Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay *

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ABSTRACT: The relative predation potentials on ichthyoplankton of the scyphomedusa *Chrysaora quinquecirrha*, the ctenophore *Mnemiopsis leidyi* and the bay anchovy *Anchoa mitchilli* from Chesapeake Bay, USA, were estimated in 3.2 m³ *in situ* mesocosm enclosures and in 1.0 m³ laboratory tanks. For all 3 predators, averaged predation mortality (d⁻¹) and volume-specific clearance rates (l d⁻¹ ml⁻¹) were higher and less variable when bay anchovy eggs were prey than when goby *Gobiosoma bosci* larvae [3.0 to ca 10.0 mm standard length (SL)] were prey. The smallest larvae (3.0 to <5.5 mm SL) were more vulnerable than eggs or larger larvae. Averaged mortality rates per scyphomedusa (0.78 and 0.32 d⁻¹ on eggs and larvae respectively) were 7 times higher than those per ctenophore (0.11 and 0.04 d⁻¹), and almost 2 times higher than those per bay anchovy (0.37 and 0.21 d⁻¹). However, volume-specific clearance rates by the relatively small bay anchovy predators were higher (ca 500 l d⁻¹ ml⁻¹) than those of the gelatinous predators. The volume-specific clearance rates of the ctenophore and medusa were only 4 and 7 % respectively of that for the anchovy. Combined species results suggest that these predators may consume 20 to 40 % daily of the fish eggs and larvae in mid-Chesapeake Bay. The scyphomedusa potentially is the most important predator on summer ichthyoplankton due to its overall abundance, high clearance rates and temporal co-occurrence with vulnerable life stages of fish.

INTRODUCTION

Predation is believed to be a major cause of high and variable mortality during the early life of marine fish (Bailey & Houde 1989). Among the potential predators are gelatinous zooplankton which may feed selectively on fish eggs and larvae (Möller 1980, 1984, Alvariño 1985, Purcell 1985, 1989, 1990, van der Veer 1985, Frank 1986, Fancett & Jenkins 1988). Reported *in situ* predation rates by gelatinous zooplankton on fish early life stages range from 0.1 % d⁻¹ (Fancett 1988) to as high as 60 % d⁻¹ (Purcell 1984, 1989). Schooling pelagic fishes also prey upon eggs and larvae and may affect abundance and dynamics of fish prey species (Hunter & Kimbrell 1980, Daan et al. 1985, Brownell 1985, 1987, Folkvord & Hunter 1986, Alheit 1987, Pepin et al. 1987, Bailey & Houde 1989, Hopkins 1989, Pepin 1989).

Experiments in large enclosures (>3 m³) that allow fish eggs and larvae, their predators and alternative prey to be stocked at abundance levels near those in the sea have provided important insight into the predation process (Laurence et al. 1979, Houde 1985, Oiestad 1985, 1988, de Lafontaine & Leggett 1987a, b, 1988, Gamble & Fuiman 1987, Fuiman & Gamble 1988, 1989, Gamble & Hay 1989, Cowan & Houde 1992, Litvak & Leggett 1992, Pepin et al. 1992). Daily mortality rates of fish larvae exposed to jellyfish predators in large enclosures have ranged from 0.02 to 1.11 d⁻¹ (Gamble & Houde 1984, Oiestad 1985, de Lafontaine & Leggett 1988, Gamble & Hay 1989, Cowan & Houde 1992), but usually were near the low end of this

reported range. Fuiman & Gamble (1988) reported mortality of herring *Clupea harengus* larvae from pelagic fish predation that averaged 32 % d^{-1} in 15.5 m^3 *in situ* mesocosms.

While several of the cited studies have documented and quantified predation by gelatinous zooplankton and fishes upon fish eggs and larvae, comparative experiments of predator potential seldom have been undertaken. Notable exceptions that employed multiple predator species in large enclosures (de Lafontaine & Leggett 1988, Fuiman & Gamble 1988, Cowan & Houde 1992, Litvak & Leggett 1992, Pepin et al. 1992) have shown that between-species differences in predation potential are related to variable encounter rates with prey, capture efficiency, probability of attack, predator size, prey size, prey abundance, presence of alternative prey and environmental conditions during the experiments. Theoretical relationships describing the rate and form of predator-prey interactions have been reviewed by de Lafontaine & Leggett (1988) and Bailey & Houde (1989).

Three abundant predators that potentially are major consumers of fish eggs and larvae in Chesapeake Bay, USA, are 2 cruising invertebrates: (1) the slow swimming (0.1 to 0.5 cm s^{-1}), small (<7.0 cm) and transparent lobate ctenophore *Mnemiopsis leidyi*; (2) the larger (5.0 to 10.0 cm), faster swimming (0.5 to 1.0 cm s^{-1}) scyphomedusa *Chrysaora quinquecirrha*, which is equipped with stinging tentacles; and (3) the rapidly swimming (6.5 to 12 cm s^{-1}) raptorial planktivorous bay anchovy *Anchoa mitchilli* (Cowan & Houde 1992). In our experiments, we estimated and compared instantaneous rates of predation mortality and clearance rates of these co-occurring, but dissimilar predators (see also Cowan & Houde 1992). We then used these predation rates to estimate the percentage of the mid-Chesapeake Bay water column that could be cleared daily by the combined predator community.

