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Abstract Although medusan predators play demonstrably important roles in a variety of marine ecosystems, the mechanics of prey capture and, hence, prey selection, have remained poorly defined. A review of the literature describing the commonly studied medusa *Aurelia aurita* (Linnaeus 1758) reveals no distinct patterns of prey selectivity and suggests that *A. aurita* is a generalist and feeds unselectively upon available zooplankton. We examined the mechanics of prey capture by *A. aurita* using video methods to record body and fluid motions. Medusae were collected between February and June in 1990 and 1991 from Woods Hole, Massachusetts and Narragansett Bay, Rhode Island, USA. Tentaculate *A. aurita* create fluid motions during swimming which entrain prey and bring them into contact with tentacles. We suggest that this mechanism dominates prey selection by *A. aurita*. In this case, we predict that medusae of a specific diameter will positively select prey with escape speeds slower than the flow velocities at their bell margins. Negatively selected prey escape faster than the medusan flow velocity draws them to capture surfaces. Faster prey will be captured by larger medusae because flow field velocity is a function of bell diameter. On the basis of prey escape velocities and flow field velocities of *A. aurita* with diameters of 0.8 to 7.1 cm, we predict that *A. aurita* will select zooplankton such as barnacle nauplii and some slow swimming hydromedusae, while faster copepods will be negatively selected.

Introduction

The importance of medusae as predators in marine ecosystems (Huntley and Hobson 1978; Moller 1980 a, 1984; Lindahl and Hernroth 1983; Purcell 1985; Matsakis and Conover 1991) has prompted the formulation of several models describing the predation process. The actual mechanism of prey encounter and capture is of critical importance to these models. Medusan encounter with prey has been described as dependent upon medusa bell diameter (Bailey and Batty 1983), tentacle spacing (Madin 1988), and fluid movements during periods of sinking by medusae (Mills 1981), but the basis for prey capture by many species of medusae remains poorly defined. For example, *Aurelia aurita*, probably the most thoroughly studied medusa, was earlier described as a microphagous feeder (Ortin 1922; Southward 1955). Later reports indicated significant ingestion by *A. aurita* of ciliates (Stoecker et al. 1987), copepods (Moller 1980 a), larval fish (Moller 1980 b, 1984; Bailey and Batty 1983; de Lafontaine and Leggett 1988; Gamble and Hay 1989) and hydromedusae (Matsakis and Conover 1991; Purcell 1991). Although *A. aurita* is reported to consume a wide variety of prey, Bamstedt (1990) calculated that the daily ration of *A. aurita* can only be met by consumption of mesozooplankton greater than 200 µm in length. No clear patterns of prey selection among mesozooplankton taxa emerge from previous reports, and *A. aurita* would appear to be a generalist, feeding unselectively upon a wide range of mesozooplankton taxonomic categories. The subumbrellar surface (Southward 1955), the exumbrellar surface (Bailey and Batty 1983) and the tentacles (Fraser 1969; Heeger and Moller 1987) have each been identified as the primary body surface used to capture this range of prey.

Different descriptions of prey selection are not limited to *Aurelia aurita*. *Cyanea capillata*, also a widely distributed scyphomedusa, has been described as selecting against copepods by Fancett (1988), while Brewer (1989) demonstrated that *Cyanea* sp. consumed primarily copepods. Thus, data on prey selection in scyphomedusae is limited, and few clear patterns emerge from what is presently known. Because scyphomedusae are important planktonic predators, the mechanics underlying prey selection and capture have significant implications for marine planktonic ecology.

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The unresolved basis of prey selection by *Aurelia aurita* and, more generally, scyphomedusae, served as the impetus for the present study. Our goal was to describe the process of prey capture by *A. aurita* and to define critical variables affecting prey selection. Our approach was to observe prey capture directly using contemporary video and optical techniques. Our results demonstrate that traditional views of scyphomedusan prey capture need to be revised to include consideration of fluid motions around swimming medusae as well as prey escape responses.

Methods

Experimental organisms

Tentaculate stage *Aurelia aurita* (Linnaeus 1758) medusae were collected from February through June in 1990 and 1991 from Woods Hole, Massachusetts and Narragansett Bay, Rhode Island, USA. Specimens used in video sequences were captured by dipping from surface waters in order to minimize damage to the medusae. Zooplankton were captured from the same sites with a 100- or 333-μm mesh net. Medusae and zooplankton were transported to the laboratory where they were maintained in incubators at field temperatures (5 to 18 °C) until used in experiments. Both medusae and zooplankton were videotaped within 48 h of capture and were not fed while in the laboratory prior to videotaping.

