J. Field Ornithol., 67(1):86–99

FOOD HABITS OF DIVING DUCKS IN THE GREAT LAKES AFTER THE ZEBRA MUSSEL INVASION

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Abstract.—Zebra mussels (*Dreissena polymorpha*) invaded the Great Lakes in the mid-1980s and quickly reached high densities. The objective of this study was to determine current consumption of zebra mussels by waterfowl in the Great Lakes region. Feeding Lesser Scaups (*Aythya affinis*), Greater Scaups (*A. marila*), Canvasbacks (*A. valisineria*), Redheads (*A. americana*), Buffleheads (*Bucephala albeola*) and Common Goldeneyes (*B. clangula*) were collected in western Lake Erie and in Lake St. Clair between fall and spring, 1992–1993 to determine food habits. All 10 Redheads, 97% of Lesser Scaups, 83% of Goldeneyes, 60% of Buffleheads and 9% of Canvasbacks contained one or more zebra mussels in their upper gastrointestinal tracts. The aggregate percent of zebra mussels in the diet of Lesser Scaups was higher in Lake Erie (98.6%) than in Lake St. Clair (54.4%). Zebra mussels (aggregate percent) dominated the diet of Common Goldeneyes (79.2%) but not in Buffleheads (23.5%), Redheads (21%) or Canvasbacks (9%). Lesser Scaups from Lake Erie fed on larger zebra mussels ($\bar{x}$ = 10.7 ± 0.66 mm SE) than did Lesser Scaups from Lake St. Clair ($\bar{x}$ = 4.4 ± 0.22 mm). Lesser Scaups, Buffleheads and Common Goldeneyes from Lake Erie consumed zebra mussels of similar size.

HÁBITOS ALIMENTICIOS DEL PATOS ZAMBULLIDORES EN LOS GRANDES LAGOS LUEGO DE LA INVASIÓN DE LA ALMEJA *DREISSENA POLYMORPHA*

Sinopsis.—La almeja *Dreissena polymorpha* invadió los Grandes Lagos a mediados de la década del 1980 y en poco tiempo alcanzó densidades sumamente altas. El objetivo de este estudio fue determinar el consumo de esta almeja por parte de los patos que utilizan estos lagos. Se coleccionaron individuos de *Aythia affinis, A. marila, A. valisineria, A. americana, Bucephala albeola* y de *B. clangula* entre el otoño y la primavera de 1992–1993, en los lagos Erie y St. Clair, para determinar los hábitos alimenticios de estas especies. El 100% de los especímenes de *A. americana,* 97% de *A. affinis,* 83% de *B. clangula,* 60% de *B. albeola,* y el 9% de *A. valisineria* ingirieron almejas. El porciento agregado de almejas en la dieta de *Aythia affinis* fue mayor en el Lago Erie (98.6%) que en el Lago St. Clair (54.4%). Las almejas (porciento agregado) dominaron la dieta de *B. clangula* (79.2%) pero no así la de *A. affinis, A. americana,* o *A. valisineria.* Los individuos de *A. affinis* del Lago Erie se alimentaron de almejas más grandes ($\bar{x}$ = 10.7 ± 0.66 mm ES) que los individuos del Lago St. Clair ($\bar{x}$ = 4.4 ± 0.22 mm). Los individuos de *A. affinis, B. albeola* y de *B. clangula* del Lago Erie se alimentaron de almejas de tamaño similar.

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Zebra mussels (*Dreissena polymorpha*) have reached high densities, especially in Lake Erie and Lake St. Clair (Leach 1993), since their introduction into the Great Lakes in the mid-1980s. Densities of zebra mussels over 700,000/m^2 have been reported at power plants on Lake Erie (Kovalak et al. 1993) and as many as 342,000/m^2 on fish-spawning reefs in Lake Erie (Leach 1993).

In Europe, Tufted Ducks (*Aythya fuligula*), Greater Scaups (*A. marila*), Common Pochards (*A. ferina*) and Common Goldeneyes (*Bucephala clangula*) commonly consume zebra mussels (de Vaate 1991, Olney 1963). In the United States, Mitchell and Carlson (1993) reported that 19 of 21 Lesser Scaups (*Aythya affinis*) entrained into a power plant in Michigan contained nearly 100% zebra mussels in their esophagi and/or proventriculi. Hamilton (1992a) and Wormington and Leach (1992) found pieces of zebra mussel shell in eight waterfowl gizzards from Lake Erie (four Buffleheads [*Bucephala albeola*], two Lesser Scaups, one Greater Scaup and one Common Goldeneye). The sample size in that study was small, however, and gizzard data are biased because of differential digestion rates of soft and hard food items (Swanson and Bartonek 1970).

