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Differential Ingestion and Digestion of Bivalve Larvae by the Scyphozoan *Chrysaora quinquecirrha* and the Ctenophore *Mnemiopsis leidyi*

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Abstract. We investigated predation on bivalve veligers by the scyphozoan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*. We found that the medusa stage of *C. quinquecirrha* captures, but does not digest, veliger larvae: 99% of oyster veligers (*Crassostrea virginica*) caught by medusae were egested alive within 7 h of capture, and 98% survived for 24 h after egestion; 98% of oyster, mussel (*Mytilus edulis*), and clam (*Mulinia lateralis*) veligers placed on the oral arms of medusae were rejected; all bivalve veligers in field-collected medusae were closed and full of tissue. Our laboratory evidence suggests that the shell of larval bivalves probably offers protection from medusae: 23% of dead, open veligers were ingested by medusae compared with 0.7% of live, closed veligers; open veligers were retained longer than closed veligers; and tissue excised from recently settled oyster larvae was ingested and digested. Freeswimming *C. quinquecirrha* ephyrae ingested but did not digest veligers. By contrast, the benthic scyphistoma stage ingested 69% of veligers that contacted their tentacles and digested 48% of those ingested. Each scyphistoma consumed an average of 1 veliger/day at densities of 0.3 veligers ml^{-1}. However, larval settlement was not reduced on oyster shells bearing scyphistomae. By contrast to the results on *C. quinquecirrha*, ctenophores egested only 4% of veligers alive, and 25% of the veligers in their gut contents were digested. Predation on veligers by ctenophores was estimated to be 0.2 to 1.7%/day in Chesapeake Bay. We conclude that *C. quinquecirrha* medusae are not important predators of bivalve veligers, but rather may reduce their mortality by consuming ctenophores, which do eat veligers.

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Introduction

Predation on planktonic larvae is one of the least understood factors affecting abundance of adult benthic invertebrates (Young and Chia, 1987). Early studies reported that the scyphomedusan *Chrysaora quinquecirrha* (DeSor) and the ctenophore *Mnemiopsis leidyi* A. Agassiz may prey heavily upon the larvae of the eastern oyster *Crassostrea virginica* (Gmelin) (Truitt and Mook, 1925; and Nelson, 1925, 1953, respectively). Both species are seasonally abundant in Atlantic coast estuaries, and co-occur with oyster larvae. Their effects on survival of oyster larvae have not been documented.

In several Atlantic coast estuaries, *M. leidyi* has been shown to be an important predator of crustacean zooplankton (*e.g.*, Cronin *et al.*, 1962; Cargo and Schultz, 1967; Bishop, 1967; Burrell, 1968; Herman *et al.*, 1968; Kremer, 1979; Deason and Smayda, 1982; Feigenbaum and Kelly, 1984; Olson, 1987) and bivalve veliger larvae (Nelson, 1925; Truitt and Mook, 1925; Burrell and Van Engel, 1976). Bivalve veligers were 75% of the prey of *M. leidyi* in New Jersey waters, and high larval settlement of three bivalve species, including oysters, occurred in years when ctenophore densities were low (Nelson, 1925). In the York River, Virginia, bivalve larvae were inversely related to the biomass of ctenophores (Burrell and Van Engel, 1976).

Studies on the feeding of scyphomedusae have shown them to eat a variety of zooplankton (reviewed in Larson, 1978; Clifford and Cargo, 1978; Feigenbaum and Kelly, 1984; Larson, 1987; Fancett, 1988; Brewer, 1989). Al-

though *C. quinquecirrha* medusae were reported to feed on oyster larvae (Truitt and Mook, 1925; Loosanoff, 1974), high numbers of oyster larvae and medusae often co-occurred (Truitt and Mook, 1925). This apparent paradox may be due to the fact that *C. quinquecirrha* medusae prey heavily upon ctenophores (Cargo and Schultz, 1967; Burrell, 1968; Miller, 1974; Feigenbaum and Kelly, 1984; Larson, 1986), thus decreasing ctenophore predation on oyster larvae.

