

Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*

R. Waggett¹ and J.H. Costello²

Biology Department, Providence College, Providence, RI 02918-0001, USA

¹Present address: Marine Science Institute, University of Texas at Austin, Port Aransas, TX 78373-1267, USA

²To whom correspondence should be addressed

Abstract. Although the lobate ctenophore *Mnemiopsis leidyi* is an influential planktonic predator, the mechanisms enabling it to capture its characteristically wide range of prey have not been systematically examined. We recorded interactions between free-swimming *M.leidyi* and two stages (nauplii, adults) of the calanoid copepod *Acartia tonsa* in order to determine a mechanistic explanation of this feeding process. Prey encounter with *Mnemiopsis* involved two different processes. The first depended on fluid motions created by the nearly continuous beating of cilia lining the four auricles. These cilia created a low-velocity flow in which *A.tonsa* nauplii were entrained (94% of naupliar encounters) and transported past the oral lobes onto the tentillae (oral tentacles). The nauplii, although capable of rapid escape responses, generally appeared to be insensitive to the current in which they were carried. The second process relied upon the collision of swimming prey with the inner surfaces of the oral lobes and was not obviously influenced by the auricular feeding currents. Adult *A.tonsa* were rarely entrained in the auricular flow, but, instead, propelled themselves into contact with the oral lobes (97% of adult encounters). Both prey capture processes functioned simultaneously. The synergistic functioning of these processes probably explains the broad patterns of prey ingestion found by *in situ* studies of *Mnemiopsis* feeding.

Introduction

Ctenophores are common marine predators and are distributed throughout the world's oceans in both surface and deep waters (Harbison *et al.*, 1978). However, their predatory impact on planktonic systems has been most fully documented in coastal environments. Copepods (Bishop, 1967, 1968; Burrell and Van Engel, 1976; Reeve and Walter, 1978; Kremer, 1979; Mountford, 1980), fish eggs and larvae (Purcell, 1985; Monteleone and Duguay, 1988; Cowan and Houde, 1992, 1993; Houde *et al.*, 1994; Purcell *et al.*, 1994) and veliger larvae (Nelson, 1925; Purcell *et al.*, 1991) are all consumed by coastal lobate ctenophores. The impact of these predators on coastal ecosystems can be profound and recent introductions of the lobate ctenophore *Mnemiopsis leidyi* have altered plankton trophic dynamics and disrupted commercial fisheries in the Black Sea (Shushkina and Musayeva, 1990; Shushkina and Vinogradov, 1991; Zaitsev, 1992; Malyshev and Arkhipov, 1993) and the Sea of Azov (Studenikina *et al.*, 1991). Therefore, predation by lobate ctenophores, particularly *M.leidyi*, can be both ecologically important to nearshore planktonic community structure and commercially important due to its potential impact on fisheries production.

The mechanical bases of prey capture by lobate ctenophores have been variously described by a number of researchers. Early researchers emphasized the importance of cilia on the auricles (Figure 1) of lobate ctenophores such as *M.leidyi* (Main, 1928; Hyman, 1940) and *Bolinopsis infundibulum* (Nagabhushanam, 1959) for

creating flow and influencing prey capture. *In situ* observers of lobate species also noted the importance of auricular currents and motions in the initiation of contact between prey and lobes or tentacles (Harbison *et al.*, 1978; Hamner *et al.*, 1987; Matsumoto and Hamner, 1988; Matsumoto and Harbison, 1993). The most recent laboratory research on lobate feeding mechanisms has focused on the essential role of the oral lobes for prey capture (*Mnemiopsis*, Reeve and Walter, 1978; *Bolinopsis*, Schulze-Robbecke, 1984). These studies emphasize the importance of swimming prey impinging on and adhering to the inner surfaces of the oral lobes. After entrapment on the lobes by sticky colloblast cells (Franc, 1978) or mucus, prey are transferred to ciliated oral grooves and transported to the mouth (Reeve and Walter, 1978). Based on these observations, lobate ctenophores such as *Mnemiopsis* have been characterized as ambush predators that either sit passively or glide slowly through the water column and capture prey that swim into their outstretched lobes.

This view of ctenophores as ambush predators is consistent with their ability to capture relatively rapidly swimming calanoid copepods. Plankton foraging

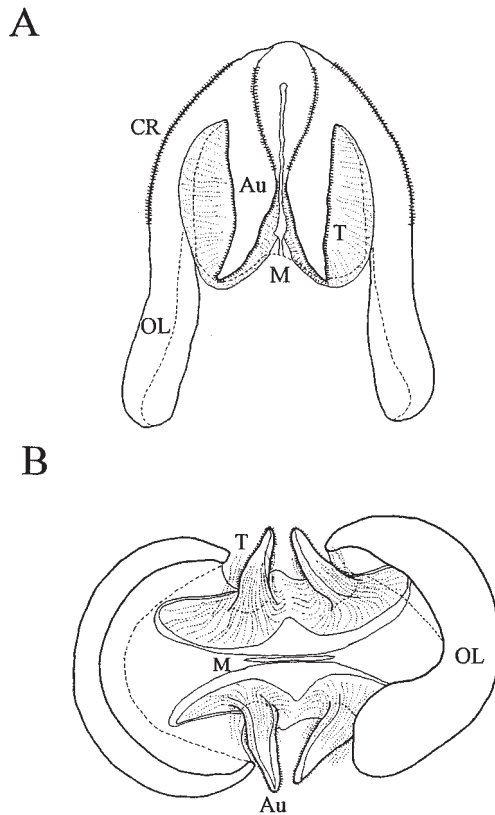


Fig. 1. *Mnemiopsis leidyi*. (A) Tentacular view. (B) Oral view. CR, ctene row; OL, oral lobe; Au, auricle; M, mouth; T, tentillae.

models (Gerritsen and Strickler, 1977) predict that a slow-moving or stationary ambush predator would encounter primarily rapidly moving prey. Therefore, actively moving prey such as late stage calanoid copepods are expected prey items for lobate ctenophores. This expectation is in agreement with studies documenting higher clearance rates for *M.leidyi* on mixed zooplankton assemblages consisting of calanoid copepods or cladocerans compared to those dominated by cyclopoid copepods or veliger larvae (Kremer, 1979). These results resemble those for tentaculate ctenophores such as *Pleurobrachia bachei* (Greene *et al.*, 1986) and imply that prey selection can be predicted based on prey swimming speeds and vulnerability after contact with the ctenophore.

