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Prey selection by the scyphomedusan predator *Aurelia aurita*

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Abstract We describe feeding behavior of *Aurelia aurita* (Linnaeus) using gut content analyses of field-collected specimens and a mesocosm experiment. The field studies were conducted in Narragansett Bay, Rhode Island, USA from March to April 1988, and the mesocosm studies were done at the Marine Ecosystems Research Laboratory at the University of Rhode Island. Patterns of prey selection changed with medusa diameter. Smaller medusae (< 12 mm diameter) consumed mostly hydromedusan prey whereas larger medusae (up to 30 mm diameter) ingested greater numbers of copepod prey. While larger medusae did feed on copepods, their diet also contained more barnacle nauplii and hydromedusae than expected from the relative abundances of these prey types in plankton samples. A marginal flow mechanism of feeding by *A. aurita* provided an explanation for the patterns of prey selection we observed in medusae of different sizes and among widely divergent prey types. Our data indicated that large prey, with escape speeds slower than the marginal flow velocities around the bell margins of *A. aurita*, made up a substantial fraction of the daily ration when they were available. Such prey species may be more important to nutrition than the more abundant copepods and microzooplankton. Successful development of young medusae may depend upon an adequate supply of slowly escaping prey.

Introduction

Conventional approaches to describing the diet of the scyphomedusan predator *Aurelia aurita* have shown this species to be capable of consuming a variety of prey types, but they have not provided a clear picture of feeding mechanics governing prey selection. Gut content analysis, the most direct approach, has shown that both soft-bodied and crustacean prey are ingested in all stages of development (Lebour 1923; Moller 1980; Matsakis and Conover 1991). These analyses have not revealed any obvious patterns in prey selection. Moller (1980) reported the major items in gut contents of young medusae 11 to 20 mm in diameter were 0.84 copepods, 0.44 herring larvae, and 0.19 cladocerans per medusa; the diet of older medusae 36 to 50 mm in diameter was similarly dominated by copepods and larval fish. On the other hand, Lebour (1923) found that gastric contents of medusae 20 to 25 mm diameter consisted primarily of crab zoeae (40 of 56 total prey recovered). Matsakis and Conover (1991) reported that large numbers of the hydromedusan, *Rathkea octopunctata*, were consumed by *A. aurita* 10 to 100 mm diameter. Patterns controlling prey selection are not evident from these reports because few details were given concerning prey abundance or digestion rates of various prey types which may affect their residence time in the gut.

Prey selection by *Aurelia aurita* has also been addressed experimentally in laboratory studies, but the results appear to conflict. Early experiments by Delap (1907) indicated that young *A. aurita* preferred hydromedusae and only ate copepods when no alternative prey were available. Bamstedt (1990) saw no evidence for selective feeding: consumption of prey by both ephyrae and older medusae was proportional to prey abundance in natural, but very dense, zooplankton assemblages. On the other hand, Stoecker et al. (1987) reported selective feeding by *A. aurita* on different types of microzooplankton and found a preference for copepod nauplii over rotifers and polychaete larvae. Studies that have concentrated on larval fish as prey clearly indicate that prey selection is a complex function of sizes, densities and capabilities of both predator and prey species, and even of types of alternative prey available (Bailey and Batty 1983; Cowan and Houde 1992).

Given the complex behavior of scyphomedusan predators and their many potential prey species, it is not surpris-

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ing that traditional field and laboratory approaches have yielded apparently conflicting information. Costello and Colin (1994) have taken an alternative, mechanistic approach, in which they assume that prey selection has a physical, quantifiable basis. They based their understanding of feeding mechanisms on microvideographic studies of fluid flows around swimming *Aurelia aurita* and proposed that prey are entrained in flows created by bell pulsation. Capture occurs when prey cannot escape flow velocities around the bell margin. They predict that prey selection should be a function of relative speeds of flows over the bell margin and escape speeds of the prey species. Prey with escape speeds that exceed the marginal flow velocities will rarely be captured and, since marginal flow velocity increases with increasing medusa diameter, prey selection should change in a predictable manner with increasing size (and age) of the medusa. Should this model prove to be correct, it could be an extremely useful tool for predicting the impact of this type of predator in the field.

