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MESOCOSMS ADRIFT: A METHOD TO ESTIMATE FISH EGG AND LARVAE MORTALITY RATES

by

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ABSTRACT

A mesocosm system was developed that can be deployed from a research vessel and set adrift with its enclosed plankton, including fish eggs, larvae and gelatinous predators. The system consists of an array of mesocosms that are 1-m diam, 5-m long and 3.2 m^3 capacity, and which are constructed of 20-μm porosity Dacron. Deployment and harvesting procedures are described. The mesocosms capture a sample of the water column and provide an assay method to examine planktonic processes in experiments of a few hours to a few days' duration. Mortality rates of bay anchovy Anchoa mitchilli eggs and yolk-sac larvae were estimated from drifting mesocosm experiments in 1989 and 1991. Overall mean instantaneous rates were 0.074 h^{-1} for eggs and 0.053 h^{-1} for larvae, indicating that 95% of a cohort of this species has died by two days after hatching. Egg and larva mortality rates were variable due to variability in initial numbers of captured eggs and larvae and due to the complex mix of predator sizes and volumes that were enclosed. An attempt (only partially successful) was made to relate observed mortalities to abundances of two enclosed gelatinous predators, a ctenophore Mnemiopsis leidyi and a scyphomedusa Chrysaora quinquecirrha. Results are discussed and compared in relation to an encounter model that predicted predation

mortality and in relation to two concurrent field experiments which provided independent estimates of egg/larvae mortality and their consumption by gelatinous predators. The drifting mesocosm method holds promise and, with modifications of experimental design, can be a valuable tool to study planktonic population processes, including those of early life stages of marine and estuarine fishes.

INTRODUCTION

Research on dynamic processes that affect survival and growth of marine fish larvae often is limited by the difficulty of mounting major field programs to estimate rates and to identify and quantify factors that contributed to mortality, promoted growth, or led to starvation. The use of enclosures (mesocosms) to examine processes that affect recruitment variability proliferated in the 1970s (Gamble et al. 1977; Øiestad 1982, 1990; Gamble 1985; Houde 1985). Mesocosms of various types and sizes, including plastic bags, mesh enclosures and seawater basins all were employed in fixed deployments to address many questions related to early life ecology of marine fishes. Many of these experiments enclosed fish larvae with natural plankton populations to determine growth and survival rates under conditions similar to those in the sea and in containers large enough to overcome some constraints of small laboratory tanks. Results often were surprising; larvae survived at high rates at prey levels previously thought to be limiting from laboratory experiments. As a consequence, predation was inferred to be the primary cause of mortality and controller of recruitment variability in the sea (Laurence et al. 1979; Øiestad 1985; Bailey and Houde 1989).

Better-focused mesocosm research in the 1980s was directed at understanding how prey levels and predators controlled the survival and growth of fish larvae. The quality as well as quantity of prey was demonstrated to be an important factor influencing growth of larvae (Frank and Leggett 1986; Cowan and Houde 1990). Predation on larvae by gelatinous zooplankton, which are thought to be major consumers of fish eggs and larvae (Purcell 1985; Bailey and Houde 1989), was studied effectively in mesocosms stocked with fish larvae and predators (deLafontaine and Leggett 1987b, 1988; Gamble and Hay 1989). Studies on the role of pelagic fish as probable significant predators on ichthyoplankton were initiated in mesocosms (Fuiman and Gamble 1988, 1989; Fuiman 1989). The significance of size-specific predation by invertebrates and fishes on fish eggs and larvae has been a subject of several recent mesocosm experiments (Cowan and Houde 1992; 1993; Litvak and Leggett 1992; Pepin et al. 1992).

Mesocosm experiments, like experiments carried out in smaller laboratory tanks, are artificial in some respects. Often they depend upon stocked populations of plankton, predators, and ichthyoplankton, usually at unnatural densities and sometimes under environmental conditions that may not resemble those in the sea. We developed a method to enclose a part of the water column with its plankton population, including ichthyoplankton, to determine mortality rates of fish eggs and larvae in short-term experiments. The method, which we term "drifting mesocosms" essentially is an assay tool in which a part of the sea is captured and the dynamics of ichthyoplankton and other zooplankton are observed under near-ambient conditions.

Our objective was to develop a method to deploy mesocosms from a research vessel that would allow estimates of mortality rates of fish eggs and larvae to be obtained over periods of one to three days. We began to design the mesocosm system in 1988. The system was modified and tested in 1989 and 1991. This report describes the system and its deployment. It also presents results from 1989 and 1991 experiments on fish egg and larval mortality and discusses the results with respect to predation potential of two gelatinous predators that were enclosed in the mesocosms. For the 1991 experiments, mortality estimates are compared with estimates obtained concurrently in field experiments carried out simultaneous to the drifting mesocosm study (Dorsey 1993; Purcell et al. 1993).

METHODS

Study Area and Species

Research was carried out in Chesapeake Bay, a large estuary on the mid-Atlantic coast of North America (Figure 1). Releases of mesocosm arrays were made at several sites, extending from the mouth of the Bay to the mid-Bay area, near the confluence of the Patuxent River.

Eggs and larvae of bay anchovy, Anchoa mitchilli, predominate during summer, when these experiments were carried out. Densities of eggs often range from 10 to 1,000 m^{-3} and yolk-sac larvae densities generally range from 1 to 100 m^{-3} (Olney 1983; Dalton 1987; Dorsey 1993). The abundance of bay anchovy, the availability of information on its biology and early life dynamics (Leak and Houde 1987; Castro and Cowen 1991; Houde and Zastrow 1991) and the experience of recent mesocosm studies on it (Cowan and Houde 1990, 1992, 1993) made bay anchovy an ideal species for the drifting-mesocosm research.

Bay anchovy females spawn daily during the peak of the spawning season in Chesapeake Bay (Luo and Musick 1991; Zastrow et al. 1991). Eggs develop rapidly and hatching occurs approximately 20-22 h after spawning at temperatures >26 °C. Thus, each experiment followed a single cohort of eggs. Virtually all larvae of bay anchovy in the mesocosms were yolk-sac larvae. Because the yolk-sac larval stage is of one-day duration, each experiment also followed a single cohort of larvae.

Two gelatinous predators were common during the times when experiments were carried out. They were the lobate ctenophore, Mnemiopsis leidyi, and the scyphomedusa Chrysaora quinquecirrha. They are important consumers of zooplankton and are hypothesized to be important predators on ichthyoplankton (Feigenbaum and Kelly 1984; Govoni and Olney 1991; Purcell 1992). The numbers and biovolumes of the gelatinous predators that were enclosed were recorded when each mesocosm experiment was ended. In some experiments, scyphomedusae were added to mesocosms to evaluate predation potential.

Mesocosm Description and Deployment

The mesocosms are 5-m long, 1-m diam cylinders constructed of 20-μm porosity dacron sailcloth. The bottom 1-m section is conical and constructed of 53-μm Nitex. Each

1-m section is supported by a 4-mm diam stainless steel ring attached to the outside of the mesocosm. The volume enclosed by a mesocosm is 3.2 m^3. A codend jar is attached to the bottom, into which all contents are drained when a mesocosm is harvested. The mesocosms are based upon a design described and illustrated by deLafontaine and Leggett (1987a) with minor modifications described by Cowan and Houde (1990). The water enclosed in the mesocosms was demonstrated to have temperatures, salinities, and oxygen concentrations similar to levels in depth profiles adjacent to the mesocosms (Cowan and Houde 1990).

To deploy the mesocosms in a drifting mode, rafts of wood and styrofoam were constructed to contain individual mesocosms. Prior to deployment, a mesocosm was bundled and secured by a line and bridle, which was tied with slip knots that could be released by a firm pull on the line when a mesocosm was dropped to the depth of deployment. A small "Zodiac" boat with two people on board was launched to assist in the deployment process. A mesocosm to be deployed was secured to a cable attached to the vessel's crane and then lowered through the hole in a raft to a depth of 5-m. The bundling line was pulled to release the slip knots and the now-opened mesocosm was brought to surface by the crane. The mesocosm, with its captured volume of water and organisms, was attached by snaphooks to the raft.

