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Rapid Increase and Subsequent Decline of Zebra and Quagga Mussels in Long Point Bay, Lake Erie: Possible Influence of Waterfowl Predation

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ABSTRACT. *Distribution and density of two introduced dreissenid species of mollusks, the zebra mussel* Dreissena polymorpha *and quagga mussel* D. bugensis, *were monitored in the Inner Bay at Long Point, Lake Erie, 1991–1995. Since populations of certain waterfowl species have been reported to alter their dietary intake and migration patterns in response to the ready availability of zebra mussels, the percent occurrence of zebra mussels in the diet of 12 duck species (552 birds) was studied concurrently, and several spring and fall aerial waterfowl surveys were flown between 1986 and 1997 (*n *= 75), to document changes in duck populations at Long Point. The first reproductive population of zebra mussels on the bay most likely appeared in 1990. After an initial rapid increase in density and colonization of the Inner Bay, zebra mussels began to steadily and consistently decline in absolute numbers, density per station and occupied area. Mean density per station in 1995 was 70% less than in 1991, the first year of rapid colonization, and 67% less than in 1992, the year of peak abundance in the bay ($P < 0.05$). Occupied area peaked in 1992, with 80% of sampling stations supporting mussels; the following 3 years showed consistent declines in the proportion of stations supporting mussels: 1993 = 75.9%, 1994 = 63.2% and 1995 = 57.1% ($P < 0.05$). Mussels in size class 0 to 5 mm were most abundant in 1991, 1993 and 1995, whereas those in size class 6 to 10 mm predominated in 1992 and 1994 ($P < 0.05$). Very few mussels over 15 mm were found. Lesser Scaup* Aythya affinis *(75.4 to 82.5 % occurrence), Greater Scaup* A. marila *(66.7 to 81.5 % occurrence), and Bufflehead* Bucephala albeola *(46.7 to 60 % occurrence) were the only three waterfowl species that consistently incorporated zebra mussels in their diet, and the mussel decline coincided with a substantial increase in the populations of these species at Long Point. Waterfowl days for Lesser and Greater Scaup combined increased rapidly from 38,500 in 1986 (prior to the zebra mussel colonization of Long Point) to 3.5 million in 1997 ($P = 0.012$). Bufflehead days increased from 4,700 to 67,000 during the same period ($P = 0.001$). Oligotrophication of Lake Erie, through reduced plankton and chlorophyll concentrations, has occurred since the invasion of zebra mussels, probably a result of filtering activities of introduced mussels. While a reduction in plankton availability may have contributed to the zebra mussel decline, high rates of waterfowl predation probably had the most substantial effect on mussel densities at Long Point. Waterfowl predation also probably influenced the size structure of the zebra mussel population, since waterfowl are size-selective foragers, and increased water clarity would have facilitated their ability to select preferred medium and large size classes of mussels. Quagga mussels, which were first detected in 1993, experienced a decline in both density and area occupied over the next two years. Quagga mussels rarely attached to soft substrates, and their decline is possibly related to the decline of suitable hard substrates, such as zebra mussels, as well as to predation by waterfowl.*

INDEX WORDS: *Zebra mussel, quagga mussel, dreissenid mussels, Long Point, Lake Erie, scaup, waterfowl, predation.*

INTRODUCTION

The zebra mussel *Dreissena polymorpha*, a bivalve mollusk originally endemic to eastern Europe, has established reproductive populations throughout the Laurentian Great Lakes since its initial introduction into Lake St. Clair in 1986 (Hebert *et al.* 1989, Neary and Leach 1992). Rapid colonization of Lake Erie by the mussel has been well documented (Griffiths *et al.* 1991). Environmental variables such as temperature, water hardness,

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availability of suitable substrate, and plankton density, which are potentially limiting (Strayer 1991), proved to be favourable in Lake Erie. Mussels spread rapidly eastwards across the lake, aided by downstream drift of their free-swimming pelagic veliger larvae, and by transportation of adults attached by byssal threads to suitable substrates, especially boats (Griffiths *et al.* 1991). In February 1990, mussel populations were found along the north shore of eastern Lake Erie between Long Point and the entrance to the Welland Canal, and frequency-length analyses of the population suggest that colonization by veligers occurred in September 1989 (Dermott and Munawar 1993, Dermott *et al.* 1993). Veligers probably also reached the Inner Bay at Long Point in fall 1989, with the first reproductive population in 1990. Although zebra mussels preferentially settle on hard substrates, they also colonize aquatic vegetation (Lewandowski 1983, Hebert *et al.* 1991). Over 90% of the Inner Bay is covered by submerged macrophytes, which has permitted colonization by zebra mussels (Petrie 1998, Knapton and Petrie 1999).

