ICES STATUTORY MEETING 1993 C.M.1993/1:42 Session S
Biological Oceanography

In situ predation rates on bay anchovy (Anchoa mitchilli) eggs and larvae by scyphomedusae (Chrysaora quinquecirrha) and ctenophores (Mnemiopsis leidyi) in Chesapeake Bay

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Abstract

We measured predation effects on eggs and larvae of bay anchovy (Anchoa mitchilli) by abundant scyphomedusae (Chrysaora quinquecirrha) and ctenophores (Mnemiopsis leidyi) from gut contents, digestion rates, and densities of predators and prey during 9 days in July 1991 at 4 stations in Chesapeake Bay. These predation effects were compared to egg and larval mortality rates measured concurrently in ichthyoplankton surveys. Mean consumption over the 20 h duration of the egg stage by medusae and ctenophores was 29% and 7%, respectively. Gelatinous predators accounted for, on average, 37% $20h^{-1}$, or 55% of the mean total egg stage mortality ($1.476\ 20h^{-1}$). Medusae consumed an average of 26% d^{-1} of the larval bay anchovy, which averaged 66% of mean total mortality ($1.232\ d^{-1}$). Predation on larvae by ctenophores was not detected. These predation effects also are compared with those measured concurrently in free-drifting 3.2 m^3 mesocosms. We conclude that medusae, which had high feeding rates but low abundances, and ctenophores, which had low feeding rates but high abundances, were important predators of bay anchovy eggs and larvae in the mesohaline region of Chesapeake Bay.

INTRODUCTION

Gelatinous zooplankton often eat the early life history stages of fishes, and their predation may be a major source of mortality (reviewed in Purcell 1985, Bailey and Houde 1989). Typically, fish eggs were incidental prey of several pelagic hydrozoans, scyphozoans, and ctenophores (reviewed in Purcell 1985). For example, fish eggs were 0.1% and 0.4% of the prey items in the scyphomedusan Stomolophus meleagris and the ctenophore Mnemiopsis leidyi, respectively (Larson 1991, Burrell and Van Engel 1976). In contrast, high proportions of prey in some scyphomedusae were fish eggs -- for Cyanea capillata (1.6 to 62.9%) and Pseudorhiza haeckeli (2.0 to 69.5%, Fancett 1988).

Fish larvae were occasional prey of most pelagic hydrozoans (reviewed in Purcell 1985), but notable exceptions were cystonect siphonophores, which ate mostly fish larvae (94-100% of the prey), and consumed 28-60% d^{-1} of the larvae present (Purcell 1981, 1984), and the hydromedusan Aequorea victoria, which ate mostly herring larvae at peak hatching (48-100% of the prey) and consumed as much as 97% d^{-1} of the larvae (Purcell 1989, Purcell and Grover 1990). Fish larvae usually were incidental prey of scyphozoans (reviewed in Purcell 1985, also Fancett 1988). Similarly, ctenophores usually contained few fish larvae (reviewed in Purcell 1985, also Frank 1986).

Gelatinous zooplankton, mainly the ctenophore Mnemiopsis leidyi and the scyphozoan Chrysaora quinquecirrha, are seasonally abundant in the mesohaline region of Chesapeake Bay, reaching maximum biomass in July - August in (Purcell et al. in press). Their main prey are crustacean zooplankton, mostly copepods Acartia tonsa (Burrell and Van Engel 1976, Purcell 1992). Both gelatinous species are believed to be important components of the pelagic food web in Chesapeake Bay (Feigenbaum and Kelly 1984, Baird and Ulanowicz 1989). They were estimated to consume up to 13% d^{-1} of the copepod production in the mesohaline region of the bay (Purcell et al. in press).

Bay anchovy (Anchoa mitchilli) is the most abundant fish species in estuaries of the U.S. Atlantic coast (Houde & Zastrow 1991). Spawning occurs throughout Chesapeake Bay, in salinities from <5 to >23 $^{o}/_{oo}$ (Dovel 1971, Olney 1983), and takes place nightly (Luo and Musick 1991; Zastrow et al. 1991), peaking in July in Chesapeake Bay (Dalton 1987). At temperatures $\geq$ 26°C, the eggs hatch in 20-24 h (Houde and Zastrow 1991).

Because both bay anchovy spawning and gelatinous zooplankton biomass peak in July in Chesapeake Bay, predation by the gelatinous species may be a major cause of egg and larval mortality. Herein, we estimate daily predation rates by medusae and ctenophores on bay anchovy eggs and larvae from gut contents, digestion rates, and abundances of the predators and prey. We compare these predation estimates with in situ mortality rates determined concurrently by the decreases in numbers of eggs and larvae in the plankton over 24 h periods (Dorsey 1993), and with mortality rates that were measured concurrently in free drifting 3.2 m^3 mesocosms (Houde et al. 1993).

MATERIALS AND METHODS

Sampling dates and locations. Four stations (Sta. 4 - 7) in mid-Chesapeake Bay were sampled in July 1991 (Table 1, Fig. 1). Sampling for zooplankton was conducted every 6-8 h, and for ichthyoplankton every 2 h, over 24 h on 9 dates. The exact location of each sampling effort was determined by the location of free-drifting mesocosms, which was

assumed to track the water mass where they were deployed near midnight on each night. Temperature, salinity and oxygen profiles were made daily with a CTD. Temperature of the surface waters was 25-28°C at all stations. The mesohaline portion of the bay is characterized by bottom waters that are depleted of oxygen (< 2 ppm O_2) during much of the summer (Table 1). Therefore, most results are reported only for waters above the pycnocline.

Gelatinous zooplankton, biomass, densities, and sizes. Medusae (Chrysaora quinquecirrha) and ctenophores (Mnemiopsis leidyi) were collected in two nets with flowmeters, and the mean densities calculated. First, a 1 m diameter, 1.6 mm mesh plankton net was towed obliquely from the surface to the pycnocline or near bottom, and back. Second, a 0.6 m diameter net with 280 μm mesh was opened near bottom and towed obliquely to the pycnocline and closed; on a second deployment, it was opened at the pycnocline and then towed to the surface. Volumes of water filtered ranged from 13 to 107 m^3, but most tows filtered 30 to 50 m^3. Each sample was poured through a sieve to retain the gelatinous plankton, then total live volume for each gelatinous species was measured in graduated cylinders. All specimens from most tows were measured immediately to the nearest mm (medusa diameter, ctenophore length). Some samples were preserved (final concentration 5% Formalin). All specimens in those samples were counted and measured later in the laboratory and live sizes calculated as in Purcell (1988, 1992).

