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Ecology of lesser scaup amphipods in the upper-Midwest: scope and mechanisms of the Spring Condition Hypothesis and implications for Migration Habitat Conservation

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**ECOLOGY OF LESSER SCAUP AND AMPHIPODS IN THE UPPER-
MIDWEST: SCOPE AND MECHANISMS OF THE SPRING CONDITION
HYPOTHESIS AND IMPLICATIONS FOR MIGRATION HABITAT
CONSERVATION**

**A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy**

In

The School of Renewable Natural Resources

**by
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May 2006**

DEDICATION

I dedicate my dissertation to my wife, Andrea C. E. Anteau, for her dedication to me over the years. Andrea has supported me as a friend, colleague, financially, and emotionally; the completion of this project would not have been possible without her tireless assistance, understanding, and sacrifices.

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TABLE OF CONTENTS

DEDICATION	ii
ACKNOWLEDGMENTS	iii
ABSTRACT	x
CHAPTER 1: GENERAL INTRODUCTION	1
THE SPRING CONDITION HYPOTHESIS	1
LITERATURE CITED	4
CHAPTER 2: NUTRIENT RESERVES OF FEMALE LESSER SCAUP DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST: A FURTHER TEST OF THE SPRING CONDITION HYPOTHESIS	7
INTRODUCTION	7
METHODS	8
RESULTS	16
DISCUSSION	22
LITERATURE CITED	28
CHAPTER 3: ESTIMATING CHANGES IN LIPID RESERVES OF LESSER SCAUP FROM PLASMA-LIPID METABOLITES	32
INTRODUCTION	32
METHODS	33
RESULTS	35
DISCUSSION	36
LITERATURE CITED	39
CHAPTER 4: ARE FEMALE LESSER SCAUP CATABOLIZING LIPID RESERVES DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST? A FURTHER TEST OF THE SPRING CONDITION HYPOTHESIS	41
INTRODUCTION	41
METHODS	43
RESULTS	48
DISCUSSION	49
LITERATURE CITED	56
CHAPTER 5: INFLUENCES OF CADMIUM, MERCURY, AND SELENIUM ON NUTRIENT RESERVES OF FEMALE LESSER SCAUP DURING WINTER AND SPRING MIGRATION	60
INTRODUCTION	60
METHODS	61
RESULTS	64
DISCUSSION	67
LITERATURE CITED	74

CHAPTER 6: AMPHIPOD DENSITIES AND INDICES OF WETLAND QUALITY ACROSS THE UPPER-MIDWEST	79
INTRODUCTION	79
METHODS	82
RESULTS	89
DISCUSSION	96
LITERATURE CITED	102
CHAPTER 7: DIET SHIFTS OF LESSER SCAUP DURING SPRING MIGRATION ARE CONSISTENT WITH THE SPRING CONDITION HYPOTHESIS	108
INTRODUCTION	108
METHODS	110
RESULTS	115
DISCUSSION	117
LITURATURE CITED	125
CHAPTER 8: DIETS OF LESSER SCAUP DURING SPRING MIGRATION THROUGHOUT THE UPPER-MIDWEST ARE CONSISTENT WITH THE SPRING CONDITION HYPOTHESIS	130
INTRODUCTION	130
METHODS	132
RESULTS	140
DISCUSSION	142
LITERATURE CITED	149
CHAPTER 9: WETLAND USE AND FEEDING BY LESSER SCAUP DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST	153
INTRODUCTION	153
METHODS	155
RESULTS	163
DISCUSSION	166
LITERATURE CITED	171
CHAPTER 10: FACTORS INFLUENCING SPRING <i>GAMMARUS</i> AND <i>HYALELLA</i> (AMPHIPODA) DENSITIES ACROSS THE UPPER-MIDWEST	175
INTRODUCTION	175
METHODS	177
RESULTS	185
DISCUSSION	188
LITERATURE CITED	195
CHAPTER 11: GENERAL CONCLUSIONS	200
THE SPRING CONDITION HYPOTHESIS	200
LITERATURE CITED	204
APPENDIX A: GLYCEROL AND TRIGLYCERIDE PROTOCOL	207