Zebra mussels have the potential to affect waterfowl distribution and abundance (Stanczykowska et al. 1990, Wormington and Leach 1992) in North America. Additionally, the bioaccumulation capacities of zebra mussels (Brieger and Hunter 1993, Busch and Schuchardt 1991, Mersch et al. 1992) may enhance the transfer of contaminants to waterfowl (de Kock and Bowmer 1993). Contaminants can negatively affect waterfowl reproduction (de Kock and Bowmer 1993) and may have secondary effects as a contaminant source for Bald Eagles (*Heliaeetus leucocephalus*) and humans. Our objectives were to determine which diving ducks currently consume zebra mussels in the U.S. portion of the Great Lakes and what proportion of their diet is now comprised of zebra mussels.

METHODS

We collected diving ducks during fall (prior to ice coverage of the lakes, November–December), mid-winter (lakes frozen, January–February) and spring (beginning of ice break-up, March–April) from January 1992 to April 1993 in three general areas of Lakes Erie and St. Clair (Fig. 1). These three general collection areas represented the major waterfowl concentrations in the U.S. portions of these two lakes (Bookhout et al. 1989). We collected ducks by shooting (Federal Permit PRT-673019, Michigan Permit SC- 785, Ohio Permits 249, 167) either from shore or from boats, generally after we had observed the ducks feeding. We immediately removed contents of the esophagus and proventriculus (upper GI tract) and stored them separately in 95% ethanol. Esophageal and proventricular contents were combined for analysis to maximize sample size (Afton et al. 1991). We determined the age and sex of waterfowl using plumage and cloacal characteristics (Carney 1964).

All food items were identified to genus or species and number of individual items counted. Frequency of occurrence (number of waterfowl

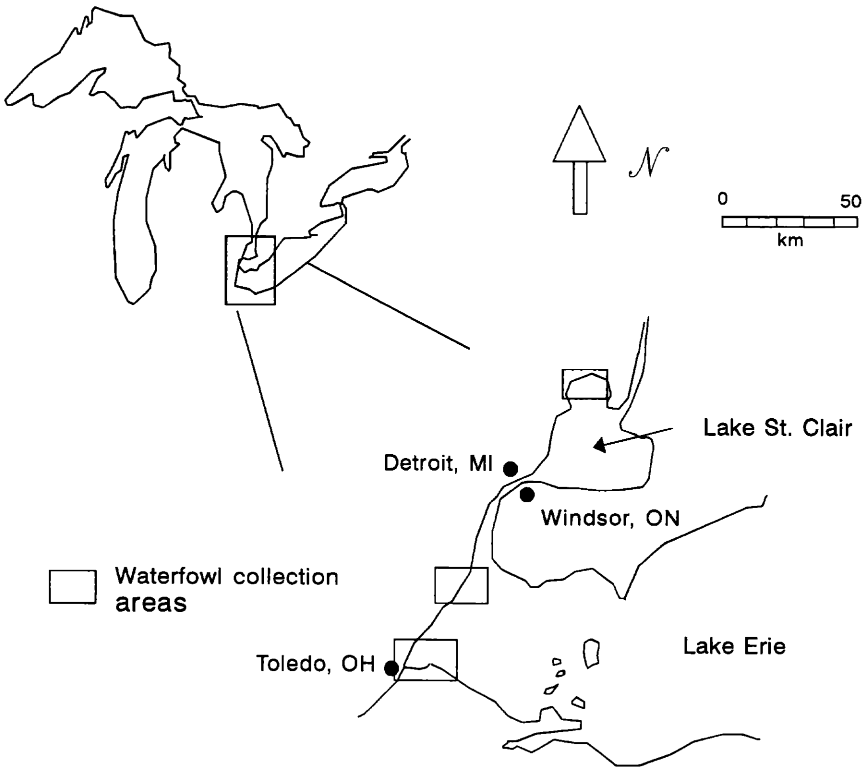

FIGURE 1. Three general locations where six species of diving ducks were collected during fall, winter, and spring, January 1992–April 1993.