Bay anchovy egg and larva densities. Two tows were made every 2 h with a 0.4 m diameter plankton net with 280 μm mesh, which was lifted vertically from near bottom to the surface. Flowmeter readings showed that 3.0 ± 1.4 m^3 of water was filtered for these tows (Dorsey 1993). Samples were preserved in 5% Formalin. Eggs and larvae were counted in the laboratory (Dorsey 1993).

Zooplankton densities. Crustacean zooplankton were collected with a diaphragm pump by filtering 50 L through a 53 μm mesh net. Each sample was integrated from three depths (surface, pycnocline, and near bottom), and preserved in 5% Formalin. In the laboratory, samples were standardized to 50 ml. Then zooplankton were counted from three 1 ml aliquots and identified to order.

Gelatinous zooplankton diet and prey selection. At the times of net sampling, medusae and ctenophores were collected individually by dip net and immediately preserved in 5% Formalin for gut content analysis. Medusae and ctenophores were not always visible to collect by dipping, therefore gut analyses do not exist for every sampling interval. In the laboratory, predator sizes were measured, and fish eggs and larvae that had been eaten were counted using a dissecting microscope. For some samples, all prey including zooplankton were counted, and electivity indices (C) were calculated from the numbers of prey m^3 and the numbers of each prey type for those samples, and the significance tested (chi square) according to Pearre (1982).

Digestion rates. Eggs were collected from 1 m^3 tanks in which bay anchovy had spawned. Medusae in 20 L containers were allowed to feed for < 10 min on eggs until several had been ingested. Each medusa was transferred to a 4 L container with filtered water (12°/$_{oo}$ salinity, 26 ± 1°C), and the eggs in the gastric pouches counted using a dissecting microscope. The numbers of eggs were counted at half hour intervals until none were seen. The periods of time between ingestion and when each egg disappeared were averaged to estimate digestion time for each medusa. Medusa diameter was measured after the experiment. The relationship of digestion time to medusa diameter and the number of eggs ingested was tested in a stepwise multiple regression. The same methods

were used to determine digestion times of newly-hatched bay anchovy larvae, except that the larvae were observed in the medusae at 15 min intervals.

Ctenophores were allowed to feed on field-collected anchovy eggs in 4 L containers for < 10 min, and then transferred to 250 ml dishes of filtered water (14‰ salinity, 24 ± 1°C). The eggs in the stomodeum were counted and observed using a dissecting microscope at 10 - 15 min intervals until they could not be recognized as eggs. Ctenophore length was measured with a ruler, and then they were preserved to determine if the egg remains could be recognized in the gut contents.

Feeding rates and predation effects. Feeding rates of medusae and ctenophores on bay anchovy eggs and larvae were calculated according to the following equation: $I = C/D \times P$, where I = number of fish eggs or larvae ingested m^{-3} h^{-1}, C = number of fish eggs or larvae in each predator, D = digestion time in hours, and P = number of medusae or ctenophores m^{-3}. To calculate the percentage eaten per hour, I then was divided by the estimated mean number of fish eggs present (no. m^{-3}) in the preceding 4 h for medusae or 1 hr for ctenophores (due to the different digestion times for these predators), plus the numbers of eggs inside the predators in a cubic meter. The same calculations were made for larvae, using larval densities from the preceding sample. The hourly predation rates were averaged on each day, converted to instantaneous rates (Z), and multiplied by 20 h for eggs and 24 h for larvae to give daily rates, which then were compared with total mortality rates from Dorsey (1993).

RESULTS

Gelatinous zooplankton biomass. Comparisons of medusa and ctenophore biomasses in paired samples above and below the pycnocline showed that both species had significantly higher biomasses in the surface waters in both day and night ($P < 0.05$, T-test for paired comparisons, Table 2). Dissolved oxygen levels below the pycnocline ranged from hypoxic (< 2 ppm) to well-oxygenated (Table 1). Some of the deeper hypoxic waters may have excluded the gelatinous species, but our sampling could not resolve the fine-scale vertical distributions. Biomasses of medusae and ctenophores did not differ between day and night, either above or below the pycnocline (Table 2). Further analyses were restricted to the surface water above the pycnocline.

Ctenophores had much greater biomasses than did medusae on 7-8 July (Sta. 4), and 23-24 July (Sta. 5)(Fig. 2). Biomasses of both predator species were greatest on those dates. Ctenophores and medusae had similar biomasses on 18 and 19 July (Sta. 7 and 6), and their combined biomasses were lower than other dates (Fig. 2).

Diet and prey selection. Bay anchovy eggs and larvae were counted from the gut contents of 117 medusae. Medusae contained from 0 - 1497 bay anchovy eggs. The number of eggs in each medusa was related to egg density (Fig. 3A), which explained 29% of the variation, and to medusa size (Fig. 3B) which explained another 12% (Table 3). From 0 to an average of 40 larvae were found in the medusae. Ctenophores contained only ≤ 3 eggs, and no larvae. Because of the comparatively low number of larvae in the medusa gut contents and eggs in the ctenophores, no regression analyses were performed.

All prey were counted from 80 medusae. Bay anchovy eggs represented from 0.1 to 90.1% (mean 21.4 ± 23.5%) of the total prey

items in each gut sample. Bay anchovy larvae were less numerous, accounting for 0 to 8.8% of the prey (mean 1.3 ± 2.6). Eggs, larvae, copepods, and cladocerans together were 95% of the total prey. Selection was positive and significant for eggs in 10 of 12 samples, for larvae in 9 of 12 samples, for copepods in 10 of 12 samples, and for cladocerans in all samples (examples in Table 4). Fish eggs were about as numerous in the diet as were copepods, even though copepod densities in situ were 400 times that of eggs (Table 4). No significant negative selection was found for fish eggs or larvae in any samples.

Digestion rates. Digestion of bay anchovy eggs by 16 medusae at 26°C averaged 3.9 ± 0.8 h. Digestion rates were not significantly related to medusa size or to the number of eggs ingested (Table 5). Digestion of 1 to 9 (mean 3.7 ± 3.1) bay anchovy larvae in the gastric pouches of 7 medusae averaged 1.1 ± 0.5 h. Therefore, 4 h and 1 h were used as the digestion times for eggs and larvae, respectively, in feeding rate calculations for medusae.

Large ctenophores (50 - 75 mm) digested 1 or 2 eggs in 37.4 ± 8.7 min (n = 20 eggs). Egg remains were found in the preserved specimens after 30 min digestion, but not after 40 min. Small ctenophores (7 - 22 mm) digested 1 or 2 eggs in 59.2 ± 23.6 min (n = 13 eggs). Because ctenophores during the field sampling were large (about 70 mm), we use 35 min as the digestion time for eggs in feeding rate calculations for ctenophores.

