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Escape of the ctenophore *Mnemiopsis leidyi* from the scyphomedusa predator *Chrysaora quinquecirrha*

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Abstract The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 is known to be eaten by the scyphomedusan *Chrysaora quinquecirrha* (Desor, 1948), which can control populations of ctenophores in the tributaries of Chesapeake Bay. In the summer of 1995, we videotaped interactions in large aquaria in order to determine whether *M. leidyi* was always captured after contact with medusae. Surprisingly, *M. leidyi* escaped in 97.2% of 143 contacts. The ctenophores increased swimming speed by an average of 300% immediately after contact with tentacles and 600% by mid-escape. When caught in the tentacles of *C. quinquecirrha*, the ctenophores frequently lost a portion of their body, which allowed them to escape. Lost parts regenerated within a few days. The striking ability of *M. leidyi* to escape from *C. quinquecirrha* may be critically important in maintaining ctenophore populations in situ.

Introduction

Chrysaora quinquecirrha scyphomedusae are known to eat *Mnemiopsis leidyi* ctenophores and can control ctenophore populations in tributaries of Chesapeake Bay (Cargo and Schultz 1967; Larson 1986; Purcell and Cowan 1995). Inverse relationships in the numbers of these two species have been described in several locations, suggesting the potential importance of predation by medusae on ctenophores (Feigenbaum and Kelly 1984; Purcell et al. 1991; Purcell and Cowan 1995). Both species are important consumers of zooplankton in the bay, and effects of medusa predation on ctenophore populations could be seen at lower trophic levels (Feigenbaum and Kelly 1984; Purcell and Cowan 1995).

Recently, Purcell and Cowan (1995) documented that *Mnemiopsis leidyi* may occur in situ with one or both lobes reduced in size by 80% or more. Lobe reduction was not caused by starvation, and other predators apparently were absent. In laboratory experiments, small *Chrysaora quinquecirrha* (≤20 mm diameter) partially consumed small ctenophores (≤20 mm in length) that were larger than themselves. Therefore, Purcell and Cowan (1995) concluded that the short-lobed condition was caused by *C. quinquecirrha* partially consuming the ctenophores. In 3.2 m^3 mesocosms, small ctenophores (≥35 mm in length) were captured more than large ones in experiments using medusae >40 mm in diameter, which suggested some escape of large *M. leidyi* from *C. quinquecirrha*. Both Larson (1986) and Purcell and Cowan (1995) mention some escape attempts by ctenophores contacted by *C. quinquecirrha.*

Many zooplankton taxa, for example, copepods, euphausiids, rotifers, medusae and siphonophores, have highly developed escape or defensive responses (reviewed by Ohman 1988; Mackie 1995). Not to be eaten by a predator obviously has a high selective advantage. Many of the escape responses involve speed, for example, the escape speeds of copepods (up to 8.3 cm s^{-1} or 105 body lengths s^{-1}) were as much as 18.6 times greater than routine swimming speeds (Heidelberg et al. 1997).

Ctenophores, however, generally are weak swimmers, propelling themselves by beating ciliary "comb plates". Species in three orders (Cydippida, Thalassocalycida and Ganeshida) remain stationary while feeding, and species in three other orders (Lobata, Cestida and Beroida) swim slowly in the oral direction (reviewed by Matsumoto and Harbison 1993)(Table 1). The cruising species that feed on zooplankton (orders Lobata and Cestida) forage at speeds of <1 to 2 cm s^{-1} (Matsumoto and Harbison 1993; Mackie 1995).

