

THE INVASION OF THE HUDSON RIVER ESTUARY BY  
THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA*, AND ITS  
SUBSEQUENT RANGE OVERLAP WITH  
THE FALSE DARK MUSSEL, *MYTILOPSIS LEUCOPHAEATA*

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## ABSTRACT

During the summer of 1992, the invasive spread of the freshwater zebra mussel, *Dreissena polymorpha*, downriver in the Hudson River Estuary was surveyed at six sites from Marlboro, NY [RKM 107] south to Tarrytown, NY [RKM 44]. Furthermore, the range of the resident estuarine false dark mussel, *Mytilopsis leucophaea*, was similarly recorded, establishing the extent of overlap between these two dreissenid mussels in the Hudson River.

As expected, *D. polymorpha* densities were highest at the northernmost site (Marlboro, NY) and decreased with increasing distance downriver. Individual *D. polymorpha* settled as far south as West Haverstraw, a site at which salinity never dropped below 2 ppt, demonstrating the invading mussels' ability to settle and survive in oligohaline waters. Densities of *M. leucophaea* were highest at the two southernmost sites (West Haverstraw and Tarrytown, NY), but individuals were found as far north as Newburgh, NY. Thus, the ranges of the two species overlapped from Newburgh to West Haverstraw [RKM 94 to 60].

Despite this overlap at three sites, the low average densities of the less abundant mussel at a given site indicate that significant sympatric settlement of these dreissenids did not occur. Thus, interactions between individuals of these two species conceived in the same year may have only minor ecological significance. This lack of significant co-occurring settlement may be a reflection of only this year's salinity regime and its limitation of settlement of both species.

The presence of *M. leucophaea* adults on rocky substrate in Constitution Marsh, where *M. leucophaea* settlement was low, suggests that the adults can tolerate a lower salinity than the veligers. A reversed tolerance in *D. polymorpha* adults for higher salinities than their veligers has been suggested by laboratory studies. Therefore, in subsequent years, as salinity changes, interactions between veligers of one species and adults of the other species are predicted to occur, at a given site with a given salinity, veligers of only one species are capable of settling in quantity, but they may encounter adults of the other species which settled in a previous year. Thus, despite non-significant co-occurring settlement, these two mussels may interact in the lower Hudson River Estuary and other North American estuaries.

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## INTRODUCTION

Introduced to the Great Lakes in 1986 via ballast water discharge (Hebert et al. 1991), the zebra mussel, *Dreissena polymorpha*, has spread to all the Great Lakes, the Illinois River, the upper St. Lawrence River, the Tennessee River, the Mississippi River, the Susquehanna River, and the Hudson River (*Dreissena polymorpha* Information Review [DPIR] 1992). This spectacular range expansion has been accompanied by the explosive population growth of this freshwater bivalve in numerous North American waters (Hebert et al. 1989, Griffiths et al. 1991), leading to profound ecological and economic impacts. *D. polymorpha*, which firmly attach to hard substrates with byssal threads, aggregate in extremely high densities, clogging water intakes (Walker 1991) and altering the dynamics of the benthic community to the point of threatening native freshwater bivalve species (Hebert et al. 1989, Walker 1991).

Based on European data, Strayer (1991) predicted that *D. polymorpha* has the capacity to, and, in all likelihood will colonize most of North America's fresh waters. Furthermore, Strayer and Smith (1992) suggested that *D. polymorpha* will likely spread to North American estuaries, based on European occurrences. While experimental studies (as summarized in MacNeill 1991a) have demonstrated the ability of *D. polymorpha* to survive low salinities of up to 12 parts per thousand (ppt), field data on the impact of salinity upon settlement, reproduction and metabolism of the zebra mussel are scarce (Carlton, pers. comm). With an established Hudson River southern limit during 1991 of Poughkeepsie, NY [122 River Kilometers (RKM) above the Battery], 1992 presented an opportunity to characterize the first invasion of *D. polymorpha* into a North American estuary.

The range extension of *D. polymorpha* into the Hudson River Estuary had been predicted to overlap the range of an estuarine resident, the false dark mussel, *Mytilopsis leucophaea*. Present in the brackish waters of the Hudson River, *M. leucophaea* [*Congeria cochleata* in the European literature] is another invader, introduced in the 1930's from the southern U.S., presumably via ballast water discharge (MacNeill 1991b). This

mussel is limited to brackish waters; in the Hudson River, Jacobson and Emerson (1961) reported individuals from the Bear Mountain Bridge [RKM 76] south to upper Manhattan [RKM 22], although its exact range and densities are unknown (Carlton, pers. comm.).

Members of the same family (Dreissenidae), *M. leucophaea* and *D. polymorpha* are morphologically similar, each have a veliger stage, attach via byssal threads, and suspension-feed. Due to these similarities, these two species would be expected to compete if their ranges overlapped. In fact, the ranges of these two species overlap in several European estuaries where *M. leucophaea* was accidentally introduced in the nineteenth century (Wolf 1969), suggesting the potential for similar overlap in North American estuaries (MacNeill 1991a, Strayer and Smith 1992). Based on the salinity tolerance of each species and Con Edison salinity data for the Hudson River, MacNeill (1991a) suggested that the likeliest region for the overlap would be between Newburgh [RKM 94] and the Bear Mountain Bridge [RKM 76] (Fig. 1). The question of interactions between these two species, however, remains largely unexplored.

I sought to test the predictions of Strayer and Smith (1992) and MacNeill (1991a), respectively: 1) Is *Dreissena polymorpha* capable of settling and surviving in the oligohaline Hudson River Estuary, with a southern limit near West Point [RKM 82] and isolated freshwater inlets further south, and 2) will the ranges of these two dreissenid mussels overlap, with the likeliest region between Newburgh and the Bear Mountain Bridge? To test these predictions, I sampled the river at six sites from Marlboro [RKM 107] to Tarrytown [RKM 44] for the presence and densities of both mussels. To determine the approximate date of settlement of the collected mussels, I also measured the mussels' shell lengths as indicators of age (Dorjelo 1992, Neumann et al. 1992, Mackie 1992). In addition to testing these questions, the potential for a mechanism of interaction between these species is explored.