Feeding rates and predation effects. Percentages of bay anchovy eggs and larvae consumed h^{-1} by medusae were calculated from gut contents, digestion rates, and densities of medusae, eggs and larvae (Table 6). The average number of eggs in each medusa ranged from 1 to 1108. Mean medusa densities were 0.02 - 0.76 m^{-3} at each sampling interval. The mean numbers of eggs in the 4 h preceding collection of medusae for gut contents were 13 - 492 m^{-3}. None of these data showed a consistent pattern of abundance related to time of day, although eggs generally decreased exponentially with time (Dorsey 1993). Predation on eggs by medusae was ≤ 1% h^{-1} in 11 samples and > 1 % h^{-1} (maximum 8.7) in 13 samples. Predation on 20 July (18:00) and on 24 July (02:00) seemed unusually low when larval densities averaged > 100 m^{-3}.

Fewer larvae than eggs were in the medusa gut contents (averages of 0 to 40.2 larvae $medusa^{-1}$, Table 6). Larvae occurred in much lower densities than eggs (3 - 204 m^{-3}). From 0 - 19% h^{-1} of the larvae were eaten by medusae. Because of the low frequency of larvae in the guts, predation could not be detected in several samples. Great variation was found in the numbers of larvae in the medusa gut contents. Unusually many larvae were eaten on 19 July (22:00) and on 21 July (24:00) at moderate larval densities, while few were eaten on 20 July (12:00 and 18:00) and on 22 July (02:00) even though larvae were numerous in the water.

Predation effects of ctenophores on bay anchovy eggs were calculated similarly (Table 7). Ctenophores contained far fewer eggs (0 - 1.6 $ctenophore^{-1}$) than did medusae. Ctenophore densities, which averaged 0.1 to 5.0 m^{-3}, were much higher than medusa densities, except at Sta. 7. Bay anchovy egg densities from the preceding net samples ranged from 1.1 to 511.7 m^{-3}. The percentages of eggs consumed were low in 15 samples (0 - 0.3% h^{-1}), but higher in 3 samples (2 - 5% h^{-1}).

Daily predation by medusae and ctenophores removed high proportions of bay anchovy eggs and larvae (Table 8). Over the 20 h egg stage, medusae were estimated to consume 9 - 45% of the eggs (mean 20 ± 18% $20h^{-1}$) and ctenophores were estimated to consume 0 - 36% (mean 7 ± 12% $20h^{-1}$). Predation by medusae was much higher (66 - 100% of the predation) than by ctenophores, except on 8 July when it was lower (24%) due to the especially high ctenophore biomass. The total predation due to both species ranged from 6 - 56% $20h^{-1}$ (mean 37 ± 19% $20h^{-1}$). Total predation differed greatly between dates at Sta. 5, from 6 to 49% $20h^{-1}$. Total daily egg mortality due to all causes was 33 - 98% $20h^{-1}$ (mean 70 ± 19%). Thus, predation represented from 4 to > 100% of the estimated daily egg mortality (mean 55 ±53%).

We calculated that 0 to > 100% d^{-1} of the larvae could be eaten by medusae (mean 26 ± 30% d^{-1}). Total daily larval mortality ranged from 34 - 99%. So, from 0 to > 100% of the total daily larval mortality was calculated to be due to medusa predation (mean 66 ± 129% d^{-1}).

DISCUSSION

Predator effects on bay anchovy eggs and larvae would depend directly on predator abundances. Ctenophore biomasses and densities in this study were 2 - 47 ml m^{-3} and 0.1 - 5 ctenophores m^{-3}. Medusa biomasses and densities were 1 - 7 ml m^{-3} and 0.02 - 0.37 medusae m^{-3}. These are typical of the mesohaline region of Chesapeake Bay and its tributaries in July. In the York and LaFayette Rivers and off Calvert Cliffs, volumes were 10 - 50 ml m^{-3} (Burrell and Van Engel 1976, Feigenbaum and Kelly 1984, Olson 1987). We can directly compare our data from Sta. 7 in 1991 with data of Purcell et al. (in press) from mid-bay stations near the same location in July to early August of 1987 and 1988. Ctenophore densities were lower in 1991 (0.08 ml m^{-3}) than in 1987 and 1988 (0.5 and 0.6 ml m^{-3}). Ctenophore biomass also was lower (2 ml m^{-3}) in 1991 than in the other years (12 and 51 ml m^{-3}). Medusae had similar densities in 1991 (0.3 m^{-3}) and in 1987 (0.9 m^{-3}), but none were found in mid-bay in 1988. Medusa biomass was higher in 1991 (2.5 ml m^{-3}) than in 1987 or 1988 (0.7 and 0 ml m^{-3}). Therefore, ctenophores may have been more important, and medusae less important, as predators of ichthyoplankton in 1987 and 1988 than in 1991. Near the mouth of Chesapeake Bay, Govoni and Olney (1991) reported densities of *Mnemiopsis leidyi* of 1 - 2 m^{-3} at one station, and of > 4 m^{-3} (maxima of 21 and 227 m^{-3}) during 11-21 June 1985. Three stations were sampled during 3-5 July 1991 in the southern Bay (Sta. 1 - 3, Fig. 1), and no *Chrysaora quinquecirrha* or *Mnemiopsis leidyi* were found (Dorsey 1993).

The importance of predation is also determined by the spatial overlap of predator and prey populations. We found that significantly more medusae and ctenophores occurred above the pycnocline than below, however they did occur in the hypoxic deeper waters. Therefore, the greatest predation by gelatinous zooplankton would be above the pycnocline. Nemazie et al. (1993) reported much greater densities of *Chrysaora quinquecirrha* medusae in surface waters at night from one 24 h vertical net series (5 tows). Our tow data do not indicate any pattern of vertical migration in seven 24 h closing net series (4 times d^{-1}).

Chrysaora quinquecirrha medusae were found to show positive selection for eggs and larvae of bay anchovy. Positive selection for fish eggs and larvae previously has been shown for the scyphomedusa *Cyanea capillata* and *Pseudorhiza haeckeli* (in Fancett and Jenkins 1988), hydromedusae *Aequorea victoria* (in Purcell 1989), and cystonect siphonophores (in Purcell 1981, 1984). For the medusae, selection

probably is positive because fish eggs and yolksac larvae are large relative to most other zooplankters, and they have little or no escape ability. Data for C. quinquecirrha indicate that ichthyoplankton do not require longer to digest (mean 3.9 h for eggs and 1.1 h for larvae) than zooplankton prey (mean 3.5 h for copepods, Purcell 1992). Therefore the frequencies of ichthyoplankton in the gut contents are not increased in relation to other prey. Mnemiopsis mccradyi showed selection for some prey types, however fish eggs and larvae were not present (Larson 1987). We did not quantify all prey of M. leidyi in the present study, and so we cannot directly evaluate selection on fish eggs or larvae here.