Escape behaviors of some oceanic ctenophores have been observed by SCUBA divers (Matsumoto and

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Table 1 Foraging and escape speeds of ctenophores. Ctenophore orders follow species names (*L* Lobata; *Cy* Cydippida; *C* Cestida; *B* Beroida). Foraging is always in the oral direction. Escape directions follow speeds (*O* oral; *A* aboral; *E* end). Escape stimuli were provided by the experimenter, except in the present study, where the stimulus was a predator. Values are means ± 1 SD (*NQ* not quantified)

Species	Foraging speed (cm s^{-1})	Escape speed (cm s^{-1})	Escape mode	Source
Bolinopsis infundibulum (L)	0.85 ± 0.27	NQ	ctenes	Matsumoto and Harbison (1993)
Mnemiopsis leidyi (L)	0.6 ± 0.3	3.2 ± 1.1 (A)	ctenes	Present study
Euplokamis dunlapae (Cy)	~ 2	~ 4 (A), 5.5 (O)	ctenes	Mackie (1995)
Ocyropsis spp. (L)	1.40 ± 1.3	7.2 ± 2.1 (A)	lobe flaps	Matsumoto and Harbison (1993)
Cestum veneris (C)	2.05 ± 0.28	~ 5–9 (E)	undulations	Matsumoto and Harbison (1993)
Velamen parallelum (C)	NQ	≤ 11 (E)	undulations	Matsumoto and Harbison (1993)
Beroe spp. (B)	3.58 ± 1.75	NQ (O)	ctenes	Matsumoto and Harbison (1993)

Harbison 1993). Divers touching the ctenophores to elicit escapes caused the ctenophores to swim away at increased speeds. Escape speeds ranged from 4 to 11 cm s^{-1} (Table 1). The escape responses generally were of short duration (<10 s) and moved the ctenophores up to several body lengths distant. Matsumoto and Harbison (1993) concluded that the escape responses probably would not be effective against visual predators. Visual predators of ctenophores include fishes (reviews by Ates 1987; Arai 1988; Harbison 1993) and euphausiids (Beyer 1992). All but one known genus (*Pleurobrachia*) of ctenophores bioluminesce upon contact (Haddock and Case 1995), and some species also eject clouds of luminous mucus or particles that may confuse visual predators (Matsumoto and Harbison 1993; Mackie 1995). Therefore, escape responses in combination with luminous displays may be effective in deterring visual predators in low-light conditions.

Ctenophores also are eaten by a variety of nonvisual predators, such as pelagic cnidarians and other ctenophore species (*Beroe* spp.)(review by Purcell 1991). In fact, the diets of semaeostome scyphomedusae, like *Chrysaora quinquecirrha*, contain many gelatinous prey. Selection for gelatinous prey by scyphomedusae seems predictable, given the large size of the prey, lack of protective covering, and apparent weak swimming abilities (Purcell 1991, 1997). That *C. quinquecirrha* selects for ctenophores can be inferred from laboratory experiments showing that ephyrae cleared larval *Mnemiopsis leidyi* at higher rates than any other prey taxon (Olesen et al. 1996). In the present study, we videotaped interactions between *C. quinquecirrha* and *M. leidyi* in order to quantify the frequency of escape, and swimming speeds of this ctenophore species before and after contact with the medusae. Our objectives were to determine if escape behavior exhibited by a ctenophore was effective against a nonvisual predator, and to examine the importance of prey escape to feeding by a scyphomedusa.

Materials and methods

Mnemiopsis leidyi A. Agassiz, 1865 and *Chrysaora quinquecirrha* (Desor, 1848) were gently dipped using a soft-mesh net from the Choptank River, Cambridge, Maryland, USA during June to August 1995. Specimens were used in experiments within 24 h of capture. The two species were held separately, unfed, in 20-liter containers of 5-μm filtered Choptank River water (11 to 12‰), for a minimum of 2 h before taping to allow acclimation to laboratory conditions (23 to 25 °C).

Two aquaria were used for videotaping encounters between medusae and ctenophores: a 38-liter tank (49.5 × 31.5 × 24.5 cm) filled with 5-μm filtered Choptank River water for only the smallest specimens; a 762-liter tank (180 × 73 × 58 cm), filled with sea water mixed with deionized water to 11 to 12‰ salinity, was used for most interactions. Water temperatures varied between 23 and 25 °C. Copepods (*Acartia tonsa*) were added in low densities to the video aquaria, which increased the activity of both ctenophores and medusae.