Certain waterfowl species have altered their dietary intake, as well as their migration patterns, to take advantage of this new food source in Lake Erie (Wormington and Leach 1992, Mitchell and Carlson 1993, Hamilton and Ankney 1994, Hamilton *et al.* 1994, Mitchell 1995, Petrie 1998). As Long Point Bay is one of the most important waterfowl staging areas in North America, duck predation may be influencing density or demographics of zebra and quagga mussels there.

Herein the rapid colonization of the Inner Bay at Long Point by zebra mussels and the subsequent decline in mussel density and occupied area are documented. Also reported are percent occurrence of zebra mussels in the diets of 12 waterfowl species and changes in abundance of those waterfowl species at Long Point since the zebra mussel invasion. Quagga mussels, *D. bugensis*, a second invading dreissenid mussel, were first located in the Erie Canal and Lake Ontario in 1991 (May and Marsden 1992) and have subsequently occupied much of Lake Erie, in some instances equalling or surpassing densities of sympatric populations of zebra mussels (Dermott and Munawar 1993, Mitchell 1995). Reproductive populations of quagga mussels were first detected in the Inner Bay at Long Point in 1993. Also reported is the occurrence of the quagga mussel in the Inner Bay at Long Point.

STUDY AREA

The Inner Bay at Long Point is located on the north shore of the Eastern Basin of Lake Erie (Fig.1). The bay is partially encompassed and protected by the Long Point peninsula, a 35 km sandspit project-

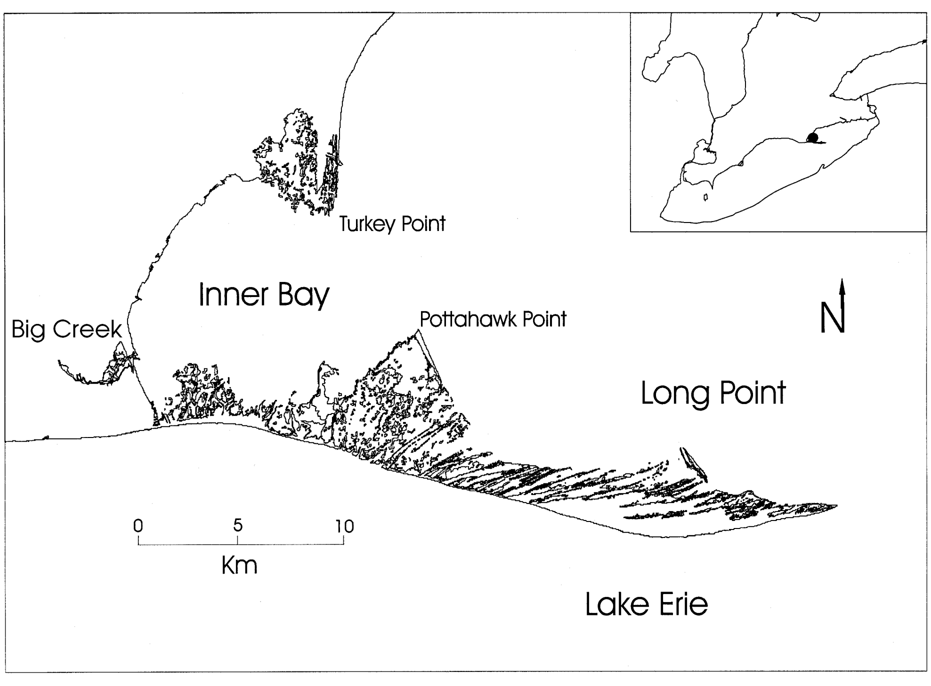

FIG. 1. Geographic location and map of Long Point's Inner Bay.

ing east into the deepest part of Lake Erie, by the north shore of the lake, and by a sand shoal extending from Turkey Point on the north shore to Pottahawk Point on the peninsula. The Inner Bay has a surface area of 78 km^2, a maximum depth of 4 m, and a mean depth of about 2 m (Reznicek and Catling 1989). Over 90% of the Inner Bay is covered with submerged macrophytes, primarily species of *Chara*, *Vallisneria*, *Najas* and *Myriophyllum* (Pauls and Knapton 1993, Petrie 1998, Knapton and Petrie 1999). The depth of the Inner Bay varies annually according to the level of Lake Erie, and sometimes daily as a result of short-term seiches induced by winds and differential atmospheric pressure (Berst and MacCrimmon 1966, Rasid *et al.* 1992). Colonization by zebra mussels probably was aided by seiches moving from east to west and thereby transporting veliger larvae into the Inner Bay.