During the spawning season, bay anchovy eggs and larvae were very important components of the diet of Chrysaora quinquecirrha medusae. Eggs and newly-hatched larvae averaged 1.8 μg nitrogen and 1.5 μg nitrogen, respectively (Tucker 1989). Eggs and larvae contributed, on average, 71 μg N medusa^{-1} d^{-1} to ingestion. Eggs were most important, contributing 80% of the bay anchovy nitrogen ingested. Nitrogen from zooplankton ingested was calculated as in Purcell (1992), and averaged 331 μg N medusa^{-1} d^{-1}. Therefore, ichthyoplankton contributed 18% of the mesozooplankton nitrogen in the diet. That nitrogen (402 μg N medusa^{-1} d^{-1}) exceeded the daily minimum nitrogen demand, as estimated by ammonium excretion, for medusae up to about 60 mm in diameter (Purcell 1992). Ctenophores are another source of nitrogen that could exceed these other sources in the diet (one 70 mm ctenophore = 3,150 μg N, Nemazie et al. 1993).

The following in situ clearance rates of bay anchovy eggs and larvae by Chrysaora quinquecirrha were similar to those calculated for other scyphomedusae. For 3 samples where mean medusa diameter was 40 mm, clearance of eggs was 1318 ± 707 L d^{-1} medusa^{-1}, and for 4 samples where mean diameter was 55 mm, clearance was 2498 ± 1120 L d^{-1} medusa^{-1}. For Stomolophus meleagris 55 mm in diameter, in situ clearance of fish eggs was 3120 L d^{-1} medusa^{-1} (Larson 1991). These rates are similar to those measured in 3.2 m^3 mesocosms, where clearance rates by C. quinquecirrha on bay anchovy eggs averaged 2983 L d^{-1} medusa^{-1} (Cowan and Houde 1993). However, in 25 L containers, clearance of fish eggs by Cyanea capillata and Pseudorhiza haeckeli 40 mm in diameter was only 140 and 400 L d^{-1} medusa^{-1}, respectively (Fancett and Jenkins 1988).

Clearance rates of bay anchovy larvae by Chrysaora quinquecirrha medusae were of the same magnitude as clearance of eggs. For 2 samples where mean medusa diameter was 40 mm, clearance rates averaged 714 L d^{-1} medusa^{-1}, and for 4 samples where mean diameter was 55 mm, clearance was 3703 ± 3765 L d^{-1} medusa^{-1}. Clearance rates of C. quinquecirrha on copepods were much lower (16 L d^{-1} medusa^{-1} for a medusa 40 mm in diameter), and can not compared to clearance rates on fish eggs or larvae due to the different characteristics of these prey (Purcell 1992). Clearance rates of goby larvae by C. quinquecirrha medusae in 3.2 m^3 mesocosms averaged 990 L d^{-1} medusa^{-1} (Cowan and Houde 1993). Aurelia aurita of 40 - 80 mm diameter cleared fish larvae from a mean of 526 L d^{-1} medusa^{-1} in 6.3 m^3 enclosures (de Lafontaine and Leggett 1987) and 1325 L d^{-1} medusa^{-1} in 5 m^3 enclosures (40 mm, Gamble and Hay 1989).

In situ clearance rates of bay anchovy eggs by Mnemiopsis leidyi in 8 samples where eggs were found were 128 ± 58 L d^{-1} ctenophore^{-1}. These are about one-third of the clearance rates measured in 3.2 m^3 mesocosms (mean 366 L d^{-1} ctenophore^{-1}), but similar to rates from 750 L containers (mean 110 L d^{-1} ctenophore^{-1}, Cowan and Houde 1993), slightly higher than rates on black drum eggs in 2.2 m^3 mesocosms (0 - 110.8 L d^{-1} ctenophore^{-1}, Cowan et al. 1992), and similar to the rates found in 200 L containers (about 61 - 168 L d^{-1} ctenophore^{-1}, Monteleone and Duguay

1988). When Monteleone and Duguay (1988) tested clearance in containers 15 - 200 L volume, they found highest rates by ctenophores in the largest containers. We did not find that M. leidyi contained any fish larvae, but Cowan and Houde (1993) calculated clearance rates of goby larvae to be 0 - 189 L d^{-1} ctenophore^{-1} in 3.2 m^3 mesocosms.

The predation effects by Chrysaora quinquecirrha on bay anchovy eggs and larvae in the mesohaline Chesapeake Bay were very high as compared with most previous estimates for scyphomedusae. From clearance rates measured in 3.2 m^3 mesocosms, in combination with published biomasses of the predators, Cowan and Houde (1993) estimated that gelatinous predators could consume 20 - 40% d^{-1} of the bay anchovy eggs and larvae in the mesohaline region of Chesapeake Bay. That estimate is similar to the means of 37% $20h^{-1}$ and 26% d^{-1} that we determined for eggs and larvae, respectively, in this study. However, Fancett and Jenkins (1988) calculated average predation rates on fish eggs and larvae in Port Phillips Bay, Australia to be only 0.1% d^{-1} by both Cyanea capillata and Pseudorhiza haeckeli, although predation in patches of medusae was higher (4 - 5% d^{-1}). Those rates were estimated from clearance rates in 25 L containers, and combined with field densities of predators and prey. Moller (1980) used gut content analysis for Aurelia aurita, and estimated that they removed 2.6 - 4.4% d^{-1} of herring larvae in Kiel Bight, Germany.

We calculated that Mnemiopsis leidyi ctenophores consumed from 0 - 36% d^{-1} (mean 7.2 $\pm$ 12.1% $20h^{-1}$) of the bay anchovy eggs, and we found no predation on larvae. From maximum clearance rates measured in 200 L containers, Monteleone and Duguay (1988) predicted much greater effects of M. leidyi, estimating that they could consume 10 - 65% of the bay anchovy eggs in Great South Bay, New York, and 11 - 55% of the yolksac larvae. Govoni and Olney (1991) used maximum clearance rates (168 L d^{-1}) from Monteleone and Duguay (1988) and field densities of M. leidyi, and estimated that ctenophores in surface waters consumed 0.1 - 14.7 eggs m^{-3} d^{-1} and 21 - 174 eggs m^{-3} d^{-1} at 2 stations at the mouth of Chesapeake Bay. These estimates compare with our range, where predation was detected, of 10 - 79 eggs m^{-3} d^{-1}.

