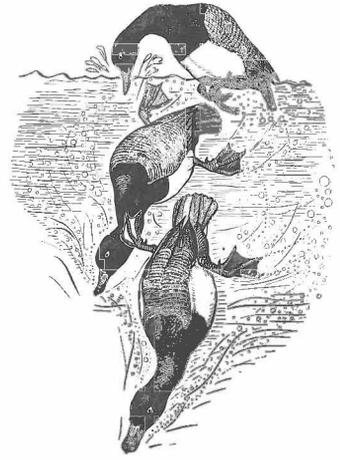


Consumption of Zebra Mussels *Dreissena polymorpha* by diving ducks in Lakes Erie and St. Clair.



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Zebra Mussels are a novel and abundant prey item for diving ducks in the Laurentian Great Lakes region. We investigated use of Zebra Mussels as food by several species of diving ducks (Greater and Lesser Scaup, Common Goldeneye, Bufflehead, White-winged Scoter and Oldsquaw) in Lakes Erie and St. Clair in 1990 and 1991. We examined 135 gizzards from ducks shot by hunters (fall) and ducks drowned in fishing nets (spring). We noted presence or absence of Zebra Mussels, and estimated lengths of mussels consumed. Mussels were eaten by all species examined and were consumed by ducks at each location. Overall, 52% of gizzards contained Zebra Mussels, including all those from Point Pelee, Ontario. Larger duck species tended to consume larger mussels, but prey sizes taken varied widely among locations. Although diving ducks probably were size-selective predators, they ate mussels from a wide size range. This suggests that at most locations where Zebra Mussels occur, some mussels of an acceptable size will always be present for ducks.

Keywords: Feeding Ecology, Diving Ducks, Biological Invasions, Zebra Mussels

Zebra Mussels *Dreissena polymorpha*, bivalves native to European lakes, have recently colonized the Laurentian Great Lakes (Griffiths *et al.* 1991, Hebert *et al.* 1991). Despite large scale environmental and economic impacts (including fouling of water, clogging of intake pipes and disruption of food webs) predicted and reported after the arrival of these prolific mussels (e.g. O'Neill & MacNeill 1989, Hebert *et al.* 1991, MacIsaac *et al.* 1992, Ludyanskiy *et al.* 1993), they provide a novel and abundant new food source for several species of diving ducks.

European waterfowl which feed on Zebra Mussels include Tufted Ducks *Aythya fuligula*, Pochards *A. ferina*, Common Goldeneyes *Bucephala clangula* and European Coots *Fulica atra* (Olney 1963, G eroudet 1966, 1978, Borowiecz 1975, Pedroli 1981, Suter 1982a, Stanczykowska *et al.* 1990). Pedroli (1981) found that mussels accounted for 99% and 93% of winter food for Tufted Ducks and Pochards, respectively, on lakes in Switzerland. Ducks in Europe have altered their migration patterns to feed on mussels in newly colonized areas, and have remained longer in regions with high mussel density (G eroudet 1966, Leuzinger 1969,

Pedroli 1981, 1982, Suter 1982a, 1982b). Ducks are also size-selective predators (Pedroli 1981, Draulans 1982, 1984, 1987), often causing large changes in size structure of mussel populations on which they feed (Wisniewski 1974, Pedroli 1977, 1981, G eroudet 1978). Such changes are often coupled with local reductions in mussel biomass (Stempniewicz 1974, Pedroli 1981, Suter 1982a, 1982c, Stanczykowska *et al.* 1990). These impacts may be of short duration, though; densities can return to normal levels by the following year if predation is not constant (Suter 1982c).

Except for Common Goldeneye, waterfowl predators of Zebra Mussels in Europe are not present in North America. However, ecologically similar species, including Greater Scaup *Aythya marila*, Lesser Scaup *A. affinis* and Bufflehead *Bucephala albeola*, are all abundant in the Great Lakes region during fall and spring migratory periods. These species, and Common Goldeneye, are known to feed on Zebra Mussels in Lake Erie at Point Pelee (Wormington & Leach 1992, Hamilton *et al.* 1994), and Lesser Scaup feed on mussels in southern Lake Michigan (Mitchell & Carlson 1993). Zebra Mussels have also been found in the giza

zard of one White-winged Scoter *Melanitta fusca deglandi* feeding in the St. Lawrence River (Guillemette *et al.* 1994). We examined the extent to which the above species, as well as Oldsquaw *Clangula hyemalis*, fed on Zebra Mussels in Lakes Erie and St. Clair in 1990 and 1991. We compared the sizes of mussels consumed by the different species and assessed the use made of Zebra Mussels as food by diving ducks in the Great Lakes.

