ILLINOIS
NATURAL HISTORY
SURVEY

Zebra Mussel Study on Lake Michigan

F-119-R

Annual Report
to
Illinois Department of Conservation

Center for Aquatic Ecology

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September 1992

Aquatic Ecology Technical Report 92/13

ZEBRA MUSSEL STUDY ON LAKE MICHIGAN

July 1, 1991 through June 30, 1992

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Submitted to
Division of Fisheries, Illinois Department of Conservation
in fulfillment of the reporting requirements of
Federal Aid Project F-119-R

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September 1992

This study was conducted under a memorandum of understanding between the Illinois Department of Conservation and the Board of Trustees of the University of Illinois. The research was performed by the Illinois Natural History Survey, a division of the Illinois Department of Energy and Natural Resources. The project was supported by funds made available through the Federal Aid in Sport Fish Restoration Act and administered by the Illinois Department of Conservation. The form and content of this report and the interpretations of the data are the responsibility of the University of Illinois and the Illinois Natural History Survey and not the Illinois Department of Conservation

Acknowledgments

Many thanks go to the following people for their work on this project: Tammy Keniry and Nan Trudeau coordinated and performed veliger and larval sampling; Mike Keniry and Wayne Brofka assisted with adult zebra mussel sampling and assembled and deployed the experimental settlement plate units; Wayne Brofka and Nan Trudeau analyzed all of the plates after retrieval; Rob Pope, Steve Robillard, and Tim Macek assisted with field work and sample processing; David Lansky provided statistical support and consultation in experimental design; and Martha Kneuer provided administrative support. Phil Fragassi and Don White of the Zion-Benton Water Treatment Plant generously provided information and access to their pump house for sampling; Don Jensen (Highland Park Water Treatment Plant), Ron Cervenka (Chicago Park District), Jim Flannery (LTV Steel), Ken Moses (Lever Brothers), Bill Hoffman (Northern Indiana Power Company), John Sapia (Bethlehem Steel), Bob Kane (Great Lakes Naval Base) and Michael Moran (Village of Glencoe Water Filtration Plant) kindly facilitated access to their sites for zebra mussel sampling; the Illinois Geological Survey provided information about their sightings of adult zebra mussels along the Illinois shoreline.

Abstract

Since their arrival in Lake St. Clair in 1986, zebra mussels (*Dreissena polymorpha*) have fouled intake pipes, navigation aids, and recreational beaches, and have had negative impacts on native species in the Great Lakes. Their ability to filter large volumes of water threatens to deplete the micro-organisms which are the base of the food chain for sport and commercially-caught fish. The mussels' high fecundity and strong attachment to hard substrates has caused major biofouling problems as well as high mortality among benthic organisms, especially native clams. The appearance of zebra mussels in Chicago in 1989 stimulated concern about predicting their local effects both on the environment and man-made installations. The objectives of this study were to (1) provide predictive information about where zebra mussels are likely to colonize in south-western Lake Michigan, (2) monitor mussel population growth and spread in the lake, (3) examine their settlement behavior, and (4) document their effects on native planktonic and benthic species. European data and diver observations in Lake Michigan indicate that all hard substrates between 2m and at least 20m depth are vulnerable to zebra mussel colonization; approximately 20% of the nearshore area is comprised of material to which zebra mussels can attach. Above 2m, the mussels will be annually removed from many areas by ice scour. Monitoring of zebra mussel veligers (larvae), settling juveniles, and adults along the Illinois and Indiana shorelines indicated that (1) by 1991 all areas of the shoreline had medium to low densities of mussels, (2) an exponential population growth was seen in 1991, and will probably continue in 1992, and (3) reproduction appears to be progressively delayed and mussel densities decrease from south to north. Settlement of juvenile mussels on experimental plates indicated that the mussels settled preferentially on the upper surface of textured, horizontal, shaded plates versus lower surfaces or smooth, vertical plates. They also strongly avoided sunlit areas. They did not show strong preferences among the various substrate materials used (wood, fiberglass, concrete, limestone, aluminum, steel, Plexiglas, glass, and PVC), but they strongly avoided galvanized steel. While it is too early in the study to infer that changes in populations of planktonic species can be attributed to zebra mussels, definite impacts of the mussels were noted on native gastropods and clams, including fingernail clams. All of these benthic species were found in some areas to be heavily encrusted with juvenile mussels. Water clarity increased dramatically between 1991 and 1992, suggesting that zebra mussels may be depleting the supply of suspended organisms and inorganic particles in the water column. This effect has already been observed for several years in Lake Erie. Consequences of this increased water clarity may include increased macrophyte growth and decreased fish catches in assessment gear due to visual avoidance of the gear.

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Introduction

One of the most critical issues facing researchers and resource managers today is the unknown ecological effect of invading non-indigenous aquatic species. The most recent invader which threatens to cause significant ecological disruption in the Great Lakes is the zebra mussel, *Dreissena polymorpha*. Since their introduction to Lake St. Clair in 1986, zebra mussels have appeared in all of the Great Lakes the major eastern inland waterways (Illinois, Hudson, Allegheny, Tennessee, Ohio, and Mississippi river drainages). Zebra mussels have a combination of characteristics which make them an especially effective invader - high fecundity, a planktonic larval stage, tolerance for a wide range of environmental conditions, and a generalist filter feeding strategy. These features, in combination with the strong attachment of adults to solid substrates, make the zebra mussel a severe nuisance to humans as well as a threat to the ecology of the Great Lakes. The mussels can clog water intake pipes in water treatment facilities, power plants, industries, and boats; they have also fouled commercial fishing nets, spawning reefs, and recreational beaches. Because they feed on planktonic organisms, the mussels may adversely impact the aquatic food web of the Great Lakes. The purposes of this study are to monitor the spread of zebra mussels in Lake Michigan, and to examine the effects of zebra mussels on native species. In particular, this study has four stated objectives:

1. Document the areas of the Illinois shoreline of Lake Michigan which will favor zebra mussel colonization.

2. Establish zebra mussel monitoring stations along the Illinois shoreline of Lake Michigan.
Zebra mussels first appeared in Lake Michigan near Chicago in 1989. By 1990 they had already begun to appear in intake pipes of shore-based industries and public utilities. Treatment of water intakes to kill attached mussels is expensive, and requires time for equipment installation. In order for utilities and marinas to be prepared to handle mussel-related problems, they need to have early warning of the appearance of zebra mussels, and information about the projected impact of the mussels. To provide this information, we monitored veligers, juvenile and adult mussels to determine when and where zebra mussels have spread in Lake Michigan along the Illinois shoreline, to determine population densities and growth rates, and to confirm predictions about areas which will be most highly colonized by zebra mussels.

3. Determine substrate preferences of zebra mussel larvae during and after settlement.
Information about zebra mussel substrate preferences is important for predicting which areas they will impact, for comparison of data from different sampling techniques, and for development of control methods. Data from European studies indicate that zebra mussel settlement densities on PVC and iron were over two orders of magnitude greater than on copper and brass (Walz 1973). Larvae avoid all plastics except PVC until the surfaces are coated with a layer of natural biological material (Van Diepen and Davids 1976). The mussels also show preferences for the undersurface of artificial substrates (Lewandowski 1976, Walz 1973). No studies have examined settlement on glass (a recommended sampling material), and no detailed examination of post-settlement movements has been made. Ultimately, an understanding of settlement preferences may lead to the development of disposable substrates which would attract zebra mussels away from critical areas such as intake pipe walls.

4. Collect pre- and post-invasion data on native benthic and planktonic populations.
Zebra mussels may affect aquatic microorganisms directly by ingestion of small species, or indirectly by depleting food sources of larger species. The mussels filter feed by ingesting any particles between 5 and 450μm (Sprung and Rose 1977). Undigested material is ejected in a mucoid ball (pseudofeces). The net effect is the sedimentation of suspended organic material. The deposition of pseudofeces may positively affect benthic and epi-benthic organisms, due to increased availability of food, or may adversely affect them due to depletion of benthic oxygen during pseudofecal decomposition. Populations of micro-

plankton may be depleted, resulting in the lowering of the forage base for zooplankton and planktivorous fish. Of particular concern is the effect of decreasing the food supply of alewife and juvenile bloater, which are important forage for salmonids and other sport fish. If zebra mussels deplete the planktonic organisms which are prey for forage fish, sport fish such as walleye, yellow perch, and salmonids are likely to be affected. Our aim was to assess changes in planktonic and benthic populations which can be attributed to the presence of zebra mussels.

When evaluating changes in planktonic and benthic populations, caution must be used in attributing changes to the presence of zebra mussels. Short-term changes in species numbers and abundance may reflect normal ecological fluctuations rather than effects due to the mussels. To confirm that local effects are due to zebra mussels, data should be collected in areas where mussels have become established, and in ecologically similar and adjacent areas which are still free of mussels. Because of the short term of this study (two years), the conclusions drawn about long-term ecological effects of the zebra mussels will necessarily be tentative.

Methods

Zebra mussel colonization potential: Natural areas where zebra mussels are likely to establish colonies were determined by first reviewing the European literature for data on mussel preferences for substrate, depth, temperature, and other environmental variables. These data were used in combination with geological descriptions of the Illinois shoreline of Lake Michigan, available from the Illinois Geological Survey, to delineate areas that have a high vulnerability to colonization (Collinson et al. 1979, Norby and Collinson 1977). Underwater surveys were conducted using scuba at 12 sites between Milwaukee and Chicago (Table 1). At sites where sufficient mussels could be found, densities were assessed by counting all zebra mussels within a 30cm or 100cm square quadrat. To avoid inadvertent selection of atypical density areas, we placed the quadrat by dropping or throwing it, and allowing it to settle unimpeded. Mussels within a minimum of four quadrats were counted at each site to estimate variance in mussel densities. Occasionally zebra mussel densities were estimated from a single quadrat, due to diver limitations such as cold or low air. No variances are available for density estimates at these sites. At sites where mussel densities were extremely low and density estimates were difficult to establish with any precision, densities are listed in Table 1 as <1 mussel/m^2. At sites where mussel densities were moderate, we removed all of the mussels within the quadrat and placed them in a bottle, then counted them in the laboratory. This method underestimated mussels if many small individuals were present, as these mussels often could not be prised whole from the substrate. In 1992, when mussel densities in most areas were extremely high, we collected representative pieces of substrate to which mussels were attached. In the laboratory, we estimated mussel densities by counting mussels within small areas (4-10cm2). We then extrapolated the counts to average densities in the field using underwater photographs of zebra mussel colonies on various substrates.

Settlement behavior and substrate choice: To test the effect of texture, color, orientation, and material on settling preferences, twelve replicate sets of settlement plate units were constructed which comprised plates of PVC, black Plexiglas, glass, clear Plexiglas, and PVC (in that order; Fig. 1). All plates were 15cm square, deployed parallel to each other on a threaded rod. The plates were separated by 2.5cm lengths of copper pipe, which is toxic to mussels, to discourage movement of settled animals between plates. The copper spacers were isolated from the plates using a stainless steel washer, to inhibit galvanic action between metal plates and the spacers (Fig. 1). All plates in half of the units were uniformly roughened using 60 grit sandpaper, except for the glass which was purchased as frosted glass. Two units of smooth plates and two units of roughened plates were deployed at each site, with one unit in each set deployed horizontally and one deployed vertically. These units comprised experiment 1. Experiment 2 tested the effect of substrate type on settlement behavior. Six replicate sets of each of the following units were constructed in the same manner as those for experiment 1: (a) plates made of limestone, steel, aluminum, and wood, and (b) concrete, galvanized steel, and fiberglass (Fig. 1). All of these units were deployed with the plates horizontal. Two replicate sets of units for experiment 1 were deployed at Burnham Harbor, Michigan City, and the Port of Indiana (Burns Harbor) on August 29 and September 4. Two replicate sets of units for experiment 2 were deployed at Michigan City, Hammond, and the Port of Indiana on August 12 and 24. All units were retrieved in early November.

Larval densities on the settlement plates were quantified by counting all of the animals within 1 cm squares in a vertical column down the middle of the plate, and in 1 cm squares in horizontal line which bisected one of the holes in the plate (Fig. 2). This design allowed quantification of the effect of the hole and the washer on the settlement of zebra mussel larvae. Larvae were not counted in squares which bordered on the edge of the plate, as handling was presumed to have dislodged some larvae from this area.