In an experiment, the first pair of mesocosms to be deployed was not secured in a raft, but was harvested immediately to provide estimates of initial abundances of ichthyoplankton and potential predators. In some experiments, a 10-mm mesh net was placed over the top of mesocosms to exclude large ctenophores and scyphomedusae. After deployment, the rafts with their mesocosms were linked by 6-m lengths of line to form an array of six units that was allowed to drift with the prevailing currents, tracking the water mass that they had sampled. A radar reflector and light were secured to a buoy on a line at the end of the mesocosm array.

The vessel tended the mesocosms during the experiments, which were of 18 to 44-h duration. The mesocosm experiment's drift track was plotted from records logged into the vessel's navigation system. At the beginning of each deployment and at each mesocosm harvest a CTD cast was made adjacent to the mesocosm array to profile temperature, salinity, oxygen, and chl a fluorescence.

In the experiments described here, pairs of mesocosms were harvested sequentially at 6 or 8-h intervals. At harvest the vessel's crane lifted the raft and mesocosm from the water, allowing its contents to drain to the codend. The mesocosm was brought aboard, the codend was flushed and its contents filtered through a 53-μm mesh sieve before being preserved in either 5% formalin or 95% ethanol for later analysis.

1989 Experiments

Six deployments were made in the period 5 to 20 July, all within 10 km of the Patuxent River mouth (Figure 1). In each experiment, six mesocosms were released. Harvests of pairs of mesocosms were made at 6-h intervals. In the first two deployments, the mesocosm arrays were tethered to the anchored vessel. In the remaining four, the mesocosms

drifted freely.

1991 Experiments

A total of 11 deployments of freely-drifting mesocosms were made in 1991 in the period 3 to 23 July. Areas of deployment are indicated on Figure 1 and in Table 1. Deployments were made, with one exception, between midnight and 04:00, at the times when maximum numbers of anchovy eggs and yolk-sac larvae were anticipated to be present. Pairs of mesocosms were harvested at 6-h intervals. Scyphomedusae were added to some of the mesocosms in designated experiments (Table 2).

In addition to the mesocosm experiments, paired vertical lifts of a 40-cm diam, 280-μm plankton net were made at 2-h intervals in the immediate vicinity of each experiment in 1991. The objective was to estimate abundances and mortality rates of bay anchovy eggs and larvae (Dorsey 1993). Results were compared with estimates from the mesocosm experiments. Specimens of the ctenophore and scyphomedusa were collected for stomach analysis during the 1991 experiments to determine consumption of anchovy eggs and larvae, from which predation mortality was estimated (Purcell et al. 1993).

Data and Analyses

Mortality rates were estimated from the decline in abundances of enclosed anchovy eggs and yolk-sac larvae during the course of an experiment. The $\log_e$ abundances of eggs or larvae were regressed on time and the exponential coefficients were estimates of the hourly mortality rates. Because all viable eggs were expected to hatch within 22 h after being spawned, adjustments of egg and larval abundances were made to account for losses of eggs attributable either to hatching or to nonviability (based upon unhatched eggs remaining $\geq$22 h after peak spawning time. An example of unadjusted and adjusted abundances in a mesocosm experiment shows how the correction procedure was applied (Figure 2).

Mortality rates were compared among areas. A correlation analysis was carried out in an attempt to relate mortality rates to environmental variables and to abundances of the gelatinous predators that were enclosed.

The effects of predator abundances on estimated mortality rates were determined by comparing mortality rates in mesocosm pairs with and without added scyphomedusae as well as examining mesocosm pairs that coincidentally had high and low gelatinous predator numbers. Abundances of eggs and larvae were examined in relation to numbers and biovolumes of the ctenophores and scyphomedusae that were enclosed in the mesocosms.

In each experiment that included the gelatinous predators, an encounter rate model that had been developed to predict the impact of gelatinous predators (Cowan and Houde 1992; Cowan et al. 1992) was applied and the modeled results were compared with the observed mortality rates of eggs and yolk-sac larvae in the experiments.

RESULTS

Mesocosm Drift Tracks

Drift tracks of mesocosm arrays were variable, dependent upon water currents in the upper 5m of the water column. Drift responded to semidiurnal tides and was sensitive to wind. Two examples of tracks from 1991 experiments are illustrated (Figure 3). In three cases, the mesocosm arrays drifted toward shoal areas from which they were towed by the Zodiac boat. These tows were <1 km and required <1 h to accomplish.

Mortality Rates

Eggs: The mean mortality rate of bay anchovy eggs in the 17 mesocosm experiments was Z = 0.074 h-1 (Table 1), which is equivalent to 79% mortality in the 21-h period between spawning and hatching. The mean rate in the six experiments near the Patuxent River mouth in 1989 was 0.090 h^{-1}; the mean rate for the eleven experiments in 1991, which were from diverse areas of the Bay, was 0.065 h^{-1}. Examples of egg abundance data and regressions fit to the data are illustrated for six of the 1991 experiments (Figure 4). The mortality rates varied widely, ranging from 0.031 to 0.156 h^{-1}. Fourteen of the 17 estimated rates were significant at the $\alpha = 0.05$ level (Table 1).

Larvae: Mortality rates of larvae (principally yolk-sac larvae) in the mesocosms also were high, and the estimates were more variable than the egg mortality rates. The mean larval mortality rate for the 17 experiments was Z = 0.053 h^{-1} (Table 1). This rate is equivalent to 72% mortality during the first day after hatch. The mean rates for experiments in 1989 and in 1991 were 0.044 h^{-1} and 0.058 h^{-1}, respectively. Larval abundance data in mesocosms were more variable than data for eggs. Only 3 of the 17 regression equations describing the change in abundance of larvae over time were significant at the $\alpha = 0.05$ level (Table 1).

Although egg and larval abundance data were variable within mesocosms, the mean mortality rates may have been estimated reasonably well. For the 17 experiments, the .95 Confidence Intervals were 0.07 $\pm$ 0.02 h^{-1} for eggs and 0.05 $\pm$ 0.03 h^{-1} for yolk-sac larvae. Based upon these estimates, the total mortality of an average cohort of bay anchovy was estimated to range from 80 to 98% during the first two days after eggs were spawned. The estimated means of the egg and yolk-sac larvae mortality rates for the 17 experiments did not differ significantly (paired t-test, $p > 0.50$).

The mortality rates estimated in the mesocosm experiments in 1991 were nearly identical to rates derived from Dorsey's (1993) plankton net surveys in the areas where the mesocosms were set. She estimated a mean egg mortality rate of 0.066 h^{-1} and a mean larval mortality rate of 0.053 h^{-1} in twelve 24-h surveys. However, the mesocosm and survey estimates of mortality were not correlated ($r = -0.19$, $p = .58$ for eggs; $r = +0.01$, $p = .99$ for larvae), suggesting that, while either method may give a reasonable estimate of mean mortality, small-scale processes in the Bay or in the mesocosms strongly influence individual survey or mesocosm results.

Mortality of eggs in the mesocosms did not differ significantly among the four areas in which the experiments were carried out in 1991 (Table 3, Figure 1). The highest recorded mean mortality (0.09 h^{-1}) occurred in area D while the lowest recorded mean mortalities (0.05 h^{-1}) occurred in areas A and B. The estimates of variances on larval mortality rates were too high to allow us to determine if there might be among-area differences (Table 3). There was no apparent relationship between the numbers or volumes of the gelatinous predators in mesocosms and the area-specific mortality rates (Tables 1 and 3).

