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Potential for Population Regulation of the Zebra Mussel, Dreissena polymorpha, in the Hudson River

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POTENTIAL FOR POPULATION REGULATION OF THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA*, IN THE HUDSON RIVER

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

Larry C. Boles

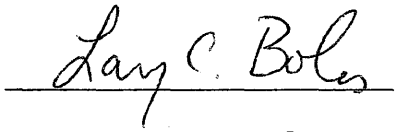
1996

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

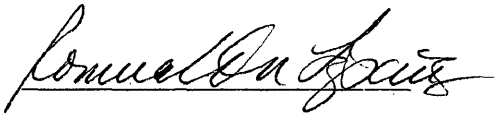
the requirements for the degree of

Masters of Arts



Larry C. Boles

Approved, May 1996



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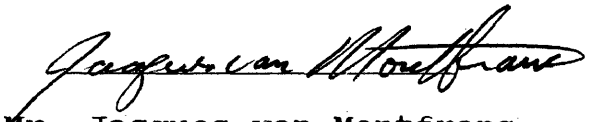

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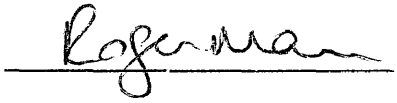

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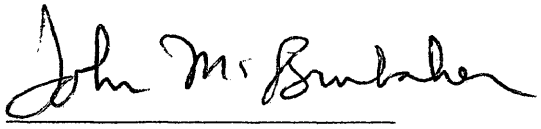

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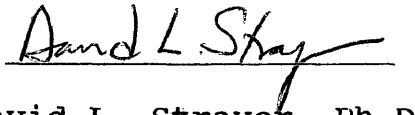

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Finally, I would like to thank all my great friends in crustacean ecology. I will miss you all and wish you the best. I especially want to thank Martha, Luis, and David for their sense of humor, companionship, and countless suggestions.

I thank the following groups and institution for the financial assistance: Tibor T. Polgar Fellowship, Hudson River Foundation Fellowship, and Virginia Sea Grant.

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ABSTRACT

I 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, New York. First, I measured distribution, abundance, and mortality rates of a zebra mussel population in the middle portion of the Hudson River . Rocks were collected along a depth gradient in the field and sampled for density and size structure of the resident mussels over the growth season. Next, I 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, I 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 predominately of a single cohort of 1+ year-class mussels (1992 year class). Sampling in August 1994 indicated a decline in *Dreissena polymorpha* density and the appearance of another dominant cohort (1994 year class). Mussel density increased dramatically with depth less than two meters 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 thought such densities are not common in the Hudson River Estuary. Thus predation does not appear to exert strong population regulation over the zebra mussel in the Hudson River, though in other estuaries where blue crabs are more abundant, population regulation by predation is feasible.

POTENTIAL FOR POPULATION REGULATION OF THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA*, IN THE HUDSON RIVER

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 upon 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 or destroy a 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*, and natural predators such as the

blue crab, *Callinectes sapidus*, and thereby provide the requisite conditions for predator-mediated control of *D. polymorpha* population dynamics.

In this investigation I 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. I conducted quantitative sampling and a series of field experiments in Hudson River freshwater habitats to determine limitations imposed by finfish and the blue crab upon 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.