with a particular food taxon divided by the total number of waterfowl) and aggregate percent (proportion of each food item in each bird averaged for all individuals; Swanson et al. 1974) were calculated for each waterfowl species. When the upper GI tract contained only animal material (n = 74), we calculated aggregate percent based on numerical data, rather than dry mass or volume, because food items were generally the same size (average length of zebra mussels = 8.1 mm, isopods = 7.8 mm, amphipods = 5.5 mm, caddisflies = 8.8 mm) and because molluscs were an important component of the diet. When upper GI tract samples contained both plant matter and animal matter (n = 8 Redheads, 2 Buffleheads), volumetric measurements of food items were taken and the volumes used to calculate aggregate percent (Bartonek and Hickey 1969, Gammonley and Heitmeyer 1990). Aggregate percent based on numbers is preferable to aggregate percent based on dry mass when molluscs are an important component of the diet because dry mass inflates the importance of molluscs in the diet due to the proportionately large mass of undigestible shell material. Additionally, numerical counts are less prone to measurement error than either the dry mass or volume methods, which is important when measuring small volumes or dry masses as in our study. Aggregate percent based on dry mass does facilitate making energy and nutritional inferences. Dry mass of zebra mussels in our study can be estimated based on their shell length (Draulans 1982). Even though methods to determine percent composition of diet differs between studies, we follow the common practice of comparing our data to other studies (Afton et al. 1991, Dirschl 1969, Gammonley and Heitmeyer 1990, Hoppe et al. 1986).

Shell length of ingested zebra mussels ≥5 mm was measured to the nearest mm and those <5 mm were measured to the nearest 0.2 mm. All zebra mussels were measured along the longest axis of the shell (Hamilton 1992b). Average size of zebra mussels was calculated for each duck and those means used for statistical comparisons. An individual duck was the measurement unit for zebra mussel size comparisons among species, ages, sexes and locations.

Data were analyzed in a step-wise manner. We used analysis of variance (ANOVA) on aggregate percent and zebra mussel size data. Bartlett's tests were used to test for homogeneity of variances prior to each ANOVA. If variances were not equal, data were rank transformed, which in all cases equalized the variances. Untransformed means ± 1 SE are presented in text and tables. When main factors and the interaction term in 2-way ANOVAs were non-significant, these factors were combined in subsequent 2-way or 1-way analyses. Similarly, sequential chi-square and/or Fisher's Exact tests were used on frequency-of-occurrence data; sexes, ages, and seasons were combined in subsequent analyses as these factors were found to be not significantly different. Differences in size distributions of zebra mussels consumed by waterfowl were tested with Kolmogorov-Smirnov two-sample tests.

RESULTS

We collected 60 Lesser Scaups, 20 Buffleheads, 11 Common Goldeneyes, 14 Canvasbacks, 10 Redheads and four Greater Scaups. Of these, 41 Lesser Scaups (the numbers collected in fall and spring were nine and 23; eight in winter), 15 Buffleheads (nine and six), six Common Goldeneyes (three and three), 11 Canvasbacks (five and five; one in winter), 10 Redheads (six and four), and one Greater Scaup (one and none) had food in their upper GI tracts. Each duck with food in its esophagus or proventriculus was included in the analyses.

Spring and fall diets.—Ninety-seven percent (31 of 32) of Lesser Scaup upper GI tracts contained at least one zebra mussel (Table 1); therefore, no statistical comparisons of frequency of occurrence between seasons, ages or sexes were made. Frequency of occurrence of zebra mussels did not differ between Lake Erie and Lake St. Clair (Fisher's Exact, $n = 32$, $P = 0.156$).

The aggregate percent zebra mussels in the upper GI tract of Lesser

TABLE 1. Frequency of occurrence and aggregate percent of foods in the upper gastrointestinal tract (esophagus and proventriculus) of five species of diving ducks from the western end of Lake Erie and Lake St. Clair during fall and spring, 1992 and 1993.