The major source of nutrients and suspended solids entering the Inner Bay is from Big Creek, the major tributary. Big Creek drains a 730 km^2, primarily agricultural-based, watershed and it has an annual discharge of about 250 x 10^6 m^3 (Berst and MacCrimmon 1966, Leach 1981, Stone and English 1993). From limnological variables measured in 1978-1979, Leach (1981) classified the Inner Bay as eutrophic on the basis of total phosphorus, nitrate-nitrogen, chlorophyll *a*, and Secchi disc transparencies. Inner Bay substrate is primarily mud at the mouth of Big Creek, where accumulated sediments from the watershed have created a deltaic deposit; sandy loam covers most of the central part and sand borders the sand shoals along eastern and southeastern boundaries (Smith 1979, Heathcote 1981). Mean water temperature between May and September is about 22°C, ranging from 18°C to 26°C, well within the optimum range for zebra mussel reproduction (Strayer 1991).

The protection afforded by the Long Point sandspit, extensive wetlands, prolific plant growth, and unique geographic location between Gulf and Atlantic coast wintering areas and prairie and arctic breeding areas, make Long Point one of the most important waterfowl staging areas in North America. Long Point Bay and its associated wetlands regularly support over 100,000 ducks, geese, and swans during peak spring and fall migration (Petrie 1998).

METHODS

An imaginary grid system was set up across the Inner Bay at 400 m intervals on a north-south axis and 500 m intervals on an east-west axis, giving a maximum number of 326 potential sampling stations. Distance between sampling stations was determined by averaging the time needed to travel between stations 400 m apart, with this initial time being determined using a LORAN-C navigational system. Transect lines were determined using two fixed shoreline points 500 m apart, and a boat was operated at full throttle for the determined length of time along each fixed transect line (Pauls and Knapton 1993).

Samples were collected at all 326 stations in 1991, 1992, and 1995, and at about every fourth station along each transect in 1993 and 1994. The sampling period spanned an equivalent time period each year, from mid-July to late August. At each station, an Ekman grab sample was collected and later analysed for all macrobenthos. Mussels were separated into zebra and quagga mussels, counted, and assigned to length categories of 5 mm increments. To approximate density per square meter, number of mussels collected per sample was multiplied by a constant of 43 (based on the fact that an Ekman dredge samples an area of 225 cm^2). Density estimates, length categories and the equation: Wet Weight (mg) = 0.051 $SL^{2.996}$, where SL = shell length (mm) (Mackie 1992), were used to estimate total mass of zebra mussels in Long Point Bay during each year. Because mussels were classified into length categories of 5mm increments, the midpoint of each increment was the length used to estimate the mass of all individuals in a size class. Substrates to which zebra mussels were attached were recorded in 1991 and in 1993 to 1995.

Distribution and density maps of zebra mussels for each year were generated using SPANS, a computerized Geographic Information System (Fig. 2). Inter-year data were compared using sign tests for presence/absence, Wilcoxon paired-sample tests were used when magnitude of change as well as direction of change was important, and goodness-of-fit G tests for analysis of frequencies (Sokal and Rohlf 1981).

The 707 ha Long Point Waterfowl Management Unit is open to controlled hunting 4 days per week. Hunters are required to report their kill to Unit office daily. Dietary samples were collected from 552 of these hunter-shot birds (12 species) between 1992 and 1994. A drawback to this simple collection method is that by not removing dietary samples immediately after collection, those samples are predisposed to post mortem digestion, resulting in a sample that is biased towards less readily digested materials. Also, since a limited number of birds had