Although this model describes capture of late stage calanoid copepods, it does not adequately explain capture of non-motile or slowly swimming prey. Field studies have demonstrated that *M.leidyi* may be an important predator of veliger larvae (Nelson, 1925; Burrell and Van Engel, 1976; Larson, 1987a) and fish eggs (Cowan and Houde, 1993). Neither of these prey types are highly motile and, based solely on encounter rate considerations, they would not be expected to be major prey items. However, clearance rates of *M.leidyi* on fish eggs and larvae may be greater than those on copepods (Monteleone and Duguay, 1988). *In situ* gut content studies (Larson, 1987a) of *Mnemiopsis mccradyi*, a congener of *M.leidyi*, demonstrate that some low-motility prey such as bivalve larvae may be positively selected in nature (as well as barnacle nauplii, calanoid and harpacticoid copepods). These data demonstrate that a simple ambush predation model does not adequately explain *M.leidyi*'s feeding patterns.

The goal of this study was to describe prey capture mechanisms quantitatively by direct observation of lobate *M.leidyi* interacting with prey characterized by different behavioral and morphological traits. We chose a prey species, the copepod *Acartia tonsa*, which is commonly encountered and consumed by *M.leidyi* in Narragansett Bay (Kremer, 1979; Deason, 1982; Deason and Smayda, 1982). *Acartia tonsa*, in common with all copepods, has a life history characterized by early naupliar stages which are morphologically and behaviorally different from later copepodite and adult stages. Previous *in situ* research (Larson, 1987a) demonstrated that *M.mccradyi* positively selects adult relative to naupliar copepod stages, and laboratory observations and Larson (1988) indicated variable capture mechanisms for these two copepod life stages. By documenting the predation process for these two prey types, we intended to quantify the influential variables affecting capture success by *Mnemiopsis*.

Method

Collection and maintenance of experimental organisms

Mnemiopsis leidyi were collected from July to October 1995 from Narragansett Bay in Barrington, RI, USA, by hand dipping into small jars. Ciliary activity and flow field experiments were performed within 72 h of ctenophore capture. Other ctenophores were maintained in the laboratory at Providence College, Providence, RI, USA, at 20°C for feeding experiments. Ctenophores maintained in the laboratory during this period grew at low rates and appeared to be in good

condition. Several cydippid stage ctenophores metamorphosed to lobate stages and many lobate individuals increased in length. These laboratory-maintained ctenophores were used in video recordings of the predation process during October–December 1995. *Acartia tonsa* copepods collected at the same site were cultured at 20°C in the laboratory until used for experimental work.

Tethering

Flow field and ciliary activity measurements were made with tethered *M.leidy*. Ctenophores were tethered by attaching a capillary pipette under slight vacuum to the apical point of the aboral end of the ctenophore near the statocyst. Practiced application of suction allowed attachment of a ctenophore to the pipette for periods up to 0.5 h without damage or apparent aberrant behavior. Longer durations of tethering often led to tissue deformation adjacent to the tether. Ctenophores used in tethered experiments swam and fed normally after release from the tether. When fed and maintained in the laboratory, these ctenophores grew and exhibited no damage as a result of the tethering process.

Microvideography

Standard rate video recordings (SVHS) using a backlit optical system (Costello and Colin, 1994) were used to detail movements of ctenophores, prey and tracer particles. A field counter labeled each sequential video frame (1/60 s per field) in order to provide temporal information. Spatial characteristics of the optical field were determined from scale bars periodically included in the recordings. Interference from motions in the unmeasured third dimension was minimized by limiting the image depth of field and by selecting particles in the focal plane for analysis. The optical system provided clear illumination of particles as well as their movements relative to the ctenophore.

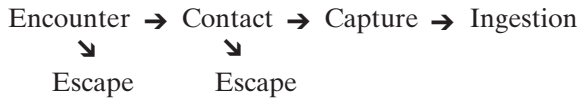
Tethered ctenophores were videotaped in a 2 l rectangular vessel. Flow patterns were visualized using fluorescein dye added with a syringe. Quantitative description of the fluid motions around *M.leidy* utilized *Artemia* sp. cysts tracked in the fluid surrounding a tethered ctenophore. Velocities in different parts of the flow field were derived from changes in cyst positions during five-field intervals (1/12 s) while the cysts passed from outside the lobes through the auricle area and beyond to the ctene rows.

Feeding studies

Adult and naupliar *A.tonsa* copepods used in feeding studies were first separated by sieving through sequential 100-, 60- and 30- μ m-mesh filters. One hundred adults were then selected individually from the 100 μ m fraction with the aid of a dissecting microscope. The adults were added to a 300 ml vessel containing 200 ml of 0.2- μ m-filtered sea water and one lobate *M.leidy* (ranging in total length from 1.5 to 2.0 cm). Four hundred nauplii of mixed stages were selected individually from the 30 μ m fraction, and added to other experimental vessels prepared

identically to those of the adult copepods. Encounters between ctenophores and copepods were recorded for ~20 min per individual ctenophore. Ctenophores selected for study were all lobate stage, but <2 cm in total length. This size group was chosen in order to minimize the disparity in dimensions between predator and prey. *Acartia tonsa* nauplii were <0.5 mm in length, and simultaneous imaging of ctenophore capture surfaces as well as prey motions was possible only when using small lobate *M.leidyi*.

