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Swimming and feeding by the scyphomedusa *Chrysaora quinquecirrha*

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Abstract The semaeostome scyphomedusa, *Chrysaora quinquecirrha* (Desor, 1848), is an abundant and important planktonic predator in estuaries and coastal waters of the eastern USA during the summer. We videotaped free-swimming medusae in the laboratory and in the field in order to determine the relationship between swimming motions and prey encounter with capture surfaces. Medusae were collected from the Choptank River (Chesapeake Bay) in September 1992 and in the Niantic River, Connecticut, USA in July 1994. We used newly hatched *Artemia* sp. nauplii and fluorescein dye to trace water motions around swimming medusae. Swimming results in a pulsed series of toroids which travel along the medusan oral arms and tentacles. Prey are entrained in this flow and the location of naupliar encounter was influenced by the phase of the pulsation cycle during which entrainment occurred. Flow-field velocities, measured by tracking particles adjacent to the bell margin during contraction, increased with bell diameter.

Introduction

The semaeostome medusa, *Chrysaora quinquecirrha*, is abundant in estuaries and near-coastal waters of the eastern USA during the summer. At these times, *C. quinquecirrha* consumes a variety of zooplankton and can directly influence copepod populations (Purcell 1992, but see Purcell et al. 1994b), fish eggs and larvae (Cowan and Houde 1993; Purcell et al. 1994a) and ctenophores (Miller 1974; Purcell and Cowan 1995). Indirect effects of predation by *C. quinquecirrha* have been suggested to play a major role in the structure and function of the Chesapeake Bay ecosystem (Feigenbaum and Kelly 1984; Baird and Ulanowicz 1989). Because this medusa consumes such a wide variety of prey types, it may appear that *C. quinquecirrha* is a generalist feeder with few patterns of prey selection, but in one study *C. quinquecirrha* selected adult copepods (Purcell 1992), in another fish eggs and larvae (Purcell et al. 1994a), and in another avoided veliger larvae (Purcell et al. 1991). The mechanisms of these selection patterns remain undefined.

Recent studies of water flow patterns created by swimming scyphomedusae have established a mechanical basis for understanding prey selection of several other scyphomedusan species (Costello and Colin 1994, 1995; Sullivan et al. 1994). These studies indicate that scyphomedusae consume taxonomically diverse prey united by a common vulnerability to entrainment in medusa-generated fluid motions. These flow patterns bring prey into contact with nematocyst-laden capture surfaces of the scyphomedusa so that prey capture is a selective process that is strongly influenced by the initial means of encounter with prey.

This issue is significant because the mechanics of prey capture varies among cnidarian predators, strongly influencing their prey selection and, hence, ecosystem impact. Many planktonic cnidarian predators are primarily stationary foragers (e.g. siphonophores), and prey selection can be predicted from filtration theory (Purcell 1981) and predator morphology (Madin 1988). Scyphomedusae, including *C. quinquecirrha*, swim almost continuously (Costello et al. unpublished), and fluid motions around the medusan capture surfaces significantly affect prey encounter and subsequent

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capture. The oral arms and tentacles of *C. quinquecirrha* trail distances equivalent to several bell diameters in the wake behind a swimming medusa. The flow patterns surrounding a semaeostome with relatively short tentacles, *Aurelia aurita*, have been described and related to prey capture (Costello and Colin 1994), but there are no quantitative descriptions of fluid flow around medusae with elongate oral arms and tentacles, such as *C. quinquecirrha*. In the present study we quantified the relationship between fluid motions and prey capture by swimming *C. quinquecirrha*. Predictions based on these patterns were then related to empirical prey selection patterns in the field.

Materials and methods

Experimental organisms

Individual *Chrysaora quinquecirrha* (Desor, 1848) were collected using a dipnet from two populations, the first in the Choptank River of Chesapeake Bay, Maryland, USA, on 1 September 1992; the second in the Niantic River, Connecticut, USA, a river flowing into Long Island Sound, throughout July 1994. Medusae were transported to the laboratory at Providence College, Rhode Island, where they were maintained in 20-liter vessels. Video recordings of medusan swimming and prey capture were made within 1 week of collection. Medusae ranged in bell diameter from 0.8 to 8.0 cm.