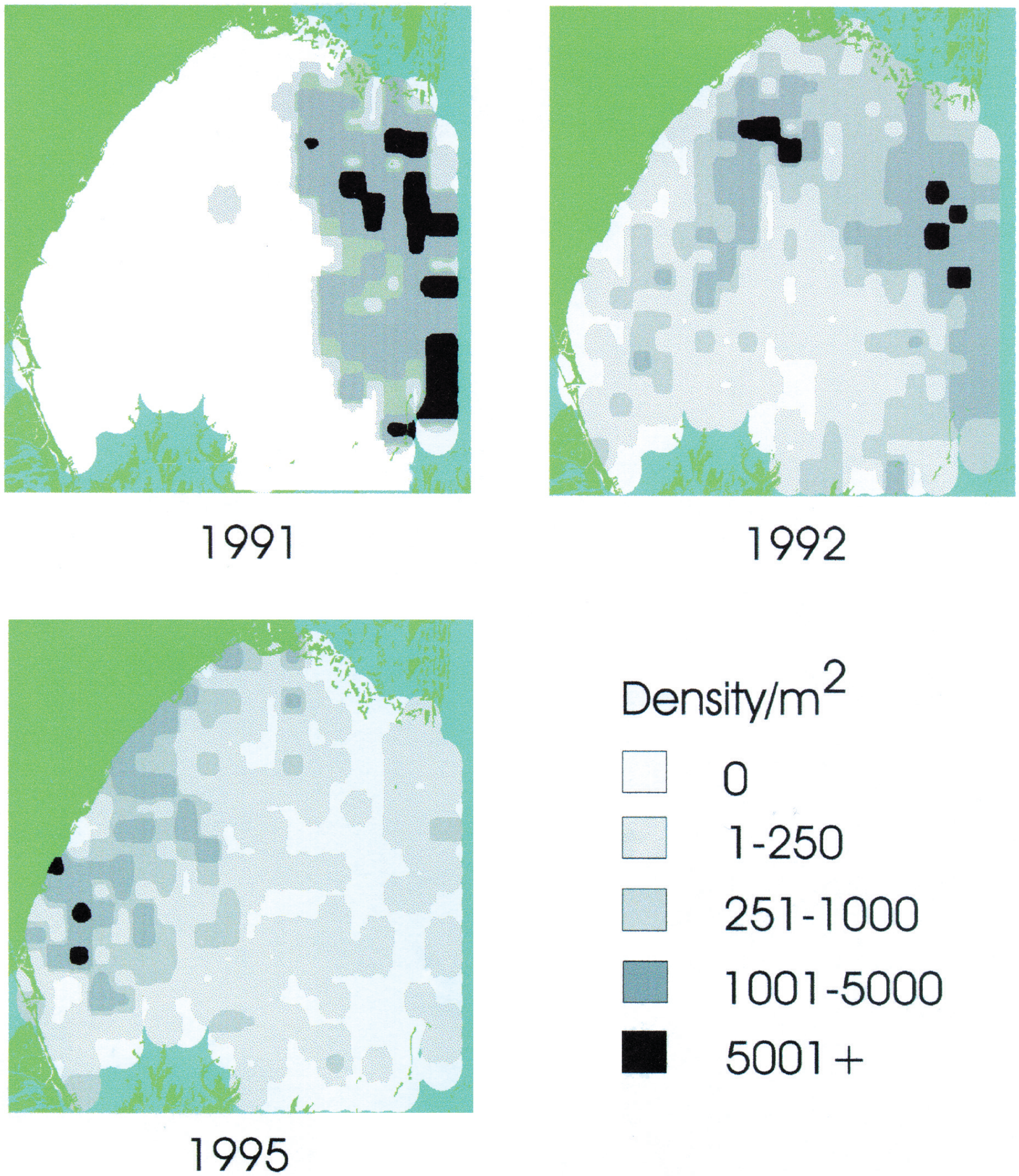

*FIG. 2. Distribution and density of zebra mussels (***Dreissena polymorpha***) in the Inner Bay at Long Point. Fig. 2(a) 1991. Fig. 2(b) 1992. Fig. 2(c) 1995.*

food items in their esophagus, the contents of the gizzard were included in the dietary analysis, potentially causing a bias towards hard foods such as zebra mussels (Swanson and Bartonek 1970). However, these sampling biases were circumvented by reporting on percent occurrence of zebra mussels in waterfowl diets rather than on the aggregate percent dry mass of individual dietary components, the objective being only to determine which species consistently consume zebra mussels at Long Point. Only birds that contained at least 0.05 g of food were analyzed.

Spring and fall aerial waterfowl surveys were conducted at Long Point during 1986, 1988, and every year between 1991 and 1997. Surveys (n = 4–7/season) were flown along a regular 250 km route by two observers in a fixed-wing aircraft at an altitude of 100 m. With the exception of the two scaup species (Lesser *Aythya affinis* and Greater *Aythya marila*) which were grouped as scaup spp., each species was identified and counted separately. Seasonal waterfowl use was subsequently calculated by averaging number of waterfowl counted between two consecutive surveys and multiplying that number by the number of days between the two survey days (Dennis *et al.* 1984). By doing this for the entire season, total number of "waterfowl days" for each species or species-group was estimated. Spring waterfowl use was calculated for the period 1 March to 15 May and fall use was calculated for the period 1 September to 15 December. Regression analysis was used to determine if total annual waterfowl days changed for each species/species-group of waterfowl at Long Point, in response to the zebra mussel invasion.