Methods

Data collection

We collected duck gizzards from hunted ducks, and from ducks drowned in fishing nets, from various locations in Lake St. Clair (42° 25' N, 82° 35' W), and from Lake Erie near Point Pelee (41° 57' N, 82° 31' W), Rondeau Bay (42° 19' N, 81° 51' W), Port Stanley (42° 40' N, 81° 10' W) and Long Point (42° 35' N, 80° 2' W). We obtained only one duck from Rondeau, so it was included with those from Point Pelee because of the geographic proximity of the two locations. A single White-winged Scoter from Long Point was included in the overall count of ducks which consumed Zebra Mussels, but these mussels were not measured and could not be included in other analyses.

We opened gizzards and separated Zebra Mussel fragments from other material with the aid of a low power magnifying lens. We did not weigh or identify other food material because gizzard contents tend to bias food identification in favour of hard bodied prey (Swanson & Bartonek 1970).

We reconstructed sizes of mussels consumed based on the lengths of mussels' internal septa found in gizzards. This is a reliable method because septa rarely break down and are easily identified from other shell fragments (Hamilton 1992a). We used separate reconstruction equations for Lakes St. Clair and Erie (Hamilton 1992a). Because it was not always possible to match left and right septa, we counted each fragment as an individual measure. Accordingly, when whole mussels were found, lengths of each side were measured and used in analyses.

Statistical analyses

All analyses were carried out using SAS statistical software (SAS Institute 1988). We tested for a pattern in Zebra Mussel use among duck species and locations based on simple presence or absence of mussel fragments (contingency Chi-square, SAS: Proc FREQ). When small sample sizes invalidated the Chi-square statistic, we used probabilities generated from Fisher's Exact Test (SAS Institute 1988).

We compared mean mussel size consumed among species using one way analyses of variance (ANOVA) (SAS: Proc GLM). Data were tested for normality prior to analysis. Most distributions were normal, and ANOVA is robust to minor violations of assumptions (Winer 1971), so the few observed deviations from normality (i.e. see Fig. 2) are unlikely to influence our results. Analyses were carried out separately for each location because we detected significant differences in mussel sizes consumed among locations, and a 2-way ANOVA combining effects of place and location was not possible because of lack of replication (i.e. not all species appeared in all locations). When overall significant effects were detected, the *a posteriori* Tukey's Test, adapted for an unbalanced design (SAS Institute 1988), was conducted to determine where differences occurred. Because some ducks consumed many more mussels than others, each observation was weighted as the inverse of the number of mussels consumed by the duck from which it came. Weightings for each duck therefore summed to 1, so each individual received equal importance in the analysis. This ensured that a duck which took many mussels did not unduly bias the results, but at the same time allowed us to maintain the inherent variability in the data, which would be lost if we used a single average mussel size taken by each duck.

We also compared size distributions of mussels consumed by ducks at each location to better assess the range in mussel sizes taken by diving ducks. We classified all mussels into one of 7 size categories (<5 mm, 5-7.99 mm, 8-10.99 mm, 11-13.99 mm, 14-16.99 mm, 17-19.99 mm and >20 mm). We compared size distributions of mussels consumed by the different species using a categorical modelling procedure (SAS: Proc CATMOD). This test detects differences in distributions and partitions the

Table 1. Number of ducks with and without Zebra Mussels in their gizzards for each species, location, and time. Number of fragments found in gizzards and used in analyses is noted.

location	species	season	with mussels <i>n</i>	without mussels <i>n</i>	fragments <i>n</i>
Long Point	Bufflehead	fall 1990	0	2	0
Long Point	Goldeneye	fall 1990	4	0	247
Long Point	Lesser Scaup	fall 1990	0	6	0
Long Point	Bufflehead	fall 1991	3	3	180
Long Point	Greater Scaup	fall 1991	6	2	179
Long Point	Lesser Scaup	fall 1991	11	7	213
Long Point	White-winged Scoter	fall 1991	1	0	^a
Point Pelee	Bufflehead	fall 1991	4	0	30
Point Pelee	Goldeneye	fall 1991	1	0	51
Point Pelee	Lesser Scaup	fall 1991	2	0	34
Port Stanley	Oldsquaw	spring 1991	19	26	169
Port Stanley	Scoter	spring 1991	4	5	51
St. Clair	Greater Scaup	fall 1990	3	3	88
St. Clair	Lesser Scaup	fall 1990	13	11	423

^anot counted or measured

variance among classification variables, in this case species effects, much as does an ANOVA for continuous data. As before, observations were weighted to ensure that all ducks received equal importance in the analysis.