Veliger and juvenile monitoring: Monitoring stations were established at 11 sites along the Illinois and Indiana shorelines (Table 1; Figure 3). Sites were either harbors or intake wells at industries and public utilities. These sites provided protection for sampling equipment from storms and vandalism; intake flows have also been shown to provide sampling areas representative of the open lake (Makarewicz 1991). Veligers were sampled every two weeks by sieving approximately 200 liters of water through a 63 micron mesh plankton net, either using a vertical tow or by pouring water through the net. Settled juveniles were sampled using three 15cm square Plexiglas plates deployed vertically in series at 3m depth. The bottom plate was removed at two week intervals, and a new plate was replaced in the middle, so that each plate was immersed for four weeks prior to collection. The top plate was used to measure total accumulation of mussels over the season. Slide racks were found to be too fragile for sampling in turbulent waters; however, a microscope slide was attached to each Plexiglas plate, and was examined to determine settlement density on a standard substrate type. These sampling protocols followed the recommendations of Marsden (1992).

Table 1. Zebra mussel monitoring sites used in 1991.

Site name	Description of site	Type of samples collected Veligers	Settled Larvae
North Point	North Point marina, adjacent to inner slips		x
Zion	Zion-Benton water treatment plant pump house	x	x
Great Lakes	Great Lakes Naval Station water treatment plant intake well	x	
Highland Park	Highland Park water treatment plant intake well	x	
Glencoe	Village of Glencoe water treatment plant	x	
Burnham Harbor	Burnham Harbor off floating dock		x
Whiting, IN	industrial plant wet well	x	x
E. Chicago 1	industrial plant intake channel	x	x
E. Chicago 1	industrial plant pump house	x	x
Gary, IN	power plant discharge channel	x	
Burns Harbor 1	industrial plant wet well	x	x
Burns Harbor 2	industrial plant cooling water discharge pipe	x	x
Burns Harbor 3	power plant cooling water discharge channel	x	
Michigan City	power plant cooling water forebay	x	x

Each water sample was analyzed by counting all veligers within each of three 1ml subsamples. Material in the water sample was kept in suspension during sub-sampling using a magnetic stirring bar. Settled mussels were quantified by counting the total number of mussels within ten replicate 1.5cm squares on each Plexiglas plate. The total number of mussels on each microscope slide was counted.

Benthic and plankton studies: During May and June we collected large zooplankton and larval fish using a 0.5m diameter, 1:4 bias plankton net with 363μm mesh.. The net was suspended from a frame mounted in front of a 17' (5.7m) Boston Whaler, and pushed at a speed of 3-4 knots. Four 0.5 mile transects were sampled in this manner approximately twice per week as weather permitted. Samples were taken after sunset as soon as complete darkness occurred. All four sites were located within one mile of Waukegan Harbor. Two sites were located at the 5m depth contour and two at 10m. All sites were marked by Loran coordinates. Samples were taken in the same manner from 1987 through 1990, from mid-May to mid-July by Bill Horns as part of another project. In the laboratory, larval fish were identified to species and counted. Zooplankton will be identified to family or genus and counted. These data will provide zooplankton and larval fish densities prior and subsequent to the zebra mussel invasion.

In June, 1991, during an unrelated study, we collected a number of snails and fingernail clams (Sphaeriids) using a 3m otter trawl. Many of these molluscs had juvenile zebra mussels attached to their shells. Consequently, in 1992 we began quantitative underwater collections of both snails and fingernail clams to attempt to estimate the impact of zebra mussels on these native taxa. Gastropods were sampled on hard substrates by picking them off the substrate within a 30cm or 100cm square quadrat. Fingernail clams were collected by trawl, and by sieving soft substrates within a quadrat through a 2 mm mesh kitchen sieve. Fingernail clams were also collected by otter trawl. All samples were preserved in 70% ethanol after being brought to the surface. In the laboratory we counted the number of zebra mussels attached to each snail or clam, and recorded the range of mussel sizes and the 'host' mollusc size. Most of these data will be reported in the next annual report.

Results

Zebra mussel colonization potential

In 1991, diver surveys revealed low densities of zebra mussels on hard substrates at all sites (Table 2). Thus, zebra mussels have colonized, to some degree, the entire shoreline from Milwaukee to south Chicago. At the northern sites, most mussels were found singly or in groups of less than five animals; in the Chicago harbors, mussels were usually clustered together in cracks and crevices. Many small (1-3mm) mussels were found at these sites, which were inadequately sampled by divers due to the inability to scrape them off rocks intact. These small mussels represented the early year class from 1991. Few mussels were found on sand or silt.

By early 1992, the change in zebra mussel densities from 1991 was dramatic. The most altered site, the bedrock hump near Waukegan Harbor marked by a green buoy, was 100% covered with zebra mussels in densities of 217,500 to 382,500 mussels per square meter. Most of the mussels were 2-10mm in length, indicating that they were spawned late in the fall of 1991.

Table 2. Adult zebra mussel densities in southwestern Lake Michigan, 1991 and 1992.

Site	Date sampled	Depth (m)	Substrate	Zebra mussel densities per m^2	Size range (mm)
1991					
Milwaukee breakwall	Aug. 15	3	cobble and gravel	none above 2m	
Black Can Reef site 1	Aug. 15	8	infilled cobble and gravel	4.5±3.1	
Black Can Reef site 2	Aug. 15	6	cobble, infilled gravel, bedrock	6±5.6	
Wind Point South Shoal	Aug. 14	7-8	cobble boulders	3.25±3.8	<18
Waukegan intake line	Jun. 20	3-10	infilled cobble, sand	<1	5-18
Waukegan green buoy reef	Jul. 10	7	flat, smooth bedrock	25±7	18-25
Fort Sheridan NE reef	Jul. 9	8	infilled cobble, gravel	<1	5-23
Fort Sheridan SW reef	Jul. 9	12	sand, infilled gravel, clay	<1	5-23
Highland Park Reef	Jul. 9	7.5	solid, smooth bedrock	110	5-21
Calumet Park, Chicago	Aug. 29	2.5	mud, silt, broken rock	**	
Burnham Harbor	Aug. 29	3.5	cobble, broken rock	41.7±55.5	
Montrose Harbor	Aug. 29	2.5	limestone blocks, sand	**	
Gary, IN	Jul. 11	>3	concrete, silt	1,644±745	5-10
1992					
Waukegan green buoy reef	July 15	7	flat, smooth bedrock		
Glencoe shoal	July 10	<2.5	bedrock; sand, infilled cobble		
Wilmette 1mi W of WR2	July 16	8-11	cobble infilled with sand		

Settlement behavior and substrate choice

Data from experiments 1 and 2 were examined graphically so that broad trends in the settling behavior of the mussels could be observed. Statistical analysis of the results is still in progress and will be submitted in a subsequent report. First, total counts from all squares on each plate were obtained. In experiment 1, data for each of the paired variables (i.e., horizontal vs vertical, rough vs smooth, dark vs light) were treated as follows: the total number of settled larvae on plate was subtracted from the total number on the corresponding plate, which was identical for all variables except one. For example, the total number of mussels on a horizontal *smooth* glass plate deployed at Burnham Harbor were subtracted from the total on a horizontal *rough* glass plate deployed at the same site to measure the relative preference for smooth versus rough surfaces. The resulting figure was divided by the total number of mussels on the two plates (or surfaces compared) to demonstrate the magnitude of the difference. If the larvae showed no preference for one factor over its alternate, across all comparisons there would be as many positive as negative calculated numbers; if one factor was strongly preferred over its alternate, the calculated figures would be mostly positive and large. Results from this analysis indicate the following: zebra mussels showed a strong preference for horizontal over vertical surfaces (Fig. 4), rough versus smooth surfaces (Figure 5) the upper surface versus the under surface of a given plate (Figure 6); they avoid sunlight (Fig. 7); they show a weak preference for black versus transparent substrates (Figure 8). In Experiment 2, no clear ranking of substrate preferences was observed except in the case of galvanized steel, which was strongly rejected (Figure 9).

Veliger and juvenile monitoring

Zebra mussel reproduction, indicated by the appearance of veligers in the water samples, was first observed at Whiting and Michigan City, Indiana, on June 3, 1991 and continued through September 23, 1991 (Table 3). Reproduction occurred at all sites along the entire Illinois and Indiana shoreline by mid-July. Peak veliger densities of over 37,000 veligers per cubic meter were noted at the southernmost sites along the lake shore.

Table 3. Summary of zebra mussel veliger monitoring along the Illinois and Indiana shorelines of Lake Michigan in 1991. Veliger counts are given as mean number of veligers per cubic meter of water. Additional data including standard deviations are given in Appendix 1.

Week of...	Zion	Great Lakes	Highland Park	Glencoe	Whiting	East Chicago1	East Chicago 2	Gary, IN	Burns Harbor	Michigan City
May 6		0	-	-	-	-	-	-	-	-
13	-		-	-	-	-	-	-	-	-
20	0	0	-	-	-	-	-	-	-	-
27	0		-	-	-	-	-	-	-	-
June 3	0		0	0	574	-	-	0	0	341
10	0	0	0	0	-	0	0	425	393	0
17	0	0	0	0	0	-			-	-
24	0		817	0	-	0	330	991	present	0
July 1	0	0	0	0	-	-	-	-	-	-
8		-	0	0	-	0	1,541	600	0	1,297
15	0	0	0		-	-	-	-	-	-
22	471		833	1,875	-	67	2,123	875	8,168	1,761
29	550	0	917	3,459	-	-	-	-	-	-
Aug. 5	1,414	-	1,867			189	5,501	37,333	7,921	2,075
12	0	307	0	341	-	-	-	-	-	-
19	0		858	-	8,298	880	5,013	18,192	37,333	1,697
26	503	0	3,667	-	-	-	-	-	-	-
Sept. 2	-	-	9,717	-	13,579	491	275	1,458	7,450	2,051
9	220	750	1,792	2,318	-	-	-	-	0	-
16	0	-	0	-	314	0	158	3,000	500	2,515
23	0	-	-	-	-	-	-	-	492	-
30	0	-	-	-	-	-	-	-	0	-
Oct 7	0	-	-	-	-	-	-	-	0	-

Settlement of juveniles was first observed at Burnham Harbor and Michigan City on July 15 (Table 4). Extreme densities of settled juveniles were noted at Burnham Harbor (144,889/m^2) and Michigan City (113,778/m^2). Settlement occurred at all sites except the East Chicago site 2; however, settlement was low at all of the East Chicago sites, Gary, and Highland Park. This result is likely due to features of these particular sites which were not conducive to settlement on our plates. For example, high turbulence at one of the East Chicago sites may have discouraged settlement.

Benthic and plankton studies

The analysis of zebra mussel impacts on native benthic and planktonic species depends upon comparing pre-invasion data and/or data from uninfested sites with post-invasion data from infested sites. Changes in native species communities can only be attributed to zebra mussels, rather than other ecological cycles or perturbations, when both sets of data are available. Currently we have only analyzed pre-invasion collections of plankton and larval fish, and we are in the process of collecting and analyzing post-invasion data. Results from these analyses will be presented in a subsequent report.

Table 4. Summary of juvenile zebra mussel settlement monitored along the Illinois and Indiana shorelines of Lake Michigan in 1991. Counts of settled juveniles are given as mean number of juveniles per square meter of Plexiglas settlement plate. Additional data including standard deviations are given in Appendix 1.

- Week of...	North Point	Zion	Highland Park	Burnham Harbor	Whiting	East Chicago1	East Chicago2	East Chicago3	Gary, IN	Michigan City
May 6	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-
27	-	-	-	-	-	-	-	-	-	-
June 3	0	0	0	-	0	-	-	-	-	-
10	-	-	0	-	-	-	-	-	-	-
17	-		0	-	0	-	-	-	-	-
24	0	-	0	-	-	0	0	0	-	-
July 1	-	0	0	0	-	-	-	-	-	-
8	-	-	0	-	-	0	0	0	-	-
15	-		0	1,333	-				-	533
22	0	0	0	-	-	0	0	0	6,400	31,605
29	0	444	0	2,667						
Aug. 5	-	-	533	-	0	444	0	0	-	8,444
12	0	0	0	-	-	-	-	-	-	-
19	-	-	0	2,222	533	444	0	1,778	-	2,667
26	0	-	0	-	-	-	-	-	-	-
Sept. 2	-	-	0	144,889	8,444	-	0	0	-	113,778
9	20,000	4,444	0	-	-	-	-	-	-	-
16	-	-	0	13,333	20,444	-	0	0	-	1,333
23	29,778	89	-	-	-	-	-	-	-	-
30	-	-	-	4,889	0	-	0	0	-	378
Oct 7	0	0	-	-	-	-	-	-	-	-

Discussion

Zebra mussel colonization potential

European data indicate that adult mussels can survive in regions with monthly mean air temperatures from -15°C to 27°C, although larval development is optimal at 20-22°C (Mackie 1989, Strayer 1991), and reproduction does not commence until the water temperature has remained above 12°C for a few weeks. Recent observations indicate that females become ripe seven weeks after releasing eggs, so several reproductive cycles may occur in a single year if the temperatures remain above 12°C (Jerrine Nichols, USFWS, Ann Arbor, personal communication). The temperature profile of Lake Michigan is conducive to a long reproductive season, and winter ice cover is sufficiently short for overwinter survival to be high. The south-western end of the lake may be particularly favored by zebra mussels due to the number of thermal plumes from industries and power plants. Zebra mussels may continue to be reproductively active all winter within a thermally elevated area such as a discharge plume.