Nothing is known of the trophic ecology of the inconspicuous benthic scyphistoma or early free-swimming ephyra stages of scyphozoans. Large numbers of *C. quinquecirrha* scyphistomae are found on oyster shell (Cargo and Schultz, 1966, 1967), which is a preferred settling substrate for oyster larvae (Kennedy and Breisch, 1981). Therefore, these scyphistomae may be predators of oyster pediveliger larvae that are preparing to settle upon oyster shells.

To test the potential importance of *C. quinquecirrha* and *M. leidyi* as predators of bivalve larvae, we compare (1) medusa and ctenophore digestion of oyster veligers, (2) rejection or ingestion of oyster, blue mussel (*Mytilus edulis* L.), and coot clam [*Mulinia lateralis* (Say)] veligers by medusae, and (3) rejection, or ingestion and digestion of oyster trochophores and veligers by the ephyra and scyphistoma stages of *C. quinquecirrha*. We also present data on bivalve veligers in gut contents of medusae and ctenophores, and *in situ* densities of those predators and veligers, to estimate the importance of predation by gelatinous zooplankton on bivalve larvae in the mesohaline region of Chesapeake Bay.

Materials and Methods

During June through August, 1987, 1988, and 1989, *C. quinquecirrha* medusae and *M. leidyi* were collected in jars from the boat basin of the Horn Point Environmental Laboratories (HPEL) on the Choptank River. In the laboratory, we used 30 μm filtered Choptank River water at ambient salinity (11–12‰) and temperature (20–27°C). After collection, medusae and ctenophores were held in 20-l plastic containers of water, and fed on *Artemia salina* nauplii for at least 12 h to clear their guts of natural zooplankton. Oyster larvae from trochophore (60 μm long) to pediveliger (270 μm) stages, and clam veligers (100–260 μm) were obtained from the HPEL hatchery. For the following experiments, veligers were separated into size fractions on screens of different mesh sizes. Mussel veligers (180 μm) were supplied by the University of Delaware, College of Marine Studies in Lewes, DE.

Digestion and survival of oyster veligers after capture by medusae and ctenophores

Individual medusae and ctenophores were exposed for 10 min either to high densities of oyster veligers alone (2–9 ml^{-1}), or to oyster veligers (0.1 ml^{-1}) with copepods (*Acartia tonsa*) as alternative prey in 4-l containers. The predators then were gently transferred twice with sieves (1 mm mesh) at 5-min intervals to 4-l containers with filtered water to remove prey adhering to their external surfaces and to dilute swimming zooplankton possibly transferred with the predators. Each predator was subsequently transferred at hourly intervals to new containers of filtered water. After the predator was removed from each container, the water was poured through a 60-μm screen, and live oyster veligers, larval shells, live copepods, and copepod exoskeletons were counted with a dissecting microscope, thus recording all prey egested each hour. Egestion times were calculated from the midpoint of each interval, so the accuracy is ±0.5 h. Living veligers that were retrieved after egestion by the medusae were put in beakers of water with food (phytoplankton *Isochrysis galbana*) to determine their survival after 24 h.

Rejection and ingestion of bivalve veligers by medusae

To examine the feeding reactions of *C. quinquecirrha* medusae to bivalve veligers and copepods, we placed medusae (15–90 mm in bell diameter) exumbrellar surface down in fingerbowls with less than 100 ml water. In this position, medusae continued to take food, and were easily examined with a dissecting microscope. Individual prey were placed by pipette on the oral arms, where prey are captured and transferred to the gastric pouches (Larson, 1986). The length of time it took prey to reach a gastric pouch (ingestion) or to be rejected from the oral arm was measured during continuous observation.

Prey in this experiment included live (closed) and freshly killed (gaping) oyster veligers, live clam and mussel veligers, live and heat-killed copepods (*Acartia tonsa*), and tissue removed from 2- to 3-day-old oyster spat (recently settled larvae). Gaping veligers were used to determine whether the larval shell caused the rejection of veligers by medusae. To obtain gaping veligers, we anaesthetized them by gradually adding seltzer water (CO_2) until the shells opened, and then rapidly heating the water to kill them. To ensure that the medusae were feeding well, live copepods, which were readily accepted, were alternated with other prey.

