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In Situ Feeding Rates of the Ctenophore *Mnemiopsis mccradyi*

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ABSTRACT: Prey ingested by *Mnemiopsis mccradyi* collected in Link Port (Indian River, east coast of central Florida) consisted mostly of copepod nauplii, barnacle nauplii, bivalve veligers, and adult copepods (*Acartia* sp., *Oithona* sp.); abundances in that order. Compared to relative in situ densities, there was an increased consumption of barnacle nauplii, bivalve veligers, and *Acartia* sp., and a decreased consumption of copepod nauplii and *Oithona* sp., implying that prey selection had occurred. In situ clearance rates (based on numbers of ingested prey, digestion rates, and in situ prey densities) for *M. mccradyi* (5 cm mean length) were 0.1 to 1.3 l h^{-1} $individual^{-1}$, depending on prey taxon. These rates are less than those measured previously in the laboratory; however, it is not possible to state if this difference is statistically significant.

Introduction

Lobate ctenophores of the genus *Mnemiopsis*, i.e., *M. mccradyi* and *M. leidyi*, may be the major predators of mesozooplankton (e.g., copepods, bivalve larvae, barnacle nauplii) in inshore waters from New England to the Gulf of Mexico (Miller 1970; Reeve and Baker 1975; Burrell and Van Engel 1976; Kremer 1976, 1979; Deason 1982).

Although a number of studies have measured feeding rates in the laboratory (Bishop 1969; Miller 1970; Kremer 1976; Reeve et al. 1978; Deason 1982), no ingestion rates have been measured in situ. There is evidence that lab-measured rates may be in error since several investigations have shown that *Mnemiopsis* cannot grow in the laboratory at normal in situ prey densities (Kremer 1976; Reeve et al. 1978).

It is important that laboratory and in situ rates be compared since lab-measured feeding rates have been extrapolated to field populations in order to predict predation rates (Bishop 1969; Miller 1970; Kremer 1976; Deason 1982). Thus, this study quantified in situ feeding rates of *Mnemiopsis mccradyi* and compared the results with those of previous laboratory studies.

Materials and Methods

Mnemiopsis mccradyi were collected during September and October 1986 at Link Port, an artificial harbor on the Indian River estuary (10 km north of Fort Pierce, east coast of Florida). At this time, in situ temperatures ranged from 27 to 31 °C. Ctenophores were abundant in the upper 1 m, averaging about 5 individuals m^{-3}, equal to a displacement volume of ~100 ml m^{-3}. For gut content analyses, animals were collected on 5 different dates (Table 1). The ctenophores (~25/date) were sampled with a dipnet from the upper 0.5 m by bringing them to near the surface and then removing them from the water using 0.5-l jars. Their total length (TL) was immediately measured to the nearest 0.5 cm (using a plastic ruler) without removing them from the water-filled jars. Specimens were then individually fixed in 4% formalin for later gut contents analyses.

For identification, ingested prey were removed from the guts of preserved ctenophores. However, this was sometimes difficult owing to the poor fixation of some ctenophores. Consequently some small prey, e.g., nauplii, could have been overlooked. Thus, zero values for the 14 specimens (12% of total 121 specimens), which apparently did not contain ingested prey, were not used in the analyses.

Prey selection was quantified using the "Log of Odds Ratio" (Gabriel 1979), a selectivity index.

Log of Odds Ratio: LOR = LN(p1q1/p2q2) where LN = natural log, p1 = percentage of prey of a given taxon in the diet, q1 = percentage of all other prey in the diet, p2 = percentage of prey of a given taxon per m^3, and q2 = percentage of all other prey per m^3. A standard error can be calculated using SE (LOR) = 1/n1p1q1 + 1/n2p2q2 where n1 = total number of prey in diet sample, n2 = total number of prey in situ per unit volume, and p1, q1, p2, and q2 as previously defined.

This index, first proposed by Fleiss (1973), has several advantages over other indices, e.g., the Ivlev Index (Ivlev 1961), Forage Ratio (Allen 1941). First, it is symmetrically distributed around 0, ranging from − infinity to + infinity (+ values = + selec-

TABLE 1. Density (number l^{-1}) (mean, standard error) of major zooplankton taxa (*Acartia, Oithona,* copepod nauplii, barnacle nauplii, bivalve veligers and polychaete larvae) collected in Link Port during Sept–Oct 1986.