Video segments in which freely swimming ctenophores and copepods interacted were analyzed frame by frame. Encounters between ctenophores and copepods were individually quantified and recorded. Interaction sequences were categorized using the terminology and criteria in Table I. Behaviors were typically related in a sequence adapted from a variety of sources (Gerritsen and Strickler, 1977; Madin, 1988):



In our study, capture always led to ingestion, so we did not emphasize the ingestion stage in our analysis. Patterns of copepod–ctenophore encounters were tabulated and classified by prey type.

The efficiency with which prey were retained after contact was measured as retention efficiency, where:

$$\text{Retention efficiency} = \frac{\text{number of captures}}{\text{number of contacts}} \times 100$$

Retention efficiency is a measure of the mechanical efficiency of the predator capture surfaces and was determined for the several portions of the ctenophore’s body which came into contact with prey.

Statistical analysis relied upon the χ^2 test (Statistica, Statsoft Inc.). Observed counts, rather than percentages, were used in all tests.

Results

Cilia and flow fields

Two distinctly different ciliary systems affected prey entrainment and capture by lobate *M.leidyi*. Cilia comprising the ctene rows (Figure 1) provide the propulsive force used in swimming and maintenance of position within the water column. Ctene row activity was highly variable (Figure 2) and stroke direction was reversible. In contrast, cilia lining the auricles beat essentially continuously (Figure 2) and unidirectionally. Occasionally, the auricular cilia ceased beating and the lobes closed rapidly, causing particles and debris which had collected in the body cavity surrounding the base of the auricles to be ejected.

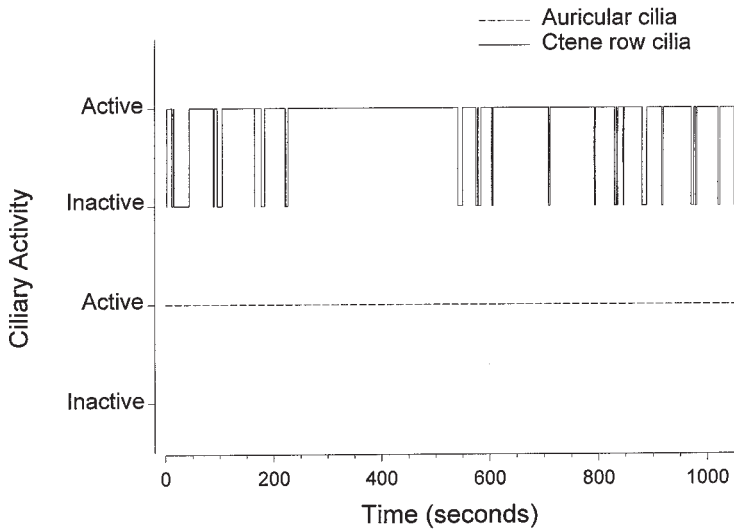


Fig. 2. A comparison of the activity of ctene rows and auricular cilia for an individual, tethered *M.leidy*. Note the irregular activity of the ctene rows and continuous beating of the auricular cilia.

Table I. Predation event categories

Behavior	Criteria
Encounter	Interaction between ctenophore and copepod within the encounter zone. Initiated either by direct contact between ctenophore and copepod or by an anticipatory response (e.g. oral lobe folding) by ctenophore prior to contact with copepod. The encounter zone was defined as the area bounded on the sides by the interior lobes of the ctenophore and extending anteriorly to the lobes for 3 mm (~2 <i>A.tonsa</i> bodylengths). Encounters resulted in either an escape from the encounter region or capture of the copepod by the ctenophore.
Contact	Physical collision of predator and prey bodies. An encounter could entail multiple contacts if the copepod was not retained and collided with another portion of the ctenophore's capture surfaces. Contacts with exterior portions of the ctenophore's body (e.g. lobe exterior) were not recorded as contacts because these could not result in capture and were outside the encounter zone.
Escape	Evasion of capture by a copepod after encounter with a ctenophore; the copepod must have left the encounter zone. Contact was not required.
Capture	Copepod subdued and consumed by ctenophore.

The auricular cilia did not contribute to forward motion and continued to beat even when a free-swimming ctenophore was stationary in the water column. Flow created by the ctene rows entrained fluid from areas adjacent to the ctene rows. Particles entrained in this fluid passed aborally alongside the exterior midbody, but did not enter the interlobe region where prey were captured (Figure 3). Dye and inert particles entrained in the flow generated by the auricular cilia traveled between the oral lobes and past the auricles. Large particles carried by this flow often contacted either the auricles or the tentillae adjacent to the ciliated food

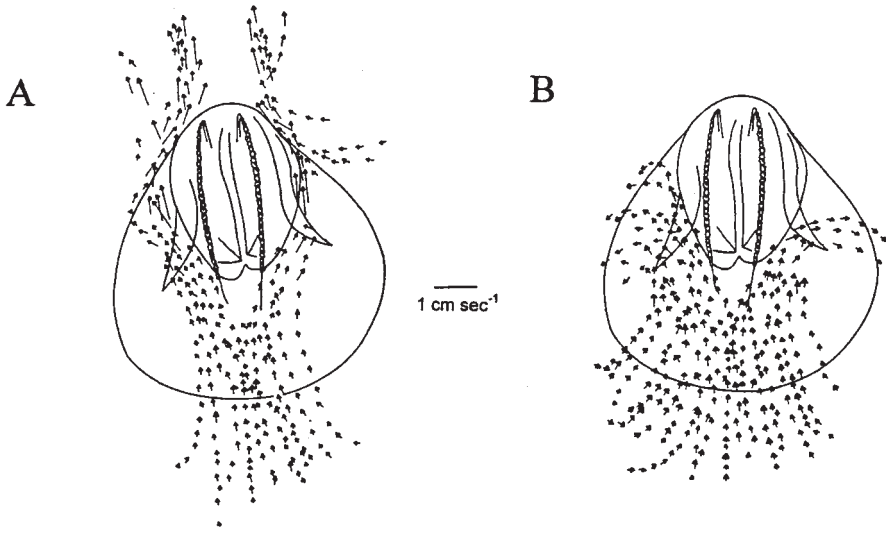


Fig. 3. Flow fields of tethered *M.leidyi* with (A) and without (B) ctene row beating. Auricular cilia were beating in both cases. Ctenophore length 2 cm. Vectors represent velocity data for flow between the oral lobes.