Throughout this discussion, we mention the container size used to measure feeding rates of gelatinous predators on fish eggs and larvae because small containers can severely bias such results. De Lafontaine and Leggett (1987) showed a 10-fold decrease in mortality rates of fish larvae as container volume increased from 0.26 to 6.35 m^3. Clearance rates of Aurelia aurita doubled over that range of volumes (de Lafontaine and Leggett 1987). Caution should be used in extrapolating results from small containers to field conditions.

In 3.2 m^3 mesocosms that were deployed each during the present study, Houde et al. (1993) were unable to quantify the effects of ctenophores and medusae on egg and larval mortality. Mortality rates were not correlated with predator numbers or volumes in the mesocosms. However, some evidence of predators were seen, because mortality rates in situ and in the mesocosms were lower at the southern bay stations (Sta. 1 - 3) where no medusae or ctenophores occurred, than in the mid-bay stations (Sta. 4 - 7) where predators were abundant (Dorsey 1993, Houde et al. 1993). In addition, greater volumes of scyphomedusae resulted in lower numbers of eggs in the mesocosms. Comparison of the egg mortality rates due to medusae and ctenophores in situ with total egg mortality in the mesocosms (Houde et al. 1993) shows that predation could have explained 56 $\pm$ 25% of the egg mortality (excluding the anomalous low data of 20 July). Predation mortality of eggs in the mesocosms predicted from an encounter rate model indicated that

predation could account for 29 ± 8% (SE) of the total egg mortality (Houde et al. 1993). Similarly, in situ predation rates on larvae could account for 46 ± 34% of the larval mortality in the mesocosms (excluding 20 July), while the encounter model predicted that predation caused 39 ± 14% (SE) of the total larval mortality in the mesocosms (Houde et al. 1993).

The scyphomedusae Chrysaora quinquecirrha and the ctenophore Mnemiopsis leidyi consumed high percentages of the bay anchovy eggs and larvae, accounting for 3 - 169% of the total egg stage mortality (mean 55 ± 53%) and 0 - 393% of the total daily larval mortality (mean 66 ± 129%). Other predators would also have contributed to mortality. The hydromedusan Nemopsis bachei was present in low numbers (0.2 ± 0.5 m^3 above the pycnocline) during our sampling. Clearance rates of N. bachei feeding on black drum eggs averaged 61 L d^{-1} $medusa^{-1}$ in 2.2 m^3 mesocosms during May 1990 near the mouth of Chesapeake Bay (Cowan et al. 1992). If we apply this clearance rate to densities of N. bachei at our stations, then this species accounted for 0 - 9% d^{-1} (mean 1.4 ± 2.7% d^{-1}) of the bay anchovy eggs consumed. The importance of egg predation by adult bay anchovy is not known, but they are thought not to be major consumers of the eggs based on stomach analysis of specimens from Chesapeake Bay (Klebasko 1991), although experiments in mesocosms indicated that they consumed eggs (Cowan and Houde 1993). We believe that scyphomedusae, which had high feeding rates but low abundances, and ctenophores, which had low feeding rates but high abundances, were important predators of bay anchovy eggs and larvae in the mesohaline region of Chesapeake Bay.

ACKNOWLEDGMENTS

This research was funded by NSF grant OCE-8701304 to E.D. Houde and NOAA grant 90NA90AA-D-SG063 to the University of Maryland Sea Grant College. We thank C.T. Baier and K.B. Heidelberg for analysis of the gut content samples, and F.P. Cresswell and N.J. Olesen for assisting with the digestion experiments. We also thank all those who assisted in the field, including the Captain and crew of the R.V. Cape Henlopen.

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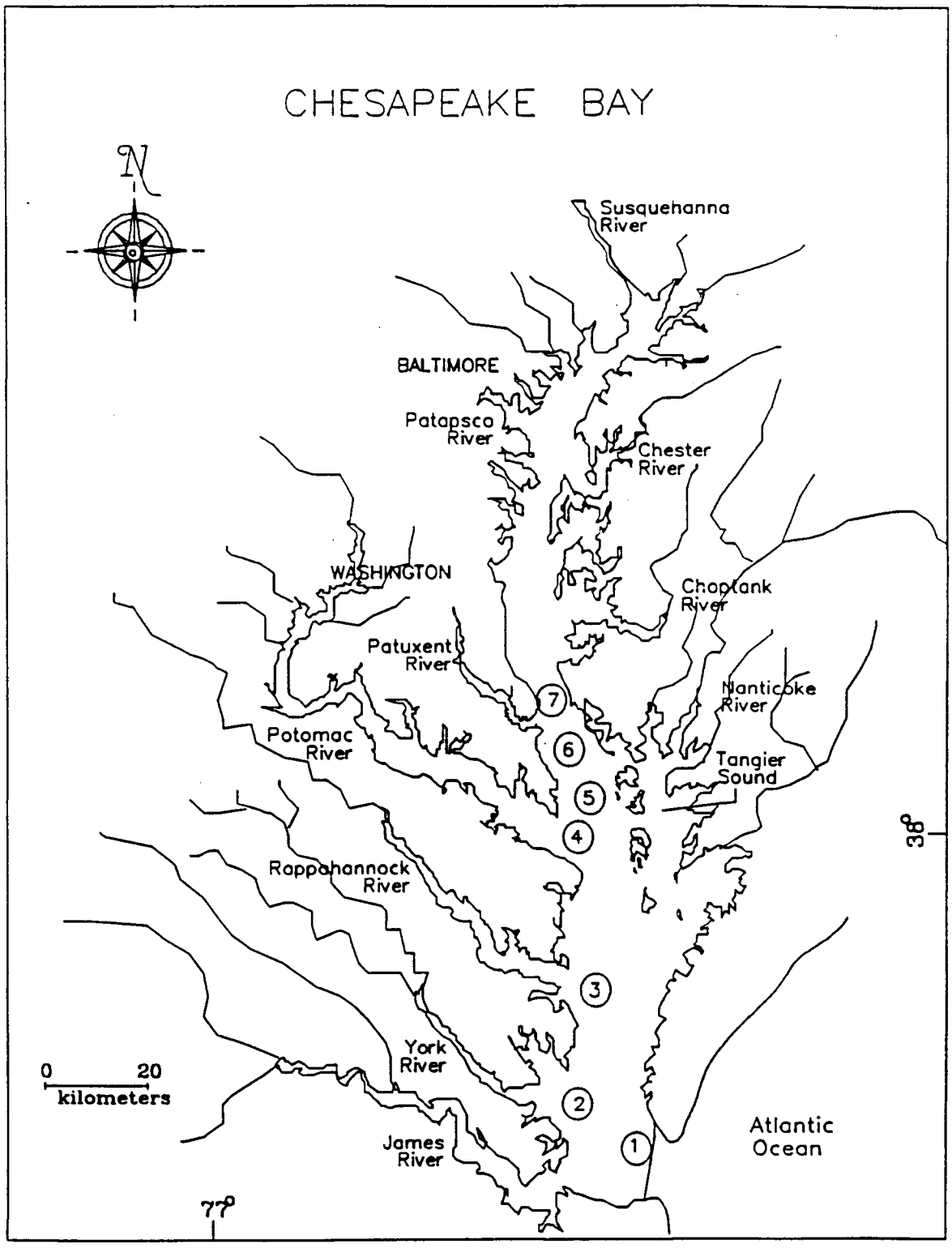

Figure 1. Sampling stations in Chesapeake Bay in July 1991.