C. quinquecirrha ephyrae 2 to 3 mm in diameter, budded from scyphistomae in the laboratory, were placed singly in a depression slide with 0.5 ml of water and a few live oyster trochophores or live oyster or clam veligers; the process of rejection or ingestion was timed after contact occurred. Scyphistomae attached to plastic slides in the laboratory were offered live oyster trochophores or veligers in 25-ml dishes, and rejection or ingestion was timed after contact.

Effect of scyphistomae on veliger settlement

To determine if *C. quinquecirrha* scyphistomae reduced oyster settlement, field-collected oyster shells containing

scyphistomae were cut into 5 to 8 cm^2 pieces and cleaned of other epifauna. Seven pieces of shell with scyphistomae (9.3 ± 3.7 individuals per shell for all experiments) and seven without were placed in 3 l of 11‰ water at 24° to 27°C in dishes of 143 cm^2 bottom area. Shell pieces were oriented so that scyphistomae were on the underside, which is their preferred location in nature (Cargo and Schultz, 1966, 1967). About 500 oyster pediveligers (179–250 μm long) were added to the dishes, plus algae (*Isochrysis galbana*) as food for the larvae and *Artemia salina* nauplii as alternate prey for the scyphistomae. The dishes were gently aerated and were covered with black plastic, because oyster veligers prefer low light levels for settlement (Ritchie and Menzel, 1969). The shell pieces were checked at 24 and 48 h for newly settled larvae. Six trials, each with two replicates, were run with different pieces of shell. There were 4 controls, each with 14 shell pieces without scyphistomae.

Scyphistoma predation and digestion rates on veligers

Predation by scyphistomae on oyster veligers was determined at the end of each trial (24 or 48 h) by counting the empty larval shells retrieved from the experimental containers. In additional predation experiments at the Chesapeake Biological Laboratory (CBL), containers were filled with 150 ml of estuary (Patuxent River) water. Each container had one plastic slide that was raised off the bottom by fishing weights so that the 3 to 20 attached scyphistomae were on the lower surface. Fifty oyster veligers (179 to 250 μm long) and algal food were added to each container. After 24 and 48 h, larvae inside scyphistomae and clear shells were counted. There were 159 trials, and 26 controls without scyphistomae to check for veliger death due to experimental manipulations. In combination with the preceding experiment, 171 predation measurements were taken.

The length of time required by scyphistomae for digestion of both closed (live) and gaping (anaesthetized and killed) oyster larvae was determined by pipetting the larvae into the tentacles and mouth region of the scyphistomae. The times of ingestion were recorded, then containers were checked at intervals for empty larval shells.

Field studies on medusae and ctenophores

In 1987, we sampled medusae, ctenophores, and bivalve veligers weekly from May to September in two tributaries of Chesapeake Bay [Broad Creek (38° 40′, 76°15′W) and Tred Avon River (38°40′N, 76°05′W)], and on three dates in both May and August, and on one day in both June and July at five stations across the Bay at the same latitude. At each station, we collected individual medusae and ctenophores by dip net and immediately preserved them in 5% formalin for dietary analysis with a dissecting microscope. All bivalve veligers in these samples were counted. Empty and open larval shells were counted separately from closed shells that contained tissue.

Densities of *C. quinquecirrha* and *M. leidyi* were measured with a 1 m diameter, 1.6-mm mesh net with flowmeter towed at 1 m depth in the tributaries (bottom depth < 4 m), and above the pycnocline in the Bay (<11 m). Medusae and ctenophores were counted from samples preserved in 5% formalin (Purcell, 1988). Densities of bivalve larvae were determined from plankton samples taken at the same times as the net tows at 1 m depth in the tributaries with a portable bilge pump, and at 1-m intervals above 11 m depth in the Bay with a submersible pump. Pump samples were filtered through a 64 μm plankton net in the field, then preserved in 5% formalin, and veligers were counted in the laboratory from whole samples or subsamples taken with a Hensen Stempel pipette.

Rates of ctenophores feeding on bivalve veligers *in situ* were estimated from individual clearance rates (Kremer, 1979) times the numbers of ctenophores per cubic meter.