Microvideography

Activities of medusae, prey and dye were observed using a backlit optical system similar to that described previously (Costello and Colin 1994). Medusae from each site were videotaped while swimming freely in 0.2 μm filtered seawater (21 °C) within rectangular vessels ranging in dimensions from $4.0 \times 8.0 \times 2.0$ to $25.5 \times 30.5 \times 18.5$ cm (width × height × depth) and volumes from 50 to 14 000 ml. Vessel choice depended upon medusa diameter since small medusae (<2 cm diameter) could swim freely in small vessels but large medusae (>5 cm diameter) required larger vessels. A field counter labeled each sequential VHS 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

$$F = h/d$$

and h is bell height and 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 anteriormost (aboral) point of the exumbrellar surface over 20-field intervals (1/3 s, t). Motion only within the two-dimensional viewing field was ensured 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 specific time interval (i) was calculated as an average according to the formula

$$u_i = \frac{x_{i+1} - x_{i-1}}{2t} \quad .$$

Acceleration (a) was calculated as

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

Reynolds number (Re) was calculated as

$$\mathrm{Re} = \frac{du}{v} \quad ,$$

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

Quantitative description of the fluid motions surrounding *Chrysaora quinquecirrha* medusae required particle tracking in the fluid surrounding the medusae. Particle velocities were used for three purposes. First, to accompany the kinematic data throughout the pulsation cycles in order to clarify variations in fluid flow during these cycles; second, to construct representative flow fields around the medusa's body during the power and recovery strokes; third, to determine the influence of medusa size on flow velocities by comparing maximum flow velocities at the bell margin (marginal flow) over a range of bell diameters. Depending on these goals, we varied the method of measurement. All particle tracking used 3-d-old *Artemia* sp. nauplii (0.3 to 0.6 mm length) as tracer particles.

Particle velocities at the bell margin were determined during five consecutive pulsation cycles for the same medusa used in the kinematic profile. Particle trajectories were measured within a square template having sides one quarter the bell diameter of the medusa (1.4 cm for the 5.45 cm diameter medusa in Fig. 1) and adjacent to the bell margin. Six particle velocities were measured for each 20-field interval (1/3 s) during the five consecutive pulsation cycles.

Flow fields during the power and recovery strokes were constructed for the same medusa used in the kinematic profile. Particle paths were collected for a 20-field interval (1/3 s) following the start of bell contraction (power stroke) and bell relaxation (recovery stroke). 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 (Costello and Colin 1994). As the swimming medusa altered orientation, so did the x–y grid, and all particle velocities were measured in relation to the bell orientation. Velocity of a particle was determined from its change in position during a 20-field interval.

Marginal flow velocity was defined as the average velocity of particles moving over the bell margin during the initial stages of the power stroke of the pulsation cycle. The power stroke was chosen for inter-medusa comparison because previous measurements had demonstrated that flow rate was maximum during this phase. Marginal flow velocity for each medusa was determined from particle trajectories measured within a square template in the same manner as the particle velocities collected over the five pulsation cycles described previously. Marginal flow velocities of 30 medusae were compared in order to determine the relationship between bell diameter and flow-field velocity. A rectangular template was scaled to the individual medusa diameter; the side dimension was 1/4 of the maximum relaxed bell diameter. Particle velocities were replicated for each medusa ($n = 8$ to 15 points) in order to ensure representative particle velocities in the flow fields. Preliminary data showed that the duration of the pulsation cycle varied widely as a function of bell diameter, so a uniform, short duration of three fields (1/20 s) was selected for marginal flow measurements following Costello and Colin (1994).

Prey capture maps

Prey capture maps were constructed for a 2.5 cm diameter medusa swimming for 20 min near the water surface in the video vessel. Locations of prey at the time of capture were mapped over

approximately 900 pulsation cycles while oral arms and tentacles remained extended. Capture of 3-d-old *Artemia* sp. nauplii was defined as an encounter with the medusa that resulted in the prey being held in position for more than 20 fields (1/3 s). The capture location and its distance from the bell margin were recorded. Prey captures near the bell margin were classified by their occurrence during the power or recovery stroke. Captures that occurred >1.5 cm from the bell margin were not readily attributable to either stroke, but to the overall flow down the body and were included in a map describing the total prey captures during the observation period.