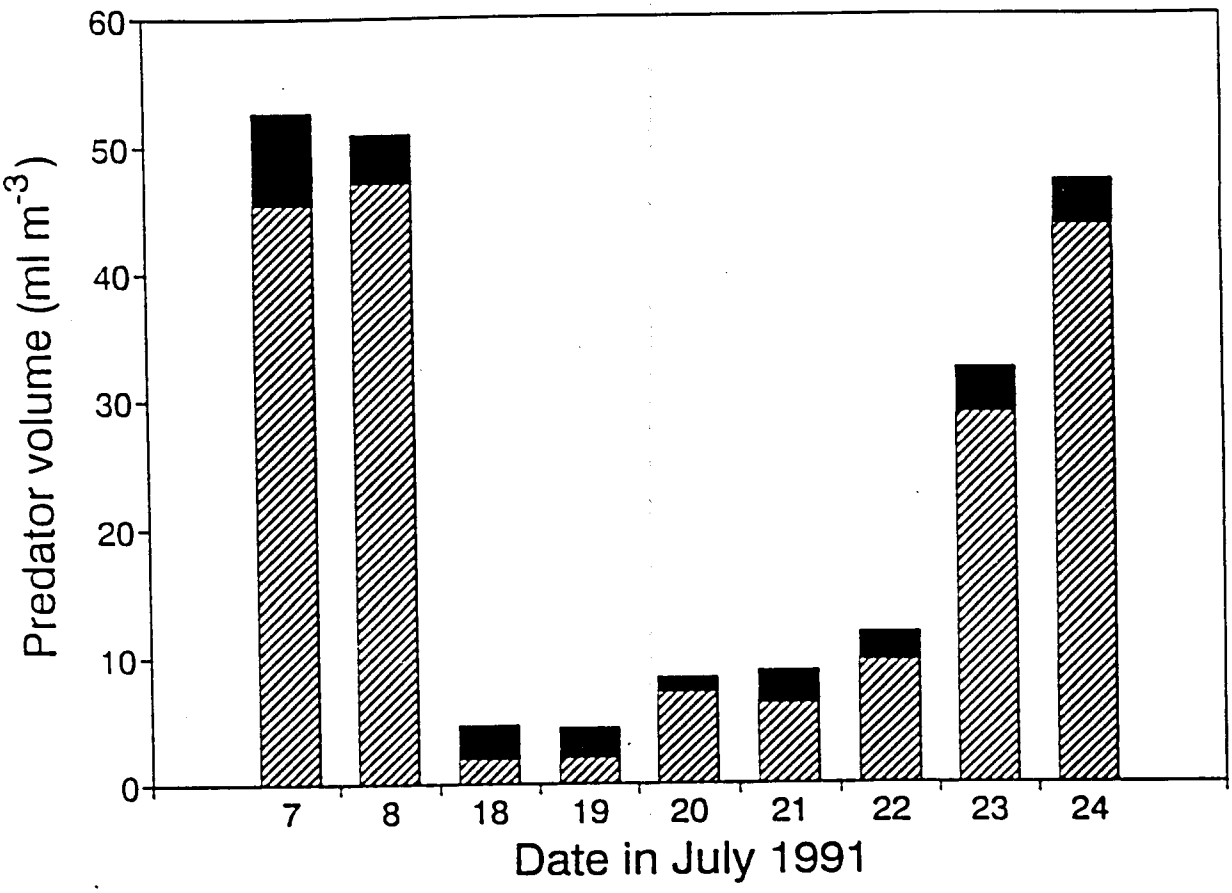

Figure 2. Chrysaora quinquecirrha and Mnemiopsis leidyi. Mean biomass (volume) of medusae (filled bars) and ctenophores (hatched bars) on each sampling date during July 1991.