Calculated waterfowl days for scaup spp. were multiplied by minimum and maximum daily mollusk consumption estimates/requirements for related species (200 to 1,025 g/d; Longcore and Cornwell 1964, Nilsson 1969, Thompson 1973, Pedroli 1981, Suter 1982) to generate an annual estimate of the proportion (based on zebra mussel biomass calculations above) of zebra mussels from Long Point Bay that were consumed by these species of waterfowl.

RESULTS

Substrate

Although zebra mussels were found attached to hard substrates such as submerged branches and shells of both living and dead freshwater mollusks (especially clams, family Unionidae, and snails, family Pleuroceridae), they were found primarily on submerged macrophytes. Overall, 81% of zebra mussels were attached to submerged macrophytes, especially species of *Chara*, *Myriophyllum*, *Najas*, *Vallisneria*, and *Potamogeton*. Quagga mussels were rarely found clinging to soft substrates and hence were frequently absent where only submerged macrophytes were present. Clusters of zebra mussels and other quagga mussels themselves were the most frequently used substrate.

Mussel Distribution

In 1991 zebra mussels were found in the eastern third of the Inner Bay, with a few scattered records in central and western parts of the bay (Fig. 2a). By 1992 (Fig. 2b), and in each subsequent year (1995, Fig. 2c), zebra mussels were found essentially throughout the Inner Bay. The only areas where mussels were consistently absent were those stations along the southeastern shore where bottom sediments were sand and no aquatic plants or hard substrates, such as mollusks, occurred.

Percent coverage of zebra mussels differed among years (Fig. 2; G = 16.9, R x C test of independence, $P < 0.001$)(Table 1). They occurred at only 87 of 326 (27%) stations in 1991, but had increased to 80% of stations the following year ($z = 8.23$, $P < 0.001$; sign test). However, the next 3 years showed consistent declines in percent occurrence, from 76% to 57%, such that the number of stations occupied in 1995 was 75 fewer than in 1992 ($z = 6.37$, $P < 0.001$; sign test). Quagga mussels were first detected in 1993. Percent occurrence at sampling stations declined from 30% in 1993, to 23% in 1994 and 17% in 1995 (G = 18.7, R x C test of independence, $P < 0.01$).

TABLE 1. Abundance of zebra mussels (ZM) in Long Point Bay (LPB), Lake Erie, 1991 through 1995, and the proportion of the total biomass potentially consumed by scaup spp.

Year	% Coverage of ZM	Density of ZM per m^2	Total Number of ZM	Total ZM Mass on LPB (kg)	Min. % of ZM[1] Eaten by Scaup spp.	Max % of ZM[1] Eaten by Scaup spp.
1991	26.7	2,050	4.27E + 10	1 188 900	22	112
1992	80	1,824	1.14E + 11	4 536 214	3	14
1993	76	830	4.92E + 10	1 339 054	46	237
1994	63	746	3.67E + 10	1 303 812	39	201
1995	57	606	2.69E + 10	758 003	43	220

[1]See methods for calculations.

Density

Mean density of zebra mussels per occupied station declined throughout the period of study (Table 1); each of the four pair-wise comparisons between successive years was significantly different (Wilcoxon paired-sample tests, $P < 0.001$). Mean density of mussels was highest in 1991 at over 2,000 individuals per station. However, considerably fewer stations were occupied by zebra mussels in 1991 than in the next 4 years. Mussel density declined from 1,824 per station in 1992 to 606 per station in 1995. Thus, mean density per station in 1995 was 70% less than in 1991, the first year of rapid colonization, and 67% less than in 1992, the year of maximum occupancy of the Inner Bay. Maximum densities also declined; in 1991, maximum densities ranged as high as 23,650/m^2, but declined in each subsequent year such that in 1995, the maximum recorded was only 5,074/m^2.

Quagga mussel densities did not approach those of zebra mussels in any of the 3 years in which they were detected. In 1993, mean density per occupied station was 406, with a maximum value of 2,064. Mean densities in 1994 and 1995 were 356 and 201, with maximum values of 1,204 and 989, respectively.

Mussel Size Distribution

Approximately 90% of zebra mussels sampled each year were less than 10 mm in length (Table 2). However, inter-year differences were substantial ($G = 46.6$, R × C test of independence, $P < 0.001$), as the proportion of mussels 0 to 5 mm and 6 to 10 mm in length, changed in magnitude. Size class 0 to 5 mm was higher in 1991, 1993, and 1995, whereas size class 6 to 10 mm was higher in 1992 and 1994 (all pair-wise comparisons, $P < 0.01$). Size distribution of quagga mussels did not differ between years (pair-wise comparisons, $P > 0.05$). About 55% of quagga mussels sampled were 0 to 5 mm, 25% 6 to 10 mm, 15% 11 to 15 mm, 3% 16–20 mm, and 2% >20 mm.