METHODS AND MATERIALS

Experimental containers. The mesocosms, which were identical to those described by de Lafontaine & Leggett (1987b), were 1 m diameter cylinders of 5 m length with a conical bottom section, giving an effective internal volume of 3.0 m^3 (3.2 m^3 total volume if filled to capacity). They were constructed from dacron sailcloth of mean mesh aperture 25 µm. The conical end section was 53 µm Nitex mesh. Mesocosms were deployed from a raft moored in 10 m depth near the mouth of the Patuxent River, a tidal tributary of the Chesapeake Bay (38° 21' N, 76° 31' W). Methods to deploy and retrieve the mesocosms have been described (Cowan & Houde 1990).

Some experiments were done in laboratory tanks of 1.3 m diameter, 0.75 m depth, and 0.75 m^3 effective internal volume (1.0 m^3 total volume if filled to capacity). The tanks were continuously supplied with Patuxent River water filtered to 5 µm. Photo period in the tank experiments was adjusted to 14 h light : 10 h dark.

Egg and larvae prey, alternative prey and predators. Experimental stocking densities of bay anchovy eggs, naked goby *Gobiosoma bosci* larvae, the predators and zooplankton which served as alternative prey were comparable to *in situ* densities in Chesapeake Bay (Dovel 1971, Brownlee & Jacobs 1987, Dalton 1987, Horwitz 1987, Olson 1987). Fertilized anchovy eggs were obtained from a laboratory-maintained spawning population and stocked at a density of 20 m^{-3} into experimental mesocosms or at 33 to 133 m^{-3} into tanks in which predators had been acclimated and starved for 12 h.

Lab-reared larvae of the goby also were used as prey in the mesocosms. Because reared larvae were available from several egg clutches and age groups, larvae with similar length distributions [3.0 to ca 10.0 mm standard length (SL)] and mean lengths were stocked in each experiment. The larvae were stocked at a density of 10 m^{-3} into mesocosms in which predators had acclimated for 12 h.

Alternative prey in mesocosms was zooplankton collected in July in the Patuxent River mouth with 53 µm mesh plankton nets and filtered through sieves to remove organisms >1 mm. The alternative prey, which was mostly *Acartia* sp. copepods, the rotifers *Synchaeta* sp. and *Brachionus* sp., and tintinnids, was added to the mesocosms to provide a nominal density of 500 l^{-1}. In the tank experiments, alternative prey was newly-hatched nauplii of *Artemia* sp., also at a nominal density of 500 l^{-1}. *Artemia* sp. was substituted for zooplankton because nuisance phytoplankton blooms and low dissolved oxygen content of Patuxent River waters in August made the collection of high numbers of live zooplankton impractical. To standardize predator hunger, alternative prey was stocked 1 h before the anchovy eggs or goby fish larvae were added to the tanks or mesocosms.

The stocking densities of the predators averaged (1) 50 ml m^{-3} ctenophores (8 to 10 per mesocosm, 3 or 4 per tank); (2) 35 ml m^{-3} medusae (1 or 2 per mesocosm, 1 per tank), and (3) 2 or 3 bay anchovies of 42.0 to 59.4 mm SL (2 to 3 per mesocosm, 2 per tank). Medusae for experiments were captured individually in buckets. Ctenophores and bay anchovies were netted, then maintained in the laboratory for several days to ensure their good condition before stocking into tanks or mesocosms.

Experimental design. Instantaneous mortality rates of anchovy eggs and goby larvae were estimated in a series of 24 h experiments in summer 1990. Predation experiments were run when mean temperature was 24.4 °C (range 21.0 to 27.6 °C) and salinity was 12.7 ppt (range 11.0 to 14.1 ppt) in the tanks and mesocosms. Several enclosures (n = 6) and tanks (n = 4) were stocked and then drained immediately to determine how efficiently eggs and larvae could be recovered. In 4 laboratory tank trials, egg recovery was 100 %. In the mesocosms, anchovy egg recovery averaged 95 % in 3 trials with alternative prey present and 96% in 3 trials with no alternative prey. In 4 mesocosm trials (2 with alternative prey), 100 % of goby larvae were recovered. In addition to recovery efficiency tests, 7 mesocosms and 6 laboratory tanks were stocked at designated egg and larva densities, but without predators, to serve as predator-free standards. The standards, run simultaneously with the predation trials, were deployed for 24 h to estimate daily egg and larvae mortality in the absence of predators.

Trials in mesocosms with anchovy eggs and goby larvae were completed on consecutive days in mid-July. On 17 July, mesocosms that contained the following combinations of predators and prey were deployed: (1) 3 mesocosms with ctenophore predators and goby larvae prey; (2) 2 with medusae predators and goby larvae prey; (3) 2 with anchovy predators and goby larvae prey; and (4) 2 with goby larvae and no predators (standards). None of the 17 July mesocosms (n = 9) contained alternative zooplankton prey. On 18 July, 2 standards with alternative prey and 2 mesocosms containing each of the predators plus goby larvae prey and alternative zooplankton prey were deployed (n = 8 enclosures). On 19 July, 3 mesocosms that contained ctenophores, 3 that held medusae predators and 3 standards, all containing anchovy egg prey, were deployed.