In Poland, maximum densities of adults were observed at depths between 2 and 12m, though in Germany mussels have been seen as deep as 44m (Stanczykoska 1964, Mackie 1989). Mussels have been trawled from the bottom of Lake Ontario at depths of 25m (Randy Owen, USF&WS, Rochester NY, pers. comm.), and mussels have been found on the walls of a 65m-deep intake tunnel adjacent to Lake Michigan (James Flannery, LTV Steel, pers. comm.). Thus, while zebra mussels may not utilize the deep central portion of Lake Michigan, they can colonize a band next to the shoreline which is several miles wide in most places. However, in most years the mussels will be removed from shallow areas (less than 2m deep) by ice scour. We have already noted this effect at inshore areas such as Glencoe Shoal. In 1992, mussel densities at the base of the shoal, at 3m depth, varied from 2,750 to 30,000 mussels per square meter, whereas no mussels were seen on any of the exposed bedrock at 1.5m.

Previous studies in Europe and elsewhere in the Great Lakes have indicated that zebra mussels will settle on a wide variety of hard substrates (Walz 1973, 1975; Lewandowski 1976, 1982; VanDiepen and Davids 1986). In areas of silt they will settle on any hard inclusions in the substrate such as pebbles or clams, often forming large clusters of mussels (Lewandowski 1982, Hebert et al. 1991, personal observations). However, broad areas of shifting substrates such as sand and silt tend to remain largely free of dense mussel colonization. The southwestern shore of Lake Michigan is largely composed of sand and small gravel, with an underlying bed of hard-pan clay (Collinson et al. 1979, Holm et al. 1987, observations during this study). Much of the substrate in the near-shore areas (i.e., within two miles of shore) is densely covered with small to large cobbles and occasional boulders, mostly set deeply into the sand and silt. Silurian bedrock reefs are scattered along the Illinois shoreline (Figure 10). Preliminary observations of one of these bedrock reefs in 1992, off Waukegan Harbor, revealed total coverage of the bedrock by zebra mussels, so that no rock was visible between the mussels. Densities were 300,000± 82,500 mussels per square meter, with the majority of mussels in the 2 to 10mm range. From diving surveys of substrate and colonization patterns of mussels in 1991 and 1992, I estimate that all hard substrates will be covered by mussels by the end of 1993, if not by fall 1992. This represents colonization of 20-40% of the lake bottom within 4 miles of shore. Mussels are also colonizing native unionid and sphaeriid clams in soft substrates, as well as gastropods and crayfish. Areas of hard-pan clay are totally devoid of mussel colonization, presumably because the substrate is too unstable for byssal attachment.

Results from our settlement experiments indicate that the mussels will settle on any of the substrates we examined (limestone, concrete, glass, Plexiglas, PVC, fiberglass, steel, wood, aluminum) except for galvanized steel. This observation confirms that the majority of man-made structures in the lake such as sheet pilings, breakwalls, boat hulls, intake structures, and navigation aids will be vulnerable to colonization. As noted above, however, structures within the range of ice scour or which do not remain in the water for periods of more than a few weeks will tend to remain free of heavy zebra mussel fouling.

Veliger and juvenile mussel monitoring

Our monitoring data clearly indicate that zebra mussel populations are well established and breeding throughout the Illinois and Indiana shorelines of Lake Michigan. These populations also appear to be in an exponential growth phase (Fig. 11), which according to European data could last for several years. Reproduction and settlement appear to be progressively delayed and somewhat lower in magnitude moving from south to north along the shoreline, as indicated by the first appearance of veligers in the water at each site (Fig. 12) and maximum densities of veligers at each site (Fig. 13). This gradient may reflect the southern point of introduction of the mussels in the lake, and the temperature gradient in Lake Michigan - not only does the southern portion of the lake naturally warm more rapidly than the northern portion, but the intensely industrialized southern shoreline produces localized thermal pollution. Preliminary data from our laboratory indicate that the mussels can continue to grow overwinter in thermally enriched discharge waters, whereas growth ceases in the unaffected lake water.

Substrate colonization

Our results indicate that settling juvenile zebra mussels prefer the upper surface of horizontal, roughened substrates over undersides, vertical substrates, or smooth substrates (Figs. 4, 5a, 5b, and 6). Preference of the mussels for dark versus transparent surfaces was not strong (Fig. 8). Mussels settled on a variety of man-made substrates, but rejected galvanized steel, presumably due to the toxicity of the zinc coating. These results compare with those from similar experiments by Kilgour and Mackie (in prep.), in which the following preferences were seen: wood > PVC > acrylic (=Plexiglas) > aluminum > galvanized iron. The results from comparing settlement on rough versus smooth vertical plates were somewhat equivocal - on horizontal plates at all sites and on vertical plates at Burnham Harbor and the Port of Indiana the mussels clearly preferred rough surfaces, whereas they tended to prefer smooth surfaces on vertical plates deployed at Michigan City (Figures 5a and 5b). No obvious reason exists for this disparity, such as mistaken coding of the plates, or an anomaly at the site.

In experiments using plates of several substrates deployed horizontally, Walz (1975) reported a marked preference of zebra mussel larvae for the undersurface of his experimental plates. However, Walz deployed each of his plates individually, so that the upper surface of each plate was exposed to sunlight. In contrast, each of our experimental plates was in shade; the upper and lower plates in each horizontal unit were used only to ensure that all the remaining plates had a plate on either side of them. Comparison of the uppermost PVC plate in each of our units with lower, shaded PVC plates showed that the mussels strongly avoided sunlit areas. On the upper, sunlit surface the mussels were often clustered in a diagonal line which matched the shadow of the brace used to hold the units together.

Zebra mussels often clustered on settlement plates around the edge of the washer which separated the plates from the copper spacers (Figs. 1 and 2). This clustering behavior was obvious when few mussels had colonized the plates, but was obscured when the plates were covered with mussels. To quantify this observation, we compared the proportion of the mussels clustered around the washer with the total mussels on each plate (Fig. 14). If the mussels were concentrated near the washer, we would expect an equivalent number of them to be found in the area adjacent to the washer and comparable unit areas elsewhere on the plate. In Fig. 14, points clustered around the labelled line indicate a distribution of mussels which is uniform with respect to the washer. On plates with low densities of mussels (less than 50 mussels in the areas counted), the density of mussels attached in the areas near the washers was much higher than elsewhere on the plate. This confirms our observations in the field, i.e., zebra mussels tend to cluster near crevices and breaks in the substrate. At high densities, other mussels provide substrate irregularities, so that the mussels are as likely to cluster with each other as against an irregularity in the actual substrate. At low densities, the mussels are more like to encounter surface irregularities than other mussels.

Results from the settlement plate experiments suggest that structures composed of galvanized steel or exposed to strong sunlight will be minimally impacted by zebra mussel colonization. These results explain in part why new colonies of mussels are usually found on the undersurface or sides of substrate material, rather than on the upper surfaces which are exposed to the most sunlight. In unrelated laboratory experiments we have also noted that pale mussels, with little or no dark striping, will tend to move more rapidly away from a brightly lit area than mussels with darkly pigmented shells. Presumably the unpigmented mussels suffer higher light penetration through their shells than dark individuals.

Our results also highlight the importance of choosing substrates carefully when monitoring for the presence of settling zebra mussels (Marsden 1992). Textured, horizontal, shaded substrates will have a higher probability of incurring settlement than smooth, vertical, brightly lit substrates, and will therefore be more useful for early detection of mussel invasion of new areas. Conversely, use of different types of substrates for quantitative estimates of zebra mussel population sizes will not yield comparable data. Monitoring programs which are intended to provide an integrated picture of zebra mussel population growth must coordinate their decisions about what settlement plate design to use.

Benthic and plankton studies

The effects of zebra mussels on densities of planktonic and benthic species cannot be examined until data from the second year of this study have been collected and analyzed. Only in 1992 did zebra mussel densities become sufficiently high that we may be able to correlate changes in planktonic and benthic populations with the presence of zebra mussels. However, several non-quantified observations and preliminary data from 1992 give an indication of the types of interactions we may expect. In a broad context, one of the observations of most concern is the heavy colonization of rocky cobble reefs by zebra mussels in south-western Lake Michigan. The Illinois shoreline of the lake is dominated by sand, bedrock, and clay substrates, so the relatively small cobble reef areas provide a rich physical habitat for a wide variety of benthic species. The crevices among the cobbles offer shelter for crayfish (*Orconectes* spp.), sculpins (*Cottus* spp.), and darters, and the cobbles provide a complex substratum for attached aquatic macrophytes, freshwater sponges, gastropods, and a variety of small crustaceans. Our observations of these reefs in 1992 indicated that zebra mussels colonize the interstitial spaces and their pseudofeces fill the smaller crevices. The physical structure of the mussel colonies also appears to trap sediments, creating large volumes of silt around the colonies which may suffocate some benthic species. The effect of the loss of shelter on crayfish and sculpins is not yet apparent. To date we have observed little direct interaction between crayfish and zebra mussels, barring collection of a dead crayfish covered in mussels. We cannot determine whether the crayfish died before or after the mussels settled, though the condition of the body suggests the latter. Zebra mussels can interfere with crayfish ecdysis (molting) by sealing the lines along which the exoskeleton usually splits. A large burden of mussels is also likely to be an energy drain on a moving crayfish.

Zebra mussels have begun to colonize the large native unionid clams in Lake Michigan, a behavior which has already been noted in Lake Erie (Hebert et al. 1991). The majority of clams picked up by our divers had from 10 to several hundred zebra mussels clustered around their anterior end. This colonization can affect the growth of the clams, and impedes their ability to dig into the substrate during storms or winter periods. Dense colonies of mussels can either seal the clam's shell closed, or prohibit the clam from closing the shell completely. Reduction of these clam populations will affect the ecosystem in Lake Michigan and also the commercial clam fishery in the Illinois and Mississippi rivers.

Our observations of mussel settlement on gastropods and sphaeriid clams indicate that the impact of the zebra mussels on native molluscs is not limited to the commercially important or 'obvious' species. Sphaeriid clams will likely suffer the same consequences of mussel settlement as do the larger clams species, but the effects will be more rapid due to the small size of the sphaeriids. The impact of settlement on snails is not clear, as they do not need to close their shells or burrow in the same way as clams. Mussel settlement near the opening to the shell could interfere with the ability of the snail to seal the opening with its operculum. The sheer mass of mussels on the shell is likely to cause an energy drain on the moving snail, and may increase the probability that the snail may be dislodged by currents or surge. Although we have only observed juvenile mussel on gastropods, the net weight of 50-100 small mussels is equivalent to that of the 'host' snail in many cases; within a few months to a year, the growing mussels will individually be larger than their host. Ultimately, the mussels could bind the snail to the substrate with their byssus threads. Reduction in populations of snails and fingernail clams will result in loss of a dietary item of several native fish, including the commercially important yellow perch.

During our settlement plate experiments we noticed a number of hydrophsycid caddis fly larvae had built cases on the plates at one site. Close examination revealed that a large proportion of the particles in their cases were juvenile zebra mussels, less than one millimeter in size. Because the plates were already in preservative when we examined them, we could not determine whether the mussels had been alive or dead when incorporated into the cases. Zebra mussels could have a positive effect on the caddis flies, by providing additional building materials if other materials are limited. More likely, the mussels may compete with the caddis flies for food, or cause a larval fly to expend extra energy to frequently shed and rebuild its case as the growing zebra mussels deform the shape of the case. We are currently devising experiments to examine the interaction between these two taxa.

Beginning in 1992, we also noted unusual water clarity throughout the sampling areas. Although Secchi depths were not taken consistently prior to 1992, the maximum Secchi depth noted between 1990 and 1991 was 4m. In contrast, 4m was the minimum Secchi depth noted during frequent measurements in 1992. Normally, periods of unusual water clarity occur due to upwellings of cold water caused by an internal seiche within the lake. A few days after the upwelling, the mixture of nutrient-rich colder water with the upper, warmer layers produces a brief plankton bloom which decreases water clarity. Prolonged water clarity is uncommon, and leads to the speculation that this event is similar to that observed in Lake Erie since 1988 - i.e., the consumption and sedimentation of algae, suspended silt particles, and small zooplankton by zebra mussels may have increased water clarity. One potential consequence of this change is that increased light levels may stimulate increased growth of aquatic macrophytes in shallow, nearshore areas. This would have negative consequences for boaters and swimmers, but may increase fish habitat. Other impacts of increased water clarity include lowered catches of fish in assessment gear such as trawls, due to visual avoidance of the gear.

