Potential Predation on Fish Eggs by the Lobate Ctenophore *Mnemiopsis leidyi* Within and Outside the Chesapeake Bay Plume*

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Abstract.– In Chesapeake Bay in June, the predatory lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* typically reach seasonal and localized abundance together. When examined at small vertical (1–3 m), horizontal (10–50 m), and temporal (6-hour) scales, the co-occurrence of *M. leidyi* and fish eggs (32.3–74.2% of which were *A. mitchilli*) was greatest in the northern reaches of the mouth of Chesapeake Bay, where the water column was well mixed, than in the southern reaches where the water column was stratified. Stratification to the south was effected by the Chesapeake Bay plume. With estimates of ctenophore clearance rate reported elsewhere and observed densities of ctenophores and fish eggs, potential predation was judged to be greatest in the northern reaches of the Bay mouth. The observation that co-occurrence and potential predation are greatest in areas where Chesapeake Bay water mixes with coastal shelf water implies that those fishes that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation.

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Predation is probably the leading cause of mortality for fertilized fish eggs and yolksac larvae because starvation is not relevant for these early-life-history stages and because the short duration of egg incubation and yolk absorption for most teleosts limits transport to areas inimical to development (Bailey and Houde 1989). Assessments of the impact of predation on cohorts of fish eggs and larvae in the ocean, however, have been hindered by three problems: two practical, the third inferential. Eggs and larvae leave little identifiable residue in the guts of predators, and, as a result, direct estimates of the extent of predation are difficult. Predators and prey, moreover, are concentrated together in collecting devices, a situation that can result in artifically high feeding rates and inflated estimates of predation. Lastly, predation is often spuriously inferred from the inverse abundance of predators and prey, when presence and absence may actually reflect spatial and temporal segregation rather than removal of prey by predators. Such misinterpretations result from failure to consider the small-scale temporal and spatial distribution of predator and prey in differing water masses (Frank and Leggett 1982, 1985).

Among the known invertebrate predators of fish eggs and larvae, coelenterates and ctenophores are likely candidates for significant predation because of their high rates of ingestion and population growth (Alldredge 1984, Purcell 1985, Monteleone and Duguay 1988). Lobate ctenophores, in particular, are major predators of small zooplankton of limited mobility (Kremer 1979, Purcell 1985, Monteleone and Duguay 1988). They capture prey by pumping water past lobes lined with mucus and secondary tentacles (Larson 1988), a feeding mechanism that is seemingly well suited for the capture of fish eggs.

In Chesapeake Bay, a lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* reach seasonal and localized abundance together, thereby providing a predator and prey pair that is ideal for an evaluation of potential predation. *Mnemiopsis leidyi* is present from late fall through midsummer, and episodically explodes in abundance between May and July (Bishop 1967, Miller 1974, Kremer and Nixon 1976, Mountford 1980). *Mnemiopsis leidyi* can exhibit appreciable predation on fish eggs (*A.*

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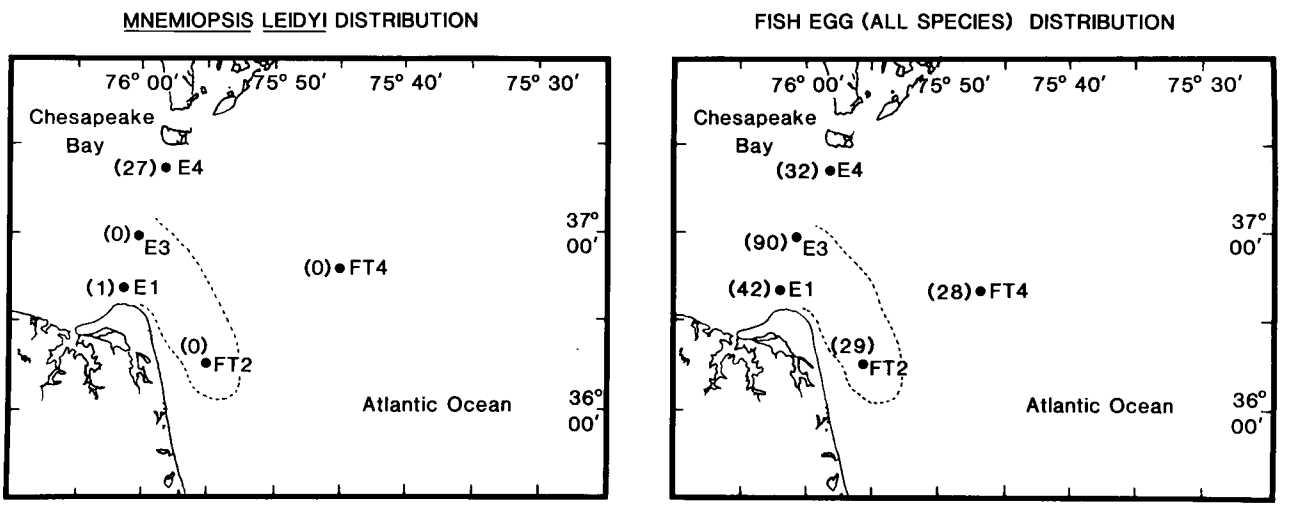