Results

Number of ducks feeding on Zebra Mussels

In total, 71 (52%) of 136 ducks contained Zebra Mussels (Table 1). There was no overall difference among species in proportion of ducks feeding on mussels ($\chi^2 = 7.227$, $df=5$, $P=0.204$). There was, however, a difference in use of mussels by ducks from

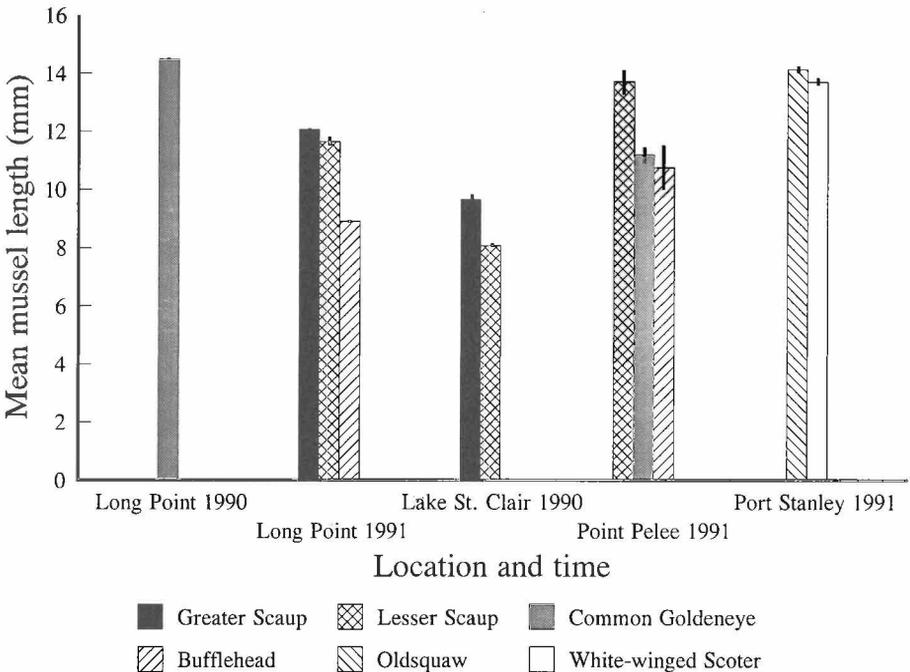


Figure 1. Mean (± 2 SE) Zebra Mussel sizes (length) consumed by duck species at the different sites in 1990 and 1991. The significance of differences among species is given in Table 2.

Table 2. Analyses of variance in mean Zebra Mussel size consumed by the different duck species in different locations. When overall significant differences occurred, species differences were identified using Tukey's Test (SAS Institute 1988).

group	df (model,error)	F	P	differences
Long Point 1991	2,569	20.30	<0.0001	Greater Scaup > Lesser Scaup Greater Scaup > Bufflehead Lesser Scaup > Bufflehead
Point Pelee 1991	2,112	5.79	0.0041	Lesser Scaup > Bufflehead Lesser Scaup > Goldeneye
St. Clair 1990	1,509	31.43	<0.0001	Greater Scaup > Lesser Scaup
Port Stanley 1991	1,218	1.24	0.2669	none

the different locations ($\chi^2=8.509$, $df=3$, $P=0.037$). This arose because of the inclusion of ducks from Port Stanley (which involved duck species not sampled elsewhere). When Port Stanley was excluded from the analysis, ducks were equally likely to consume Zebra Mussels at all locations ($\chi^2=4.805$, $df=2$, Fisher's Exact $P=0.0985$). In this sample, 48 of 82 ducks (58.5%) contained mussels (Table 1).