Date	*Acartia*	*Oithona*	Copepod N.	Barnacle N.	Bivalve V.	Poly. L.
16 September	7.6, 3.4	36, 2.2	117, 10	4.2, 0.8	2.6, 0.7	1.9, 0.3
28 September	2.0, 0.5	15, 2.2	27, 4.7	2.1, 0.4	3.2, 0.8	7.1, 1.3
5 October	1.1, 0.4	7.0, 1.0	23, 10	7.7, 0.4	4.4, 1.4	4.7, 0.5
12 October	1.9, 0.6	14, 1.2	67, 10	10, 1.7	4.0, 0.9	2.5, 0.3
28 October	3.2, 7.1	11, 2.7	84, 11	5.9, 1.0	9.0, 2.2	2.7, 0.5

tion, − values = negative selection, zero = no selection), and secondly a standard error can be calculated (Gabriel 1979).

Gut clearance times (time between ingestion of prey and egestion of wastes) were measured after individual ctenophores (n = 30, 3–6 cm TL) had been placed in separate containers of 64-μm-filtered seawater for 4 h at 25–27 °C, to completely clear their guts. They were then fed small numbers of copepodites and adult *Acartia* sp. (mostly *A. tonsa*), or smaller prey (i.e., copepod nauplii, barnacle nauplii and *Oithona* sp. copepodites and adults). After 5 min the water was changed to remove any remaining prey, and the course of digestion was followed using a binocular microscope.

Zooplankton samples (0.2 m^3) were taken at the beginning and end of each hour-long, ctenophore sampling period (done between 1200–1600 hours). Replicated vertical tows (1–0 m) were made within 10 m of where the ctenophores were collected, using a 50 cm, 64-μm mesh net.

Subsamples, taken with a Stempel pipet (representing $1/10$ to $1/50$ of the total sample), were placed in a circular tray for counting. Between 400 and 500 zooplankters were counted in each subsample.

The apparent in situ clearance rates (rates at which ctenophores removed prey from the water column) were estimated from data on the number of prey ingested, the gut clearance time, and the in situ prey density (Larson 1985). ACR = NPG·(GCT·PD)$^{-1}$, where ACR = clearance rate 1 h^{-1} individual^{-1}, NPG = number of prey ingested per ctenophore, GCT = gut clearance time (h), and PD = prey density (no. l^{-1}).

Results

Of the 121 ctenophores (mean = 5 cm TL, range = 3–6 cm TL) collected, 107 contained identifiable ingested prey. However many specimens also contained unidentifiable crustacean remains. More than 1,700 prey items belonging to at least 15 prey taxa were found (Table 2). The major prey (making up 85% of total) were copepod nauplii, barnacle nauplii, bivalve veligers, and *Acartia* sp. adults and copepodites. The numbers of ingested prey were low, averaging 15.8 ± 1.4 SE (standard error) per ctenophore. However, there was considerable variation in the number of ingested prey (maximum = 70). The coefficient of variation (CV) for total number of prey in the gut equaled 94%. For individual prey taxa, the variation was even greater (i.e., for *Acartia* sp., CV = 204%; for copepod nauplii, barnacle nauplii, and bivalve veligers, CV = 130–150%). Of the 10 dominant prey taxa, CV was lowest for *Oithona* sp. (CV = 82%).

Gut clearance times (GCT) ranged from 0.33 h to 1.5 h (n = 30), depending on prey size and number of prey consumed. For small prey (e.g., <1 mm TL: copepod nauplii, barnacle nauplii, *Oithona* sp.), GCT averaged 0.5 h (range = 0.3–0.6 h) and was mostly independent of the numbers of prey in the gut (between 10–50 prey). For larger prey (i.e., adult *Acartia* sp. (1–2 mm TL), GCT averaged about 1 h (range = 0.8–1.5 h) and was dependent on the number of prey in the gut. When 1 to 10 large prey were ingested, GCT was approximately 1 h.

The zooplankton samples were dominated by the following taxa: copepod nauplii, *Oithona* sp., barnacle nauplii, bivalve veligers, polychaete larvae,

TABLE 2. Results of gut content analyses of freshly collected *Mnemiopsis mccradyi* (n = 107) from Link Port, Florida.

Prey	Total in Gut	Percent of Total
Copepod nauplii	543	32
Barnacle nauplii	364	21
Bivalve veligers	316	19
Acartia sp. (adults + copepodites)	222	13
Oithona sp. (adults + copepodites)	57	3
Oikopleura dioica	51	3
Misc. other copepods (*Paracalanus, Temora,* cyclopoids, harpacticoids)	50	3
Brachyuran zoea	41	2
Polychaete larvae	24	1
Tintinids	13	<1
Gastropod veligers	11	<1
Isopods	7	<1
Sagitta hispida	6	<1
Barnacle cyprids	6	<1
Tunicate larvae	3	<1
Tanaids	2	<1
Shrimp mysis	1	<1
Nematodes	1	<1
	Total = 1,718	

TABLE 3. Coefficient of variation (mean, standard error) of numbers of zooplankton among subsamples, replicate tows, and among samples collected on different dates.