In the present study we used Costello and Colin's (1994) model as a framework for explaining patterns of prey selectivity observed in previously unpublished field and laboratory data on the diet of *Aurelia aurita*. The data were collected prior to formulation of their hypothesis but contain sufficient information about medusa diameter and prey availability to allow comparison with the model predictions. Our analysis indicates that the model has a degree of predictive capability but also that specific details of the model regarding capture of copepods may need modification. Nevertheless, consideration of the marginal flow mechanism of feeding has provided insights about nutrition in *A. aurita* that might otherwise not have been evident from more traditional approaches.

Methods

Field study

Weekly collections of *Aurelia aurita* (Linnaeus) were made during daylight hours from early March to late April 1988 at three stations in Narragansett Bay, Rhode Island, USA representing a north-south transect including the upper bay (Providence River), mid-bay (Greenwich Bay) and lower mid-bay (Wickford Cove). To supplement the daytime collections, additional samples were taken at midnight at all stations on 31 March 1988. Additional tows were made from areas of the mid-bay where *A. aurita* were observed to be particularly abundant on 6 and 20 April 1990. Collections to characterize zooplankton abundance and composition were made simultaneously.

Two tows per station were made with a 60-cm diameter bongo net fitted with paired 303-μm and 1000-μm mesh nets equipped with General Oceanics flow meters. Tows were oblique, sampling from surface to near bottom, and ranged from 2 to 5 min duration depending on water depth, which was approximately 14 m in the Providence River and 5.5 m in Greenwich Bay and Wickford Cove. Samples were preserved immediately after collection in 6% buffered formalin. Abundance estimates of jellyfish and larger zooplankton were made by counting the entire contents (for medusae) or subsamples of the 303-μm mesh sample. Abundance of smaller zooplankton was estimated by pumping 18 liters of water through a 20-μm mesh screen while the hose was being drawn through the entire water column. Diameters of *Aurelia aurita* were measured from specimens preserved for 1 mo in 6% formalin and were related to diameter of live specimens by the equation $D_l=0.665+1.3\ D_p$ ($n=20$, $r^2=0.942$), where D_l and D_p refer to diameters of live and preserved specimens, respectively. Gut content analyses were made only on medusae from the 1000-μm mesh sample. This mesh size collected virtually no prey along with *A. aurita* thus eliminating bias due to net-feeding. The percentage of jellyfish which lost gut contents when preservative was added was determined by examining 30 medusae collected from 13 m^3 enclosures for visible gut contents and by preserving them for varying periods before reexamination. An additional 23 medusae which had fed on either copepods or larval fish in the laboratory were observed while adding the preservative.

We have used the electivity index "C" from Pearre (1982) to define prey selection because it is a commonly used index for studies of medusan feeding behavior. This index is derived from the chi square formulation allowing comparison of average numbers of prey $medusa^{-1}$ and average numbers of prey m^{-3}. Values of this index range from −1 to +1. Statistical significance was based on the chi square statistic as suggested by Pearre (1982). Apparent prey selectivity may be biased due to differing digestion rates of each prey type; these differences were taken into account in the data from the enclosure study by determining selectivity from daily ration values corrected for digestion time in the manner of Larson (1991). Digestion times were measured directly for larval fish and copepods in laboratory experiments. Individual medusae were incubated at 7 °C, fed single prey and observed every 15 min until digestion was complete. Digestion times for other prey types (barnacle nauplii and harpacticoid copepods) were estimated from values reported by Larson (1991) for digestion by *Stomolophus meleagris* of similar prey types. He reported that barnacle nauplii took 35% longer to digest than copepods. Our values were adjusted accordingly.