Species, location, food taxa (*n*)	Frequency of occurrence (%)	Aggregate %	
		x̄	SE
Lesser Scaup (32)			
Lake Erie (27)			
Mollusca			
zebra mussels	27 (100)	98.6	0.94
Amnicola walkeri	1 (4)	0.2	0.19
Physella integra	1 (4)	0.9	0.93
Sphaeriidae	1 (4)	<0.1	
Isopoda			
Caecidotea sp.	2 (7)	0.2	0.13
Annelida	2 (7)	0.1	0.11
Lake St Clair (5)			
Mollusca			
zebra mussels	4 (80)	54.4	19.92
Amnicola walkeri	3 (60)	2.6	1.58
Pleurocera acuta	2 (40)	20.2	19.95
Physella integra	1 (20)	1.0	1.00
Valvata sp.	1 (20)	0.8	0.80
Gyraulus sp.	1 (20)	1.2	1.20
Sphaeriidae	1 (20)	1.2	1.20
Ferrissia parallela	1 (20)	0.1	0.10
Amphipoda			
Hyalella/ Gammarus spp.	4 (80)	14.4	12.21
Isopoda			
Caecidotea sp.	1 (60)	3.0	1.48
Diptera	1 (40)	1.3	1.18
Fish	1 (20)	<0.1	
Bufflehead (15)			
Lake Erie			
Mollusca			
zebra mussels	9 (60)	23.5	8.83
Amnicola walkeri	1 (7)	0.6	0.60
Amphipoda			
Hyalella/ Gammarus spp.	10 (67)	46.6	10.42
Isopoda			
Caecidotea sp.	3 (20)	8.8	6.72
Trichoptera			
Hydropsyche sp.	1 (7)	4.8	4.80
Tricoptera adult	1 (7)	<0.1	
Odonata			
Enallagma sp.	1 (7)	3.6	2.45
Crustacea	1 (7)	1.1	1.13
Plants			
wildcelery winterbuds	1 (7)	6.1	6.13
Polygonum sp. seeds	1 (7)	6.7	6.67
Common Goldeneye (6)			
Lake Erie			
Mollusca			
zebra mussels	5 (83)	79.2	16.35
Physella integra	1 (17)	0.3	0.33

TABLE 1. Continued.

Species, location, food taxa (n)	Frequency of occurrence (%)	Aggregate %	
		x̄	SE
Amphipoda			
Hyalella/Gammarus spp.	2 (33)	5.8	5.44
Isopoda			
Caecidotea sp.	2 (33)	14.8	11.03
Canvasback (11)			
Lake Erie (3) and Lake St. Clair (8)			
Mollusca			
zebra mussels	1 (9)	9.1	9.09
Plants			
wildcelery winterbuds	10 (91)	90.9	9.09
Redhead (10)			
Lake Erie (4)			
Mollusca			
zebra mussels	4 (100)	50.5	28.58
Plants			
Potamogeton sp.	2 (50)	49.5	28.58
Lake St. Clair (6)			
Mollusca			
zebra mussels	6 (100)	1.3	0.98
Plants			
Potamogeton sp.	6 (100)	98.7	0.98

Scaups in Lake Erie (98.6%) was greater than in Lake St. Clair (54.4%) (Table 1, $F_{1,29} = 17.97$, $P < 0.001$). Aggregate percent of zebra mussels in the upper GI tract did not differ between ages or seasons (age, season, and interaction, $F_{1,23} = 0.56$, < 0.01, 2.39; $P = 0.463$, 0.993, 0.136, respectively) or between sexes ($F_{1,25} = 1.48$, $P = 0.235$) for Lesser Scaups in Lake Erie. Food habits of Lesser Scaups in Lake St. Clair were more variable than food habits in Lake Erie; six taxa comprised >95% of the food items in Lake St. Clair compared with only one taxon, zebra mussels, comprising >95% of the food items in Lake Erie.

Sixty percent of Buffleheads contained one or more zebra mussels (Table 1). Frequency of occurrence of zebra mussels did not vary by sex (Fisher's Exact, $P = 1.00$, $n = 15$) or season ($P = 0.136$, $n = 15$).

No one food item dominated in the upper GI tracts of Buffleheads (Table 1). Approximately 47% of Bufflehead food items consisted of amphipods. Nearly 24% of Bufflehead diet was composed of zebra mussels; aggregate percent did not differ by sex or season (sex, season, and interaction $F_{1,5} = 0.08$, 0.29, < 0.01; $P = 0.793$, 0.613, 0.954, respectively).