Trials in the tanks (n = 22 tanks) were completed over a 3 wk period in August and September. On a given day, stocking density of egg prey was based in part on their availability in laboratory spawns. For each predator type, 1 tank with alternative prey (*Artemia* sp. nauplii), 1 tank without and 1 standard was set up each day except on 2 d when no *Artemia* sp. was available. Predators for tank experiments were randomly selected from populations held in the laboratory and recently acclimated to feeding on *Artemia* sp. At the termination of all experiments, the predators were removed by dip-netting, then the contents of the containers (fish eggs, larvae, alternative prey) were quickly collected (5 to 20 min) and preserved in 4 % buffered formalin sea water.

Goby larvae were measured within 24 h after the end of each experiment to the nearest 0.1 mm. Survivors were classified by 0.5 mm length classes,

where length class 3.0 represented larvae from 3.0 to 3.4 mm SL, length class 3.5 from 3.5 to 3.9 mm, etc. Live gelatinous predator wet volumes (ml) were measured to 1.0 ml by volume displacement in a graduated cylinder. Bay anchovy predators were measured to the nearest 0.1 mm SL before obtaining their wet volume (to 1.0 ml) by displacement.

Predation rate estimates. The instantaneous predation mortality rate (Z) was estimated from an exponential model:

$$Z = \frac{\ln N_c - \ln N_p}{t} \qquad (1)$$

where N_p = final number of eggs and larvae in an experimental container with predators, corrected for mean recovery rate of prey from tanks or mesocosms; N_c = final number of eggs and larvae in predator-free containers, corrected for mean recovery rate; and t = the duration of the experiment in days.

The instantaneous mortality rate per predator $(Z \text{ pred}^{-1})$ was calculated as:

$$Z_1 = Z/P \qquad (2)$$

where P = number of predators.

Standardized mortality rates (i.e. corrected for predator size effects) for each series of experiments employing the same predator and experimental container were calculated (modified from de Lafontaine & Leggett 1988) as:

$$Z_p = \frac{Z_1 (\Sigma P_v/n)}{v} \qquad (3)$$

where n = number of experimental units (containers) in an experiment; Z_p = standardized instantaneous predation mortality rate $(\text{d}^{-1} \text{ pred}^{-1})$; $\Sigma P_v/n$ = grand mean volume (ml) of all predators (of the same species) in an egg or larva experiment employing the same experimental container type; and v = mean volume of the predator(s) in the experimental container being standardized.

Volume-specific clearance rates for each series of experiments that employed the same predator and experimental container were calculated as:

$$F_s = V Z_p/(\Sigma P_v/n) \qquad (4)$$

where F_s = volume-specific clearance rate $(1 \text{ d}^{-1} \text{ ml}^{-1})$; and V = volume of the experimental container (l).

RESULTS

Predator-free standards

The overall mean mortality rate of bay anchovy eggs in predator-free standards was significantly

Table 1 *Mnemiopsis leidyi*. Summary of results of experiments using the ctenophore as a predator on fish eggs and larvae in 3.2 m³ mesocosms and 1.0 m³ laboratory tanks

Mean predator volume (ml)	Total predator volume (ml)	Effective container volume (m³)	Prey density (no. m⁻³)	Alternative prey (ca 500 l⁻¹)	Mortality rate Z_p (d⁻¹ pred⁻¹)	Clearance rate F_s (l d⁻¹ pred⁻¹)
A. Anchovy eggs as prey						
20	160	3.0	18.8	None	0.11	20.5
16	160	3.0	20.6	None	0.13	24.2
16	160	3.0	20.0	None	0.10	18.8
16	50	0.75	66.7	None	0.25	11.7
16	50	0.75	33.3	None	0.13	6.0
13	50	0.75	100.0	None	0.17	7.9
16	50	0.75	69.3	*Artemia* sp.	0.14	6.5
16	50	0.75	133.3	*Artemia* sp.	0.08	3.7
B. Goby larvae as prey						
20	160	3.0	10.0	None	0.05	7.1
23	160	3.0	10.0	None	0.06	8.2
20	160	3.0	10.0	None	0.07	9.2
23	160	3.0	10.0	Zooplankton	0.00	0.0
20	160	3.0	10.0	Zooplankton	0.01	1.3

lower in the laboratory tanks (0.11 d⁻¹) than in the mesocosms (0.19 d⁻¹) (Mann-Whitney U; p = 0.01). Higher mortality in the mesocosms probably was due to handling stress caused by conveyance to the enclosure site. Egg mortality in the predator-free laboratory tanks did not differ between tanks with or without *Artemia* sp. nauplii alternative prey. Mortality of goby larvae in mesocosms lacking predators was negligible and was not dependent on presence of zooplankton alternative prey. In four 24 h trials, 99.2 % of the goby larvae survived in the predator-free standards.