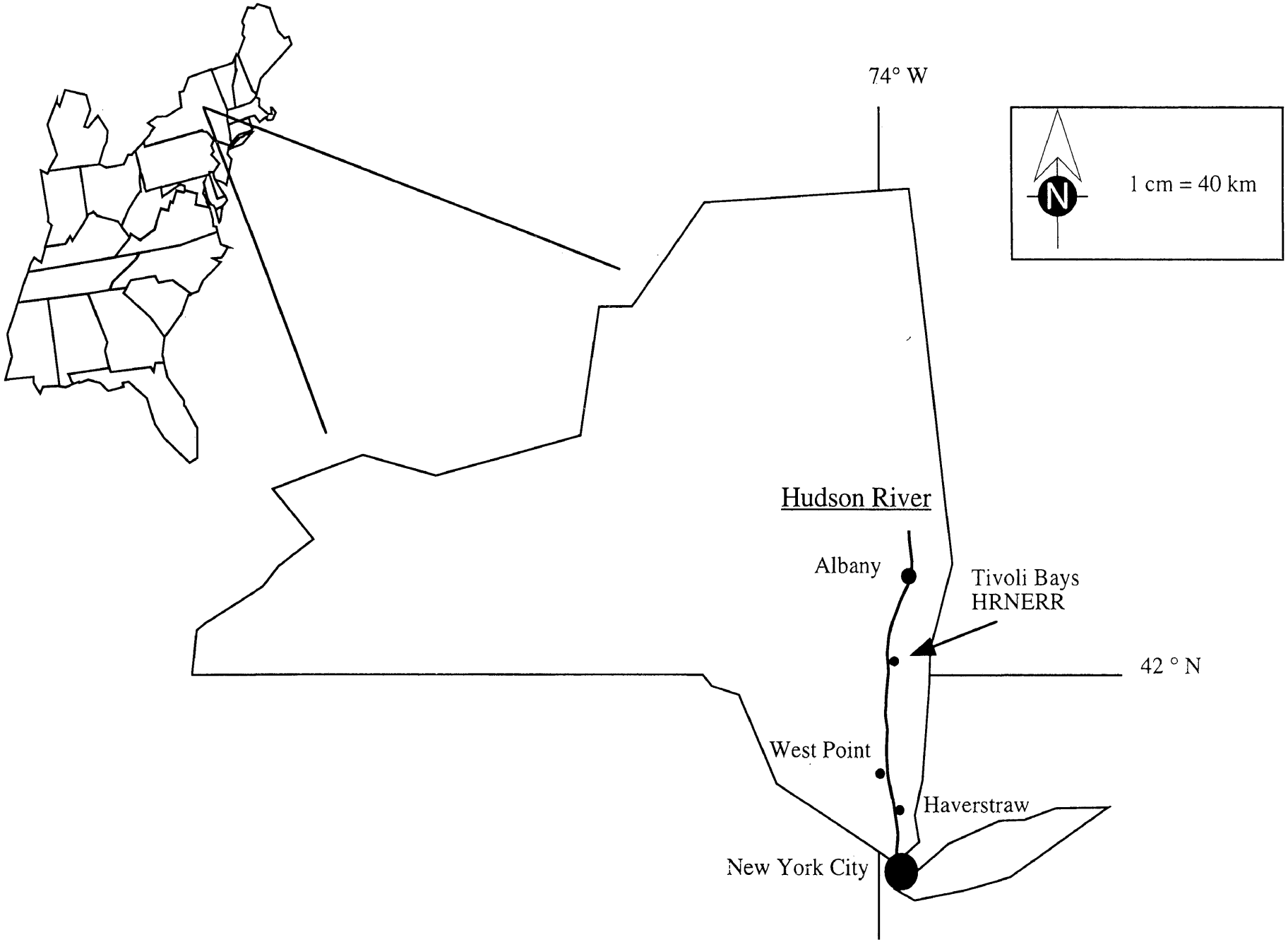
The potential predator prey system

The zebra mussel most likely invaded the Great Lakes in 1985 or 1986, with the first collection reported in Lake St. Clair on June 1, 1988 (Hebert *et al.* 1989). The

bivalves were most likely introduced in their larval veliger stage by the dumping of ballast water from a large ocean going ship, one of the most common methods of exotic species introduction (Carlton 1992). Zebra mussels had spread to most western European low-salinity ports by the mid 1800's from its original range in the drainage basins of the Black, Caspian, and Aral Seas in Eastern Europe. Just as canal building in Europe facilitated the spread of the prolific mollusk, the construction of the St. Lawrence Seaway provided an avenue of introduction into the North American Great Lakes. Once established in Lake St. Clair, *D. polymorpha* rapidly colonized western Lake Erie, and now occurs in all the Laurentian Great Lakes. Hebert *et al.* (1989) reported that zebra mussels from Lake St. Clair and western Lake Erie exhibited high genetic diversity which indicated the population was founded by a large number of individuals and not by a single chance introduction.

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, New York (Fig. 1) (Strayer *et al.* 1993). The rapid colonization of North American waters has been facilitated by its high fecundity (30,000 eggs/female/year), a free-swimming larval stage that is unlike 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).

Figure 1. Map of the study area.


74° W
N
1 cm = 40 km
Hudson River
Albany
Tivoli Bays
HRNERR
42 ° N
West Point
Haverstraw
New York City

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, due to 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 & 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, *C. sapidus*, 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 foraging from late spring through autumn in Chesapeake Bay (Hines *et al.* 1987, 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 & 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 is 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 & 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 mussels and preferred the largest individuals available (Molloy *et al.* 1994).

METHODS

Study site

I 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, New York (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 due to 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 m to 20 m during the four sampling periods. Rocks with attached mussels were transported to the laboratory in padded coolers to minimize handling mortality. I estimated zebra

mussel density on each rock by removing all live individuals that fell within a 16 cm^2 plastic grid place 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 measured to the nearest millimeter using Vernier calipers. Six replicate rock samples were examined during each month of the study yielding 24 samples during the one year period. Mean zebra mussel densities were used to estimate both inter- and intra-annual mortality rates. Shell length data were used to construct size-frequency distributions.