Gelatinous Predators

We were unable to quantify the effect of the two major gelatinous predators in causing mortality of anchovy eggs and larvae in the mesocosms. Egg and larval mortality rates were not correlated with numbers or volumes of the ctenophore M. leidyi and the scyphomedusa C. quinquecirrha. There were some indications that these two predators did contribute to observed mortalities of eggs in the drifting mesocosms. The three experiments in the lower Bay in 1991 (Figure 1, Area A, Tables 1 and 3), which had no gelatinous predators, had a mean egg mortality rate of 0.048 h^{-1} compared to a mean rate of 0.071 h^{-1} for the eight remaining experiments in 1991 which had gelatinous predators enclosed. Over a 21-h incubation period, this difference in mortality rates would generate a 14% difference in survival at time of hatching.

In the four experiments in 1991 into which two scyphomedusae were added to one of each of the pairs of mesocosms (Table 2), there was only slight evidence that the added predation capacity caused an increase in egg mortality rate. For the mesocosms without medusae added, mean mortality rate was 0.09 h^{-1} while the rate was 0.10 h^{-1} in mesocosms with the two added predators. Two examples of declines in egg abundances from these experiments are illustrated. One indicates a possible increase in mortality rate due to predator addition (Expt. 91-2-4) but the second indicates no change in mortality rate (Expt. 91-2-6) (Figure 5).

The examination of mesocosm pairs that were harvested at the same times revealed that, on average, there was a deficit in numbers of anchovy eggs in the mesocosm with the greater volume of the two gelatinous predators. This method of indexing the effects of predator abundance indicated that egg numbers per mesocosm were reduced by 1.1 and 1.7 per ml of predator in the 1989 and 1991 experiments, respectively. Most of the deficits were attributable to volumes of the scyphomedusa, rather than the ctenophore or the combined volumes of the two predators. Considering the scyphomedusa alone, egg numbers per mesocosm were reduced by -25.9 and -8.7 per ml of scyphomedusa in 1989 and 1991, respectively.

Modeled Predation

The application of an individual-based, encounter model to the 1991 data on initial egg and larvae abundances in the mesocosms, for the observed gelatinous predator numbers and sizes, predicted that, on average, 29% and 39% of the total egg and larval mortalities were caused by the ctenophores and nettles in experiments with the predators present (Table

4). The model predicted that the enclosed predators imposed mean mortality rates of 0.016 h^{-1} and 0.014 h^{-1} on eggs and larvae, respectively. In the absence of the ctenophore and scyphomedusa predators, the predicted mortality rates in these mesocosm experiments would have been 0.055 h^{-1} and 0.048 h^{-1} for eggs and larvae, respectively, compared to the observed rates of 0.062 and 0.071 h^{-1} (Table 4).

DISCUSSION

A method was developed to allow routine deployment of 3.2 m^3 mesocosms from research vessels to be used in short-term experiments to study dynamic interactions in the plankton. The method can be used successfully under most weather conditions in large estuaries and probably in coastal seas. It is essentially an assay methodology which allows a portion of the environment to be enclosed and the dynamics of naturally-occurring populations to be evaluated. The technique allows addition or exclusion of predators and prey to manipulate the system and predict the responses of natural plankton populations to increased predation pressure. To our knowledge, this report is the first on the use of such a system, although Owens et al. (1985) described a free-floating, portable mesocosm designed to study nutrient cycling in marine environments.

We applied the drifting mesocosm method to estimate mortality rates of bay anchovy eggs and yolk-sac larvae in the Chesapeake Bay and to relate observed rates to potential predation pressures, especially from gelatinous zooplankton. Mortality rates of eggs were estimated with fair precision, but larval rates were poorly estimated in individual experiments, probably because the less abundant yolk-sac larvae were more patchily distributed and the numbers enclosed during deployments were both fewer and more variable. The mean of coefficients of variation (100 $s/\bar{x}$) for the 11 individual experiments in 1991 was 17.3% for egg mortality rates but it was 39.6% for the larval mortality rates. The mean mortality rates of both eggs and larvae were similar to mean rates estimated in concurrent ichthyoplankton surveys carried out in the same areas as the mesocosm deployments (Dorsey 1993). However, the daily rates from the ichthyoplankton surveys and the mesocosm rates on the same days often were not concordant.

We believe that realistic Baywide and area-specific estimates of bay anchovy egg mortalities were derived from the drifting mesocosm deployments. The mean instantaneous rate in 1991 was 0.065 h^{-1}, which corresponds to a daily (24-h) loss rate of 79%. Dorsey's (1993) concurrent field surveys produced a mean egg mortality rate of 0.066 h^{-1}, also equal to a daily loss rate of 79%. Mean mortality rates for yolk-sac larvae in 1991 were 0.058 h^{-1} and 0.053 h^{-1} in the mesocosm and field survey, respectively, which are equivalent to 75% and 72% daily mortalities. These high rates indicate that most of a cohort's mortality in bay anchovy occurs before the end of the yolk-sac larva stage. At the mean rates estimated in the drifting mesocosms during 1989 and 1991, 95% of a cohort would have died by 48 h posthatch.

The egg and yolk-sac larva mortality rates are similar to those estimated or inferred in other studies on bay anchovy. Leak and Houde (1987) estimated an approximate 86% mortality of eggs in Biscayne Bay, Florida, and Castro and Cowen (1991) estimated that the

egg and yolk-sac larvae experienced a mean mortality of 88% d^{-1} in Great South Bay, New York.

Mortality rates of older bay anchovy larvae apparently decline but still remain high. Leak and Houde (1987) estimated rates throughout the larval stage of 0.30 to 0.45 d^{-1} and Castro and Cowen (1991) estimated rates in the range 0.24 to 0.48 d^{-1}. Loos and Perry (1991) showed that larval mortality rates declined continuously with increasing size for bay anchovy in a subestuary of the Chesapeake Bay. Larvae <3.0 mm length (<2 days posthatch) died at rates in excess of 0.50 d^{-1}, rates similar to our mesocosm estimates and to those of Dorsey (1993) in the Chesapeake Bay proper. Loos and Perry (1991) found that larvae >10 days old had mortality rates <0.20 d^{-1}. It is interesting to note that Cowan and Houde (1990) estimated a mean mortality rate from hatching until 16-22 days posthatch of only 0.16 d^{-1} for bay anchovy larvae, based upon eggs stocked in moored mesocosms deployed in a raft near the mouth of the Patuxent River. They had excluded gelatinous predators from those mesocosms and suggested that the low mortality rates were a consequence of low predation risk, a result in accord with other mesocosm experiments in which predators were excluded (e.g. Øiestad 1990).

It was difficult to show that the two major gelatinous predators were responsible for a significant fraction of the mortality that occurred in the drifting mesocosms. Cowan and Houde (1992, 1993), based upon results from mesocosm experiments on a moored raft and upon encounter rate modeling, had predicted that 20-40% of the bay anchovy egg and larvae population could be consumed daily by the usual abundances of the ctenophore and the scyphomedusa in Chesapeake Bay. Our application of the encounter rate model to the numbers of anchovy eggs and larvae, and the gelatinous predator numbers and sizes in the drifting mesocosm experiments during 1991, indicated that mean mortalities of 18% (eggs) and 14% (larvae) from ctenophore and scyphomedusa predation could be expected Baywide, and that 29% (eggs) to 39% (larvae) might die from predation by the jellyfish in areas of the Bay where the two gelatinous predators occurred. In another concurrent set of experiments in 1991, Purcell et al. (1993) showed that approximately 40% d^{-1} egg mortality and 36% d^{-1} larval mortality could have been caused by the two gelatinous predators during the experimental period, based upon stomach analysis and digestion rate determinations. In addition, Purcell et al. (1993) estimated that 33 and 36% of the total egg and larvae mortalities, respectively, were attributable to combined predation by the two jellyfishes.