Laboratory study

Prey selection by *Aurelia aurita* was also assessed in two large enclosures (5 m deep, 13 m^3 volume) maintained by the Marine Ecosystems Research Laboratory at the University of Rhode Island. Details of enclosure design were reported by Oviatt et al. (1986). The enclosures are outdoors, allowing natural lighting and photoperiod. Mixing was induced periodically with a vertical plunger on a schedule that simulated tidal energy inputs. Temperature was controlled with heat exchangers and was kept at 7.5 °C for this experiment. On 8 April 1990 the enclosures were filled simultaneously with a natural plankton assemblage by pumping unfiltered water from lower Narragansett Bay. The following day 40 *A. aurita* (30±3 mm diameter) were hand-dipped from surface waters at the Greenwich Bay station (mid-Narragansett Bay) and immediately transferred to one of the two enclosures. Both enclosures also contained a known number of fish larvae, *Pleuronectes americanus*, (1300 in each enclosure) which had been counted and added to the natural plankton assemblage. Plankton and fish abundances were compared in the enclosures with and without *A. aurita* present 4 d after the medusae had been added. Zooplankton and larval fish abundances were determined from replicate net tows (202-μm mesh, 0.25-m diameter) drawn from bottom to top of the enclosures during the mixing cycle.

To conclude the experiments medusae were dipped from the enclosure with a long handled bucket and immediately preserved for gut content analysis. Final abundances of larval fish were determined by draining the entire contents of the enclosures through a 303-μm mesh net.

Prey selection patterns of the medusae in the enclosure were determined by two independent techniques: (1) From differences in zooplankton abundance between the enclosures with and without medusae added. Analysis of variance was used to determine significance of differences in zooplankton abundance between the enclosures with and without medusae added. Differences in abundances of prey species between the two enclosures were used to determine prey selection. (2) From gut content analysis of all medusae removed at the end of the experiment. Gut contents, digestion rates and the

electivity index "C" were used to determine prey selection as described above.

Results

Field study

Aurelia aurita were present at all three stations. Abundances ranged from 0.5 to 30 m^{-3} and were highest at the Providence River and Greenwich Bay stations (Fig. 1). Medusa diameter increased from a minimum of 2.8 mm in early March to a maximum of 37 mm at the end of April. Copepods (primarily *Acartia hudsonica* and *Oithona similis*) were always the most abundant zooplankton (Fig. 1). Two species of hydromedusae, *Obelia sp.* and *Rathkea octopunctata*, were present in lower numbers until late March.

Gut content data from medusae removed from the 1000-µm mesh tows were left uncorrected for losses due to preservation because these losses proved to be negligible. Only 3 of 53 medusae regurgitated gut contents upon addition of preservative and these had fed on, but not fully completed ingestion of, fish larvae. We did observe that very small medusae in samples preserved for more than 1 yr had become fragile and prey could be inadvertently dislodged from the gastric pouches, so only those samples analysed within a year of collection are reported here.

Several trends were clearly apparent in the gut content data. Species composition of prey recovered from *Aurelia aurita* was very similar across stations on the same date but varied considerably with time, and hence, with medusa diameter (Table 1, Fig. 2). Gut contents of medusae 3 to 12 mm diameter contained almost exclusively hydromedusae while gut contents of medusae greater than 14 mm diameter contained more calanoid copepods (Fig. 2 A). A decline in numbers of hydromedusae in Narragansett Bay after 1 April 1988 was correlated with the change in diet. On 15 April both large and small medusae of *A. aurita* were collected simultaneously, allowing a comparison of the diet of small medusae with that of larger medusae during this period of reduced hydromedusan abundance. Very few of these small medusae (averaging 9 mm) had fed (Fig. 2 B) and, while hydromedusae were still present in the diet, copepods made up a larger fraction of prey. In contrast most larger medusae had fed and calanoid copepods were very numerous in the diet, although hydromedusae were also eaten (Table 1, Fig. 2).

Gut contents of medusae collected at night did not differ from daytime data in any consistent way. At one station fewer prey were found in guts at night, while at the other station, more prey were found at night. Types of prey consumed were not apparently different during the day or night (Table 1).

There was significant positive electivity for hydromedusae on every date for every size class of medusae (Table 2). There was significant negative electivity for copepods by small medusae. Larger medusae from Narragansett Bay exhibited no significant selection for or against copepods except on one date. Electivities for copepod nauplii were always negative.