APPENDIX B: B-HYDROXYBUTYRATE PROTOCOL.....	208
APPENDIX C: MASS CHANGES OF RECAPTURED LESSER SCAUP	209
APPENDIX D: CORRELATION BETWEEN TAPEWORM ABUNDANCE AND LIPID RESERVES OF FEMALE LESSER SCAUP	211
APPENDIX E: SIGHTINGS OF COLOR-MARKED SCAUP DURING SPRING MIGRATION.....	212
VITA.....	213

ABSTRACT

I tested the scope of the Spring Condition Hypothesis in explaining the continental population decline of lesser scaup (*Aythya affinis*; hereafter scaup) and explored potential mechanisms affecting female body condition to assist conservation efforts for population recovery.

Lipid reserves of females currently are lower than historical values during spring migration throughout Iowa, Minnesota, and North Dakota; females catabolized lipids throughout this area (indexed by concentrations of plasma-lipid metabolites, which accounted for 75% of the variation in mass change). My results indicate that a large segment of the continental scaup population likely is affected by decreased lipid reserves, which could cause reductions in breeding propensity and reproductive success.

Hepatic cadmium was negatively correlated with lipid reserves of females during spring migration; however, current cadmium concentrations only accounted for 11% of the observed decrease in lipid reserves of females between Illinois and Minnesota.

Wetland use by scaup was positively correlated with amphipod densities throughout the upper-Midwest, indicating a preference for amphipods. Amphipod densities were markedly lower ($1 - 12 \text{ m}^{-3}$) and scaup were consuming fewer amphipods in the upper-Midwest relative to historical records. Scaup probably must spend more time searching for food within and among wetlands than they did historically. Fish occurred in 74, 78 – 84, and 31 – 45% of wetlands in Iowa, Minnesota, and North Dakota, respectively, whereas historically they occurred in only 10 – 20% of wetlands. Amphipod densities were negatively correlated to fish densities and sedimentation. My

results indicate that there has been a decrease in amphipod densities throughout the upper-Midwest, which likely is causing the observed decreases in lipid reserves of scaup.

My results generally were consistent with the Spring Condition Hypothesis and indicate that wetland restoration efforts are needed throughout the upper-Midwest, but especially in Iowa and southern Minnesota. Managers should provide abundant populations of amphipods (over 26 m^{-3} geometric mean across the landscape) and target wetlands that: (1) have large ($> 500 \text{ m}$ diameter) open-water zones, (2) are deep enough to support over-wintering populations of amphipods, (3) allow management of fish communities, and (4) the surrounding land can be managed to reduce sedimentation.

CHAPTER 1: GENERAL INTRODUCTION

THE SPRING CONDITION HYPOTHESIS

Scope of the Spring Condition Hypothesis

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly since 1978 (Austin et al. 1998, Afton and Anderson 2001); population estimates were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. Recruitment of lesser scaup apparently has declined since 1978, and female survival rates have declined relative to that of males (Afton and Anderson 2001). The segment of the scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through the upper-Midwest comprises a major component of the continental population and likely is experiencing the largest decline in numbers (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup (Afton 1984, Afton and Ankney 1991, Anteau 2002, Anteau and Afton 2004). The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas in lower body condition than in the past (Afton and Anderson 2001). Female scaup currently are migrating through Northwestern Minnesota and arriving on a breeding area in southwestern Manitoba with fewer lipid reserves than did those historically (Anteau 2002, Anteau and Afton 2004). Anteau and Afton (2004) hypothesized that the observed decreases in lipid reserves were indicative

of a landscape-level decline in lipid reserves, occurring somewhere between western Illinois and Northwestern Minnesota. I examined lipid reserves and body mass of female scaup collected during spring migration across the upper-Midwest, in order to test the scope of the Spring Condition Hypothesis (Chapter 2).