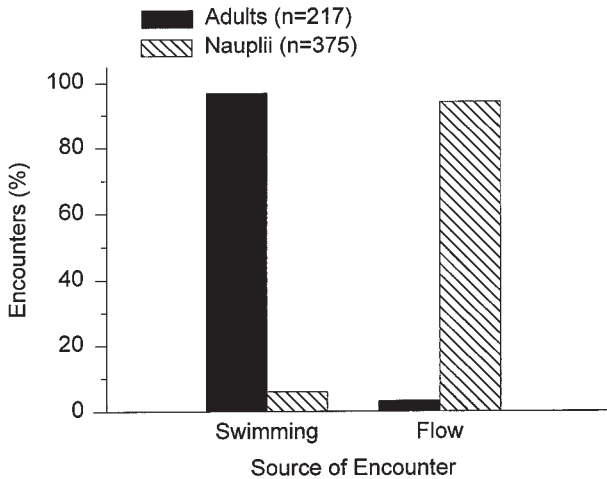


Fig. 4. The proportion of *A.tonsa* adult and naupliar encounters with the ctenophore, *M.leidyi*, attributed to either a self-propelled approach by the copepod (Swimming) or entrainment of the copepod in the auricular flow field (Flow). The total number of recorded encounters (n) is listed for adults and nauplii.

groove leading to the mouth (Figure 1). The auricles of *M.leidyi* are flexible and, when contacted by a particle or prey item, actively redirected the particle towards the tentillae. The tentillae themselves were flexible and retractable. Generally, the tentillae streamed aborally in the auricular flow from their origins at the

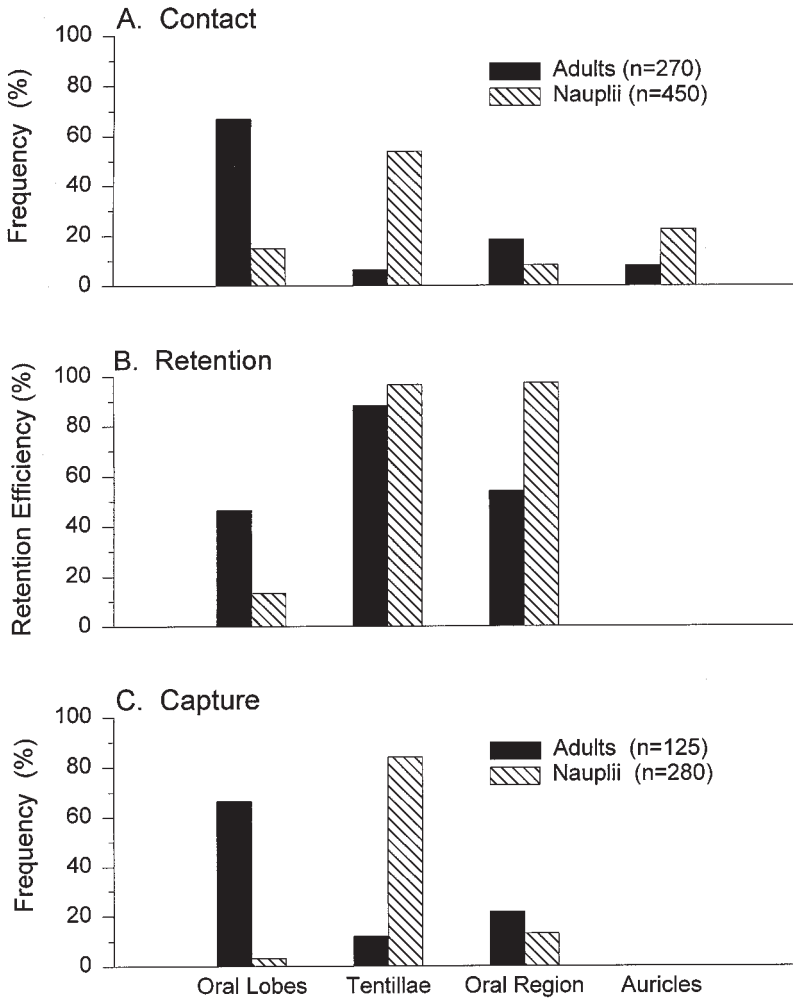


Fig. 5. The proportions of *A.tonsa* adult and nauplii contacts (A), the efficiency with which they were retained (B) and the location of capture (C) for different body surfaces of the ctenophore *M.leidy*. The total number (*n*) of recorded contacts and captures is listed for adults and nauplii.

margin of the oral groove. At full length, the tentillae sometimes extended past the auricles and outside the body of the ctenophore into the surrounding fluid.

The predation process: stage-dependent variations in capture of Acartia by Mnemiopsis

The two copepod life stages encountered free-swimming *Mnemiopsis* differently (χ^2 , $P < 0.0001$; Figure 4). Nauplii were most commonly entrained within the auricular flow field. In contrast, adult *A.tonsa* typically initiated encounters by swimming into the vicinity of the ctenophore.

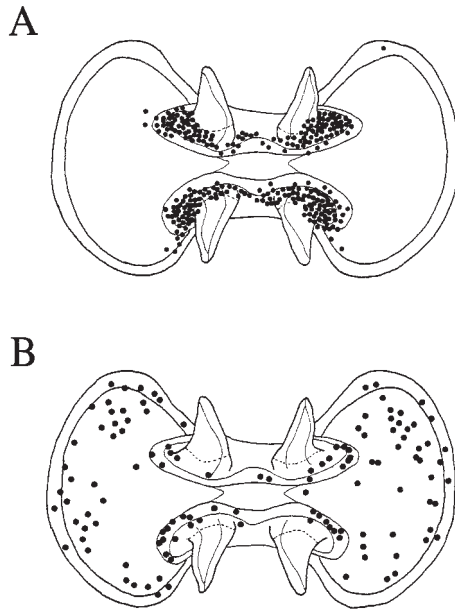


Fig. 6. Composite image summing individual prey capture locations on the ctenophore *M.leidyi*. **(A)** Capture locations of *A.tonsa* nauplii (based on captures by six ctenophores). **(B)** Capture locations of *A.tonsa* adults (based on captures by nine ctenophores).