Anchovy eggs as prey

The mortality rates of anchovy eggs per ctenophore predator (Z_p) in the mesocosms and tanks ranged from 0.08 to 0.25 d⁻¹ (Table 1). Even though ctenophore size was not correlated with mortality rates, mortality and clearance rates were standardized for consistency among experiments. Volume-specific clearance rates (F_s) ranged from 3.7 to 24.2 l d⁻¹ ml⁻¹ (Table 1). Presence of *Artemia* sp. as alternative prey had no demonstrable effect on ctenophore predation rate on bay anchovy eggs (Table 2) (Mann-

Table 2. Effects of presence of alternative zooplankton prey on the predation rate on fish eggs and larvae by the ctenophore *Mnemiopsis leidyi*, scyphomedusa *Chrysaora quinquecirrha* and anchovy *Anchoa mitchilli*. Given are estimates of mean mortality (Z_p) and clearance (F_s) rates and coefficients of variation (CV) about the means. Probability values (p) are from Mann-Whitney U-tests (*p ≤ 0.05). Egg experiments were in 1.0 m³ laboratory tanks. Goby larvae experiments were in 3.2 m³ mesocosms

Predator	Prey	Alternative prey	N	Mortality rate Z_p (d⁻¹ pred⁻¹) Mean	CV%	p > U	Clearance rate F_s (l d⁻¹ pred⁻¹) Mean	CV%	p > U
Mnemiopsis leidyi	Eggs	Present	2	0.11	25.9	0.25	5.1	34.7	0.25
	Eggs	Absent	3	0.18	26.4		8.5	0.3	
	Larvae	Present	2	0.01	100.0	0.08	0.7	141.4	0.08
	Larvae	Absent	3	0.06	10.7		8.2	18.9	
Chrysaora quinquecirrha	Eggs	Present	2	1.80	57.0	0.56	22.7	36.8	0.56
	Eggs	Absent	3	2.08	31.5		26.1	10.4	
	Larvae	Present	2	0.37	57.2	0.68	25.6	76.5	0.68
	Larvae	Absent	2	0.26	55.1		17.5	47.1	
Anchoa mitchilli	Eggs	Present	3	0.22	9.7	0.05*	77.5	13.3	0.05*
	Eggs	Absent	3	1.25	14.3		450.9	10.0	
	Larvae	Present	2	0.04	60.7	0.12	94.0	87.8	0.12
	Larvae	Absent	2	0.37	87.4		834.0	114.7	

Table 3. *Chrysaora quinquecirrha*. Summary of results of experiments using the scyphomedusa as a predator on fish eggs and larvae in 3.2 m³ mesocosms and 1.0 m³ laboratory tanks

Mean predator volume (ml)	Total predator volume (ml)	Effective container volume (m³)	Prey density (no. m⁻³)	Alternative prey (ca 500 l⁻¹)	Mortality rate Z_p (d⁻¹ pred⁻¹)	Clearance rate F_s (l d⁻¹ pred⁻¹)
A. Anchovy eggs as prey						
120	120	3.0	20.6	None	0.63	31.7
65	130	3.0	20.6	None	0.89	44.8
55	110	3.0	20.0	None	0.81	40.6
62	62	0.75	33.0	None	1.79	22.5
44	44	0.75	133.0	None	2.43	30.5
53	53	0.75	80.0	None	2.01	25.3
23	23	0.75	69.3	*Artemia* sp.	2.27	28.6
55	55	0.75	106.7	*Artemia* sp.	1.33	16.8
B. Goby larvae as prey						
39	78	3.0	10.0	None	0.17	11.6
32	64	3.0	10.0	None	0.34	23.4
55	110	3.0	10.0	Zooplankton	0.58	39.6
50	100	3.0	10.0	Zooplankton	0.17	11.6

Whitney *U*; p = 0.25), although the power to detect differences was low due to small sample size.

Bay anchovy eggs suffered high mortalities, Z_p = 0.63 to 2.43 d⁻¹ pred⁻¹ from predation by the scyphomedusa in the tanks and mesocosms (Table 3), which resulted in volume-specific clearance rates that ranged from 16.8 to 44.8 l d⁻¹ ml⁻¹. The presence of *Artemia* sp. as alternative prey also did not protect anchovy eggs from predation by *Chrysaora quinquecirrha* (Table 2; Mann-Whitney *U*; p = 0.56).

Bay anchovy cannibalized its eggs (Table 4). The standardized mortality rates (Z_p) in the tanks ranged from 0.19 to 1.32 d⁻¹, rates comparable to those of the gelatinous predators. The relatively high volume-specific clearance rates (F_s) of the anchovy ranged

from 69.9 to 478.1 l d⁻¹ ml⁻¹. Presence of *Artemia* sp. nauplii as alternative prey resulted in a 5-fold reduction in egg cannibalism by bay anchovy (Table 2; Mann-Whitney *U*; p = 0.05).

The mortality rates induced by the ctenophore, scyphomedusa, or bay anchovy in the 1.0 m³ tanks were not correlated with initial anchovy egg densities in the range 33 to 133 eggs m⁻³ (Fig. 1), nor were they related to the variable temperatures and salinities during these experiments (Spearman's correlation, p > 0.05).

Goby larvae as prey

Estimated mortality rates (Z_p) of goby larvae from ctenophore predation ranged from 0.00 to 0.07 d⁻¹ in

Table 4. *Anchoa mitchilli*. Summary of results of experiments using the bay anchovy as a predator on fish eggs and larvae in 3.2 m³ mesocosms and 1.0 m³ laboratory tanks