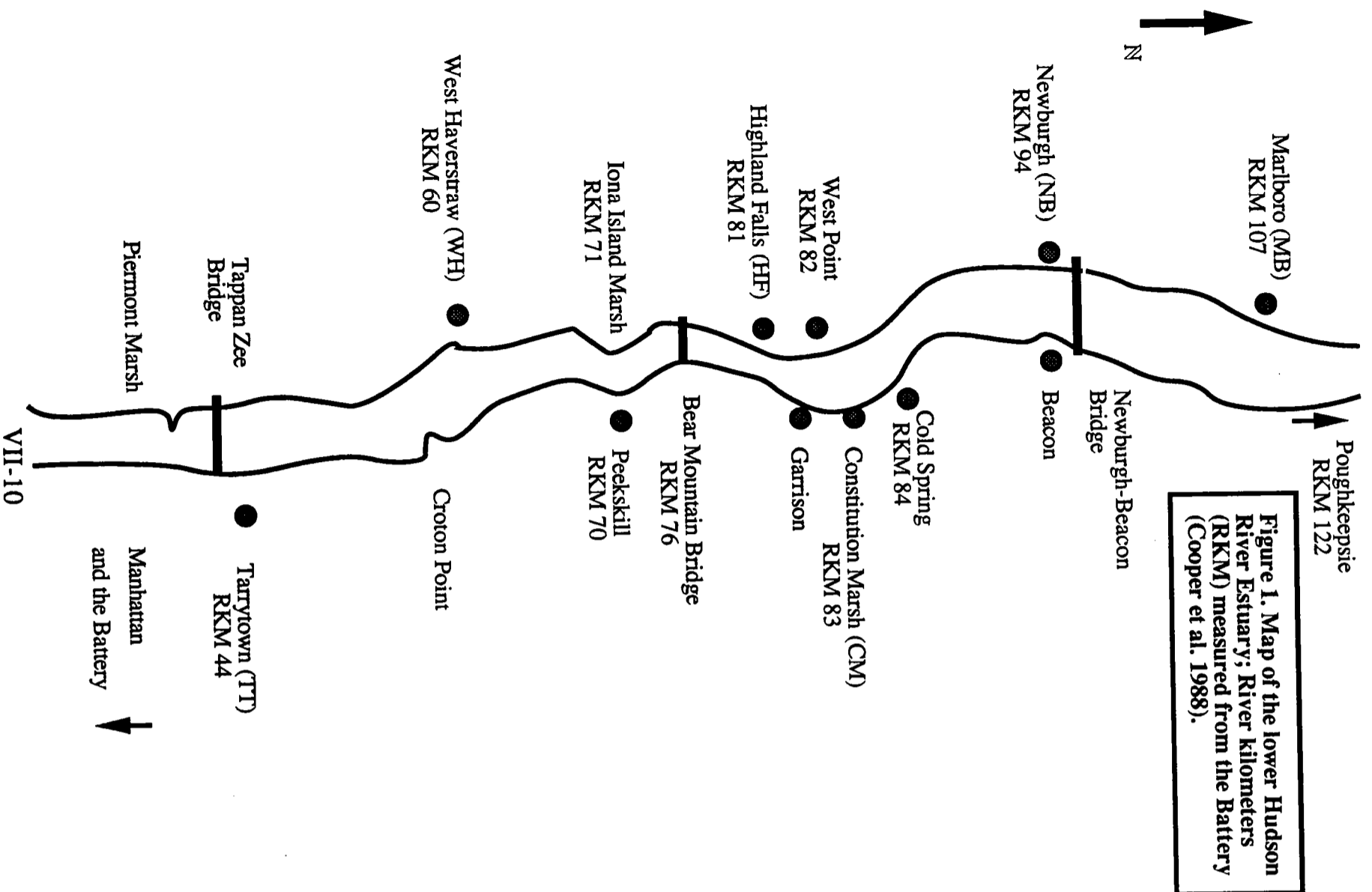


Figure 1. Map of the lower Hudson River Estuary; River kilometers (RKM) measured from the Battery (Cooper et al. 1988).

**METHODS**

Five sites were established on the Hudson River to sample the probable zone of range overlap between the two mussels. From south to north, the sites were: Tarrytown Marina (Tarrytown), Haverstraw Marina (West Haverstraw), Highland Falls Marina (Highland Falls), Gull Harbor Marina (Newburgh), and the Marlboro Yacht Club (Marlboro). These sites ranged from the Tappan Zee Bridge to north of the Newburgh-Beacon Bridge (Fig. 1). All sites were along the river's edge, except for the Haverstraw Marina, which is in a protected cove receiving freshwater from a nearby stream. All are affected by diurnal tides and each site is subject to considerable boating activity.

On May 15, 1992, three arrays were suspended from floating docks at each site (15 arrays total). Each array consisted of a polypropylene line holding 15 3x5" roughened PVC plates, intended as settlement surfaces for the dreissenid mussels. In addition, each array was weighted with a standard cinder block (with an average surface area of 0.462 m<sup>2</sup>) to keep the array vertical in the water column. Attached to floating docks, each array remained at a constant depth of 2.5 m.

On a weekly basis, the PVC plates were removed from each site, stored in freshly collected river water, and transported in coolers to the Hudson River Foundation's laboratory in Garrison, NY (near Bear Mountain Bridge). All plates from the sites were immersed and examined under a 50x microscope, with a fiber-optic light to prevent heating the specimens. Plates were searched for settled fouling organisms. Dreissenid mussels were identified non-destructively by examining external characteristics as outlined in MacNeill (1991b), and confirmed initially with dissection. Other macro-organisms were identified with the assistance of Dr. Jim Carlton. All plates were returned to their originating sites within 12 hours. Plates were examined weekly from June 3, 1992 until August 18, 1992.

Settlement on the cinder blocks was also used as an alternative measure of mussel densities. Note that cinder blocks received no special treatment during the weekly plate

removals. All but one of the cinder blocks were retrieved between September 19, 1992 and October 2, 1992; the final cinder block (#3 at Highland Falls) was lost in the second week of September due to line breakage. However, on October 15, this block was located and salvaged from about 6 m of water with a trawl.