Statistics

Our results are presented as the mean ± one standard deviation. Comparisons on the numbers of prey rejected or ingested were by contingency tables and Chi-square tests, and comparisons of the retention times of different prey species were by one-way analysis of variance. In results reported here as significantly different, the statistical probability is less than 0.001, unless stated otherwise.

Results

Digestion and survival of oyster veligers after capture by medusae and ctenophores

Chrysaora quinquecirrha medusae captured copepods and oyster veligers (80–270 μm long). Ninety-three percent of the copepods were digested, compared with only 1% of the veligers (Table I). Medusae egested copepod remains in less than 5 h, and the few undigested copepods were

Table I

Numbers of copepods and oyster veligers digested after capture by Chrysaora quinquecirrha *medusae and* Mnemiopsis leidyi

Species	Captured	Digested	Predators tested
C. quinquecirrha			
copepods	12,143	11,276 (93%)	110
oyster veligers	4,800	48 (1%)	100
M. leidyi			
oyster veligers	333	316 (96%)	28

Table II

Percentages of oyster veligers of different sizes surviving for 24 h after egestion by Chrysaora quinquecirrha *medusae. Numbers of egested veligers are in parentheses*

	Time inside medusa (h)					
Veliger size	<1	1–2	2–3	3–4	4–5	5–6
<100 μm	96.3	88.9	75.0	72.7	—	100
	(164)	(18)	(12)	(11)	(0)	(2)
100–200 μm	99.6	95.2	97.1	94.1	71.4	91.7
	(1559)	(272)	(102)	(51)	(14)	(12)
>200 μm	99.4	100	93.9	81.8	100	66.7
	(335)	(65)	(33)	(11)	(6)	(3)

dead. Undigested veligers were egested in less than 7 h, with over 90% egested in less than 2 h. Medusae egested shells of the 48 veligers that were digested in 3.4 ± 1.8 h at 22 to 27°C. Digested veligers included 31 small (<100 μm) and 17 medium (100–200 μm), but no large (>200 μm) veligers. These numbers represent 0.03%, 0.006%, and 0% of the numbers of veligers ingested in each size class. Medusae digested veligers less than 100 μm long significantly more frequently than those in both larger size classes. More medium sized veligers were digested than large ones ($P < 0.05$). Ctenophores digested significantly more oyster veligers (96%) than did medusae (1%) (Table I), and egested 333 empty larval shells in 2.0 ± 1.0 h at 19.5 to 20.5°C.

Many veligers egested by medusae were alive. Overall, 98.4% of 2670 veligers that we retrieved after egestion by medusae survived for 24 h afterward. Veligers smaller than 100 μm long showed significantly lower survival than larger veligers (Table II). Veligers retained for more than 2 h showed significantly lower survival than those retained for less than 2 h (Table II). Differences between the <1 h and the 1–2 h groups, and among the groups >2 h were not significant ($P > 0.2$ for all comparisons).

Rejection and ingestion of bivalve veligers by medusae

Prey placed on an oral arm of *C. quinquecirrha* medusae were immediately rejected, or they were taken briefly inside the oral arm by the medusae before rejection, or they were transported inside the oral arm and then to a gastric pouch (ingestion). Medusae rejected significantly more live oyster veligers (99.3%) from the oral arms than live copepods (1.5%) (Table III). The numbers of live oyster, mussel, and clam veligers rejected were not significantly different ($P = 0.2$ to 0.8).

The closed shell protected veligers from ingestion and digestion by medusae. Open oyster veligers were rejected significantly less than closed, live ones, but the difference between closed and open mussel larvae was not significant

Table III

Numbers of oyster, mussel, and clam veligers, copepods, and oyster spat tissue rejected, ingested, and digested by Chrysaora quinquecirrha *medusae, ephyrae, and scyphistomae*

Prey	Rejected	Ingested	Digested	Specimens tested
		Medusae		
Veligers				
Oyster—live	134	1	1	22
Oyster—dead	41	12	—	12
Oyster—shells	22	0	0	2
Mussel—live	91	4	—	8
Mussel—dead	16	0	0	1
Clam—live	74	1	0	14
Oyster spat tissue	6	27	≥10	9
Copepods—live	7	451	451	57
—dead	20	137	—	8
		Ephyrae		
Veligers				
Oyster—live	18	26	0	28
Clam—live	77	7	5	14
Trochophores	3	117	≥105	26
		Scyphistomae		
Veligers				
Oyster—live	9	32	12	19
Clam—live	9	8	7	12

— = Not quantified because we were unable to track the prey.