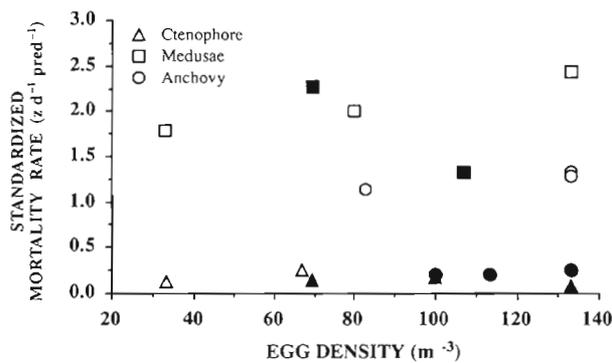| Mean predator volume (ml), SL	Standard length (mm)	Total predator volume (ml)	Effective container volume (m³)	Prey density (no. m⁻³)	Alternative prey (ca 500 l⁻¹)	Mortality rate Z_p (d⁻¹ pred⁻¹)	Clearance rate F_s (l d⁻¹ pred⁻¹)
A. Anchovy eggs as prey							
1.9	55.9	3.8	0.75	82.7	None	1.13	410.1
2.5	59.4	5.0	0.75	133.3	None	1.28	464.5
2.0	54.9	4.0	0.75	133.3	None	1.32	478.1
1.8	55.2	3.5	0.75	113.3	*Artemia* sp.	0.20	70.8
2.2	56.6	4.3	0.75	100.0	*Artemia* sp.	0.19	69.9
2.0	54.8	4.0	0.75	133.3	*Artemia* sp.	0.25	91.9
B. Goby larvae as prey							
1.0	42.0	3.0	3.0	10.0	None	0.09	200.0
1.4	43.9	2.8	3.0	10.0	None	0.66	1467.9
1.3	48.5	4.0	3.0	10.0	Zooplankton	0.07	161.5
1.7	48.0	5.0	3.0	10.0	Zooplankton	0.01	26.5

Fig. 1. Standardized instantaneous mortality (Z d^{-1} $pred^{-1}$) rate due to predation by ctenophore *Mnemiopsis leidyi*, scyphomedusa *Chrysaora quinquecirrha* and bay anchovy *Anchoa mitchilli* on bay anchovy eggs in relation to initial egg density (m^{-3}) in the 1.0 m^3 tanks. Filled symbols indicate presence of alternative prey

the mesocosms (Table 1); clearance rates ranged from 0.0 to 9.2 l d^{-1} ml^{-1}. The presence of zooplankton as alternative prey did not significantly reduce mortality rates of goby larvae due to ctenophore predation (Table 2; Mann-Whitney U; $p = 0.08$).

The goby larvae mortality rate (Z_p) caused by scyphomedusa predation was high (0.17 to 0.58 d^{-1}), although lower than that of anchovy eggs (Table 3). Volume-specific clearance rates (F_s) also were lower and ranged from 11.6 to 39.6 l d^{-1} ml^{-1}.

The goby larvae mortality rates (Z_p) caused by bay anchovy predation were variable (Table 4), with mortality rates ranging from 0.01 to 0.66 d^{-1}. As a consequence, volume-specific clearance rates (F_s) also were variable (Table 4), ranging from 26.5 to 1467.9 l d^{-1} ml^{-1}. Presence of alternative zooplankton prey may have protected goby larvae from predation by bay anchovy (Table 2). The mean goby larvae mortality and clearance rates increased more than 9-fold when alternative prey was absent, but high variability in the 2 trials (Table 4) and low statistical power masked what may have been significant effects (Mann-Whitney U; $p = 0.12$).

Prey size effects

Goby larvae 3.0 to ca 10.0 mm SL were equally vulnerable to ctenophore predation (Regression analysis; Arcsin % mortality on larvae length class; $p > 0.05$). Mortality, which was variable in the 5 trials (Fig. 2), averaged 54 % for length classes that were tested. Bay anchovy eggs apparently were slightly more vulnerable (63 %) to ctenophore predators than were most larva length classes.

The vulnerability of goby larvae to predation by the scyphomedusa declined as larvae lengths increased (Fig. 2). Vulnerability was highest (100 % mortality) for the smallest larvae (3.0 to < 4.5 mm SL). If the derived equation is extrapolated, one would predict no mortality (arcsin % Z = 0) for goby larvae of lengths > 11.4 mm SL. Anchovy eggs, which were not included in the regression analysis, appear to have been less vulnerable than the smallest goby larvae (Fig. 2).

The vulnerability of goby larvae to predation by bay anchovy also decreased as lengths of larvae increased (Fig. 2). Larvae 3.0 to < 4.0 mm SL were 100 % vulnerable. Some anchovy eggs and some > 4.0 mm SL goby larvae did survive to the end of the 24 h experiments.
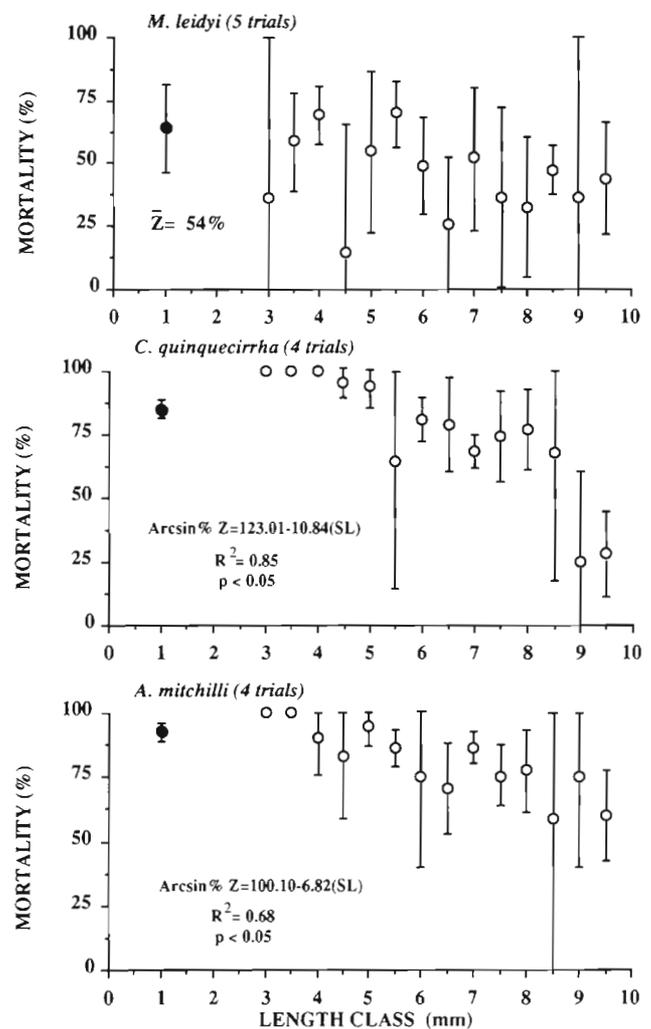