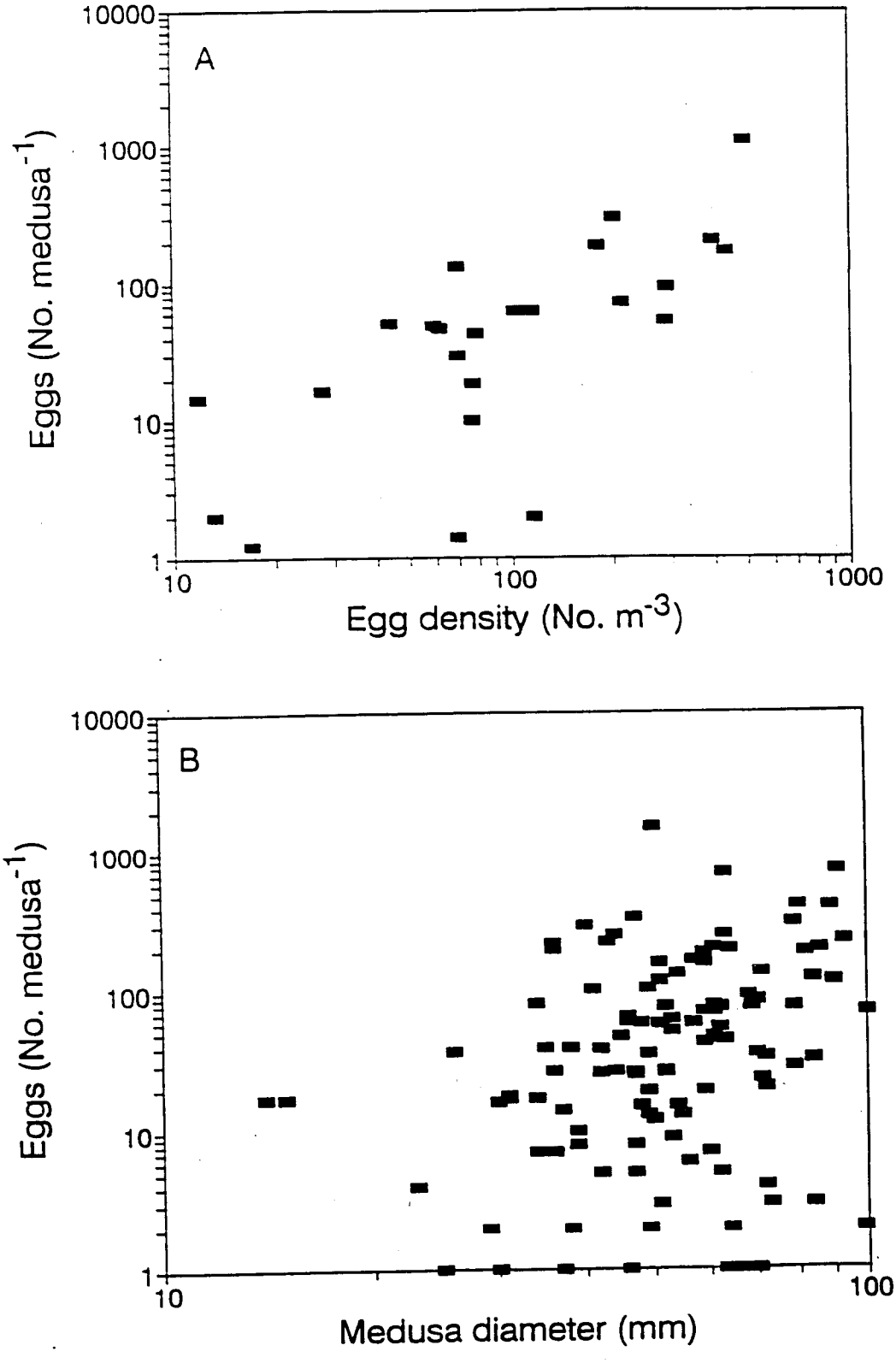

Figure 3. Chrysaora quinquecirrha. Numbers of bay anchovy eggs in medusa gut contents as related to A. egg density (average in preceding 4 h) and to B. medusa diameter.

Table 1. Sampling dates, locations, maximum sampling depths, and dissolved oxygen concentrations above and below the pynocline in Chesapeake Bay during July 1991. Depths of the pynocline are in parentheses.

Date	Sta.	Location	Depth (m)	Dissolved oxygen (ppm) Above	Below
July, 1991					
7-8	4	37° 56-59' W 76° 10-14' W	16 (8-10)	2.8 - 8.2	0.8 - 4.4
18	7	38° 23-26' N 76° 21-22' W	21 (10)	3.1 - 7.4	0.1 - 4.9
19	6	38° 16-20' N 76 ° 17-18' W	23 (11)	6.3 - 7.5	0.1 - 6.3
20-24	5	38° 04-09' N 76° 11-15' W	27 (12)	3.2 - 7.0	0.3 - 5.6

Table 2. Chrysaora quinquecirrha and Mnemiopsis leidyi. Biomass (ml m^{-3}) above and below the pycnocline during day and night. The numbers of tows are in parentheses.

Species and depth	Day	Night
C. quinquecirrha		
Above	3.10 ± 3.78 (9)	2.86 ± 3.15 (11)
Below	1.13 ± 2.07 (9)	1.16 ± 1.57 (11)
M. leidyi		
Above	19.15 ± 23.46 (9)	18.81 ± 24.30 (10)
Below	6.62 ± 10.18 (9)	11.49 ± 18.14 (10)

Table 3. Chrysaora quinquecirrha. Multiple regression analysis of bay anchovy egg density (mean in 4 h period prior to collection of gut sample), and preserved medusa diameter on the number of eggs in 117 medusae in situ. Regression equation: $\log Y = 0.83 \log X_1 + 1.33 \log X_2 - 2.49$; multiple $r = 0.579$; ANOVA $F = 26.96$, $p = 3.3 \times 10^{-10}$*, SE of estimate = 0.57

Variable	Range	Mean	Partial r^2	F	P
X_1, Eggs m^{-3}	13.2 - 492.3	183.3	0.290	43.79	$<1 \times 10^{-5}$*
X_2, Diameter (mm)	14 - 125	55.3	0.117	14.14	$<3 \times 10^{-4}$*
Y, Eggs $medusa^{-1}$	0 - 1497	96.4	---	---	---

* statistically significant

Table 4. Chrysaora quinquecirrha. Bay anchovy eggs, larvae and major zooplankton taxa in the diet of medusae and in situ in 1991, and indices of prey selection (C) according to Pearre (1982). No. of medusae examined are in Table 6. * $p < 0.005$

	Fish eggs	Fish larvae	Copepods	Cladocerans	Other Zooplankton
18 July 04:00					
No. prey medusa^{-1}	199.4	4.6	187.2	13.1	1.5
No. prey L^{-1}	0.39	0.16	61.0	2.7	71.1
C	0.621*	0.040*	0.004*	0.014*	---
19 July 22:00					
No. prey medusa^{-1}	189.1	45.0	279.6	61.6	4.1
No. prey L^{-1}	0.12	0.04	25.3	4.0	30.0
C	0.531*	0.252*	0.028*	0.037*	---

Table 5. Chrysaora quinquecirrha. Multiple regression of live medusa diameter and the initial number of bay anchovy eggs per medusa on digestion time of fish eggs in laboratory experiments at 26° C. n = 16 medusae. No variables significantly affected digestion time.

Variable	Range	Mean	Partial r^2	F	P
X_1, Diameter (mm)	23 - 44	32.2	0.157	2.61	0.13
X_2, Eggs medusa^{-1}	9 - 52	24.7	0.004	0.06	0.18
Y, Digestion time (h)	3.7 - 5.2	3.9			

Table 5. Chrysaora quinquecirrha. Calculation of predation (% eaten L^{-1}) effects on bay anchovy eggs and larvae from analysis of the numbers of eggs and larvae in the gut contents of medusae, and the densities of medusae, eggs, and larvae for sampling times in July 1991. Digestion times = 4 h for eggs and 1 h for larvae. Mean medusa densities are from 3 or 4 plankton tows.