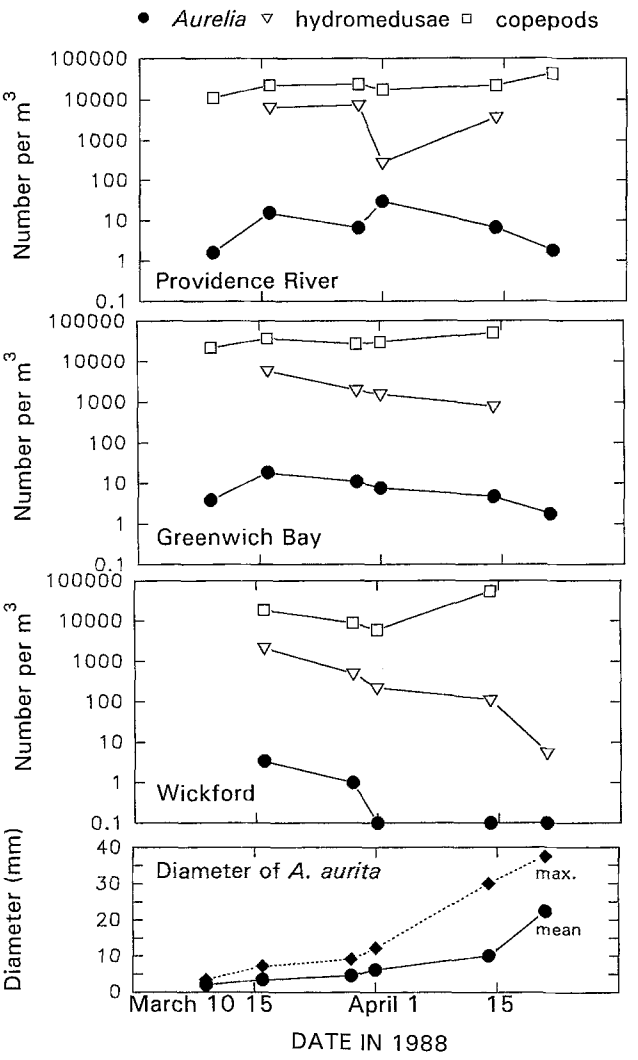

Fig. 1 *Aurelia aurita.* Abundances of the scyphomedusan and two prey types (hydromedusae and copepods) at three stations in Narragansett Bay during March and April of 1988. Average diameters (continuous line) and maximum diameters (dotted line) of individual *A. aurita* pooled for all stations

Laboratory study

Initial samples to characterize zooplankton composition of the mesocosms immediately after they were filled indicated that *Aurelia aurita*, which are usually rare in lower Narragansett Bay, were not initially present in either enclosure (Fig. 3). Zooplankton samples were dominated by copepods (primarily *Acartia hudsonica* and *Oithona similis*), and no hydromedusae were present in the plankton at that time. Total zooplankton abundances in the enclosure with *A. aurita* were significantly reduced relative to abundances in the control enclosure after 4 d (Fig. 3). Numbers of juvenile copepods (copepodites) actually increased in

Table 1 *Aurelia aurita* gut contents. Medusae from Narragansett Bay (1988 and 1990) and a mesocosm (*MERL*) enclosure (1990). Location 1: Providence River; Location 2: Greenwich Bay; Location 3: Wickford Cove. Number of each prey type recovered reported. "Other" refers to rotifers for small medusae and a combination of rotifers, harpacticoid copepods and cladocera for medusae ≥8.0 mm. Medusa diameters (mean ± SD) were measured on preserved specimens