In summary, a number of direct and indirect effects of zebra mussels in the nearshore area of southwestern Lake Michigan have been noted or hypothesized by our observations so far. Many of these effects may result in delayed, long-term changes in the invertebrate and fish community in the lake. In the ongoing segment of this study we will continue to collect quantitative data which will demonstrate the short-term, direct effects of zebra mussels, and allow us to predict the direction and magnitude of long-term changes.

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Appendix 1. Data from zebra mussel veliger and settled juvenile monitoring along the Illinois and Indiana shorelines of Lake Michigan, 1991. Descriptions of sites are given in Table 1. Dashes indicate absence of data.

		water	secchi	sample	liters	veligers/m^3		larvae/m^2 (Plexiglas)		larvae/m^2
Date	Site	temp	depth	depth	sampled	mean	S.D.	mean	S.D.	(glass slide)
7-Jun	North Point	-	-	-	-	-	-	0	-	-
26-Jun	North Point	-	-	-	-	-	-	0	-	-
23-Jul	North Point	-	-	-	-	-	-	0	-	-
2-Aug	North Point	24	1	-	-	-	-	0	-	-
16-Aug	North Point	-	-	-	-	-	-	0	-	-
30-Aug	North Point	25	2.4	-	-	-	-	0	-	
13-Sep	North Point	20	1.2	-	-	-	-	20,000	13,937	11,200
25-Sep	North Point	13	0.9	-	-	-	-	29,778	21,979	1,449
11-Oct	North Point	12	1	-	-	-	-	0	-	-
24-May	Zion	7.5	1.2	4.05	795	-	-	-	-	-
30-May	Zion	8	1.1	1.4	216	-	-	-	-	-
7-Jun	Zion	15	-	4	283	-	-	0	-	-
14-Jun	Zion	13.5	1	3	212	-	-	-	-	-
20-Jun	Zion	17	1	3	212	-	-		-	-
28-Jun	Zion	13	1.2	3	212	-	-		-	-
5-Jul	Zion	16.5	1	3	212	-	-	0	-	-
19-Jul	Zion	16	0.25	2.8	198	-	-	-	-	-
26-Jul	Zion	22	1.4	3	212	471	817	-	-	-
2-Aug	Zion	21	1.1	3	212	550	953	444	1,405	-
9-Aug	Zion	21	0.5	3	212	1,414	707	-	-	-
15-Aug	Zion	21	1	3	212	0	0	0	-	-
23-Aug	Zion	21.5	1	3	212	0	0	-	-	-
30-Aug	Zion	16	1.2	3	212	503	436	-	-	-
13-Sep	Zion	9.5	1.1	3	212	220	381	4,444	5,543	3,200
20-Sep	Zion	8	1.4	3	212	0	0	-	-	-
25-Sep	Zion	12	1.6	3	212	0	0	89	-	-
4-Oct	Zion	11	0.7	3	212	0	0	-	-	-
11-Oct	Zion	11.5	0.9	3	212	0	0	0	-	-
	-									
9-May	Great Lakes	8	1.9	3	589	-	-	-	-	-
23-May	Great Lakes	8	1.8	2	393	-	-	-	-	-
10-Jun	Great Lakes	14	1.8	3.5	247	-	-	-	-	-
20-Jun	Great Lakes	15	1.4	3	212	-	-	-	-	-
5-Jul	Great Lakes	14.5	1.8	3.5	247	-	-	-	-	-
18-Jul	Great Lakes	18.5	1	3	212	-	-	-	-	-
2-Aug	Great Lakes	21	1.4	3	212	-	-	-	-	-
16-Aug	Great Lakes	22	1.8	3	212	307	531	-	-	-
30-Aug	Great Lakes	20	1.6	2	141	0	0	-	-	-
13-Sep	Great Lakes	14.5	2	2.2	156	750	1,299	-	-	-
26-Sep	Great Lakes	12	1.6	2.2	156	-	-	-	-	-

Appendix 1. continued.

		water	secchi	sample	liters	veligers/m^3		larvae/m^2 (Plexiglas)		larvae/m^2
Date	Site	temp	depth	depth	sampled	mean	S.D.	mean	S.D.	(glass slide)
3-Jun	Highland Park	-	-	mixed	200	-	-	-	-	-
11-Jun	Highland Park	-	-	mixed	200	-	-	-	-	-
17-Jun	Highland Park	64	-	mixed	200	-	-	-	-	-
24-Jun	Highland Park	-	-	mixed	200	817	1,415	-	-	-
1-Jul	Highland Park	-	-	mixed	200	-	-	-	-	-
9-Jul	Highland Park	75	-	mixed	200	-	-	-	-	-
15-Jul	Highland Park	74	-	mixed	200	-	-	-	-	-
22-Jul	Highland Park	64	-	mixed	200	833	1,443	-	-	-
29-Jul	Highland Park	76	-	mixed	200	917	1,588	-	-	-
5-Aug	Highland Park	75	-	mixed	200	1,867	1,617	-	-	533
12-Aug	Highland Park	74	-	mixed	200	0	0	-	-	-
16-Aug	Highland Park	74	-	mixed	200	858	1,487	-	-	-
19-Aug	Highland Park	76	-	mixed	200	1,917	1,660	-	-	-
26-Aug	Highland Park	74	-	mixed	200	3,667	3,175	-	-	-
5-Sep	Highland Park	75	-	mixed	200	9,717	8,096	-	-	-
9-Sep	Highland Park	68	-	mixed	200	1,792	1,642	-	-	-
16-Sep	Highland Park	60	-	mixed	200	0	0	-	-	-
5-Jun	Glencoe	-	-	8.3	587	-	-	-	-	-
10-Jun	Glencoe	-	-	8.3	587	-	-	-	-	-
18-Jun	Glencoe	-	-	8.3	587	-	-	-	-	-
24-Jun	Glencoe	-	-	8.3	587	-	-	-	-	-
1-Jul	Glencoe	-	-	8.3	587	-	-	-	-	-
11-Jul	Glencoe	-	-	8.3	587	-	-	-	-	-
24-Jul	Glencoe	-	-	8.3	587	1,875	532		-	-
1-Aug	Glencoe	-	-	8.3	587	3,459	1,483		-	-
9-Aug	Glencoe	-	-	-	-	-	-		-	160
16-Aug	Glencoe	-	-	8.3	587	341	295		-	533
11-Sep	Glencoe	-	-	8.3	587	2,318	1,328	-	-	-
3-Jul	Burnham Harbor	-	-	-	-	-	-	0	-	-
17-Jul	Burnham Harbor	-	-	-	-	-	-	1,333	3,000	-
4-Aug	Burnham Harbor	-	-	-	-	-	-	2,667	3,108	4,267
18-Aug	Burnham Harbor	-	-	-	-	-	-	2,222	2,342	2,133
31-Aug	Burnham Harbor	-	-	-	-	-	-	144,889	49,010	86,000
16-Sep	Burnham Harbor	-	-	-	-	-	-	13,333	15,108	-
29-Sep	Burnham Harbor	-	-	-	-	-	-	4,889	3,279	7,467
7-Jun	Whiting	18.5	-	2.5	247	574	993	0	-	-
21-Jun	Whiting	23	-	3	212	-	-	0	-	-
8-Aug	Whiting	26.5	-	-	-	-	-	0	-	-
22-Aug	Whiting	27	-	3	212	8,298	754	0		533
4-Sep	Whiting	28	-	3	212	13,579	3,288	-	-	-
18-Sep	Whiting	24	-	3	212	314	272	20,444	10,307	-
2-Oct	Whiting	20.5	-	-	-	-	-	0	-	-

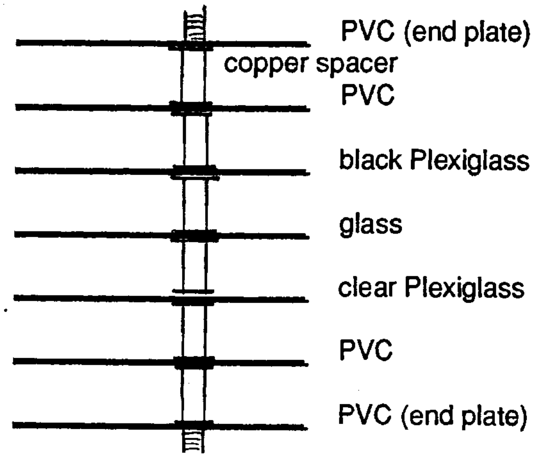
Appendix 1. continued.

Date	Site	water temp	secchi depth	sample depth	liters sampled	veligers/m^3		larvae/m^2 (Plexiglas)		larvae/m^2 (glass slide)
						mean	S.D.	mean	S.D.	
13-Jun	E. Chicago 1	22	-	2.5	177	-	-	-	-	-
27-Jun	E. Chicago 1	26	-	surface	100	-	-	0	-	-
11-Jul	E. Chicago 1	28	-	surface	160	-	-	0	-	-
25-Jul	E. Chicago 1	27	-	surface	200	67	115	0	-	-
8-Aug	E. Chicago 1	25	-	2.5	177	189	327	0		-
22-Aug	E. Chicago 1	27	-	1.5	106	880	762	0		-
4-Sep	E. Chicago 1	26	-	2.4	170	491	851	0	-	-
18-Sep	E. Chicago 1	23	-	2	141	0	0	0	-	-
13-Jun	E. Chicago 2	27	-	3	212	-	-	-	-	-
27-Jun	E. Chicago 2	26	-	3	212	330	572	0	-	-
11-Jul	E. Chicago 2	28	-	3	212	1,541	1,334	0	-	-
25-Jul	E. Chicago 2	27	-	3	212	1,415	708	0	-	-
8-Aug	E. Chicago 2	25	-	3	212	5,501	681	0	-	-
22-Aug	E. Chicago 2	26.5	-	3	212	5,013	395	1,778	3,108	1,067
4-Sep	E. Chicago 2	29	-	surface	200	275	476	0	-	-
18-Sep	E. Chicago 2	27	-	surface	200	158	274	0	-	-
6-Jun	Gary, IN	19	-	3.5	212+	-	-	-	-	-
13-Jun	Gary, IN	20.5	-	surface	212+	425	735	-	-	-
27-Jun	Gary, IN	21	-	surface	212+	991	991	-	-	-
11-Jul	Gary, IN	24	-	surface	200	600	520	-	-	-
25-Jul	Gary, IN	24	-	surface	200	875	217	-	-	6,400
8-Aug	Gary, IN	22	-	surface	200	37,333	8,401	-	-	-
22-Aug	Gary, IN	22	-	surface	200	18,192	4,506	-	-	-
4-Sep	Gary, IN	22.5	-	surface	200	1,458	505	-	-	-
18-Sep	Gary, IN	19	-	surface	200	3,000	1,132	-	-	-
21-Aug	Port of Indiana 1	23	1.2	surface	200	37,333	289	-	-	-
4-Sep	Port of Indiana 1	22-	-	surface	200	7,450	3,725	-	-	-
9-Sep	Port of Indiana 1	67	-	-	200	0	0	-	-	-
16-Sep	Port of Indiana 1	68	-	-	200	500	866	-	-	-
23-Sep	Port of Indiana 1	65	-	-	200	458	794	-	-	-
30-Sep	Port of Indiana 1	63	-	-	200	0	0	-	-	-
7-Oct	Port of Indiana 1	-	-	-	200	0	0	-	-	-
21-Aug	Port of Indiana 2	23	-	mixed	200	84,667	5,508	-	-	-
4-Sep	Port of Indiana 2	73	-	mixed	200	0	0	-	-	-
9-Sep	Port of Indiana 2	66	-	mixed	200	0	0	-	-	-
16-Sep	Port of Indiana 2	69	-	mixed	200	0	0	-	-	-
23-Sep	Port of Indiana 2	64	-	mixed	200	492	852	-	-	-
30-Sep	Port of Indiana 2	62	-	mixed	200	0	0	-	-	-
7-Oct	Port of Indiana 2	-	-	mixed	200	0	0	-	-	-

Appendix 1. continued.

