1997

Potential For Population Regulation Of The Zebra Mussel By Finfish And The Blue Crab In North American Estuaries

Larry C. Boles
Virginia Institute of Marine Science

Rom Lipcius
VIMS

Journal of Shellfish Research, Vol. 16, No. 1, 179–186, 1997.

POTENTIAL FOR POPULATION REGULATION OF THE ZEBRA MUSSEL BY FINFISH AND THE BLUE CRAB IN NORTH AMERICAN ESTUARIES

LARRY C. BOLES* AND ROMUALD N. LIPCIUS
Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

ABSTRACT We conducted a series of descriptive and manipulative experiments aimed at quantifying the abundance, natural mortality, and effectiveness of predators in controlling the zebra mussel, *Dreissena polymorpha*, in the Hudson River Estuary. First, we measured distribution, abundance, and mortality rates of a zebra mussel population in the middle portion of the Hudson River Estuary, NY. Rocks were collected along a depth gradient in the field and sampled for the density and size structure of the resident mussels over the growth season. Next, we either allowed access (controls) or denied access (predator exclusion) to predators in field experiments with rocks harboring a known number of zebra mussels to estimate natural mortality. Finally, we conducted manipulative field experiments to test the effectiveness of the blue crab, *Callinectes sapidus*, at consuming zebra mussels by presenting similar rocks to crabs in field enclosures. Field sampling in June, July, and August 1993 indicated a dense (~30,000 mussels/m^2) population composed of a single cohort of 1 + year-class mussels. Sampling in August 1994 indicated a decline in *D. polymorpha* density. Mussel density increased dramatically with depth less than 2 m below the spring low tide mark. In cage experiments, blue crabs caused mortality rates that were an order of magnitude higher than those measured for the local predator guild, which was primarily composed of finfish. Localized extinctions of zebra mussels within one growth season were predicted in areas where blue crab densities approach 0.1 crabs/m^2.

KEY WORDS: Zebra mussel, blue crab, population regulation, predation

INTRODUCTION

Predation can regulate community structure and the dynamics of marine benthic species (Peterson 1979, Paine 1980). Predator-prey interactions in marine systems are particularly complex and may be relatively stable because they are dominated by guilds of generalist predators capable of switching among numerous prey species (Peterson 1979, Hines et al. 1990). The abundances of such generalist predators are not coupled to their benthic prey and, therefore, are capable of controlling the dynamics of these prey species or driving them to local extinction without being dependent on any single species for their persistence. (Murdoch et al. 1985). Generalist predators have long been cited as regulators of population structure in the classic studies of the marine intertidal zone (Connell 1970, Paine 1974). In this setting, a successful predator may prevent the establishment of or destroy monoculture of a competitively dominant species (Paine 1992). The varied nature of the predator's diet is necessary for it to persist during periods of low abundance of the dominant prey species. Such features potentially characterize predator-prey interactions between the exotic zebra mussel, *Dreissena polymorpha* (Pallas), and natural predators such as the blue crab, *Callinectes sapidus* (Rathbun), and thereby provide the requisite conditions for predator-mediated control of *D. polymorpha* population dynamics.

The zebra mussel was first discovered in the Hudson River in 1991 and has since expanded to its salinity limit (3–6 ppt) near Haverstraw, NY (Strayer et al. 1993). The rapid colonization of North American waters has been facilitated by its high fecundity (30,000 eggs/female per year), a free-swimming larval stage that is unlike that of any native freshwater bivalve, and the apparent lack of effective competitors and predators (Hebert et al. 1991, Lemma et al. 1991, MacIsaac et al. 1991, Strayer 1991). As a consequence, *D. polymorpha* often occurs at densities exceeding 10,000 mussels/m^2 and has thereby become a major and costly nuisance (Cooley 1991, Griffiths et al. 1991). Zebra mussels attached to hard substrates by their byssal fibers form large colonies, which can choke off water intake pipes at power plants and municipal water treatment plants and also produce biofouling problems on boats, navigational aids, and beaches.

Moreover, as a result of its salinity tolerance (up to approximately 5 ppt), the zebra mussel is expected to colonize and expand into most North American waters, including the low-salinity portions of estuaries such as Chesapeake Bay (Bij de Vaate 1991, Strayer 1991, Strayer and Smith 1993). Thus, the potential exists for *D. polymorpha* to become a serious pest throughout its environmentally delineated range in North American waters, unless predation or competition can effectively regulate the zebra mussel in its distribution and abundance.

The blue crab is a large (males up to 227-mm carapace width [CW]), epibenthic omnivore occurring in various habitats along the northwest Atlantic Ocean, Gulf of Mexico, and Caribbean Sea (Williams 1984). Blue crabs serve as both prey and consumers and are abundant and actively forage from late spring through autumn in Chesapeake Bay (Hines et al. 1987, Hines et al. 1990). The diet of Chesapeake Bay blue crabs consists of bivalves, crabs (both blue crabs and xanthids), fish, and polychaetes, and to a lesser extent, amphipods and isopods (Hines et al. 1990, Mansour and Lipcius 1991). Blue crab ecology in the Hudson River has not been well studied, and consequently, the abundance and range of the species within the system are not understood. Previous research has shown that *C. sapidus* is common in the freshwater and low-salinity regions of the estuary in some years (Stein and Wilson 1992). Strayer et al. (1993) reported that blue crabs in the Hudson River included zebra mussels in their diet. Laboratory experiments demonstrated that adult male blue crabs readily consumed zebra

*Corresponding address: Department of Biology, CB#3280, University of North Carolina, Chapel Hill, NC 27599-3280.

mussels and preferred the largest individuals available (Molloy et al. 1994).

In this investigation, we quantified abundance patterns and natural mortality rates of *D. polymorpha* in the field and tested the hypothesis that predation by *C. sapidus* and naturally occurring finfish predators might serve to limit the zebra mussel in the Hudson River Estuary and in other North American estuaries. We conducted quantitative sampling and a series of field experiments in Hudson River freshwater habitats to determine limitations imposed by finfish and the blue crab on zebra mussel abundance and distribution. Further trials compared the effectiveness of the blue crab and the local predator guild (primarily, finfish species) in controlling zebra mussel abundance. The specific objectives of the investigation included: (1) a description of *D. polymorpha* abundance and distribution, (2) measurement of natural mortality of *D. polymorpha* and identification of likely predators, and (3) testing the feasibility of biological control of *D. polymorpha* by *C. sapidus* and finfish in the Hudson River.

METHODS

Study Site

We conducted field experiments and collected samples on the eastern shore of the Hudson River in the Tivoli Bays Region of the Hudson River National Estuarine Research Reserve, NY (42°05′N, 73°55′W) (Fig.1). The tidal freshwater habitat was approximately 160 km north of the mouth of the estuary. In this region, the benthic environment of the Hudson was characterized by large stones and cobbles covering a steeply sloping bottom that reached over 20-m depths in some areas. The tidal range was approximately 1.0 m, and underwater visibility was poor (<3 m) during the study periods because of suspended particles.

Zebra Mussel Sampling

In the first component of this study, rocks were sampled by SCUBA divers during June, July, and August 1993, and again in August 1994, to examine the density and size structure of the zebra mussel population. Divers collected rocks haphazardly by hand at depths ranging from 3 to 20 m during the four sampling periods. Rocks with attached mussels were transported to the laboratory in padded coolers to minimize handling mortality. We estimated zebra mussel density on each rock by removing all live individuals that fell within a 16-cm^2 plastic grid placed on the rock's surface. Mussels were removed by pulling the byssal fibers from the substrate surface with forceps. These mussels were counted, and their shell lengths were measured to the nearest millimeter with Vernier calipers. Six replicate rock samples were examined during each month of the study, yielding 24 samples during the 1-y period. Mean zebra mussel densities were used to estimate both inter-annual and intra-annual mortality rates. Shell length data were used to construct size-frequency distributions.