In situ videography

Medusae were observed in situ by SCUBA divers in order to determine flow-field structure under field conditions. In situ video recordings were made using a SONY TR81 camera with zoom lens contained within an Amphibico underwater housing. Fluorescein dye was ejected from a syringe near swimming medusae by one diver while a second diver videotaped dye patterns around swimming medusae. Line drawings of the video images were made with the assistance of a Bioscan Optimas image analysis system.

Results

Kinematics

The kinematic profile for a 5.45 cm diameter *Chrysaora quinquecirrha* traveling 2.8 vertical cm illustrates the relationship between bell shape, motion and particle velocities during swimming (Fig. 1). Forward motion, expressed as increased vertical position, occurred only during periods of bell contraction, indicated by increased bell fineness (F_i). During bell relaxation, indicated by decreased F_i, the medusa actually decreased its vertical distance or went backwards. While there was net forward motion over the entire cycle, the forward progress made during the contraction phase was partially counteracted by backward motions as the bell relaxed. This resulted in cyclic positive and negative variations in medusan velocity and acceleration over the course of pulsation cycles. The net flow was characterized by relatively high Re numbers averaging 343 (range: 22 to 792). The velocities of particles near the bell margin varied over the pulsation cycle. Maximum particle velocities (2.63 cm s^{-1}) occurred during the contraction phase, while minimum values (0.25 cm s^{-1}) accompanied the recovery phase (Fig. 1).

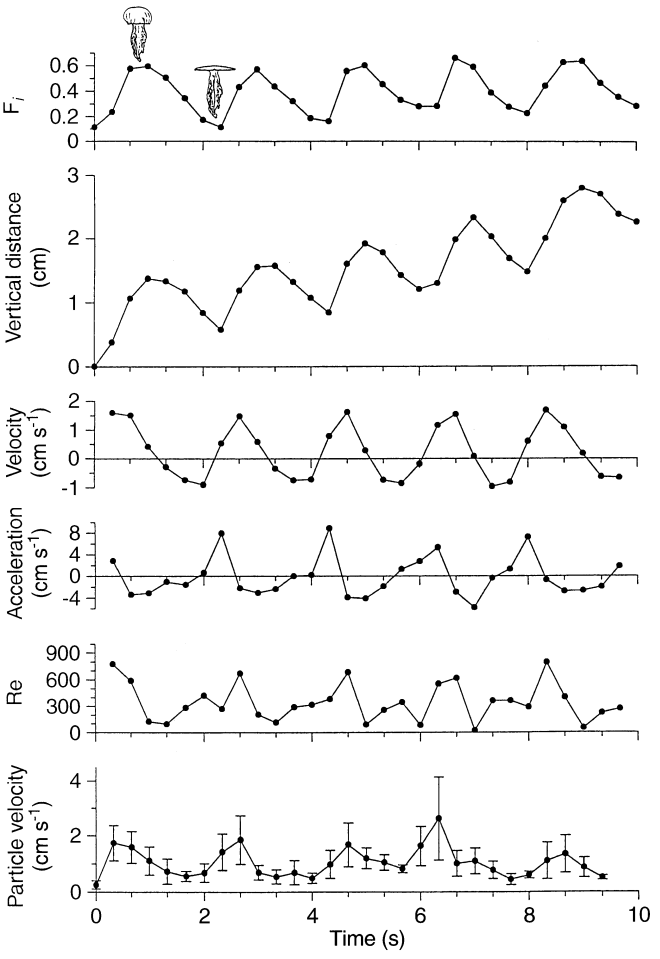

Fig. 1 *Chrysaora quinquecirrha*. Instantaneous bell fineness (F_i), vertical position of the medusa in the water column, velocity, acceleration, Reynolds number (*Re*), and particle velocity determined from a swimming medusa, 5.45 cm diameter. The medusa is shown with full bell contraction and in the uncontracted state (tentacles not shown). Particle velocities were measured at the bell margin over 1/3-s intervals; six velocities were used for each point. *Error bars*: 95% confidence intervals around the mean particle velocity