Mean size of mussels consumed

Large species of ducks at each location (with the exception of Port Stanley) appeared to take the largest mussels (see Bellrose (1980) for average sizes of duck species). At Long Point in 1991, Greater Scaup ate larger mussels than did Lesser Scaup, and both scaup species took larger prey than did Bufflehead (Figure 1, Table 2). Lesser Scaup took larger mussels than did Common Goldeneye and Bufflehead at

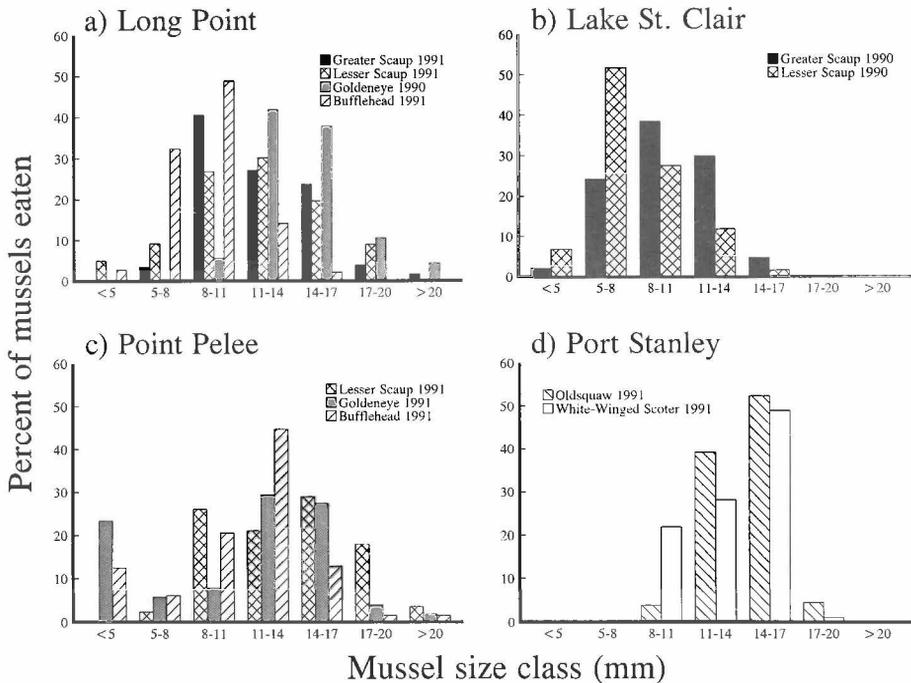


Figure 2. Size-frequency distributions of Zebra Mussels consumed by the different duck species in 1990 and 1991 at each sampling location. The Y-axis refer to percent of all mussels eaten by a species (within sites) which fall into the various size categories. Observations were weighted such that each duck received equal importance (see methods).

Table 3. Categorical analysis of Zebra Mussel size frequency distributions consumed by each duck species in each location. Significant effects indicate that size distributions of mussels consumed differ among the species.

location	comparisons	χ^2	df	P
Long Point 1991	Bufflehead, Greater Scaup, Lesser Scaup	102.00	12	<0.0001
St. Clair 1990	Greater Scaup, Lesser Scaup	33.86	6	<0.0001
Point Pelee 1991	Common Goldeneye, Bufflehead, Lesser Scaup	18.03	12	0.1147
Port Stanley 1991	White-winged Scoter, Oldsquaw	15.92	6	0.0142

Point Pelee (**Figure 1, Table 2**). At Lake St. Clair in 1990, Greater Scaup took significantly larger mussels than did Lesser Scaup (**Figure 1, Table 1**). Finally, there was no statistical difference among mussel sizes eaten by White-winged Scoters and Oldsquaws at Port Stanley (**Figure 1, Table 2**).

Size distribution of mussels consumed

Size distribution of mussels consumed at Long Point differed among species (**Table 3**). Greater and Lesser Scaup consumed a greater proportion of large mussels, and took a somewhat wider range of mussel sizes, than did Bufflehead (**Figure 2**), though all species appeared to feed on mussels of many different sizes. It is notable that Common Goldeneye in 1990 ate mussels much larger than did any of the species in 1991 (**Figure 2**), but these could not be compared to the 1991 birds because available mussel sizes may have differed. At Lake St. Clair in 1990, Greater and Lesser Scaup consumed a similar range of mussel sizes, but most frequently taken size classes for Greater Scaup were larger than for Lesser Scaup, generating a significant difference between the two distributions (**Table 3, Figure 2**). There was no overall difference in size-frequency distributions of mussels consumed by the three species of ducks at Point Pelee, and all species took mussels from a similar size range (**Table 3**). However, Common Goldeneye and Bufflehead tended to make greater use of small mussels than did Lesser Scaup (**Figure 2**). Distributions of mussels taken by Oldsquaw and White-winged Scoters at Port Stanley differed significantly, with scoters feeding more heavily on 8-11 mm mussels, but the range taken by the two species was similar (**Table 3, Figure 2**).