TABLE 2. Proportional size distribution (in 5 mm increments) of zebra mussels over a 5-year period in Long Point's Inner Bay.

	Percent				
Year	0–5	6–10	11–15	16–20	> 20
1991	46.3	44.4	8.2	1.1	0
1992	28.7	55.2	14.7	1.2	0.1
1993	50.4	38.6	10.4	0.6	0
1994	30.6	58.5	9.3	1.0	0.6
1995	68.8	20.4	7.7	2.4	1.0

Waterfowl Diets and Surveys

Five hundred and fifty-two ducks contained sufficient dietary samples (> 0.05 g) to be included in the analysis. Of 12 species that were sampled, 6 were diving ducks and 6 were dabbling ducks. Individuals of 5 of the 12 species had consumed zebra mussels, and only Lesser Scaup (75 to 83% occurrence), Greater Scaup (67 to 82%), and Buffleheads (47 to 60%) consistently ate zebra mussels (Table 3). Given their inability to forage in deep water, and their normally herbivorous/granivorous diet, it was not surprising that dabbling ducks did not consume zebra mussels.

Waterfowl days, for all species combined, increased from 3.7 million in 1986 to 7.7 million in 1997 ($P = 0.034$). However, most of this increase (88%) can be attributed to those species that consume zebra mussels. Scaup spp. and Buffleheads were the only species that consistently ate zebra mussels (Table 3) and they were also the only species that significantly increased use of Long Point after colonization by zebra mussels (all other species, $P > 0.05$) (Figure 3). These increases were substantial: waterfowl days for scaup spp. increased from 38,500 in 1986, before colonization by zebra mussels, to 3.5 million in 1997 ($r^2 = 0.614$, $P = 0.012$). Bufflehead days increased from 4,700 to 67,000 during the same period ($r^2 = 0.837$, $P = 0.001$). Peak spring counts for scaup spp. increased from 3,761 birds in 1986 to 22,435 birds in 1997 ($P < 0.001$), and fall counts increased from 1,925 to 50,966 birds during this period ($P = 0.058$). Peak spring counts for Buffleheads increased from 31 birds in 1986 to 920 birds in 1997 ($P = 0.007$), and fall counts increased from 216 to 1,618 birds during this time ($P = 0.018$). With the exception of 1992, when zebra mussel densities were at their peak and scaup densities were relatively low, scaup spp. alone were theoretically capable of consuming between 22 and 112% of zebra mussels on Long Point Bay in 1991 and between 43 and 220% by 1995 (Table 1).

DISCUSSION

The first reproductive population of zebra mussels in the Inner Bay at Long Point probably occurred in 1990. Mussels rapidly increased over the

TABLE 3. Percent occurrence of zebra mussels and unidentified shells in the diets of 12 species of waterfowl collected at Long Point, Lake Erie, 1992 through 1995.

Species		n	Feeding Guild	% Zebra Mussels	% Unidentified Shells	Maximum %[1] Occurrence
Lesser Scaup	*Aythya affinis*	57	Diver	75	61	83
Greater Scaup	*Aythya marila*	27	Diver	67	59	82
Bufflehead	*Bucephala albeola*	15	Diver	47	33	60
Redhead	*Aythya americana*	45	Diver	11	4	11
Canvasback	*Aythya valisineria*	44	Diver	0	0	0
Common Goldeneye	*Bucephala clangula*	10	Diver	0	0	0
Black Duck	*Anas rubripes*	60	Dabbler	5	0	5
Green-winged Teal	*Anas crecca*	42	Dabbler	0	0	0
Gadwall	*Anas strepera*	24	Dabbler	0	0	0
Wood Duck	*Aix sponsa*	35	Dabbler	0	0	0
American Wigeon	*Anas americana*	149	Dabbler	0	0	0
Mallard	*Anas platyrhynchos*	44	Dabbler	0	0	0

[1]All birds with zebra mussels or unidentified shells in their diet.

next 2 years, such that maximum density and distribution were reached by fall 1992. The ability of this species to rapidly colonize embayments and shallow lakes has been well documented. For instance, zebra mussel densities peaked on dammed Rhine delta lakes (surface area 60 km^2) within 2 years of colonization (Smit *et al.* 1993). After their rapid invasion of the Inner Bay, zebra mussels declined in overall distribution as well as in abundance. Quagga mussels also declined after colonizing the Inner Bay in 1993. Quagga mussels rarely attached to soft substrates and most frequently attached to zebra mussels or other quagga mussels. Thus, the decline in zebra mussel density during 1993 to 1995 resulted in fewer potential substrates for quagga mussels and may have contributed to their decline.