When brought out of the river, blocks were immediately cleared of all mussels visible to the naked eye in natural light. Furthermore, percent cover was determined with random point sampling for two other predominant species, the barnacle, *Balanus eburneus*, and a colonial hydroid. All mussels were counted, except for the mussels collected at the Marlboro site where, due to the great numbers of *D. polymorpha*, subsamples were taken from random portions of each block and totals were extrapolated to the entire block. Mussels at least 2 mm long were externally identified and random subsamples of 25 individuals were measured. Dissections were performed at random to confirm external identifications.

Rocks from Constitution Marsh [RKM 83] were also sampled as an additional measure of dreissenid densities. Rocks were collected at random by hand on October 19, 1992 from the two south channels of the marsh. Only the surfaces deemed suitable for dreissenid settlement (i.e., not buried or covered) were sampled. At low tide, the mid-channel depth was about 1 m, and I searched the entire channel width. Mussels visible to the naked eye in natural light were collected, and identified and measured under a 50x microscope. I measured the areas of the searched rock surfaces and calculated density estimates.

Finally, on a weekly basis, I measured temperature and salinity at each site. Temperature was taken at the water surface and at 2 m. Salinity was initially measured only from the surface, but in the month of August, salinity was measured at 2 m as well. The Institute of Ecosystems Studies and the Millbrook School, both in Millbrook, NY, provided monthly precipitation data for May through September.

For data analysis, the SuperAnova program (Macintosh) was used. In examining the cinder block density data, dreissenid species and site were the main factors (the nested block within site factor was pooled into the residual term [ $P=0.5006$ ]). For analysis of size differences, dreissenid species and site were again the main factors, and data from Constitution Marsh were included. To test all pair-wise comparisons, the least squares means method was used.

## RESULTS

### Variation in Physical River Characteristics:

Over the summer, water temperatures climbed at all sites and fell off dramatically in the fall. The highest temperatures were reached at West Haverstraw (Fig. 2). Dual salinity measurements differed by less than 0.5 ppt so only surface salinities are shown (Fig. 3). Salinity fluctuated at each site but the three most northern sites were clearly less salty than the two southern sites. Additionally, Tarrytown was noticeably more saline than West Haverstraw (Fig. 3). Note that a salt-wedge did not migrate upriver over the summer.

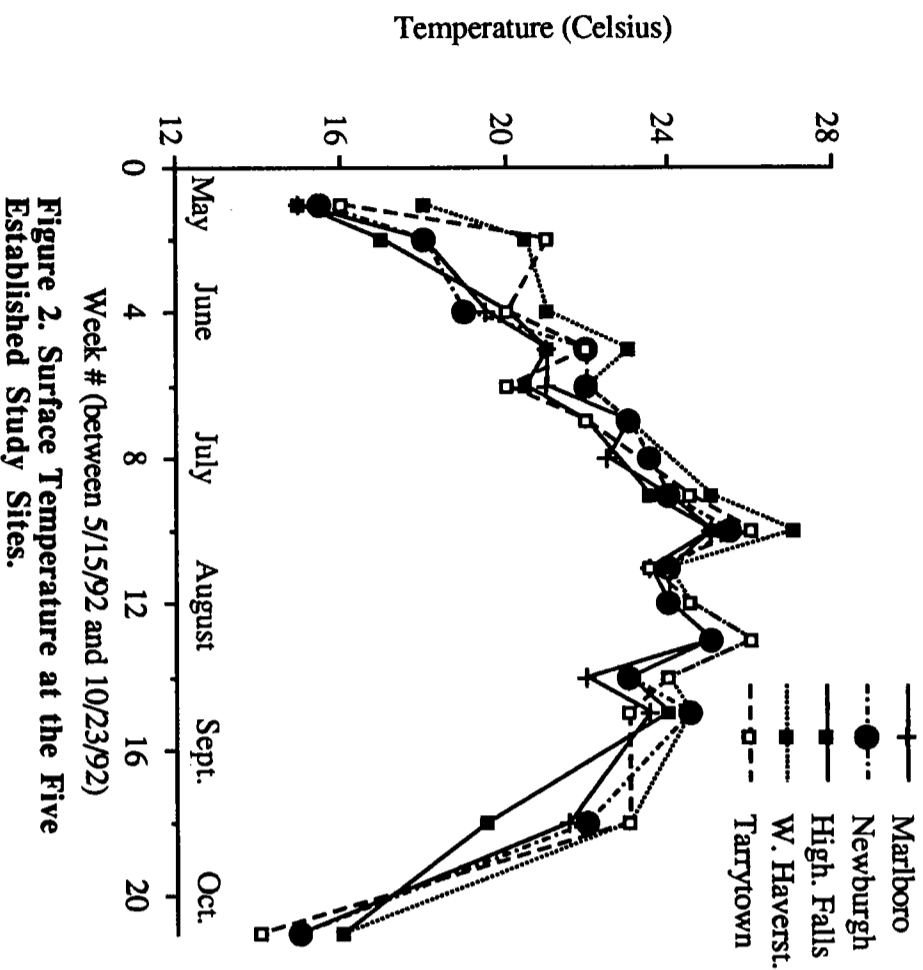


Figure 2. Surface Temperature at the Five Established Study Sites.

