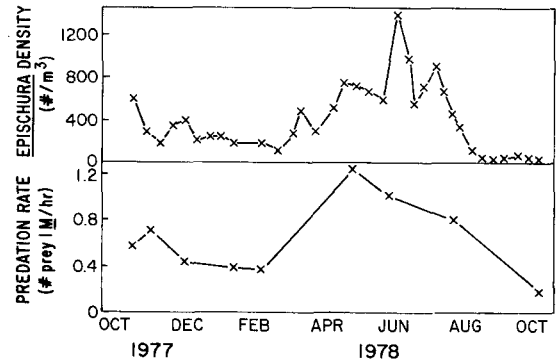

Fig. 3. Seasonal changes in the prey density and mean field predation rates of *Mysis relicta (M)*. Each depicted density of *Epischura* is the mean of three replicate tows at the index station (from Rybock 1978).

types were determined from the laboratory experiments.

The functional responses of adult mysids to changes in the density of both *Epischura* and *Diaptomus* were measured in the laboratory (Fig. 4).
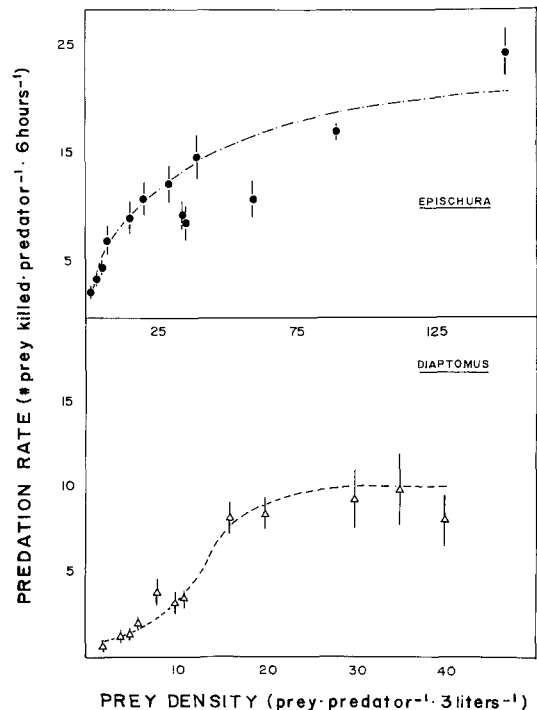

Fig. 4. Functional response curves for *Mysis relicta*. Depicted are the means ± standard error of the predation rates at each density of prey per predator. These values are the means of the predation rates of each mysid per treatment at each repetition of the trial. Curves were visually fitted.

Fig. 2 *In situ* functional response curve for *Mysis relicta*. The prey density is the mean density of *Epischura* from three replicate tows. O = index station; X = Emerald Bay; △ = laboratory data added for comparison (adapted from Rybock 1978).

Although the predation rate of *Mysis* was usually greater when *Epischura* were offered as prey, the overall shapes and magnitudes of the responses were not very different at densities greater than 3 per liter. The functions describing the relationship between predation rate and prey density were both curvilinear. Our results were consistent with those of Cooper & Goldman (1982), who found a decrease in the clearance rate of *Mysis* as the density of both prey types increased above a certain level.

Rybock found *Mysis* capable of handling and ingesting an adult *Epischura* in 7 min (not including search and capture time). A maximum predation rate of 8 prey per hour could only occur at densities which effectively eliminated search and capture time. The maximum predation rates measured in the field and the laboratory were lower than this hypothetical maximum rate. Even before reaching these rates the functional response curve already had begun to level off, indicating that handling time limits search time, or time spent resting between feeding, or satiation limits the predation rate at high densities of prey.

The effect of absolute and relative prey densities on the preference for either prey species by *Mysis* was examined. In Fig. 5, the average field density of *Epischura*, *Diaptomus* and the combined density of both prey was plotted against the preference for *Epischura* measured at each density. Based on the field data, C(E) was greater than 1 for 6 of the 9 field dates which indicated a positive preference for *Epischura* over *Diaptomus*. There was a significant decrease in C(E) as the abundance of *Epischura* increased above $100/m^3$ ($p < 0.05$, $r^2 = 0.52$). A similar (but not statistically significant) decrease in C(E) occured with the total prey density. There were too few data points at high prey densities to determine the relationship of C(E) to *Diaptomus* density.