Medusae and ctenophores were gently transferred to the aquaria in 1- to 4-liter beakers. Medusae acclimated in the video aquaria for 5 to 30 min, while individual ctenophores were acclimated simultaneously in 4-liter containers of water from the video aquaria and then gently released into the video aquaria. One to three medusae and three to five ctenophores were used in each taping session. All encounters resulted solely from the swimming behaviors of the ctenophores and medusae. Interactions in which aquarium surfaces interfered were not analyzed. Each medusa was used for a 1 to 1.5 h taping session. Medusa diameter then was measured with a ruler by placing them exumbrellar side down on a flat surface. Ctenophore length was measured with a ruler before acclimation while each ctenophore was just covered by water in a shallow dish. Each ctenophore was used for five or less contacts with a medusa. The water in the aquaria was replaced after each session.

Interactions were filmed in three dimensions (3-D) with an NEC TI-22A CCD camera and a Yashika Hi-8 video camera (30 frames s^{-1}). The two cameras were mounted at a 90° angle to each other on a platform or tripod that could be moved laterally and raised and lowered as needed to follow interactions in the tanks. The paired video recordings were synchronized by a flash from a strobe light immediately before each interaction. The focal distance was held constant throughout each interaction. Scale was determined by a ruler inserted near the specimens and videotaped immediately after each interaction. Light for videotaping was provided by a bank of five 40-W fluorescent bulbs above the aquaria, which did not seem to affect the behaviors of the medusae or ctenophores.

Videotape analysis was done with a Sony Hi-8 video cassette recorder deck (Model EV-S2000 NTSC) and a Panasonic monitor (Model CTL-2770S). The location of contact on both the jellyfish and the ctenophore, direction of ctenophore escape, distance covered by the escape, ctenophore lobe contraction, loss of ctenophore body parts, medusa tentacle contraction, and change in medusa swimming direction caused by contact were recorded for 143 contacts. The numbers of interactions in various categories differed because parts of some interactions could not be clearly discerned from the tapes. Ctenophore swimming speeds and directions ($n = 20$) and distance of escape ($n = 26$) were determined in 3-D for contacts with medusa tentacles by marking their locations on the

video monitor every five frames (1/6 s). Because ctenophores often rotated as they swam, ctenophore positions were determined by marking the front and back edges and then using the midpoint on a line connecting the two points. The paths were traced and the distances, speeds, and directions of swimming quantified using a Jandel Scientific Sigma Scan digitizing pad and software. The two videotapes for each interaction were analyzed separately. Then the distances and speeds were determined in 3-D from the following equation: distance (mm) $= (a^2 + b^2)^{1/2}$, where a is distance traced on the video monitor from Camera 1, and b is distance on Camera 2 times the cosine of the angle of travel. This angle was manipulated to always be positive. Multiplying the distance travelled by the cosine of the angle for one camera removed the vertical distance so that it was included only once. The traced distances were converted to actual distances by adjusting according to the scale videotaped during each encounter. Swimming speed (mm s^{-1}) equalled the distance travelled during each five frames multiplied by 6 to get 1-s intervals.

Results

Of the 143 contacts between *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, only four (2.8%) resulted in capture and ingestion of a ctenophore. No obvious relationship existed in the sizes of the ctenophores that were captured and the sizes of the successful medusae, however, the length of the captured ctenophore was less than medusa diameter in each case (Fig. 1). In a few other cases, the ctenophores were held for 1 to 10 min, but eventually escaped with severe damage.