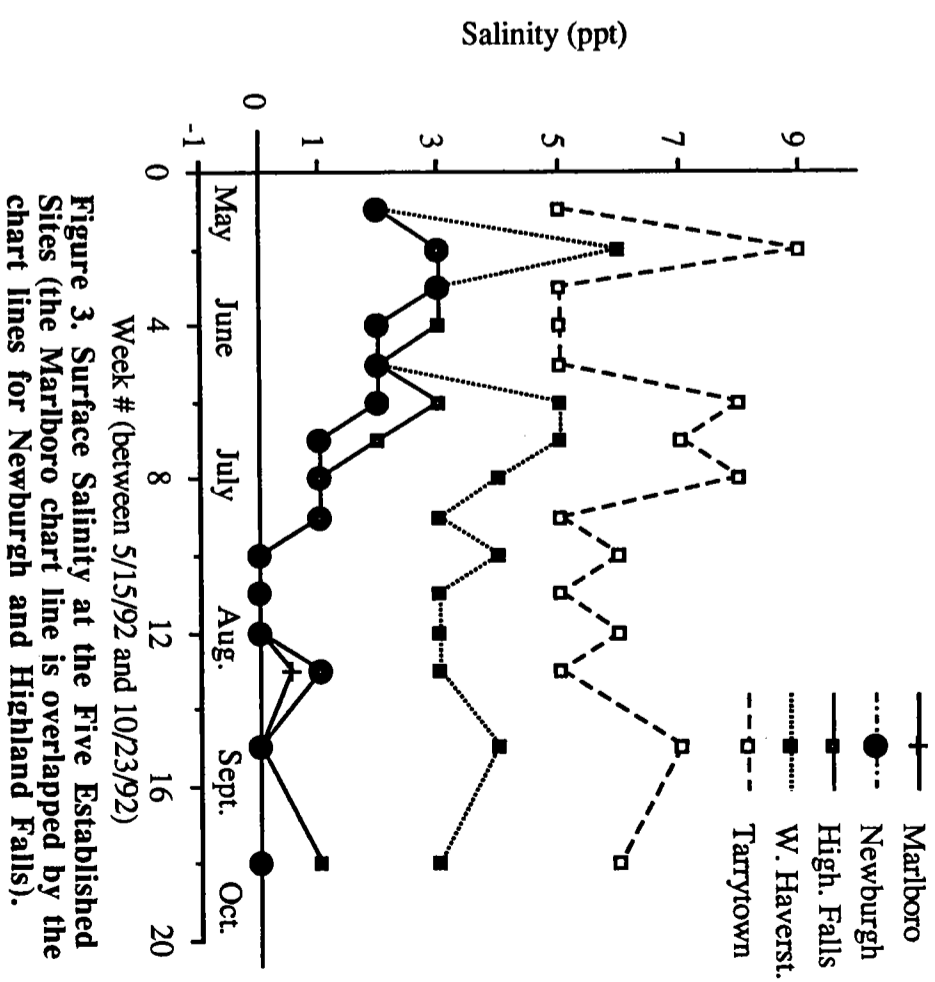


Figure 3. Surface Salinity at the Five Established Sites (the Marlboro chart line is overlapped by the chart lines for Newburgh and Highland Falls).

Monthly rainfall as recorded in Millbrook, NY was lower than the long-term average for each month between May and September with the notable exception of July, which was extremely wet (Table 1).



**Table 1. Comparison of 1992 Institute of Ecosystems Studies Precipitation Data with the Millbrook Schools Long-term [1951-1980] Data for Millbrook, NY (provided by IES with permission).**

Time Period	1992 (mm)	Long-term Avg. (mm)
May	72.3	85.5
June	78.7	93.7
July	149.3	92.7
August	66.2	100.3
September	47.0	94.2
June-August	294.2	286.7
May-September	413.8	466.4

**Presence/Absence of Fouling Organisms:**

Juvenile bivalves were first observed in early June on the PVC plates from Tarrytown, followed by plates from West Haverstraw (Table 2). Settled bivalves were first observed at Marlboro and Newburgh at the end of June, followed by Highland Falls in mid-July. Mussels 300 microns to 2 mm long could not be identified to species level due to the morphological similarity; at the two southern sites, however, several mussels on the plates grew longer than 2 mm and were identified as *M. leucophaeata*.

Based on observation of the plates and blocks, as well as on-site records, *D.*

*polymorpha* was found from Marlboro south to West Haverstraw, and *M. leucophaeata* from Tarrytown north to Newburgh (Table 3); thus, the ranges of these two species currently overlap at three of the five sites (Newburgh, Highland Falls, and West Haverstraw). Four other species were identified: the barnacle, *Balanus eburneus*, the blue crab, *Callinectes sapidus*, a colonial hydroid (species unknown) and the water chestnut, *Trapa natans*. With the exception of *C. sapidus*, which was found throughout the study

range, each of the these species' ranges are generally similar to the range of one of the two dreissenid mussels (Table 3).

**Table 2: Number of Juvenile Bivalves Observed on the PVC Plates at the Five Established Sites by Week (TT=Tarrytown, WH=West Haverstraw, HF=Highland Falls, NB=Newburgh, MB=Marlboro, and an \* indicates the number of individuals identified --- all were *M. leucophaeata*).**

Date	TT	WH	HF	NB	MB
6/2	4	0	0	0	0
6/9	0	0	0	0	0
6/16	0	3	0	0	0
6/21	0	11	0	0	0
6/29	0	5	0	1	1
7/6	0	1	0	0	6
7/13	0	3	0	3	2
7/20	1*	3	4	0	1
7/27	1*	8**	5	1	0
8/4	2*	11****	2	3	0

**Table 3: Presence/Absence Records for Six Species at the Five Established Sites (X indicates presence, - indicates absence, and site labels as in Table 2).**

Species	South					North				
	TT	WH	HF	NB	MB	TT	WH	HF	NB	MB
<i>D. polymorpha</i>	-	X	X	X	X	-	-	-	-	-
<i>M. leucophaeata</i>	X	X	X	X	-	-	-	-	-	-
<i>B. eburneus</i>	X	X	X	X	-	-	-	-	-	-
Colonial hydroid	-	-	X	X	X	-	-	-	-	-
<i>T. natans</i>	-	-	X	X	X	-	-	-	-	-
<i>C. sapidus</i>	X	X	X	X	X	-	-	-	-	-