Date	Location	No. medusae	Diameter (mm)	Total prey	Calanoid copepods	Copepod nauplii	Barnacle nauplii	Harpacticoid copepods	Hydromedusae	Other
1988										
Mar 11	1	10	2.3±0.8	5	0	0	0	0	4	1
	2	25	2.8±0.6	7	2	1	1	0	0	3
Mar 18	1	25	3.3±0.8	22	0	0	0	0	20	2
	2	25	3.3±0.8	18	0	0	0	0	16	2
	3	25	3.5±0.7	14	0	0	1	0	10	3
Mar 29	1	25	4.6±1.8	48	1	0	2	0	40	5
	2	25	3.5±1.4	31	1	0	1	0	29	0
Apr 1	1	71	5.6±2.5	66	3	0	2	5	56	0
	1 night	70		11	1	0	0	0	10	0
	2	23	5.8±2.8	12	1	0	0	0	11	0
	2 night	28		30	6	0	2	1	21	0
Apr 15	1	38	8.0±3.2	37	9	7	0	0	16	5
		9	20±4.1	74	30	8	2	4	23	7
	2	31	8.9±2.2	10	3	4	0	0	0	3
		30	22.2±3.9	151	30	56	25	10	9	21
Apr 22	1	26	14.9±3.6	110	44	41	5	10	1	9
	2	3	34±4.3	35	18	1	7	6	0	3
1990										
Apr 6	2	20	17.8±4.0	95	38	3	27	5	16	6
Apr 20	2	20	22.0±4.2	136	48	4	34	3	9	38
Apr 13	Enclosure	32	26.6±4.1	215	45	25	98	24	0	23

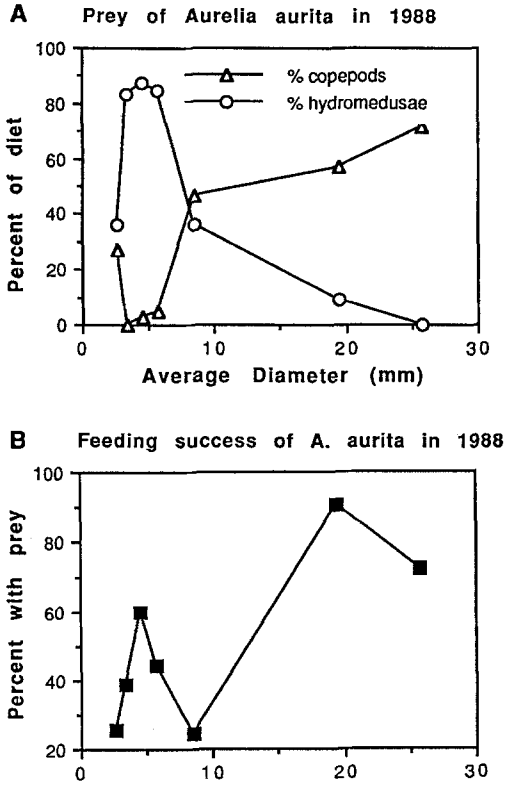

Fig. 2 *Aurelia aurita*. Data from Narragansett Bay, all stations sampled in 1988 combined. **A** Dominant prey types recovered from gut contents plotted versus medusa diameter. **B** Percent of individuals in each size category containing prey

both enclosures during the 4-d experimental period. This was to be expected because April is the period of most rapid population growth for spring species of copepods in Narragansett Bay (Durbin and Durbin 1981). Predation by *A. aurita* apparently did not prevent an increase in copepods but did reduce the size of the increase relative to that in the enclosure without predators.

Diet of *Aurelia aurita* in the enclosure consisted primarily of copepods, barnacle nauplii, harpacticoid copepods and fish larvae (Fig. 4). Electivity calculations based on gut contents indicated that far more barnacle nauplii and fewer copepods were ingested than would be expected from the relative abundance of these taxa in the plankton (Table 2). These electivity values were corrected for differing digestion times of copepods and larval fish, which we measured to be 3.5 ± 1.2 and 2.3 ±0.1 h, respectively. Gut analysis of *A. aurita* collected from mid-Narragansett Bay during the same time period as the enclosure experiment indicated that a large number of barnacle nauplii naturally occurred in their diet (Table 1). In the enclosure, electivity was not significantly different from zero for harpacticoid copepods (+0.04) and larval fish (+0.02). Calculation of prey types consumed based on abundance differences between mesocosms with and without medusae resulted in nearly identical values to those calculated from gut content analysis (Fig. 4).