(Table III). Open oyster veligers also were retained significantly longer in the oral arms than were closed veligers (Table IV). Empty larval shells were never ingested (Table III). Oyster spat tissue was ingested significantly more frequently than either open or closed oyster veligers (Table III). Dead copepods were rejected significantly more often

Table IV

Percentages of bivalve veligers that were retained for five time intervals in the oral arms of Chrysaora quinquecirrha *medusae. The numbers of veligers tested are in the "Rejected" column in Table III*

	Time inside oral arm (min)					
Prey	<1	1–2	2–4	4–10	>10	Maximum time (min)
Oysters						
live	16	31	19	19	16	45
dead	12	24	20	5	39	156
Mussels						
live	9	31	12	24	24	70
Clams						
live	2	10	8	15	65	91

than live ones (Table III), but most dead ones were still accepted as food.

Although nearly all veligers were eventually rejected from the oral arms of *C. quinquecirrha* medusae, differences in retention time existed among the three bivalve species tested (Table IV). Most live veligers were rejected in less than 10 min. Live mussel veligers were retained somewhat longer than live oysters, but the difference was not significant ($P = 0.2$). Clams were retained significantly longer before rejection than were oysters and mussels.

Comparisons among life history stages of *C. quinquecirrha* showed that ephyrae and scyphistomae ingested proportionately more oyster and clam veligers than did the medusae (Table III). Ingestion of oyster veligers differed significantly between medusae and ephyrae, and between medusae and scyphistomae; however, differences between ephyrae and scyphistomae were not significant ($P = 0.1$). Ingestion of clam veligers differed significantly between scyphistomae and medusae, and between scyphistomae and ephyrae; however the difference between medusae and ephyrae was not significant ($P = 0.1$).

Of the ingested veligers, scyphistomae digested significantly more oysters than did ephyrae (Table III), but not clams ($P = 0.9$). Thus, ephyrae behaved more like medusae than scyphistomae in that they digested few oyster veligers. Ephyrae digested five clam veligers in 1.8 to 20.6 h (mean 10.6 ± 8.3 h).

Comparisons between types of veligers showed that ephyrae ingested significantly more oyster than clam veligers (Table III), but digested significantly more clams than oysters. In contrast, scyphistomae ingested significantly more clam than oyster veligers ($P < 0.05$), and digested significantly more clams than oysters ($P < 0.05$). These results suggest that clam and oyster veligers are captured with different success by ephyrae and scyphistomae, and that oyster veligers show greater resistance to digestion than do clam veligers once captured.

Because individual oyster trochophore larvae were difficult to observe due to their small size (<60 μm), we were successful at offering them only to ephyrae, which ingested and digested significantly more trochophores than veligers (Table III).

Effect of scyphistomae on veliger settlement

No settlement of oyster veligers occurred in three of six experiments. Veligers in three experiments and one control settled preferentially on the lower surfaces of the shell pieces, even those with *C. quinquecirrha* scyphistomae. Numbers of spat on the upper/lower shell surfaces were: shells with scyphistomae 19/69; without scyphistomae 22/49; control 22/77. No significant differences in spat settlement were seen among shell pieces with or without scyphistomae, which were on the lower surfaces ($P > 0.2$ for all comparisons). Total settlement was greater in the control container (average of seven veligers settled per shell), where there were no scyphistomae, as compared with the experimental containers (average settlement of two per shell), probably because predation by scyphistomae reduced the numbers of veligers.