Fig. 2. Percent mortality of bay anchovy *Anchoa mitchilli* eggs and naked goby *Gobiosoma bosci* larvae in mesocosm experiments imposed by ctenophore *Mnemiopsis leidyi*, scyphomedusa *Chrysaora quinquecirrha* and bay anchovy *Anchoa mitchilli* predators in relation to size of prey, ± 1 SE. Egg mortality rates are represented by length class = 1 mm (●). Regression parameter estimates were obtained after arcsin transformation of percent data for goby larvae

A linear regression (Fig. 2) extrapolated to arcsin % $Z = 0$, suggests that larvae ≥ 14.8 mm SL would not be vulnerable to predation by 42.0 to 48.0 mm SL bay anchovy.

DISCUSSION

The 3 predators readily ate bay anchovy eggs and naked goby larvae. The mortality rate imposed by *Chrysaora quinquecirrha* on eggs and larvae was particularly high (Table 5). Rates for all of the predators were independent of initial anchovy egg prey density, indicating that number of prey consumed was proportional to number encountered. This result is similar to that reported previously for gelatinous zooplankton and fish predators feeding on fish eggs (Monteleone & Duguay 1988) or larvae (de Lafontaine & Leggett 1988, Fuiman & Gamble 1988, 1989, Gamble & Hay 1989). The mortality rates of bay anchovy eggs and naked goby larvae from predation by bay anchovy were lower than rates imposed by the medusa (Table 5). But, anchovy clearance rates were higher because their volumes were small. Both the mortality and clearance rates imposed by the ctenophores were low compared to the medusa and anchovy.

Small goby larvae (3.5 to 5.5 mm SL) were more vulnerable to predation by the medusa and anchovy than were anchovy eggs or larger goby larvae. Perhaps surprisingly, vulnerability of the goby larvae to the ctenophore did not decline significantly for the length classes tested (3.0 to ca 10.0 mm SL). This result, albeit based on variable data, appears to contrast with the prediction that progressively larger larvae will have declining vulnerability to cruising invertebrate predators (Bailey & Houde 1989). Monteleone & Duguay (1988) speculated that transparency and slow movements of *Mnemiopsis leidyi* contributes to a lack of visual (i.e. low apparent looming effect; Webb 1981) detection and escape response by bay anchovy larvae.

The vulnerability of goby larvae to predation by the bay anchovy was in part consistent with that expected for raptorial-feeding fishes (Bailey & Houde 1989). In theory, larva vulnerability to predation initially should increase as length increases and then decline rapidly as length approaches limits imposed by the predator's mouth gape (Bailey & Houde 1989, Fuiman 1989). In our experiments, mortality rate of goby larvae from bay anchovy predation was highest for the smallest larvae, declining consistently as lengths increased. There was no evidence that the smallest goby larvae were less vulnerable than those of intermediate lengths.

Folkvord & Hunter (1986) proposed that, for fish predators, little or no predation can occur when larvae are longer than 50% of the predator's length. Based upon extrapolation of a linear relationship between vulnerability and length, we estimated that goby larvae became invulnerable to the 40 to 50 mm long bay anchovy predators at approximately 15 mm SL, which is 33% of the predators length. A similar extrapolation of the data presented by Pepin et al. (1992) and Litvak & Leggett (1992) for sticklebacks *Gasterosteus aculeatus* feeding on capelin *Mallotus villosus* larvae suggests that capelin may no longer be vulnerable to predation when they are 26 to 30% as long as the sticklebacks. If vulnerability declines faster in larvae that are longer than those that we tested, as Fuiman (1989) found for cannibalistic herring *Clupea harengus*, then 15 mm SL might be an overestimate of the length of zero vulnerability of goby larvae to bay anchovy predation.