Traditional measures of body condition (e.g., size-adjusted body mass and lipid, protein, and mineral reserves) of scaup likely are influenced by a combination of environmental factors at specific collection sites and at preceding migration stopover areas (Anteau and Afton 2004); thus, these measures of body condition potentially are affected by habitat factors over a large and unknown area. An assessment of where scaup are accumulating or catabolizing lipid reserves is needed throughout the upper-Midwest to further test and determine the scope of the Spring Condition Hypothesis. I evaluated whether plasma-lipid metabolites (triglyceride and β -hydroxybutyrate) are useful in predicting daily lipid change (DLC) in scaup during spring migration (Chapter 3). I subsequently examined DLC of migrating female scaup collected throughout the upper-Midwest to identify where females are accumulating or catabolizing lipid reserves in spring (Chapter 4).

Mechanisms of the Spring Condition Hypothesis

Female scaup currently migrating throughout the upper-Midwest are catabolizing lipids and have low lipid reserves, suggesting they are nutritionally stressed (Anteau and Afton 2004; Chapters 2, 4); moreover, there has been an apparent concomitant decline in breeding success of scaup (Afton and Anderson 2001, Koons 2001, Koons and Rotella 2003). Therefore, it is important to understand the mechanisms causing females to be in poor condition. One prediction of the Spring Condition Hypothesis is that food

availability (abundance of prey) and/or forage quality (nutritional value of prey) on northern stopover areas have declined. Custer et al. (2003) and Anteau and Afton (2004) hypothesized that trace-element contaminants might also inhibit the ability of female scaup to accumulate nutrient reserves during spring migration.

Accordingly, I examined potential mechanisms of the Spring Condition Hypothesis by (1) testing the influence of trace elements (cadmium, mercury, and selenium) on the accumulation of nutrient reserves of female scaup during spring migration (Chapter 5) and (2) determining whether there has been a decline in availability and/or quality of scaup foods on spring stopover areas in the upper-Midwest (Chapters 6, 7, 8). Specifically, I examined food availability and forage quality of scaup by: (1) assessing amphipod (preferred food) availability and indices of wetland quality across the upper-Midwest in relation to published historical data (Chapter 6); (2) testing for decreases in forage quality by examining historical and current diets of scaup at 2 areas of Minnesota and 1 in Manitoba (Chapter 7); and (3) examining forage quality at a landscape scale by determining whether female scaup are able to procure preferred foods across the upper-Midwest (Chapter 8).

Migration Habitat Conservation

Food availability and quality of female scaup are low or have decreased recently during spring migration in the upper-Midwest (Anteau and Afton 2006; Strand 2005; Chapters 6, 8). Accordingly, conservation, restoration, and management of wetland habitats used by scaup during spring migration are goals of a major conservation plan in the upper-Midwest (Ducks Unlimited 2004). However, further information is needed concerning scaup habitat and feeding behavior to help efficiently target conservation

activities to wetlands and areas that would be most beneficial for scaup. Therefore, I examined how wetland characteristics and food availability influenced wetland use and feeding by scaup and identified areas or regions in the upper-Midwest that are in most need of conservation efforts (Chapter 9).

Amphipods seemingly are a preferred food for scaup during spring and summer in the upper-Midwest (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Anteau (2002) and Anteau and Afton (2004) hypothesized that amphipod populations have declined across the upper-Midwest, due to landscape-scale increases in (1) abundance or foraging effectiveness of fish and/or (2) anthropogenic caused sedimentation into wetlands. I examined potential factors (e.g., fish, sedimentation, and other interacting factors) influencing densities of amphipods in semipermanent and permanent wetlands throughout the upper-Midwest to assist conservation efforts in restoring abundant populations of amphipods in this area (Chapter 10).