**Densities of the Dreissenid Mussels:**

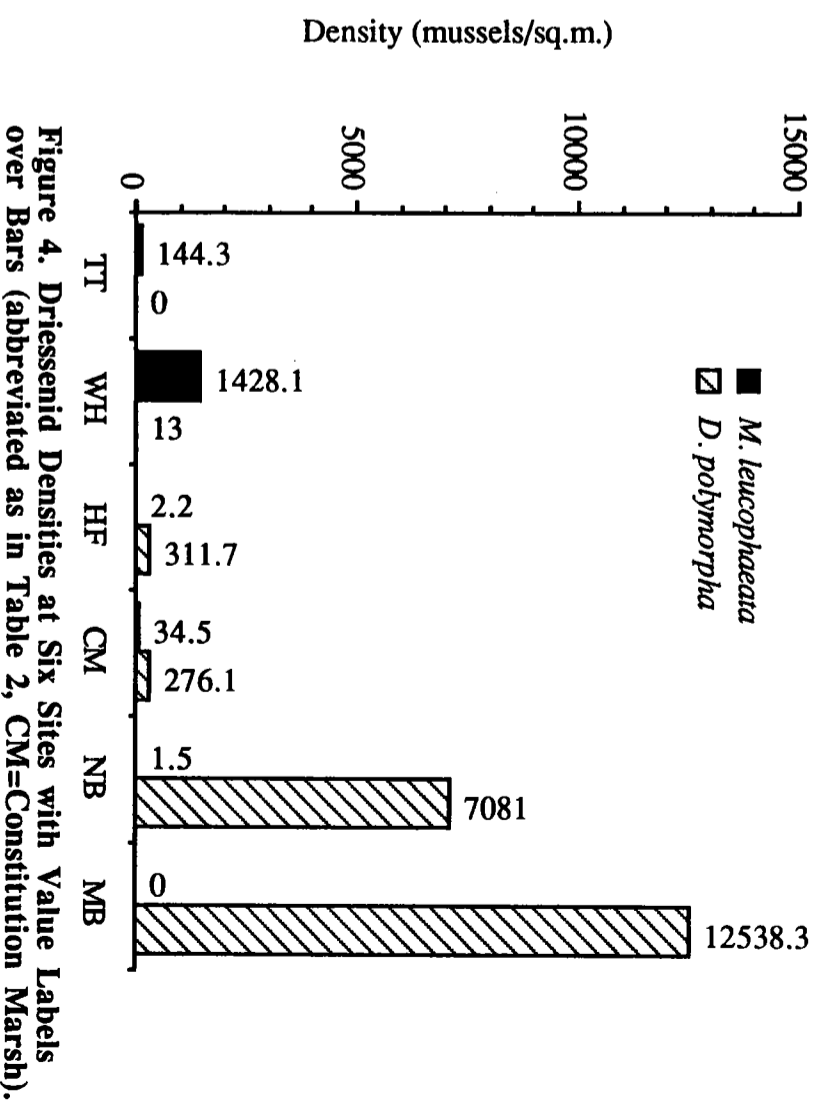
Despite the initial settlement of the mussels on the PVC plates, few to no mussels maintained themselves on the plates from one week to the next. It appeared that either the plates or the handling discouraged permanent settlement; juvenile bivalves were occasionally observed crawling off the plate, suggesting a handling effect. Alternatively, juvenile mortality is very high or veligers routinely relocate. This deterrent effect precluded accurate assessment of mussel densities on the PVC plates; therefore, only the cinder blocks and natural substrate were sampled for mussel densities.

*Dreissena polymorpha* cinder block densities were significantly highest ( $P < 0.0001$ ) at Marlboro, decreased at each more southern site, were very low at West Haverstraw, and were not found at Tarrytown. *M. leucophaeata* densities on the cinder blocks, on the other hand, were highest ( $P < 0.0209$ ) at West Haverstraw, decreased significantly ( $P < 0.0114$ ) at the more northern sites, and were not found at Marlboro (Fig.

4). Additionally, there was a significant species by site interaction (Table 4). Thus, while overlap occurred, the density of the less abundant dreissenid species was significantly lower than the density of the predominant mussel at each of the three overlap sites (Fig. 4).

At Constitution Marsh, where sampling was carried out on the natural rocky substrate, *M. leucophaeata* density was slightly higher than the average density found on the cinder blocks at the neighboring Highland Falls site, while *D. polymorpha* density was slightly lower than the corresponding average density at Highland Falls (Fig. 4).

Additionally, the percent cover of *Balanus eburneus* and a colonial hydroid followed a pattern generally similar to the dreissenid densities (Fig. 5).



**Figure 4. Dreissenid Densities at Six Sites with Value Labels over Bars (abbreviated as in Table 2, CM=Constitution Marsh).**

Table 4. ANOVA Table for the Dreissenid Species by Site Interaction. Data from Constitution Marsh (CM) were not included, and the Block(Site) factor was pooled into the residual because it was not significant [P=0.5006].

Source	df	Sum of Sq.	Mean Sq.	F	P
Dreissenid Species	1	1.01E8	1.01E8	257.34	<0.0001
Site	4	1.75E8	4.39E7	111.51	<0.0001
SpeciesXSite	4	2.13E8	5.32E7	135.37	<0.0001
Residual	20	7.87E6	3.93E5		

Dependent Variable=Mussel Density

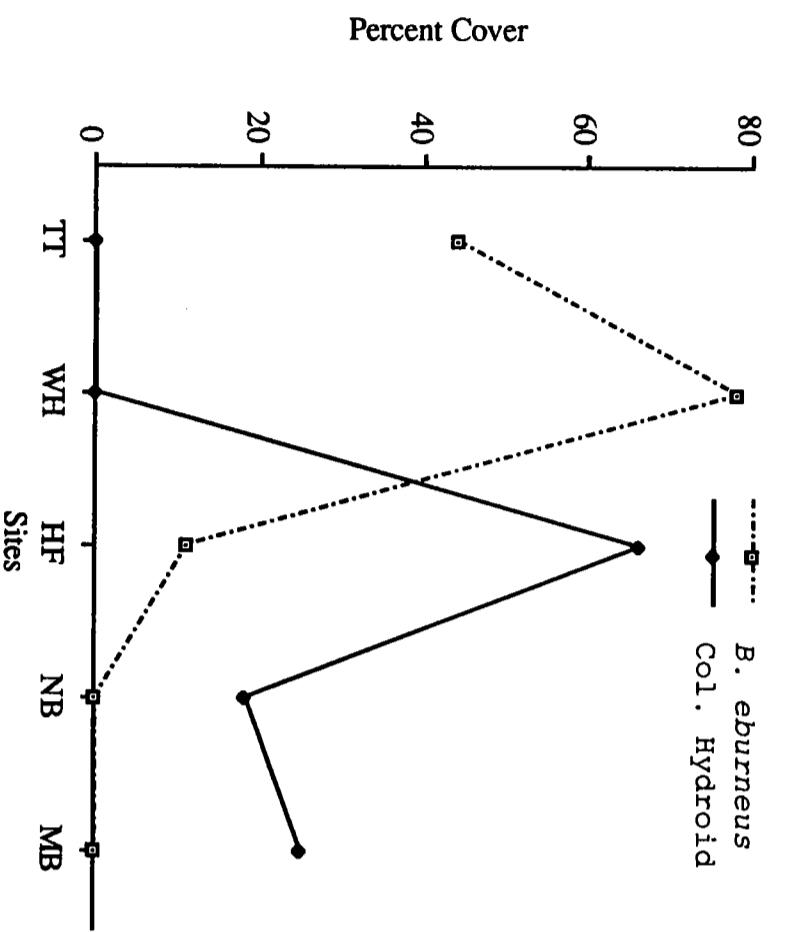


Figure 5. Percent Cover of a Barnacle and Colonial Hydroid on the Cinder Blocks at the Five Established Sites.