Zebra mussels are suspension feeders that indiscriminately and prolifically filter biotic and abiotic material from the water column (Ten Winkle and Davids 1982, Holland 1993). MacIsaac *et al.* (1992) calculated that zebra mussels on Hen Island Reef in western Lake Erie were capable of filtering a water column of 7 m between 3.5 and 18.8 times per day and Bunt *et al.* (1993) found that zebra mussels 11 mm or less in length were theoretically capable of filtering up to 96% of the water column per day in western Lake Erie. These prolific filtering capabilities can reduce planktonic diatom availability (Holland 1993), the primary food source of zebra mussels, which could precipitate a density-dependent decline in zebra mussel populations. For instance, planktonic diatoms declined by up to 90%, and water transparency increased by 100% since the invasion of zebra mussels in Hatchery Bay in western Lake Erie (Holland 1993).

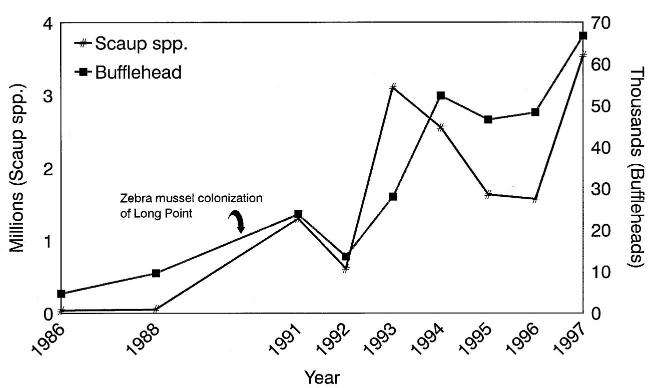

FIG. 3. Changes in the waterfowl day use of scaup spp. and Buffleheads at Long Point Bay, Lake Erie, 1986 to 1998.

The volume of water in the Inner Bay (78 km^2) is about 156×10^6 m^3; thus, there are about 2,000 L of water over each square meter of lake bottom. In 1992, average density of zebra mussels was 1,461 mussels/m^2 (1,824 mussels/m^2 for each occupied station × 80.1 % station occupancy) and most were less than 10 mm in length (Table 2). Thus, using Bunt *et al.*'s (1993) allometric equation for pumping rates $PR = 0.057 \cdot SL^{1.82}$, the clearance rate of the Inner Bay would have been about 17 days. Clearly, the filtering rate of zebra mussels in the Inner Bay at Long Point was considerably slower than in western Lake Erie. This can be attributed to the fact that a lack of hard substrates has prevented zebra mussels from reaching the high densities recorded in western Lake Erie (up to 233,000/m^2, Leach 1993). Whereas, phytoplankton densities have probably declined somewhat in Long Point Bay since zebra mussel colonization (Nicholls and Hopkins 1993, Petrie 1998), and this food exploitation may have contributed to the observed decline in zebra mussel densities, food limitation may not be the principal cause of the decline at Long Point.

Superimposed on possible depletion of food resources by zebra mussels is the direct impact of waterfowl predation on zebra mussel populations. Long Point is probably the most important waterfowl staging area on the Great Lakes, and it is particularly important for diving ducks (Dennis *et al.* 1984, Petrie 1998). Diving ducks, primarily of the genera *Aythya* and *Bucephala*, have modified their migration and overwintering patterns in response to availability of zebra mussels (Wormington and Leach 1992, review in Hamilton *et al.* 1994), and minor to severe reductions in mussel densities have occurred where populations of these ducks have increased (Stanczykowska 1977, Stanczykowska *et al.* 1990, Pedroli 1981, Suter 1982, Hamilton *et al.* 1994). There was a substantial increase in total waterfowl use of Long Point Bay between 1986 and 1997, most of which can be attributed to increased use by scaup spp. The combined Lesser and Greater Scaup use of Long Point Bay increased 92-fold between 1986 and 1997, despite a substantial decline in the North American population of scaup spp. (Dilworth-Christie and Dickson 1997). Of 84 Lesser and Greater Scaup collected at Long Point, 82% had consumed zebra mussels. Although Bufflehead numbers at Long Point are substantially lower than those of scaup spp., they have also altered movement patterns and diet composition in response to availability of zebra mussels.