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CHAPTER 2: NUTRIENT RESERVES OF FEMALE LESSER SCAUP DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST: A FURTHER TEST OF THE SPRING CONDITION HYPOTHESIS

INTRODUCTION

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly since 1978 (Austin et al. 1998, Afton and Anderson 2001); annual population estimates were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. Recruitment of lesser scaup apparently has declined since 1978, and female survival rates have declined relative to that of males (Afton and Anderson 2001). The segment of the scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through the upper-Midwest comprises a major component of the continental population and likely is experiencing the largest decline in numbers (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup (Afton 1984, Afton and Ankney 1991, Anteau 2002, Anteau and Afton 2004). The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas in lower body condition than in the past (Afton and Anderson 2001). Female scaup migrating through Northwestern Minnesota in 2000 – 2001 (hereafter NW00) had fewer lipid reserves than did those historically (Anteau 2002, Anteau and Afton 2004). Anteau and Afton (2004) hypothesized that the observed decreases in lipid reserves at NW00 were indicative of a landscape-level decline in lipid

reserves, occurring somewhere between western Illinois and Northwestern Minnesota. Migrating female scaup currently are catabolizing lipid reserves across the upper-Midwest, except in western Illinois (Chapter 4); thus, body condition of females leaving western Illinois may be a good predictor of that for females on subsequent stopover areas in the upper-Midwest.

I evaluated annual variations in body mass of females in western Illinois and its relation to that of females stopping in Northwestern Minnesota to determine whether such variability was important when interpreting body condition of females across the upper-Midwest. I used NW00 as a reference to compare lipid reserves and body mass of female scaup collected during spring migration across the upper-Midwest, to test the potential scope of the Spring Condition Hypothesis. If this hypothesis has a large scope, lipid reserves of females in regions across the upper-Midwest would be similar to or lower than those found to be lower than historical values (NW00). I analyzed body mass to allow comparisons with other studies for which lipid-reserve data were not available. Finally, I described regional variations in protein and mineral reserves of female scaup during spring migration in the upper-Midwest.

METHODS

Study Area

Pool 19.-I used Pool 19 of the Mississippi River (Figure 2.1; between Hamilton and Niota, IL; hereafter Pool 19) to reference scaup body condition prior to migrating into the upper-Midwest. Pool 19 has been described in detail by Thompson (1973) and Havera (1999).