Scyphistoma predation and digestion rates on veligers

A total of 4409 oyster veligers were consumed by *Chrysaora quinquecirrha* scyphistomae in 171 predation experiments, as evidenced by the presence of empty shells. In contrast, only 9 empty shells were retrieved from 27 controls without scyphistomae. No significant differences existed between the ingestion rates measured at 24 and 48 h, therefore the results were pooled. The initial densities of larvae in the experimental and control containers averaged 0.31 ± 0.06 veligers ml^{-1}. Over the range of prey density (0.1–0.7 veligers ml^{-1}), the number of larvae consumed per scyphistoma per day (range 0–13) was positively correlated with larval density ($r = 0.26$, $P < 0.01$). On average, each scyphistoma consumed 0.9 ± 0.6 veligers/day. As many as 15 larvae were observed within a single scyphistoma. These results indicate that scyphistomae are more effective predators on oyster veligers than are medusae. However, we observed that after a few hours, scyphistomae sometimes expelled ingested larvae, which began swimming again. These larvae then were available for recapture.

Closed bivalve veligers were very resistant to digestion by scyphistomae. Closed D-stage clam veligers were digested in 37.5 to 41 h (mean 39.2 ± 1.2 h, n = 34), and clam pediveligers were digested in 4 to 47 h (mean 30.6 ± 15.6 h, n = 6). Scyphistomae that had ingested one or two closed oyster pediveligers egested empty shells in 24 to 67 h (mean 34.6 ± 12.9 h, n = 13). Three pediveligers removed from scyphistomae after 18.5 h appeared to be healthy. In contrast, open oyster pediveligers were digested in only 1.3 to 5.1 h (mean 3.7 ± 0.8 h, n = 32).

Field studies on medusae and ctenophores

Field-collected *M. leidyi* and *C. quinquecirrha* medusae both contained bivalve veligers. In 67 medusae, the shells of all 77 veligers were closed and full of tissue, indicating that they had not been digested. By contrast, 19 of 76 (25%) of the shells in 9 ctenophores were open and empty, indicating complete digestion. The proportions of open and closed shells in medusae and ctenophores were significantly different. Ctenophores contained more veligers (an average of six each) than did medusae (about one each). This may be because the ctenophores were collected in Chesapeake Bay, where veliger densities were much greater than in the tributaries, which was where the medusae were collected for diet studies (Table V).

Table V

Densities (numbers m^{-3}) of Chrysaora quinquecirrha *medusae,* Mnemiopsis leidyi, *and bivalve veligers in Chesapeake Bay and the Broad Creek and Tred Avon River tributaries from May to August, 1987, and the percentages of veligers consumed per day by* Mnemiopsis

	Chesapeake Bay				Tributaries			
Month	Medusae	Ctenophores	Veligers	Veligers* consumed per day (%)	Medusae	Ctenophores	Veligers	Veligers* consumed per day (%)
May	0	0.3 ± 0.5	13,826 ± 11,491	0.2 ± 0.2	0–0.3	0.2–33.1	—	—
June	0	2.7 ± 1.6	14,210 ± 8,145	1.0 ± 0.6	5.4 ± 5.8	0	1786 ± 1550	0
July	0.1 ± 0.1	0.1 ± 0.1	60,032 ± 97,380	0.2 ± 0.2	9.6 ± 4.2	0	419 ± 279	0
August	0.6 ± 0.7	0.7 ± 0.8	12,284 ± 15,234	1.7 ± 1.9	7.2 ± 3.7	0	1421 ± 1060	0

* Percentage daily consumption estimated from ctenophore filtering rates (Kremer, 1979).
— = No data.

To estimate the importance of predation on veligers by medusae and ctenophores in nature, we measured *in situ* densities of *M. leidyi, C. quinquecirrha,* and bivalve veligers in May through August, 1987 (Table V). Ctenophores occurred in the Bay throughout this period, but they were excluded from the tributaries by high densities of medusae that fed on them from June through August. Medusae were much less abundant in the Bay than in the tributaries. Sampled densities of bivalve veligers were much greater in the Bay than in the tributaries, possibly due to different efficiencies of the pumps used to collect them. If we assume that only ctenophores ate the bivalve veligers, then 0.2 to 1.7% of the veligers were consumed daily in the main Bay, and none were eaten in the tributaries during that period (Table V).

Discussion

A surprising result of this study is that *Chrysaora quinquecirrha* medusae do not ingest or digest bivalve veliger larvae. Three lines of evidence lead to this conclusion. (1) Medusae that caught swimming veligers egested them alive. (2) Veligers placed on oral arms were subsequently rejected. (3) Veligers in the gut contents of field-collected medusae were closed and full of tissue. The ephyra stage ingested oyster veligers but did not digest them. By contrast, scyphistomae egested some living veligers, but many were retained and eventually digested.