Table 2 *Aurelia aurita*. Electivity values (the index "C") for selected prey types consumed. Prey species were grouped into broad taxanomic categories (i.e., all species of calanoid copepods). Environmental concentrations of plankton were obtained from counts of 20-μm mesh screened samples for all prey except copepodite and adult copepods, whose abundance was estimated from 202 μm-mesh net tows. Some dates for which gut contents are available (Table 1) omitted because data on environmental concentration of zooplankton were missing. Values significantly different from no selection ($p \leq 0.1$) indicated with asterisk. If a particular prey was not found in the guts, this is indicated with a dash. Electivities from the enclosure study were corrected for digestion time of each prey type

Date	Stn	Diameter (mm)	Hydromedusa	Calanoid copepods	Barnacle nauplii	Copepod nauplii
1988						
Mar 18	1	3.3	+0.75*	–	–	–
	2	3.3	+0.74*	–	+0.01	–
	3	3.5	+0.68*	–	–	–
Mar 29	2	4.5	+0.86*	–0.88*	+0.10	–
Apr 1	1	5.6	+0.77*	–0.50*	+0.02	–
	2	5.8	+0.72*	–0.13	+0.02	–
Apr 15	1	8.0	+0.54*	+0.13	–	–0.49*
		17–30	+0.33*	+0.29*	+0.09	–0.53*
	2	8.9	–	+0.05	–	–0.15*
		14–25	+0.18*	+0.08	+0.34*	–0.44*
1990						
Apr 13	Enclosure	26.6	–	–0.21*	+0.22*	No data

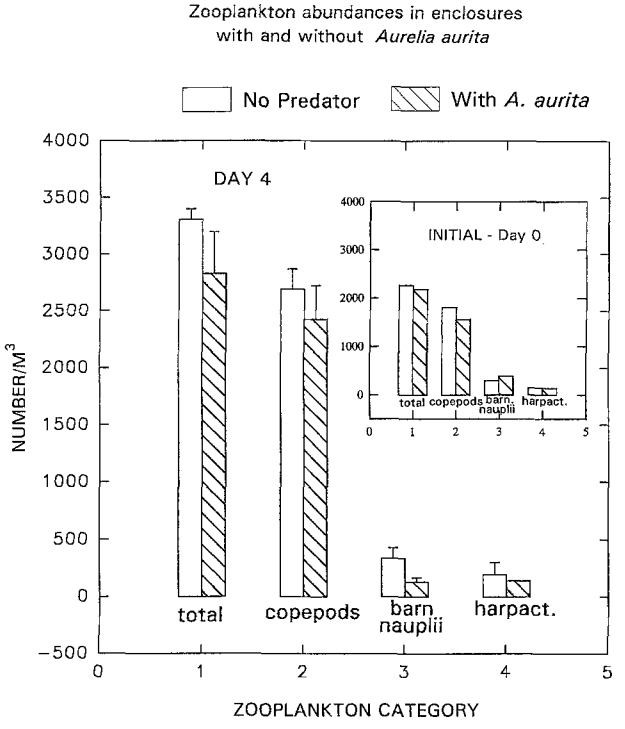

Fig. 3 Plankton abundances in MERL enclosures with and without *Aurelia aurita*. Error bars indicate SD of three replicate net tows (202-μm mesh) in each enclosure. Insert indicates starting conditions before adding medusae; main graph indicates abundances 4 d later. A two-factor (tank and species) analysis of variance on log 10 transformed abundance data for all species indicated significant difference between enclosures with and without *A. aurita* ($p < 0.01$; interaction term, $p < 0.1$); (*harpact* harpacticoids)