Flow fields

Bell contraction caused particles in water near the bell margins to be accelerated posteriorly (orally) towards the tentacles and oral arms suspended from the bell (Fig. 2A). Particle velocities were greatest in the fluid immediately adjoining the bell margin at the beginning of bell contraction. Fluid from this area formed a vortex as it was entrained and swept downward with the bell margin; the paths of particles in this fluid were curved in the outlines of these vortices. During the subsequent recovery phase, the bell relaxed and became more flattened (low F_i) and fluid, traced by particle paths, flowed inwards through the tentacles into the manubrium and subumbrellar space (Fig. 2B). Particles entrained in vortices during the previous power stroke continued their rotational motion further down the length of the medusa throughout at least two subsequent pulsation cycles (Fig. 2B), but particle paths became less distinct as they progressed down the oral arm and tentacle mass.

Flow-field velocities past the bell margin during the power stroke increased linearly with bell diameter over the range (0.8 to 8.0 cm diameter) of medusae measured (Fig. 3). There was no significant difference in the relationship between bell diameter and marginal flow velocity for medusae from the two sample sites (ANCOVA, $p = 0.18$). Due to the higher average velocities and orally directed flow patterns, particles were

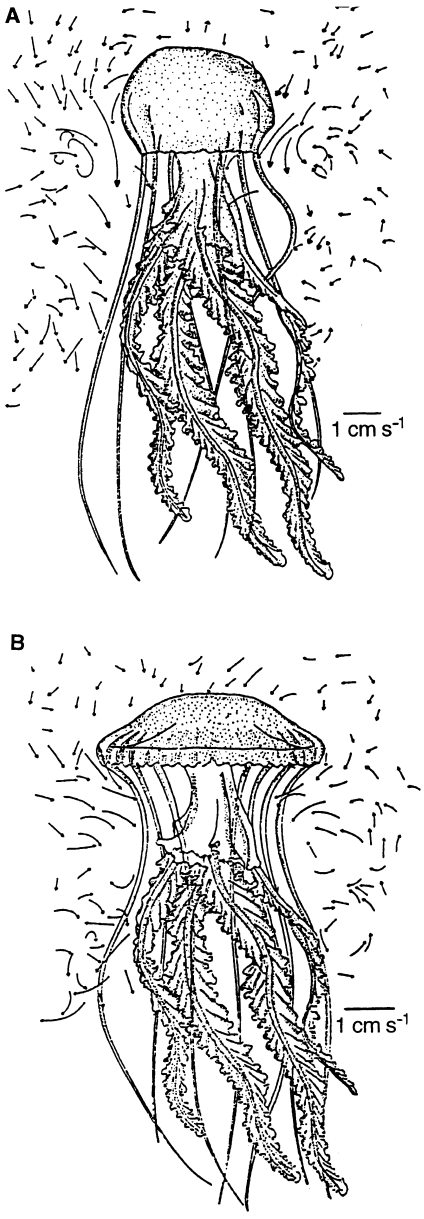

Fig. 2 *Chrysaora quinquecirrha.* Particle paths around a swimming medusa during **A** power and **B** recovery strokes. Particle data collected from images taken over 1/3-s intervals while the camera was stationary and medusa swam through the field of view. Medusa position represents midpoint of the sample interval. Medusa was the same as used in Fig. 1 (5.45 cm diameter)

carried below the bell margin during the power stroke and encountered the oral arms and tentacles several millimeters below the bell margin. In contrast, during the recovery stroke, fluid moved past the bell margin into the subumbrellar space and encountered the tentacles and upper portions of the oral arms.

Prey capture

Artemia sp. nauplii were captured on both the oral arms and tentacles located proximally to the bell (Fig. 4A, B).