In the laboratory, *Mysis* were offered *Epischura* and *Diaptomus* at different ratios (0.143–7) and at 3 different total abundances (8, 40 and 60 prey per 3 l). Preference of *Mysis* for *Epischura* was plotted as a function of the ratio of *Epischura* to *Diaptomus*. These curves were compared between the three total densities (Fig. 6a, b). Identical trends
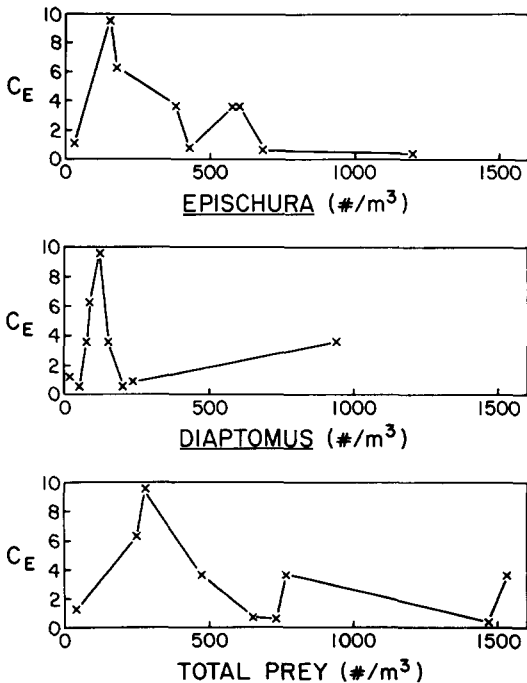

Fig. 5. Preference for *Epischura* by *Mysis* in the field as a function of *Epischura*, *Diaptomus*, and total prey density (*Epischura* plus *Diaptomus*).
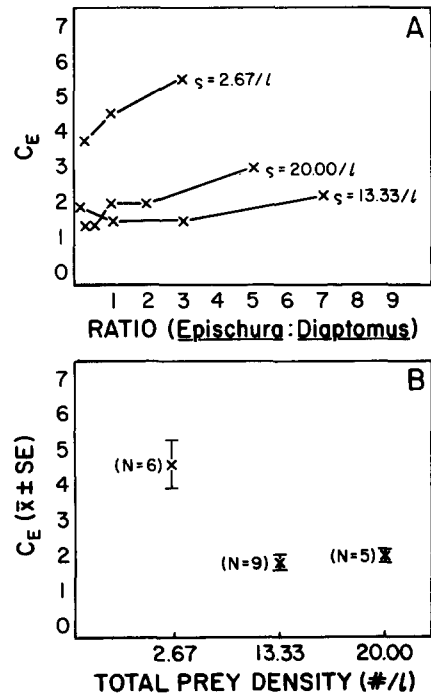

Fig. 6. Preference for *Epischura* by *Mysis* in the laboratory experiments as a function of the relative density of *Epischura* and *Diaptomus* (6a), and the total prey density (6b). δ = sum of *Epischura* and *Diaptomus* in each treatment; N = number of estimates of C_E used in calculation of the mean $C_e \pm$ standard error.

were found when preference was calculated with the measure proposed by Manly (1974; see Folt 1982).

C(E) increased slightly at all three total densities as the relative abundance of *Epischura*, increased. This trend was most pronounced at the lowest total density. The values of C(E) were greatest for all ratios at the lowest total density (8 prey per 3 l). The mean C(E)'s for all treatments at each total prey density were calculated and plotted in Fig. 6b. The mean preference at the lowest prey density was significantly higher than mean preference in either of the other experiments (p <0.02). The mean C(E) at the two highest total prey densities did not differ significantly. Apparently, the mechanism which resulted in a greater representation of *Epischura* in the diet was more effective at low prey densities. Possible explanations are presented below.

Discussion

In this paper we examined some effects of life in a changing environment on the feeding behavior of a pelagic predator. Specifically, the effects of changes in density and prey type on predation rate and the selection of prey were measured. Despite probable differences between individuals in the field in their past histories and abilities to use certain prey items, a positive correlation between predation rate and prey density was demonstrated. The preference by *Mysis* for specific prey items was also correlated with the density of prey. However, in this instance, an increase in total prey abundance was associated with a decrease in the preference for the preferred prey, *Epischura*.

Changes in the predation rate of *Mysis* as a function of the density of both prey types were curvilinear (Fig. 2). At low densities, even relatively small differences in the number of available prey (e.g. from 4 to 6 prey per predator per liter) resulted in a measurable difference in mean feeding rates. The functional response curves for both prey increased at a decreasing rate above 6 to 7 prey per predator per liter (termed threshold density). Thus at high densities, large differences in the number of available prey (e.g. from 7 to 13 prey per predator per liter) did not result in a significant change in the mean predation rates. Variations among individuals (as the standard error about the mean predation

rate) in their predation rates on the same food resulted from either differences in ability to capture prey successfully, in the feeding history of animals (hunger, experience), or in their responses to capture and handling stress prior to the laboratory acclimation period.