Date	Site	water temp	secchi depth	sample depth	liters sampled	veligers/m^3 mean	S.D.	larvae/m^2 (Plexiglas) mean	S.D.	larvae/m^2 (glass slide)
6-Jun	Port of Indiana 3	19.5	-	surface	212+	-	-	-	-	-
13-Jun	Port of Indiana 3	19	-	surface	212+	393	681	-	-	-
27-Jun	Port of Indiana 3	22	-	surface	212+	21,250	14,958	-	-	-
11-Jul	Port of Indiana 3	24	-	2.6	184	-	-	-	-	-
25-Jul	Port of Indiana 3	28	-	2	141	8,168	2,021	-	-	-
8-Aug	Port of Indiana 3	22.5	-	3	212	7,921	1,132	-	-	-
6-Jun	Michigan City	15.5	0.65	3.5	247	341	596	-	-	-
13-Jun	Michigan City	20	0.6	3	212	-	-	-	-	-
27-Jun	Michigan City	23	0.6	3	212	-	-	-	-	-
11-Jul	Michigan City	24	0.4	3	212	1,297	1,297	0		533
25-Jul	Michigan City	25	1.1	3	212	1,761	1,571	31,605	12,261	20,000
8-Aug	Michigan City	21	0.45	3	212	2,075	1,797	8,444	5,719	16,000
22-Aug	Michigan City	22	0.9	3	212	1,697	0	2,667	7,012	3,200
4-Sep	Michigan City	22	0.8	3	212	2,051	1,184	113,778	51,881	3,200
18-Sep	Michigan City	21	1	3	212	2,515	981	1,333	2,147	813
2-Oct	Michigan City	17	2.1	3	-	-	-	378		2,667

Figure 1. Settlement plate units used for testing substrate preferences of settling zebra mussels. In Experiment 1, each replicate consisted of four such units - two deployed horizontally (one with roughened plates and one with smooth plates), and two deployed vertically (one with roughened plates and one with smooth plates). In Experiment 2, a replicate consisted of the illustrated unit plus a second unit constructed using plates made of fiberglass, steel, and concrete.


Settlement Plate Unit (Experiment 1)

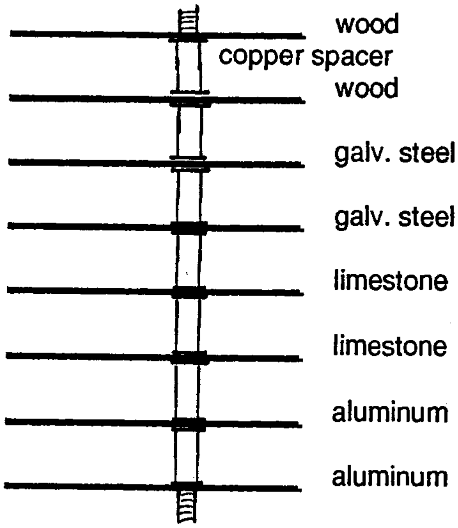

Settlement Plate Unit (Experiment 2)

Figure 2. Zebra mussel settlement plate, showing areas used for counting settled mussels. The dotted line indicates the position of the washer which was used to separate the plates from the copper spacers between each plate.

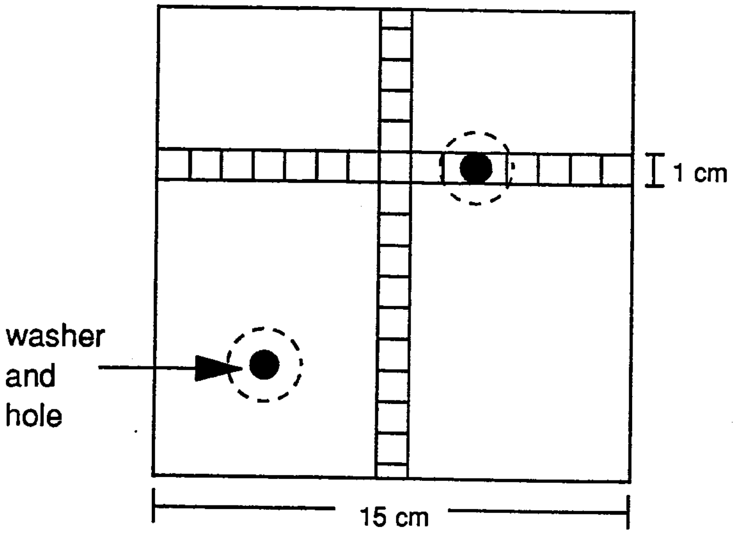


Figure 3. Zebra mussel monitoring sites used in southwestern Lake Michigan in 1991.

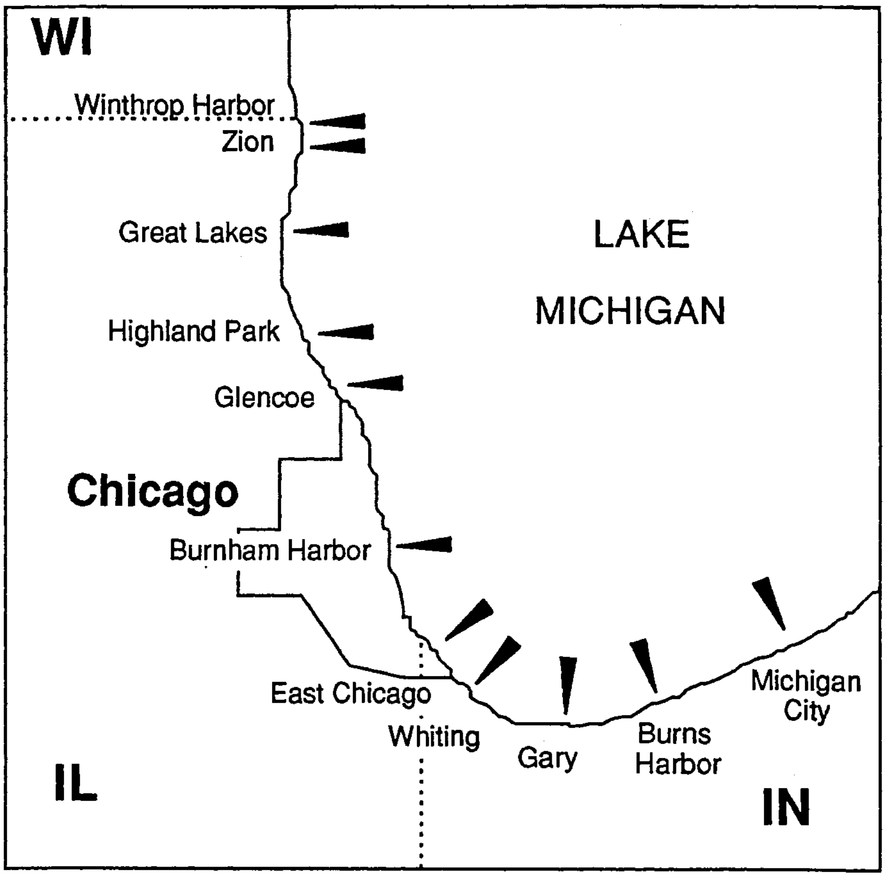


Figure 4. Juvenile zebra mussel settlement on horizontal (upper and lower surfaces) versus vertical plates. Each bar represents the difference between mussel density on a horizontal versus a vertical surface of comparable plates, divided by the total number of mussels on the plate. Bars above the x-axis indicate higher densities of mussels on upper or lower surfaces of horizontal plates; bars below the x-axis indicate higher densities on the vertical surfaces.

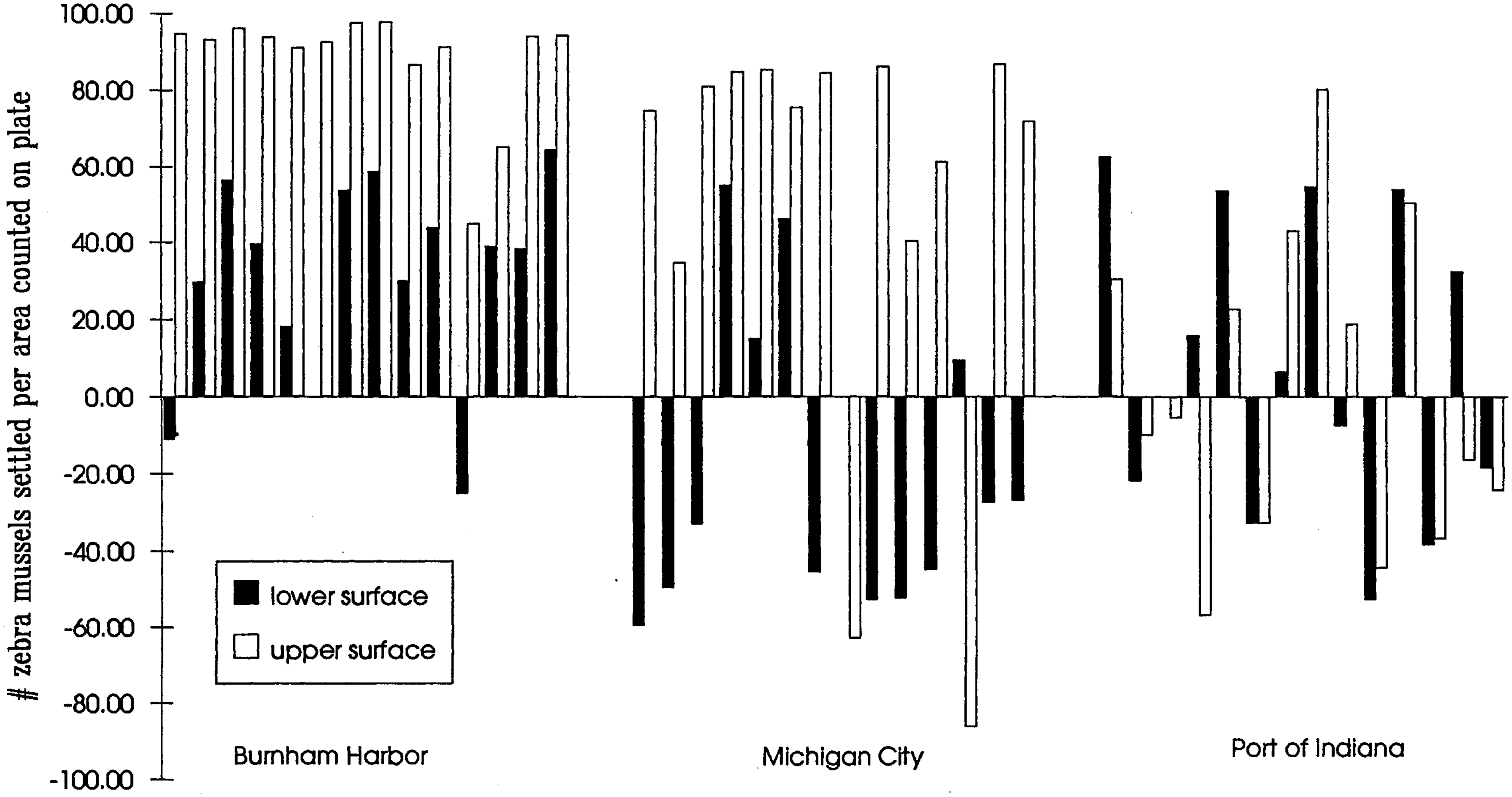


Figure 5a. Juvenile zebra mussel settlement on rough versus smooth vertical plates of various materials. Each bar represents the difference between mussel density on a rough versus a smooth surface of plates of the same material, divided by the total number of mussels on both surfaces. Bars above the x-axis indicate higher densities of mussels on the rough plates; bars below the x-axis indicate higher densities on the smooth surfaces.