Discussion

Ducks feeding in Lakes Erie and St. Clair have clearly altered their food habits to include Zebra Mussels since the arrival of these bivalves in North America. More than half of the birds examined, including all of those from Point Pelee and nearly 60% of those from Long Point in 1991, contained mussels. This is consistent with European observations, where birds have frequently altered their diets to include Zebra Mussels shortly after they became available (Pedroli 1977, 1981, Géroudet 1978). Notably, this change has been shown by duck species that use different habitats. Oldsquaws typically feed farther from shore in deeper water than do the other species in the study (Bellrose 1980). Hence, Zebra Mussels have provided a common food source for diving duck species feeding in different locations and under different foraging constraints.

Except for Point Pelee, the sampling locations in our study represent traditional staging grounds for migratory diving ducks (McCullough 1981). Diving ducks began feeding at Point Pelee during fall only after the 1988 arrival (Griffiths *et al.* 1991) of Zebra Mussels in the area (Wormington & Leach 1992). This difference may explain why all ducks from Point Pelee contained Zebra Mussels, whereas some ducks from other locations had not eaten mussels before collection. Alternative foods were present in the other areas, so some ducks may not have switched to Zebra Mussels. At Point Pelee, however, ducks were probably there only because of the presence of Zebra Mussels (see Leuzinger 1969, Géroudet 1978, Pedroli 1981 and Suter 1982b for European examples of changes in waterfowl migration patterns and staging grounds in response to Zebra Mussels), so

mussels were almost certainly their main food source.

It is possible that some ducks from our study areas (other than Point Pelee) did not contain Zebra Mussels because mussels were not present where they fed. We used SCUBA gear to do extensive bottom surveys in the area where ducks were collected at Point Pelee (Hamilton 1992b). The substrate was blanketed with mussels, and no other obvious food sources were present. Ducks from other sites were shot by hunters or caught in fish nets, and, although we know that mussels were present in the general area, we know nothing of particular sites where ducks fed immediately before collection.

We found a general tendency at most sites for larger duck species to take larger Zebra Mussels. This is not a surprising result, but it is notable that although there were differences among sizes of mussels taken, all species took a very broad and overlapping range of prey. Mussel sizes taken by species also differed greatly among sites. Ducks from Point Pelee took larger mussels than did their conspecifics in other areas. Mussel size distributions tend to change considerably over times and locations (Stanczykowska 1977, Bij de Vaate 1991, Griffiths *et al.* 1991, Hebert *et al.* 1991), so it is probable that the range of available prey differed among sites, causing ducks to take mussels of different sizes.

Diving ducks are typically size-selective predators when feeding on Zebra Mussels (Draulans 1982, 1984, 1987). The caloric value of a mussel increases exponentially with shell length (Draulans & Wouters 1988), but shells also thicken as mussels grow, so neither very large nor very small mussels are as profitable as medium-sized mussels. However, ducks feeding in the Great Lakes appear to feed on mussels of widely varying sizes. Mitchell & Carlson (1993) found that Lesser Scaup in Lake Michigan fed most heavily on small mussels averaging 4.1 mm in length. This contrasts with our observation that ducks selected much larger than average mussels at Point Pelee (Hamilton *et al.* 1994). Clearly,

although Lesser Scaup may take larger mussels when available, even very small mussels are sufficiently profitable to attract ducks.

Conclusions

Duck species in our study fed mostly on medium-sized mussels, but also ate many smaller mussels. This broad range of acceptability may help to explain why Zebra Mussels have so quickly become an important food source for diving ducks in the Great Lakes. It also suggests that mussels will remain important for ducks in the future. Clearly, selection of Zebra Mussels by diving ducks is related to mussel size availability, and further work, in which mussel availability and sizes taken are quantified, is needed to determine the nature of this relationship and its implications for ducks and Zebra Mussels in the Great Lakes region. Ducks are unlikely to eliminate mussels (Hamilton *et al.* 1994), and the high reproductive and growth rates of the mussels virtually ensure that, given the variability of mussel sizes consumed in our study, mussels of acceptable sizes will be available for ducks each year.

We have shown that ducks do feed on Zebra Mussels in the Laurentian Great Lakes. However, we have no information on the possible long term effects of this food source on duck populations. Further study, concerning nutritional quality and contaminant levels of Zebra Mussels, as well as condition and population changes of duck species using this new food source, is required to address this question. Monitoring of newly invaded lakes for changes in local duck populations may allow us to assess the impact of Zebra Mussels on staging grounds and migration patterns of diving ducks. This would permit study of the link between ducks and their newly introduced prey, and, combined with knowledge of the value of Zebra Mussels as a food source, would help to determine the true impact of Zebra Mussels on North American duck populations.

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