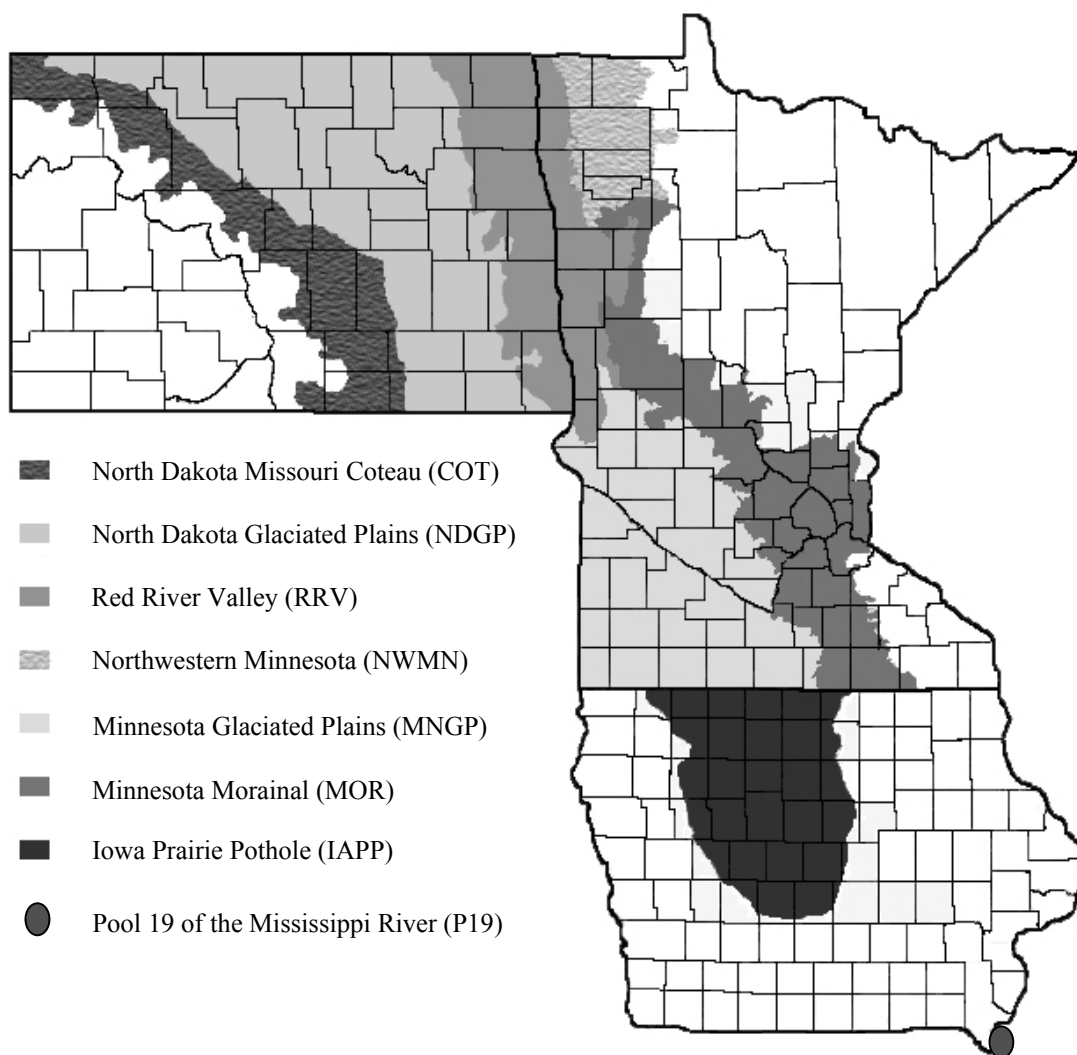


Figure 2.1. Map of the study area depicting 7 eco-physiographic regions and Pool 19 of the Mississippi River for lesser scaup collections during spring migration in the upper-Midwest, 2003 – 2005. Areas in white were not sampled.

Upper-Midwest.—My study area here included the Prairie Pothole Regions in Iowa, Minnesota, and North Dakota (Figure 2.1), which comprise the most important spring migration stopover areas for scaup, based on observations of wildlife biologists and managers, band-recovery data, sightings of color-marked scaup, and aerial surveys in spring (Low 1941; Afton and Hier 1985; Afton et al. 1991; Pace and Afton 1999; Minnesota Department of Natural Resources, unpublished data; North Dakota Game and Fish Department, unpublished data). I stratified the 3-state area into 7 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 2.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

Sampling Design and Allocation

Pool 19.—In springs 2003 – 2005, I attempted to collected 25 female scaup at Pool 19 to examine annual variation and reference body mass prior to their migration into the upper-Midwest each spring.

Reference group.—I used data collected from Northwestern Minnesota in 2000 and 2001 (NW00) as a reference group to make *a priori* comparisons with other upper-Midwest regions because body mass and lipid-reserve levels of females have decreased there relative to historical data (Anteau 2002, Anteau and Afton 2004). In springs 2003 – 2005, I also attempted to collect 15 females annually at each of the same sites in Northwestern Minnesota (hereafter NWMN; Agassiz National Wildlife Refuge [NWR] and Thief Lake and Roseau River Wildlife Management Areas [WMA]; Table 2.1).

Table 2.1. Regions, years, dates, and numbers of female lesser scaup (N) collected during spring migration in the upper-Midwest, including numbers collection sites (S) and numbers of candidate townships (T) for random selection of collection sites.