Mussel Shell Lengths:

There was a significant (P < 0.0001) difference in the average shell lengths of these two species by site (Table 5). *M. leucophaea* individuals from Newburgh were significantly shorter than those from Tarrytown and West Haverstraw (P < 0.0373, Fig. 6). More notably, however, the average length of *M. leucophaea* at Constitution Marsh was significantly longer than the average length of *M. leucophaea* at any of the five established sites (P < 0.0001). Furthermore, the average length at Constitution Marsh (14.93 mm) was about 2.5x greater than the next longest average *M. leucophaea* length (5.97 mm at Tarrytown), and about 4.0x the average length of conspecifics from the geographically closest site (3.73 mm at Highland Falls). Additionally, the minimum individual *M. leucophaea* shell length at Constitution Marsh was greater than the maximum individual *M. leucophaea* shell length at any of the four other sites where it was found (Fig. 6).

Table 5. ANOVA Table for the Dreissenid Species by Site Interaction. Data from Constitution Marsh (CM) were included in this calculation.

Source	df	Sum of Sq.	Mean Sq.	F	P
Dreissenid Species	1	45.69	45.69	12.05	0.0007
Site	5	610.40	122.08	32.19	<0.0001
SpeciesXSite	3	285.59	95.20	25.10	<0.0001
Residual	168	637.21	3.79		

Dependent Variable=Shell Length

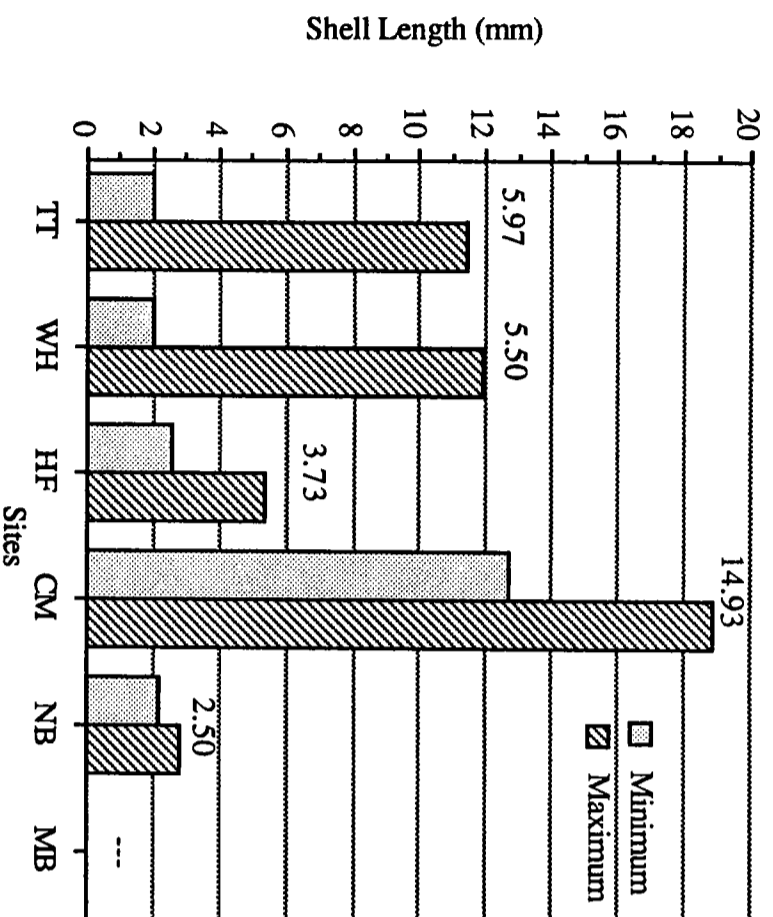


Figure 6. The Shell Length Data for *Mytilopsis leucophaeata* at the Six Sites (average shell length for the population at each site is displayed above the graph bars).

For *D. polymorpha* (Fig. 7), the average shell length of individuals from Constitution Marsh was significantly longer ( $P < 0.0001$ ) than the average for *D. polymorpha* at the three northern sites (Highland Falls, Newburgh, and Marlboro); individuals from the marsh, however, were only about 1.8x greater than the average length of *D. polymorpha* from Highland Falls (3.58 mm) and were not significantly longer than *D. polymorpha* collected from West Haverstraw (average 5.80 mm). Also, *D. polymorpha* at the three northern sites were, on average, significantly shorter than the average *D. polymorpha* at West Haverstraw ( $P < 0.0011$ ). Furthermore (Fig. 7), unlike the *M. leucophaeata* case, the shortest individual *D. polymorpha* shell length at Constitution Marsh was shorter than the maximum individual *D. polymorpha* shell length at any of the four other sites at which *D. polymorpha* was found.