Consumption of zebra mussels by waterfowl generally requires limited search and handling time. This is probably particularly true at Long Point, as most zebra mussels are attached to vegetation rather than to rocks and unionid shells. When prey become super-abundant and easily exploited, waterfowl tend to concentrate their foraging efforts on that food source; other pochard species exclusively consume zebra mussels when they are readily available (Pedroli 1981). If this is true for scaup spp. at Long Point, then these two species alone could have theoretically consumed between 22 and 112% of the zebra mussels at Long Point Bay in 1991, and between 43 and 220% by 1995. Clearly, predation by these waterfowl species alone could have caused the decline in zebra mussel distribution and abundance in Long Point Bay. Importantly, several other species of waterfowl (Oldsquaw *Clangula hyemalis*, White-winged Scoter *Melanitta fusca deglandi*, Hamilton and Ankney 1994) and fish (French 1993, Morrison *et al.* 1997) reportedly consume zebra mussels, and probably also contributed to the declining zebra mussel population at Long Point. While not documented in this study, probably because of small sample size (n = 10), Common Goldeneyes *Bucephala clangula* also consume zebra mussels in Lake Erie (Hamilton and Ankney 1994). However, although high rates of waterfowl consumption probably suppressed the population of zebra mussels in Long Point Bay, their high fecundity and dispersal capabilities probably prevents their eradication from the bay.

These results indicate an alternation of numerical dominance by mussels in 0 to 5 and 6 to 10 mm size classes, with very few mussels over 15 mm occurring in the Inner Bay (Table 2). If there was gradual food depletion from 1992 onward, one would expect the size of zebra mussels to decline, or to be inversely related to size of the zebra mussel population. There were marked changes in dominant size classes from one year to the next, but the changes did not indicate a gradual linear reduction in food availability (Table 2). This alternation may indicate years of higher food and temperatures causing fast growth alternating with years of poorer food and lower temperatures leading to slow growth. Such heterogeneity in size and cohort structure in zebra mussel populations in Lake St. Clair has been ascribed to intraspecific competition differentially influencing growth rates (Hebert *et al.* 1991).

More notable is that approximately 90% of zebra mussels, during all years, were < 10 mm in length and that very few were > 15 mm (Table 2). This may be attributed to size selective predation by foraging ducks, as heavy predation rates result in entire size cohorts being absent from zebra mussel populations (Wisiniewski 1974, Pedroli 1977). Waterfowl at Long Point concentrated most foraging effort on zebra mussels that were > 8 mm long (Hamilton and Ankney 1994), and, in western Lake Erie, waterfowl preferentially took medium and large mussels over the more common small ones (Hamilton *et al.* 1994). Furthermore, increased water clarity of Long Point Bay would facilitate visual prey selection, thereby increasing the capability of ducks to select larger size zebra mussels. Such selective predation would also suppress the reproductive capabilities of the population, as mussels do not reproduce until they are between 5 and 9 mm in length (Morton 1969, Stancykowska 1977, Mackie 1992), and female fecundity increases exponentially with age (Walz 1978).

CONCLUSION AND MANAGEMENT IMPLICATIONS

After an initial rapid increase in density and distribution in the Inner Bay at Long Point, zebra mussels steadily declined in absolute numbers, density per station and occupied area. The filtering activities of zebra mussels have increased water clarity and reduced availability of their plankton food source throughout Lake Erie, and this has probably contributed to the zebra mussel decline. However, there has been a substantial increase in scaup spp. and Bufflehead populations at Long Point since the colonization of zebra mussels, and these species consume large quantities of these mussels. Increased use of Long Point Bay by scaup spp. and Buffleheads is most likely a consequence of not only more birds staging in the area, but also of birds remaining for longer periods in response to this food source.

Zebra mussels are filter feeders and accumulate contaminants more readily than native Great Lakes bivalves (Brieger and Hunter 1993). These contaminants are subsequently passed up the food chain to the waterfowl that consume them. Lesser Scaup, Greater Scaup, and Buffleheads collected on western Lake Erie had elevated tissue concentrations of many contaminants compared to other species that consume aquatic plants (Mazak *et al*. 1997). This may be problematic, as transfer of contaminants from zebra mussels to waterfowl can adversely affect reproductive output (Scholten *et al.* 1989, de Kock and Bowmer 1993). Therefore, although scaup spp. and Buffleheads have shown functional and numerical responses to high populations of zebra mussels in the lower Great Lakes, consumption of these introduced mussels may in turn be indirectly influencing their survival and/or reproductive output, and by extension, continental populations.

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