Figure 1

Positions of stations and mean station densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at the mouth of Chesapeake Bay. Dotted line indicates position of the Chesapeake Bay plume.

mitchilli) in the laboratory (Johnson 1987, Monteleone and Duguay 1988), but while it consumes some fish larvae in Chesapeake Bay (Burrell and Van Engel 1976), its predation on fish eggs in the field is not documented. *Anchoa mitchilli* spawns in the Bay in spring and summer and its eggs typically account for over 90% of all fish eggs present between May and August (Olney 1983).

The mouth of the Bay is characterized by water masses that differ spatially in both the vertical and horizontal dimensions (Boicourt et al. 1987) and provides hydrographic structure capable of shaping the spatial distribution of planktonic animals. Its complex hydrography is dominated by a buoyant plume characterized by a horizontal scale of 10–100 km, a vertical scale of 5–20 m, and a temporal scale of 1–10 days (Boicourt et al. 1987). As a result, the small-scale vertical and horizontal distributions of predator and prey can be observed synoptically in water columns of different structure within a confined study area.

Here we describe the small-scale spatial and temporal co-occurrence of *M. leidyi* and fish eggs at the mouth of Chesapeake Bay and assess potential predation.

Methods

Sampling protocol

Three stations were allocated across the mouth of Chesapeake Bay with two additional stations on the continental shelf (Fig. 1) such that some stations were within and others outside of the typical boundaries of the Chesapeake Bay plume (Boicourt et al. 1987). Each station was occupied for 30 hours between 11 and 21 June 1985 (the sampling period at station E1 was interrupted for 24 hours by vessel failure). At each station, hydrographic profiles (temperature, salinity, and specific gravity anomaly σ_t) and plankton collections at three nominal depths (surface, within the pycnocline, and below the pycnocline) were obtained once at four diel intervals (dawn, noon, dusk, and midnight). Fish eggs and ctenophores were collected with a 1-m Tucker trawl equipped with three 202-μm mesh nets, General Oceanic flow meters, and an Applied Microsystems Limited temperature, salinity, and depth recorder and towed at approximately 100 cm/second. Nets were opened at depth and fished along a horizontal trajectory for 30–60 seconds each; for subsurface strata, the trawl was lowered while the vessel was stopped and its nets were fished along a horizontal trajectory at depth. The trawl was positioned at nominal depth strata by the trigonometry of the warp angle and length. Triplicate samples were obtained at the surface; duplicate, discrete-depth samples were obtained within and below the pycnocline. With these sampling procedures, the trawl sampled on small vertical (1–3 m) and horizontal (10–50 m) scales.

All plankton collections were passed through a 6.4-mm mesh screen to separate ctenophores from ichthyoplankton. Ctenophores retained on this screen were fixed to prevent dissolution following the methods of Gosner (1971), then rinsed and preserved in 5%

formalin solution. Ichthyoplankton was preserved in either 5% formalin or 95% ethanol. All *M. leidyi* and fish eggs were counted except in those samples of exceptionally high ctenophore volume, where ctenophore number was estimated by volumetric subsampling and multiplication. Counts of ctenophores and fish eggs were averaged for replicate collections taken at a depth stratum and diel interval.