Because the ctenophores foraged with the oral end leading, the oral end of the ctenophores contacted medusae in 49% of the interactions, which was significantly more than the side (30%) or the aboral end (21%; Chi-square, $p < 0.05$)(Table 2). There was a significant dependence between location of contact and escape direction (*G*-test of independence, $G = 89.02$, $df = 7$, $p << 0.001$). When touched on either end, *Mnemiopsis leidyi* escaped in the opposite direction significantly more often than continuing in the same direction (Chi-square, $p << 0.05$)(Table 2; Fig. 2). When contacted on the side,

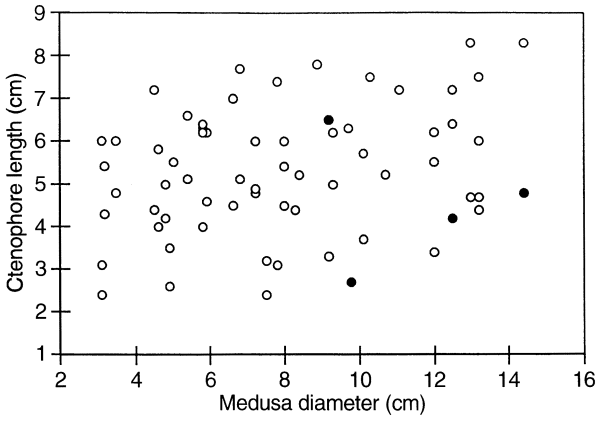

Fig. 1 *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*. Sizes of ctenophores that contacted medusae in laboratory aquaria. All ctenophores escaped after contact except for four individuals, which are marked by *solid circles*. *Open circles* represent ≥1 contact. 139 escapes and 4 captures equalled 143 contacts total

Table 2 *Mnemiopsis leidyi*. Locations of contacts with scyphomedusae (*Chrysaora quinquecirrha*) and ctenophore escape directions

Escape direction	Location of contact on ctenophore			
	Oral	Aboral	Side	Total
Aboral	66	3	24	93
Oral	1	24	11	36
None	1	2	7	10
Total	68	29	42	139

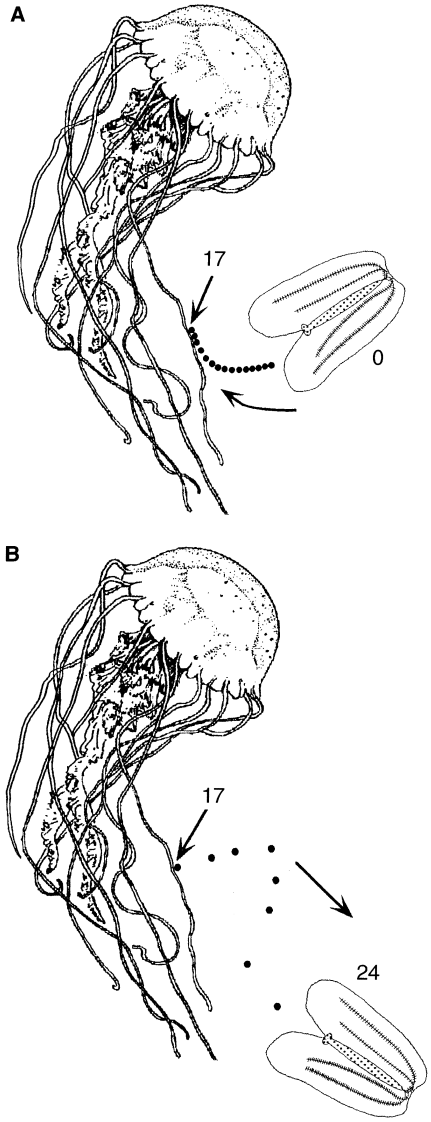

Fig. 2 *Mnemiopsis leidyi*. Approach and escape of a ctenophore contacting a medusa (*Chrysaora quinquecirrha*) as traced from a videotape. *Dots* indicate the position of the oral edge of the ctenophore at 1/6 s intervals. **A** The ctenophore approached with the oral end leading and **B** escaped with the aboral end leading. The greater escape speed of the ctenophore is illustrated by the wide spacing between dots in **B** as compared with the slower foraging speed in **A**. The medusa was 9.3 cm in diameter and the ctenophore was 6.2 cm in length. 0 is the initial ctenophore position, 17 is the 1/6 s interval when contact occurred, and 24 is the last interval represented

ctenophores escaped significantly more often towards the aboral end (Chi-square, $p < 0.05$).