The Type II functional response curve described by Holling (1959) was hypothesized to represent the response of invertebrate arthropod predators to changes in prey density. However zooplankton predators have been reported with Type I (Dodson 1975; Jamieson 1980), Type II (Jamieson 1980; Pastorak 1980); bell-shaped (Pastorak 1980) and Type III (Akre & Johnson 1979; Johnson & Crowley 1980) functional response curves. A Type II response occurs when the time a predator spends handling prey (e.g. catching, killing, eating, resting and grooming) reduces search time, and sets an upper limit to the number of prey that can be eaten per unit time. Handling time can be significant for zooplankton predators (Li & Li 1979; Kerfoot *et al.* 1980). Therefore, it was expected that the functional response curves for *Mysis* on both prey would rise at a decelerating rate with increases in prey density.

Sigmoid responses (Type III) have been found for a range of vertebrate and invertebrate predators. Many biological factors result in curves this shape. For example, if the ability of the predator to capture prey increased with the number of encounters with the prey (hence prey density), handling times would decrease at higher prey densities. This could cause an increase in predation rate with prey density as depicted in a Type III functional response curve. The functional response curves for *Mysis* with *Epischura* as prey fit the Type II model, since there was a decelerating rise in predation rate as *Epischura* density increased. In contrast, a sigmoid curve provided the best visual fit when *Diaptomus* were the prey available. The greatest differences between the responses to the two species occurred at the lowest prey densities. This result indicated that differences in the ability of *Mysis* to capture successfully either species or the ability of either species to escape were greatest at lower densities.

Variation in the abundance of prey each predator encounters can result in large differences among individual predators in the amount of food eaten during a nocturnal feeding migration. A predator
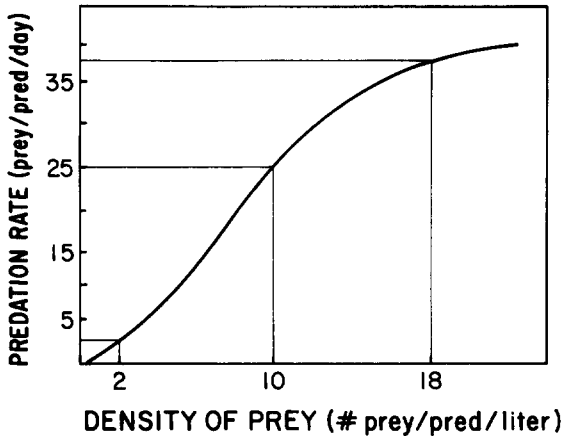
Fig. 7. Hypothetical functional response curve.

with the hypothetical functional response curve depicted in Fig. 7, which spent the night in a patch with a constant density of 10 prey per predator, would have consumed 24 prey. However, if it spent half of its time with a constant density of 2 prey per predator and half with a density of 18 prey per predator, it would have consumed only 20 prey that night. When the functional response is non-linear, the predation rate of the predator at the average density of prey is not equal to the average of the predation rates in different sized patches.

An even greater cause of variation among individuals in the number of prey consumed results when predators spend disproportionate periods of time with high or low densities of prey. For example, a predator foraging all night with a constant density of 18 prey per predator would have consumed over 35 prey that night.

We have demonstrated that great differences exist spatially and temporally in the distribution and abundance of the zooplankton in Lake Tahoe. One effect of this heterogeneity on the mysid population was hypothesized to be large variation among individuals in the number and type of prey consumed. Large variations in growth rate and fitness among mysids which were separated in the lake for extended periods of time could occur, if the numbers of prey available differed among those areas and were below the threshold density.

However, in different areas of the lake (or different times of the year)where the abundance of prey per predator was above the threshold density, the predation rates of individual mysids would not vary greatly. Any variability in growth and fitness in these areas may not correlate strongly with prey abundance.

In both the laboratory experiments and the field collections, *Mysis* usually included a disproportionately high ratio of *Epischura* to *Diaptomus* in its diet. However, in 1-prey experiments, *Mysis* preyed effectively on *Diaptomus* and in some cases preference for *Diaptomus* in the field was positive (Fig. 5). Changes in prey preference by *Mysis* may result in part from a change in the ability of *Mysis* to prey on *Diaptomus*. Several potential causes of the measured change in *Mysis* predation rate on *Diaptomus* are: 1) *Mysis* becomes more adept at capturing and handling *Diaptomus* as a function of the number of encounters (of density) with *Diaptomus*; 2) the ability of *Diaptomus* to escape decreases with encounter frequency or density; or 3) additional interactions (e.g. Folt & Goldman 1981) between *Diaptomus* and *Epischura* affect the escape ability of *Diaptomus*. At present we are unable to determine which of these mechanisms causes the decrease in predation rate by *Mysis* on *Diaptomus* at low density.