We conducted a series of five underwater transects in August 1993 to characterize the depth distribution of *D. polymorpha* at the study site. Four random rock samples were collected using SCUBA along depth profiles to determine density using the same method as above. The four samples at each depth were located along a marked transect line that was positioned by divers. A random number table was used to select the four marks along the line at which a rock would be taken. Densities reflect the average number of animals per area of rock surface, not area of river bottom. At each collection site, a visual estimate of percent coverage was also taken with a haphazardly placed circular grid (25 cm in diameter). Samples were collected along a transect at increasing depths (0.5-m increments) until 100% coverage was observed at all four sample locations. Transects were conducted at 0.5-, 1.0-, 1.5-, 2.0-, and 2.5-m depths. These values were corrected to reflect depth below spring low tide levels using published tide tables.

Field Experiments

The second component of the study involved manipulative field experiments conducted in late July and early August 1993. We first

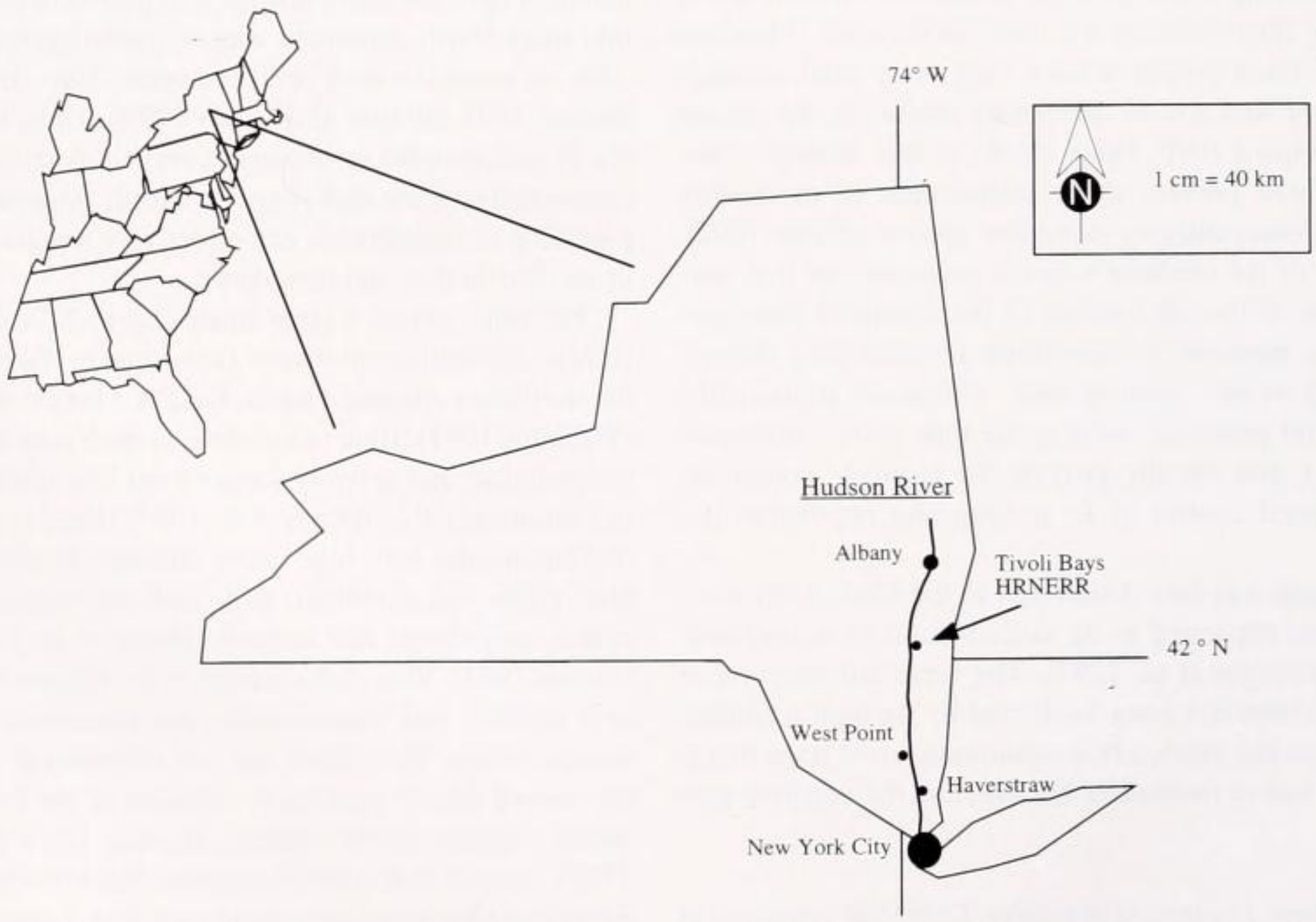

Figure 1. Map of study area in the vicinity of the Hudson River National Estuarine Research Reserve (HRNERR).

measured mortality rates of *D. polymorpha* due to predation. Rocks with attached mussels were collected from the Hudson River by divers and maintained in laboratory aquaria for 72 h to ensure the health of experimental animals. Zebra mussels that actively siphoned water and closed their shells when agitated were considered healthy. After this observation period, mussels were removed from aquaria and placed in dissecting trays. We then began removing mussels from the rock's surface until only 100 live zebra mussels remained attached. Mussels were first removed from the outside surfaces of each rock so that each clump of 100 mussels resembled a naturally occurring cluster. Sixteen of these rocks with 100 attached mussels were then transported back to the field and placed in enclosures for the experiment. Cages were constructed of 2.5-cm plastic mesh, covered 1 m^2 of substrate, and were 0.7 m tall. Sixteen cages were arranged in four rows of four cages, with 1 m spacing between each, and treatments were interspersed (Fig. 2). Each treatment was replicated eight times. Control treatments comprised fully enclosed cages protecting one rock with 100 precounted mussels. Experimental cages were topless, had only two sides, and thus exposed the experimental rock to predation. After 14 days, the rocks were removed from the cages and the surviving mussels were enumerated.

The final experiment used the same field enclosures and another set of rocks with 100 precounted mussels prepared in the same manner. In this trial, 18 interspersed cages were fully enclosed and hard intermolt male blue crabs were introduced as predators (Fig. 3). Six cages contained small crabs (60- to 80-mm CW), and six cages contained large crabs (110- to 130-mm CW). Six cages contained only rocks with 100 precounted mussels and served as controls. After 72 h, crabs were removed and surviving mussels were enumerated. Each blue crab was examined to confirm that it had survived the entire experimental period.

In both field experiments, the proportional mortality of *D. polymorpha* was calculated by subtracting the number of surviving mussels from the original number of mussels and then dividing that result by the original number of mussels. Differences between treatments were analyzed by use of an analysis of variance (ANOVA) model, with arcsine-transformed proportional mortality as the dependent variable and cage treatment as a fixed factor. Scheffe's test was used to examine contrasts among the three treatments in the second field experiment. Data were examined for normality and tested for homogeneity of variance with an F_{max} test. (Sokal and Rohlf 1980).