Microvideography

Standard rate video recordings (VHS) were used to detail movements of medusae, prey and their surrounding fluids. Two approaches were used to describe flow around free-swimming medusae: dye studies for qualitative information on flow patterns and particle studies for quantitative assessment of fluid velocities.

Medusae were observed while swimming freely in 0.22-μm filtered seawater within rectangular vessels ranging in dimensions from 4.5×8.0×2.0 cm to 25.5×30.5×18.5 cm (width×height×depth) and volumes from 50 to 14000 ml. Vessel size was influenced by two considerations. First, since only videotape of free-swimming medusae that were more than a bell radius away from the vessel wall was used for analysis, the vessel had to be large enough to allow medusae to swim freely while minimizing contact with walls. Second, image clarity and particle tracking were favored by limiting the depth of the viewing field. The choice of vessel size optimized these factors and depended upon medusa diameter. A syringe was used to add fluorescein dye for qualitative flow studies. Capture of 4-d old *Artemia* sp. nauplii (0.3 to 0.6 mm length) by medusae ranging from 1 to 3 cm diameter was observed in order to determine principal capture surfaces. Aliquots of exponentially growing cultures of a large (approximately 100 μm diameter) diatom, *Coscinodiscus* sp., were added to the vessels in order to trace particle motions. Large medusae (>3 cm diameter) required larger tracer particles; 4-d old *Artemia* sp. nauplii were used for these medusae. Previous observations had demonstrated that while *Artemia* sp. nauplii move their appendages extensively, their net swimming velocity is low and they are readily captured and ingested by *Aurelia aurita*.

Activities of predator, prey and tracer particles were observed using a backlit optical system. 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. The optical system provided clear illumination of particles as well as their movements in relationship to the medusae.

Alterations in bell shape were quantified by the fineness ratio, F, where

$$F = h/d \tag{1}$$

and h is bell height while d is bell diameter. Instantaneous fineness ratio, F_i, represents the fineness ratio during the midpoint of an interval used for measurement of medusa velocity. F_i was determined to quantify variations in bell morphology during the pulsation cycle. The fineness ratio of the bell at rest in its uncontracted state corresponds closely to the minimum F_i value, whereas maximum F_i corresponds to full bell contraction.

Medusa motion was measured from sequential changes in position (x) of the anterior most point of the exumbrellar surface over five field (1/12 s) intervals (t). Motion only within the two-dimensional viewing field was assured by using a sequence in which bell orientation was level and the medusa swam from bottom to top of the viewing field.

The velocity (u) for a time interval (i) was calculated as an average according to the formula

$$u_i = \frac{x_{i+1} - x_1}{2t} \tag{2}$$

Acceleration (a) was calculated as

$$a_i = \frac{x_{i+1} + x_{i-1} - 2x_i}{t^2}. \tag{3}$$

Reynolds number (Re) was calculated as

$$\mathrm{Re} = \frac{du}{v}, \tag{4}$$

where u is medusa velocity and v is the kinematic viscosity of seawater.

Escape velocities of prey were determined using the same optical system but without medusae in the experimental vessel. With the exception of *Artemia* sp. nauplii, all the species utilized co-occurred in the field with *Aurelia aurita* medusae. Three prey groups, listed as copepodites, copepod nauplii and barnacle nauplii, were not identified to generic level. Adult copepods, *Temora longicornis* and *Acartia hudsonica*, were captured with a 333-μm mesh net. The hydromedusae, *Obelia* sp. and *Rathkea octopunctata*, were collected with a 102-μm mesh net. 3-d old, yolk-sac stage, winter flounder larvae (*Pleuronectes americanus*) were provided by G. Klein-McPhee. Prey escape was initiated either by direct stimulation with a probe or by slight vibration of the experimental vessel. Escape velocities were determined from the time duration and distance covered between in-

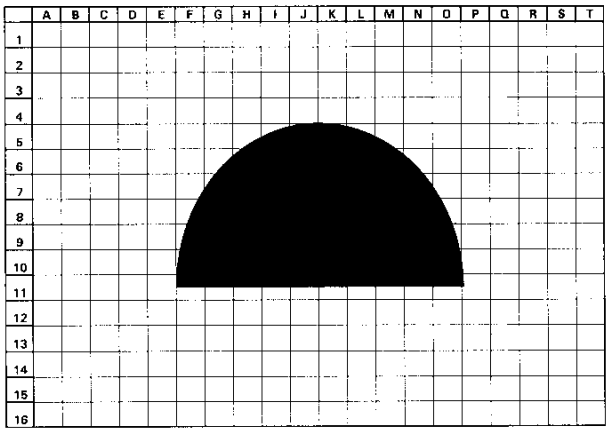


Fig. 1 *Aurelia aurita*. Calculation of fluid motions surrounding a swimming medusa by transposing an x-y grid over video sequences and measuring particle motions within grid cells

itial body movement and final resting position during an escape event.