The escape response caused the ctenophores to reverse direction in 114 of the 139 escapes (82%). In addition, ctenophores abruptly closed their lobes in 70.6% of 109 contacts where the lobes were clearly open before contact (Table 3). Lobes closed in response to contacts both with the bell and tentacles of medusae. *Mnemiopsis leidyi* closed its lobes more often when escaping orally (83%) than when escaping aborally (65%), however, a *G*-test of independence and Williams' corrections for a 2×2 table and 1 degree of freedom showed no significant dependence ($p > 0.10$).

Escapes after contact with medusa tentacles were more vigorous than escapes after contact with the swimming bell. Speeds from the latter escapes were not quantified because the bell interfered with tracking the ctenophore. The ctenophore escapes after contact with tentacles lasted 4.0 ± 1.7 s and consisted of an initial phase of rapid acceleration, where speed increased from means of 6 to 32 mm s^{-1} (equivalent to 0.1 to 0.6 body lengths s^{-1}), and then gradually decreased (Fig. 3; Table 4). This represented a sixfold increase from foraging speed to maximum escape speed (Table 4). Linear and logarithmic regression analyses showed no significant relationships between ctenophore size and speed (both in millimeters per second and body lengths per second) before, after contact, or in mid-escape (highest $r^2 = 0.295$, $n = 20$). The small size range of ctenophores used for speed measurements (3.3 to 7.8 cm) may explain the lack of a significant trend. Escape swimming carried the ctenophores an average of 95 mm distance (1.8 ± 0.8 body lengths). There were no significant differences among oral (22) and aboral (4) escape speeds or distances (Mann–Whitney *t*-statistics).

In 14 of the 82 escapes from tentacle contact, pieces of the ctenophore were seen to tear off and remain attached to the medusa's tentacles. When maintained in a container with copepods for food, ctenophores sustaining various degrees of damage healed completely within 3 d. Small pieces torn off the ctenophores would not have been visible on the videotapes.

Ctenophores made contact with a medusa's tentacles about 60% of the time and with the bell about 40% (Table 5). When contact was made in the middle or lower portions of the tentacles, the tentacles contracted and shortened substantially. Upon contact with a ctenophore, medusae often changed swimming direction, usually turning toward the point of contact (Table 5). This action sometimes resulted in further contacts with the ctenophore.

Table 3 *Mnemiopsis leidyi*. Occurrence of lobe contractions and escape directions after contact between ctenophores with open lobes and scyphomedusae (*Chrysaora quinquecirrha*)

Escape direction	Lobe contraction		
	Contraction	No contraction	Total
Aboral	48	26	74
Oral	24	5	29
None	5	1	6
Total	77	32	109

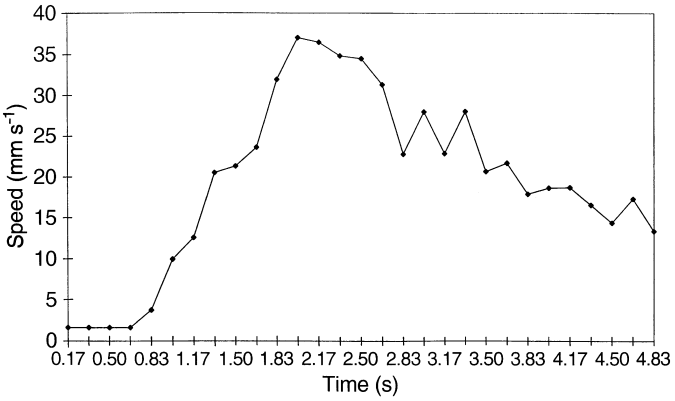

Fig. 3 *Mnemiopsis leidyi*. Ctenophore swimming speed (mm s^{-1}) during a typical interaction with a *Chrysaora quinquecirrha* medusa as measured over 1/6 s intervals by video analysis. The ctenophore was foraging in the oral direction when it contacted a tentacle of the medusa at 0.665 s. Thereafter, swimming was in the aboral direction as the ctenophore escaped. The ctenophore was 4.2 cm in length