The morphological site at which *Acartia* made contact with *Mnemiopsis* also varied greatly between the two groups of copepods. Nauplii entrained in the auricular flow passed between the oral lobes and made first contact with tentillae, the auricles or the region surrounding the mouth itself, including the oral groove (Figure 5A). Late stage copepods occasionally contacted these surfaces; however, the major contact sites of late stage copepods were the interior surfaces of the oral lobes. In contrast, few (<20%) of the nauplii contacted the oral lobes.

The body location at which capture occurred closely resembled patterns of contact distributions (Figure 5). An important difference between these patterns was the absence of captures on the auricles. Prey which contacted the auricles (nauplii more frequently than adults) subsequently either escaped or contacted one of the other capture surfaces. Most nauplii were captured on the tentillae (84%), whereas most adults (66%) were captured on the oral lobes (Figure 5C). A composite map of capture site distributions (Figure 6) illustrates the difference in capture locations between the two copepod groups.

Differences in capture locations between the two copepod groups were not explained by differences in retention rates of various capture surfaces for the two copepod groups. High retention rates and high proportions of capture coincided in only one case: that of naupliar capture on tentillae. In that case, high proportions of contacts by nauplii on the tentillae coupled with high retention rates subsequently resulted in high capture rates (Figure 5B). High retention rates without high contact rates did not result in high capture rates for any capture

surface. For example, the oral region was as efficient as the tentillae at retaining nauplii (97% for both the oral region and tentillae), but the low proportion of nauplii contacting the oral region resulted in a low overall contribution as a capture site. Likewise, although the high retention rate of the tentillae was not significantly different between nauplii and adults (χ^2 , $P = 0.08$; Figure 5B), the tentillae contributed a significantly lower proportion of adult than naupliar captures (χ^2 , $P < 0.0001$; Figure 5C) because few adults contacted the tentillae (Figure 5A). The primary role of contact location was further demonstrated by the predominance of adult captures on the oral lobes. The retention efficiency of adults on the oral lobes was significantly lower than that of the tentillae (χ^2 , $P < 0.0001$; Figure 5B), but, nevertheless, the oral lobes were the predominant capture surface for adult copepods (Figure 5C). In this case, the relatively low retention efficiency of the oral lobes was less important than the predominance of the oral lobes as the primary adult contact sites. Therefore, differential body surface retention efficiencies explain little of the variation in capture locations between copepod life stages. Instead, the relationship between the mechanisms by which encounters were initiated (flow entrainment versus self-propelled swimming) and subsequent contact locations largely explains capture location patterns for the two *Acartia* life stages.

Discussion

Mnemiopsis leidyi is a complex predator with an array of different structures and behavioral patterns synergistically contributing to its foraging success. Encounters with *A.tonsa* nauplii and adults revealed two major routes by which prey are encountered and captured. The first, transport via feeding currents generated by the auricular cilia, was the predominant mechanism producing encounters with the nauplii. The second mechanism, entrapment on the broad oral lobes, was effective with the larger, rapidly swimming adult *A.tonsa*. Each pathway of prey capture was suited to specific prey characteristics.

Entrainment and sieving through the tentillae selects for prey whose swimming speeds are less than the flow field velocities generated by the auricular cilia. In this study, nauplii rarely attempted to escape while being carried by the auricular flow towards the auricles and tentillae. Instead, the nauplii were often motionless and apparently unaware of their imminent capture. It is unlikely that this behavioral pattern was unusual or an experimental artifact. Similar behavior by calanoid copepod nauplii has been noted during interactions with other gelatinous predators (Sullivan *et al.*, 1997). Nauplii that did attempt to escape (most commonly when in close proximity to the auricles, oral region or tentillae) demonstrated a capacity for rapid, vigorous escape swimming. Therefore, we do not interpret the lack of escape behaviors by nauplii prior to contact as due to an inability to escape. More probably, the nauplii fail to detect the predator's presence. Previous research on *A.tonsa* swimming behavior has demonstrated that nauplii swim infrequently relative to later copepodite and adult stages (Buskey, 1994). Further, *A.tonsa* nauplii are much less sensitive to shear in flows than are adults and escape much less frequently in a suction flow (Fields and Yen, 1997).

The low velocity flows created by *M.leidyi*'s four auricles may not produce enough shear to surpass the threshold necessary to generate an escape response until the nauplii are within the curtain of tentillae floating adjacent to the auricles. In contrast, adult *A.tonsa* are more active, rapid swimmers (Buskey, 1994) and are responsive to much lower shear rates (Fields and Yen, 1997). As a result, adults would be less likely to be entrained by auricular flow fields and, if entrained, unlikely to remain passive as shear rates increased near the tentillae and auricles.

Prey capture via flow field entrainment resembles descriptions by earlier investigators and may be the mechanism underlying the capture of a wide range of non-motile and slowly swimming prey by *M.leidyi*. The description by Main (1928) of feeding by *M.leidyi* focused on capture and transport of bivalve larvae by ciliary mechanisms. Hyman (1940) considered *M.leidyi* to be primarily a mollusk larva predator that utilized feeding currents to entrain prey. Based on the work of these and other investigators, the flow-field based mechanisms we describe for capture of *A.tonsa* nauplii probably apply to non-motile prey such as fish eggs (Purcell, 1985; Monteleone and Duguay, 1988; Cowan and Houde, 1992, 1993; Houde *et al.*, 1994; Purcell *et al.*, 1994) as well as relatively slowly-swimming prey such as bivalve larvae (Nelson, 1925; Purcell *et al.*, 1991) and protozoans (Stoecker *et al.*, 1987).