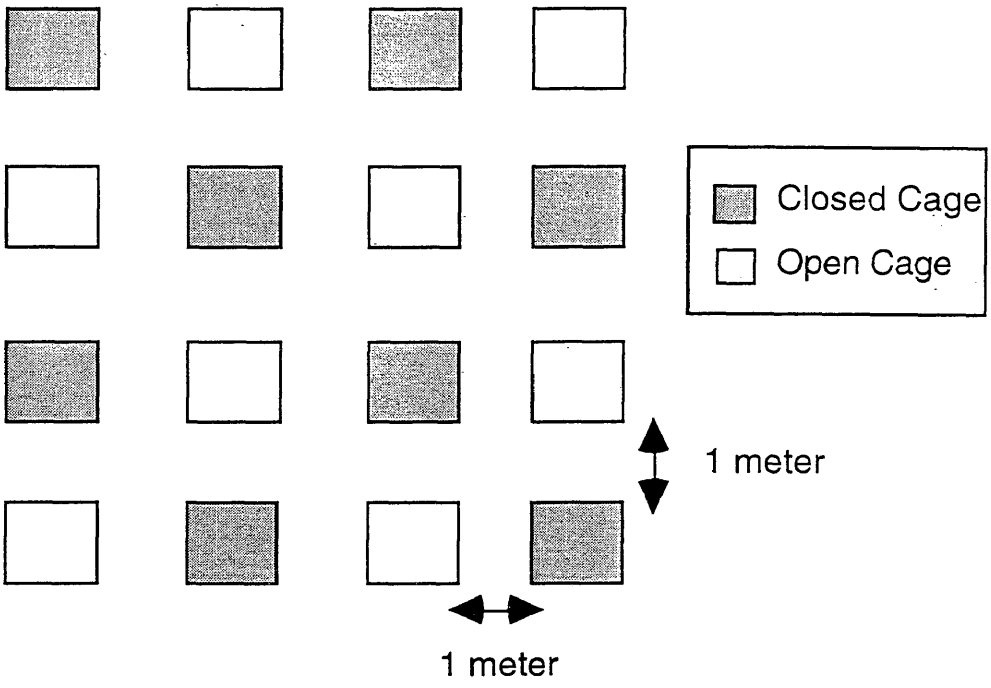
I conducted a series of five underwater transects in August, 1993 to characterize the depth distribution of *D. polymorpha* at the study site. Four random rock samples were collected using SCUBA along depth profiles to determine density using the same method as above. The four samples at each depth were 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 samples would be taken. At each collection site a visual estimate of percent coverage was also taken using a haphazardly-placed circular grid (25 cm diam.). Samples were collected at increasing depth profiles (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. I first 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 hours to ensure the health of experimental animals. Zebra mussels that actively siphoned water and closed their shells when agitated were considered healthy. Following this observation period, mussels were removed from aquaria and placed in dissecting trays. I 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).

Figure 2. Configuration of cages for first field experiment.

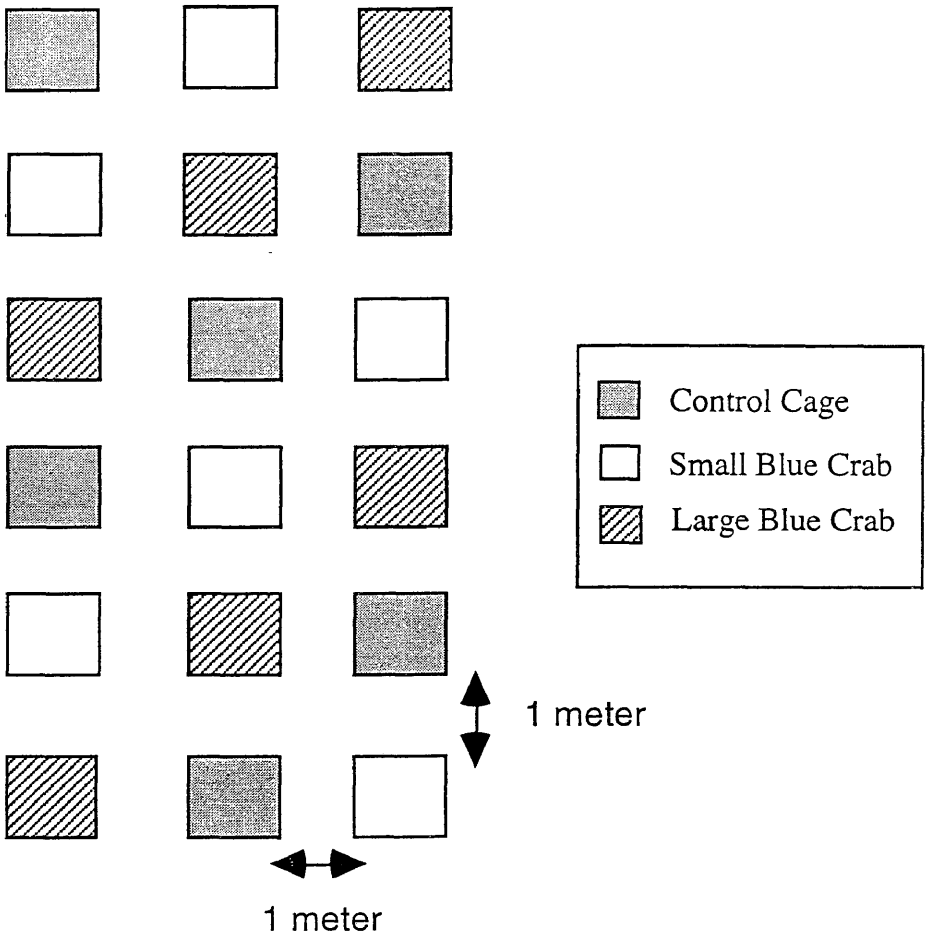

Closed Cage
Open Cage
1 meter
1 meter

Each treatment was replicated 8 times. Control treatments comprised fully-enclosed cages protecting one rock with 100 pre-counted mussels. Experimental cages were topless and 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 enumerated.

The final experiment utilized the same field enclosures and another set of rocks with 100 pre-counted 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 (60-80 mm carapace width (CW)) and six cages contained large crabs (110-130 mm CW). Six cages contained only rocks with 100 pre-counted mussels and served as controls. After 72 hours, crabs were removed and surviving mussels enumerated. Each blue crab was examined to confirm that it had survived the entire experimental period.

In both field experiments 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 using an ANOVA model with angularly (arcsine) transformed proportional mortality as the dependent variable and cage treatment as a fixed factor. Scheffe's test was used to

Figure 3. Configuration of cages for second field experiment.