We were unable to show statistically significant relationships between gelatinous predator abundances or biovolumes and the estimated mortality rates of anchovy early life stages under the conditions of these experiments. This outcome resulted in part from the high variability in initial numbers of eggs or larvae in each mesocosm. Initial abundances could only be estimated from the mean abundances in the pair of mesocosms harvested at the beginning of each experimental deployment. A better design will be necessary in future experiments to more precisely estimate initial mean abundances and the mean abundances at each time that mesocosms are harvested. At this time, we do not know the best way to index predator numbers or volumes with respect to their predation potential in the mesocosms. There can be a mix of predator types, sizes and numbers in the mesocosms that will affect estimates of predator and prey swimming speeds and encounter rates, and susceptibilities of

eggs and larvae in complex ways that are not presently appreciated.

Predators in addition to the ctenophore and scyphomedusa have not been considered here, but other invertebrates and fishes also are potentially important. We unintentionally enclosed fish (adult bay anchovy and atherinids) occasionally in our deployments of the drifting mesocosms. Fish are potential consumers of bay anchovy eggs and larvae (Cowan and Houde 1993). Invertebrates such as amphipods, isopods and predaceous copepods are enclosed in the mesocosms but to date their predation potentials have not been evaluated. Cowan et al. (1992b) found that the small ($\leq$10 mm diam) hydromedusa Nemopsis bachei was an effective predator on eggs of black drum (Pogonias cromis) in moored mesocosm experiments carried out in Chesapeake Bay. At times, N. bachei might be a significant predator on bay anchovy eggs but it was uncommon during our research and only a few specimens were enclosed in the mesocosms. Finally, we have not considered possible consumption of fish eggs and larvae by $<$10 mm length individuals of the ctenophore, M. leidyi. Potential predation by such small ctenophores, which can be extremely abundant, was not accounted for in our mesocosm experiments.

Fish eggs and larvae are relatively uncommon components of the plankton and enclosed volumes of 3.2 m^3 are a relatively small and potentially highly variable sample of the sea. In future applications on fish eggs and larvae, more replications will be required to estimate initial abundances and to estimate abundances at each succeeding harvest. This will allow more precise estimates of means and rates. It is easily feasible to double the number of deployments. Each mesocosm takes approximately 7-10 min to deploy. An array of 6 drifting mesocosms, plus the two that were harvested immediately to initialize abundances, required 2 h to deploy in the 1991 experiments. At current prices, each mesocosm unit plus its raft and all hardware costs $770 U.S. A doubling of effort is affordable and an array of 12 mesocosms could be deployed within a 4-h period. Our preliminary analysis of variability in abundances of eggs and larvae, and of sample sizes required to have reasonable confidence in detecting differences among experiments in mean abundances, mortality, or the potential effects of predators, suggests that this level of effort would be sufficient for an abundant species such as bay anchovy.

Another potential solution to the sampling problem is to increase mesocosm size. Mesocosms up to 1.5 m diam and of 8-10 m^3 capacity could be deployed from many research vessels, although securing the mesocosm into its raft will become a significant problem as mesocosm size increases. Deployments of mesocosms of variable sizes could be carried out to address scaling issues, although it seems unlikely that mesocosms of volumes much less than those described here would be useful for experiments on fish early life stages. On the other hand, smaller units might be very acceptable to assay the dynamics and interactions of the smaller and more abundant components of plankton communities.

REFERENCES

Bailey, K.M. and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1-83.

Castro, L. and R.K. Cowen. 1991. Environmental factors affecting the early life history of bay anchovy Anchoa mitchilli in Great South Bay, New York. Mar. Ecol. Prog. Ser. 76:235-247.

Cowan, J.H., Jr., R.S. Birdsong, E.D. Houde, J.S. Proest, W.C. Sharp and G.B. Mateja. 1992. Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. Estuaries 15:392-402.

Cowan, J.H., Jr. and E.D. Houde. 1990. Growth and survival of bay anchovy (Anchoa mitchilli) larvae in mesocosm enclosures. Mar. Ecol. Prog. Ser. 68:47-57.

Cowan, J.H., Jr. and E.D. Houde. 1992. Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae and planktivorous fish. Fish. Oceanogr. 1:113-126.

Cowan, J.H., Jr. and E.D. Houde. 1993. The relative predation potentials of scyphomedusae, ctenophores, and planktivorous fish on ichthyoplankton in Chesapeake Bay. Mar. Ecol. Prog. Ser. 95:55-65.

Cowan, J.H., Jr., E.D. Houde and K.A. Rose. 1992. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. Int. Council Explor. Sea, C.M. 1992/L:32. 17 pp.

Dalton, P. 1987. Ecology of Anchoa mitchilli eggs and larvae in the mid-Chesapeake Bay. M.S. Thesis, Univ. Maryland, College Park. 104 pp.

deLafontaine, Y. and W.C. Leggett. 1987a. Evaluation of in situ enclosures for larval fish studies. Can. J. Fish. Aquat. Sci. 44:54-65.

deLafontaine, Y. and W.C. Leggett. 1987b. Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish. Can. J. Fish. Aquat. Sci. 44:1534-1543.

deLafontaine, Y. and W.C. Leggett. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Can. J. Fish. Aquat. Sci. 45:1173-1190.

Dorsey, S.E. 1993. Daily variability in mortality of bay anchovy (Anchoa mitchilli) eggs and yolk-sac larvae in Chesapeake Bay, USA. M.S. Thesis, Univ. Maryland, College Park. 109 pp.

Feigenbaum, D. and M. Kelly. 1984. Changes in the lower Chesapeake Bay food chain in the presence of the sea nettle Chrysaora quinquecirrha (scyphomedusa). Mar. Ecol. Prog. Ser. 19:39-47.

Frank, K.T. and W.C. Leggett. 1986. Effect of prey abundance and size on the growth and survival of larval fish: An experimental study employing large volume enclosures. Mar. Ecol. Prog. Ser. 34:11-22.

Fuiman, L.A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. Mar. Ecol. Prog. Ser. 51:291-299.

Fuiman, L.A. and J.C. Gamble. 1988. Predation by Atlantic herring, sprat and sand eels on herring larvae in large enclosures. Mar. Ecol. Prog. Ser. 44:1-6.

Fuiman, L.A. and J.C. Gamble. 1989. Influence of experimental manipulations on predation of herring larvae by juvenile herring in large enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer 191:359-365.

Gamble, J.C., J.M. Davies and J.H. Steele. 1977. Loch Ewe bag experiment, 1974. Bull. Mar. Sci. 27(1):146-175.

Gamble, J.C. 1985. More space for the sparsely distributed: an evaluation of the use of large enclosed experimental systems in fish larval research. Int. Counc. Explor. Sea, C.M. 1985/Mini-Symp. 2:1-13.

Gamble, J.C. and S.J. Hay. 1989. Predation by the scyphomedusan Aurelia aurita on herring larvae enclosures: effects of predator size and prey starvation. Rapp. P.-v. Réun. Cons. int. Explor. Mer 191:366-375.

Govoni, J.J. and J.E. Olney. 1991. Potential predation on fish eggs by the lobate ctenophore Mnemiopsis leidyi within and outside the Chesapeake Bay plume. Fish. Bull., U.S. 89:181-186.

Houde, E.D. 1985. Mesocosms and recruitment mechanisms. Int. Council Explor. Sea, C.M. 1985/Mini-Symposium/No. 4. 12 pp. plus 2 tables and 1 figure.

Houde, E.D. and C.E. Zastrow. 1991. Bay anchovy. pp. 8-1 to 8-14. In: Funderburk, S.L., J.A. Mihursky, S.J. Jordan and D. Riley (eds.), Habitat requirements for Chesapeake Bay Living Resources, 2nd Edition. Living Resources Subcommittee, Chesapeake Bay Program. Annapolis, MD.

Laurence, G.C., T.A. Halavik, B.R. Burns and A.S. Smigielski. 1979. An environmental chamber for monitoring "in situ" growth and survival of larval fishes. Trans. Am. Fish. Soc. 108:197-203.