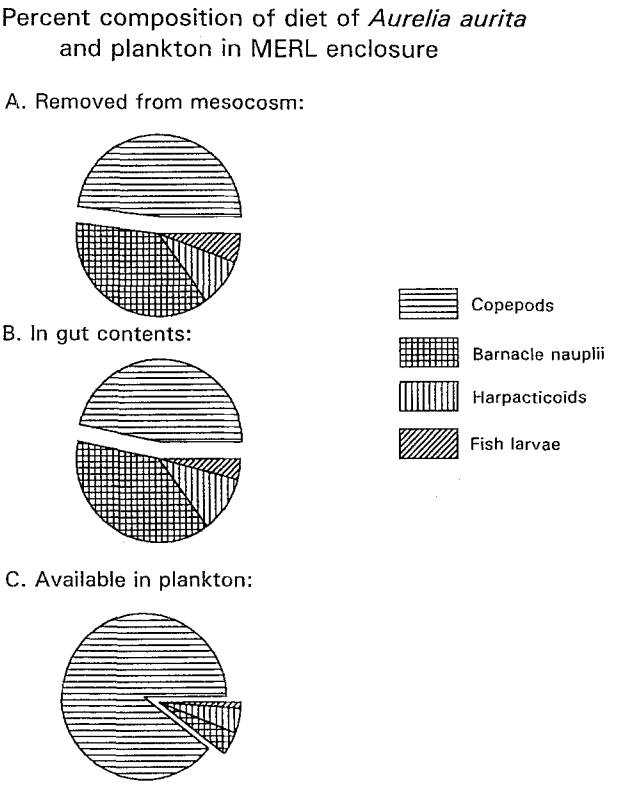

Fig. 4 *Aurelia aurita*. Percent composition of the diet in enclosure experiment. **A** Values obtained from differences in plankton abundances in mesocosms with and without medusae (shown in Fig. 3). **B** Values obtained from gut analysis. **C** Composition of plankton at

Discussion

Aurelia aurita clearly "selected" certain prey types over others. By this we mean that diet could not have been predicted solely from a knowledge of prey abundances in the environment. Soft-bodied hydromedusan prey, and one crustacean prey, barnacle nauplii, were preferred prey types over the more abundant copepods. The data also strongly suggest that small medusae, < 10 mm diameter, rarely fed on calanoid copepods. In fact, very few small medusae contained any visible prey remains when hydromedusae were rare. Larger medusae ingested more calanoid copepods than smaller ones, but also contained other, less abundant prey types in higher numbers than would have been predicted from relative abundance of these prey types in the plankton.

Our data are consistent with other studies indicating prey selection by *Aurelia aurita* (Delap 1907; Bailey and Batty 1983; Stoecker et al. 1987), but the mechanisms governing prey selection were not immediately evident to us, especially since the preferred prey, hydromedusae and barnacle nauplii, are such dissimilar taxa. Since one of our goals was to develop a greater predictive capability for prey consumed in novel environments, we looked to the model of Costello and Colin (1994) for insight.

We propose that medusa – fluid interactions are useful for explaining why particular prey types were important in the diet of *Aurelia aurita*. Costello and Colin (1994) hypothesize that relative speeds of the medusan flow field (termed the marginal flow velocity) and prey escape speeds should successfully predict prey selection patterns. Positively selected prey should be characterized by escape speeds slower then the marginal flow velocities of a medusa; negatively selected prey escape by swimming faster than marginal flow velocities. Larger bell diameters are associated with higher marginal flow speeds, allowing faster prey to be captured as the medusa grows. In fact, prey selected by *A. aurita* in our study, hydromedusae and barnacle nauplii, have very slow or negligible escape responses (Costello and Colin 1994). Also consistent with their predictions was our finding that prey selection changes with increasing medusa diameter – prey with faster escape responses (copepods) were more readily consumed by the larger medusae and the smaller medusae were apparently rarely able to capture copepods. Costello and Colin (1994, Fig. 7 therein) indicate that live medusae ca. 30 mm in diameter (22.6 mm diameter in preserved medusae) should be able to capture copepod nauplii but that older calanoid copepods have such rapid escape velocities that their capture by the marginal flow mechanism appears prohibited even by much larger medusae. We found that gut contents of medusae larger than 10 mm diameter (preserved) contained copepod nauplii and older copepod stages as well (Table 1, Fig. 2). Capture of copepods by medusae of the size classes reported here is not explained by the marginal flow mechanism proposed by Costello and Colin (1994) and may occur by another mechanism. Alternatively, poorly understood aspects of copepod escape behavior may alter the simple relationship proposed between escape velocity and marginal flow capture. The latter possibility is supported by evidence that copepods exhibit complex behavioral responses to mechanical stimuli which may affect their escape abilities (Costello et al. 1990; Marrase et al. 1990) and by experiments of Haury et al. (1980) showing that 29% of adult copepods escaped in the wrong direction, directly into the path of their presumed predator.