Control Cage
Small Blue Crab
Large Blue Crab
1 meter
1 meter

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).

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

I recorded over eight hours of underwater video using a Sony 8mm video recorder with remote water-proof cameras in August of 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 meter in all directions but did allow it to capture images of fish swimming along the river's bottom.

Whenever possible, I 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, August 1993 and August 1994). These were checked daily for the presence of blue crabs and rebaited when necessary.

RESULTS

Abundance of zebra mussels rapidly increased with increasing depth and reached constant values less than 2 meters 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, $p<.05$), and appeared to reach an asymptote in density at 0.6-1.6 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 shell length. Mean shell length increased 24% over the three month 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-July period was

Figure 4. Depth distribution of mean *Dreissena polymorpha* density (± 1 s.d.) in the Tivoli Bays region of the Hudson River. Bar denotes nonsignificant differences.

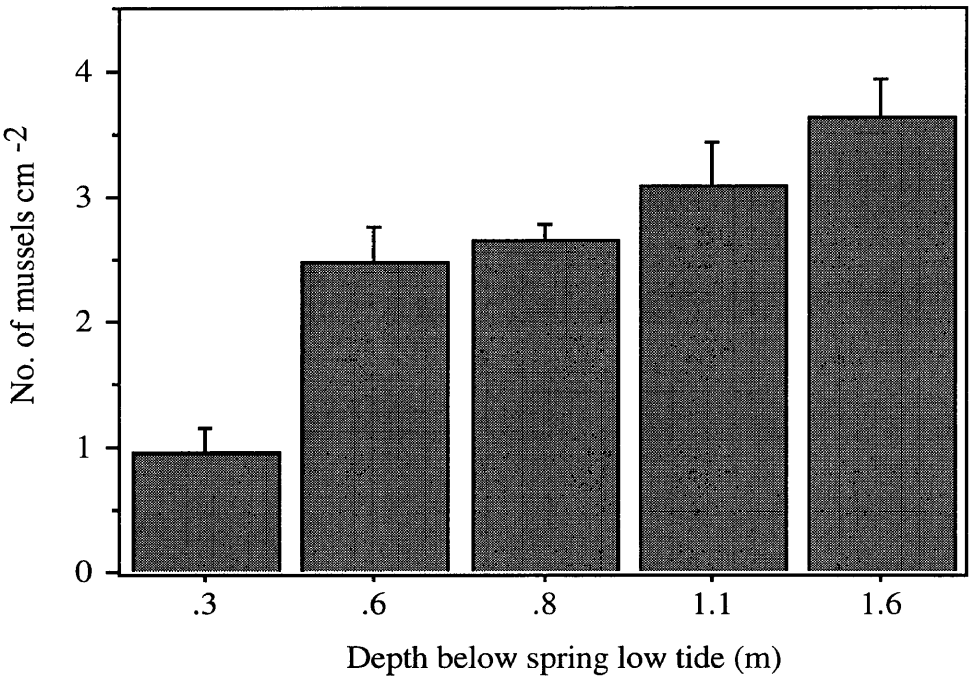
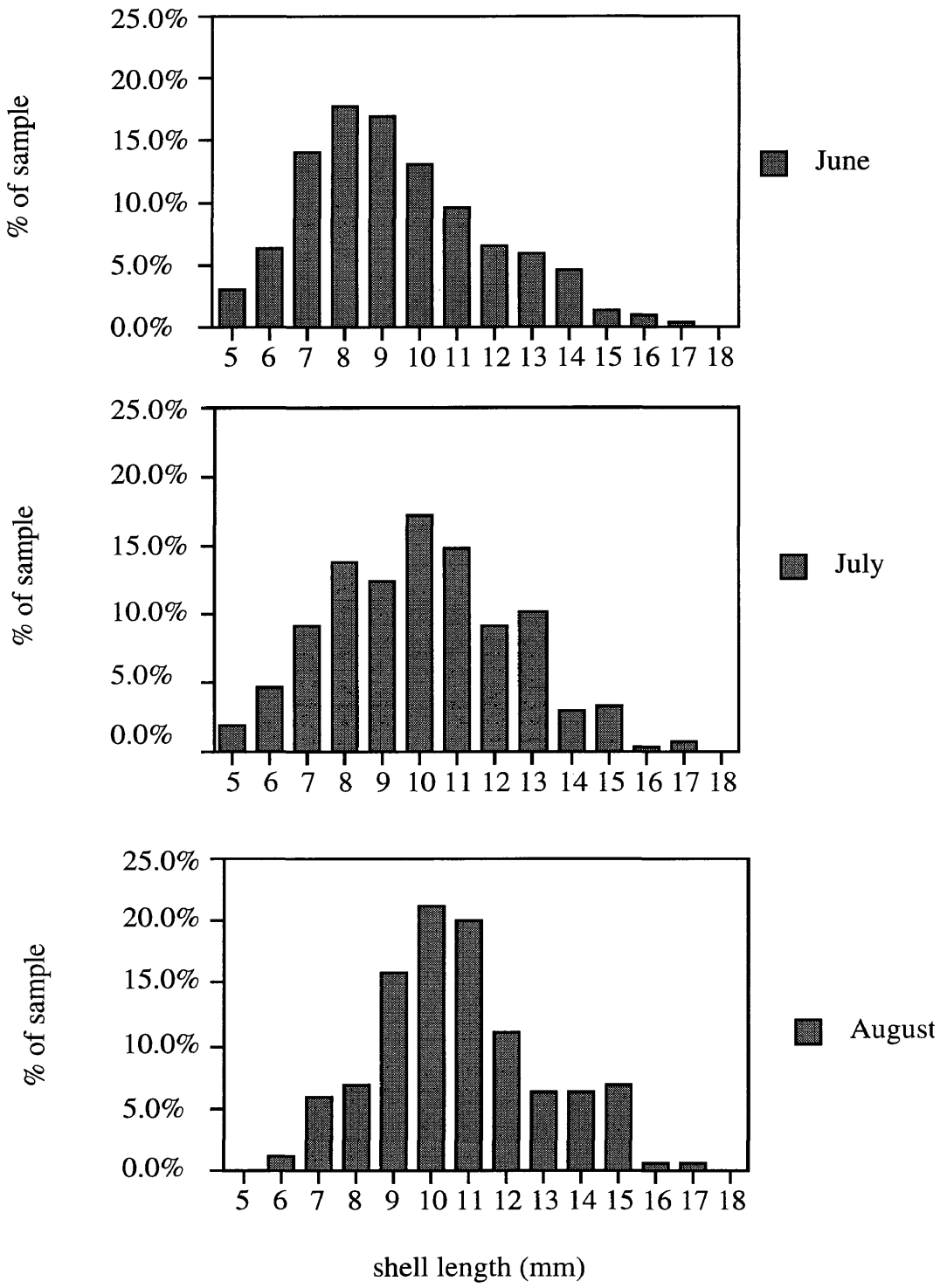