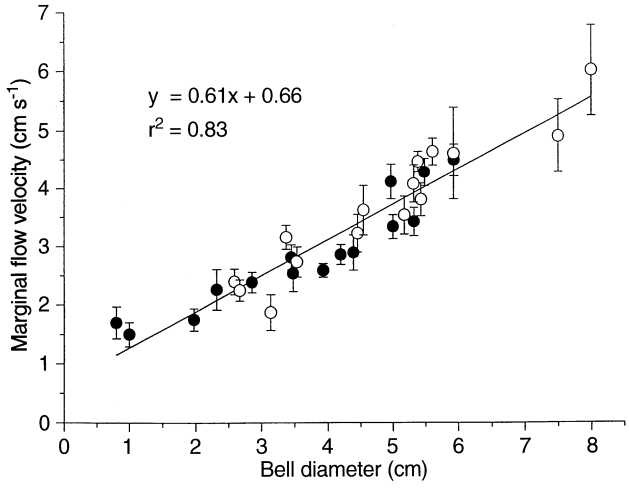

Fig. 3 *Chrysaora quinquecirrha.* Marginal flow velocities of medusae of varying bell diameters. Each data point represents a different medusa (○ Chesapeake Bay medusae; ● Niantic River medusae). Particle velocities were measured over 1/20-s intervals at the bell margin. Eight to 12 velocities were determined for each medusa. *Error bars*: 95% confidence intervals around the mean velocity

While most captures occurred near the bell margin, the location of capture relative to the bell margin was influenced by the phase of the pulsation cycle during which the prey was entrained in the flow around the medusa. For example, prey entrained in the vortex shed during the power stroke were more likely to be carried further from the bell before encountering the oral arms and tentacles (Fig. 4A) than were prey entrained in the fluid refilling the subumbrellar space during the recovery stroke (Fig. 4B). A number of prey that were captured more distally down the oral arms or tentacles could not be readily classified as being captured during a distinct phase of the pulsation cycle. This was because the wake posterior to the bell consisted of a continuous series of pulsed vortices. Prey that passed a distance of greater than approximately 1.5 cm from the bell margin before encountering a capture surface became part of a pulsed but continuous flow in which the location of encounter with the medusa was unpredictable and uncoupled from concurrent bell pulsations. Capture locations of these prey were mapped but not attributed to a specific stage of the pulsation cycle (Fig. 4C). Many prey escaped by passing through the wake without encountering a capture surface.

The pulsed vortex structure of the medusan wake was recorded with in situ video of medusae swimming in the Niantic River on 8 July 1994 (Fig. 5A). Vortices formed at the bell margin during the power stroke and persisted as the medusa swam forward, pulling its oral arms and tentacles through the wake. Vortices expanded after formation but visible structure dissipated rapidly so that the maximum number visible in the wake never exceeded two to three vortices.