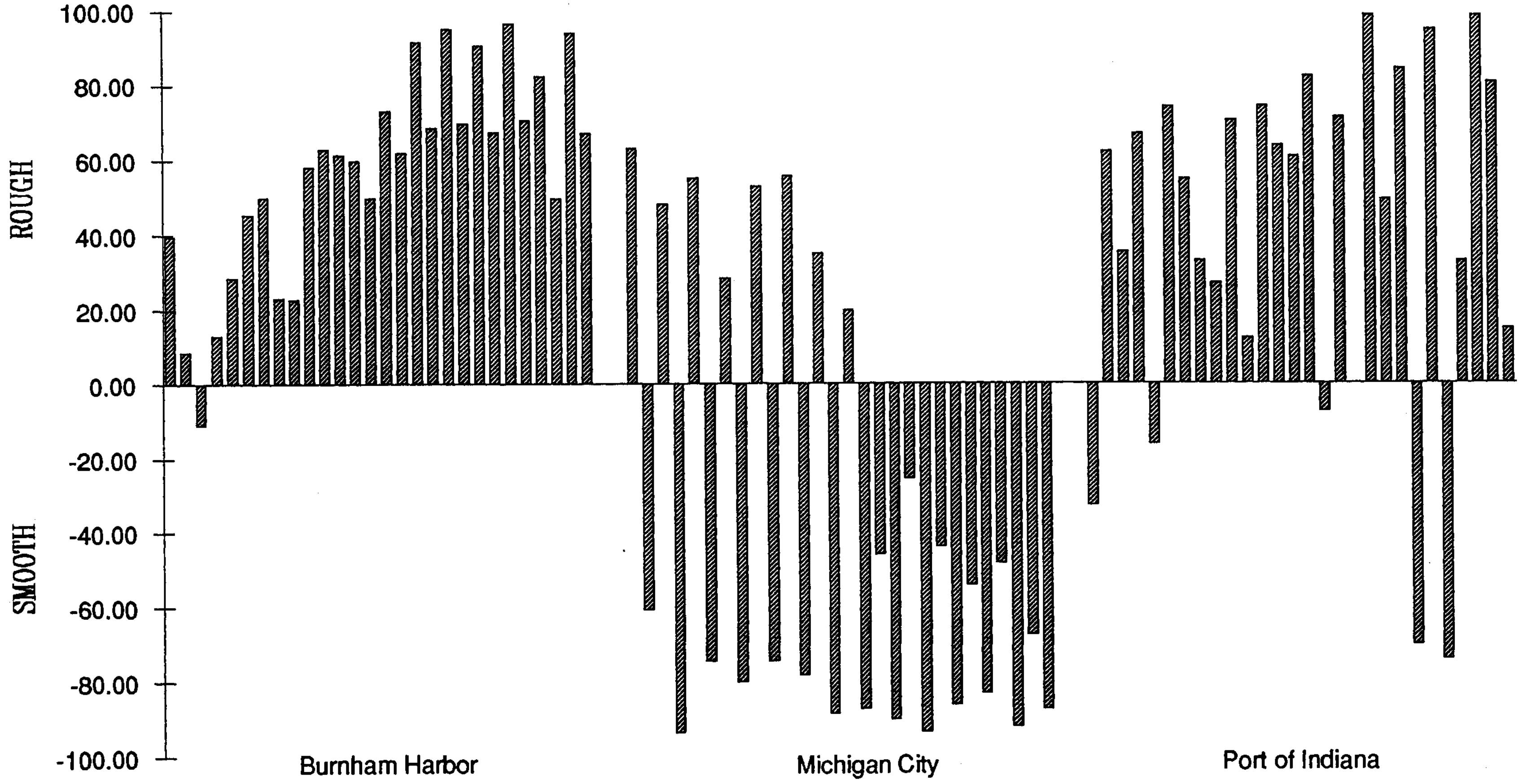


Figure 5b. Juvenile zebra mussel settlement on rough versus smooth horizontal plates (upper surface only) of various materials. Each bar represents the difference between mussel density on a rough versus a smooth surface of plates of the same material, divided by the total number of mussels on both surfaces. Bars above the x-axis indicate higher densities of mussels on the rough plates; bars below the x-axis indicate higher densities on the smooth surfaces.

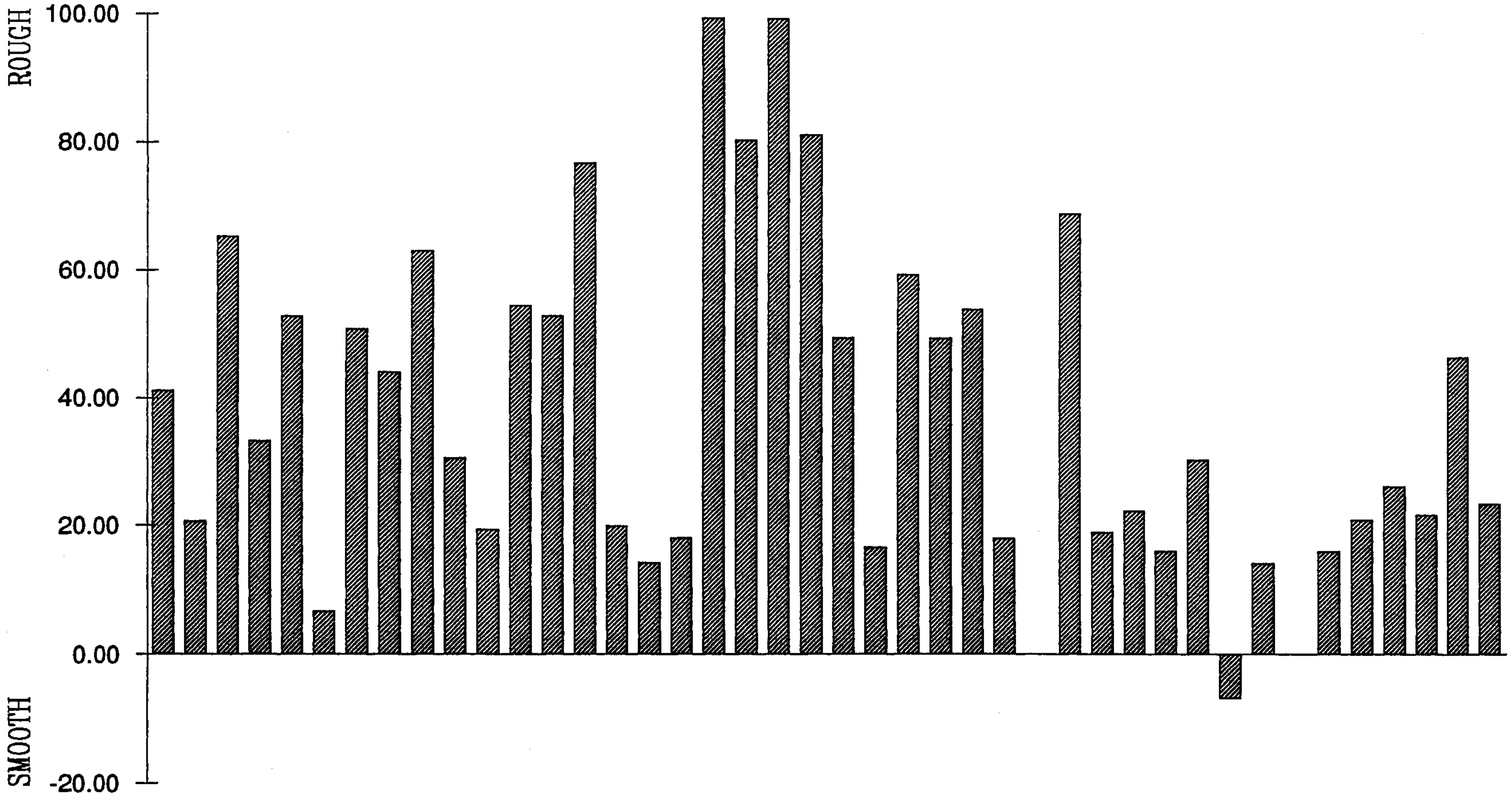


Figure 6. Juvenile zebra mussel settlement on upper versus lower surfaces of horizontal plates. Each bar represents the difference between mussel density on an upper surface versus density on a lower surface of the same plate, divided by the total number of mussels on the plate. Bars above the x-axis indicate higher densities of mussels on the upper surface; bars below the x-axis indicate higher densities on the under-surface.

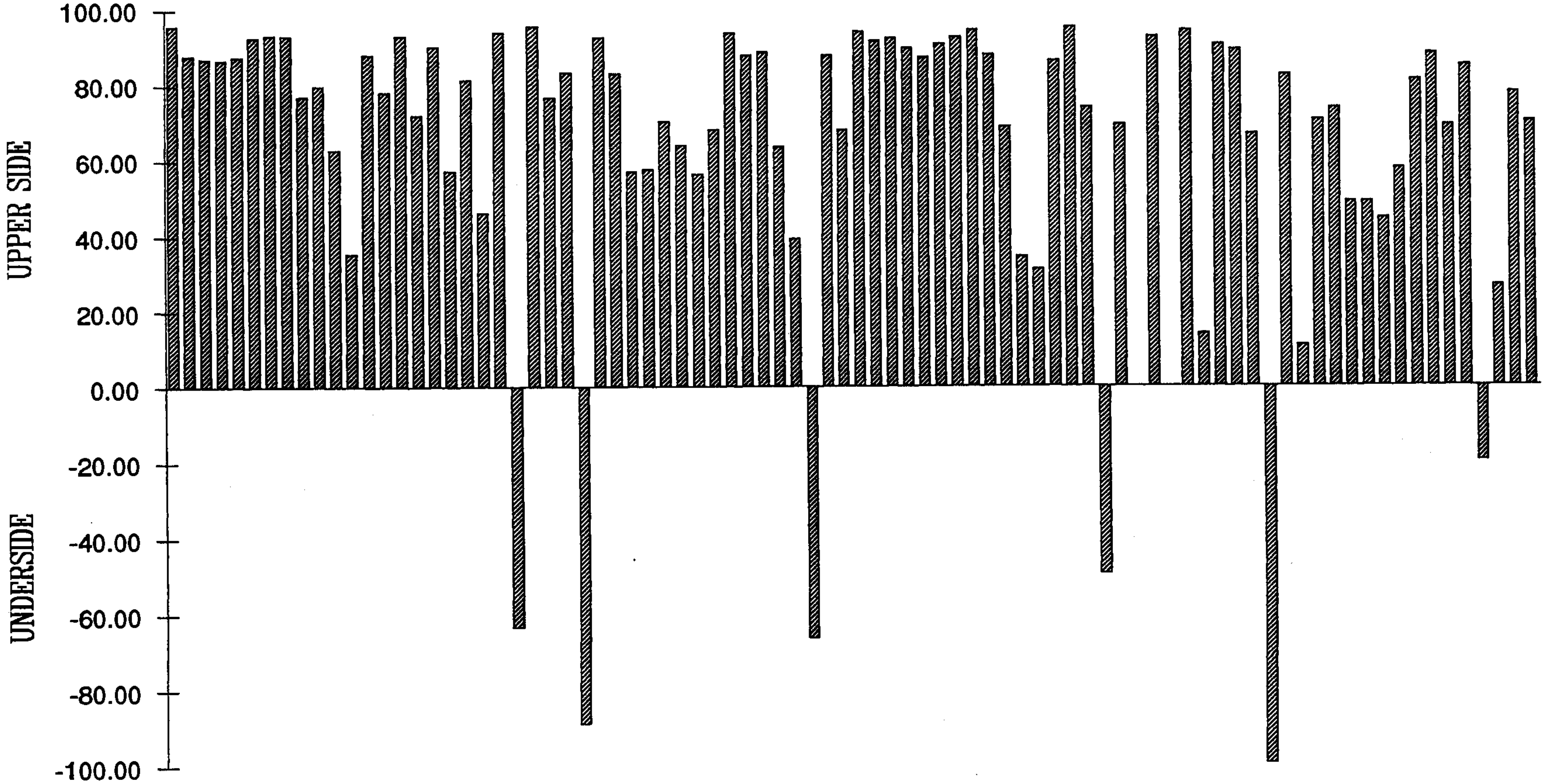
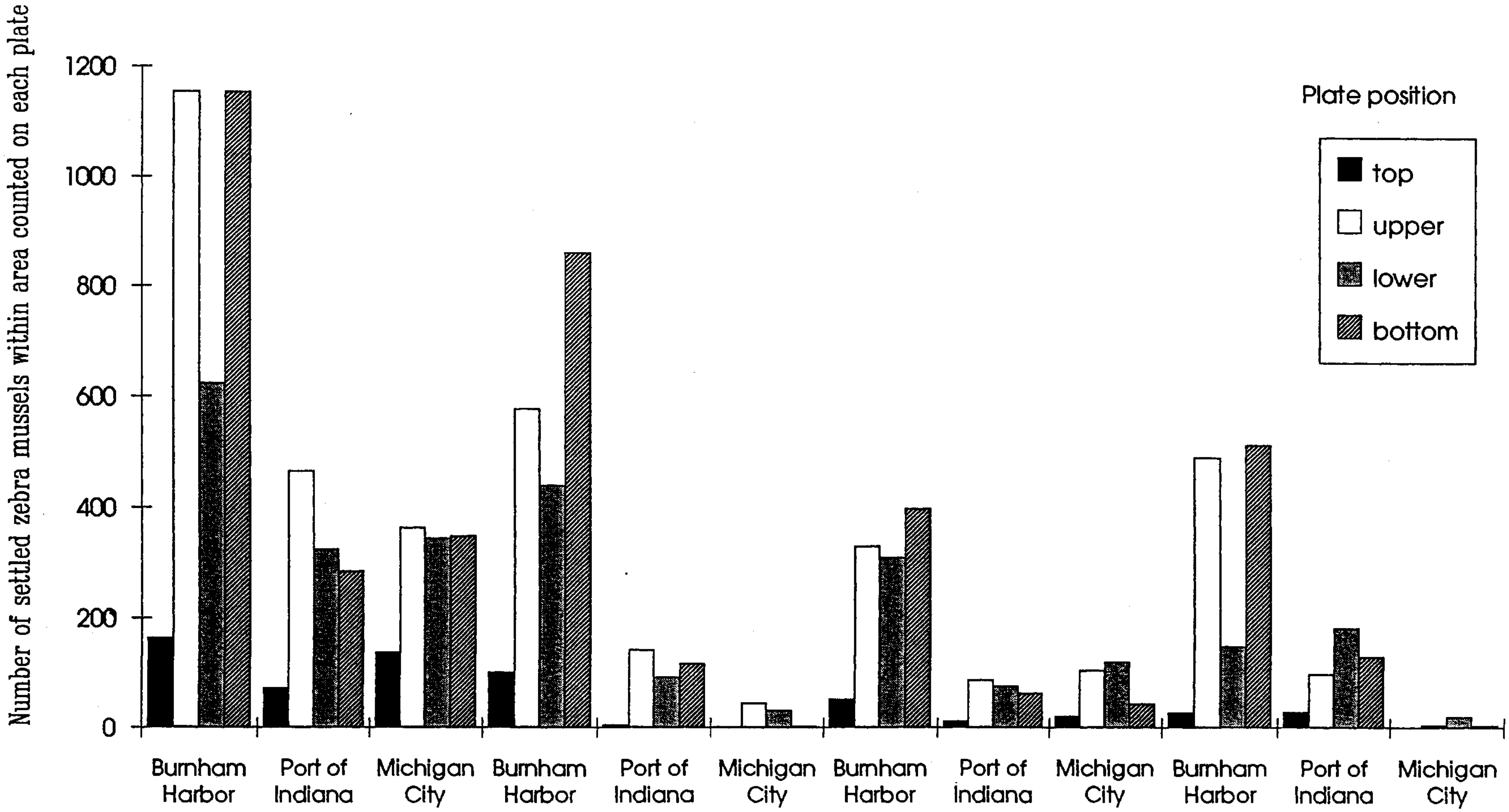


Figure 7. Juvenile zebra mussel settlement on plates exposed to sunlight (top plates) versus plates in constant shadow (upper, lower, and bottom plates). The plates are grouped by the settlement plate unit in which they were deployed.