Source of Variation	Coefficient of Variation				
	Acartia	*Oithona*	Copepod N.	Barnacle N.	Bivalve V.
Subsample	18.9, 2.6	10.4, 1.5	8.8, 2.0	18.2, 3.5	24.4, 3.4
Replicate	28.5, 5.4	15.9, 4.2	26.6, 5.1	23.0, 5.4	34.1, 5.2
Sample date	49.5, 10.0	22.9, 8.1	6.5, 1.4	25.5, 8.6	46.8, 15.3

and *Acartia* sp. adults and copepodites, in that order (Table 1). Most of these zooplankton were important in the diet of *M. mccradyi* (Table 2).

Errors in estimating prey densities were partitioned among subsamples, replicates, and samples taken on different sampling dates (Table 3). The coefficient of variation ranged from 9% to 24% between subsamples, 16% to 34% between replicates, and 7% to 50% among samples from different dates depending on the taxon.

Calculated clearance rates varied from 0.1 to 1.3 (mean = 0.6) $l\ h^{-1}$ $individual^{-1}$, depending on the prey (Table 4). For *Acartia* sp. adults and copepodites as well as other similarly-sized copepods, gut clearance times of 1 h were used; for smaller prey, a value of 0.5 h was applied, except for bivalve veligers for which 1 h was considered appropriate because digestion was possibly slowed owing to their tightly closed valves. Because the numbers of ingested prey were highly variable, coefficients of variation were large, ranging from 82% to 204%.

Prey ingested by *Mnemiopsis mccradyi* were those which were relatively numerous in the plankton; however, there was evidence of prey selection. For example, copepod nauplii and *Oithona* sp. were under-represented in the guts relative to in situ abundance, whereas barnacle nauplii, bivalve veligers, and *Acartia* sp. were more abundant relative to zooplankton densities (Table 5).

Discussion

Mnemiopsis leidyi is a selective predator. Burrell and Van Engel (1976) found that bivalve veligers, barnacle nauplii, and polychaete larvae were more abundant in the diet relative to in situ densities. In this study, evidence suggests that there was positive selection for some prey (i.e., *Acartia* sp., harpacticoids, bivalve veligers, and barnacle nauplii) and negative selection for others (i.e., *Oithona* sp. and copepod nauplii). Some form of prey selection is thought to occur in all gelatinous predators (Larson 1985).

The high variability in the number of prey ingested by *M. mccradyi* (e.g., CV = 204% for *Acartia* sp.) could be due to several factors (e.g., differences in ingestion rates, or digestion rates, or prey densities). The first two factors can probably be eliminated because of the variability in the ratios of ingested prey taxa. If the large variance was due to high or low ingestion rates, or rapid or slow digestion by individual ctenophores, then it follows that if *Acartia* copepods were abundant in the gut of a ctenophore, then similarly large numbers of other prey would also be found and vice versa. However, this was not the case, there was no obvious relationship between numbers of individual prey taxa in the guts of specific ctenophores. Thus, variable prey densities appear to be the most probable cause of this variance.

Reeve (1980) concluded that ctenophores were probably dependent on high density micro-scale prey patches because laboratory-measured ingestion rates were too low at average prey densities to support ctenophore growth. Results herein support this patch-foraging hypothesis.

Estimated in situ clearance rates for *Mnemiopsis mccradyi* of 5 cm TL ranged from 0.1 to 1.3 $l\ h^{-1}$ $individual^{-1}$ (at 27–30 °C), depending on the prey taxa ingested. Lab-measured clearance rates for *Mnemiopsis* sp. ctenophores feeding on small cala-

TABLE 4. Apparent in situ clearance rates (mean, standard error) for *Mnemiopsis mccradyi* feeding on various zooplankton prey (n = 107).

Prey	Clearance Rates ($l\ h^{-1}$ $individual^{-1}$)
Acartia sp.	0.9, 0.15
Oithona sp.	0.1, 0.06
Copepod nauplii	0.2, 0.07
Barnacle nauplii	1.3, 0.23
Bivalve veligers	0.6, 0.14

TABLE 5. Prey selectivity values (Log of odds ratio) for *Mnemiopsis mccradyi* feeding on various zooplankton prey (i.e., *Acartia*, harpacticoid copepods, *Oithona*, copepod nauplii, barnacle nauplii, and bivalve veligers). Positive values indicate positive selection, negative values indicate negative selection.