No. of mussels cm -2
0
1
2
3
4
.3
.6
.8
1.1
1.6
Depth below spring low tide (m)

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


25.0%
20.0%
15.0%
10.0%
5.0%
0.0%
% of sample
5 6 7 8 9 10 11 12 13 14 15 16 17 18
June
July
August
shell length (mm)

0.008 d^{-1} and decreased to 0.005 d^{-1} during the July-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 in 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 substrate. This indicated a ~35% decrease in overall zebra mussel abundance during the 12 month 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 two-year old class. The average density of that year class (1.18 individuals/cm^2) represents a 61% decrease in zebra mussel abundance.

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 two-week period. In the open cages,

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

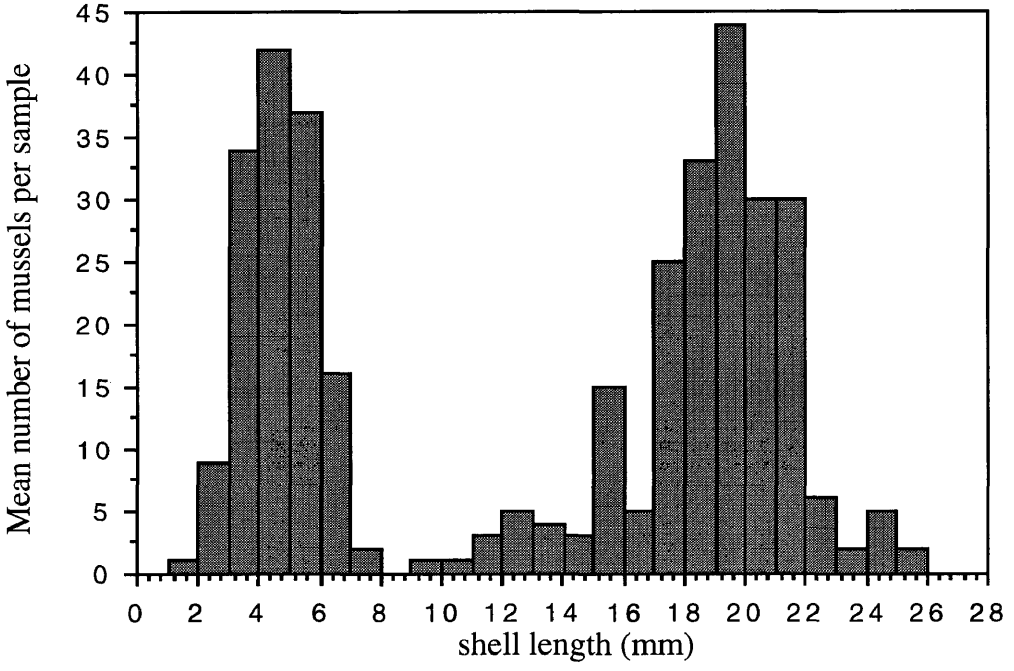
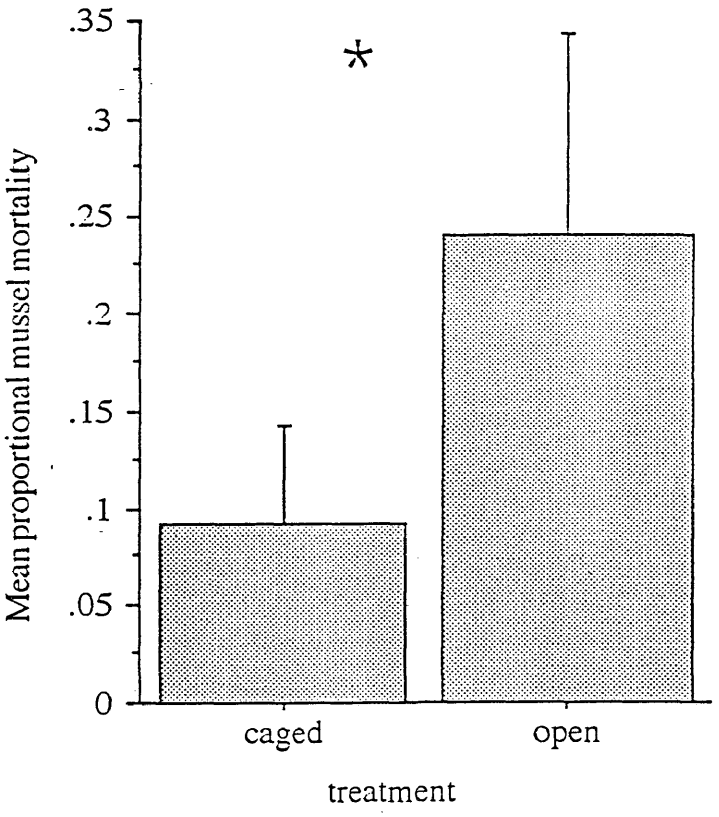