Region	Year	Dates	N	S	T
Iowa Prairie Pothole	2004	6 - 9 April	27	3	43 ^a
	2005	30 March – 4 April	27	3	
Minnesota Morainal	2003	20 April - 9 May	19	4	348 ^b
	2004	10 - 15 April	12	4	
	2005	8 - 16 April	30	4	
Minnesota Glaciated Plains	2003	9 - 29 April	33	4	285 ^b
	2004	8 - 19 April	30	4	
	2005	10 - 15 April	34	4	
Northwestern Minnesota ^c	2003	1 - 13 May	26	3	
	2004	4 - 13 May	44	3	
	2005	23 - 28 April	35	3	
Red River Valley	2003	17 April – 10 May	26	3	66 ^b
	2004	24 April - 2 May	17	3	
	2005	17 - 21 April	26	3	
North Dakota Glaciated Plains	2003	15 April - 2 May	60	6	364 ^b
	2004	20 April – 11 May	46	6	
	2005	9 April - 2 May	59	6	
North Dakota Missouri Coteau	2003	14 - 23 April	30	3	208 ^b
	2004	15 - 22 April	30	3	
	2005	7 April - 1 May	30	3	

^a Townships that contain at least 200 hectares total of semipermanent and permanent wetlands.

^b Townships that contain at least 200 hectares of semipermanent wetlands.

^c Fixed collection sites (same each year – see methods).

Random site selection.-I used constrained-random sampling techniques to select collection sites in all other regions. I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 2.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck North Dakota, unpublished data; S. Piepgras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or permanent wetlands. I then allocated numbers of collection sites among the 6 regions (3 to 6 sites per region; Table 2.1) based on region size and number of candidate townships available (Table 2.1, Figure 2.1). Each region was divided into equal-sized sub-regions based on latitude, such that there was 1 collection site per sub-region annually (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 collection sites for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 2.1).

Random collection sites.-Each collection site (27,972 ha) was comprised of three 36-square-mile townships in order to insure adequate collection opportunities; however, in some instances (17 % of townships where collections occurred) I had to replace townships with another randomly selected township because selected township no longer had suitable scaup habitat (semipermanent or permanent wetlands) or had little or no scaup use. I attempted to collect 10 females from each collection site. I randomly

selected new townships annually without replacement within each sub-region, from the list of candidate townships, to maximize representation of spatial variability in nutrient reserves of scaup. In 2004 and 2005, I further constrained township selection so that the centrum of the second and third townships selected were within 50 km of the centrum of the first randomly selected township, to minimize travel by field crews.

Collection of Specimens

I collected female scaup randomly with a shotgun, without the use of decoys to avoid associated biases (Pace and Afton 1999); collections were conducted exactly as in Afton et al. (1991) and Anteau and Afton (2004, 2006). In all regions, I attempted to collect females that were feeding. I generally timed collections to occur during the middle of migration, coinciding with relatively large numbers of migrating scaup present within each sub-region. I collected 641 female scaup from the upper-Midwest study area in springs 2003 – 2005 (Table 2.1). However, in the Iowa Prairie Pothole (IAPP) region, I only collected scaup in 2004 – 2005. Scaup were collected from 98 different townships (9 in Iowa, 46 in Minnesota, and 43 in North Dakota) and 3 different fixed locations (in NWMN) in 2003 – 2005, representing 7.5 % of the candidate collection townships in the upper-Midwest. At Pool 19, I also collected 22, 20, and 25 female scaup in springs 2003 – 2005 (March 21 – 27 each year).