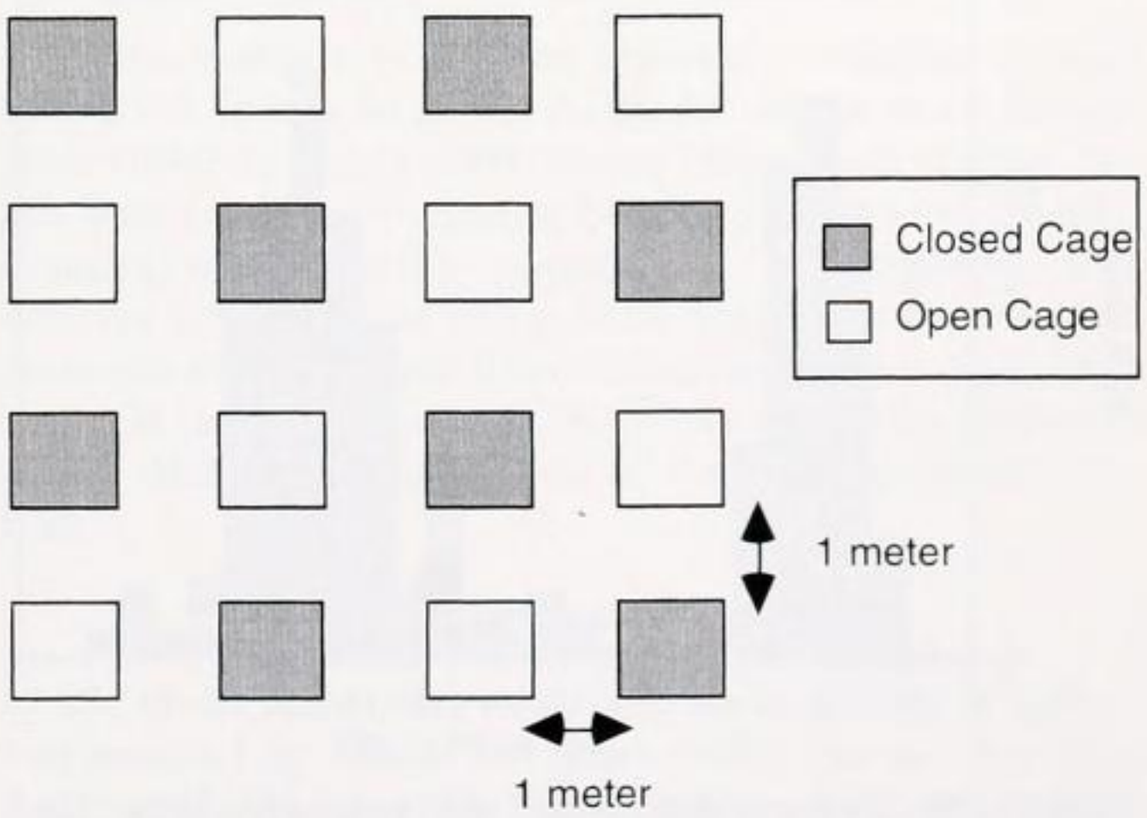

Figure 2. Configuration of cages for the first field experiment.

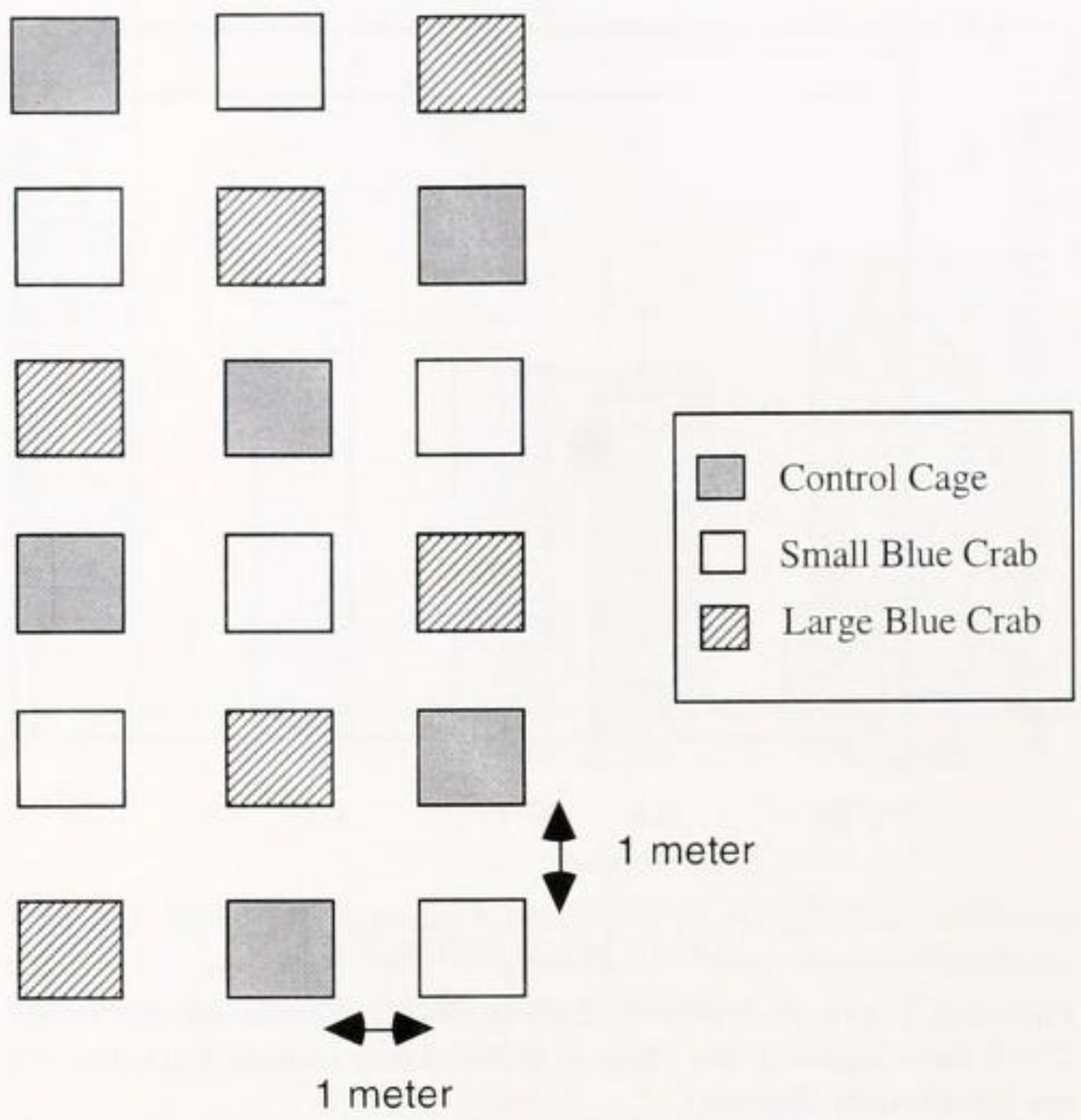

Figure 3. Configuration of cages for the second field experiment.

Instantaneous per capita mortality rates (z) were calculated for each period during the study using the estimated zebra mussel densities. The rate was calculated by:

$$z = \frac{-\ln\left(\frac{Nt}{No}\right)}{t}$$

where the instantaneous rate (z) takes into account the original number of mussels (N_o) and the number of mussels (N_t) surviving some period of time (t). This rate (z) was also used to compare zebra mussel mortality rates from the two caging experiments.

Identification of Potential Predators

We recorded over 8 h of underwater video using a Sony 8-mm video recorder with remote waterproof cameras in August 1994. The remote camera was anchored to the rocky substrate using large concrete bricks and pointed at rocks covered with zebra mussels. Poor underwater visibility limited the camera's field of view to approximately 1 m in all directions but did allow it to capture images of fish swimming along the river's bottom. Whenever possible, we identified these fish to the lowest possible taxonomic level.