Estimation of co-occurrence

Our intention was to assess the small-scale co-occurrence of ctenophores and eggs relative to the water masses overlying these stations and to then evaluate potential predation. Because the depth of each sample occasionally varied from the nominal and the trawl consequently fished through hydrographic discontinuities, some collections were omitted from consideration. Collections omitted were those in which salinity values, recorded during each 30–60 second fishing interval, varied outside a range of 1.5‰. This procedure eliminated seven of 35 collections at station E1 and none at E4, the two stations where ctenophores and fish eggs were consistently present and where we focused our assessment of potential predation.

Estimates of potential predation

We estimated potential predation, for each depth and diel interval, as the product of clearance rate (the volume of water cleared of all prey per unit time per ctenophore), times the end points of the range of density of ctenophores (the number of ctenophores per unit volume, averaged for replicates), times the end points of the range in density of fish eggs (again averaged for replicates). A clearance rate of 168 L/day was used from Monteleone and Duguay (1988), who found that the clearance rate of fish eggs was independent of egg density (as well as the presence of alternate prey) and was positively and linearly related to experimental vessel size. This clearance rate was the highest rate observed for ctenophores 4.5–5.0 cm in length feeding in the largest vessels employed and falls roughly within the range of values reported elsewhere (Larson 1987). A sample of 10 preserved ctenophores from our collections averaged 8.5 mL in volume which converts to an average length of 4 cm (Kremer and Nixon 1976). We did not account for shrinkage.

Results

Distribution and co-occurrence

Mnemiopsi leidyi and fish eggs were consistently present only at stations E1 and E4 (Fig. 1). Pulses in densities of *M. leidyi* were evident, but did not conform to specific diel intervals or tidal phases (Figs. 2, 3). Egg density showed a diel pattern, with peak densities from dusk to dawn. Eggs of *Anchoa mitchilli* accounted for an average of 74.2% (range 23.0–98.5%) of the fish eggs at station E1 and 32.3% (range 0–62.9%) at E4.

Mnemiopsis leidyi and fish eggs were, for the most part, vertically segregated at station E1, but co-occurred, particularly in surface water, at E4. Vertical segregation at E1 (Fig. 2) reflected the physical stratification of the water column with a warm, low-salinity, surface-layer characteristic of the Chesapeake Bay plume overlying a cool, higher-salinity, bottom-layer characteristic of coastal shelf water (Boicourt et al. 1987). At E1, in the southern reaches of the mouth of the Bay, surface collections within the plume yielded higher egg densities, while subsurface collections yielded higher *M. leidyi* densities. Station E4, in the northern reaches and outside the plume, was unstratified with no thermo-, halo-, or pycnocline (Fig. 3). Water at this station apparently was a mixture of Chesapeake Bay water and coastal shelf water, likely the result of tidal, rather than wind, mixing. Winds, often responsible for mixing at the mouth of the Bay (Ruzecki 1981), were light to moderate during this sampling period (1–8 m/second).

Potential predation

Overall, potential predation was greater in the unstratified northern reaches of the mouth of the Bay outside the plume (E4) than in the southern reaches stratified by the plume (E1), because of greater temporal and spatial co-occurrence of *M. leidyi* and fish eggs there. Range estimates of potential population predation were 0.1–14.7 eggs per m^3/day at E1, and 0–174.3 at E4 (Table 1).

Discussion

The assessment of ichthyoplankton predation in the field has been based historically on the examination of predator gut contents or on the strength of a negative correlation of predator and prey densities, even though biases may result from the lability of fish eggs and larvae in the guts of predators, from the feeding of predators within the collecting device used to sample predator and prey (Purcell 1985), and from the spurious inference of cause and effect drawn from correlation analysis (Frank and Legget 1982, 1985). Few have resolved successfully the first two problems (Bailey and Houde 1989, Purcell 1989, Purcell and Grover 1990). In regard to the latter, the importance of small-scale spatial and temporal distribution of predator and prey

in evaluating predation is apparent across the mouth of Chesapeake Bay. Potential predation in the southern reaches where the Chesapeake Bay plume overlays coastal shelf water was low because of the relative lack of vertical co-occurrence there. In the northern reaches where the water column was well mixed, *M. leidyi* and fish eggs co-occurred in a more or less well-mixed water column, and as a result our estimates of potential predation were high.

The application of parameter estimates derived from laboratory predation experiments to the evaluation of the impact of gelatinous planktivores on their prey in nature, an approach that avoids field sampling errors, has other pitfalls (Purcell 1985). These problems relate to the unrealistic confines of experimental vessels, which constrain movement and small-scale hydrodynamics, and to unnaturally high experimental densities of predator and prey (Sullivan and Reeve 1982, de Lafontaine and Leggett 1988). The result is often artificially low estimates of clearance rate, values that are then used as functions in mathematical operations that range from simple multiplication of clearance rate and predator density (e.g., Reeve et al. 1978) to complex models that involve the swimming and foraging velocities and ambit geometries of motile predators and prey, and the turbulence of the environment in which they are embedded (e.g., Bailey and Batty 1983, Rothschild and Osborn 1988, Evans 1989). The simple approximation used herein was justified, in part, by the behavior of *M. leidyi* feeding on immobile fish eggs. Lobate ctenophores feed as a moving pump, pumping water continuously through mucus- and tentacle-lined lobes, while either swimming vertically or hovering (Larson 1988), and changing position in response to low prey density (Reeve et al. 1978). While the geometry of the predatory field of *M. leidyi* is unknown, we assume, given forage velocities of from 1–3 mm/second for its congener *M. mccradyi* (Larson 1987), that it encounters new water continuously. Although the gut capacity of lobate ctenophores is small, *M. leidyi* egests superfluous food in a mucus bolus when its gut is full and continues feeding; egested fish eggs, embedded in this bolus, are either dead or moribund (Johnson 1987).

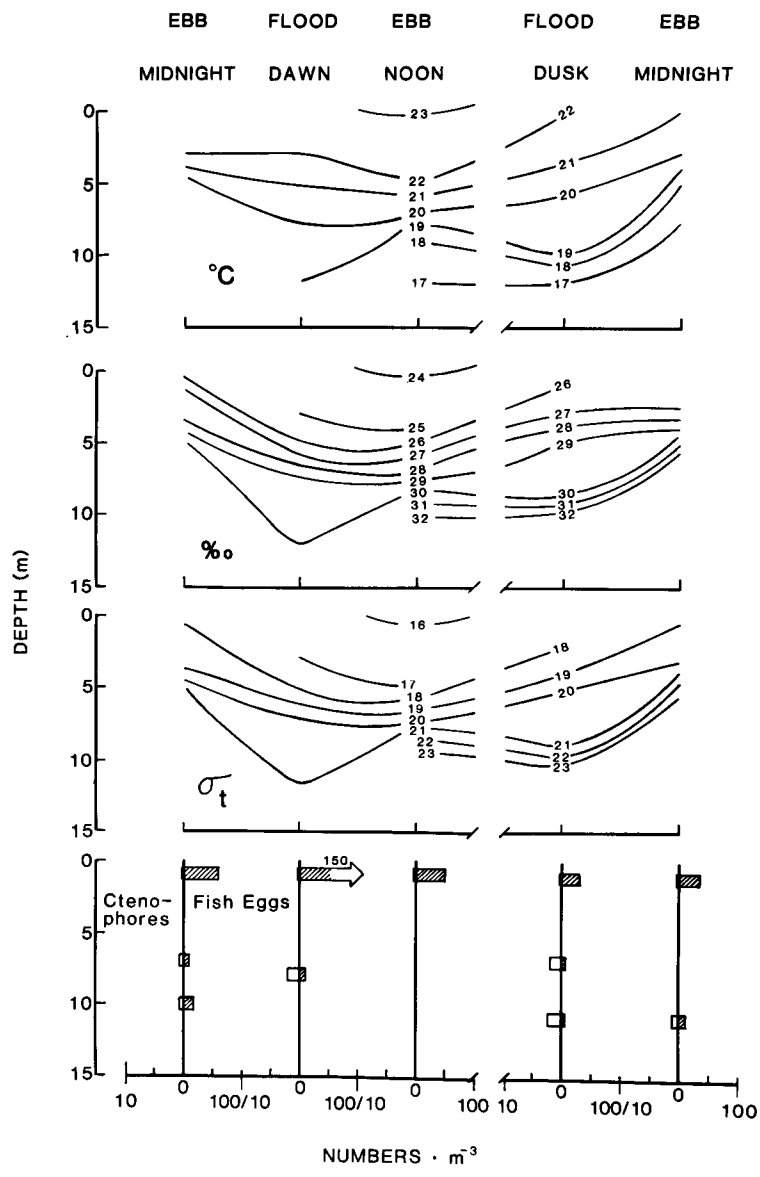

Figure 2

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at station E1 at the mouth of Chesapeake Bay. Vessel failure caused a 24-hour interruption in sampling between noon and dusk.

The observation that co-occurrence of *M. leidyi* and fish eggs, and consequently potential predation, is greatest in areas where Chesapeake Bay water mixes with coastal shelf water, coupled with the observation that *M. leidyi* are more abundant in regions of higher salinity within other estuaries, implies that those fishes

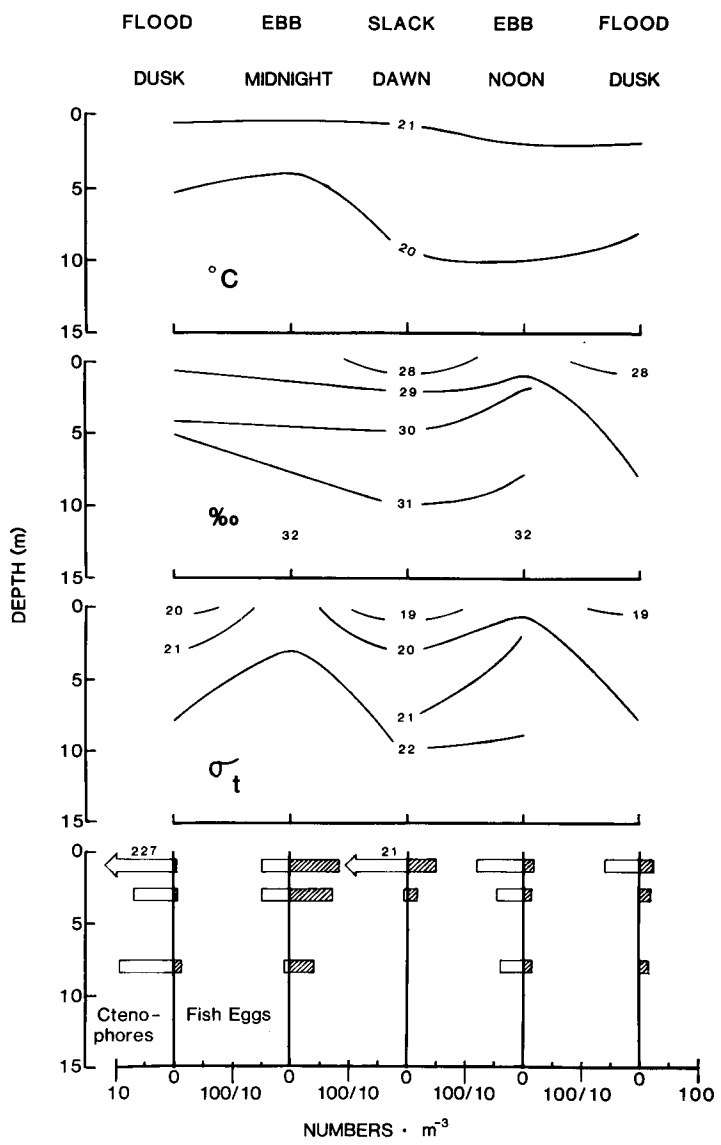

Figure 3

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at station E4 at the mouth of Chesapeake Bay.

Table 1

Potential predation of the lobate ctenophore *Mnemiopsis leidyi* on fish eggs at the mouth of Chesapeake Bay. Values are the end points of the range over five diel intervals.

	Potential predation rate (eggs/m^3 × day)	
Strata	Station E1	Station E4
Surface	0.1–14.7	21.0–174.3
Pycnocline	1.6–4.4	0–68.8
Below pycnocline	0.5–3.8	0–25.1

that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation. Estuaries typically fluctuate between stratified and unstratified conditions as a result of lunar periodicity and meteorological forcing. A survival advantage may be afforded by spawning in association with the predator free surface waters of the Chesapeake Bay plume.

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