The larval shell may protect bivalve veligers from ingestion by *C. quinquecirrha* medusae. The rapid rejection of veligers from the oral arms suggests that medusae either do not recognize veligers as food items because of the shell, or that veligers provide a "distasteful" stimulus. Larvae of an echinoderm (*Acanthaster planci*) and an ascidian (*Ecteinascidia turbinata*) contain chemicals that make them unpalatable to planktivorous fishes (Lucas *et al.,* 1979; Young and Bingham, 1987).

The sensing and recognition of food must take place in the oral arms of the medusae, as indicated by the differences in ingestion of copepods and veliger larvae. This recognition may involve a mechanical stimulus from active prey, as suggested by the facts that more living, active copepods were ingested than dead ones, and that immobile veligers nearly always were rejected. Recognition also may be due to chemical stimuli, because more open oyster veligers, which presumably leaked body fluids, were ingested than closed ones. The various bivalve species also may present different stimuli, as suggested by the different retention times of oyster, mussel, and clam veligers in the medusae.

The larval shell probably protects veligers from digestion as long as they remain closed within the predators. Veligers were retained for up to 7 h in medusae, and then egested alive. Veligers were removed alive from scyphistomae after 18 h, but closed oyster pediveligers eventually were digested in over 24 h. By contrast, newly killed veligers with open shells were digested by scyphistomae in 3 to 5 h. Therefore, open veligers apparently are more susceptible to digestion than closed ones. Digestion of some veligers may be due to their injury by the scyphistomae's nematocysts at capture, causing the shells to open. Presumably, this also could explain why a few veligers were digested by the medusae.

Suspension-feeding benthic invertebrates can be important predators of pelagic larvae (Thorson, 1946). Bivalve larvae have been found in the stomach contents of their own and other bivalve species (summarized in Mileikovsky, 1974; Young and Chia, 1987). However, oyster larvae taken into the mantle cavities of six mollusk species were rejected in the pseudofeces, from which they may be able to escape (MacKenzie, 1981). A few veligers were ingested and eliminated in the feces of these mollusks, from which they could not escape (MacKenzie, 1981).

Oyster veligers also were rejected unharmed by a barnacle (*Balanus eburneus*) and a polychaete (*Polydora ligni*) (in MacKenzie, 1981), but the common barnacle (*Balanus improvisus*) ate oyster veligers in Chesapeake Bay (Steinberg and Kennedy, 1979).

From earlier studies, Mileikovsky (1974) concluded that bivalve veligers often could pass alive through the guts of primarily herbivorous feeders. However, no larvae were known to pass alive through primarily carnivorous feeders, although protectively coated gametes of a polychaete (*Melinna palmata*) passed through fish (*Acipenser stellatus*) feeding on the adult worms (in Mileikovsky, 1974). Numerous examples exist of benthic cnidarians feeding on bivalve veligers (Young and Chia, 1987). Also, oyster veligers were eaten by the common sea anemone *Diadumene leucolena* in Chesapeake Bay (Steinberg and Kennedy, 1979). To our knowledge, our study presents the first evidence of bivalve veligers passing alive through a carnivorous predator, the medusa stage of *Chrysaora quinquecirrha*.

The diets of several species of pelagic cnidarians are reported to include bivalve veligers, but the numbers of veligers in siphonophores (Purcell, 1981) and hydromedusae (reviewed in Purcell and Mills, 1988) usually were less than 1% of the prey items. Similarly, the scyphomedusae *Aurelia aurita* and *Stomolophus meleagris* in the Gulf of Mexico, and *Mastigias* sp. in Jellyfish Lake, Palau, contained small numbers of bivalve veligers (Purcell, unpub. data). However, bivalve veligers were 25 to 67% of the prey in the hydromedusan *Proboscidactyla flavicirrata* (Purcell and Mills, 1988), and 40 to 80% of the prey in the scyphomedusan *Cyanea* sp. (Brewer, 1989). None of the above studies distinguished between digested or undigested veligers.