July 1991	Station	Time	No. medusae examined	No.eggs medusa^{-1}	Medusae m^{-3}	No.eggs eaten m^{-3} h^{-1}	No.eggs m^{-3}	% eggs eaten h^{-1}	No. larvae medusa^{-1}	No. larvae eaten m^{-3}	No. larvae m^{-3}	% larve eaten h^{-1}
6-7	4	0200	4	16.5	0.24	1.0	27.6±31.8	3.5	2.2	0.5	23.0	2.3
7	4	1000	2	63.0	0.13	2.0	115.4±36.2	1.8	0.5	0.06	29.5	0.2
8	4	0400	4	10.0	0.37	0.9	76.4±43.3	1.2	0.2	0.1	6.0	1.6
8	4	1600	2	51.0	0.11±0.01	1.4	433.8±11.8	0.3	0	0	2.8	0
18	7	0400	8	210.1	0.02±0.02	1.0	394.3±384.3	0.3	4.6	0.1	164.4	0.05
18	7	1600	15	54.2	0.25±0.06	3.4	371.0±191.2	0.9	5.5	1.4	48.8	2.8
18	7	2200	7	30.4	0.76±0.34	5.8	69.3±71.6	7.7	3.6	2.7	24.1	10.2
19	6	1000	6	173.5	0.02±0.02	0.9	370.6±96.7	0.2	12.5	0.2	158.4	0.1
19	6	1600	8	72.0	0.38±0.28	6.8	211.8±233.9	3.1	0.9	0.3	5.1	6.1
19	6	2200	8	188.3	0.23±0.19	10.8	124.8±94.2	8.0	39.4	9.2	39.8	18.7
20	5	1200	2	94.0	0.06±0.05	1.4	289.0±110.3	0.5	0	0	33.7	0
20	5	1800	5	1.4	0.06±0.04	0.02	116.0±96.2	0.02	0.8	0.05	129.5	0.04
20-21	5	0200	7	133.6	0.10±0.02	3.3	84.4±68.0	3.7	1.0	0.1	36.8	0.3
21	5	1600	2	1107.5	0.10±0.04	27.7	492.4±69.5	5.3	0	0	11.4	0
21	5	2400	4	63.5	0.07±0.04	1.1	276.3±254.9	0.4	40.2	2.8	123.8	2.2
21-22	5	0200	5	49.2	0.10±0.02	1.2	59.1±81.6	2.1	0	0	204.0	0
22	5	0800	2	43.5	0.10±0.07	1.1	78.8±30.6	1.4	0	0	6.1	0
22	5	1400	3	47.0	0.10±0.02	1.2	61.6±22.7	1.9	0	0	17.2	0
22	5	2200	5	1.2	0.12±0.08	0.04	16.9±18.1	0.2	1.6	0.2	13.4	1.4
22-23	5	0200	5	18.8	0.22±0.06	1.0	77.2±118.5	1.3	0	0	48.4	0
23	5	1600	1	302.0	0.08±0.02	6.0	202.7±44.0	2.9	0	0	22.2	0
23-24	5	0200	5	2.0	0.15±0.09	0.1	115.9±178.8	0.06	2.2	0.3	87.0	0.4
24	5	1600	2	2.0	0.11±0.02	0.05	13.2±3.7	0.4	0	0	6.2	0
24	5	2200	5	14.6	0.04±0.04	0.15	13.9±6.2	1.0	4.6	0.2	9.4	1.9

Table 7. Mnemiopsis leidyi. Calculation of predation effects (% eaten h^{-1} on bay anchovy eggs from analysis of the numbers of eggs in the gut contents of ctenophores, and the densities of ctenophores and eggs for sampling times in July 1991. Digestion time = 35 min. Mean ctenophore densities are from 3 or 4 plankton tows.

July 1991	Station	Time	No. cteno. examined	No. eggs $cteno^{-1}$	Cteno. m^{-3}	No. eggs eaten m^{-3} h^{-1}	No. eggs m^{-3}	% eggs eaten h^{-1}
7	4	0200	5	0	1.65	0	68.6	0
7	4	1000	6	0.7	5.02	6.0	136.3	4.2
7	4	1600	5	0	4.51	0	22.5	0
8	4	0430	4	0.8	3.08	4.2	76.7	5.2
8	4	1000	5	0.4	2.60±0.30	1.8	85.8	2.1
8	4	1630	1	0	3.15±1.00	0	59.9	0
18	7	1300	4	0.6	0.07±0.03	0.07	448.9	0.02
18	5	1700	3	0	0.09±0.04	0	200.6	0
20	5	1130	7	1.6	0.20±0.06	0.5	400.1	0.1
20	5	1730	6	0	0.54±0.44	0	203.1	0
21	5	1630	1	3.0	0.20±0.04	1.0	511.7	0.2
22	5	0830	3	0.7	0.15±0.03	0.2	85.6	0.2
23	5	1000	4	0	1.11±0.94	0	213.3	0
23	5	1530	5	0.6	0.57±0.11	0.6	187.6	0.3
23	5	2230	1	0	1.22±0.44	0	1.4	0
24	5	0130	5	0	1.90±0.22	0	1.1	0
24	5	1500	5	0	2.40±0.65	0	7.6	0
24	5	2130	5	0	0.85±0.16	0	6.7	0

Table 8. Anchoa mitchilli. Total egg mortality over the 20 h stage duration, the eggs consumed by medusae and ctenophores, and the percentages of egg mortality that was due to predation on sampling dates in July 1991. The percentages of predation due to medusae are in parentheses.[a] Calculated from Dorsey (1993).

	Total egg Mortality[a]		Eggs consumed (%)		Egg mortality due to predation
July 1991	Z $20h^{-1}$	% $20h^{-1}$	Z $20h^{-1}$	% $20h^{-1}$	%
7	0.980	62.5	0.818 (65.8)	55.6	83.5
8	1.24	71.1	0.632 (24.0)	46.8	51.0
18	1.62	80.2	0.624 (96.8)	46.4	38.5
19	0.84	56.8	0.771 (100)	53.7	91.8
20	1.60	79.8	0.060 (83.9)	6.0	3.8
21	0.40	33.0	0.676 (94.1)	49.1	169.0
22	2.00	86.5	0.322 (87.0)	27.5	16.1
23	0.90	59.3	0.444 (95.5)	35.8	39.8
24	3.70	97.5	0.098 (100)	9.4	2.6

Table 9. Anchoa mitchilli. Total daily larval mortality, the percentages of larvae consumed daily by medusae, and the percentages of larval mortality that were due to that predation on sampling dates in July 1991. [a] calculated from Dorsey (1993).

	Total larval mortality [a]		Total larvae consumed		Larval mortality due to predation
July 1991	Z d^{-1}	% d^{-1}	Z d^{-1}	% d^{-1}	%
7	4.248	98.6	0.302	26.1	7.1
8	0.408	33.5	0.192	17.5	47.1
18	0.864	57.8	1.067	65.6	123.5
19	0.528	41.0	2.080	87.5	393.9
20	0.528	41.0	0.005	4.8	1.0
21	1.392	75.1	0.201	18.2	14.4
22	1.728	82.2	0.084	8.1	4.9
23	0.672	48.9	0	0	0
24	0.720	51.3	0.048	4.7	6.7