Six baited crab pots were also fished near the study site during periods of sampling and field experimentation (June, July, and August 1993 and August 1994). These were checked daily for the presence of blue crabs and rebaited when necessary.

RESULTS

The abundance of zebra mussels rapidly increased with increasing depth and reached constant values less than 2 m below the surface. Samples collected along depth transects beginning at the spring low tide mark indicated a significant effect of depth (Fig. 4; ANOVA, $F = 13.88$ $df = 4,15$, $p < 0.0001$). Abundance at the shallowest depth (0.26 m) was significantly lower than at the four deeper stations (Scheffe's test, critical value = 1.329, $p < 0.05$),

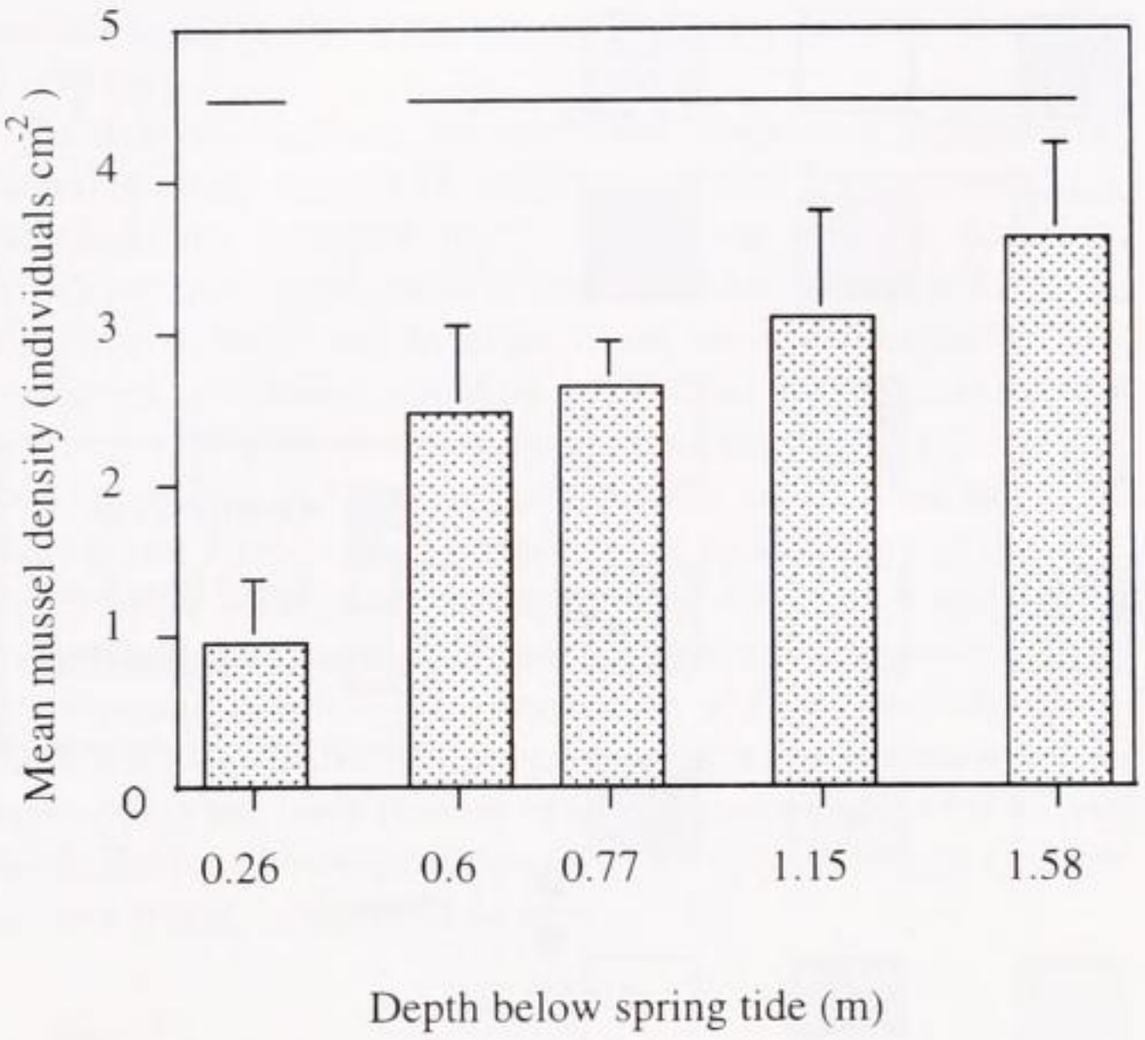

Figure 4. Depth distribution of mean *D. polymorpha* density in the Tivoli Bays region of the Hudson River. Lines connect bars that are not significantly different.

and appeared to reach an asymptote in density at 0.6 to 1.6-m depths (Fig. 4). Density values observed at the 1.6-m transect were similar to those observed at deeper depths during subsequent sampling.

Size-frequency distributions from 1993 (Fig. 5) revealed a single cohort with no individuals exceeding 20 mm in shell length. Mean shell length increased 24% over the 3-mo period from 9.83 mm in June to 11.51 mm in July, and to 12.19 mm in August. Mean mussel density decreased from 4.40 individuals/cm^2 in June to 3.69 individuals/cm^2 in July. Mussel density continued to decrease from 3.69 individuals/cm^2 in July to 3.04 individuals/cm^2 in August. The instantaneous mortality rate (z) of zebra mussels during the June to July period was 0.008/day and decreased to 0.005/day during the July to August period.

Size-frequency distributions (Fig. 6) of zebra mussels sampled from rocks in the Hudson River in August 1994 revealed a trimodal population composed of two year-classes. The first, centered around 5-mm shell length, was composed of mussels that settled either late in the fall of 1993 or early in the summer of 1994. The second group, averaging around 20-mm shell length, most likely settled in 1992. Overall, average mussel density was 1.96 individuals/cm^2 of rock substrate. This indicated a ~35% decrease in overall zebra mussel abundance during the 12-mo period from August 1993 to August 1994. However, the density estimates from 1993 were based only on the population that was represented here by the 2-y-old class. The average density of that year-class (1.18 individuals/cm^2) represents a 61% decrease in zebra mussel abundance.