Leak, J.C. and E.D. Houde. 1987. Cohort growth and survival of bay anchovy Anchoa mitchilli larvae in Biscayne Bay, Florida. Mar. Ecol. Prog. Ser. 37:109-122.

Litvak, M.K. and W.C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. 81:13-24.

Loos, J.J. and E.S. Perry. 1991. Larval migration and mortality rates of bay anchovy in the Patuxent River. NOAA Tech. Rept., NMFS 95.

Luo, J. and J. Musick. 1991. Reproductive biology of the bay anchovy in Chesapeake Bay. Trans. Am. Fish. Soc. 120:701-710.

Øiestad, V. 1982. Application of enclosures to studies on the early life history of fishes. pp. 49-62, In: Grice, G.D., M.R. Reeve (eds.), Marine mesocosms, biological and chemical research in experimental systems. Springler-Verlag, New York.

Øiestad, V. 1985. Predation on fish larvae as a regulatory force, illustrated in mesocosm studies with large groups of larvae. NAFO Sci. Counc. Stud. 8:25-32.

Øiestad, V. 1990. Specific applications of meso- and macrocosms for solving problems in fisheries research. pp. 136-154, In: Lalli, C.M. (ed.), Enclosed experimental marine ecosystems: a review and recommendations. Coastal and Estuarine Studies 37. Springer-Verlag: New York, Berlin, Heidelberg.

Olney, J.E. 1983. Eggs and early larvae of the bay anchovy, Anchoa mitchilli, and the weakfish, Cynoscion regalis, in lower Chesapeake Bay with notes on associated ichthyoplankton. Estuaries 6:20-35.

Owens, N.J.P., E.M.S. Woodward, R.K. Chivers, P.J. Willerton, R.F.C. Mantoura and P.H. Burkill. 1985. A portable mesocosm for use in offshore and oceanic studies. Int. Council Explor. Sea, C.M. 1985/Mini-Symposium Poster No. 18.

Pepin, P., T.H. Shears and Y. deLafontaine. 1992. Significance of body size to the interaction between a larval fish (Mallotus villosus) and a vertebrate predator (Gasterosteus aculeatus). Mar. Ecol. Prog. Ser. 81:1-12.

Purcell, J.E. 1985. Predation on fish eggs and larvae by pelagic cindarians and ctenophores. Bull. Mar. Sci. 37:739-755.

Purcell, J.E. 1992. Effects of predation by the scyphomedusan Chrysaora quinquecirrha on zooplankton populations in Chesapeake Bay, USA. Mar. Ecol. Prog. Ser. 87:65-76.

Purcell, J.E., D.A. Nemazie, S. Dorsey, J.C. Gamble and E.D. Houde. 1993. In situ predation rates on bay anchovy eggs and larvae by scyphomedusae and ctenophores in Chesapeake Bay, USA. Int. Council Explor. Sea, C.M. 1993/L:42, Sess. S.

Zastrow, C.E., E.D. Houde and L.G. Morin. 1991. Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy Anchoa mitchilli in mid-Chesapeake Bay. Mar. Ecol. Prog. Ser. 73:161-171.

Table 1. Chesapeake Bay drifting mesocosm experiments, 1989 and 1991. Summary data from mesocosms on dates, locations, bay anchovy egg and larvae instantaneous mortality rates, gelatinous zooplankton mean numbers and volumes per 3.2 m^3 mesocosm. Standard errors of estimates are given in parentheses. Locations are illustrated in Figure 1. Location A = York River area. Location B = Potomac River area. Location C = Cove - Cedar Point areas. Location D = Pt. No Pt. area. * = significant at 0.05 level. ** = significant at 0.01 level.

Experiment	Date	Location	Instantaneous Mortality Rates (h^{-1})		Gelatinous Zooplankton in Mesocosms			
					Ctenophore		Scyphomedusa	
			Eggs	Larvae	Mean No.	Mean Vol. (ml)	Mean No.	Mean Vol. (ml)
89-1-1	5 July 1989	Patuxent River mouth	0.1564** (0.0136)	0.1020 (0.1082)	0.38	2.05	0.38	1.72
89-1-2	6 July 1989	Patuxent River mouth	0.1025** (0.0197)	+0.0001 (0.0221)	0.00	0.00	2.00	72.79
89-1-3	7 July 1989	Patuxent River mouth	0.0776* (0.0240)	+0.0034 (0.0254)	5.50	34.05	0.38	0.63
89-2-1	18 July 1989	Patuxent River mouth	0.0434** (0.0100)	+0.0644 (0.0566)	7.50	81.02	0.13	0.66
89-2-2	19 July 1989	Patuxent River mouth	0.0592 (0.0454)	0.1019 (0.0145)	14.29	138.64	0.14	1.86
89-2-3	20 July 1989	Patuxent River mouth	0.1008** (0.0254)	0.1261 (0.0546)	6.88	67.03	0.25	0.15
1989 Means			0.0900 (0.0163)	0.0437 (0.0313)	5.76	53.80	0.54	12.97
91-1-1	3 July 1991	A	0.0454** (0.0078)	0.0554 (0.0555)	0.00	0.00	0.00	0.00
91-1-2	4 July 1991	A	0.0306 (0.0285)	0.0538 (0.0474)	0.00	0.00	0.00	0.00
91-1-3	5 July 1991	A	0.0669** (0.0116)	0.1770* (0.0391)	0.00	0.00	0.00	0.00

Table 1. (Continued).

Experiment	Date	Location	Instantaneous Mortality Rates (h^{-1})		Gelatinous Zooplankton in Mesocosms			
					Ctenophore		Scyphomedusa	
			Eggs	Larvae	Mean No.	Mean Vol. (ml)	Mean No.	Mean Vol. (ml)
91-1-4	7 July 1991	B	0.0410 (0.0197)	0.0231 (0.0211)	10.50	133.38	0.50	13.50
91-1-5	8 July 1991	B	0.0496** (0.0057)	+0.0632 (0.0315)	8.62	118.63	1.13	3.88
91-2-1	18 July 1991	C	0.0640** (0.0172)	0.0706** (0.0140)	0.12	2.50	0.25	5.00
91-2-2	19 July 1991	C	0.0565** (0.0176)	0.0997 (0.0399)	0.63	18.63	0.75	7.88
91-2-3	20 July 1991	D	0.1167** (0.0202)	0.0897 (0.0385)	0.43	7.43	1.86	40.14
91-2-4	21 July 1991	D	0.1542** (0.0153)	+0.0109 (0.0350)	0.63	19.00	0.88	19.25
91-2-5	22 July 1991	D	0.0371* (0.0149)	0.0586 (0.0299)	0.00	0.00	0.75	33.88
91-2-6	23 July 1991	D	0.0481* (0.0127)	0.0802 (0.0268)	0.00	0.00	0.84	31.48
1991 Means			0.0646 (0.0113)	0.0576 (0.0186)	1.90	27.23	0.63	14.09
1989 and 1991 Combined Means			0.0735 (0.0095)	0.0527 (0.0159)	3.26	36.61	0.60	13.69

Table 2. Drifting mesocosm experiments, 1991. Mortality rates of bay anchovy eggs in four experiments in which two scyphomedusae were added to one of each pair of mesocosms. Mortality rates are compared in mesocosms with and without the added scyphomedusae. * = significant at 0.05 level. ** = significant at 0.01 level.

Experiment	Date	Instantaneous Mortality Rates (h^{-1})	
		Without Additional Scyphomedusae	With Two Scyphomedusae Added
91-2-3	20 July 1991	0.1213**	0.1151*
91-2-4	21 July 1991	0.1393**	0.1666**
91-2-5	22 July 1991	0.0344	0.0450
91-2-6	23 July 1991	0.0570*	0.0555
Mean		0.0880	0.0955
Standard Error		0.0251	0.0283

Table 3. Area-specific summaries of drifting mesocosm experiments, 1991. Summary statistics of bay anchovy egg and larvae mean mortality rates (Z) in four areas of the Chesapeake Bay (Figure 1). Numbers in parentheses are mortality rates estimated from ichthyoplankton surveys on the same dates (Dorsey 1993).