If in the field the density of *Diaptomus* is low, or high densities are infrequently encountered or encountered for short periods of time, we would expect a higher proportion of *Epischura* in the diet of mysids. In fact, positive preference for *Diaptomus* may only occur when there is a great increase in the density of *Diaptomus* for a prolonged period. This may explain why, despite the ability of *Mysis* to prey effectively on *Diaptomus* in the laboratory, average field predation rates on this species were low.

We demonstrated that both feeding rates and prey preferences of *Mysis relicta* depended on the abundance of prey. The impact of changes in the composition and density of the prey community on both predator and prey populations can only be evaluated if variations in the field densities are measured and individual responses at each density are known.

References

Akre, B. G. & Johnson, D. M., 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. J. Anim. Ecol. 48: 702–720.

Cassie, R. M., 1959. Microdistribution of plankton. N. Z. J. Sci. 2: 398–409.

Cooper, S. D. & Goldman, C. R., 1980. Opossum shrimp predation on zooplankton Can. J. Fish. aquat. Sci. 37: 909–919.

Cooper, S. D. & Goldman, C. R., 1982. Preliminary studies of factors affecting predation rates of Mysis relicta. Can. J. Fish. aquat. Sci. (in press).

Dagg, M., 1977. Some effects of patchy food environments on copepods. Limnol. Oceanogr. 22: 99–107.

Dodson, S. J., 1975. Predation rates of zooplankton in Arctic ponds. Limnol. Oceanogr. 20: 426–433.

Fasham, M. J. R., 1978. The statistical and mathematical analysis of plankton patchiness. Annu. Rev. Oceanogr. mar. Biol. 16: 43–79.

Folt, C. L., 1982. The effects of species interactions on feeding and mortality of zooplankton. Ph. D. thesis. Univ. of Calif., Davis.

Folt, C. L. & Goldman, C. R., 1981. Allelopathy in zooplankton: a mechanism for interference competition. Science 213: 1133–1135.

Goldman, C. R., 1981. Lake Tahoe: two decades of change in a nitrogen deficient oligotrophic lake. Verh. int. Verein. Limnol. 21: 45–70.

Hopkins, T. L., Baird, R. C. & Millikin, D. M., 1973. A messenger operated closing trawl. Limnol. Oceanogr. 18: 488–490.

Holling, C. S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

Jamieson, C. D., 1980. The predatory feeding of copepodid stages III to adult Mesocyclops leukarti (Claus). in: Kerfoot, W. C., (Ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, New Hampshire 793 pp.

Johnson, D. M. & Crowley, P. H., 1980. Odonate 'hide and seek' habitat-specific rules? in: Kerfoot, W. C. Kerfoot (Ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, New Hampshire 793 pp.

Kerfoot, W. C., Kellogg, D. L., Jr., & Rudi Strickler, J., 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses. In Kerfoot W. C. (Ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, New Hampshire 793 pp.

Li, J. L. & Li, H. W., 1979. Species-specific factors affecting predator–prey interactions of the copepod Acanthocyclops vernalis with its natural prey. Limnol. Oceanogr. 24: 613–626.

Lewis, W. M., Jr., 1978. Comparison of spatial and temporal variation in the zooplankton of a lake by means of variance components. Ecology 59: 666–671.

Manly, B. F. S., 1974. A model for certain types of selection experiments. Biometrics 30: 281–294.

Morgan, M., 1979. The dynamics of an introduced population of Mysis relicta (Loven) in Emerald Bay and Lake Tahoe, California-Nevada. Ph. D. thesis. Univ. of California, Davis.

Murdoch, W. W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39. 335–354.

Pastorak, R. A., 1980. Selection of prey by Chaoborus larvae: a review of new evidence for behavioral flexibility. in Kerfoot, W. C. (Ed.) Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, New Hampshire 793 pp.

Richerson, P. J., 1969. Community ecology of the Lake Tahoe plankton. Ph. D. thesis, Univ. of California, Davis. 111 pp.

Rybock, J. T., 1978. Mysis relicta loven in Lake Tahoe; vertical distribution and nocturnal predation. Ph. D. thesis, Univ. California, Davis. 118 pp.