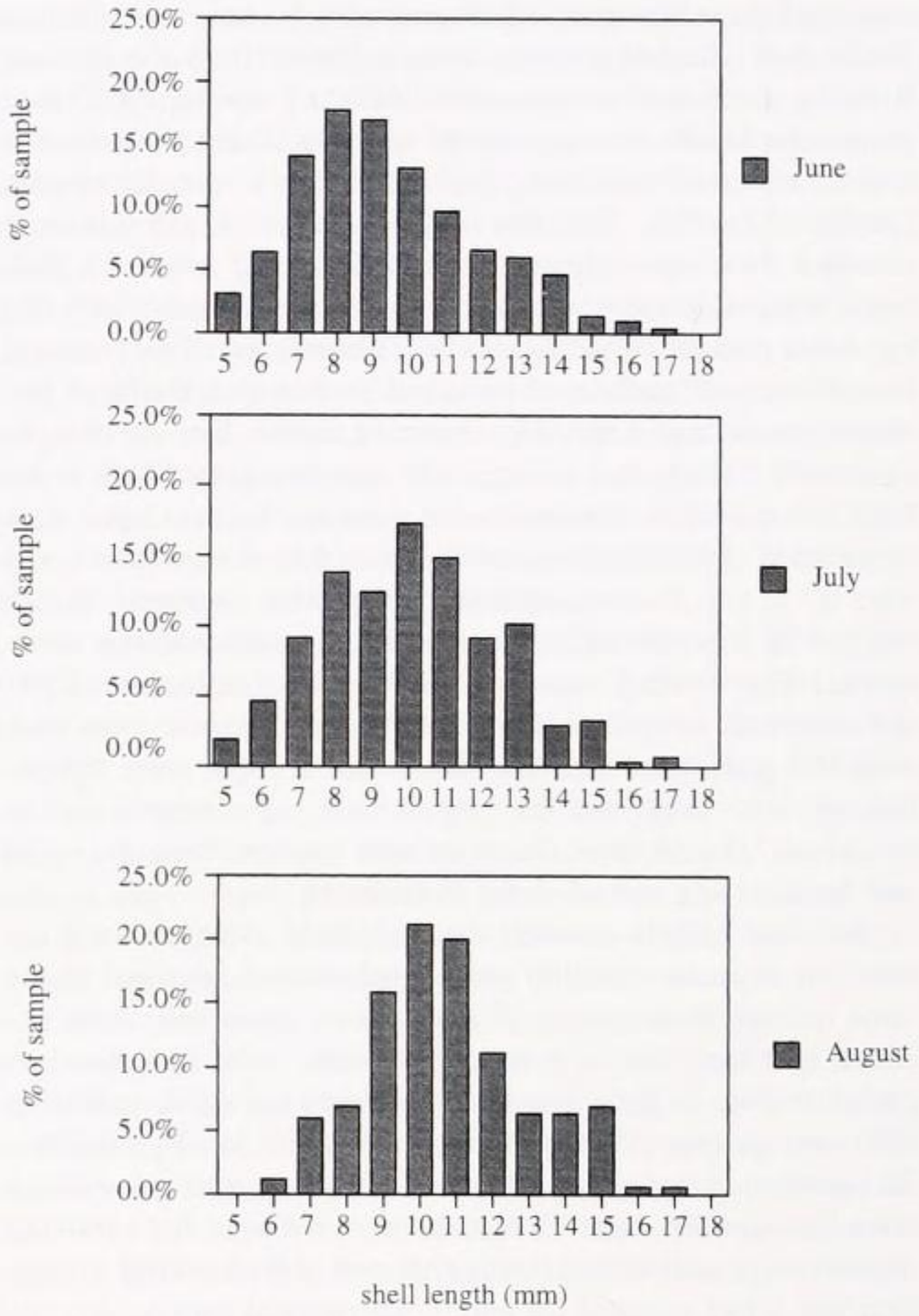

Figure 5. Size-frequency distributions of *D. polymorpha* in the Tivoli Bays region of the Hudson River in 1993.

Field Experiments

Mean zebra mussel mortality in the first manipulative experiment was significantly greater (ANOVA, $F = 13.43$, $df = 1,14$, $p < 0.0026$) in the experimental treatments (Fig. 7). Mussels in the closed-cage controls suffered less than 10% mortality over the 2-wk period. In the open cages, attached *D. polymorpha* experienced 24% mortality. The resulting 14% mortality was attributed to the effects of local predators. Zebra mussels in the open cages experienced an instantaneous mortality rate of 0.013/day during the experiment.

The introduction of male blue crabs produced higher mortality rates in the second field experiment. Large blue crabs consumed nearly 40% of the prey in 72-h trials (Fig. 8), correcting for the 10% mortality in the controls during the trial period. The control

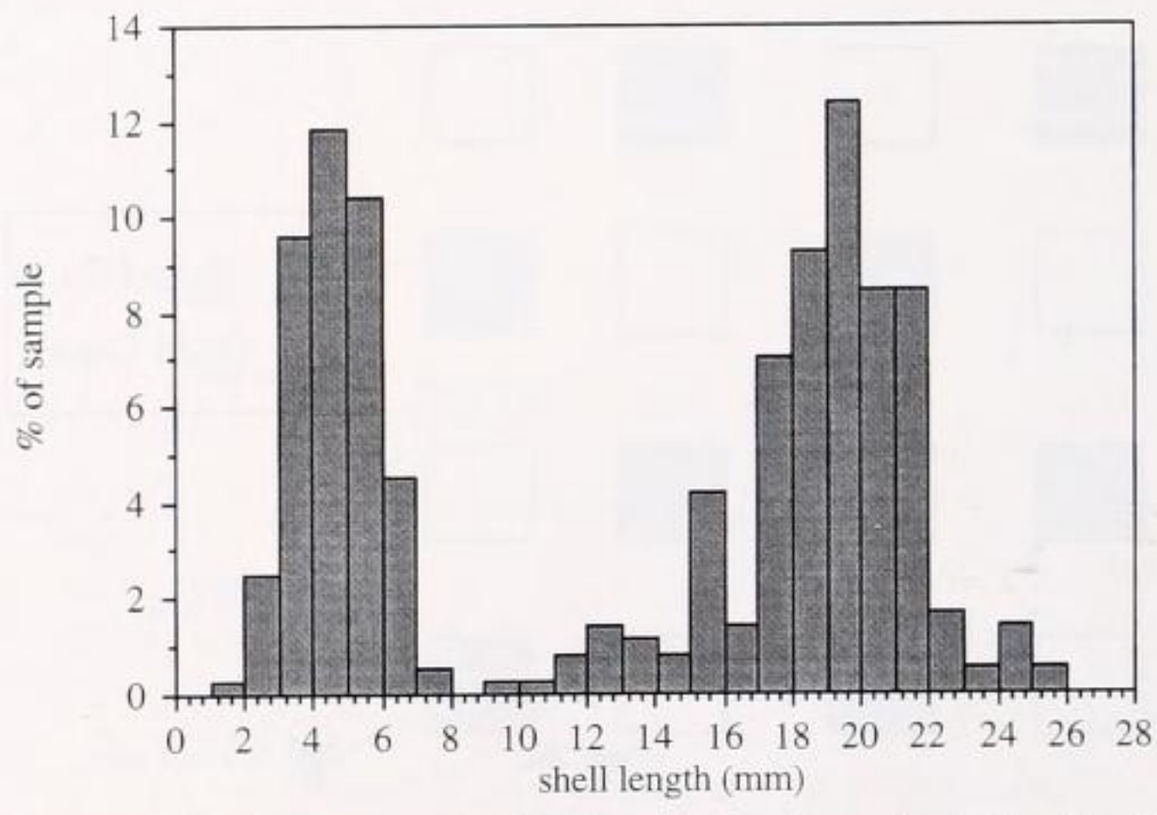

Figure 6. Size-frequency distributions of *D. polymorpha* in the Tivoli Bays region of the Hudson River in 1994.