We also observed more negative electivity values for copepod nauplii than for older copepods (Table 2), the reverse of the pattern expected if escape speeds are the only factor governing capture of these prey types. Given that negative electivities for copepod nauplii have also been observed by Purcell (1992) for another scyphomedusa, *Chrysaora quinquecirrha*, future research efforts might well be directed at defining differences in patterns of encounter and capture involving nauplii versus copepodite and adult copepods.

Our data confirm the prediction of the model of Costello and Colin (1994) that weakly swimming prey will be preferentially captured. The specific details of a model that explains how larger medusae catch fast moving prey have yet to be worked out. While not entirely consistent with our data, the model has provided a valuable framework for its interpretation and insights which were not obvious from the gut content data alone. In turn, the data suggest refinements needed in the model. Other models of predation which do not account for escape patterns of prey, such as those which rely on encounter probabilities to predict diet (Gerritson and Strickler 1977), do not appear to fit the data as well as that of Costello and Colin (1994). If encounter probabilities dominated the capture process, one would expect that faster moving prey, such as copepods, would always dominate the diet. Our data indicate that prey escape speeds are one important factor governing which prey will be captured but that a full understanding of predation mechanics awaits further investigation of both predator and prey behaviors.

We also suggest that important inferences concerning the nutrition of young (small) medusae can be drawn from the data we have presented. Successful development may be very dependent on an abundant supply of slowly escaping prey types. In our study these prey appeared to be hydromedusae, which were very evident in the gut contents. It is also possible that nutrition of young medusae may depend on food sources or prey types, such as microzooplankton, which do not leave visible remains in the guts. *Aurelia aurita* is known to consume microzooplankton, but the relative importance of these prey in their diet has been little studied. Our own data suggest that ingestion of relatively few hydromedusae could supply a daily ration of 25% body carbon for medusae 6 mm in diameter, whereas feeding rates on smaller prey must be quite high to supply equivalent amounts of carbon (Table 3). In fact, frequency of hydromedusae in the guts of 3 to 6 mm diameter *A. aurita* ranged from 0.4 to 1.2 medusa^{-1} (Table 1). Using preliminary unpublished data we estimate a 6-h digestion time for 3 to 6 mm medusae feeding on *Rathkea octopunctata*. This allows calculation of feeding rates ranging from 1.6

Table 3 *Aurelia aurita*. Feeding rates of medusae (6 mm diameter) necessary to achieve a daily ration of 25% (% body C d^{-1}) on the designated prey type. Feeding rate (no. of prey d^{-1}) calculated assuming a carbon weight of 61 µg ephyra^{-1} based on the regression for diameter versus C developed by Matsakis and Conover 1991. Carbon weights for prey based on sources indicated

Prey category	Carbon (µg)	Feeding rate (no. d^{-1})	Source
Ciliates	0.02	750	Putt and Stoecker (1989)
Nauplii[a]	0.05	300	Durbin and Durbin (1978)
Copepod[b]	2.50	6	Durbin and Durbin (1978)
Rathkea octopunctata			
Juvenile	2.49	6	Matsakis and Conover (1991)
Adult	3.89	4	

[a] Nauplius of *Acartia clausi*, Stage N IV, assuming carbon 50% dry weight
[b] Copepodite of *A. clausi*, Stage C V

to 4.8 *R. octopunctata* d^{-1}, a rate sufficient to obtain a significant proportion of the daily ration needed for growth. On the other hand, carbon requirements would be difficult to meet unless feeding rates on nauplii or ciliates were very high (Table 3).

Young *Aurelia aurita* may feed primarily upon relatively large prey with slow escape responses. This observations has broad applicability among the scyphomedusae because morphology and size of the early developmental stages are similar. It is a conclusion that is also consistent with the detailed, if qualitative, observations of early investigators of nutrition in scyphomedusae (reviewed by Russell 1970) that *Chrysaora* spp., *Cyanea* spp. and *Aurelia* spp. were dependent on a diet of hydromedusae and ctenophores.

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