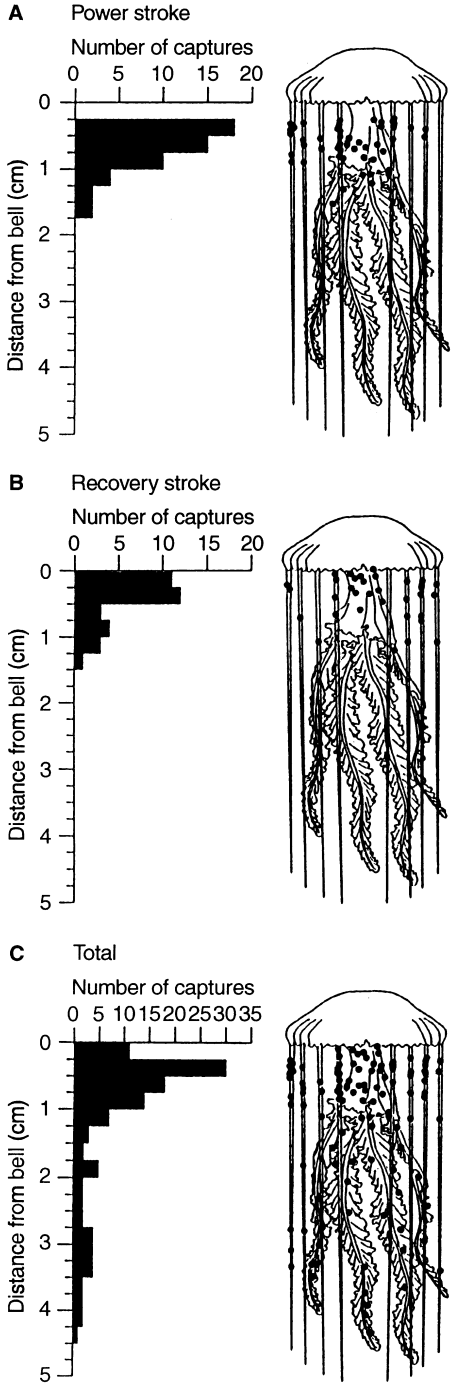

Fig. 4 *Chrysaora quinquecirrha.* Locations of *Artemia* sp. nauplii encountered and captured by a swimming 2.5 cm diameter medusa during **A** power and **B** recovery strokes. Medusa bell is shown in relaxed state so that capture locations can be directly compared between pulsation stages. **C** Total prey captures over a 20-min interval included captures not attributable to a specific portion of the pulsation cycle

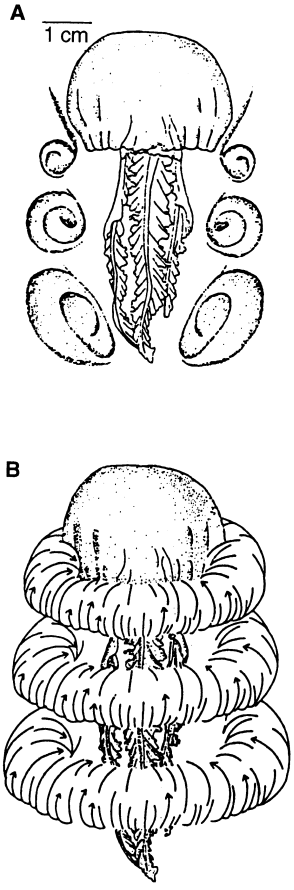

Fig. 5 *Chrysaora quinquecirrha.* **A** Line drawing of vortex structure for a 4.9 cm diameter medusa. Three vortices were formed during power strokes of three consecutive pulsation cycles. Areas between vortices represent recovery strokes of these cycles. Dimensions based on in situ video from Niantic River. Tentacles not shown. **B** Schematic illustration of toroidal wake of a swimming medusa based on previous panel. *Arrows* show direction of water flow

Discussion

From a functional perspective, the morphology of *Chrysaora quinquecirrha* represents a paradox shared with many other medusae but unusual among the metazoa. *C. quinquecirrha* swims almost continuously (Costello et al. unpublished), yet its capture surfaces are located at the posterior (oral) end of the body. Other cruising predators have typically evolved capture surfaces (proboscis, eversible pharynx, chelae, mouthparts, teeth) at the leading, or anterior, end of the body (Barnes et al. 1993). The functional problem is that of moving the prey to the capture surfaces. *C. quinquecirrha*, like a variety of other scyphomedusae (Costello and Colin 1995), uses bell contractions to push fluid and entrained prey along its capture surfaces. The fluid flow along these body surfaces takes the form of a series of pulsed vortices produced by alternating contraction and relaxation of the bell. Locations of prey capture corresponded closely to the phase of the bell pulsation cycle. We have analyzed this flow in two dimensions because this perspective is most readily visualized and documented, but the true nature of the flow would be more appropriately viewed in three dimensions (Fig. 5B). Due to the radial symmetry of medusae, flow along the capture surfaces is actually a series of pulsed toroids which provide a complex, unsteady mechanical signal to entrained prey.