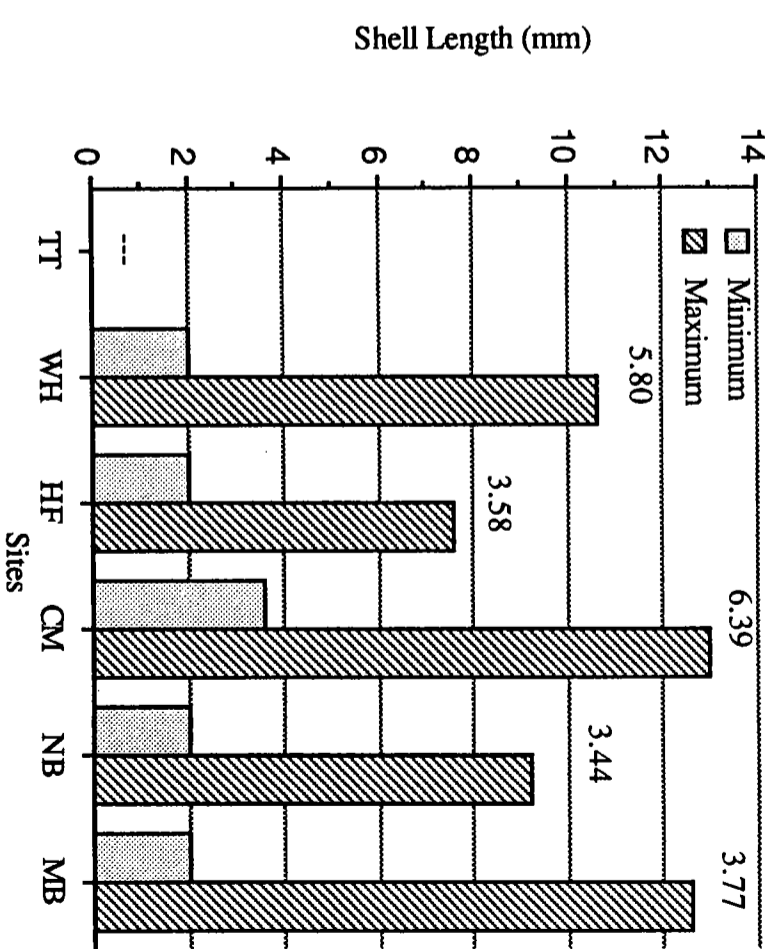


Figure 7. The Shell Length Data for *Dreissena polymorpha* at the Six Sites (average shell length for the population at each site is displayed above the graph bars).

#### DISCUSSION

The presence/absence data confirmed the predictions of Strayer and Smith (1992) and MacNeill (1991a); i.e., *D. polymorpha* 1) successfully settled and survived in the lower Hudson River Estuary, invading as far south as West Haverstraw, and 2) overlapped the range of *M. leucophaeata* from at least Newburgh south to West Haverstraw.

These ranges, as predicted by salinity tolerances of European populations, were similar to the patterns observed for a variety of other species, roughly broken down into "upriver" (*D. polymorpha*, *T. naans*, and a colonial hydroid) and "downriver" species (*M. leucophaeata* and *B. eburneus*). With the exception of *C. sapidus* which ranged

throughout this portion of the estuary, each of these observed patterns closely correlates with the salinity regime: three "fresher" sites (Marlboro, Newburgh, and Highland Falls) and two more saline sites (West Haverstraw and Tarrytown).

Despite this real encroachment by *D. polymorpha*, the potential for interactions with *M. leucophaeata* is debatable given the extremely low cinder block densities of the less common mussel at each of the three overlap sites. At Newburgh and Highland Falls, where the sites were dominated by *D. polymorpha*, *M. leucophaeata* was present in extremely low densities (1.5/m<sup>2</sup> and 2.2/m<sup>2</sup>, respectively), and the reverse was true at West Haverstraw, where *M. leucophaeata* dominated (13.0 *D. polymorpha*/m<sup>2</sup>). Thus, while these two species' ranges overlap, interactions between these dreissenid mussels appear to have been minor over this season on the cinder blocks.

However, data collected from natural rocky substrate at Constitution Marsh suggest an alternate route leading to interactions between these mussels. Although the density of *M. leucophaeata* was significantly lower than that of *D. polymorpha* density (34.5/m<sup>2</sup> vs. 276.1/m<sup>2</sup>), it was higher than the *M. leucophaeata* cinder block density at neighboring Highland Falls (2.2/m<sup>2</sup>), suggesting that the cinder block sampling may have underestimated *M. leucophaeata* densities. Furthermore, the average shell length of *M. leucophaeata* collected at Constitution Marsh was longer than the averages for the members of the same species collected at any of the other sites, and about 4x the average length of *M. leucophaeata* collected on the cinder blocks at Highland Falls. Additionally, the shortest *M. leucophaeata* collected on the rocks of Constitution Marsh (12.7 mm) was longer than the longest *M. leucophaeata* collected on any of the cinder blocks (11.9 mm at West Haverstraw). These data suggest that *M. leucophaeata* collected at Constitution Marsh either 1) were older than the individuals collected on the cinder blocks or 2) grew faster than the mussels settled on the blocks. Indirect evidence based on *D. polymorpha* suggests that the latter argument is unlikely.

The average length of *D. polymorpha* collected at Constitution Marsh was significantly longer than the average length of *D. polymorpha* from Marlboro, Newburgh, and Highland Falls, but not West Haverstraw; the average length of *D. polymorpha* at the two most northern sites may have been depressed by the extremely high densities of late-burst young mussels produced by parent populations to the north. Additionally, the longest *D. polymorpha* collected on the rocks of Constitution Marsh (13.0 mm) was only slightly longer than the longest *D. polymorpha* found on any cinder block (12.6 mm at Marlboro). These relatively minor size differences suggest that the physical characteristics (e.g. flow, productivity) of Constitution Marsh did not dramatically increase growth of *D. polymorpha* and, presumably, the very similar *M. leucophaeata*.

Returning to the former argument, the larger size differences in the average length of *M. leucophaeata*, as well as the relatively long minimum size at Constitution Marsh, suggest that the *M. leucophaeata* collected at Constitution Marsh may be older than the *M. leucophaeata* collected on the cinder blocks. All of the *M. leucophaeata* on the cinder blocks settled on or after May 15, 1992, the date of block submersion, while individuals from Constitution Marsh appear to have settled in a previous year. Despite the low settlement of *M. leucophaeata* in 1992 in Highland Falls and, presumably, Constitution Marsh, the previously settled individuals in Constitution Marsh survived the summer, accounting for the higher densities on the rocks than on the cinder blocks.