Table 4 *Mnemiopsis leidyi*. Swimming speed before, immediately after, and in mid-escape following contact with the tentacles of scyphomedusae (*Chrysaora quinquecirrha*) ($n = 20$). Distances covered during escapes also are given ($n = 26$). Ctenophores were foraging in the oral direction prior to contact and escaped in the aboral direction (*SD* standard deviation)

	Swimming speeds and distance			
	Mean	SD	Minimum	Maximum
Before contact (mm s^{-1})	6	3	2	11
After contact (mm s^{-1})	19	7	7	30
Middle of escape (mm s^{-1})	32	11	12	55
Change				
Before to after (%)	311	218	56	800
Before to middle (%)	614	414	91	1733
Escape distance (mm)	95	45	25	229

Table 5 *Chrysaora quinquecirrha*. Locations of contact by ctenophores (*Mnemiopsis leidyi*), and the proportions of those contacts in which medusae reoriented towards the side of contact. Percentages given in *brackets*

Region of contact	No. of contacts	No. changing direction
Bell	56 [39.4]	12 [21]
Upper tentacle	36 [25.4]	16 [44]
Mid tentacle	24 [16.9]	4 [17]
Lower tentacle	26 [18.3]	1 [4]

Discussion and conclusions

For an animal with low escape swimming speeds (means of 32 mm s^{-1} or 0.6 body lengths s^{-1}), the ctenophore

Mnemiopsis leidyi escaped from its predator, *Chrysaora quinquecirrha*, with surprising frequency (95% of 82 contacts with tentacles). To our knowledge, escape frequencies of a ctenophore from a natural predator have not been determined previously. Strand and Hamner (1988) found similar frequencies of escape (96%) by the scyphomedusa *Aurelia aurita* from the scyphomedusa *Phacellophora camtschatica*, and small *A. aurita* were captured more frequently than large. Small ctenophores and hydromedusae were not seen to escape from *P. camtschatica*.

Costello and Colin (1994) hypothesized that prey captured by the scyphomedusa *Aurelia aurita* have escape velocities less than the velocity of the swimming-generated flow at the bell margin ("marginal flow velocity"). Thus, the medusa-generated flow would overwhelm escape swimming of slow prey and draw them into the tentacles. Marginal flow velocities of *Chrysaora quinquecirrha* medusae used in the present study ranged from 2.5 to 9.8 cm s^{-1} (calculated from Ford et al. 1997). The escape speeds of *Mnemiopsis leidyi* (1.2 to 5.5 cm s^{-1}) generally were less than these calculated marginal flow velocities, and according to the above hypothesis, many ctenophores should have been captured. Escape of *M. leidyi* was not stimulated by the swimming-generated flow, however, and ctenophore contact with the medusae generally was not caused by the ctenophores being swept into the tentacles by the swimming-generated water flow.

Escape swimming of *Mnemiopsis leidyi* was an average of six times faster than foraging speeds, and transported the ctenophores an average of 95 mm distance (about 2 body lengths). This is comparable to another lobate species, *Bolinopsis infundibulum*, which exhibited escape speeds (unmeasured) similar to foraging speeds (9 mm s^{-1}), which transported the ctenophores 1 to 3 body lengths (Matsumoto and Harbison 1993), and to a cydippid species (*Euplokamis dunlapae*), which also used ciliary swimming in escape (Mackie 1995)(Table 1). Foraging speeds of other species examined were similar (14 to 20 mm s^{-1}), however, those species (*Ocyropsis* spp., *Cestum veneris*, and *Velamen paralellum*) used muscular contractions for escape swimming and reached much greater speeds (50 to 110 mm s^{-1}) than species using ciliary swimming (Table 1).