Five of six Common Goldeneyes contained at least one zebra mussel (Table 1). Zebra mussels dominated in the diet (79%); isopods and amphipods also were consumed.

Wildcelery winterbuds (*Vallisneria americana*) were the dominant food (91%) in Canvasback upper GI tracts (Table 1). Only one Canvasback, collected from Lake Erie, contained zebra mussels in its upper GI tract.

TABLE 2. Size (mm) of zebra mussels consumed by six species of diving ducks in the western end of Lake Erie and Lake St. Clair during fall and spring, 1992 and 1993.

Location and species	x̄	SE	n[a]	Minimum[b]	Maximum[b]
Lake Erie					
Greater Scaup	13.4		1	2.4	23
Common Goldeneye	12.0 A[c]	1.55	5	1.6	23
Lesser Scaup	10.7 A	0.60	27	0.8	23
Canvasback	9.7		1	2.8	15
Bufflehead	7.7 AB	1.45	9	0.8	18
Redhead	6.3 B	2.61	4	0.2	18
Lake St. Clair					
Lesser Scaup	4.4	0.22	4	0.8	9
Redhead	3.2	0.25	6	1.2	7

[a] Number of ducks used to calculate mean zebra mussel shell lengths.
[b] Minimum and maximum sizes determined from all zebra mussels consumed by each species.
[c] Means with same letter are not significantly different (F = 3.51; df = 3,42; P = 0.023, Bonferroni mean separation).

This individual was collected while it was dabbling along the shoreline during a period of low water caused by a seiche (Bookhout et al. 1989). One Canvasback and one Lesser Scaup were collected from a mixed feeding flock of Lesser Scaups and Canvasbacks. The Canvasback had only wildcelery winterbuds and the Lesser Scaup had only zebra mussels in their upper GI tracts.

All 10 Redheads contained at least one zebra mussel in their upper GI tracts (Table 1). The difference in aggregate percent of zebra mussels between Lakes Erie and St. Clair approached significance ($F_{1,8}$ = 3.51, P = 0.098). This lack of difference resulted from the large variance of Lake Erie Redheads; two of four Redheads contained 99% vegetation, whereas the other two Redheads contained 100% zebra mussels. The zebra mussels that eight of 10 Redheads were eating (six of six Redheads from Lake St. Clair and two of four Redheads from Lake Erie) were attached to the stems of vegetation.

Only one Greater Scaup (immature female from Lake Erie) contained food in its upper GI tract. Ninety-nine percent of the food in its upper GI tract was zebra mussels and 1% was a snail, *Pleurocera* sp.

Size of zebra mussels.—Size of zebra mussels consumed did not differ between male and female Lesser Scaups (Table 2, $F_{1,18}$ = 2.69, P = 0.118) or between male and female Buffleheads (Table 2, $F_{1,7}$ = 1.12, P = 0.325). There were no seasonal differences in size of zebra mussels eaten by Lesser Scaups (Table 2, $F_{1,18}$ = 2.57, P = 0.126) or Buffleheads ($F_{1,7}$ = 1.21, P = 0.308). Lesser Scaups from Lake Erie ate larger zebra mussels than Lesser Scaups from Lake St. Clair (Table 2, $F_{1,30}$ = 16.19, P < 0.001). Using Lake Erie data only, Lesser Scaups, Buffleheads and Common Goldeneyes consumed zebra mussels of similar size, and Lesser Scaups and

