



## Autumn diet of greater scaup, lesser scaup, and long-tailed ducks on eastern Lake Ontario prior to zebra mussel invasion

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**Abstract** Diving ducks staging on the lower Great Lakes have responded to the introduction and subsequent population increase of zebra mussels (*Dreissena polymorpha*) by consuming this readily available food. However, nutritional and contaminant-related implications of recent dietary shifts are hindered by the fact that few studies have documented foods consumed by diving ducks before zebra mussels invaded the Great Lakes in 1988. We examined diets of greater scaup (*Aythya marila*), lesser scaup (*Aythya affinis*), and long-tailed ducks (*Clangula hyemalis*) collected from eastern Lake Ontario during autumn 1986 and 1987 to determine differences among the 3 species. Gastropods were the main food item of greater (92% aggregate dry mass) and lesser scaup (86%), but they consumed relatively small amounts (3% and 7%, respectively) of amphipods. In contrast, amphipods made up 66% of the diets of long-tailed ducks; gastropods were 28% of their diet. Amphipod populations have increased and native gastropods decreased in the presence of zebra mussels in the lower Great Lakes, such that zebra mussel invasion likely has had greater dietary implications for scaup than for long-tailed ducks. Dietary shifts from nonfilter-feeding gastropods to filter-feeding zebra mussels likely contributed to elevated contaminant burdens in lesser and greater scaup on the lower Great Lakes. We encourage further research into the diet-, nutrient-, and contaminant-related implications of zebra mussel induced ecological changes to the Great Lakes.

**Key words** amphipods, *Aythya affinis*, *A. marila*, *Clangula hyemalis*, diet, *Dreissena polymorpha*, Great Lakes, greater scaup, lesser scaup, long-tailed duck, waterfowl, zebra mussel

The lower Great Lakes historically supported large concentrations of diving ducks during spring and autumn migration (Dennis et al. 1984). The invasion of zebra mussels (*Dreissena polymorpha*) into the Great Lakes during the mid-1980s altered the macroinvertebrate food base (Griffiths et al. 1991, Hebert et al. 1991), which has consequences for

waterfowl distribution, abundance, and diets. For example, after introduction of zebra mussels, numbers of greater (*Aythya marila*) and lesser scaup (*A. affinis*) and long-tailed ducks (*Clangula hyemalis*) have increased greatly on the lower Great Lakes during migration and winter (Wormington and Leach 1992, Petrie and Knapton 1999, Petrie and Schum-

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mer 2002). Several subsequent food-habits studies have shown that zebra mussels are consumed by all molluscivorous diving ducks and some omnivorous species (Mitchell and Carlson 1993, Hamilton and Ankney 1994, Petrie and Knapton 1999).

Ecological events and conditions on staging areas can affect waterfowl survival and reproductive output (Pace and Afton 1999, Afton and Anderson 2001, Austin et al. 1998, Anteau 2002), and there is growing interest in the effect that consumption of zebra mussels is having on the nutrient-reserve dynamics and contaminant burdens of diving ducks (Mitchell and Carlson 1993, Guillemette et al. 1994, Hamilton and Ankney 1994, Petrie and Knapton 1999). Zebra mussels are filter feeders that accumulate quantities of heavy metals, trace elements, and organic contaminants in their tissues (Doherty et al. 1993, Mills et al. 1993, Robertson and Lauenstein 1998). These contaminants can be passed up the food chain to waterfowl that consume them (Custer and Custer 2000; S.A. Petrie, Long Point Waterfowl and Wetlands Research Fund, unpublished data), which could influence nutrient-reserve acquisition, reproductive output, or survival. To place in context the nutritional and contaminant-related effects of zebra mussel consumption on waterfowl, it is important to document waterfowl diets prior to this ecological change.

Lesser scaup, greater scaup, and long-tailed ducks feed extensively on macroinvertebrates (Thompson 1973, Peterson and Ellarson 1977, Rofritz 1977, Hoppe et al. 1986, Afton et al. 1991, Afton and Heir 1991), but selection of foods by these species varies with study location and season, largely as a response to resource availability and nutritional requirement. Although all 3 species now consume zebra mussels on the Great Lakes (Hamilton and Ankney 1994, Petrie and Knapton 1999), little is known about their foods prior to this dietary shift. Furthermore, although zebra mussels have increased the overall availability of benthic invertebrates to foraging waterfowl (Barton

1988, Dermott et al. 1993), they also have caused substantial changes in nutrient cycling and substrate complexity that has affected the native benthic invertebrate community (Griffiths 1993). For example, amphipod densities increased and densities of native Unionids decreased in the presence of zebra mussels (Mackie 1991, Kuhns and Berg 1999). Therefore, information on diets of diving ducks prior to zebra mussel introduction is needed to understand whether prey switching was the result of a simple dietary shift or a zebra mussel-induced decline in historical foods.

We quantified and compared the diets of lesser scaup, greater scaup, and long-tailed ducks before zebra mussels were a readily available food source in the Prince Edward County area of Lake Ontario, one of the principal staging areas for these species on the Great Lakes (Dennis et al. 1984, Ross 1989). We predicted that there would be limited sex-, age-, and species-specific differences in diets of lesser and greater scaup, as they are closely related, primarily carnivorous, and were collected outside the reproductive period. Based on previous food-habits studies, we further predicted that long-tailed ducks would eat more amphipods and less gastropods than the 2 scaup species.

## Methods

### *Field collection*

From 31 Oct–24 Nov 1986, we obtained



Large numbers of diving ducks feed and rest on the lower Great Lakes during spring and fall migrations. Photo by Shannon Badzinski.

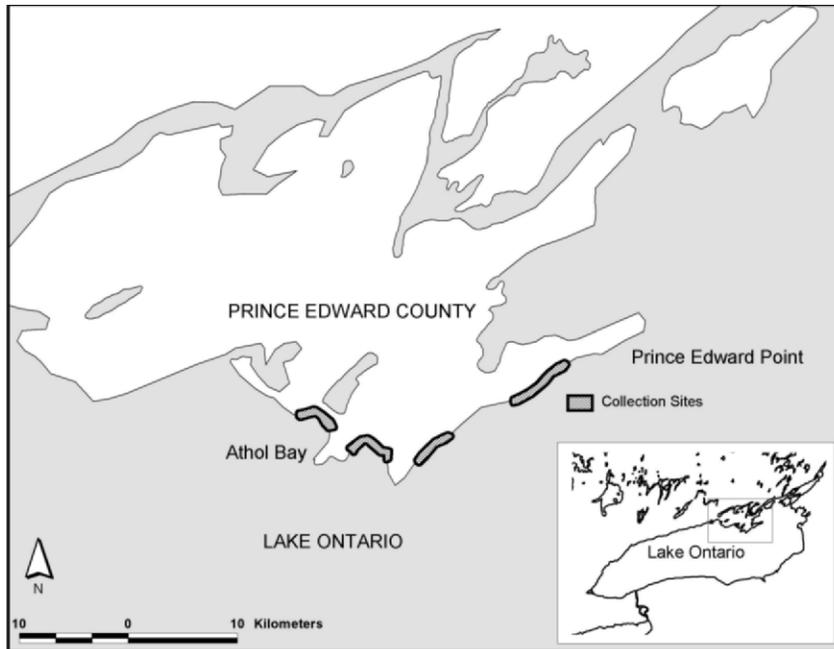


Figure 1. Geographic location of the Prince Edward County area of Lake Ontario and areas where greater scaup, lesser scaup, and long-tailed ducks were captured in commercial fishing nets from Athol Bay to Prince Edward Point, Ontario, Canada.

greater scaup ( $n=66$ ), lesser scaup ( $n=117$ ), and long-tailed ducks ( $n=13$ ) that were accidentally captured in commercial fishing nets in Lake Ontario; the shoreline off which they were caught extended from West Bank on the north side of Athol Bay ( $43^{\circ}53.2'N$ ,  $77^{\circ}16.9'W$ ) to Prince Edward Point ( $43^{\circ}55.6'N$ ,  $76^{\circ}52.3'W$ ), Ontario, Canada (Figure 1). We obtained an additional 32 long-tailed ducks from nets in the same region during 16–24 Nov 1987. All ducks were caught in monofilament or multistrand gill nets (2 m high, 11.5-cm mesh size) set along the lake bottom, usually at depths of 3 to 8 m (range: 2–30 m). Except for one catch of 77 birds, most birds were caught as individuals or small groups (5–10 birds). In most studies of food habits, waterfowl are observed foraging prior to collection to ensure they have ingested food (Swanson et al. 1974). Because gill nets were set below the water, all birds in our study probably were actively foraging when captured. Indeed, most ducks had large amounts of food in their esophagi, and only 1 collected duck lacked food. We did not inject alcohol or formalin down the throats of birds upon collection, but carcasses cooled rapidly because they were submerged and frozen shortly after being removed from nets.

### Laboratory methods

We thawed the birds in the lab at room temperature; esophageal and proventricular contents were removed, identified, and counted. We conducted sorting and identification under a dissection microscope (10X ocular) in a gridded  $9 \times 9$ -cm petri dish. We extracted all biotic material with tweezers and identified it to the lowest taxonomic level possible (Wiggins 1978, Clarke 1981, Peckarsky et al. 1990, Jokinen 1991). We then labelled sorted samples and placed them in vials containing 80% ethyl alcohol. We dried subsamples of each food item separately at  $60^{\circ}C$  for 24 hours and weighed ( $\pm 0.001$  g) them

on a digital balance. We calculated the dietary mass of each food item by multiplying the median mass of a subsample for a specific item by the number of individual food items counted in each bird's dietary sample. Because shells usually are not digested by waterfowl, we adjusted the estimated dry mass of molluscs to eliminate shell mass; based on equations in Mackie and Flippance (1983), we determined that the tissue contribution to dry mass of gastropods and polycypods was 26 and 28%, respectively.

For statistical analyses we grouped most food items into categories based on taxonomic order, but gastropods were divided further into families. We summarized data for each category of food as aggregate percent (proportion) dry mass and percent frequency of occurrence (Swanson et al. 1974). We used aggregate proportion dry mass of food categories as response variables in all statistical analyses, but we converted them to aggregate percent dry mass for presentation. We investigated residuals from all statistical models for normality by inspecting normal probability plots. Residuals from the raw proportion data were not distributed normally. Therefore, we transformed the data with an arcsine square root transformation (Zar 1996), which increased normality of residuals in all statistical models.

### Statistical analyses

We used multivariate analysis of variance (MANOVA) to determine whether overall diets differed among greater scaup, lesser scaup, and long-tailed ducks (PROC GLM, MANOVA, SAS Institute Inc. 1990). Because sex of 17 of 45 long-tailed ducks had not been determined and the 1986 sample for this species was small, we combined data for all species across years and sexes for this analysis. We included "species" as a class variable to examine overall variation in aggregate proportion dry mass for valvatids, hydrobids, bithyniids, pluerocerids, lymnaeids, physids, planorbids, pelycypods, trichopterans, dipterans, amphipods, and isopods. In both sets of analyses, when multivariate tests of species effects were significant ( $P < 0.05$ ), we examined overall significance of the individual univariate models ( $P < 0.05$ ) and then used Tukey's Honest Significant Difference (HSD) tests to determine interspecific differences in consumption of specific food items. We also investigated whether aggregate proportion dry mass of total gastropods (i.e., sum of valvatids, hydrobids, bithyniids, pluerocerids, lymnaeids, physids, and planorbids) differed among the 3 diving duck species by using a separate univariate Analysis of Variance (ANOVA) (PROC GLM; SAS Institute Inc. 1990); Tukey's HSD test was used to identify differences among means of the 3 diving duck species.

Because of large samples and positive sexual identification of all greater ( $n_{\text{female}} = 30$ ,  $n_{\text{male}} = 35$ ) and lesser scaup ( $n_{\text{female}} = 27$ ,  $n_{\text{male}} = 90$ ), we could investigate overall dietary differences (valvatids, hydrobids, bithyniids, pluerocerids, lymnaeids, physids, planorbids, pelycypods, trichopterans, dipterans, amphipods, and isopods) between species and sexes via MANOVA. We analyzed variation in consumption of dietary items by species and sex, and the interaction between class variables (species  $\times$  sex); food-habits data for greater and lesser scaup are reported by species-sex groups. We also report the species and sex coefficients, or effect sizes; these values are the magnitude (+ or -) of difference between: 1) greater scaup relative to lesser scaup and 2) female relative to male scaup species. We also investigated whether aggregate proportion dry mass of total gastropods differed between species and sexes or among species-sex groups (species  $\times$  sex) via ANOVA.

In multivariate analyses we used Wilks' lambda as the test statistic for identification of important effects. For all univariate models, we examined  $F$ -

statistics based on type III sums of squares and report means ( $\pm$  SE). Statistical models and differences between or among means are considered statistically significant at  $P \leq 0.05$ , but worthy of biological interpretation and discussion at  $P \leq 0.10$ .

## Results

### *Comparison of diets of greater scaup, lesser scaup, and long-tailed ducks*

Overall diets of greater scaup, lesser scaup, and long-tailed ducks differed during autumn migration at Lake Ontario (MANOVA, species effect: Wilks'  $\lambda = 0.28$ ,  $P \leq 0.001$ ; Table 1). Gastropods comprised 91.7 and 86.2% of the dry mass of greater scaup and lesser scaup diets, respectively, but significantly less (27.5%) of the autumn diet for long-tailed ducks (Table 1). We found gastropods in 100, 99, and 93% of samples collected from greater scaup, lesser scaup, and long-tailed ducks, respectively (Table 2). On a dry-mass basis, valvatids, hydrobids, bithyniids, lymnaeids, physids, and planorbids were more prevalent in the diets of greater and lesser scaup compared to long-tailed ducks; greater scaup consumed more pluerocerids than did long-tailed ducks and lesser scaup, which both consumed similar amounts of these gastropods (Table 1).

Although gastropods were important foods, bivalves, insects, and crustaceans contributed substantially to diets of these 3 diving duck species during autumn at Lake Ontario (Tables 1, 2). Bivalves and pelycypods occurred in 61, 73, and 53% of the diets of greater scaup, lesser scaup, and long-tailed ducks, respectively (Table 2), but their contribution to biomass consumed did not differ among species (Table 1). Aquatic insects, including trichopterans, dipterans, ephemeropterans, and coleopterans, were eaten by all 3 species (Table 2). Relative mass of trichopterans consumed did not differ among species, but long-tailed ducks ate slightly more dipterans than did scaup species (Table 1). Crustaceans, especially amphipods and isopods, were eaten by greater scaup, lesser scaup, and long-tailed ducks, but ostracods, decapods, and conchostracas were eaten by some, but not all, species (Table 2). Amphipods comprised 65.6% of the dry mass of long-tailed duck diets, but they contributed much less to the diets of greater scaup (3.1%) and lesser scaup (6.7%; Table 1). As compared to amphipods, isopods contributed much less to diets of scaup species and long-tailed ducks, as mass of this food did not differ substantially

Table 1. Aggregate percentage (%) dry mass of food items consumed by greater scaup ( $n_{1986} = 66$ ), lesser scaup ( $n_{1986} = 117$ ), and long-tailed ducks ( $n_{1986} = 13$ ,  $n_{1987} = 32$ ) on Lake Ontario during autumn.

| Food item               | Species effect <sup>a</sup> |              | Mean ( $\pm$ SE) <sup>b</sup> |                 |                  |
|-------------------------|-----------------------------|--------------|-------------------------------|-----------------|------------------|
|                         | $F_{2,225}$                 | $P^c$        | Greater scaup                 | Lesser scaup    | Long-tailed duck |
| Mollusca                |                             |              |                               |                 |                  |
| Gastropoda <sup>d</sup> | 134.71                      | $\leq 0.001$ | 91.7 (2.7) a                  | 86.2 (2.0) a    | 27.5 (3.3) b     |
| Valvatidae              | 14.06                       | $\leq 0.001$ | 10.5 (1.2) a                  | 9.3 (1.0) a     | 2.5 (1.5) b      |
| Hydrobiidae             | 19.42                       | $\leq 0.001$ | 29.7 (2.7) a                  | 33.3 (2.0) a    | 12.7 (3.3) b     |
| Bithyniidae             | 9.75                        | $\leq 0.001$ | 18.4 (2.5) a                  | 17.4 (1.9) a    | 6.5 (3.1) b      |
| Plueroceridae           | 10.94                       | $\leq 0.001$ | 11.2 (1.4) a                  | 3.5 (1.0) b     | 2.6 (1.7) b      |
| Lymnaeidae              | 20.39                       | $\leq 0.001$ | 1.0 (0.4) a                   | 2.3 (0.3) a     | 0.2 (0.5) b      |
| Physidae                | 31.83                       | $\leq 0.001$ | 5.9 (0.7) a                   | 3.8 (0.5) a     | 0.3 (0.8) b      |
| Planorbidae             | 7.68                        | $\leq 0.001$ | 1.0 (0.4) a                   | 2.3 (0.3) b     | 0.2 (0.5) c      |
| Pelecypoda/Bivalvia     | 0.66                        | 0.52         | 3.9 (1.5)                     | 5.1 (1.1)       | 3.8 (1.9)        |
| Arthropoda              |                             |              |                               |                 |                  |
| Insecta                 |                             |              |                               |                 |                  |
| Trichoptera             | 2.53                        | 0.08         | 1.1 (0.4)                     | 1.5 (0.3)       | 2.1 (0.5)        |
| Diptera                 | 7.44                        | $\leq 0.001$ | 0.1 (0.1) a                   | 0.3 (0.1) a     | 0.8 (0.2) b      |
| Ephemeroptera           |                             |              |                               | Tr <sup>e</sup> | Tr               |
| Coleoptera              |                             |              | Tr                            |                 |                  |
| Crustacea               |                             |              |                               |                 |                  |
| Amphipoda               | 158.89                      | $\leq 0.001$ | 3.1 (2.4) a                   | 6.7 (1.8) a     | 65.6 (2.9) b     |
| Isopoda                 | 2.50                        | 0.08         | 0.2 (0.1) a                   | 0.2 (0.1) a     |                  |
| Ostracoda               |                             |              |                               |                 | Tr               |
| Decapoda                |                             |              | Tr                            |                 |                  |
| Conchostraca            |                             |              |                               | Tr              |                  |
| Arachnida               |                             |              |                               |                 |                  |
| Acari                   |                             |              | Tr                            | Tr              | Tr               |
| Fish                    |                             |              | Tr                            |                 |                  |
| Aquatic vegetation      |                             |              | Tr                            | Tr              | Tr               |

<sup>a</sup> Overall species effect was significant (MANOVA: Wilks'  $\lambda = 0.28$ ,  $P \leq 0.001$ ).

<sup>b</sup> Means followed by the same letters do not differ (Tukey's HSD test,  $P > 0.05$ ).

<sup>c</sup>  $P$ -values are from univariate  $F$ -tests of species effects.

<sup>d</sup> Univariate species effect was significant (ANOVA:  $R^2 = 0.55$ ,  $F_{2, 225} = 134.71$ ,  $P \leq 0.001$ ).

<sup>e</sup> Tr = trace amount (aggregate % mass  $< 0.01$ g) of a food item present.

among the diets of the 3 species (Table 2). We found aquatic vegetation in all 3 species (Table 2), but it contributed little in terms of dry mass ( $< 0.01\%$ ) to their diets (Table 1).

### Comparison of diets of female and male scaup species

There were no differences in overall diets among species-sex groups (species  $\times$  sex effect: MANOVA, Wilks'  $\lambda = 0.94$ ,  $P = 0.538$ ), but aggregate percent dry mass of food items in diets differed between species (MANOVA, Wilks'  $\lambda = 0.79$ ,  $P \leq 0.001$ ) and females and males (MANOVA, Wilks'  $\lambda = 0.80$ ,  $P \leq 0.001$ ) (Table 3). Gastropods occurred in nearly all

greater and lesser scaup, but frequency of occurrence of each gastropod family varied between species and sexes. Bivalves, aquatic insects, and crustaceans occurred in diets of each species, but their occurrence in the diets was lower than those of most gastropod families (Table 4). Greater scaup generally ate greater quantities of gastropods than did lesser scaup (Table 3). Looking at consumption of individual gastropod families, greater scaup ate 8% more pluerocerids than did lesser scaup, but lesser scaup ate slightly more planorbids (Table 3). Male greater and lesser scaup both consistently ate more bithyniids and valvatids than did females, whereas female greater and lesser scaup consistently ate a much larger percentage of lymnaeids than did males of each species (Table 3).

Pelecypods and aquatic insects, especially trichopterans and dipterans, occurred in a large percentage of diets of male

and female greater and lesser scaup (Table 4), but their dry-mass contributions were smaller than those for most gastropods (Table 3). There were no interspecific or intersexual differences in the aggregate percent dry mass of pelecypods and trichopterans (Table 3). Amphipods made up a slightly larger percentage (4.5%) of the diets of lesser than greater scaup, and there was a tendency for females of both species to eat a slightly larger percentage (3.8%) of amphipods (Table 3).

## Discussion

Although lesser and greater scaup eat large quan-

Table 2. Frequency of occurrence (%) of food items consumed by greater scaup ( $n_{1986}=66$ ), lesser scaup ( $n_{1986}=117$ ), and long-tailed ducks ( $n_{1986}=13$ ,  $n_{1987}=32$ ) during autumn on Lake Ontario.

| Food item           | Greater scaup | Lesser scaup | Long-tailed duck |
|---------------------|---------------|--------------|------------------|
| Mollusca            |               |              |                  |
| Gastropoda          | 100           | 99           | 93               |
| Valvatidae          | 76            | 83           | 49               |
| Hydrobiidae         | 89            | 97           | 71               |
| Bithyniidae         | 62            | 62           | 18               |
| Pluerozeridae       | 65            | 61           | 42               |
| Lymnaeidae          | 81            | 92           | 38               |
| Physidae            | 77            | 80           | 16               |
| Planorbidae         | 53            | 80           | 27               |
| Pelecypoda/Bivalvia | 61            | 73           | 53               |
| Arthropoda          |               |              |                  |
| Insecta             |               |              |                  |
| Trichoptera         | 49            | 67           | 62               |
| Diptera             | 27            | 37           | 42               |
| Ephemeroptera       |               | 1            | 9                |
| Coleoptera          | 2             |              |                  |
| Crustacea           |               |              |                  |
| Amphipoda           | 49            | 81           | 91               |
| Isopoda             | 17            | 33           | 7                |
| Ostracoda           |               |              | 9                |
| Decapoda            | 2             |              |                  |
| Conchostraca        |               | 1            |                  |
| Arachnida           |               |              |                  |
| Acari               | 3             | 10           | 20               |
| Fish                | <1            |              |                  |
| Aquatic vegetation  | 38            | 35           | 80               |

tities of animal matter, there is considerable geographical and seasonal variation in taxa that are consumed (Austin et al. 1998, and references therein). For example, lesser scaup primarily feed on amphipods during spring and summer in the Midwest of Canada and the United States (Bartonek and Hickey 1969, Rogers and Korschgen 1966, Afton and Heir 1991, Afton et al. 1991), but eat mainly molluscs during spring on Keokuk Pool of the Mississippi River (Thompson 1973). Diets of greater scaup primarily consist of molluscs during winter on the east and west coasts of North America (Cronan 1957, Vermeer and Levings 1977). However, when molluscs were scarce during winter on the Detroit River, greater scaup consumed oligochaetes and wild celery (*Vallisneria spiralis*) (Jones and Drobney 1986).

Although some studies unfortunately have included gizzard contents, there appears to be consensus that scaup species eat large quantities of

molluscs when they are readily available (Cronan 1957, Rogers and Korschgen 1966, Thompson 1973, Hoppe et al. 1986, Wahle and Barclay 1993). Although scaup on Lake Ontario had a diverse diet, molluscs were their primary food item during autumn on Lake Ontario prior to invasion by zebra mussels. But lesser scaup, especially females, had a higher proportion and frequency of occurrence of amphipods in their diets. Reasons for sex- and species-specific differences in dietary intake are unclear but likely reflect differences in prey selection because many birds were captured together in commercial fishing nets while foraging. Because both lesser scaup and long-tailed ducks have been reported to consume large quantities of amphipods in other studies (Bartonek and Hickey 1969, Rogers and Korschgen 1966, Peterson and Ellarson 1977, Afton and Heir 1991, Afton et al. 1991), we suggest that dietary differences identified in this study are the result of differences in foraging behavior, prey-size selection, or niche partitioning.

Although scaup species and long-tailed ducks consumed gastropods, they were less important in diets of long-tailed ducks, which primarily ate amphipods prior to invasion of zebra mussels. In fact, long-tailed ducks ate substantially more amphipods than did both species of scaup. Long-tailed ducks on Lake Michigan primarily ate amphipods (Peterson and Ellarson 1977) or oligochaetes (Rofritz 1977). Although long-tailed ducks did not seem to selectively forage for molluscs on the Great Lakes (Peterson and Ellarson 1977), they did consume large quantities of them in marine habitats (Bagge et al. 1973, Stott and Olson 1973, Goudie and Ankney 1986). Furthermore, Peterson and Ellarson (1977) concluded that long-tailed ducks were largely opportunistic foragers because they ate the most abundant prey items present at a foraging location.

Frequency of occurrence of plant matter was somewhat higher in long-tailed ducks, a species that has been classified as a carnivore (Barnes and Thomas 1987), compared to both omnivorous species of scaup. Thirty to 85% of long-tailed ducks collected from several different areas of Lake Michigan consumed plant material, but vegetative mass made up only a small percentage of their total diets (Peterson and Ellarson 1977). Jones and Drobney (1986) concluded that over half of the vegetation in scaup diets was plant debris ingested incidentally. Because plant matter and bryozoans occurred only in trace amounts in diets of ducks in

Table 3. Aggregate percentage (%) dry mass of food items consumed by female and male greater scaup (Grsc:  $n_{\text{Female}}=30$  and  $n_{\text{Male}}=35$ ) and lesser scaup (Lesc:  $n_{\text{Female}}=27$  and  $n_{\text{Male}}=90$ ) during autumn 1986 on Lake Ontario.

| Food item               | Species effect <sup>a,b</sup> |           | Sex effect <sup>b</sup> |              | Effect sizes ( $\pm$ SE)   |                              |               | Mean ( $\pm$ SE) |              |            |  |  |  |  |
|-------------------------|-------------------------------|-----------|-------------------------|--------------|----------------------------|------------------------------|---------------|------------------|--------------|------------|--|--|--|--|
|                         | $F_{1,178}$                   | $P$       | $F_{1,178}$             | $P$          | Grsc vs. Lesc <sup>c</sup> | Female vs. Male <sup>d</sup> | Greater scaup |                  | Lesser scaup |            |  |  |  |  |
|                         |                               |           |                         |              |                            |                              | Female        | Male             | Female       | Male       |  |  |  |  |
| Mollusca                |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Gastropoda <sup>e</sup> | 6.69                          | 0.01      | 0.05                    | 0.50         | 6.3 (2.5)                  | -3.4 (2.6)                   | 89.8 (3.0)    | 93.3 (2.9)       | 83.6 (3.1)   | 87.0 (2.0) |  |  |  |  |
| Valvatidae              | 0.45                          | 0.50      | 10.16                   | 0.002        | 1.6 (1.4)                  | -4.6 (1.5)                   | 7.4 (1.7)     | 12.0 (1.6)       | 5.8 (1.7)    | 10.4 (1.1) |  |  |  |  |
| Hydrobiidae             | 0.44                          | 0.51      | 2.41                    | 0.12         | -2.3 (2.8)                 | -4.5 (3.0)                   | 27.6 (3.4)    | 32.1 (3.3)       | 29.9 (3.5)   | 34.3 (2.3) |  |  |  |  |
| Bithyniidae             | 1.12                          | 0.29      | 13.09                   | $\leq 0.001$ | 3.2 (2.5)                  | -10.5 (2.7)                  | 12.5 (3.1)    | 23.0 (3.0)       | 9.3 (3.2)    | 19.8 (2.0) |  |  |  |  |
| Pluoceridae             | 13.70                         | $< 0.001$ | 0.04                    | 0.85         | 8.0 (1.5)                  | -0.3 (1.6)                   | 11.2 (1.9)    | 11.5 (1.8)       | 3.3 (1.9)    | 3.6 (1.2)  |  |  |  |  |
| Lymnaeidae              | 3.21                          | 0.08      | 24.27                   | $\leq 0.001$ | -4.8 (2.3)                 | 15.6 (2.5)                   | 23.8 (2.8)    | 8.2 (2.7)        | 28.6 (2.9)   | 13.0 (1.9) |  |  |  |  |
| Physidae                | 2.35                          | 0.13      | 0.48                    | 0.49         | 2.2 (0.7)                  | -0.4 (0.8)                   | 5.7 (0.9)     | 6.1 (0.9)        | 3.5 (0.9)    | 3.9 (0.6)  |  |  |  |  |
| Planorbidae             | 16.69                         | $< 0.001$ | 2.83                    | 0.09         | -1.5 (0.5)                 | 1.3 (0.5)                    | 1.7 (0.6)     | 0.4 (0.5)        | 3.2 (0.5)    | 2.0 (0.4)  |  |  |  |  |
| Pelecypoda/Bivalvia     | 0.40                          | 0.53      | 0.69                    | 0.41         | -0.1 (1.7)                 | -0.2 (1.8)                   | 3.9 (2.0)     | 4.0 (1.9)        | 5.0 (2.1)    | 5.1 (1.3)  |  |  |  |  |
| Arthropoda              |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Insecta                 |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Trichoptera             | 2.32                          | 0.13      | 0.66                    | 0.42         | -0.4 (0.4)                 | 0.3 (0.4)                    | 0.9 (0.5)     | 1.2 (0.4)        | 1.3 (0.5)    | 1.6 (0.3)  |  |  |  |  |
| Diptera                 | 3.07                          | 0.08      | 1.35                    | 0.25         | -0.02 (0.01)               | 0.01 (0.01)                  | 0.2 (0.1)     | 0.0 (0.1)        | 0.1 (0.1)    | 0.2 (0.1)  |  |  |  |  |
| Ephemeroptera           |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Coleoptera              |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Crustacea               |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Amphipoda               | 10.10                         | 0.002     | 3.48                    | 0.06         | -4.5 (1.8)                 | 3.8 (1.8)                    | 5.2 (2.1)     | 1.4 (2.0)        | 9.7 (2.2)    | 5.8 (1.4)  |  |  |  |  |
| Isopoda                 | 3.41                          | 0.07      | 0.68                    | 0.41         | -0.07 (0.01)               | -0.01 (0.01)                 | $< 0.1$ (0.1) | 0.2 (0.1)        | 0.2 (0.1)    | 0.1 (0.1)  |  |  |  |  |
| Decapoda                |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Conchostraca            |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Arachnida               |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Acari                   |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Fish                    |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |
| Aquatic vegetation      |                               |           |                         |              |                            |                              |               |                  |              |            |  |  |  |  |

<sup>a</sup> Overall species  $\times$  sex interaction (MANOVA: Wilks'  $\lambda=0.94$ ,  $P=0.4770$ ) was not found, but species (MANOVA: Wilks'  $\lambda=0.78$ ,  $P=\leq 0.001$ ) and sex (MANOVA: Wilks'  $\lambda=0.81$ ,  $P=\leq 0.001$ ) main effects were identified.

<sup>b</sup>  $F$ - and  $P$ -values are from univariate analyses of species and sex effects.

<sup>c</sup> Species effect sizes are Grsc mean-Lesc mean.

<sup>d</sup> Sex effect sizes are Female mean-Male mean.

<sup>e</sup> Univariate ANOVA ( $R^2=0.04$ ,  $F_{3,178}=2.12$ ,  $P=0.08$ ) indicated no species  $\times$  sex interaction ( $F_{1,178}=0.16$ ,  $P=0.69$ ) or sex main effect ( $F_{1,178}=0.39$ ,  $P=0.53$ ), but did indicate a species main effect ( $F_{1,178}=6.71$ ,  $P=\leq 0.001$ ).

Table 4. Frequency occurrence (%) of food items consumed by female and male greater scaup ( $n_{\text{Female}}=30$  and  $n_{\text{Male}}=35$ ) and lesser scaup ( $n_{\text{Female}}=27$  and  $n_{\text{Male}}=90$ ) during autumn 1986 on Lake Ontario.

| Food item           | Greater scaup |      | Lesser scaup |      |
|---------------------|---------------|------|--------------|------|
|                     | Female        | Male | Female       | Male |
| Mollusca            |               |      |              |      |
| Gastropoda          | 100           | 100  | 100          | 99   |
| Valvatidae          | 67            | 83   | 63           | 88   |
| Hydrobiidae         | 87            | 91   | 96           | 98   |
| Bithyniidae         | 50            | 71   | 37           | 70   |
| Plerocercidae       | 63            | 65   | 52           | 63   |
| Lymnaeidae          | 87            | 77   | 96           | 91   |
| Physidae            | 73            | 80   | 74           | 82   |
| Planorbidae         | 57            | 49   | 67           | 83   |
| Pelecypoda/Bivalvia | 53            | 66   | 56           | 78   |
| Arthropoda          |               |      |              |      |
| Insecta             |               |      |              |      |
| Trichoptera         | 50            | 46   | 48           | 73   |
| Diptera             | 23            | 29   | 37           | 37   |
| Ephemeroptera       |               |      | 4            |      |
| Coleoptera          |               | 3    |              |      |
| Crustacea           |               |      |              |      |
| Amphipoda           | 53            | 43   | 85           | 80   |
| Isopoda             | 13            | 17   | 26           | 36   |
| Decapoda            |               | 3    |              |      |
| Conchostraca        |               |      | 4            |      |
| Arachnida           |               |      |              |      |
| Acari               | 3             | 3    | 7            | 11   |
| Fish                |               | <1   |              |      |
| Aquatic vegetation  | 43            | 31   | 26           | 38   |

our study, and all 3 species ate macroinvertebrates almost exclusively, we also believe that consumption of these food items was primarily incidental.

Historically, lesser and greater scaup primarily fed on gastropods during autumn migration on eastern Lake Ontario. The introduction of zebra mussels has provided a readily available food source that is now being eaten by both scaup species. Although dietary proportions were not provided, Hamilton and Ankney (1994) reported that 52% of lesser scaup and 65% of greater scaup collected during autumn on lakes St. Clair and Erie had consumed zebra mussels. Petrie and Knapton (1999) reported that over 80% of scaup collected during autumn on Lake Erie had consumed zebra mussels. Thus, lesser and greater scaup appear to have switched from a diet dominated by native gastropods to one dominated by exotic zebra mussels.

Densities greater than 100,000 zebra mussels per m<sup>2</sup> in lakes St. Clair and Erie have been reported

(Griffiths et al. 1991, MacIsaac et al. 1992); Petrie and Knapton (1999) reported densities ranging from 2,050/m<sup>2</sup> in 1991 to 606/m<sup>2</sup> in 1995 on Long Point Bay, Lake Erie. Native bivalves are considerably less abundant in the lower Great Lakes; Lake St. Clair averaged 10 individuals/m<sup>2</sup> prior to zebra mussel introduction (Nalepa and Gauvin 1988). Furthermore, zebra mussels tend to displace native gastropods when they invade an area (Hebert et al. 1991). Therefore, the dietary switch by scaup probably resulted from the greater availability of zebra mussels and possibly zebra mussel-induced declines in traditional scaup foods.

Long-tailed ducks fed primarily on amphipods during fall on Lake Ontario. Since the introduction of zebra mussels, gammarid amphipod abundance has increased, often by several orders of magnitude, in the Great Lakes (Howell et al. 1996, Kuhns and Berg 1999). Thus, colonization of zebra mussels may have increased availability of traditional long-tailed duck foods in some parts of the Great Lakes. Unfortunately, few comprehensive food habits and energetics studies have been conducted on long-tailed ducks using the lower Great Lakes since zebra mussels were introduced. Nineteen of the 45 (42%) long-tailed ducks that Hamilton and Ankney (1994) collected during spring on Lake Erie had consumed zebra mussels. Given the high percent occurrence of native gastropods in their diet prior to arrival of zebra mussels, it is not surprising that long-tailed ducks have incorporated zebra mussels into their diets. It is unknown, however, whether long-tailed ducks have simply replaced the native gastropods in their diets with zebra mussels or have actually begun to replace the traditional amphipod component of their diets with this novel food item. We propose that unless Peterson and Ellarson (1977) are correct in their assertion that long-tailed ducks are opportunistic foragers, the introduction of zebra mussels probably had less influence on dietary composition of long-tailed ducks than on both scaup species.

## Management implications

Prior to zebra mussel colonization, there was limited dietary overlap between long-tailed ducks and scaup during autumn on eastern Lake Ontario, as long-tailed ducks primarily consumed amphipods and scaup primarily consumed gastropods. Amphipod populations generally have increased and native gastropods decreased in the presence of

zebra mussels in the lower Great Lakes (Howell et al. 1996, Kuhns and Berg 1999). Thus, invasion of zebra mussels possibly had greater dietary implications for greater and lesser scaup than for long-tailed ducks. Although little is known about the historic contaminant burdens in long-tailed ducks that stage and over-winter on the lower Great Lakes, recent studies (post-zebra-mussel invasion) from this region have shown that lesser and greater scaup have high contaminant burdens, especially selenium (Custer and Custer 2000, S. A. Petrie, Long Point Waterfowl and Wetlands Research Fund, unpublished data). We suggest that increased anthropogenic inputs of selenium to the lower Great Lakes, combined with dietary shifts from nonfilter-feeding gastropods to filter-feeding zebra mussels, likely has contributed to these high contaminant burdens. We also suggest that other molluscivorous waterfowl that consume zebra mussels [e.g., bufflehead (*Bucephala albeola*), common goldeneye (*B. clangula*), scoters (*Melanitta* spp.)] may be affected and that waterfowl that over-winter on the lower Great Lakes may be more susceptible to acute contaminant acquisition than birds that stage for short periods during spring and autumn.

We conclude that the ready availability of exotic zebra mussels has resulted in dietary convergence among several waterfowl species staging and over-wintering on the Great Lakes; nutrient-reserve, contaminant, behavioral, and habitat use implications of this convergence require further study.

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