Date	*Acartia*	*Harpacs*	*Oithona*	Copepod N.	Barnacle N.	Bivalve V.
			−0.84			
16 September	1.7	3.0		−0.74	1.6	1.0
28 September	1.5	1.8	−2.6	−0.95	1.5	1.4
5 October	1.8	0.35	−2.4	−0.24	0.36	0.65
12 October	0.81	0.47	−0.40	0.14	0.79	0.75
28 October	0.92	0.70	−1.8	0.25	1.2	0.87
Mean	1.4	1.3	−1.6	−0.31	1.1	0.94

TABLE 6. Estimated mean clearance rates for *Mnemiopsis* sp. ctenophores of 5 cm total length.

Taxon	Clearance Rate (l h^{-1} $ind.^{-1}$)	Temperature (°C)	Reference
Mnemiopsis leidyi	1–2	16–24	Miller (1970)
Mnemiopsis leidyi	0.7[a]	20–25	Kremer (1976)
Mnemiopsis mccradyi	2.2[a]	26	Walter (1976)
Mnemiopsis mccradyi	0.1–1.3[b]	27–30	data herein

[a] Interpolated from values in paper.
[b] Depending on prey taxon.

noid copepods ranged from 0.7 to 2.5 l h^{-1} $individual^{-1}$ (Table 6). Although it appears as if estimated in situ and laboratory-measured clearance rates for *M. mccradyi* are different, potential sources of bias must be first considered. One factor which affects the accuracy of clearance rate estimates is variability in prey densities. Both in the laboratory and in situ, prey densities are difficult or impossible to accurately measure when prey aggregate at interfaces (lab) or are patchy over small space scales (in situ). Another factor is that prey kept in the lab may not be able to escape predators as readily as they would in situ because they are weakened by starvation or from repeatedly avoiding predators in confined quarters. Thus, differences in clearance rates of <100% may not be significant; however, further studies are needed before it can be assumed that laboratory and in situ rates are comparable.

Clearance rates are prey-species dependent. Kremer (1976) found that laboratory clearance rates for *M. leidyi* were lower when veligers and cyclopoids were the prey than when calanoids and cladocerans were presented as food. In this study, in situ rates varied by an order-of-magnitude depending on the prey taxa.

Interpretation of the results of feeding studies can be aided by foraging theory. Foraging theory predicts that a number of factors affect zooplankton feeding rates, e.g., prey behavior, especially swimming speed and direction, prey vulnerability (ability to escape), and relative prey availability (prey density and distribution) (Gerritsen and Strickler 1977; Green et al. 1986).

In this study, clearance rates were highest for ctenophores feeding on barnacle nauplii and *Acartia* sp. adults which have relatively high swimming speeds (0.5–2 mm s^{-1}) (Anderson 1974; Miller et al. 1982; Fulton and Wear 1985; Green et al. 1986), and lowest for those feeding on *Oithona* sp. and copepod nauplii which swim at lesser speeds (0.1–0.3 mm s^{-1}) (Anderson 1974; Fulton and Wear 1985).

Although there was an apparent relationship between in situ clearance rates and prey swimming speeds, foraging theory predicts that this would only be so only if predator speed is relatively low in comparison to that of the prey (Gerritsen and Strickler 1977). However, at least in the laboratory, *M. mccradyi* can forage at rates of up to 1 cm s^{-1} (although mean rates are much less) (Larson unpublished), in which case prey speeds of 2 mm s^{-1} would have little effect on clearance rates. Nevertheless, because there appears to be a relationship between ctenophore clearance rates and prey swimming speeds, it appears that the foraging speeds of *Mnemiopsis* are low, i.e., 1–3 mm s^{-1}. However, this requires further study.

One other factor must also be taken into account, i.e., relative prey availability. If prey were randomly distributed, relative prey availability would be proportional to relative prey densities. However, evidence presented herein suggests that this was not the case. The large coefficients of variation (100 to 200%) for numbers of ingested prey suggest that prey distributions were patchy. It is unlikely that such variation could be due solely to vertical stratification of prey because *Mnemiopsis* tends to forage vertically (Reeve and Walter 1978; Larson unpublished) and therefore prey would have been equally available to all ctenophores, resulting in a low variance for the numbers of ingested prey.

The size scale of the prey patches in Link Port was probably less than that sampled by the net (<0.2 m^3) because the variance of the plankton densities was relatively low. Moreover, since *Mnemiopsis* foraging rates are only 2 l h^{-1} or less, these patches probably occur over distances of centimeters rather than meters. From estimates of in situ clearance rates, it appears that patches of *Acartia* sp. may have reached densities of up to 15 times greater than mean values. Because few ctenophores (about 10% of the population) were able to exploit these dense prey patches, it appears that the patches were trophicly unimportant. The significance of prey patches to gelatinous predators requires further investigation.

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