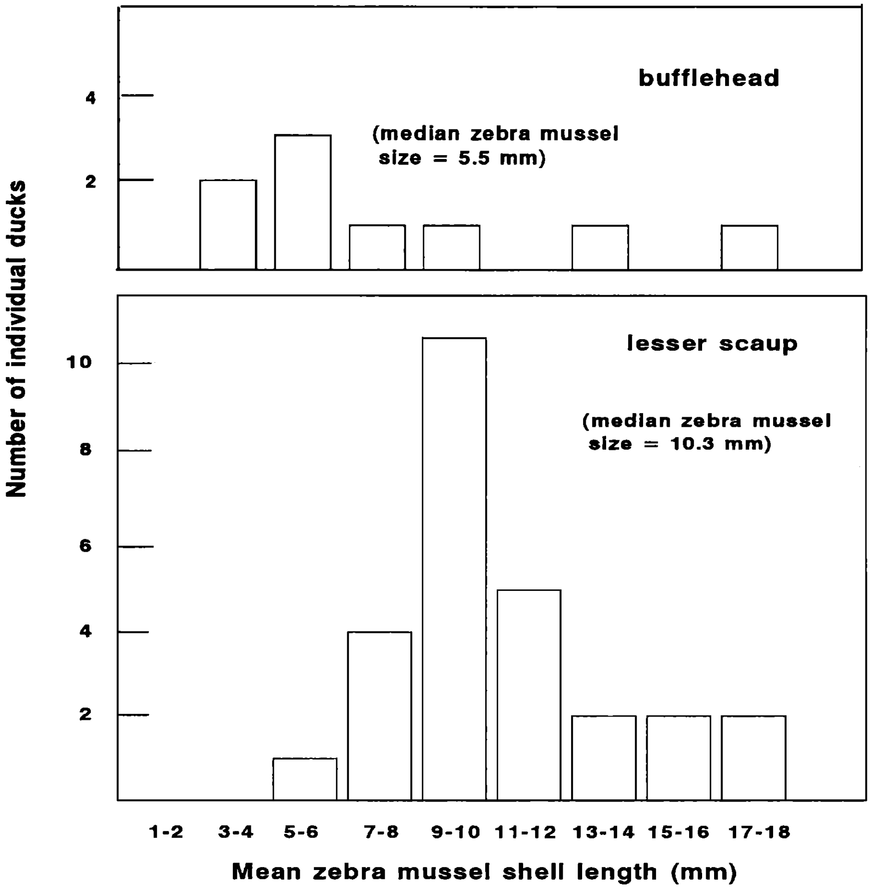

FIGURE 2. Size distribution of zebra mussels from the upper gastrointestinal tracts of Lesser Scaups and Buffleheads collected from Lake Erie during fall 1992 and spring 1993.

Goldeneyes consumed larger zebra mussels than Redheads ($F_{3,42} = 3.51$, $P = 0.023$).

The size of zebra mussels consumed by Redheads did not differ between Lake Erie and Lake St. Clair (Table 2, $F_{1,8} = 0.70$, $P = 0.426$). The average size of zebra mussels eaten by Redheads when zebra mussels were the only food present in the upper GI tract was 10.1 ± 0.27 mm ($n = 2$). Average size of zebra mussels attached to vegetation in the Redhead's upper GI tract was 2.9 ± 0.43 mm ($n = 8$).

Although the mean size of zebra mussels eaten by Buffleheads and Lesser Scaups did not differ, the size distribution of zebra mussels consumed by Lesser Scaups was larger than those consumed by Buffleheads (Kolmogorov-Smirnov, $P < 0.05$) (Fig. 2). The median size of zebra mussels eaten by Buffleheads was 5.5 mm compared with 10.3 mm for Lesser Scaups.

Winter season.—Eight of nine Lesser Scaups collected in an area of open water influenced by the hot water discharge of a power plant contained 100% gizzard shad (*Dorosoma cepedianum*); one Lesser Scaup contained 100% zebra mussels. One Canvasback collected from the same area contained 100% gizzard shad also.

DISCUSSION

Zebra mussels are now the dominant food consumed by Lesser Scaups and Common Goldeneyes in western Lake Erie and northern Lake St. Clair. Zebra mussels will probably remain an abundant food source for waterfowl in Lakes Erie and St. Clair in the future (Leach 1993). Zebra mussels are less important in the diets of Buffleheads and Redheads, and of little importance to Canvasbacks. The dominance of zebra mussels in the diet of Lesser Scaups was expected because of the wide variety of food items and the predominance of molluscs in the diet of migrating and wintering Lesser Scaups in some geographic areas. Nearly 100% of Lesser Scaup diet was dwarf surfclams (*Mulinia lateralis*) in Louisiana (Harmon 1962), 79% was fingernail clams (*Sphaerium* sp.) in Iowa (Thompson 1973), and 50% was Asiatic clams (*Corbicula fluminea*) in South Carolina (Hoppe et al. 1986). In Canada and Minnesota, 33–85% of the diet was amphipods (Afton et al. 1991, Dirschl 1969), whereas chironomids dominated in California (44%, Gammonley and Heitmeyer 1990) and Louisiana (46%, Afton et al. 1991).