The importance of feeding currents is not unique to *Mnemiopsis* among the lobate ctenophores. Nagabhushanam (1959) observed that the lobate ctenophore *B.infundibulum* relied upon auricular flow to entrain prey for capture. *In situ* observations of other lobate genera have also indicated an important role for the auricles in prey capture (Matsumoto and Hamner, 1988; Matsumoto and Harbison, 1993). Therefore, both flow field generation and auricular movements affecting prey trajectories may be important, although rarely quantified, components of the predation apparatus of a variety of lobate ctenophores.

Mnemiopsis has evolved an alternative mechanism for capture of highly motile adult calanoid copepods such as *A.tonsa*. These plankters swim too frequently and escape too vigorously to be entrained within the auricular flow field. Instead, strongly swimming prey collide with the interior surface of the large oral lobes which *Mnemiopsis* extends while swimming slowly forward or sitting in ambush. Retention efficiencies of the lobes were not high compared to the tentillae (Figure 5B), but the responsive nature of the lobes to prey presence partially compensated for the lower retention rates of copepods contacting those surfaces. The response patterns of *Mnemiopsis* to adult copepods affects the capture success of these prey and are the subject of a related study (Costello *et al.*, in press).

The relative importance of either feeding mechanism depends upon the availability of alternative prey types. When low motility or slowly swimming prey such as copepod nauplii or veliger larvae dominate the plankton, the most likely means of prey encounter and capture by *M.leidyi* would be flow entrainment and tentacle sieving. This may explain earlier observations of extensive feeding by *M.leidyi* on mollusk larvae (Nelson, 1925) and the belief that *M.leidyi* is primarily a predator upon planktonic larvae (Hyman, 1940). However, the use of oral lobes for feeding probably predominates when copepodite and adult copepods are the most

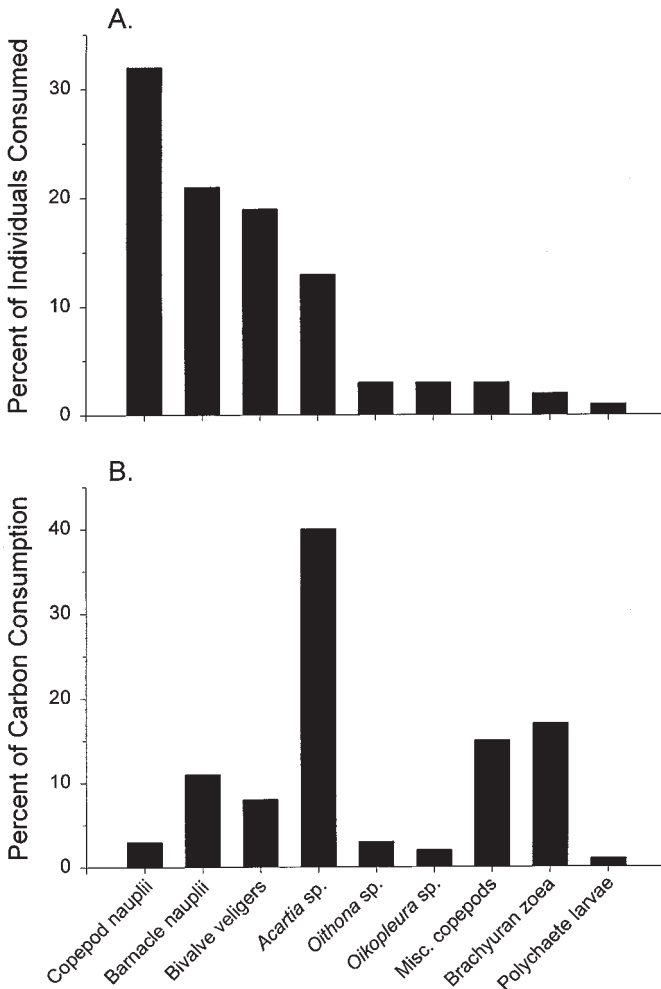


Fig. 7. *In situ* diet of *M.mccradyi*. (A) Percentage of gut contents comprised of various prey categories. Data are from Larson (1987a), but limited to prey categories contributing $\geq 1\%$ of the total number of prey in guts. (B) Approximate percentage contribution by various prey categories to total carbon intake, based on data from (A). Carbon equivalents for prey items taken from Larson (1987b) (copepod nauplii, barnacle nauplii, *Acartia* sp., *Oithona* sp., *Oikopleura* sp., miscellaneous copepods) and Ikeda (1974) (bivalve veligers, brachyuran zoeae, polychaete larvae).

numerous available prey. As a result, researchers focusing on ingestion of adult copepod prey would be expected to describe the oral lobes as the primary capture site of *Mnemiopsis* (Reeve and Walter, 1978). When a mixture of prey was available, as in the *in situ* studies of Larson (1987a), nauplii and slowly swimming prey such as veliger larvae were more frequently caught than adult copepods (Figure 7A). Barnacle nauplii were also frequently caught, but the mechanism of their capture is uncertain because, although they are poor escape swimmers, barnacle nauplii do swim frequently and may be captured primarily on the oral lobes. The

numerical dominance of copepod nauplii and slow swimmers such as veliger larvae in gut contents obscures the important fact that, from a nutritional perspective, late stage copepods were the dominant carbon contributors to *M.maccradyi*'s diet (Figure 7B). Therefore, although auricular flow and prey sieving may be the numerically dominant prey capture mechanism, collision and entrapment of late stage copepods on the oral lobes may be the pathway responsible for the greatest nutritional input to the ctenophore. Both mechanisms of prey capture are certainly important contributors to feeding by *Mnemiopsis* and, together, provide flexibility in the utilization of whichever prey component is available within the highly variable planktonic environment.