A quantitative description of the fluid motion surrounding an *Aurelia aurita* medusa utilized particles tracked in the fluid surrounding the bell during the initial stages of the recovery stroke. The recovery stroke was chosen for examination because prior observation indicated that most particle captures occurred during this phase of the bell pulsation cycle. Flow field images were taken while the camera was stationary and the medusa swam through the field of view. The flow field was constructed from several pulsation cycles because no single cycle contained enough appropriately located and focused particles to describe the entire flow field. We measured the flow field by superimposing an *x-y* grid on a video sequence of a free-swimming medusa (Fig. 1). As the swimming medusa altered orientation, so did the *x-y* grid. Therefore, all particle velocities were measured in relation to the medusa's bell orientation. Velocities in different parts of the flow field were measured from different cells in the *x-y* grid. All measurements were made at the same phase of the recovery stroke – three fields (1/20 s) after the stroke began. Velocity of a particle was determined from its change in position during a three-field interval.

Marginal flow velocity was defined as the average velocity of particles flowing past the bell margin during the initial stages of the recovery stroke of the bell pulsation cycle. Marginal flow velocity for each medusa was determined from particle trajectories measured within a rectangular template located adjacent to the bell margin at the onset of the recovery stroke. The rectangular template was scaled to individual medusa diameter; the long dimension was 1/4 of and the height was 1/8 of the maximum relaxed bell diameter. Particle velocities were replicated for each medusa ($n=8$ to 32 points) and among individual medusae in order to assure representative particle velocities in the medusan flow fields.

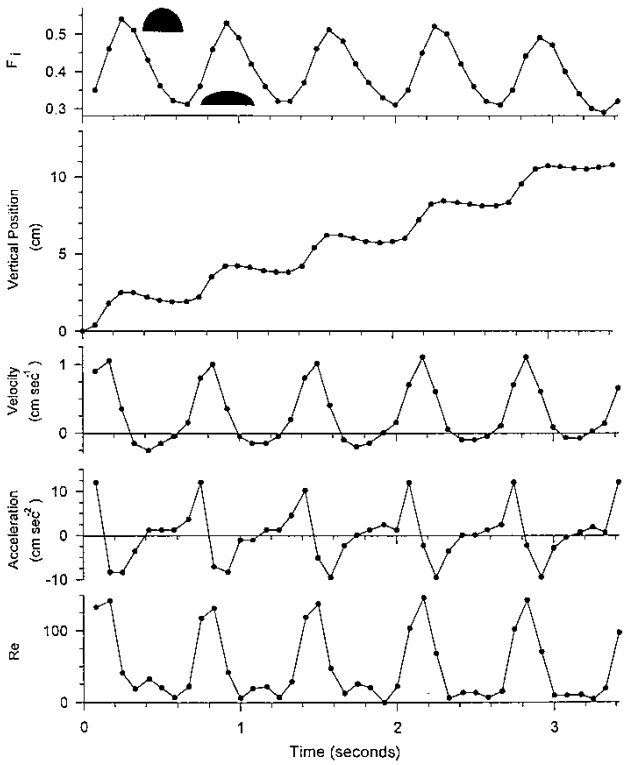


Fig. 2 *Aurelia aurita*. Instantaneous bell fineness (F_i), vertical position of the medusa in the water column, velocity, acceleration and Reynolds number (Re) determined from swimming by a 1.6-cm diameter medusa