Probable effect of containment

We did not examine effects of container volume directly, but we believe that experiments with *Mnemiopsis leidyi* and *Chrysaora quinquecirrha* in containers smaller than 2.0 to 3.0 m^3 may overestimate predation capacity. Mortality rates of anchovy eggs im-

Table 5. Summary of results of predation experiments in 3.2 m^3 mesocosms using ctenophore *Mnemiopsis leidyi*, scyphomedusa *Chrysaora quinquecirrha* and anchovy *Anchoa mitchilli*; mean ($\pm$ 1 SE) instantaneous mortality rates per predator (Z_p, d^{-1} pred^{-1}) and standardized clearance rates (F_s, l d^{-1} ml^{-1})

Predator	Bay anchovy egg prey			Naked goby larvae prey		
	n	Z_p	F_s	n	Z_p	F_s
Ctenophore	3	0.11 ± 0.02	21.17 ± 3.16	5	0.04 ± 0.03	5.16 ± 4.18
Medusa	3	0.78 ± 0.12	39.03 ± 4.51	4	0.32 ± 0.19	21.55 ± 12.93
Anchovy	6	0.37 ± 0.58[a]	550.00 ± 104.07[a]	4	0.21 ± 0.32	463.98 ± 858.81

[a]Anchovy predation mortality and clearance rates of eggs are estimates from 1.0 m^3 tanks corrected for container volume effects (Steel & Torrie 1980)
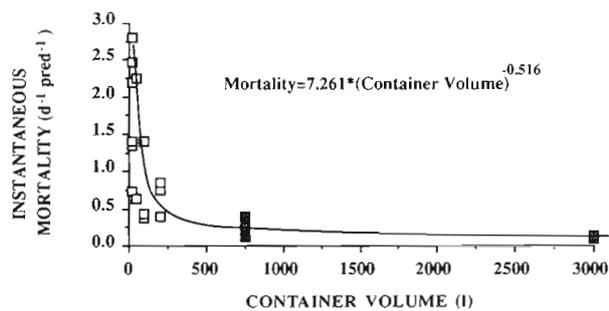
Fig. 3. Bay anchovy *Anchoa mitchilli* egg mortality (d^{-1}) due to lobate ctenophore *Mnemiopsis leidyi* as a predator with respect to container volume (l) based on our data in 1.0 m^3 tanks and 3.2 m^3 mesocosms (□) and data from Monteleone & Duguay (1988) in 15 to 200 l aquaria (□)

posed by the ctenophore predators were, on average, > 1.5 × higher in the 1.0 m^3 tanks than in the 3.2 m^3 mesocosms (Table 1), indicating that predation mortality was inversely related to container volume even in our relatively large containers. Combining our results and those of Monteleone & Duguay (1988) for ctenophores of 4.5 to 5.0 cm (ca 15 ml) suggests that large increases in mortality rates are expected in containers smaller than 500 l (Fig. 3). Results with the medusa predator (Table 3) appear similar and perhaps are even more affected by small container volumes.

De Lafontaine & Leggett (1987a) demonstrated, with subsequent support by Gamble & Hay (1989), that experiments with medusae as predators in ≥3.0 m^3 enclosures should yield predation rates on fish larvae that are similar to those in the sea. Our results support those conclusions with respect to the ctenophore *Mnemiopsis leidyi*, and the scyphomedusa *Chrysaora quinquecirrha*.

Temporal variability and co-occurrence of predators and prey

Among factors likely to influence the relative potential of the 3 predators to affect recruitment of fish in the Chesapeake Bay are (1) the year-to-year variability in predator abundances; and (2) the temporal and spatial overlap between predators and vulnerable life stages of fishes. The ctenophore *Mnemiopsis leidyi* usually appears in May, increases rapidly in abundance until mid-June or early July, after which abundance and biomass decline until fall (Bishop 1967, Miller 1974, Feigenbaum & Kelly 1984, Olson 1987). It sometimes 'swarms' in abundance and biomass (> 100 ml m^{-3}) between May and July (Bishop 1967, Miller 1974). Over its range, the densest populations of sea nettle *Chrysaora quinquecirrha* occur in the Chesapeake Bay

(Feigenbaum & Kelly 1984, Olson 1987). It usually appears in June but is not abundant until early July. Bay anchovy *Anchoa mitchilli* is the most abundant fish in the Chesapeake Bay and is present throughout the year (Hildebrand & Schroeder 1928, Horwitz 1987, Luo 1991).

Eggs and larvae of the bay anchovy dominate the ichthyoplankton in mid-Chesapeake Bay during summer when its eggs account for 96 % of all fish eggs (Olney 1983), peaking in abundance in July when predator numbers are relatively low, but increasing (Olney 1983, Dalton 1987). Peak abundance of the ctenophore occurs before the spawning peak of bay anchovy. In contrast, abundance of the medusa usually increases dramatically in July when bay anchovy eggs and larvae are most abundant and susceptible to predation. Adult or juvenile bay anchovy that are large enough to cannibalize eggs and larvae are in relatively low abundance during the spawning season (Horwitz 1987, Newberger 1989) which may limit their importance as predators. Moreover, field studies of diets of bay anchovy (Vazquez 1989, Johnson et al. 1990, Klebasko 1991) suggest that it, unlike some anchovy species (Hunter & Kimbrell 1980, Brownell 1985, 1987, Alheit 1987, Valdés et al. 1987), is not strongly cannibalistic or predacious on ichthyoplankton.

Predation rates by bay anchovy, which does not filter-feed, on eggs and larvae in our experiments were reduced in the presence of alternative prey, indicating that it preferentially selects zooplankton prey when available. In contrast, predation by the cruising gelatinous zooplankton was not demonstrated to have been affected by presence of alternative prey, supporting the hypothesis that some jellyfish and ctenophore predators are non-selective and probably do not satiate at prey densities usually occurring *in situ* (de Lafontaine & Leggett 1988, Monteleone & Duguay 1988, Bailey & Houde 1989, Cowan & Houde 1992). Selective feeding by bay anchovy, however, does not preclude the possible importance of fish predation on ichthyoplankton in Chesapeake Bay. Its consumption of ichthyoplankton, combined with that of other abundant fishes, such as the filter-feeding Atlantic menhaden *Brevoortia tyrannus*, potentially is significant.