The importance of predation on oyster larvae by scyphistomae in nature is difficult to predict because there are few density estimates for scyphistomae or for oyster veligers near the estuary bottom. Only 2.8 ± 3.1% of oyster shells had scyphistomae in the York River, Virginia (Cones and Haven, 1969). One third of those shells had an average of more than 10 scyphistomae per shell (maximum 21), and densities were <1 to 53 scyphistomae m^{-2} of bottom. However, 53.4 ± 25.3% of oyster shells contained scyphistomae in eleven tributaries of the Chesapeake Bay in Maryland, and 70% of those shells had more than 10 individuals (maximum 200; Cargo, unpub. data). Predation by scyphistomae on oyster veligers in those tributaries probably would be higher than in the York River.

The predation rate of one oyster veliger scyphistoma^{-1} day^{-1} from our laboratory experiments should be applied to field conditions with caution, because the experimental larval densities (100–700 l^{-1}, mean 300 l^{-1}) were generally high in comparison with densities of pediveligers in bottom waters. Oyster veliger densities were generally less than 14 l^{-1} near the bottom in Broad Creek and the Tred Avon River, but one sample had 134 l^{-1} (Seliger *et al.*, 1982). Densities of oyster veligers > 200 μm long were 23 to 215 l^{-1} near the bottom in the James River, Virginia (Andrews, 1983). Mortality in our laboratory experiments could be higher than in the field because veligers that were expelled undigested by scyphistomae in our experiments could have been repeatedly ingested, eventually resulting in death, while veligers in nature might have escaped.

Molluscan trochophore larvae lack a shell, and are probably vulnerable to predation by all life history stages of *C. quinquecirrha*. We could only follow the fate of trochophores offered to ephyrae, which did ingest and digest them. In nature, trochophores may be distributed throughout the water column, and may seldom encounter benthic scyphistomae. Although medusae do consume some copepod nauplii and rotifers of the same size as trochophores (about 60 μm), such small animals were only a few percent of the prey items (Purcell, unpub. data). Therefore, medusae probably do not capture many trochophores in nature. Depending on temperature, the trochophore stage lasts only 24 to 30 h, so this period of vulnerability to predators is short, compared with the 6 to 18 day veliger stage of various bivalve species (Loosanoff and Davis, 1963). Ctenophores readily ingested and digested veligers, and they probably also eat trochophores, because they consume many copepod nauplii (Purcell, unpub. data) and ciliates (Stoecker *et al.*, 1987) of the same size.

Quaglietta (1987) studied potential predation by *Mnemiopsis leidyi* on larvae of the hard clam *Mercenaria mercenaria* in Great South Bay, New York. Clam veligers and ctenophores co-occurred in July through December, and were most abundant in August through September. Ctenophore feeding reached a maximum in September, with an average of 11 and 36% of the water cleared of prey per day in 1985 and 1986, respectively. Both the biomass of ctenophores and their estimated predation on veligers were greater during Quaglietta's (1987) study in Great South Bay than during our study in Chesapeake Bay.

Predation on bivalve veligers by *M. leidyi* during our study was apparently limited to Chesapeake Bay, because the ctenophores were not found in Broad Creek and Tred Avon River after the appearance of *C. quinquecirrha* medusae in June. Predation by medusae on *M. leidyi* also may have reduced ctenophore densities in the main Bay. We conclude that not only do *C. quinquecirrha* medusae not consume bivalve veligers, but the medusae may reduce other predation on them by feeding on ctenophores.

In the mesohaline region of Chesapeake Bay, *C. quinquecirrha* medusae are present during June through September or October (Cargo and Schultz, 1966). Therefore,

medusae could reduce ctenophore predation on veligers of *Crassostrea virginica,* as well as other bivalves such as *Ischadium recurvum* Rafinesque, *Macoma mitchelli* Dall, *Mulinia lateralis, Mytilopsis congeria* (Conrad), and *Tagelus plebeius* (Lightfoot) which spawn throughout the summer (Shaw, 1965; Kennedy, pers. obs.). However, bivalve species that spawn only in the spring and autumn in Chesapeake Bay, *e.g., Macoma balthica* (L.) and *Mya arenaria* (L.) (Shaw, 1965), would be most vulnerable to predation by *M. leidyi.*

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