The two pathways of prey encounter and capture can function simultaneously and synergistically. Auricular cilia continued to beat and generate flow fields even as adult copepods were captured on the oral lobes. The independence of the two pathways may explain the observation that various densities of alternative large prey (*Acartia hudsonica* adults and *Artemia* sp. nauplii) did not affect clearance rates of *M.leidyi* feeding on *Anchoa mitchilli* eggs relative to treatments with eggs alone (Monteleone and Duguay, 1988). The synergistic interaction of the two pathways was demonstrated by observations of *Mnemiopsis* preying upon two copepod species (*Acartia tonsa* and *Oithona colcarva*) characterized by different motility patterns. Adult *O.colcarva* copepods swam infrequently and were entrained by the auricular flow fields generated by *Mnemiopsis*. However, once within the interlobe space, *Oithona* typically attempted to escape and most frequently contacted, and were captured on, the oral lobes (Costello *et al.*, in press). Therefore, depending upon prey characteristics, different components of the two principal capture pathways can be combined during prey capture. The complementary functioning of these mechanisms probably underlies the broad taxonomic range of prey ingested by *Mnemiopsis in situ*.

The efficiency with which *Mnemiopsis* captures different prey types is not reflected in electivity indices or comparisons of feeding rates between different prey types described in other studies. For example, Larson (1987a) found that *M.mccradyi* consumed lower proportions of copepod nauplii and *Oithona* sp. than would be expected based on the *in situ* proportions of these prey in the plankton. In other words, *Mnemiopsis* appeared to select these prey negatively. Likewise, Kremer (1979) found that *M.leidyi* feeding rates on cyclopoid copepods and veliger larvae were 25% of the rates observed when calanoid copepods or cladocerans dominated the available prey. The relatively low feeding rates on copepod nauplii and cyclopoids could be interpreted as resulting from low retention efficiencies for these prey. However, contrary to that interpretation, overall retention efficiencies of nauplii were significantly higher than for adults in this study (62% versus 46%, respectively; χ^2 , $P < 0.0001$). There was no significant difference in retention efficiencies of *Mnemiopsis* feeding on *A.tonsa* or *O.colcarva* adults (Costello *et al.*, 1999). Therefore, negative *in situ* selection of copepod nauplii and cyclopoid copepods does not reflect lower prey retention efficiencies for these prey by *Mnemiopsis*. Instead, selection patterns more probably result from the different mechanisms by which prey encounter the ctenophore predator. Both *Oithona* and *Acartia* nauplii were encountered via

entrainment in auricular flow. In contrast, *Acartia* adults (positively selected prey in other studies) were encountered via self-propelled swimming into *Mnemiopsis*' oral lobes. At equivalent prey densities, rapidly swimming prey, such as *Acartia* adults, are more likely to contact the slowly swimming *Mnemiopsis* due to their relative velocities and large ambits (Gerritsen and Strickler, 1977; Buskey *et al.*, 1993) than are the low-motility prey, such as *Oithona* and *Acartia* nauplii, entrained within auricular flow fields. In this case, the major patterns of *Mnemiopsis* prey selection are more strongly influenced by the mechanism of prey encounter than by subsequent stages (contact, capture, ingestion) in the predation process.

The most important consequence of multiple capture mechanisms is the wide feeding niche occupied by *Mnemiopsis* in marine planktonic food chains. In nature, *Mnemiopsis* affects a wide spectrum of planktonic prey by acting as both an ambush predator capturing mobile zooplankton such as adult copepods and simultaneously filter feeding on small prey entrained within feeding currents. The widespread occurrence of ciliated auricles and finely spaced tentillae among lobate ctenophores suggests that our findings on prey capture may not be an isolated trait of *Mnemiopsis*, but may also apply to other members of the Lobata (Costello and Coverdale, 1998). If so, then the predatory impact of lobate ctenophores may be substantially underestimated by focusing estimates of trophic impact solely on consumption of adult copepods and ignoring the role of lobate ctenophore predation on groups as small as the microplankton.

Acknowledgements

The authors are grateful to S.Colin, P.Kremer, L.Madin, R.Rapoza, B.Schulte, A.Selle, J.R.Strickler, C.Suchman and B.Sullivan for discussion and review of this manuscript. Financial support for this research was provided by the National Science Foundation (OCE 9103309 to J.H.C.).

References

- Bishop,J.W. (1967) Feeding rates of the ctenophore, *Mnemiopsis leidyi*. *Ches. Sci.* **8**, 259–261.
- Bishop,J.W. (1968) A comparative study for feeding rates of tentaculate ctenophores. *Ecology*, **49**, 996–997.
- Burrell,V.G. and Van Engel,W.A. (1976) Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York Estuary. *Estuarine Coastal Mar. Sci.*, **4**, 235–242.
- Buskey,E.J. (1994) Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia*, **292/293**, 447–453.
- Buskey,E.J., Coulter,C. and Strom,S. (1993) Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. *Bull. Mar. Sci.*, **53**, 29–43.
- Costello,J.H. and Colin,S.P. (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar. Biol.*, **121**, 327–334.
- Costello,J.H. and Coverdale,R. (1998) Planktonic feeding and evolutionary significance of the lobate body plan within the Ctenophora. *Biol. Bull.*, **195**, 247–248.
- Costello,J.H., Loftus R. and Waggett,R. The influence of prey detection on capture success by the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. *Mar. Ecol. Prog. Ser.*, in press.
- Cowan,J.H. and Houde,E.D. (1992) Size dependent predation on marine fish larvae by ctenophores, scyphomedusae and planktivorous fish. *Fish. Oceanogr.*, **1**, 113–125.