Upon contact of the oral end with *Chrysaora quinquecirrha*, *Mnemiopsis leidyi* often would rapidly close its lobes, and the escape occurred with the streamlined aboral end leading (Fig. 2). Lobe closures did not appear to cause an initial burst of speed (Fig. 3), but the resulting streamlining probably increased speed overall and reduced the volume occupied by the ctenophore, which should reduce the chances of further contacts. Additionally, the vigorous closures that often occurred when tentacles touched the lobes helped to dislodge some of the medusae's tentacles.

The ctenophores also enhanced their escape ability by losing pieces of tissue attached to the medusa tentacles. The power to lose and regenerate body parts is a common strategy in nature for escaping predators, and *Mnemiopsis leidyi* has excellent regenerative powers. Coonfield (1936) found that when *M. leidyi* was cut in half in the laboratory, most of the pieces that maintained the apical organ regenerated fully. Purcell and Cowan (1995) found that damaged ctenophores healed quickly, but that fecundity and probably clearance rates were reduced. It seems that their gelatinous composition allows ctenophores to escape by sacrificing a portion of their bodies and subsequently experiencing a short period of reduced fitness.

In each of the four capture events, the ctenophore was considerably smaller than the medusa that captured it. Similarly, Purcell and Cowan (1995) found that small ctenophores were more likely to be consumed in 24-h experiments and that medusae had higher clearance rates on small ctenophores. During our study, small ctenophores (≤3 cm) were plentiful in early June, but as *Chrysaora quinquecirrha* appeared, small ctenophores began to disappear and were rare by early July, with the smallest being ≥4 cm. Size distributions of ctenophores in spring and summer in Chesapeake Bay during other years also followed this pattern (Purcell 1988; Purcell and Cowan 1995).

The primary reaction of *Chrysaora quinquecirrha* to contact with *Mnemiopsis leidyi* was a change in swimming direction. When contact was made on the upper tentacles or bell edge, *C. quinquecirrha* frequently moved towards the point of contact. This may be simply because contact by a ctenophore on the upper tentacle could pull that edge of the bell down and change the swimming direction towards the point of contact. Active pursuit of ctenophore prey by *C. quinquecirrha* was not observed.

Both *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* are important in the ecology of Chesapeake Bay. Both are important consumers of zooplankton and ichthyoplankton (Kremer 1979; Deason and Smayda 1982; Govoni and Olney 1991; Purcell 1992; Cowan and Houde 1993; Purcell et al. 1994a, b). The intraguild predation by medusae on ctenophores leads to complex community-level effects that actually could reduce predation on zooplankton and ichthyoplankton populations (Greve 1981; Feigenbaum and Kelly 1984; Purcell 1991; Cowan and Houde 1993). Purcell and Cowan (1995) speculated that predation by *C. quinquecirrha* on *M. leidyi* may contribute to the existence of high zooplankton standing stocks, and lower ichthyoplankton mortality rates during the summer in Chesapeake Bay, because of the high feeding and reproductive rates of *M. leidyi*.

The striking ability of *Mnemiopsis leidyi* to escape from *Chrysaora quinquecirrha* may be of great importance in maintaining ctenophore populations. Whether or not the ctenophore populations persist may depend critically on the times at which populations of the two species develop. Typically, small ctenophores are present before ephyrae of *C. quinquecirrha* appear in May (Purcell and Cowan 1995). The young medusae feed on

the small ctenophores (Olesen et al. 1996), and if the medusa population is large, they may consume all of these small ctenophores in tributaries (Purcell and Cowan 1995). However, if the medusa population is small or delayed due to low salinities and/or temperatures (Cargo and Schultz 1967; Purcell personal observation), the ctenophores can grow large and thus escape from medusae, allowing the ctenophores and medusae to coexist.

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