Mean number of mussels per sample
45
40
35
30
25
20
15
10
5
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28
shell length (mm)

Figure 7. Mean proportional mortality of *Dreissena polymorpha* in open and closed cage treatments. Asterisk denotes significance.


.35
.3
.25
.2
.15
.1
.05
0
*
Mean proportional mussel mortality
caged
open
treatment

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 d^{-1} 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 mortalities in the 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 = .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 eight hours 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.

Figure 8. Mean proportional mortality of *Dreissena polymorpha* in control, small crab, and large crab treatments. Bar denotes nonsignificant differences. Asterisk denotes significance.

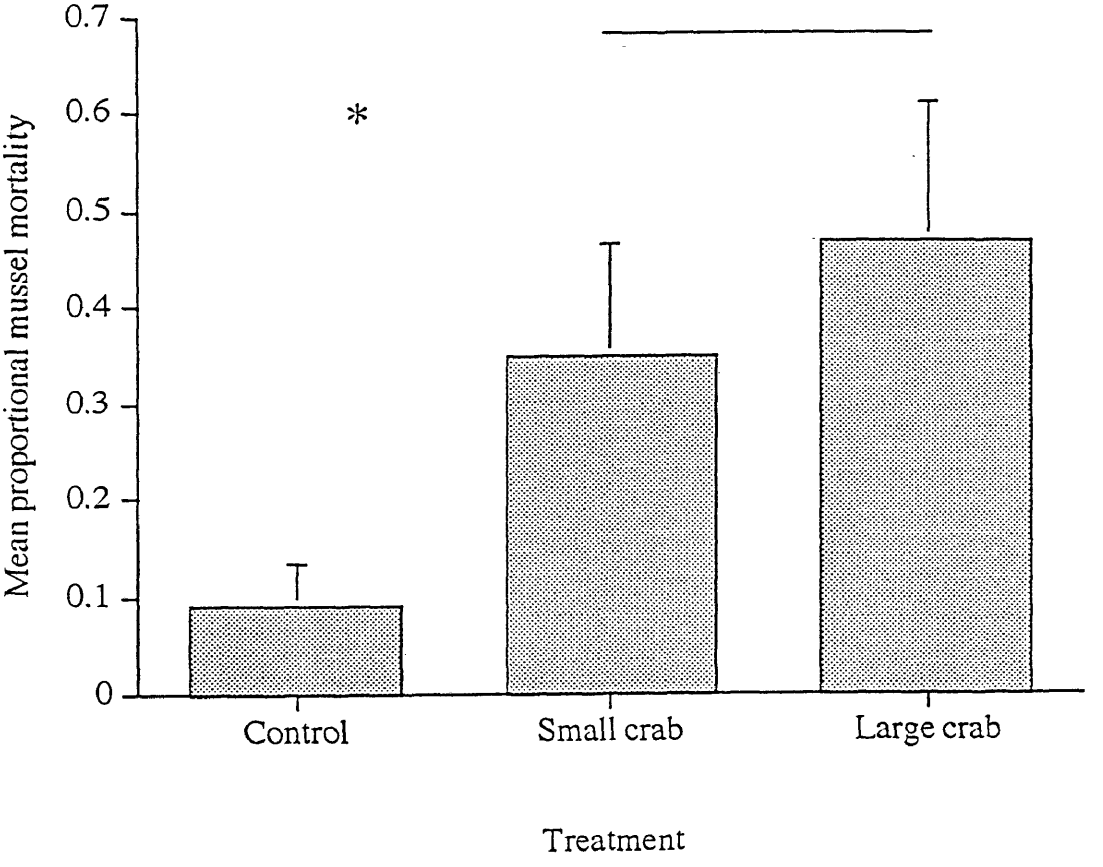

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
Mean proportional mussel mortality
Control
Small crab
Large crab
Treatment

Table 1. Mean *Dreissena polymorpha* instantaneous mortalities summarized from 1993 field experiments.