Food habits of Lesser Scaups consisted of gizzard shad during periods when the lakes were iced covered, usually during January and February (Assel et al. 1983). Waterfowl were forced to leave or move into the remaining areas of open water (CMC, unpubl. data) at the mouths of rivers, power plant water discharge points, and ice leads. Shad were plentiful and may have been the only food available in the power plant discharge areas (CMC, pers. obs).

Only about 25% of Bufflehead diets was zebra mussels in Lake Erie; amphipods dominated (47%). Buffleheads in California consumed mainly seeds of *Scirpus robustus, Polygonum lapathifolium* and *Potamogeton pectinatus* (34% of diet), corixids (water boatman, 29%) and chironomids (22%); molluscs comprised ≤11% of the diets (Gammonley and Heitmeyer 1990). Cottam's (1939) compilation of waterfowl diets (mainly from gizzards) indicated that insects (41%), crustaceans (17%) and molluscs (16%) were the main foods in the diet of Buffleheads.

Nearly 80% of Common Goldeneye diet was zebra mussels in Lake Erie. Prior to the invasion of the zebra mussels, Common Goldeneye diets in the nearby Detroit River were comprised of 37% wildcelery winterbuds, 9% oligochaetes and 7% decapods; molluscs were found in only trace amounts (Jones and Drobney 1986). Cottam (1939) indicated that crustaceans (32%) and insects (28%) were the dominant components in

Common Goldeneye diets (mainly from gizzards) with molluscs comprising <10%.

Canvasbacks fed primarily on wildcelery winterbuds in Lakes Erie and St. Clair, probably because this aquatic vegetation was widely available (CMC, pers. obs.). Few individuals consumed zebra mussels. Canvasbacks switched to a diet of Baltic macoma (*Macoma balthica,* 82%) (data mainly from gizzard samples, Perry and Uhler 1988) when the submersed aquatic vegetation declined in Chesapeake Bay (Bayley et al. 1978, Haramis and Carter 1983, Orth and Moore 1981). In North and South Carolina aquatic vegetation predominated in the diet of Canvasback when available, otherwise Baltic macoma dominated (gizzard data, Perry and Uhler 1982). On the upper Mississippi River Canvasbacks consumed ≥99% wildcelery winterbuds and *Sagittaria rigida* tubers (Korschgen et al. 1988) even though invertebrate foods were available (C. E. Korschgen, pers. comm.).

The Canvasback that was collected while feeding alongside a Lesser Scaup was eating 100% wildcelery winterbuds whereas the Lesser Scaup was eating 100% zebra mussels. This may suggest a preference for wildcelery winterbuds by Canvasbacks and a preference for zebra mussels by Lesser Scaups. The one Canvasback that was eating zebra mussels was apparently taking advantage of zebra mussels that were exposed due to low water conditions created by a seiche.

In Lakes Erie and St. Clair eight of 10 Redheads consumed mainly above-ground portions of *Potamogeton* spp. and incidently ingested zebra mussels which were attached to the vegetation stems. In two of six Redheads in Lake Erie, however, zebra mussels were the only food in the GI tract. This dominance of vegetation in the diet is consistent with other studies of Redhead food habits. Redheads in North Carolina ate predominately shoalgrass (*Halodule wrightii*) (from gizzard data mainly, Perry and Uhler 1982) as did Redheads in Louisiana (83% & 67% of diet as determined from esophagi and proventriculi) (Michot and Nault 1993) and Texas (Koenig 1969). On the Mississippi River in Wisconsin, 65% of Redhead's diet was wildcelery winterbuds (Korschgen et al. 1988).

Zebra mussels consumed by ducks, except for the eight Redheads mentioned above, were present as individual mussels. We did not find clumps of zebra mussels still held together by their byssal threads nor zebra mussels still attached to a substrate such as vegetation or rock. This was true even for Buffleheads that consumed very small zebra mussels. This observation suggests that zebra mussels were either plucked individually from the substrate or if pulled off in clumps then the clumps were separated in the duck's mouth prior to swallowing.