Experiment	Date	Location	Eggs		Larvae	
			Z (h^{-1})	S.E.	Z (h^{-1})	S.E.
91-1-1	3 July	A	0.0476	0.0105	0.1081	0.0341
91-1-2	4 July		(0.0410)		(0.0597)	
91-1-3	5 July					
91-1-4	7 July	B	0.0453	0.0043	+0.0294	0.0319
91-1-5	8 July		(0.0555)		(0.0970)	
91-2-1	18 July	C	0.0602	0.0038	0.0863	0.0118
91-2-2	19 July		(0.0615)		(0.0290)	
91-2-3	20 July		0.0890	0.0280	0.0529	0.0218
91-2-4	21 July	D	(0.0613)		(0.0450)	
91-2-5	22 July					
91-2-6	23 July					

Table 4. Predation-induced (via ctenophores and scyphomedusae) mortality rates of bay anchovy eggs and larvae predicted from an individual-based, encounter rate model, compared with the estimated mortality rates in drifting mesocosm experiments that included gelatinous predators, Chesapeake Bay, 1991. Experiment summary statistics are given in Table 1. The encounter rate model is described by Cowan and Houde (1992) and Cowan et al. (1992). A = Model-Predicted, predation-induced Z, h^{-1}. B = Mesocosm-Estimated Z, h^{-1}.

EGGS

Experiment	A	B	A/B
91-1-4	0.029	0.041	0.71
91-1-5	0.021	0.050	0.42
91-2-1	0.003	0.064	0.05
91-2-2	0.007	0.056	0.13
91-2-3	0.022	0.117	0.18
91-2-4	0.018	0.154	0.12
91-2-5	0.018	0.037	0.49
91-2-6	0.012	0.048	0.26
Mean	0.016	0.071	0.29
Standard Error	0.003	0.015	0.08

LARVAE

Experiment	A	B	A/B
91-1-4	0.019	0.023	0.84
91-1-5	0.020	0.063	0.31
91-2-1	0.004	0.071	0.05
91-2-2	0.007	0.100	0.07
91-2-3	0.020	0.090	0.23
91-2-4	0.013	0.011	1.17
91-2-5	0.015	0.059	0.26
91-2-6	0.014	0.080	0.18
Mean	0.014	0.062	0.39
Standard Error	0.002	0.011	0.14

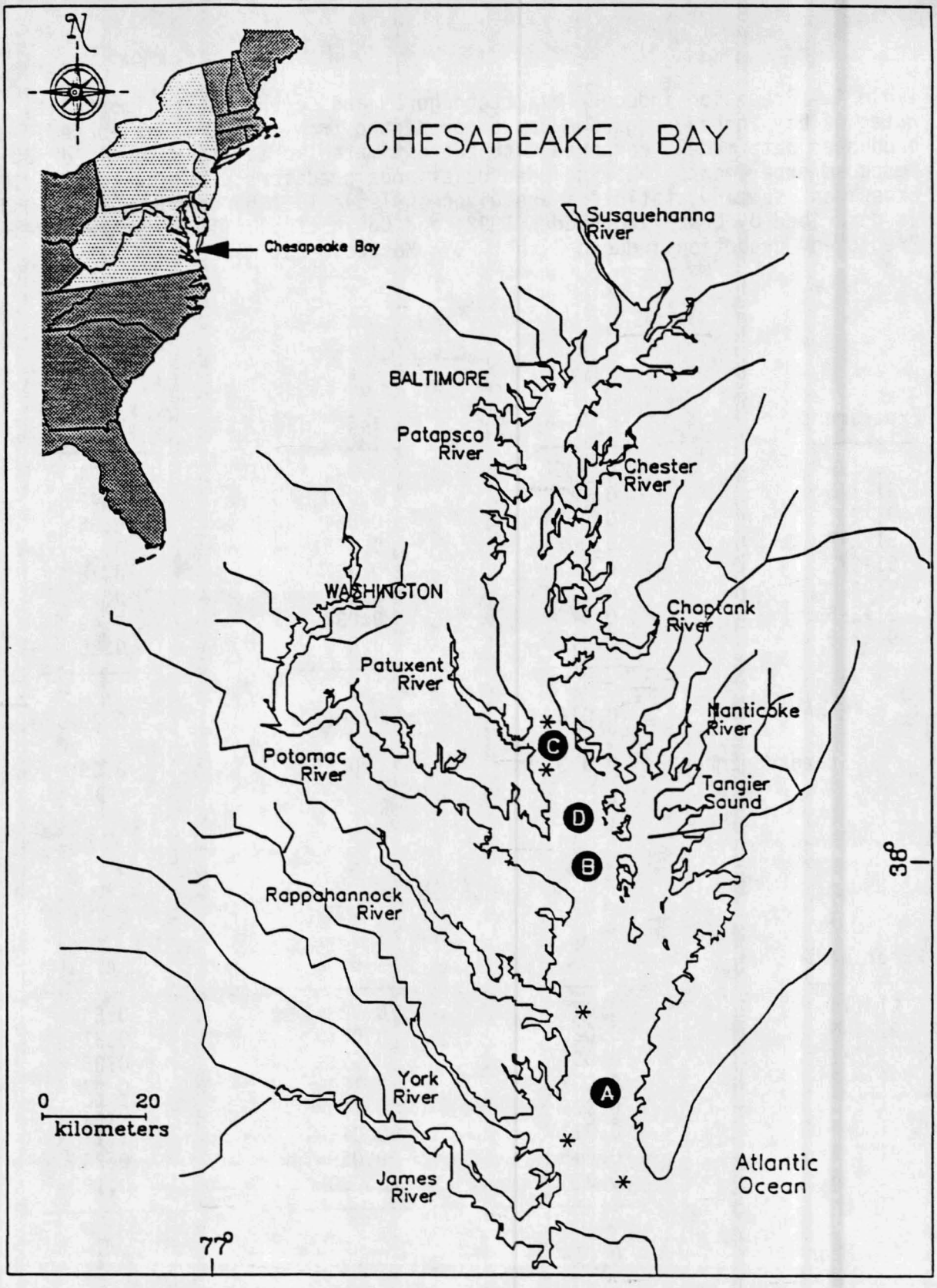

Figure 1. Map of Chesapeake Bay showing drifting mesocosm experimental sites and areas, 1989 and 1991. All of the 1989 experiments were carried out within 10 km of the area designated C. The three experimental sites in area A and two experimental sites in area C during 1991 are designated by asterisks. Two experiments were run in area B and four in area D during 1991.