Condition	Technique	Instantaneous Mortality Rate (d^{-1})
Natural Predators	Size-Frequency Analysis	.007
Natural Predators	Field Experiments, Exposed	.013
Small Blue Crabs	Predator Enclosures	.119
Large Blue Crabs	Predator Enclosures	.185

Table 2. Potential piscine predators (based on French 1993) of *Dreissena polymorpha* observed in the Hudson River Estuary by underwater video system.

Common name	Scientific name	Potential Predator	Observed Predation
Pumpkinseed	*Lepomis gibbosus*	yes	yes
Redbreast sunfish	*Lepomis auritus*	yes	yes
Common carp	*Cyprinus carpio*	yes	no
Smallmouth bass	*Micropterus dolomieui*	no	no
Various minnows	several genera	no	no

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 significantly 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 3000 mussels/m^2 (Bij deVaate 1991).The densities reported here (~30,000 mussels/$m^{2)}$ are well within the ranges observed in North American waters (Dermott & 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).

I 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 d^{-1} from June to July and 0.005 d^{-1} from July to August. These estimates were lower than those observed in the predator-exclusion experiment (0.013 d^{-1}). The higher mortality rates associated within the manipulative experiment suggested some caging effect. Hall *et al.* (1990) found that while caging treatments can be a powerful research technique, care must be taken in the analysis of results to separate any confounding effects of the method. The presence of a partial cage structure in this experimental treatments may have increased predation rates by attracting more fish.

The success of the zebra mussel in North America can be attributed at least in part to the lack of effective natural predators. In Europe, mussels are preyed upon by eels (de Nie 1982), other fish (Daoulas & Economidis 1984), and ducks (Draulans 1984). The role of predation in the recent invasion of North American waters by the zebra mussel is not well documented. At least six species of piscine predators capable of consuming zebra mussels were reported by French (1993)(Table 2) but most of these are

uncommon in the Hudson River. Only two of these, the pumpkinseed, *Lepomis gibbosus*, and the red-breasted sunfish, *Lepomis auritus*, were observed consuming *D. polymorpha* during this study. More recently, Hamilton *et al.* (1994) found that diving ducks in Lake Erie have included zebra mussels in their diet, thus leading to ephemeral reductions in mussel biomass in shallow areas. This study is the first attempt to measure the effects of predation on an estuarine population of *D. polymorpha*.

Predation often functions to control invertebrate species in benthic environments (Virnstein 1977, Brönmark 1988). For exotic species, one of the leading causes of failure to become established in new environments is predation (Lodge 1993). Before the invasion of the zebra mussel, perhaps the most infamous exotic bivalve was the Asiatic clam, *Corbicula fluminea*. Similarly to the zebra mussel, this organism led to problems including biofouling and displacement of native bivalve species. Strong predation pressure by several native fish species limited the success of the Asian clam in colonizing at least one potential habitat area (Robinson and Wellborn 1988).

I have suggested that the blue crab might be an effective predator capable of controlling the population dynamics of the zebra mussel. Consumption of *D. polymorpha* by *C. sapidus* was reported soon after the invasion of the Hudson River (Strayer *et al.* 1993). Molloy *et al.* (1994)

reported a marked reduction of zebra mussels in the mid-Hudson in 1992, which coincided with high abundance of blue crabs. The observation of high mortality rates in 1992 supported my hypothesis and encouraged my field experiments. The probable characteristics of this predator-prey system which render it amenable to control of *D. polymorpha* by *C. sapidus* include:

(1) *D. polymorpha* is an epibenthic colonizer of hard, accessible substrates.

(2) *D. polymorpha* achieves a relatively small adult size, apparently well within the minimum size capabilities of *C. sapidus* predation (Eggleston 1990 a, b);

(3) *D. polymorpha* lives in large, discrete aggregates readily apparent to epibenthic predators;

(4) *C. sapidus* is a generalist predator independent of the densities of any particular prey species (Lipcius & Hines 1986, Hines *et al.* 1990).

(5) *C. sapidus* readily consumes bivalves, including mussels (Seed 1980, Blundon & Kennedy 1982, Arnold 1984, Lipcius & Hines 1986, Eggleston 1990a, b).

(6) The functional response of *C. sapidus* to bivalves in habitats providing high encounter

rates, such as hard substrates accessible to a predator, is inversely density-dependent (Eggleston 1990a, b), which leads to localized extinction of the prey (Lipcius & Hines 1986).

(7) *C. sapidus* aggregates at high-density prey patches (Hines *et al.* 1990, Mansour & Lipcius 1991), and

(8) *C. sapidus* can tolerate and actively forage in the full range of salinities from marine to freshwater (DeFur *et al.* 1987).

The results of my crab predation experiment provided support for the hypothesis that dense populations of blue crabs can be more effective in reducing zebra mussel abundance than local finfish or invertebrate predators. *D. polymorpha* mortality rates caused by *C. sapidus* were nearly twice those caused by the local predator guild in only 20% of the time. The instantaneous mortality rates (z) observed in the various treatments were used to estimate the time (t) until zebra mussel population levels reached 1% of their current values (Table 3) by the formula:

$$t = \frac{\ln No - \ln Nt}{z}$$

where No is the initial number of mussels and Nt is the number of mussels at the end of the experimental period. Assuming predation by *C. sapidus* would occur over roughly a

Table 3. Estimated time to 1% of 1993 zebra mussel abundance based on instantaneous mortality rates observed in field experiments.