Waterfowl from both lakes that were specifically foraging on zebra mussels consumed zebra mussels that averaged 8–12 mm long. Mussels that were attached to vegetation, primarily from Lake St. Clair, and incidentally consumed were smaller ($\bar{x}$ = 3 mm). The size distribution of zebra mussels in the areas where we collected waterfowl is unknown, but waterfowl consumed sizes close to the size deemed most profitable for female (9–10 mm) and male (13–14 mm) Tufted Ducks (de Leeuw and Van

Eerden 1992). The modal size of zebra mussels eaten by six ducks at Point Pelee, Ontario was 11–13 mm (Hamilton et al. 1994). This size was larger than the modes in our study; however, Hamilton et al. (1994) disregarded all mussels <5 mm in length when calculating modes, so their modal value is biased high. In our study, 38% of zebra mussels eaten by Lesser Scaup and 50% of zebra mussels eaten by Bufflehead were ≤5 mm.

Diving duck numbers, especially Lesser Scaups and Canvasbacks, and their duration of stay have increased on Lake Erie and Lake St. Clair since the arrival of zebra mussels (Wormington and Leach 1992; E. N. Kafcas and J. Weeks, unpubl. data). Canvasback seem to have benefitted indirectly from the arrival of zebra mussels because the increased water clarity (Holland 1993) has allowed wildcelery to proliferate (E. N. Kafcas, pers. commun.). This alteration of distribution patterns could increase survival rates for wintering diving ducks because some do not travel the additional 500–1300 km to the Atlantic or Gulf Coasts and some migrate late, after the hunting seasons have closed. In contrast, more than 15,000 diving ducks died of starvation in Switzerland and the Netherlands when their feeding areas froze over for an extended period in late winter (Suter and Van Eerden 1992). Body reserves of these birds were not sufficient to survive a 29-d period when ice covered zebra mussel beds and physiological condition prevented them from moving south so late in the winter.

Body masses of Lesser Scaups and Buffleheads in this study (CMC, unpubl. data) were similar to body masses reported from spring migrants in California (Gammonley and Heitmeyer 1990) and wintering waterfowl in New York (Ryan 1972). Lipid content of Lesser Scaups from Lake Erie (5–46%, CMC, unpubl. data) was also similar to lipid levels in fall migrant Lesser Scaups in Manitoba (Austin and Fredrickson 1987). These mass comparisons may indicate that zebra mussels are an adequate winter food. Energetic constraints of zebra mussels as a food should be examined experimentally, however. Waterfowl may need to consume greater volumes of and spend more time feeding when consuming zebra mussels, a low-energy food (4389 cal/g dry mass [Stanczykowska and Lawacz 1976]) compared with other higher energy foods (Driver et al. 1974, Jorde et al. 1995, Perry et al. 1986). The low energy content of zebra mussels may be partially compensated for, however, by their high abundance and easy availability.

Because zebra mussels are known to accumulate contaminants such as polychlorinated biphenyls (Brieger and Hunter 1993), it will be important to determine whether waterfowl are being affected by increased contaminant exposure, especially in areas of known pollution such as the Detroit and Maumee Rivers (Hoke et al. 1990, Smith et al. 1985). Reduced reproduction has been identified in Tufted Ducks fed zebra mussels from a contaminated basin in the Netherlands (de Kock and Bowmer 1993).

ACKNOWLEDGMENTS

We thank A. F. Boysen, T. Cichecki, G. Chandler, R. Hamric, C. O. Kochanny, E. N. Kafcas, K. Lee and L. W. Tisch for help collecting waterfowl; N. R. Adams, R. W. Ainslie, C. W. Blair,

J. Bresciami, Buds Fine Dining, Burr Marine, Schmidt Marine, Selfridge Air National Guard Base, Surf North Restaurant, Toledo Edison Power Plant and U.S. Army Corps of Engineers for access to their properties; J. R. P. French, III, M. T. Lesinski and B. A. Manny for assistance in identifying food items, and J. E. Austin, J. H. Gammonley, C. E. Korschgen, W. L. Green, M. E. Heitmeyer, G. A. Swanson, and four anonymous reviewers for comments on the manuscript.

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Received 26 Jan. 1995; accepted 17 Apr. 1995.