Thus, the low salinity at Highland Falls seems to have inhibited *M. leucophaeata* settlement in that region of the river in this summer. However, salinity in the Hudson River Estuary varies with the level of precipitation; increased rainfall increases the downriver flow, pushing the salt wedge further south, and vice versa. In July, 1992, a month of very high precipitation, salinity was relatively low at Highland Falls. Based on the time of appearance of settled bivalve juveniles at Highland Falls and the densities on the cinder blocks, veligers were in the water column during this time and *M. leucophaeata* settlement was very low. In other periods of low rainfall or drought, however, the salinity

of the water at Highland Falls would be expected to increase. In such cases, *M. leucophaeata* would be expected to settle in that region and possibly further north, as suggested by the larger individuals collected in Constitution Marsh. Furthermore, these settled individuals, now consuming food and occupying space (possible limiting factors), are capable of surviving decreases in salinity at least as great as that recorded in Highland Falls in 1992. Similarly, *Dreissena polymorpha* may echo this pattern; in "wet" years, *D. polymorpha* can settle at "fringe" sites (i.e. West Haverstraw) and possibly survive subsequent years at that site by tolerating annual increases in salinity.

Thus, the cinder block data suggest that *D. polymorpha* and *M. leucophaeata* will not settle in abundance at the same site at the same time; i.e. one species' settlement correlates with the inhibition of the other's settlement. However, the data from Constitution Marsh demonstrate the ability of *M. leucophaeata* to survive in an area where the salinity is below the "preferred" level (as indicated by the lack of *M. leucophaeata* settlement at Highland Falls). Experimental studies (summarized in MacNeill 1991a, Strayer and Smith 1992) further suggest the converse ability of *D. polymorpha*. Therefore, in the field, interactions between these two species could be expected when newly settled mussels of one species encounter previously settled individuals of the other species from a prior time period when the salinity of the region was different. This long-term effect is likely to have a stronger detrimental impact upon *M. leucophaeata*; in "wet" years, when the overlap sites are available to *D. polymorpha* settlement, dense settlement is possible. Thus, in subsequent years, when these same sites are available for settlement by *M. leucophaeata* based on increased salinity, *D. polymorpha* may already occupy a great deal of the available space. In the converse situation, the lower densities of *M. leucophaeata* are not likely to present the same space limitation problem to *D. polymorpha*.

The question of the future of the *D. polymorpha* invasion of the Hudson River Estuary also needs to be addressed; is the invasion likely to continue downriver next year? The data from this summer suggest that *D. polymorpha* may not spread much further south

in the river, except in isolated fresh-water inlets. First, no *D. polymorpha* were found at Tarrytown by the end of September, 1992; in all likelihood, *D. polymorpha* had access to this site, since the veliger stage lasts an average of 2 weeks and the closest recorded mature population (settled in 1991) was in Poughkeepsie, 78 km upriver. Furthermore, the large quantity of human river-traffic was a likely source of hitchhiking *D. polymorpha* veligers and newly-settled juveniles to Tarrytown throughout the summer of 1992. Despite the obvious opportunity for *D. polymorpha* to invade Tarrytown, none were observed at that site, indicating that *D. polymorpha* is not likely to spread much further downriver without a great change in the river's salinity.

While *D. polymorpha* may not spread much further south, the densities at each site of occurrence may increase dramatically as more veligers are supplied from upstream and produced by local mature individuals. The high productivity of the Hudson River Estuary (Gladden et al. 1988) could support much greater densities; thus, *D. polymorpha* may present both an economic and ecological threat similar to that seen in the Great Lakes and the fresh water portion of the Hudson River.

### CONCLUSIONS

Several conclusions can be drawn from this study:

1. Strayer and Smith's (1992) prediction that *D. polymorpha* was capable of invading the Hudson River Estuary to West Point [RKM 82] and isolated "fresher" inlets was validated; *D. polymorpha* was found as far south in the Hudson River as West Haverstraw [RKM 60], a site influenced by a fresh water source and downriver of West Point;

2. MacNeill's (1991a) prediction that the ranges of *D. polymorpha* and *M. leucophaea* would overlap was also confirmed; the two mussels co-occurred from Newburgh to West Haverstraw [RKM 94 to 60]:

3. The highest densities of each mussel correlated well with the salinity data (*D. polymorpha* was most dense at the four "fresher" sites (including Constitution Marsh), while *M. leucophaea* was most dense at the two saltier sites): Thus, while the two dreissenid mussels overlapped, at any site of overlap the average density of the less abundant mussel was very low relative to the predominant mussel's average density;

4. Based on the shell length data, live *M. leucophaea* collected at Constitution Marsh [RKM 83] appeared to have settled in a previous year demonstrating the capability of the adults to survive a 1992 decrease in salinity that deterred *M. leucophaea* settlement: Similar differential adult-veliger tolerances are predicted for *D. polymorpha* based on prior laboratory studies;

5. Interactions, such as competition, therefore, are unlikely to play a dominant role between individuals of either species settling in a given year; however, interactions between these two species can be expected to be more significant between mature individuals of one species (from a prior year) and newly settled individuals of the other species; and

6. The *D. polymorpha* invasion of the Hudson River Estuary has reached an apparent southern limit near West Haverstraw [RKM 60]; densities of *D. polymorpha* at sites within this range are expected to increase, potentially to nuisance levels.

#### RECOMMENDATIONS

This study raises many questions, of which the most pressing is whether densities of these dreissenid mussels at the sites of overlap will increase in subsequent years as salinity fluctuates annually. Studies similar to this one could be repeated in the following years; if, for example, Highland Falls experiences a higher salinity in the summer of 1993,

any change in *D. polymorpha* and/or *M. leucophaea* settlement could be correlated to this change and compared to the results from 1992. Furthermore, experimental work should be done on the impact of non-optimal salinity upon each dreissenid's settlement success, metabolism, and reproductive success; under controlled conditions, does low salinity (0-1 ppt) negatively impact *M. leucophaea*, and does high salinity (4-6 ppt) harm *D. polymorpha*?

Secondly, due to the overlap of these dreissenids and the probable increasing densities in that zone of overlap, possible interactions between these species should be investigated, including 1) competition for food and space, 2) veliger predation and cannibalism by each mussel of both species, and 3) differential vulnerability of the two mussels to predation (i.e. the blue crab, *C. sapidus*).

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