Condition	Technique	Estimated time (t)
Natural Predators	Size-Frequency Analysis	657
Natural Predators	Field Experiments, Exposed	354
Small Blue Crabs	Predator Enclosures	39
Large Blue Crabs	Predator Enclosures	24

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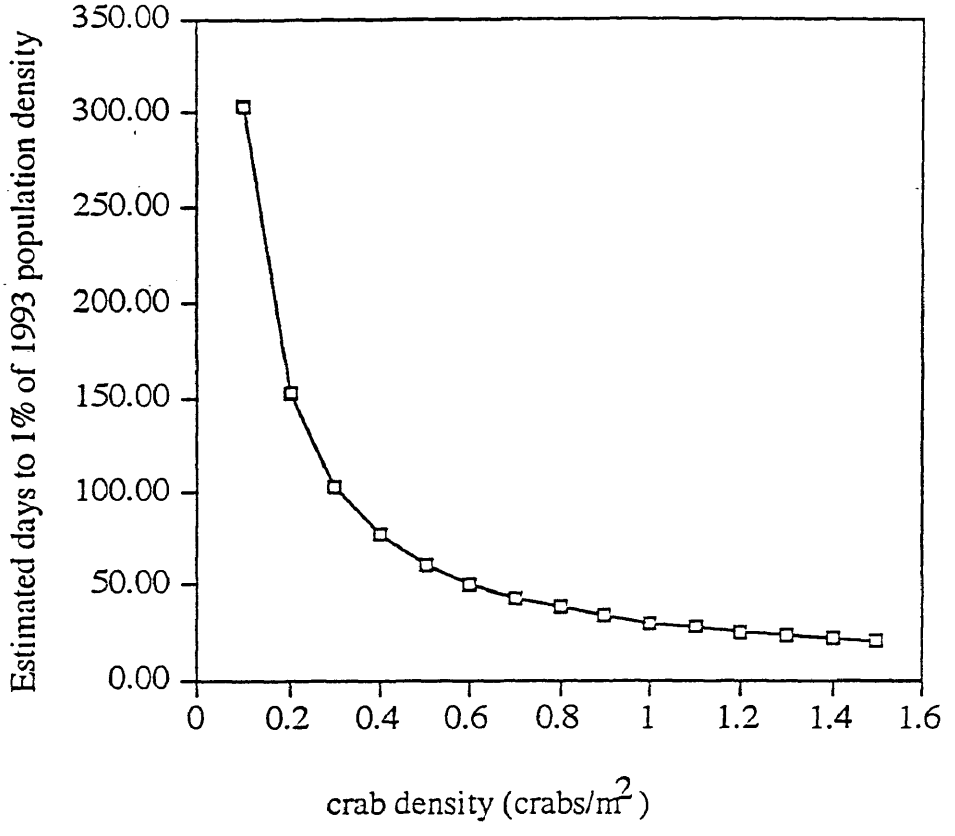
100-day period (given the usual absence of blue crabs in the oligohaline portions of estuaries during cooler months), significant reductions of zebra mussels are predicted within one summer (Fig. 9). At my measured predation rates, blue crab densities of 0.1 crabs/m^2 would drastically reduce the abundance of *D. polymorpha* in one season. A significant decrease in the mussel population would be expected whenever crab densities and predation rates approach or surpass these levels. Hines *et al.* (1987) reported summer densities of 0.10-0.73 crabs/m^2 in a subestuary of Chesapeake Bay in Maryland. During part of the study, water temperature and salinity conditions in the area were similar to those found in the Hudson River estuary.

Blue crab densities in the Hudson River system are relatively low, varying from almost zero to moderate densities capable of 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.

Figure 9. Projected localized extinction rates (days) for *Dreissena polymorpha* at various blue crab densities based on instantaneous mortality rates observed in this study.


Estimated days to 1% of 1993 population density
350.00
300.00
250.00
200.00
150.00
100.00
50.00
0.00
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
crab density (crabs/m2)

This conclusion is supported by the recent estuary wide investigation by Strayer *et al.* (in press) which points to competiton 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.

The introduction of the zebra mussel, *Dreissena polymorpha*, into North America was initially considered a regional problem of special concern for states and provinces bordering the Great Lakes. However, the exotic bivalve spread quickly across New York's inland waters and has been present in the Susquehanna River since 1991 (Lange and Cap 1992). The potential for zebra mussel to spread down to northern Chesapeake Bay was the initial impetus for this research. Further interest was generated by the observations of massive zebra mussel mortality in the

summer of 1991 in the Hudson River in areas with an abundance of blue crabs (Molloy *et al.* 1994).

Baker *et al.* (1993) reviewed the criteria for predicting zebra mussel invasions in the Mid-Atlantic region. They rated both freshwater and estuarine habitats on susceptibility to introduction and probability of establishment of *Dreissena polymorpha* based on several physical characteristics. Obviously, biotic factors may also have a large impact on the success of zebra mussel populations in estuarine systems like Chesapeake Bay. The recent work by Strayer *et al.* (in press) suggests that intra-specific competition for food resources will prevent zebra mussels in rivers and estuaries from reaching the great densities that have been observed in the Great Lakes. I believe that my work demonstrates if *Dreissena polymorpha* ever reaches the low salinity waters of the Chesapeake Bay it will likely encounter the added regulatory pressure of predation by blue crabs.

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