Results

Swimming mechanics and fluid motions

Aurelia aurita generally swam continuously with tentacles extended. Movement was dependent upon thrust generated by cyclic alterations in the bell form of the medusa. Although continuous, the swimming motions of *A. aurita* can be divided into two essential phases, the power and the recovery strokes, and quantified by alterations in instantaneous bell fineness (F_i, Fig. 2). The relative durations of the two strokes were different; the power stroke was shorter than the recovery stroke (approximately 0.25 vs 0.4 s for Fig. 2). During the power stroke, contraction of circular muscles reduced the bell diameter, so that F_i increased, and exerted pressure on the fluid contained within the bell cavity. That pressure forced water out of the bell cavity in a jet directed posterior to the medusa. Reaction to the posteriorly directed jet thrust the medusa forward and accelerated it to maximum velocity. The greatest change in position of the medusa within the water column occurred during this phase of the pulsation cycle. The second phase, the recovery stroke, began after the circular muscles relaxed, causing the bell diameter to increase, so that F_i decreased. During the recovery stroke, the volume of the subumbrellar space increased and was filled with fluid adjacent to the medusa. Cessation of the propulsive jet slowed forward motion while refilling of the subumbrellar cavity from behind the medusa actually caused a negative velocity, or backwards motion, of the medusa. This was evident in both the vertical position and velocity profiles (Fig. 2). It is important to note that the negative component of the velocity profile was small relative to the positive component. If the same fluid were used for refilling the bell as for the propulsive jet, the medusa would expel and recollect the same fluid volume. In this case, the positive and negative components of the velocity profile would roughly balance, resulting in back and forth oscillatory motion with no net movement. As demonstrated by the vertical position data (Fig. 2), this did not occur. Instead, refilling occurred primarily via water intake over the bell margin.

Jet propulsion resulted in unsteady flow patterns in the fluid surrounding *Aurelia aurita*. This pattern is demonstrated by the Re of the flow surrounding a swimming *A. aurita* (Fig. 2). Re varied from 0, immediately at the end of the recovery stroke, to almost 150 during the power stroke. Both the velocity and the direction of the flow alternated during each pulsation cycle.

Video analysis demonstrated that prey capture by *Aurelia aurita* was strongly dependent upon flow alternations created by swimming medusae. During the power stroke, fluid adjacent to the bell margin is entrained and follows the bell through its arc of movement. Fluid and entrained

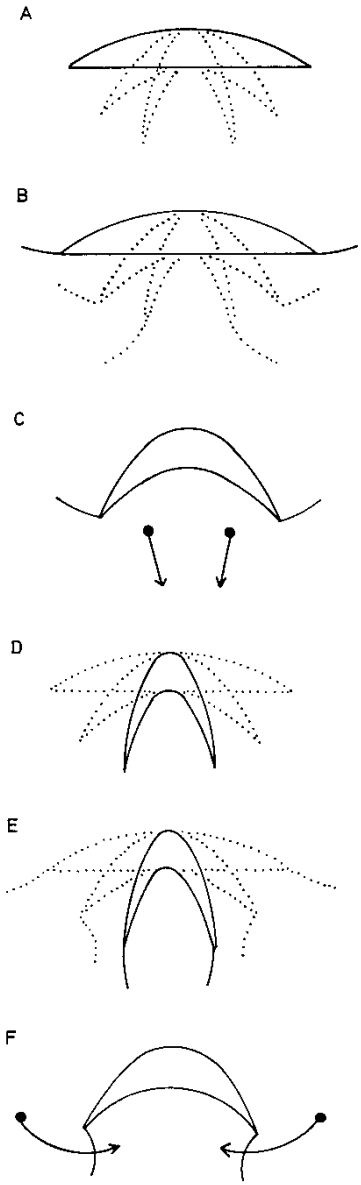


Fig. 3 *Aurelia aurita*. Schematic representation of the relationships between bell pulsation, fluid motion and prey capture. All drawings represent cross-sections. **A** Change in bell form during power stroke; continuous lines represent initial position while dotted lines represent successive bell positions. **B** Identical to **A** except for addition of tentacle position during power stroke. **C** Bell and tentacle position in mid-power stroke; arrows represent motion of fluid and entrained particles. **D** Change in bell form during recovery stroke; continuous line represents initial position while dotted lines represent successive bell positions. **E** Identical to **D** except for addition of tentacle position during recovery stroke. **F** Bell and tentacle position in mid-recovery stroke; arrows represent motion of fluid and entrained particles (including prey). Note that not all fineness values are representative of actual medusae

particles are brought from positions adjacent to the lower bell to a position near the bell margin. As the bell recoils to its relaxed form (the recovery stroke), the bell margin sweeps an arc outward and the subumbrellar cavity refills with water (Fig. 3). The decreased pressure in the subumbrellar cavity during refilling creates a flow into the subumbrellar cavity; fluid moves past the bell margin and into the subumbrellar cavity. Prey entrained within this fluid are either sieved through tentacles lining the bell margin or directly encounter the oral arms or subumbrellar surface. These surfaces, particularly the tentacles and oral arms, are richly provided with nematocysts (Heeger and Moller 1987) and were observed in our experiments to be the major capture sites. Prey captured on the tentacles were removed by the flexible oral arms and passed along ciliated grooves within the oral arms to the gut in the manner described by Southward (1955).