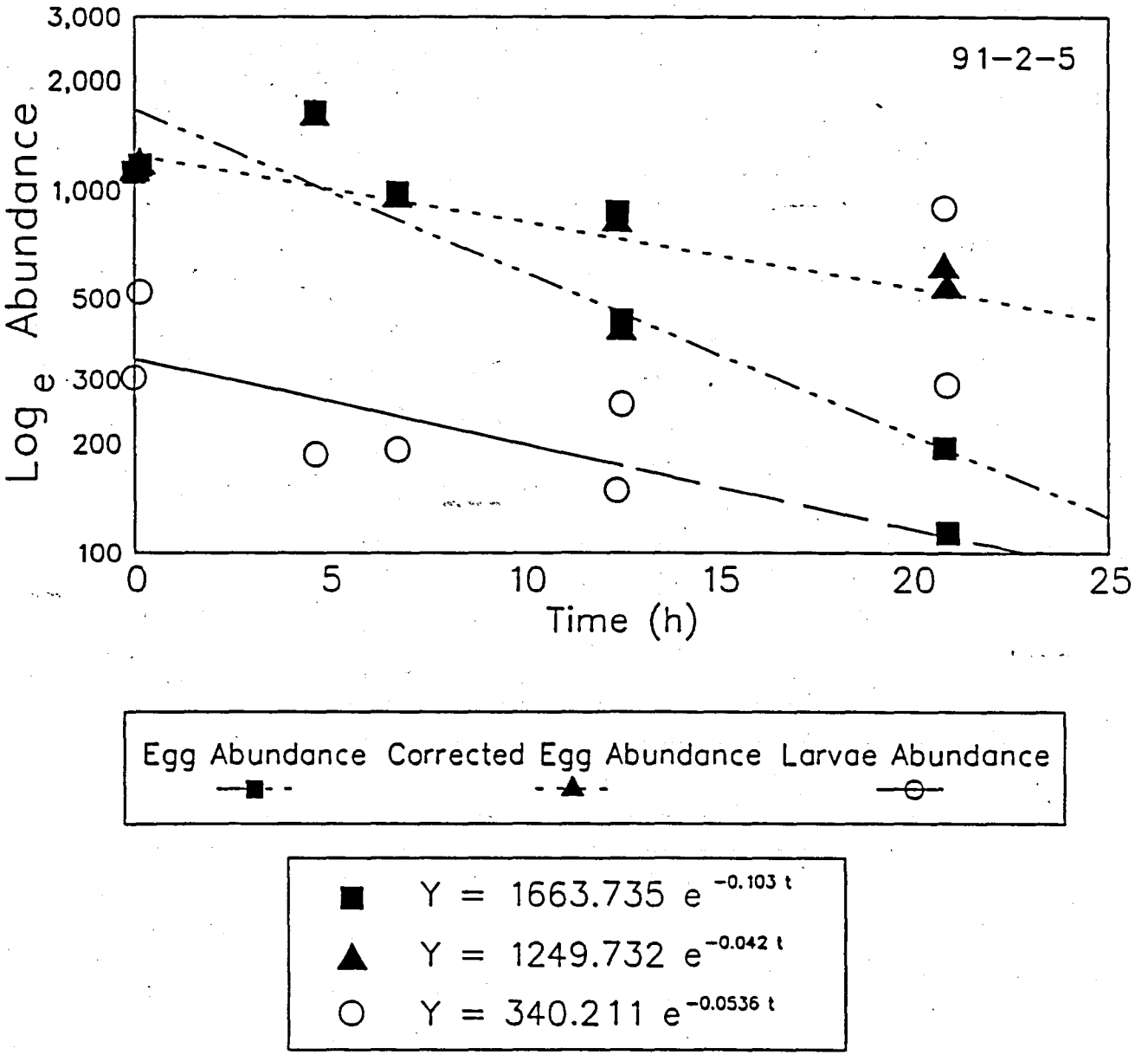

Figure 2. Example of adjustment procedure to correct egg abundances. Unadjusted and adjusted egg abundances in mesocosm experiment 91-2-5 (see Table 1). The adjustment corrects egg numbers to account for hatching of eggs at time >20 h and for nonviable eggs (mean value of 0.0052 h^{-1} in 1991 and variable values in 1989). The equation to describe decline in larval abundance is fitted only to data <20 h after time 0. The difference between mean observed larval abundance and predicted abundance (from the equation) at observation times >20 h is the adjustment factor that estimates the number of eggs which hatched into larvae.

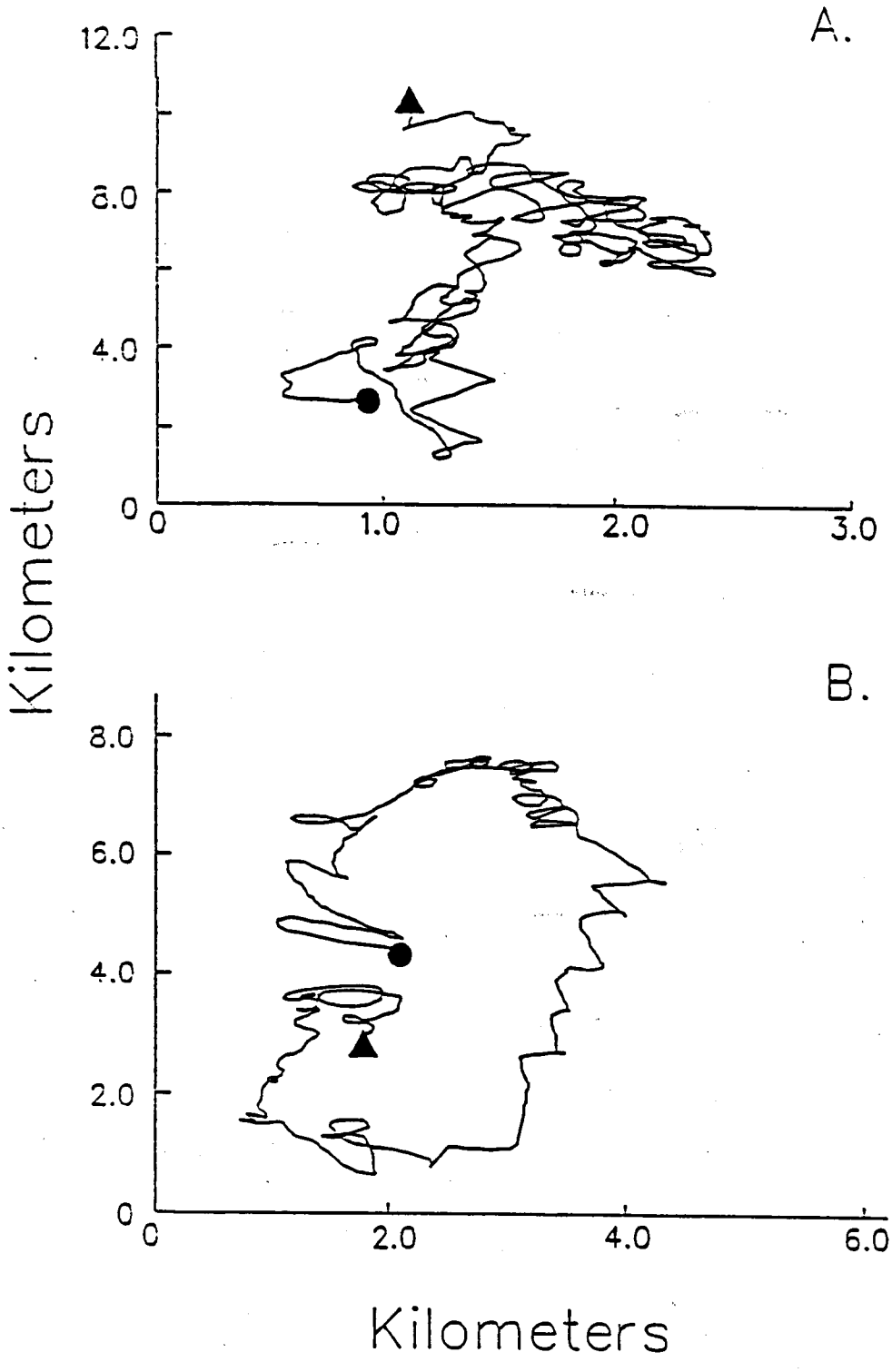

Figure 3. Two examples of mesocosm-array drift tracks, 1991. ● -- start. ▲ -- end.

A. Experiment 91-2-2, 19 July 1991. This experiment was carried out in area C and is designated by the asterisk south of C on Figure 1.

B. Experiment 91-1-3, 5 July 1991. This experiment was carried out in area B at the mouth of the Rappahannock River (Figure 1).