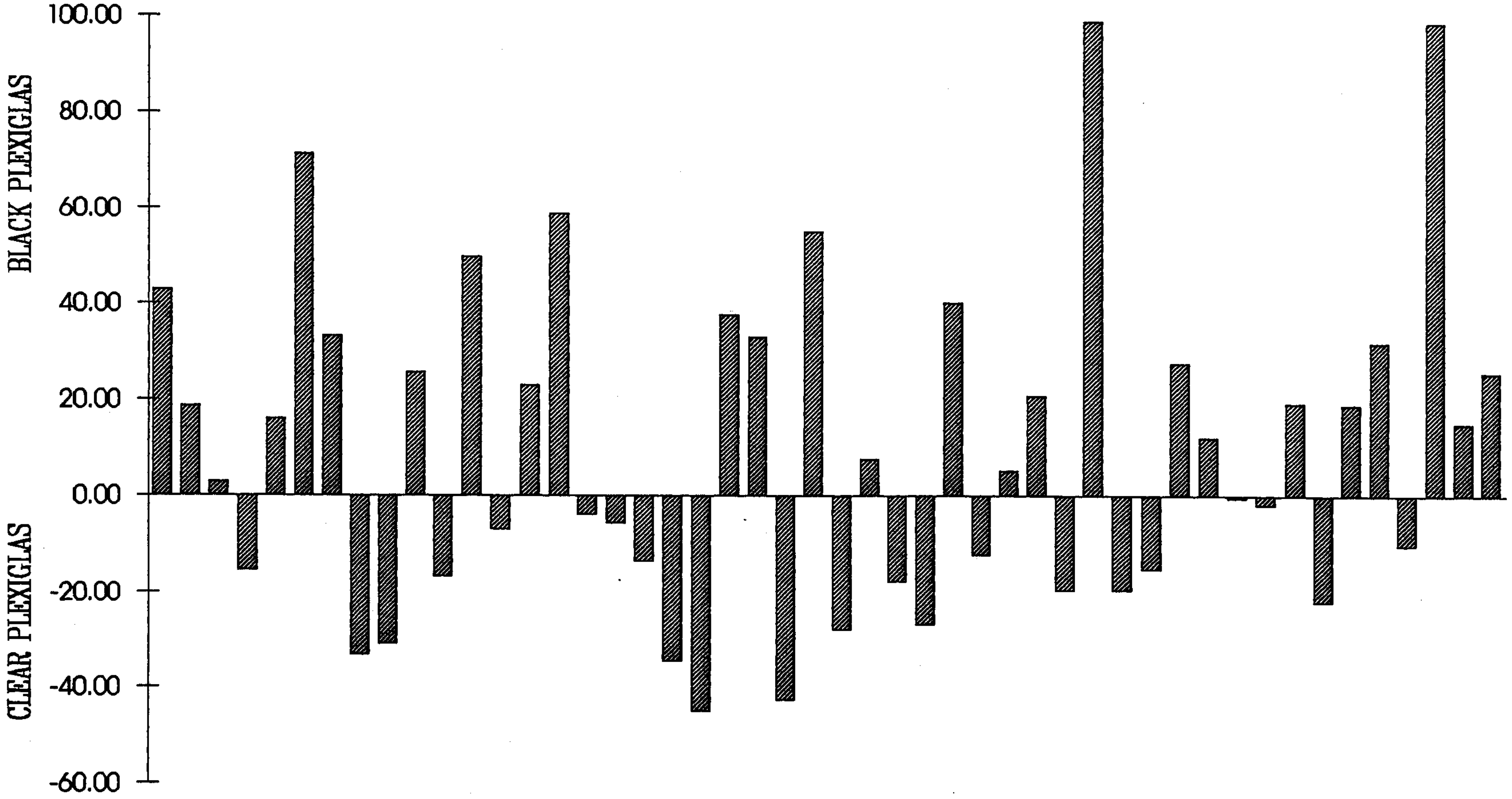


Figure 8. Juvenile zebra mussel settlement on black versus transparent Plexiglas plates. Bars above the x-axis indicate higher densities of mussels on the black plates; bars below the x-axis indicate higher densities on the transparent plates.

Figure 9. Juvenile zebra mussel settlement on the upper and lower surfaces of horizontal plates of different materials.

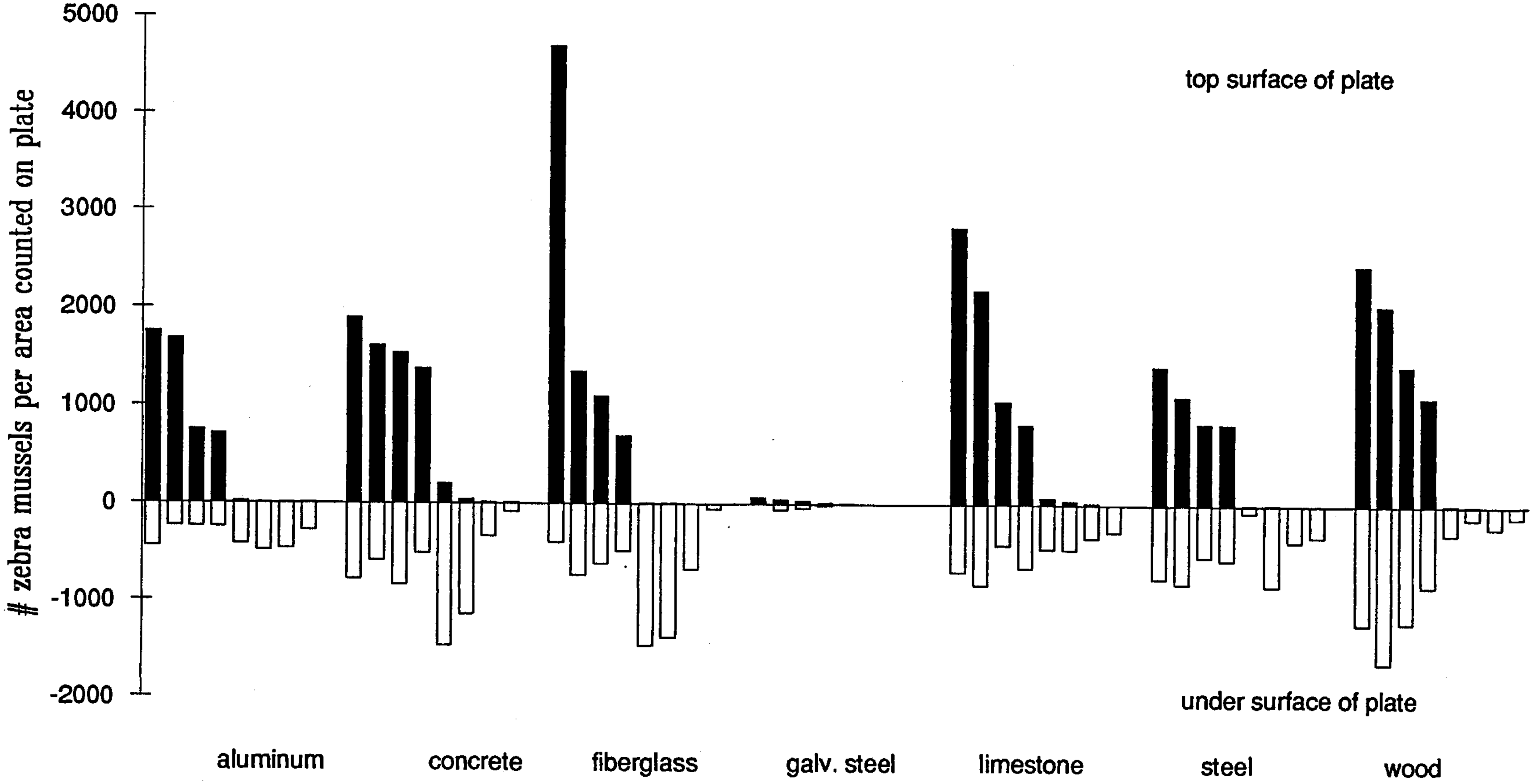


Figure 10. Bedrock reefs along the Illinois shoreline of Lake Michigan (from Collinson et al. 1979)

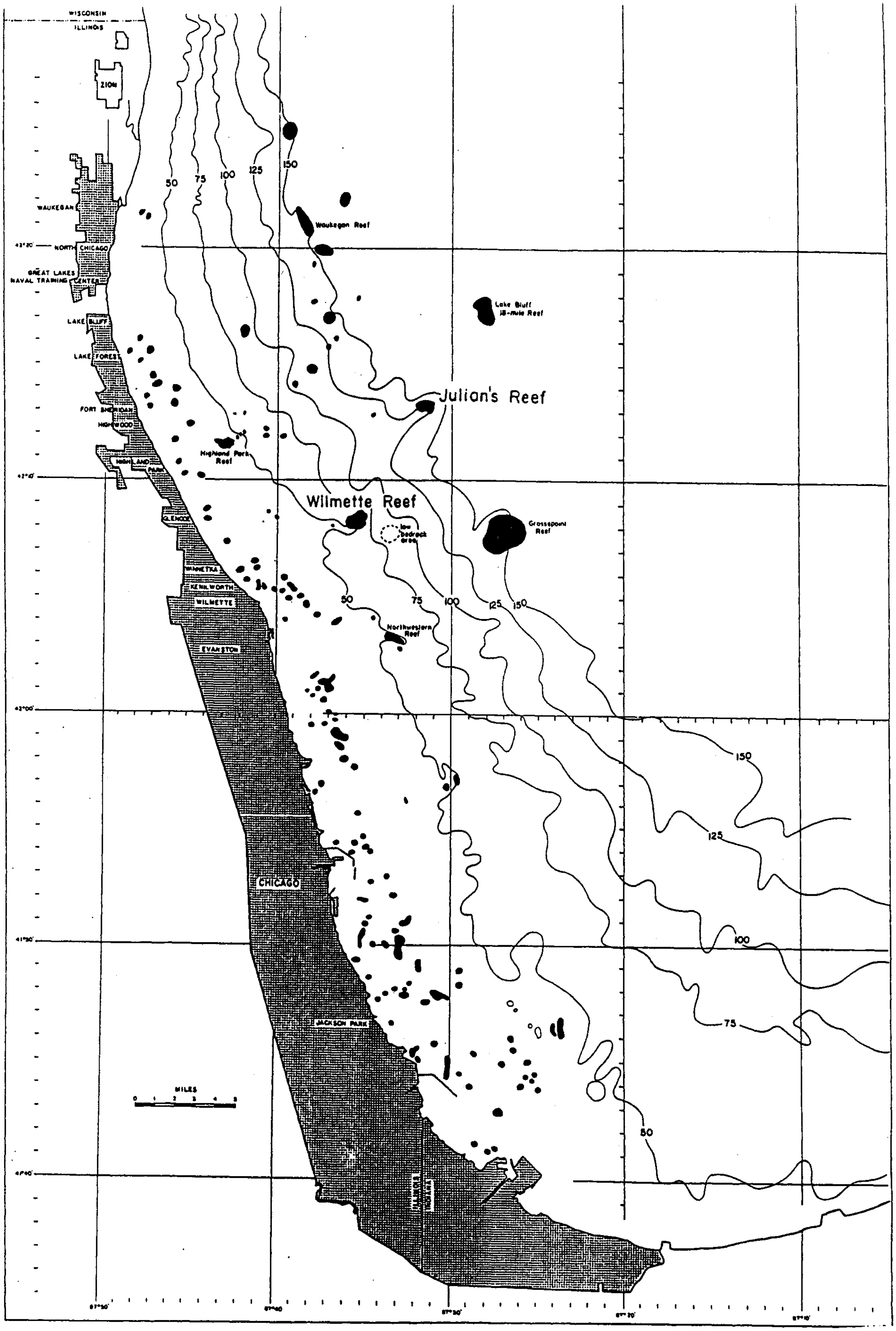


Figure 11. Pattern of reproduction of zebra mussels in Lake Michigan in 1991 as indicated by veliger densities in the water column.