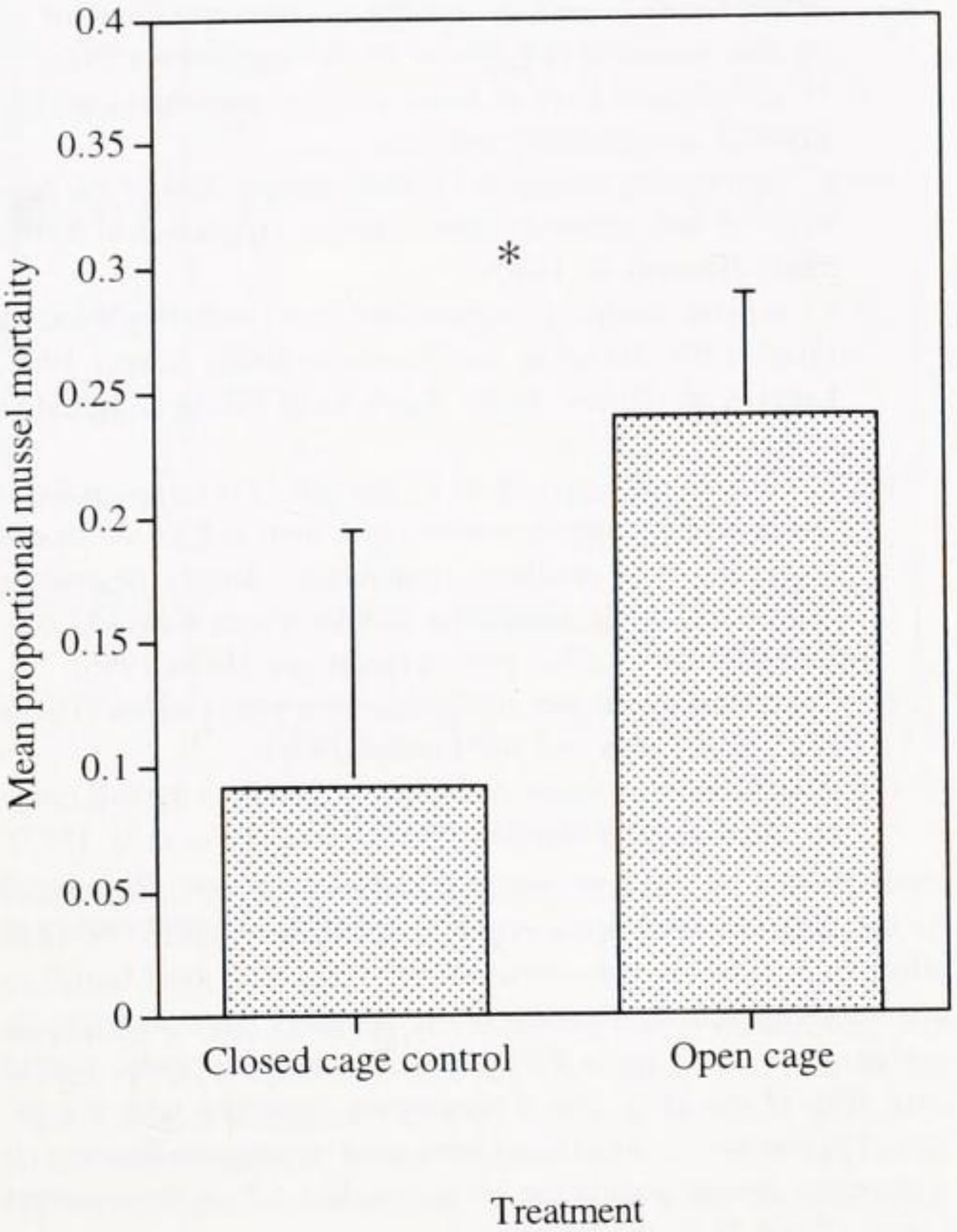

Figure 7. Mean proportional mortality of *D. polymorpha* in open- and closed-cage treatments. Asterisk denotes significant difference.

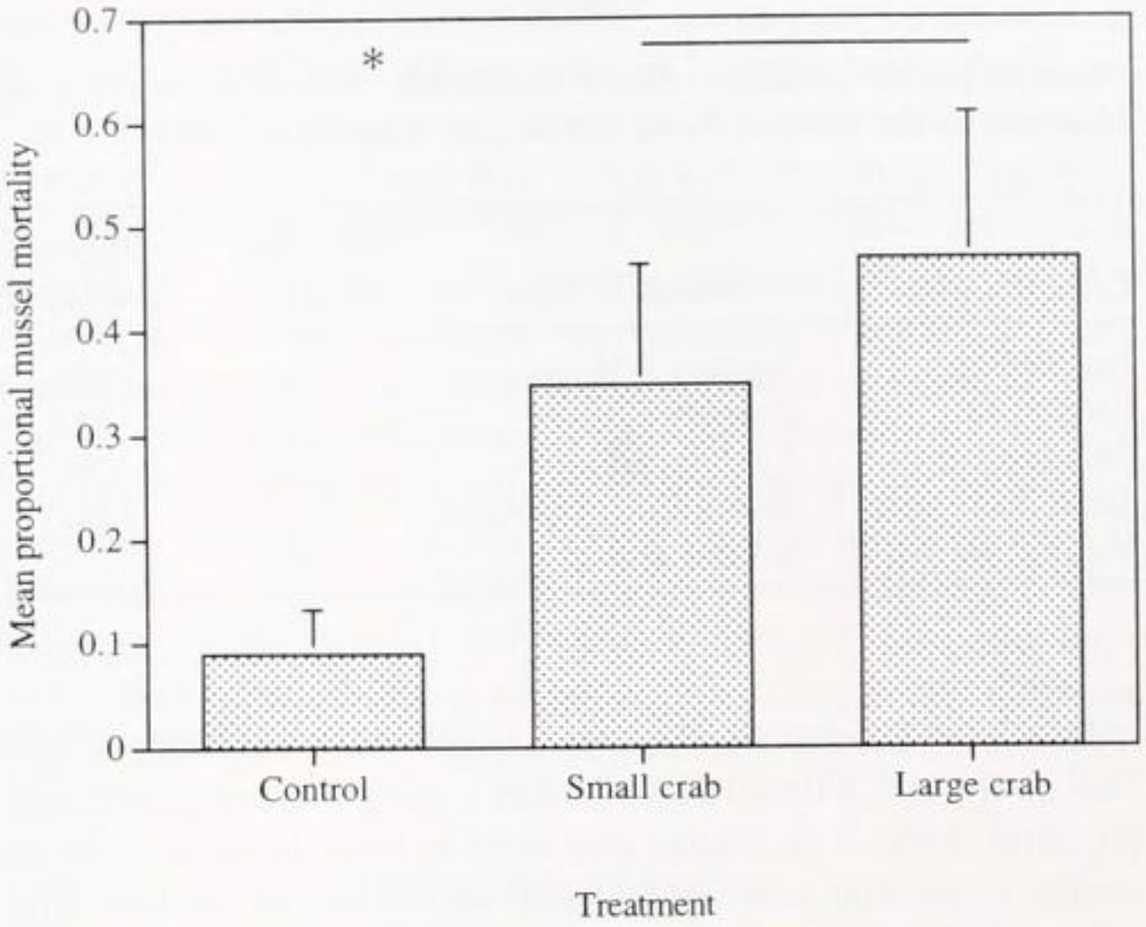

Figure 8. Mean proportional mortality of *D. polymorpha* in control, small crab, and large crab treatments. Asterisk denotes significant difference. Bar denotes nonsignificant difference.

mortalities in this experiment were similar to those in the first field experiment and were attributed mainly to the handling and transport of mussels between the field and laboratory. Although the effect of the crab treatments was highly significant (ANOVA, $F = 19.21$, $df = 2,15$, $p < 0.0001$), mussel mortalities did not differ significantly between large and small crab treatments (Scheffe's test, critical value = 0.169, $p > 0.05$). Corrected instantaneous mortality rates (z) indicated that mortality rates were an order of magnitude higher in those treatments containing blue crabs than in those exposed to natural predators (Table 1).