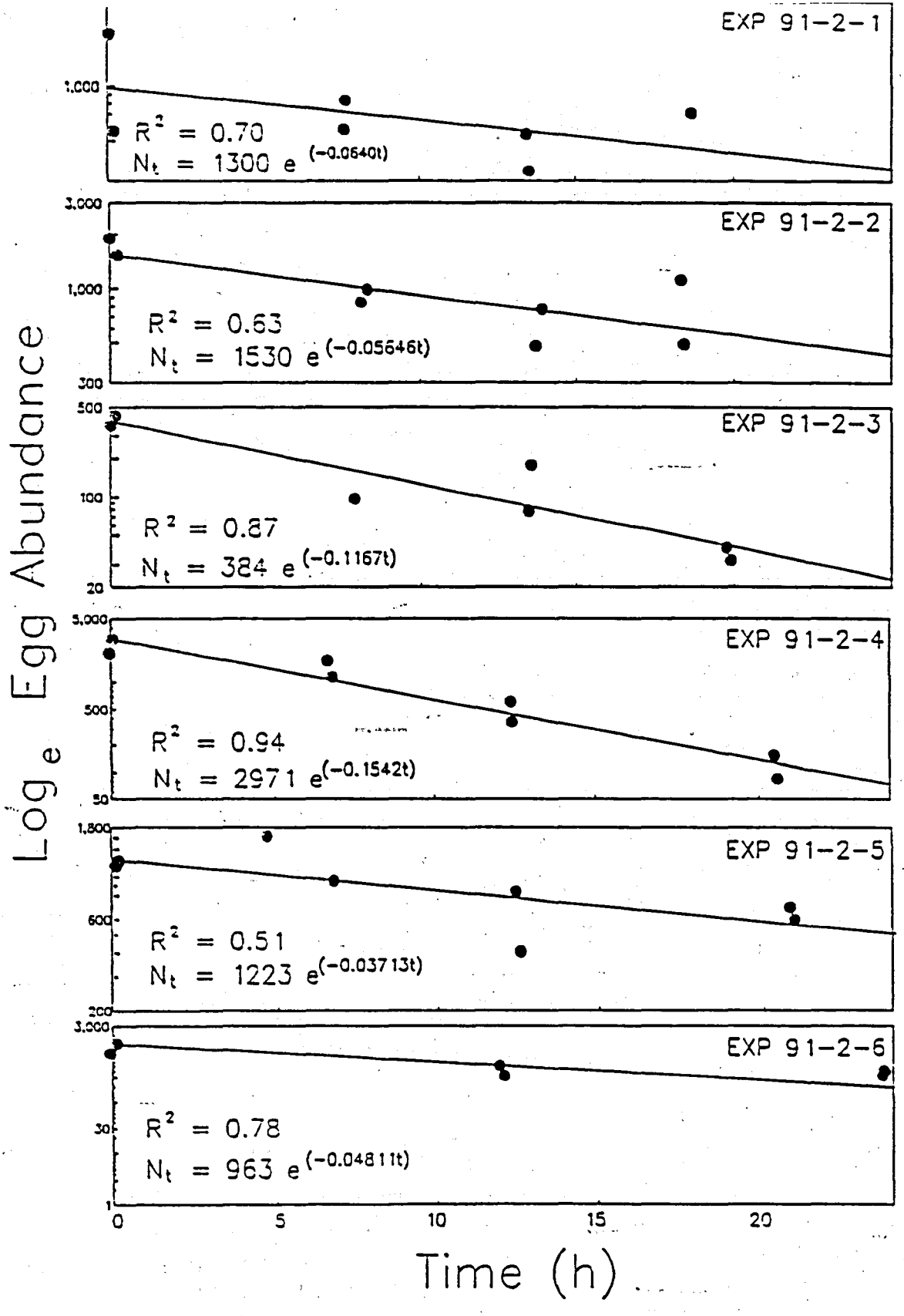

Figure 4. Egg mortality rates, 1991. Adjusted egg abundances (number per mesocosm) and exponential models describing declines in abundances over time for six drifting mesocosm experiments in 1991. Experiment locations, dates, and summary statistics are given in Table 1.

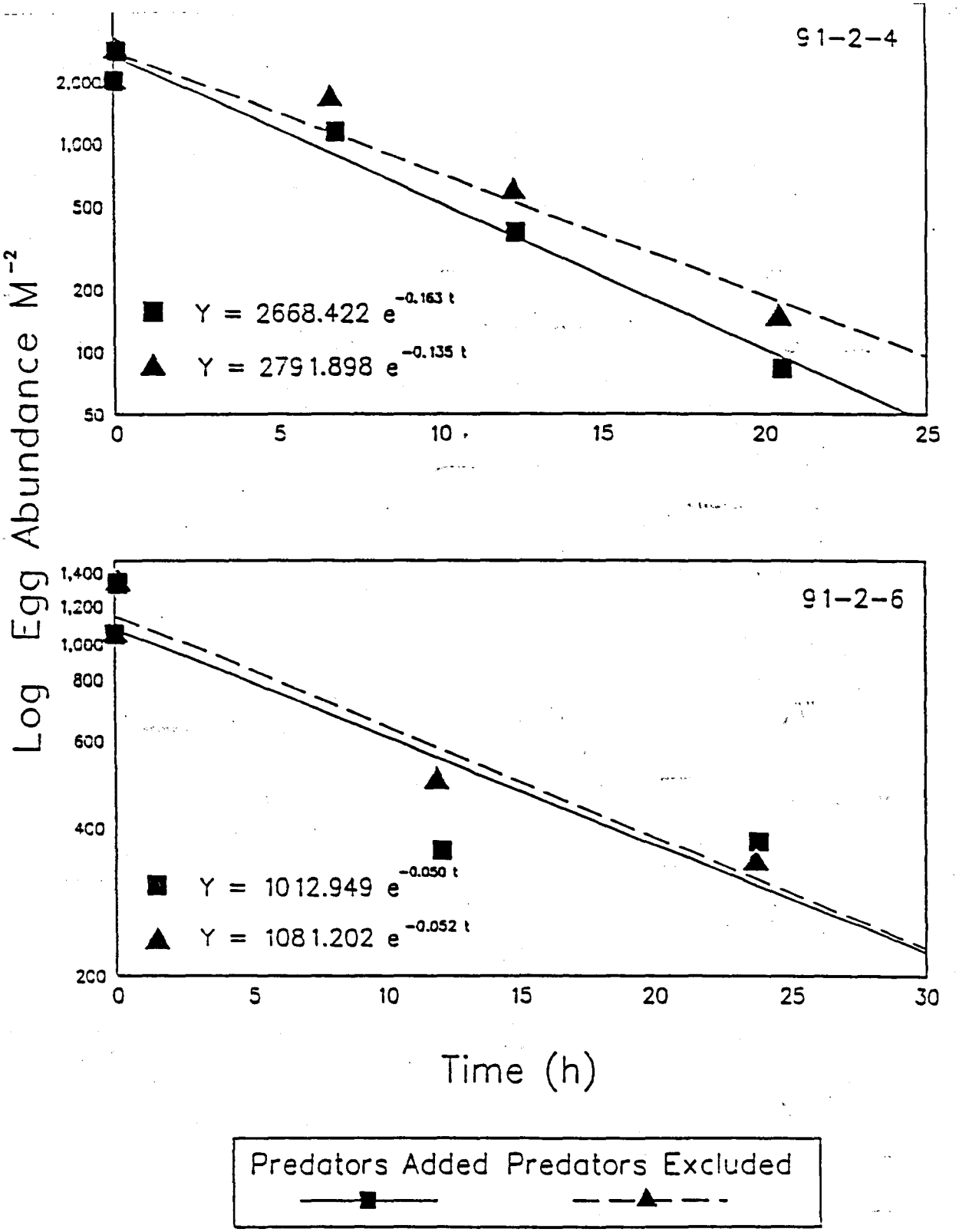

Figure 5. Egg mortality rates. A comparison of the declines in egg abundances in pairs of mesocosms; one of each pair received two added scyphomedusae predators at the time the experiment began. Equations describe the declines in abundance in each case.

A. Experiment 91-2-4, 21 July 1991, area D (Figure 1).

B. Experiment 91-2-6, 23 July 1991, area D (Figure 1).

An apparent increase in mortality is observed in 5A but not in 5B.