Mortality rates of bay anchovy eggs and larvae in Chesapeake Bay are high. Instantaneous mortality rates were estimated to be near 1.5 d^{-1} for eggs and 0.29 to 0.32 d^{-1} for larvae (Loos & Perry 1991, Houde unpubl.). The probable cause of the high mortalities is predation. Using the clearance rate estimates from our mesocosms (l d^{-1} ml^{-1}), combined with 5 yr mean (1976 to 1980) biomass (ml m^{-3}) estimates of the gelatinous predators in the mid-Bay (Olson 1987), we estimated
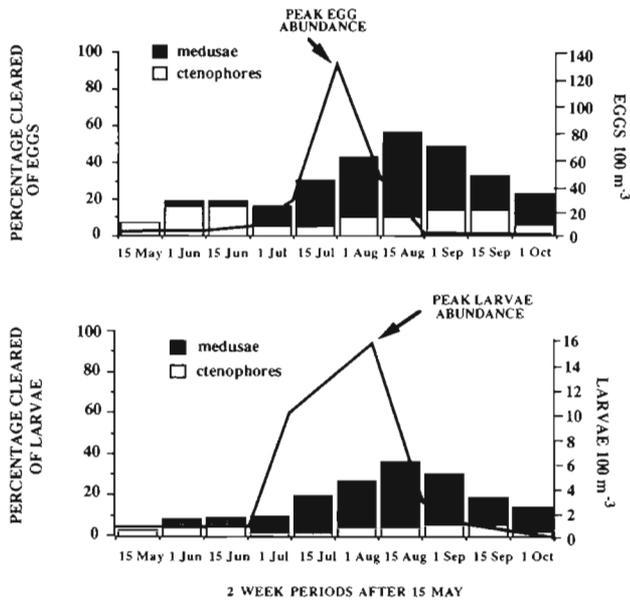
Fig. 4. Estimated percentage of the water column that could be cleared daily of fish eggs and larvae by gelatinous predators (ctenophore *Mnemiopsis leidyi* and scyphomedusa *Chrysaora quinquecirrha*) in mid-Chesapeake Bay, assuming that each predator cleared a unique volume. Estimates were derived from experimental volume-specific clearance (F_s, $l\,d^{-1}\,ml^{-1}$) rates combined with 5 yr average gelatinous predator biomass (ml wet volume m^{-3}) in the mid-Bay (Olson 1987). Bay anchovy egg and larva densities are 4 yr means from Dalton (1987)

the percentage of the water column that could be cleared daily by the gelatinous predators (Fig. 4), assuming that each predator cleared a unique volume. The estimates, while speculative, indicate that the gelatinous predators, especially the medusa, have the potential to consume a high percentage (20 to 40 % daily) of the eggs and larvae of bay anchovy in mid-Chesapeake Bay. This result agrees well with the recent findings of Purcell (1992) who reported that *Chrysaora quinquecirrha* may consume 2 to 78 % d^{-1}, depending on location, of the crustacean zooplankton standing stock in Chesapeake Bay. Predation rates in the tributaries are high, averaging 20 to 50 % d^{-1} (maximum 94 % d^{-1}) of the zooplankton biomass (Purcell 1992).

The medusa *Chrysaora quinquecirrha* probably is the most important predator of summer ichthyoplankton in Chesapeake Bay. However, the medusa is not randomly distributed in the bay and small-scale horizontal or vertical patchiness has been shown to affect its predation potential on zooplankton (Purcell 1992). Govoni & Olney (1991) also have demonstrated that the ctenophore *Mnemiopsis leidyi* is non-uniformly distributed, both horizontally and vertically, in lower Chesapeake Bay and proposed that vertical stratifica-

tion can either isolate fish eggs and larvae from predation or, alternatively, enhance predation probability by *M. leidyi*. *C. quinquecirrha* feeds primarily on crustacean zooplankton (Cargo & Schultz 1966, Feigenbaum et al. 1982, Purcell 1992) and on the ctenophore *M. leidyi* (McNamara 1955, Cargo & Schultz 1967, Feigenbaum & Kelly 1984) in Chesapeake Bay. Estimates of *C. quinquecirrha* feeding rates on the ctenophore population in the bay have ranged from 36 to ≥100 % d^{-1} (Miller 1974, Feigenbaum & Kelly 1984). If those estimates are correct, predation by *C. quinquecirrha* on ctenophores may indirectly influence its own predation potential on ichthyoplankton, by satiating its consumption needs (Cowan & Houde 1992), and the potential of the ctenophore by reducing its numbers in Chesapeake Bay. Consequently, year-to-year variability in gelatinous predator abundances and temporal successions will influence ichthyoplankton survival. In some years ctenophore abundance during July in Chesapeake Bay remains high and/or *C. quinquecirrha* abundance is low (Olson 1987). Such variability may have a significant effect on trophic interactions that can affect recruitment of summer-spawning fishes. Examination of such interactions and consequences of variable predator abundances is an important topic for future research on fish recruitment in Chesapeake Bay.

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