Potential Predators

Approximately 8 h of 8-mm underwater videotape revealed several fish species occupying the benthic habitat of the Hudson River (Table 2). French (1993) reported that several of these species were capable of consuming bivalves such as zebra mussels. Consumption of mussels by pumpkinseed, *Lepomis gibbosus*, was observed in the video, as well as in the field, by divers on several occasions. Baited crab pots fished during sampling periods in 1993 and 1994 caught no blue crabs. Blue crabs were neither observed during video monitoring nor seen by divers during the study period.

DISCUSSION

The spread of the zebra mussel into the Hudson River Estuary was predicted by Strayer and Smith (1993) and has been well documented. Mussels at the Tivoli site were found at very high densities on hard substrata and were differentially distributed with depth. The distribution of increasing mussel density with depth was consistent with the hypothesis that physical factors (e.g., desiccation, ice scour) restrict the upper limit of the vertical abundance of *D. polymorpha* in the Hudson River Estuary. Zebra mussels have been reported in the intertidal region of the St. Lawrence Estuary (Mellina and Rasmussen 1994), but no exposed mussels were observed in this study. Mussels at the shallowest depths (<0.5 m) were most often found in sheltered areas, on the vertical surfaces of rocks or in crevices.

Zebra mussels in European lakes and large rivers occur at densities near 3,000 mussels/m^2 (Bij de Vaate 1991). The densities reported here (~30,000 mussels/m^2) are well within the ranges observed in North American waters (Dermott and Munawar 1994). Size-frequency distributions of *D. polymorpha* in the Hudson River indicated that the population was composed of a single cohort spawned the previous year (Jenner and Janssen-Mommen 1993). Given the planktonic larval stage of the mussel, the likely parental population was several kilometers upriver of the Tivoli Bays site (Strayer et al. 1993).

We estimated the natural mortality of zebra mussels from both field sampling and predator-exclusion experiments. In the first case, mussels experienced instantaneous mortality rates of 0.008/day from June to July and 0.005/day from July to August. These estimates were lower than those observed in the predator-exclusion experiment (0.013/day). The higher mortality rates associated

TABLE 1.

Mean zebra mussel mortalities summarized from 1993 field experiments.

Condition	Technique	Instantaneous Mortality Rate/Day
Natural predators	Size-frequency analysis	0.007
	Field experiments, exposed	0.013
Small blue crabs	Predator enclosures	0.119
Large blue crabs	Predator enclosures	0.185

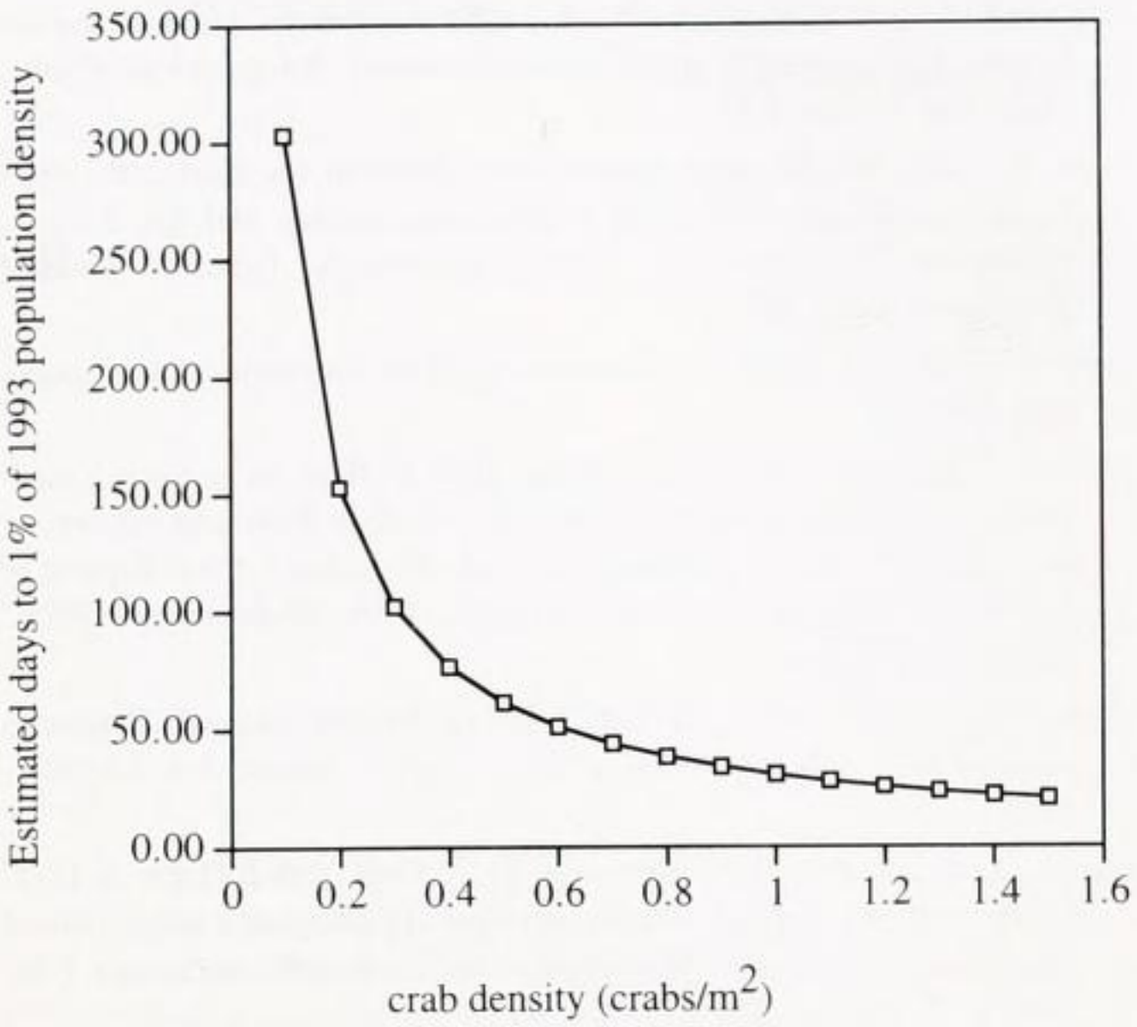

Figure 9. Projected localized extinction rates (days) for *D. polymorpha* at various blue crab densities.

supporting a small commercial fishery in some years (Stein and Wilson 1992). In this study, no crabs were caught in several baited traps, and local fishermen indicated that there were few blue crabs in the middle portion of the Hudson River in 1993 and 1994. Hence, biological control of the zebra mussel in the Hudson River caused by blue crab predation is unlikely.

In conclusion, *D. polymorpha* will not be regulated by the local predator guild in the Hudson River unless predator abundance increases significantly. This conclusion is supported by the recent estuary-wide investigation by Strayer et al. (1996), which points to competition for food resources as the most important regulatory mechanism in the Hudson River. In particular, the blue crab is capable of controlling zebra mussel abundance if the predator abundance increases to levels approximating 0.1–1.0 crabs/m^2, depending on crab size. Localized extinctions of zebra mussels within a 100-day growth season, like those observed by Molloy et al. (1994), are possible at these crab densities, given the rates of predation measured in this study (Fig. 9). It is not yet known if blue crab populations reach this level in the Hudson River. Such densities are common in other estuaries, such as Chesapeake Bay, and indicate that the zebra mussel may be regulated in estuaries near the southern limit of its predicted range, where blue crabs are more abundant.