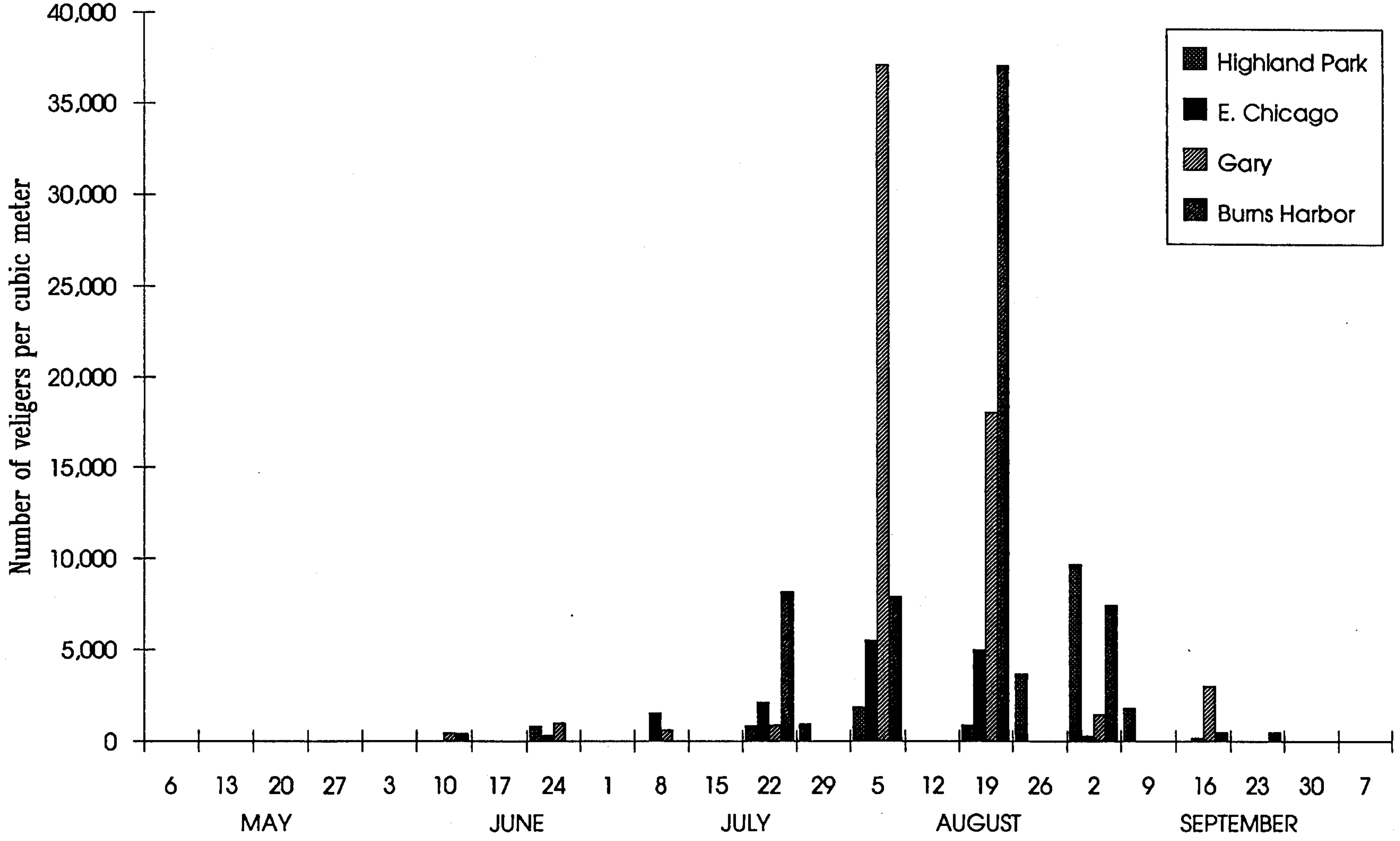


Figure 12. First appearance of zebra mussel veligers at each of the sites monitored in 1991.

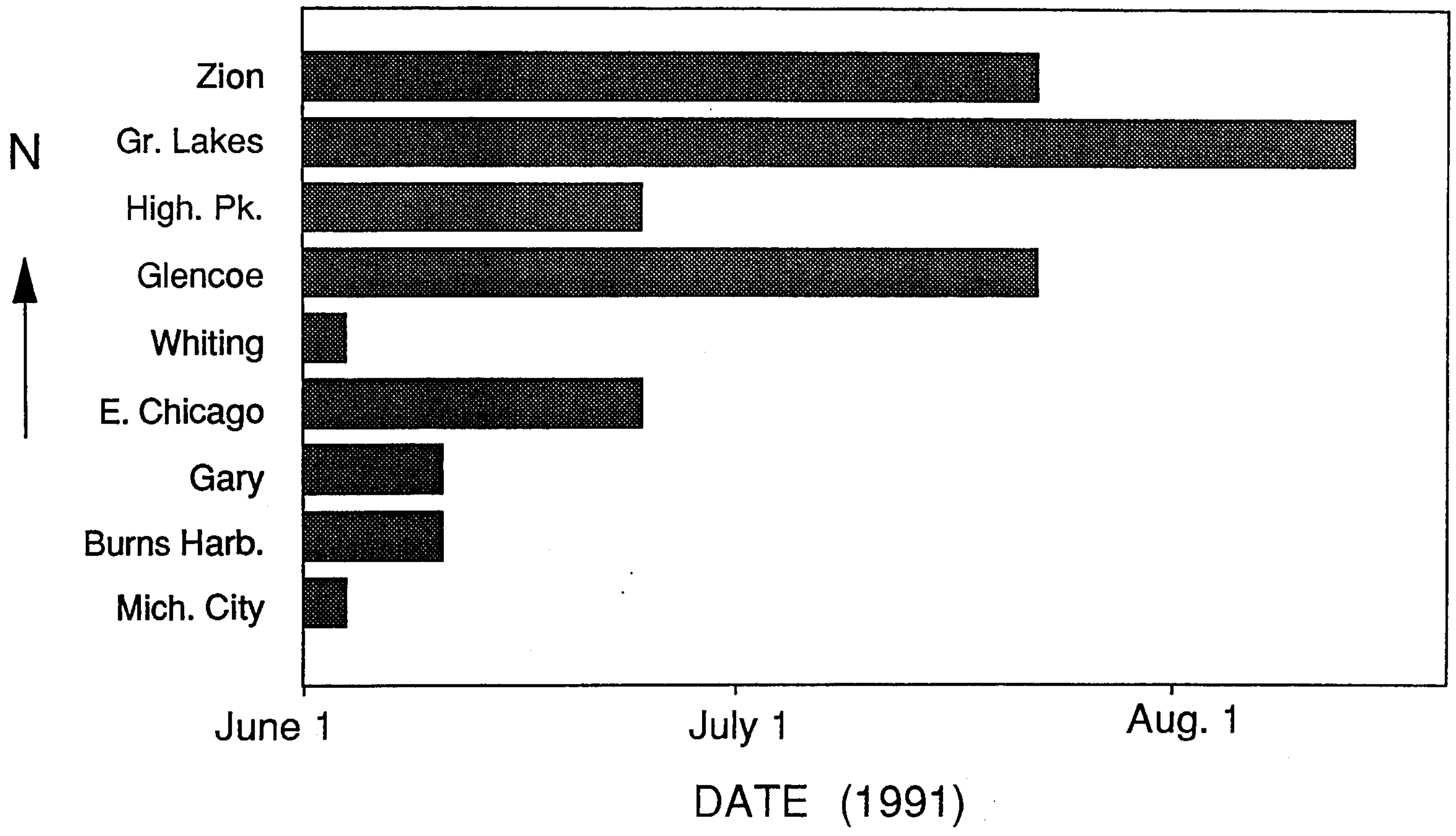


Figure 13. Maximum densities of zebra mussel veligers at each of the sites monitored in 1991.

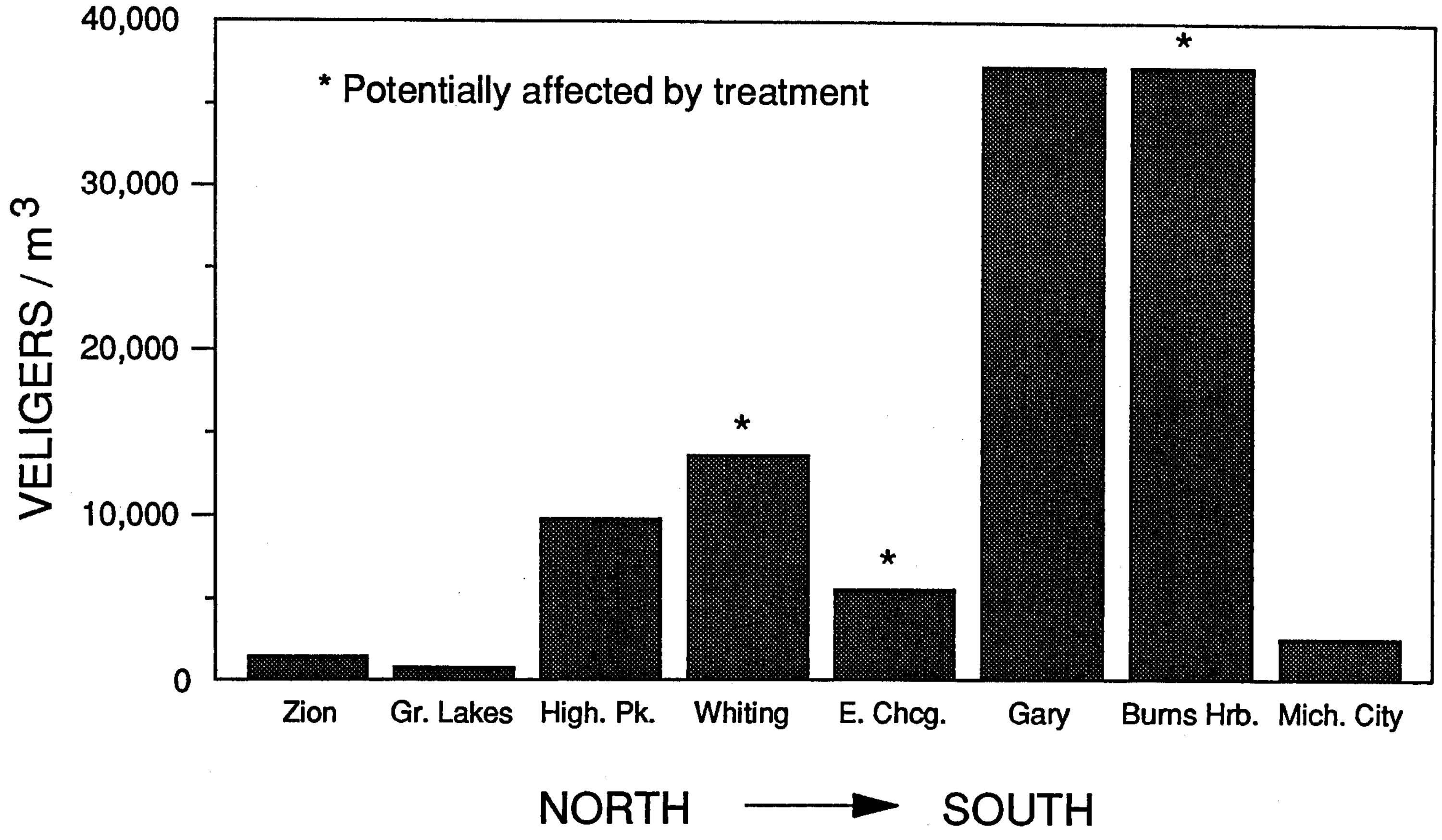


Figure 14. Zebra mussel settlement adjacent to washers on the experimental plates compared with total density of zebra mussels on each plate.