Kinematic analysis provides insight into the functional relationship between swimming and water flow. Swimming kinematics of *Chrysaora quinquecirrha*

resemble those of another oblate medusan predator, the hydromedusa *Aequorea victoria* (Colin and Costello 1996). A 5.0 cm diameter *A. victoria* and a 5.45 cm diameter *C. quinquecirrha* had similar velocities (max. 1.91 and 1.68 cm s^{-1}, respectively) and accelerations (max. 4.9 and 8.9 cm s^{-1}, respectively). The flow around each species was characterized by maximum Re values in the 10^2 to 10^3 range (max. 787 and 791, respectively), indicating that inertial forces predominated relative to viscous forces during swimming for both species (Vogel 1994). The velocities and accelerations of these oblate medusae are low in comparison to other smaller, more prolate (streamlined) medusae. For example, a smaller (1.0 cm diameter), slowly swimming (not rapid escape swimming) hydromedusa, *Aglantha digitale*, had peak velocities >5.0 cm s^{-1} and accelerations >40 cm s^{-1}, substantially higher than those of the much larger *A. victoria* and *C. quinquecirrha*. From the perspective of translating their bodies through water, oblate medusae such as *C. quinquecirrha* appear to be inefficient relative to more prolate forms such as *A. digitale*. Nevertheless, an analysis of hydrodynamic forces during medusan swimming shows that oblate medusae, such as *C. quinquecirrha*, are very effective at moving the fluid surrounding their body during swimming (Colin and Costello 1996). Indeed, it may be that their body form and function has evolved primarily to perform work on the fluid around them, in the form of toroidal flow through prey capture surfaces, rather than for efficient translation through a fluid. The relevance of fluid considerations to feeding by *C. quinquecirrha* is supported by the correspondence between prey capture locations and swimming-generated currents.

What patterns of in situ prey selection would be expected based solely on fluid interactions? Since *Chrysaora quinquecirrha* swims almost continuously (Costello et al. unpublished), it may be described as a cruising forager (Gerritsen and Strickler 1977; Greene 1986). Based on this pattern, we would expect it to capture primarily slowly moving planktonic prey. The primary prey consumed by another cruising scyphomedusa, *Aurelia aurita*, had escape swimming velocities less than the marginal flow velocities for *A. aurita* (Costello and Colin 1994; Sullivan et al. 1994). Because marginal flow increases with bell diameter, we would expect an increasing range of prey species to be consumed by larger diameter *C. quinquecirrha*. Immobile prey, such as fish eggs, and slowly moving prey, such as early stage fish larvae, barnacle nauplii, veliger larvae, ctenophores, and many copepod nauplii would be the expected prey of most sizes of *C. quinquecirrha* (Fig. 6). Copepodites and adult copepods characteristically escape at >5 cm s^{-1} and would not be expected to be major prey items. We would expect only the largest medusae to capture some of the slower copepodites.

Do observed feeding patterns correspond to predictions based on flow patterns? Early laboratory studies (Delap 1901; Lebour 1923) described *Chrysaora quinquecirrha* as selecting soft-bodied prey and consuming

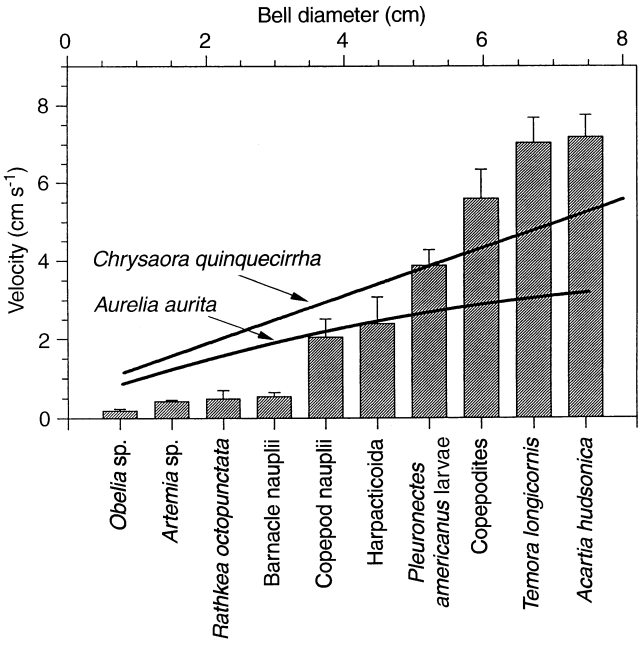

Fig. 6 *Aurelia aurita* and *Chrysaora quinquecirrha.* Comparison of zooplankton escape velocities with regressions of marginal flow velocities over bell diameters of medusae (regression for *A. aurita* and zooplankton escape velocities from Costello and Colin 1994)