- Cowan, J.H. and Houde, E.D. (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **95**, 55–65.
- Deason, E.E. (1982) *Mnemiopsis leidyi* (Ctenophora) in Narragansett Bay, 1975–79: abundance, size composition and estimation of grazing. *Estuarine Coastal Shelf Sci.*, **15**, 121–134.
- Deason, E.E. and Smayda, T.J. (1982) Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. *J. Plankton Res.*, **4**, 203–217.
- Fields, D.M. and Yen, J. (1997) The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J. Plankton Res.*, **19**, 1289–1304.
- Franc, J.M. (1978) Organization and function of Ctenophore colloblasts: an ultrastructural study. *Biol. Bull.*, **155**, 527–541.
- Gerritsen, J. and Strickler, J.R. (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.*, **34**, 73–82.
- Greene, C.H., Landry, M.R. and Monger, D.C. (1986) Foraging behavior and prey selection by the ambush entangling predator *Pleurobrachia bachei*. *Ecology*, **67**, 1493–1501.
- Hamner, W.M., Strand, S.W., Matsumoto, G.I. and Hamner, P.P. (1987) Ethological observations on foraging behavior of the Ctenophore *Leucothea* sp. in the open sea. *Limnol. Oceanogr.*, **32**, 645–652.
- Harbison, G.R., Madin, L.P. and Swanberg, N.R. (1978) On the natural history and distribution of oceanic ctenophores. *Deep-Sea Res.*, **25**, 233–256.
- Houde, E.D., Gamble, J.C., Dorsey, S.E. and Cowan, J.H., Jr (1994) Drifting mesocosm: the influence of gelatinous zooplankton on mortality of bay anchovy, *Anchoa mitchilli*, eggs and yolk sac larvae. *ICES J. Mar. Sci.*, **51**, 383–394.
- Hyman, L.H. (1940) *The Invertebrates, Vol. 1, Protozoa through Ctenophora*. McGraw-Hill, New York.
- Ikeda, T. (1974) Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido Univ.*, **22**, 1–88.
- Kremer, P. (1979) Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries*, **2**, 97–105.
- Larson, R.J. (1987a) *In situ* feeding rates of the ctenophore *Mnemiopsis mccradyi*. *Estuaries*, **10**, 87–91.
- Larson, R.J. (1987b) Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. *Neth. J. Sea Res.*, **21**, 35–44.
- Larson, R.J. (1988) Feeding and functional morphology of the lobate Ctenophore *Mnemiopsis mccradyi*. *Estuarine Coastal Shelf Sci.*, **27**, 495–502.
- Madin, L.P. (1988) Feeding behavior of tentaculate predators: *in situ* observations and a conceptual model. *Bull. Mar. Sci.*, **43**, 413–429.
- Main, R.J. (1928) Observations of the feeding mechanism of a ctenophore, *Mnemiopsis leidyi*. *Biol. Bull.*, **55**, 69–78.
- Malyshev, V.I. and Arkhipov, A.G. (1993) The ctenophore *Mnemiopsis leidyi* in the Western Black Sea. *Hydrobiologia*, **29**, 39–44.
- Matsumoto, G.I. and Hamner, W.M. (1988) Modes of water manipulation by the lobate ctenophore *Leucothea* sp. *Mar. Biol.*, **97**, 551–558.
- Matsumoto, G.I. and Harbison, G.R. (1993) *In situ* observations of foraging, feeding and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida and Beroida. *Mar. Biol.*, **117**, 279–287.
- Monteleone, D.M. and Duguay, L.E. (1988) Laboratory studies of predation by the ctenophore *Mnemiopsis leidyi* on the early stages in the life history of the anchovy, *Anchoa mitchilli*. *J. Plankton Res.*, **10**, 359–372.
- Mountford, K. (1980) Occurrence and predation by *Mnemiopsis leidyi* in Barnegat Bay, New Jersey. *Estuarine Coastal Mar. Sci.*, **10**, 393–402.
- Nagabhushanam, A.K. (1959) Feeding of a ctenophore, *Bolinopsis infundibulum* (O.F. Muller). *Nature*, **189**, 829.
- Nelson, T.C. (1925) On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. *Biol. Bull.*, **48**, 92–111.
- Purcell, J.E. (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. Mar. Sci.*, **37**, 739–755.
- Purcell, J.E., Cresswell, F.P., Cargo, D.G. and Kennedy, V.S. (1991) Differential ingestion and digestion of bivalve larvae by the scyphozoan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*. *Biol. Bull.*, **180**, 103–111.
- Purcell, J.E., Nemazie, D.A., Dorsey, S., Houde, E.D. and Gamble, J.C. (1994) Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **114**, 47–58.
- Reeve, M.R. and Walter, M.A. (1978) Nutritional ecology of ctenophores—a review of recent research. *Adv. Mar. Biol.*, **15**, 249–287.

- Schulze-Robbecke,A.C. (1984) Functional morphology of *Bolinopsis infundibulum* (ctenophore). *Helgol. Meeresunters.*, **38**, 47–64.
- Shushkina,E.A. and Musayeva,E.I. (1990) Structure of planktonic community of the Black Sea epipelagic zone and its variation caused by invasion of a new ctenophore species. *Oceanology*, **30**, 225–228.
- Shushkina,E.A. and Vinogradov,M.Yi. (1991) Long-term changes in the biomass of plankton in open areas of the Black Sea. *Oceanology*, **31**, 716–721.
- Stoecker,D.K., Verity,P.G., Michaels,A.E. and Davis,L.H. (1987) Feeding by larval and post-larval ctenophores on microzooplankton. *J. Plankton Res.*, **9**, 667–683.
- Studenikina,Ye.I., Volovik,S.P., Mirzoyan,A.I. and Luts,G.I. (1991) The ctenophore *Mnemiopsis leidyi* in the Sea of Azov. *Oceanology*, **31**, 722–725.
- Sullivan,B.K., Suchman,C. and Costello,J.H. (1997) Mechanisms of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. *Mar. Biol.*, **130**, 213–222.
- Zaitsev,Yu.P. (1992) Recent changes in the trophic structure of the Black Sea. *Fish. Oceanogr.*, **1**, 180–189.

Received on February 1, 1999; accepted on May 9, 1999