Tentacle orientation altered predictably during the bell pulsation cycle as shown schematically in Fig. 3. Tentacles may sometimes actually be longer relative to the bell diameter than illustrated. Individual medusae can rapidly alter tentacle length. However, the relationship between tentacle length and bell diameter was relatively constant over the range of bell diameters we examined. During the initial power stroke, the tentacles followed the bell margin (the tentacles originate at the bell margin) downward, sweeping an arc wider than the bell diameter. We observed some prey captured on the tentacles during this phase, but relatively few. Most of the observed captures occurred during the recovery stroke. During this phase, tentacles lagged behind the outward arc of the recovering bell margin. The tentacles were then aligned perpendicular to the flow into the subumbrellar surface and acted as sieves which intercepted particles entrained in the flow.

Flow fields, capture surfaces and marginal flow velocities

The mechanics of particle capture we have detailed differ significantly from previous descriptions of medusan prey capture mechanisms. In order to explain these differences and identify the appropriate variables influencing captures of different types of prey, we examined the flow fields surrounding tentaculate *Aurelia aurita*, concentrating on the initial recovery stroke. It was at this phase of the pulsation cycle that we noted most prey captures.

Velocity vectors for particles surrounding medusae at the beginning of the recovery stroke were greatest around the bell margin and were directed away from the anterior portion of the bell (Fig. 4). Forward motion of a medusa moved fluid adjacent to the front of the bell in the direction of the medusa. This mass of water created a "bow wave", and reduced pressure near the bell margin caused fluid to flow around the bell. Vortices shed at the bell margin, as well as alterations in the direction of flow due to bell pulsation, resulted in a turbulent wake behind the medusa. The net result was that most particles flowed along, but not into, the exumbrellar surface and were accelerated around the bell margin. Fig. 5 schematically describes

streamline flow around a tentaculate *Aurelia aurita* during the initial stages of the recovery stroke and emphasizes the importance of viewing a swimming medusa as a solid (although not rigid) object parting the fluid through which it swims.

Flow around the bell margin brought particles into contact with the tentacles. Due to the potential importance of these flows for prey entrainment and capture, marginal flow velocities were recorded for a range of medusae with different bell diameters (from 0.8 to 7.1 cm). Marginal flow velocities increased with bell diameter (Fig. 6).

While we observed most captures of *Artemia* sp. nauplii by tentaculate *Aurelia aurita* to occur on the tentacles, we also observed some exumbrellar captures. Our observations indicate that prey transport down the exumbrella is not continuous as might be expected of ciliary transport, but is saltatory, and occurs coincident with bell contraction. Fig. 7 illustrates movement of an *Artemia* sp. nauplii down the exumbrellar surface towards the bell margin of a 1.0-cm diameter *A. aurita* medusa. The medusa swam intermittently, and only during periods of bell contraction (high F_i) did the nauplii move measurably along the exumbrellar surface. These data suggest that alterations in boundary layer flow along the exumbrellar surface may be the primary means of large prey transport along the exumbrella. Bell contraction and exumbrellar prey movement coincide with maximum velocities of the fluid adjacent to the bell and, hence, decreased boundary layer thickness as well as maximum velocities of the fluid surrounding the attached prey. Durations of prey motion were short (< 0.25 s) and would not be obvious to an observer without some means of optical recording and playback. Prey velocities and the durations of prey movement increased as the prey proceeded down the bell (Fig. 7). This pattern may be due to the gradation in fluid velocities which occur along the bell. Portions of the bell near the margin experience greater fluid velocities over their surface during pulsation (Fig. 4) and, hence, greater boundary layer thinning. Higher particle velocities along the exumbrellar surface near the bell margin probably result from the relatively greater alterations in boundary layer flow in this region. We observed several instances in which prey incapable of self-propulsion broke loose from the exumbrellar surface near the bell margin during bell contraction and were subsequently lost by the medusa. Thus, while cilary movement of prey almost certainly occurs, our observations indicate that transport of large prey along the exumbrellar surface occurs concurrently with rhythmic alterations in boundary layer flow accompanying bell contraction and relaxation.

Flow and prey escape velocities

Prey escape velocities were measured for comparison with marginal flow velocities. Escape velocities varied greatly among taxonomic groups (Fig. 8). Adult *Temora longicornis* and *Acartia hudsonica* and copepodites, achieved the highest escape velocities of the plankton recorded. Both these groups possessed escape speeds in excess of the mar-

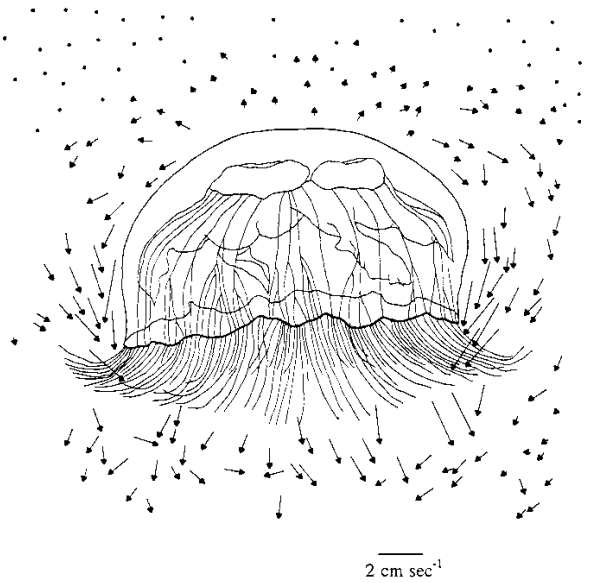
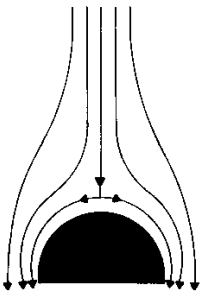


Fig. 4 *Aurelia aurita.* Velocity vectors for tracer particles during initial stages of recovery stroke. Vector data collected from flow field images taken at 1/20-s intervals while camera was stationary and medusa swam through the field of view. Medusa position represents midpoint of sample interval. Medusa diameter was 3.6 cm

Fig. 5 *Aurelia aurita.* Streamline flow around a medusa during initial stages of recovery stroke. Medusa body is frame of reference for streamline flow



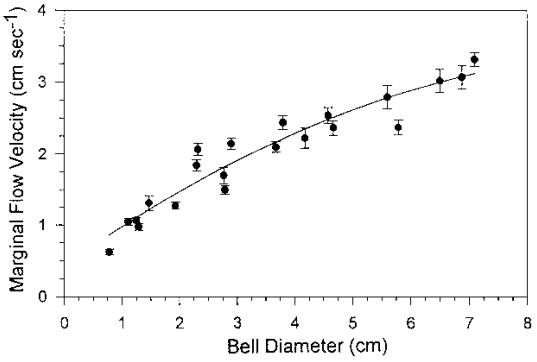


Fig. 6 *Aurelia aurita.* Marginal flow velocities of medusae of varying bell diameters. Each data point represents a different medusa. 8 to 32 velocities determined for each medusa; error bars represent 95% confidence intervals round the mean velocity. Error bars including within graphic symbol for those points without apparent error bars

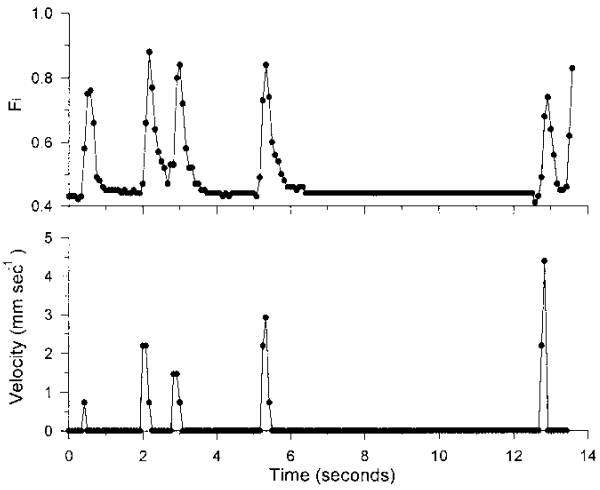


Fig. 7 *Aurelia aurita.* Relationship between fineness ratio (bell height/diameter) of medusa during bell pulsation cycle (top) and velocity of prey (*Artemia* sp. nauplii) transport along exumbrellar surface (bottom). Prey was moved from mid-bell to bell margin. Prey became enmeshed in marginal tentacles at ca. 13 s. (F_i instantaneous bell fitness)

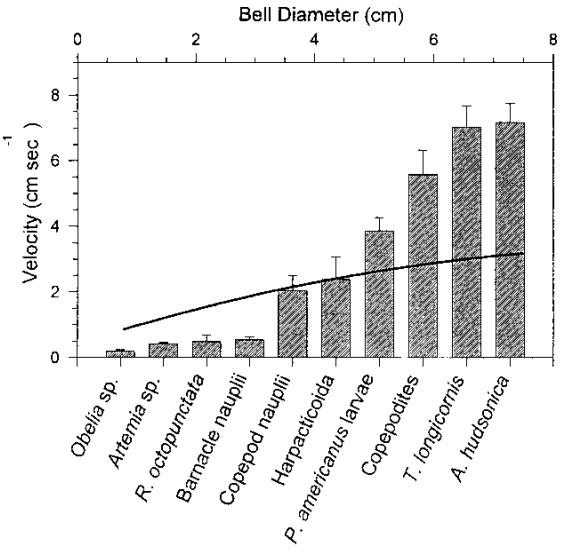


Fig. 8 *Aurelia aurita.* Marginal flow velocities of medusae (continuous curve, top *x*-axis) and escape velocities of prey (hatched bars, bottom *x*-axis). Continuous curve represents polynomial fit of data from Fig. 6. Prey escape velocities are means and 95% confidence intervals of 8 to 20 replicates for each prey category (*R. octopunctata, Rathkea octopunctata*; *P. americanus, Pleuronectes americanus*; *T. longicornis, Temora longicornis*; *A. hudsonica, Acartia hudsonica*)

ginal flow velocities of the full size range (0.8 to 7.1 cm diameter) of *Aurelia aurita* measured. Escape velocities of yolk-sac stage (approximately 0.4 mm length) winter flounder larvae represent maximum escape velocities. These escape velocities agree well with burst swimming speeds of a variety of fish larvae (Bailey and Houde 1989). However, many of the larvae exhibited poorly developed escape responses; a large number either did not respond or responded variably to prodding with a probe. Because harpacticoid copepods and copepod nauplii were not identified to species, it is unclear whether variability within these groups was intra- or inter-specific. *Artemia* sp. nauplii had essentially no escape response. Although they swam quite rapidly in the presence of mechanical stimulation, they had no burst speed capacity. In this regard, they resembled barnacle nauplii, which also had very low escape velocities. The two hydromedusae, *Obelia* sp. and *Rathkea octopunctata*, both escaped slowly. *R. octopunctata* could accelerate by rapid bell contraction, but the velocities achieved were relatively low.

Discussion

These findings have several implications for the ecology of planktonic medusae. First, the physical basis of prey encounter with *Aurelia aurita* provides a framework within which quantitative models of predation by *A. aurita*, and other similar medusan predators, can be proposed and tested. Our first hypothesis is that prey encounter with capture surfaces of *A. aurita* will be a function of marginal flow velocity and prey escape velocity (Fig. 8). Prey that are slower than the marginal flow should reach capture surfaces of *A. aurita*. Escape velocities of common zooplankton taxa indicate that calanoid copepods, usually the most numerically abundant and most available potential prey for *A. aurita*, should be difficult to capture using the marginal flow mechanism proposed here. In contrast, other taxa, including barnacle nauplii and hydromedusae, should be most susceptible to this mode of feeding. Therefore, prey "selection", those prey consumed as compared to the prey available in the plankton, should be affected by the physical mechanism of prey capture. If this mechanism dominates feeding selectivity by *A. aurita*, we would expect the diet of *A. aurita* to change as the medusa grows because more planktonic taxa would be susceptible to entrainment in the medusan flow field as bell diameter increases. Since *A. aurita* appears seasonally in most locations, the impact of this predator on the planktonic community should be affected by the relative timing of developmental stages of predator and prey populations.

Our approach to prey selection by *Aurelia aurita* emphasizes the importance of processes underlying the initial encounter between predator and prey. Purcell and Mills (1988) have documented the relationship between nematocyst structure and prey selection in hydromedusae. Their approach differs from ours in their emphasis upon factors determining post-encounter prey selection. While nematocyst type appears to limit prey selection in a variety of medusae, particularly hydromedusae, *A. aurita* is capable of capturing both soft- and hard-bodied prey. Sullivan et al. (1994) found that both hydromedusae and barnacle nauplii were important food items for *A. aurita* in Narragansett Bay and, as noted previously, other investigators report a

wide range of prey types utilized by *A. aurita*. Thus, initial prey encounter and the factors underlying encounter events, play a decisive role, while nematocyst structure is probably of less significance in determining the composition of the diet of *A. aurita*.

We believe that the biomechanical perspective on prey capture clarifies prey selection patterns in *Aurelia aurita*. Field data on prey selection by *A. aurita* of different developmental stages experiencing variable prey availability are largely consistent with predictions arising from the marginal flow mechanism. Whereas *A. aurita* has previously been viewed as a generalist feeder, it is clear that slowly escaping prey, including hydromedusae and barnacle nauplii, are staple items in the natural diet of this medusa (Sullivan et al. 1994).

The limitations of the capture mechanism we describe are determined by the relative sizes and velocities of predators and prey. Many zooplankton are of low mass or velocity and essentially follow streamline flow into tentacles of adult *Aurelia aurita*. Ciliates, fish eggs, barnacle nauplii, many harpacticoid copepods, some copepod nauplii, and small hydromedusae, such as *Obelia* sp., are small and slow enough to be captured in this way. Zooplankton that are large or that swim rapidly relative to *A. aurita* may possess higher momentum than the fluid surrounding the medusa. In these cases, a prey organism may not be entrained in the flow around the medusa but could directly encounter any capture surface, including the exumbrella. Bailey and Batty (1983) noted that *A. aurita* with diameters of 0.5 to 2.5 cm captured approximately 1.0-cm long larval herring (*Clupea harengus*) almost solely on the exumbrellar surface. In this case, the prey were probably too large, relative to the predator, to be entrained by the medusan flow field. However, field populations of *A. aurita* may be larger relative to their prey (Moller 1984), and tentacular capture of fish larvae may be common. The escape velocities we measured for the winter flounder larvae (Fig. 8) represent maximum escape speeds and are similar to the burst swimming speeds reported for a variety of fish larvae (Bailey and Houde 1989). However, many of the larvae observed in the laboratory exhibited poorly developed escape responses. If larval fish escape responses are as variable in field populations as those we measured in the laboratory, only a fraction of the larvae encountered by *A. aurita* in the field may actually be capable of maximum escape speeds.

Rapidly escaping zooplankton may also possess sufficient momentum to evade the fluid flow around *Aurelia aurita*. In contrast to slow or poorly escaping prey, the usually more abundant copepods are harder to catch and are probably less important to the nutrition of *A. aurita* than has previously been thought. However, copepods are common in the diet of *A. aurita* (Moller 1980a; Sullivan et al. 1994), and their capture by the marginal flow velocity mechanism appears prohibited by their rapid escape responses (Fig. 8). This implies that capture of copepods occurs by means other than the marginal flow mechanism, or that escape velocities alone may be insufficient to account for copepod escape behavior. The latter is supported by evidence that copepods exhibit complex behavioral responses to mechanical stimuli which may impair these escape abilities (Haury et al. 1980; Costello et al. 1990; Marrase et al. 1990; Hwang et al. 1994). These results underscore the need for further investigation into behaviors of both the predator and prey species.

This work has implications for the relationship between medusan morphology and foraging mode. Medusae exhibit a wide range of body forms varying from elongate and streamlined to oblate and bluff. Foraging strategies also vary among medusae from active cruising to sedentary ambush patterns (Mills 1981; Leonard 1982; Madin 1988; Costello 1992). We suggest that medusan morphologies and foraging strategies are coevolved traits. Streamlining reduces pressure drag in moderate and high Reynolds number flows and may be estimated by the fineness ratio of the medusan bell in the relaxed state. Energy expenditure during swimming increases exponentially as fineness ratio decreases (Daniel 1983, 1985). Forms with low fineness ratios moving at moderate Reynolds number flows, such as *Aurelia aurita*, dissipate energy as vortex rings in their wake. The 1.6 cm diameter medusa used for the measurements in Fig. 3 had a fineness ratio of approximately 0.3, while powerfully swimming hydromedusae have fineness ratios of 2.0 or greater (Costello 1992). The low fineness ratio of *A. aurita* results in relatively inefficient propulsion relative to medusae with more streamlined morphologies. The bell morphologies of cruising medusan predators, such as *A. aurita*, may not reflect natural selection for maximum propulsive efficiency. It is the propulsively inefficient body form of *A. aurita* which effectively creates fluid motions used to capture prey. Low propulsive efficiency, coupled with high fluid disturbance, serves to maintain feeding efficiency for *A. aurita*.

Such a high drag body morphology in a continuously swimming organism may appear maladaptive; however, the widespread distribution and frequent occurrence of *Aurelia aurita* attests to the success of its combination of propulsion with prey capture. *A. aurita* is not unique in this regard. Oblate morphologies characterize a number of scyphomedusae that are cruising foragers. The mechanism we report for *A. aurita* may underlie prey capture and selection by a number of medusan species, particularly scyphomedusae.

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