copepods only when ctenophores and small medusae were depleted as prey choices. More recent quantitative studies have documented that while fish eggs and larvae, barnacle nauplii and other slow moving prey are present in the gut, copepodites and strongly moving adult copepods frequently predominate in the gut contents of medusae preserved in the field, and weakly moving veliger larvae are seldom found in medusa guts (Purcell 1992; Purcell et al. 1994a; Sullivan et al. unpublished). Further, adult copepods were positively and copepod nauplii negatively selected (Purcell 1992). Therefore, some in situ patterns of prey selection appear to disagree with predictions based on fluid flow. Several factors may influence these inconsistencies. First a fluid-based model predicts encounter between medusa and prey but provides no information on subsequent components of the predation cycle. This cycle starts with encounter but is followed by capture, ingestion, and digestion of prey by the predator (Holling 1959). The latter components cannot be ignored for a number of predator–prey interactions. For example, whereas many copepod nauplii encounter coral polyp tentacles, most escape, presumably because a nauplius provides an insufficient stimulus to elicit the necessary response by tentacular nematocysts of the polyp (Heidelberg et al. 1997). Similarly, veliger larvae are both encountered and captured by *C. quinquecirrha,* but are rapidly released alive (Purcell et al. 1991). Therefore, although both these prey types may be entrained and encountered, subsequent interactions at the capture and ingestion phases of the predation cycle limit the capacity of a flow-based model to

predict in situ prey selection patterns. Further, although simple escape velocities may address the vulnerability of many taxa to medusan feeding currents, there is sufficient evidence of the complexity of prey behavior (Purcell et al. 1987; Strand and Hamner 1988; Hwang et al. 1994; Trager et al. 1994) to suggest that other factors also affect prey vulnerability. Additionally, important gelatinous prey such as ctenophores (Miller 1974; Purcell and Cowan 1995) may be encountered, captured and ingested yet not be counted in gut contents due to rapid digestion and tissue dissolution in formalin preservatives (Purcell 1992). Hence, specific types of predator–prey interactions as well as methodological considerations affect the applicability of a flow-based model for predicting in situ selection patterns of *C. quinquecirrha* medusae.

Knowing these limitations, what is the importance of flow-based encounter in prey selection by *Chrysaora quinquecirrha*? Although clearance rates (volume of water cleared predator^{-1} time^{-1}) are prone to the same limitations as gut content data for describing prey selection, they do express feeding rate on a fluid volume basis and give an indication of the relative efficiency with which different prey items are extracted from the medium. Average clearance rates of a *C. quinquecirrha* medusa 40 mm in diameter differ greatly with prey type (review by Purcell 1997): on copepods 16 liters d^{-1} (Purcell 1992); on fish eggs and larvae averages of 714 and 1318 liters d^{-1}, respectively (Purcell et al. 1994a); and on ctenophores, 309 litres d^{-1} (Purcell and Cowan 1995). These data indicate that although copepods may form a major component of the diet of *C. quinquecirrha*, fish eggs and larvae, and ctenophores when they are present, are more efficiently removed by *C. quiquecirrha* from the surrounding fluid than are copepods.

We suggest that fluid motions created by bell pulsations during swimming play a central role in prey encounter by *Chrysaora quinquecirrha*. Comparison of the relative magnitudes of the marginal flow velocity for a specific diameter medusa, and the escape velocity of a specific prey type, allows prediction of the encounter rate of that prey type by capture surfaces of the medusa. Actual field selection patterns additionally reflect specific predator–prey interactions at several stages in the predation process subsequent to the encounter between prey and the medusan flow field. A successful prey selection model for *C. quinquecirrha* must incorporate these other interactions to predict in situ selection patterns. An improved understanding of in situ feeding by *C. quinquecirrha* should address the relationship between bell diameter and in situ selection and the complex interactions between medusae and copepods.

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