ACKNOWLEDGMENTS

We thank the Hudson River Foundation, the Commonwealth of Virginia, and the New York State Museum for research support. Special thanks are given to D. Molloy, J. Waldman, C. Nieder, D. Strayer, and B. Blair for field support and advice. D. Molloy, D. Strayer, J. Bence, R. Meehan, and two anonymous reviewers provided helpful comments on the manuscript. This research was conducted while the senior author was supported by the Tibor T. Polgar Fellowship from the Hudson River Foundation, the Hudson River Foundation Graduate Fellowship, and a research assistantship from the Caribbean Marine Research Center. This is Contribution Number 2043 of the Virginia Institute of Marine Science, The College of William and Mary.

LITERATURE CITED

Arnold, S. K. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne). *J. Exp. Mar. Biol. Ecol.* 80:207–219.

Bij de Vaate, A. 1991. Distribution and aspects of population dynamics of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in the lake Ijsselmeer area (The Netherlands). *Oecologia* 86:40–50.

Blundon, J. A. & V. S. Kennedy. 1982. Mechanical and behavioral aspects of the blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. Exp. Mar. Biol. Ecol.* 65:47–65.

Brönmark, C. 1988. Effects of vertebrate predation on freshwater gastropods: an exclosure experiment. *Hydrobiologia* 169:363–370.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several species of *Thais*. *Ecol. Monogr.* 40: 49–78.

Cooley, J. M. 1991. Zebra mussels. *J. Great Lakes Res.* 17:1–2.

Daoulas, C. C. & P. S. Economidis. 1984. The feeding of *Rutilus rubilio* (Bonaparte) (Pisces, Cyprinidae) in Lake Trichonis, Greece. *Cybium* 8:29–38.

DeFur, P. L., D. Nusbaumer & R. J. Lewis. 1987. Physiological aspects of molting in blue crabs from the tidal fresh-water Potomac River, Virginia. *J. Crustacean Biol.* 8:12–19.

Dermott, R. & M. Munawar. 1994. Invasion of Lake Erie offshore sediments by *Dreissena,* and its ecological implications. *Can. J. Fish. Aquat. Sci.* 50:2298–2304.

deNie, H. W. 1982. A note on the significance of larger bivalve molluscs (*Anodonta* spp. and *Dreissena* sp.) in the food of the eel (*Anguilla anguilla*) in Tjeukemeer. *Hydrobiologia* 95:307–310.

Draulans, D. 1984. Sub-optimal mussel selection by tufted ducks *Aythya fuligula:* test of a hypothesis. *Anim. Behav.* 32:1192–1196.

Eggleston, D. B. 1990a. Foraging behavior of the blue crab, *Callinectes sapidus,* on juvenile oysters, *Crassostrea virginica:* effects of prey density and size. *Bull. Mar. Sci.* 46:62–82.

Eggleston, D. B. 1990b. Behavioral mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus,* feeding on juvenile oysters, *Crassostrea virginica. J. Anim. Ecol.* 59:615–630.

French, J. R. P. 1993. How well can fishes prey on zebra mussels in eastern North America? *Fisheries* 18:13–19.

Griffiths, R. W., D. W. Schlosser, J. H. Leach & W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48:1381–1388.

Hall, S. J., D. Raffaelli & W. R. Turrell. 1990. Predator-caging experiments in marine systems: a reexamination of their value. *The American Naturalist* 136:657–672.

Hamilton, D. J., C. D. Ankney & R. C. Bailey. 1994. Predation of zebra mussels by diving ducks: an exclosure study. *Ecology* 75:521–531.

Hebert, P. D. N., C. C. Wilson, M. H. Murdoch & R. Lazar. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha. Can. J. Zool.* 69:405–409.

Hines, A. H., A. M. Haddon & L. A. Weichert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67:105–126.

Hines, A. H., R. N. Lipcius & A. M. Haddon, A. M. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs (*Callinectes sapidus*) in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36:55–64.

Jenner, H. A. & J. P. M. Janssen-Mommen. 1993. Monitoring and control of *Dreissena polymorpha* and other macrofouling bivalves in the Netherlands. pp. 537–554. *In:* T. F. Nalepa and D. W. Schlosser (eds.). Zebra Mussels: Biology, Impact, and Control. CRC Press, Boca Raton, FL.

Lemma, A., L. Wolde-Yohannes, P. C. Fraleigh, P. L. Klerks & H. H. Lee. 1991. Endod is lethal to zebra mussels and inhibits their attachment. *J. Shellfish Res.* 10:361–366.

Lipcius, R. N. & A. H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361–1371.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8:133–137.

MacIsaac, H. J., W. G. Sprules & J. H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics? *Can. J. Fish. Aquat. Sci.* 48:2051–2060.

Mansour, R. A. & R. N. Lipcius. 1991. Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. *Mar. Ecol. Prog. Ser.* 72:239–246.

Mellina, E. & J. B. Rasmussen. 1994. Occurrence of zebra mussel (*Dreissena polymorpha*) in the intertidal region of the St. Lawrence Estuary. *J. Freshwater Ecol.* 9:81–84.

Molloy, D. P., J. Powell & P. Ambrose. 1994. Short-term reduction of adult zebra mussels (*Dreissena polymorpha*) in the Hudson River near Catskill, New York: an effect of juvenile blue crab (*Callinectes sapidus*) predation? *J. Shellfish Res.* 13:367–371.

Murdoch, W. M., J. Chesson & P. L. Chesson. 1985. Biological control in theory and practice. *The American Naturalist* 125:344–366.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between and dominant competitor and its principal predator. *Oecologia* 15:93–120.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49:667–685.

Paine, R. T. 1992. Food web analysis through field measurements of per capita interaction strength. *Nature* 355:73–75.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment communities of estuaries and lagoons. pp. 233–264. *In:* R. J. Livingston (ed.). Ecological Processes in Coastal and Marine Systems. Plenum Publishing Corporation, New York.

Robinson, J. V. & G. A. Wellborn. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea:* fish predation effects. *Oecologia* 77:445–452.

Seed, R. 1980. Predator-prey relationships between the mud crab, *Panopeus herbstii,* the blue crab, *Callinectes sapidus,* and the Atlantic ribbed mussel, *Geukensia* (=*Modiolus*) *demissa. Estuarine Coastal Mar. Sci.* 11:445–458.

Sokal, R. R. & F. J. Rohlf. 1980. *Biometry.* W.H. Freeman and Company, New York.

Stein, J. J. & K. A. Wilson. 1992. Blue crab, *Callinectes sapidus,* distribution and habitat utilization in the lower Hudson River and tributaries. pp. VI-1–24. *In:* J. R. Waldman and E. A. Blair (eds.). Final Reports of the Tibor T. Polgar Fellowship Program, 1991. Hudson River Foundation, New York.

Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha,* in North America. *Can. J. Fish. Aquat. Sci.* 48:1389–1395.

Strayer, D. L., J. Powell, P. Ambrose, L. C. Smith, M. L. Pace & D. T. Fischer. (1996). Arrival, spread, and early dynamics of a zebra mussel (*Dreissena polymorpha*) population in the Hudson River Estuary. Can. J. Fish. Aquat. Sci. 53(5):1143–1149.

Strayer, D. L., J. Powell, B. Walton & E. Mellina. 1993. Spread of zebra mussels in the Hudson River estuary in 1992. *Dreissena Polymorpha Information Review* 4:5.

Strayer, D. L. & L. C. Smith. 1993. The distribution of *Dreissena polymorpha* in estuaries and brackish waters. pp. 715–728. *In:* T. F. Nalepa and D. W. Schlosser (eds.). Zebra Mussels: Biology, Impact, and Control. CRC Press, Boca Raton, FL.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58:1199–1217.

Williams, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC.