Notes

Diet of Lesser Scaup Wintering on Lake Pontchartrain, Louisiana

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Abstract

The lesser scaup *Aythya affinis* has been a species of conservation concern since continental breeding populations began declining in the 1980s. The causes of this decline are likely multifaceted, but cross-seasonal effects are believed to play a prominent role: females unable to acquire sufficient nutrient reserves during winter and spring migration have poor survival and breeding success. Understanding scaup diet composition and prey selection can help managers not only diagnose mechanisms underlying wintering scaup distributions, but may also help direct management actions to increase forage availability and quality. We evaluated the diet of 60 scaup collected from a major wintering site in Louisiana, Lake Pontchartrain. Scaup consumed almost entirely mollusks, especially targeting medium-sized (6–16 mm) common rangia clams *Rangia cuneata*, which were strongly selected relative to their availability. Eighty-two percent of scaup consumed dark false mussels *Mytilopsis leucophaeata* and 57% consumed dwarf surf clams *Mulinia lateralis*; both foods were selected by scaup, but were uncommon in benthic samples. On the other hand, small snails *Texadina sphinctostoma*, *Probythinella protera* were common in dredge samples but were either avoided or consumed in proportion to their availability. We conclude that medium-sized common rangia clams and dark false mussels are the most consumed foods for scaup wintering on Lake Pontchartrain, and hypothesize that annual variation in prey populations may be an important proximate driver of scaup abundance.

Keywords: bivalve; duck; food; mollusk; preference; selection; waterfowl

Received: May 14, 2019; Accepted: September 13, 2019; Published Online Early: September 2019; Published: December 2019

Citation: Stroud CN, Caputo CE, Poirrier MA, Ringelman KM. 2019. Diet of lesser scaup wintering on Lake Pontchartrain, Louisiana. *Journal of Fish and Wildlife Management* 10(2):567–574; e1944-687X. https://doi.org/10.3996/062018-JFWM-059

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Introduction

The continental breeding population of lesser scaup *Aythya affinis* (hereafter scaup) declined for 20 y between the mid-1980s and the mid-2000s, and despite recent increases, remains 13% below the long-term average of 5.02 ± 0.04 million (USFWS 2017). Hypotheses for this decline include reduced female survival (Koons et al. 2006) and reduced recruitment (Arnold et al. 2016). These factors could in turn be caused by changes in breeding habitat quality (Drever et al. 2012; Ross et al. 2015) and prebreeding declines in body condition (Afton and Anderson 2001; England et al. 2018). For example, nutrient reserves acquired at wintering or spring migration areas are important predictors of scaup survival and reproductive success (Afton and Ankney 1991; Pace and Afton 1999; Anteau and Afton 2004).

Afton and Anderson (2001) formalized these ideas, and they developed the spring condition hypothesis, which postulates that reproductive success has declined relative to historic levels because female scaup are arriving on breeding grounds in poorer body condition than in the past. They hypothesized that poorer body condition was a result of reduced availability or quality of food resources on wintering, spring migration, or breeding areas. In support of the spring condition hypothesis, amphipod food resources have declined at many spring staging areas in the Midwest, forcing scaup to consume less nutritious mollusks (Anteau and Afton 2006, 2008). As a result of this shift in diet, scaup lipid reserves in Minnesota and Manitoba were nearly 30% lower in the early 2000s as compared with the 1980s (Anteau and Afton 2004). Because of declines in foraging quality at spring migration areas in the upper Midwest, it may be increasingly important for scaup to depart major wintering areas with larger nutrient reserves (Austin et al. 2000).

The Mississippi Flyway, which winters approximately 40% of the continental scaup population, has experienced the largest population declines (Afton and Anderson 2001). Louisiana winters 91% of the scaup in the Mississippi Flyway (Afton and Anderson 2001), and one area in Louisiana that hosts large numbers of scaup is Lake Pontchartrain, a large estuarine lagoon just north of New Orleans (Kinney 2004). However, scaup numbers on Lake Pontchartrain fluctuate drastically. For example, aerial surveys flown by the Louisiana Department of Wildlife and Fisheries estimated more than 1 million birds present in December 2006, whereas zero scaup were counted that previous January (Stroud et al. 2019).

One potential source for this variation in scaup abundance is coincident variation in food availability on Lake Pontchartrain. Mollusks are a primary food source for wintering scaup throughout their range (Hoppe et al. 1986; Custer and Custer 1996), and indeed are common in Lake Pontchartrain (Poirrier et al. 2008). However, scaup diets in Louisiana have been shown to be highly variable among sites: scaup consumed primarily fish on Lake Borgne (Rogers and Korshgen 1966), primarily seeds on Catahoula Lake (Moore et al. 1998), and primarily midge larvae (Chironomidae) on Rockefeller Wildlife Refuge (Afton and Ankney 1991). Specific to Lake Pontchartrain, Bowman (1973) noted an abundance of common rangia clams *Rangia cuneata* (hereafter, rangia) and dark false mussels *Mytilopsis leucophaeata* present in scaup diets, but did not collect data on prey availability in the benthos or the size classes of mollusks that were consumed (sensu Custer and Custer 1996; Richman and Lovvorn 2004). Understanding these details of prey selection is important for diving ducks, which selectively consume species and sizes of mollusks on the basis of handling times, meat-to-shell ratios that affect nutrients relative to passage rate, and avoidance of prey that may be too large to ingest (Draulans 1982; Bustnes and Erikstad 1990; De Leeuw 1992; Hamilton et al. 1999; Richman and Lovvorn 2004). Moreover, these data are critical on Lake Pontchartrain, where mollusk species assemblages and size distributions are dynamic through time in response to major disturbance events (e.g., spillway openings and hurricanes) (Poirrier et al. 2009). Our goal was to determine important diet items for scaup wintering on Lake Pontchartrain, especially in relation to their availability in the benthic substrate. Specifically, our objectives were to 1) determine diet composition (prey species and size class) of scaup collected from Lake Pontchartrain, 2) estimate concurrent prey availability in the estuary, and 3) evaluate dietary selection by comparing prey consumption to availability.

Methods

Lake Pontchartrain is a 1,630 km^2 oligohaline estuarine lagoon in southeastern Louisiana with an average salinity of 3.9 parts per thousand, an average depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). Scaup begin to arrive in the Lake Pontchartrain area between late October and the middle of November (Baldassarre 2014). We attempted to collect scaup from a $\sim$400-km^2 area on the northern lobe of Lake Pontchartrain during daylight hours between November 2016 and January 2017 and collections were attempted in the same area during each sampling occasion. Collections were incidentally concentrated in this portion of the Lake because that was where scaup commonly congregated. We collected scaup opportunistically from fast-moving boats to avoid biases associated with collecting ducks over decoys (Greenwood et al. 1986). They were collected using 12-gauge shotguns and #2 steel shot, under U.S. Fish and Wildlife Service scientific collecting permit MB74481B-0, Louisiana Department of Wildlife and Fisheries scientific collecting permit LNHP-15-074, and Louisiana State University AgCenter Animal Care and Use Committee protocol A2015-20. Immediately after collection, we injected scaup esophagi with 10% buffered formalin to prevent further digestion (Afton and Ankney 1991). In the lab, we dried scaup with consumer hair dryers to remove excess water, and determined age and sex by examining rectrices and wing plumage (Carney 1992). We measured body mass (with ingesta) and made morphometric measurements, including body length, culmen length and width, tarsometatarsus length, wing chord length, and longest rectrix width measured to the nearest millimeter (Afton and Ankney 1991; Hohman et al. 1995). Ingesta mass was not subtracted from total body mass (Hine et al. 1996; Vest et al. 2006).

We removed the esophagus and proventriculus (with ingesta) and placed them into containers filled with 10% buffered formalin (Afton et al. 1991). We used a dissecting microscope to sort esophageal and proventricular contents by species into 5-mm size classes based on length. Esophageal and proventricular contents were combined for analysis to maximize sample size (Afton et al. 1991). We excluded contents from the gizzard and intestines, because the gizzard imposes a sampling bias by retaining harder food items (Dirschl 1969; Swanson and Bartonek 1970). After sorting, we enumerated diet items in each species and size class, placed them into tin cups, and dried them in an oven for 24 h at 60°C (Afton et al. 1991). After drying we determined the dry mass of each species and size class to the nearest 0.1 mg.

To sample the mollusks available to foraging scaup, we collected three replicate dredge samples near six randomly selected scaup collection sites using a 15-cm^2 petite Ponar dredge (Abadie and Poirrier 2000; Brammer et al. 2007; Poirrier et al. 2008). This scale of sampling was sufficient for our purposes, because the benthic community of Lake Pontchartrain is characterized by low diversity and is relatively invariant across the spatial and temporal scale of our study (Poirrier et al. 2009; Poirrier and Caputo 2015). We rinsed and sieved samples using a Wildco 12-L, 0.6-mm sieve bucket (Science First/Wildco, Yulee, FL), and then preserved them in 10% Borax-buffered formalin with rose Bengal stain (Abadie and Poirrier 2000; Brammer et al. 2007; Poirrier et al. 2008). In the laboratory, we rinsed samples in a 0.5-mm sieve and sorted mollusks into 5-mm size classes on the basis of length and enumerated. We converted mollusk counts into an estimate of the number of individuals/m^2 by extrapolating from the surface area sampled by the petite Ponar dredge (225 cm^2) (Abadie and Poirrier 2000; Brammer et al. 2007; Poirrier et al. 2008). We calculated food availability by averaging benthic invertebrate abundances across the three replicate Ponar dredges and the six locations.

We used linear regression to determine whether the total number of food items consumed (dependent variable) varied by sex, age (independent factor variables), time of collection, or collection date (independent continuous variables). Although Poisson or negative binomial error structures are commonly used for analyses of count data (Zar 2009), after examining regression diagnostic plots, we selected a Gaussian error structure because it provided the best fit to the data. For scaup that consumed more than five food items (Reinecke and Owen 1980), we described consumption using three different metrics (Swanson et al. 1974; Prevett et al. 1979): 1) the frequency of occurrence of a food item, given all items that were eaten; 2) the aggregate percent dry weight of a food type, given the weight of all food types eaten; 3) the percentage of scaup that consumed a food item out of all scaup that were collected.

We calculated selection indices to assess dietary preferences (Manly et al. 1993). Selection index values ranged from 0 to ∞; values $>$ 1.0 indicated that scaup showed positive selection for a prey species and values $<$ 1.0 indicated avoidance. We defined the selection index as: $\hat{w}_i = \hat{o}_i / \hat{p}_i$, where $\hat{w}_i$ was the selection index for food item i, $\hat{o}_i$ was the proportion of a food type in the diet, and $\hat{p}_i$ was the proportion in which it was available on Lake Pontchartrain. We conducted all analyses in Program R (version 3.5.0, R Core team 2018); we report means $\pm$ standard error unless otherwise specified. We judged variables to be nonsignificant if $\alpha > 0.05$. Data are provided as Table S1, *Supplemental Material*.

Results

We collected 60 scaup on Lake Pontchartrain unevenly spaced across 5 d between 7 December 2016 and 20 January 2017 at 40 locations. Successful collection attempts were limited to days with calm winds and seas, with slightly foggy and overcast conditions improving collection success. We collected 53 males and 7 females composed of 42 adults and 18 juveniles. Sex, age, and collection time did not affect the number of prey items or total dry weight of prey consumed (all $P > 0.05$). Scaup consumed significantly more prey later in the season. Our regression model indicated that the number of food items consumed increased by 0.6 prey items per day through the season ($P < 0.05$). These trends were driven largely by the last two sampling occasions; using collection date as a factor, we found that scaup food consumption increased by 24.8 items on the last collection date ($P < 0.05$).

Scaup diets

Five species of mollusks (Figure 1) comprised 98% of the total number of food items and nearly 100% of the aggregate dry weight consumed. Rangia was the dominant food item eaten, accounting for 43% of the total number of food items ingested (Table 1) and 25 of the 28 individuals (89%) that had food items in the upper digestive tract consumed rangia. Scaup consumed a total of 353.2 g of rangia (Table 2), which represented 60% of the dry weight for all food items consumed. About half (51%) of the rangia eaten were 6–11-mm long, which accounted for 22% of all food items ingested. Although rangia $\geq$ 11 mm to $<$ 16 mm long accounted for only 8% of the total number of food items consumed, the size class represented 36% of the aggregate dry weight ingested. Combined, these two medium-size classes of rangia represented 55% of the aggregate dry weight for all food items consumed. The dark false mussel was the second most consumed species (82% of individuals consumed mussels), accounting for 26% of total number of food items and 37% of the total dry weight ingested.

Although 57% of scaup consumed dwarf surf clams *Mulinia lateralis*, the prey species only represented 3% of the total number of food items and 1% of the aggregate dry weight consumed (Table 1). Two species of snails *Texadina sphinctostoma* and *Probythinella protera* were consumed in moderate numbers (Table 2), but accounted for $<$ 2% of aggregate dry mass. Insects from the orders Coleoptera and Diptera combined to account for 2% of the total number of food items eaten and less than 1% of the aggregate dry weight consumed. Five individuals also ingested trace amounts of plant material; insects and plants were not included in selection analysis because their availability was not assessed in dredge samples for this paper.

Prey availability and selection

Texadina sphinctostoma was the most abundant prey species in the benthic dredge samples (Table 2), representing 59% of the total number of food items available (Table 3, Figure 2). Rangia was the second most abundant species; abundance among rangia size classes decreased with increasing size classes (Table 2). Compared with other prey species, dark false mussels and

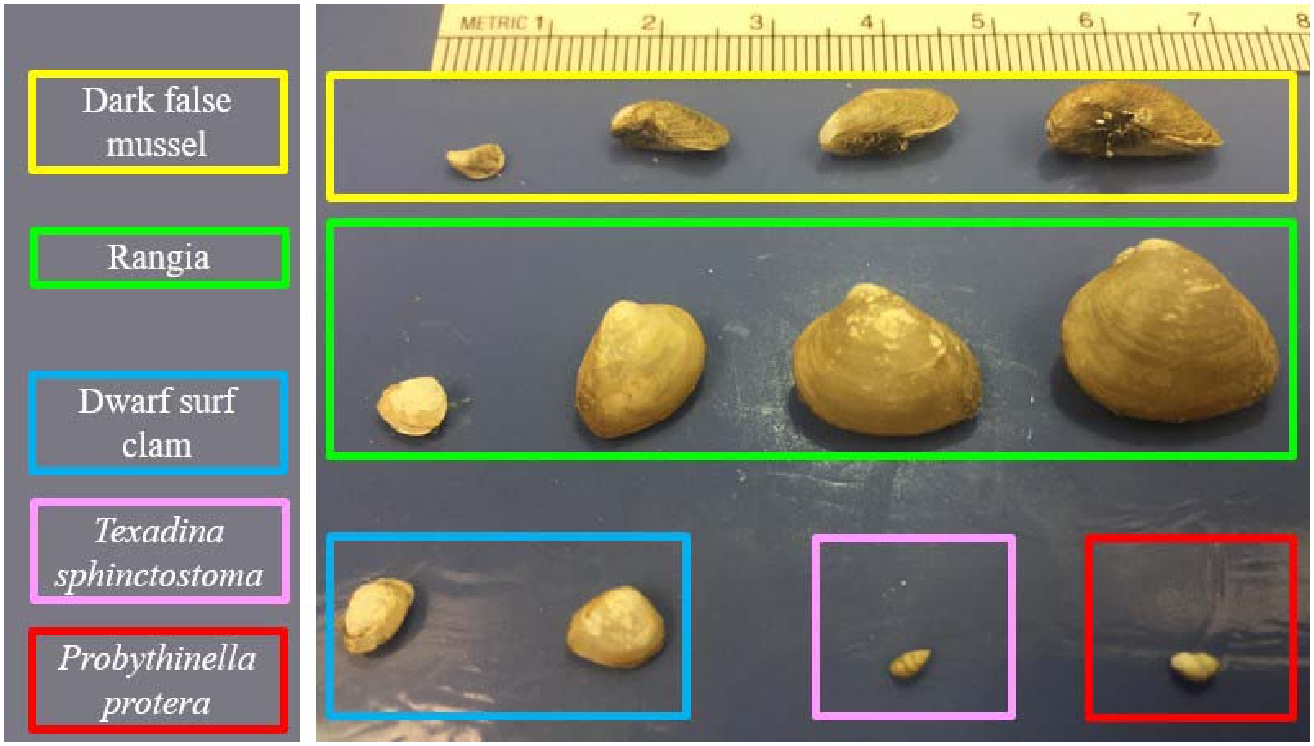

Figure 1. Photograph of mollusk prey species consumed by lesser scaup *Aythya affinis* on Lake Pontchartrain, Louisiana, April 4, 2017.

dwarf surf clams were relatively rare in the benthic dredge samples, with both species accounting for $< 4\%$ of the total number of food items available (Table 3).

Dark false mussels were the most selected mollusk, followed by dwarf surf clams (Table 3, Figure 2). However, large selection index values for these species were partially an artifact of their relative rarity in the dredge samples (Table 2). Scaup selected rangia as a species and the three smallest size classes (0 to < 6 mm, ≥ 6 mm to < 11 mm, and ≥ 11 mm to < 16 mm) (Table 3). Selection index values indicated that scaup avoided *T. sphinctostoma*, but *P. protera* was consumed in proportion to its availability in the benthos.

Discussion

Wintering scaup feed primarily on mollusks, often of a particular species or size (Afton et al. 1991; Custer and Custer 1996; Richman and Lovvorn 2004). Our results confirmed that scaup wintering on Lake Pontchartrain fed almost exclusively on mollusks, in accordance with previous work conducted by Bowman (1973). Rangia and dark false mussels were the dominant prey species consumed by scaup on Lake Pontchartrain and accounted for large percentages of the total number of food items and dry weight consumed. Rangia is often a dominant species in the benthic community on Lake Pontchartrain (Poirrier et al. 2009), and the species likely

Table 1. Percent occurrence of food items, aggregate percent dry weight, and frequency of food item occurrence in lesser scaup *Aythya affinis* that were collected during the winter of 2016–2017 from Lake Pontchartrain, Louisiana.

Food item	% of Total food items	Aggregate % dry weight	% Occurrence among scaup
Rangia (*Rangia cuneata*) (0 to $<$ 6 mm)	12.3	3.9	64.3
Rangia ($\geq$ 6 to $<$ 11 mm)	21.9	19.1	89.3
Rangia ($\geq$ 11 to $<$ 16 mm)	8.4	35.6	67.9
Rangia ($\geq$ 16 to $<$ 21 mm)	0.1	1.3	3.6
Rangia total	42.6	59.9	89.3
Dwarf surf clam (*Mulinia lateralis*)	2.8	1.2	57.1
Dark false mussel (*Mytilopsis leucophaeata*)	25.5	36.8	82.1
Texadina sphinctostoma	9.3	0.6	21.4
Probythinella protera	17.3	1.5	35.7
Insecta	2.4	0.0	14.3
Amphipoda	0.1	$<$ 0.1	3.6

Table 2. Total food items consumed by lesser scaup *Aythya affinis* and their availability on Lake Pontchartrain, Louisiana during the winter of 2016–2017.

Food item	Number of food items consumed	Dry weight consumed (g)	Number of food items available (mean ± SE per m^2)
Rangia (*Rangia cuneata*) total	497	353.2	274.7 ± 36.0
Rangia (0 to < 6 mm)	143	23.1	145.7 ± 34.1
Rangia (≥ 6 to < 11 mm)	255	112.6	71.7 ± 15.2
Rangia (≥ 11 to < 16 mm)	98	209.7	52.6 ± 21.6
Rangia (≥ 16 to < 21 mm)	1	7.9	4.8 ± 3.3
Dwarf surf clam (*Mulinia lateralis*)	33	7.2	7.2 ± 5.2
Dark false mussel (*Mytilopsis leucophaeata*)[a]	298	217.1	38.2 ± 14.7
Texadina sphinctostoma	108	3.5	805.1 ± 158.2
Probythinella protera	202	8.6	250.8 ± 67.2
Insecta	28	0.2	Not estimated
Amphipoda	1	< 0.1	Not estimated
Total	1,167	589.6	1,376.0 ± 355.3

[a] Dark false mussels also attach to hard surfaces not sampled by the benthic dredge, and so availability may be underestimated.

represents a large component of annual scaup diets on the estuary. Dark false mussels were the second most important prey species, accounting for over a quarter of the total quantity of food items eaten and 37% of the aggregate dry weight consumed. Dark false mussels attach to hard surfaces, such as rocks, artificial reefs, walls, or pilings (Oliver et al. 1998; Bamber and Taylor 2002), all of which are found on Lake Pontchartrain. Thus, it is possible that dark false mussels provide scaup with an easily accessible food source at reliable locations, and indeed, several of our collection locations were near the Lake Pontchartrain Causeway.

Dark false mussels were strongly preferred by scaup relative to their abundance in the benthic dredge surveys. However, dark false mussels are poorly sampled by dredge surveys because they attach to bridge pilings, seawalls, and other artificial structures. The selection index estimate reported here for dark false mussels is therefore likely inflated because availability was underestimated by our sampling protocols. In addition, underestimating the proportional availability of dark false mussels would lead to an overestimate of the proportional availability of rangia, meaning that true selection for those clams may be even stronger than reported here. Regardless, both rangia and dark false mussels were consumed by most scaup in significant numbers, and we conclude that they are important food items on Lake Pontchartrain.

Larger clams contain more nitrogen, lipids, and energy (kJ) than smaller clams (Richman and Lovvorn 2004), and so it is intuitive to expect scaup to maximize the size of prey items consumed. However, several studies have shown that scaup and other diving ducks more commonly select small- or intermediate-sized clams, possibly because of differing handling times, more advantageous meat-to-shell ratios, and risk avoidance of very large prey (Bustnes and Erikstad 1990; Hamilton et al. 1999; Richman and Lovvorn 2004). For example, clams < 12 mm long comprised 90% of scaup diets in the San Franscisco Bay (Richman and Lovvorn 2004). Similarly, we found that 80% of rangia ingested by scaup on Lake Pontchartrain were < 11 mm long, and that medium size classes of rangia were strongly selected relative to their availability.

Dwarf surf clams were also a selected food type, and indeed, wintering scaup often consume substantial amounts of dwarf surf clams if they are available (Cronan 1957; Harmon 1962; Uhler 1982). For example, in southwest Louisiana, dwarf surf clams represented over 99% of the total number of food items consumed (Harmon 1962). During our study, these clams represented less than 1% of the total food available during the winter of 2016–2017, likely limiting their biological importance to wintering scaup. However, since they are more abundant at higher salinities (Poirrier et al. 2009), dwarf surf clams would likely comprise a higher

Table 3. Selection index for lesser scaup *Aythya affinis* diet items on Lake Pontchartrain, Louisiana. Estimates from insects and amphipods were not included because availability data were not collected.

Food item	Proportion consumed	Proportion available	Selection index
Rangia (*Rangia cuneata*) (0 to < 6 mm)	0.12	0.11	1.16
Rangia (≥ 6 to < 11 mm)	0.22	0.05	4.20
Rangia (≥ 11 to < 16 mm)	0.08	0.04	2.20
Rangia (≥ 16 to < 21 mm)	< 0.01	< 0.01	0.25
Rangia total	0.43	0.20	2.13
Dwarf surf clam (*Mulinia lateralis*)	0.03	0.01	5.43
Dark false mussel (*Mytilopsis leucophaeata*)[a]	0.26	0.03	9.19
Texadina sphinctostoma	0.09	0.59	0.16
Probythinella protera	0.17	0.18	0.95
Total	0.98	1.00	23.53

[a] Dark false mussels also attach to hard surfaces not sampled by the benthic dredge, and so availability may be underestimated.

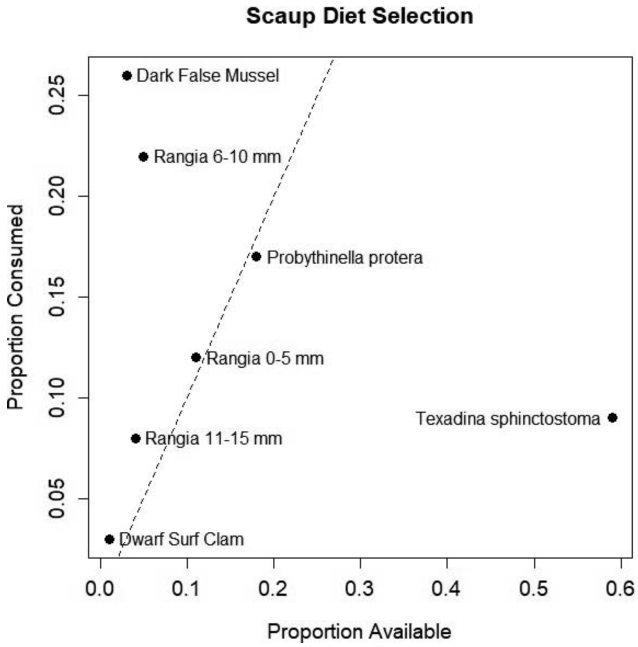

Figure 2. Diet selection diagram for lesser scaup *Aythya affinis* foraging on mollusks in Lake Pontchartrain, Louisiana during the winter of 2016–2017. Strongly preferred foods cluster at the upper left of the diagram, above the 1:1 selection ratio line. Preference for dark false mussels (*Mytilopsis leucophaeata*) may be overestimated because they also attach to hard surfaces not sampled by the benthic dredge.

percentage of scaup diets on Lake Pontchartrain in years when the salinity is higher. On the other hand, although *T. sphinctostoma* and *P. protera* accounted for sizable percentages of the total number of food items consumed, preference analyses indicated that *T. sphinctostoma* was avoided by scaup and *P. protera* was consumed in proportion to its availability. Because of their small size and low meat-to-shell ratios, the value of *T. sphinctostoma* or *P. protera* to wintering scaup is lower than other food sources on Lake Pontchartrain.

Because benthic invertebrate diversity is low on Lake Pontchartrain, it seems likely that the community of mollusks we sampled constitute the majority of scaup diets in most years. However, given the potential for extreme annual changes in the benthic community (e.g., following a hurricane), diet composition is likely to change from year to year (Poirrier and Caputo 2015). On Lake Pontchartrain, hooked mussel *Ischadium recurvum* abundance is usually low but the species can become superabundant in years of higher salinity on the estuary (Poirrier and Caputo 2015). Although no scaup consumed the hooked mussel in our study, scaup are known to consume the species at other wintering locations (Perry et al. 2007). Thus, it seems likely that scaup may feed on hooked mussels when the salinity is high on the estuary.

Finally, we found that scaup consumed more food later in the season, especially on the last two collection dates. We are confident that this is a not simply a site effect, because on those dates we collected scaup from multiple locations. It is possible that premigratory hyperphagia could be partially responsible for this result, because scaup seem to leave Lake Pontchartrain by February (C. Stroud, personal observation). On the other hand, Anteau and Afton (2004) did not see increases in scaup body condition until the birds left Louisiana, and conditions farther north in the flyway have more important effects on breeding demographics. Lake Pontchartrain at least provides foraging resources sufficient to support large populations of scaup in most years, but additional research is needed on whether prey abundance is driving interannual variation in scaup use (while this paper was undergoing peer review, Stroud et al. [2019] published results that link scaup abundance to the abundance of medium-sized rangia clams).

Supplemental Material

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Table S1. File provides raw data from which analyses were conducted.

Found at DOI: https://doi.org/10.3996/052019-JFWM-036.S1 (21 KB XLSX).

Reference S1. Carney SM. 1992. Species, age and sex identification of ducks using wing plumage. Washington, D.C.: U.S. Department of the Interior, U.S. Fish and Wildlife Service.

Found at DOI: https://doi.org/10.3996/052019-JFWM-036.S2 (2.74 MB PDF).

Reference S2. [USFWS]. U.S. Fish and Wildlife Service. 2017. Waterfowl population status, 2017.

Found at DOI: https://doi.org/10.3996/052019-JFWM-036.S3 (3.96 MB PDF).

Acknowledgments

Funding for this project was provided by the Louisiana Department of Wildlife and Fisheries, Ducks Unlimited Canada, The Institute for Wetland and Waterfowl Research (Waterfowl Research Foundation Fellowship), and the Louisiana State University AgCenter. We thank R. Keim for the use of his boat, M. Anteau and A. Afton for advice on scaup collection, and P. Wightman and J. White for assistance collecting scaup. We thank the Associate Editor and three anonymous reviewers for their comments on an earlier draft of this manuscript.

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