Specimen Preparation

I recorded body mass immediately upon collection (± 1 g), and then preserved esophageal and proventricular contents by slowly injecting a 10% buffered formaldehyde solution down the esophagus with a syringe (Chapter 8). Specimens then were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections. In

the laboratory, carcasses were thawed, reweighed (± 1 g), and the following morphometrics were recorded: (1) total length (± 1 mm), from tip of longest rectrix to tip of bill with bird stretched on its back, (2) keel length (± 0.1 mm; externally measured), (3) wing cord (± 1 mm; Carney 1992), (4) rectrix length (± 1 mm), from body to tip of longest rectrix, and (5) tarsus bone (± 0.1 mm; Dzubin and Cooch 1992). I then removed and weighed upper- and lower-gut contents (Anteau 2002). Carcass preparation and body composition analyses were contracted to the Avian Energetics Laboratory (AEL) of Bird Studies Canada, Port Rowan, Ontario. At AEL, carcasses were weighed (± 0.01 g), dried to a constant mass, reweighed, and homogenized so that carcass could pass through a 2-mm sieve (see Anteau and Afton 2004). Nutritional analyses of prepared carcasses were conducted exactly as in Afton and Ankney (1991). Following analyses, estimates of lipid, protein, and mineral reserves were estimated exactly as in Anteau and Afton (2004).

Statistical Analyses

Annual variation. -I conducted a principal components analysis of the correlation matrix for morphometrics: body length (total length – rectrix length), wing cord, tarsus bone, and keel length (PROC PRINCOMP; SAS Institute 2002) separately for females collected from Pool 19 and Northwestern Minnesota in 2000 – 2005. I then used the first principal component scores (PC1; for each location) to index body size (Afton and Ankney 1991). For both locations separately, I tested for annual differences in body mass of females collected in 2000 – 2005 with an analysis of covariance (ANCOVA; PROC MIXED; SAS Institute 2002), with year as a class variable and PC1 as a covariate. I used the PDMIX800 macro (Saxton 1998) in each model to get Tukey-Kramer adjusted

mean letter groupings for years. I then used a linear regression to test if annual mean body mass of females at Pool 19 explained variation in body mass in Northwestern Minnesota (PROC REG; SAS Institute 2002).

I conducted a third principal components analysis of the correlation matrix on the same morphometrics (PROC PRINCOMP; SAS Institute 2002) for all females collected from across the upper-Midwest in 2003 – 2005. I tested for annual variations in body mass and lipid reserves (lipid, protein, and mineral) of females collected in 2003 – 2005 with separate ANCOVAs (PROC MIXED; SAS Institute 2002), in which year, region, and sub-region within region were class variables and PC1 was a covariate. These analyses indicated that body mass ($F_{2, 615} = 0.11$; $P = 0.895$) and lipid reserves ($F_{2, 615} = 0.67$; $P = 0.513$) were similar among years 2003 – 2005; thus, year was excluded from subsequent models.

Lipid reserves and body mass in the upper-Midwest.-I conducted a fourth principal components analysis of the correlation matrix on the same morphometrics, which included an additional 70 females collected in NW00 as a reference group (Anteau and Afton 2004; PROC PRINCOMP; SAS Institute 2002). I tested for regional differences in lipid reserves and body mass of females with separate ANCOVAs (PROC MIXED; SAS Institute 2002) in which region and sub-region within region were class variables and PC1 was a covariate. I specified NW00 as a separate region, and conducted *a priori* tests by contrasting body mass or lipid reserves of females collected in NW00 to those of all other regions using the Dunnett-adjusted pdiff-control option of the least-squares means statement for region (PROC MIXED; SAS Institute 2002).

Protein and mineral reserves in the upper-Midwest.- I examined regional variations in protein and mineral reserves of females collected from the upper-Midwest in 2003 – 2005 with separate ANCOVAs (PROC MIXED; SAS Institute 2002), in which year, region, and sub-region within region were class variables and PC1 was a covariate. I used PC1 scores from the third principal components analysis to index body size in these analyses (Afton and Ankney 1991). I used the PDMIX800 macro (Saxton 1998) in each model to get Tukey-Kramer adjusted mean letter groupings for each region and year (if significant at *alpha* 0.05).

RESULTS

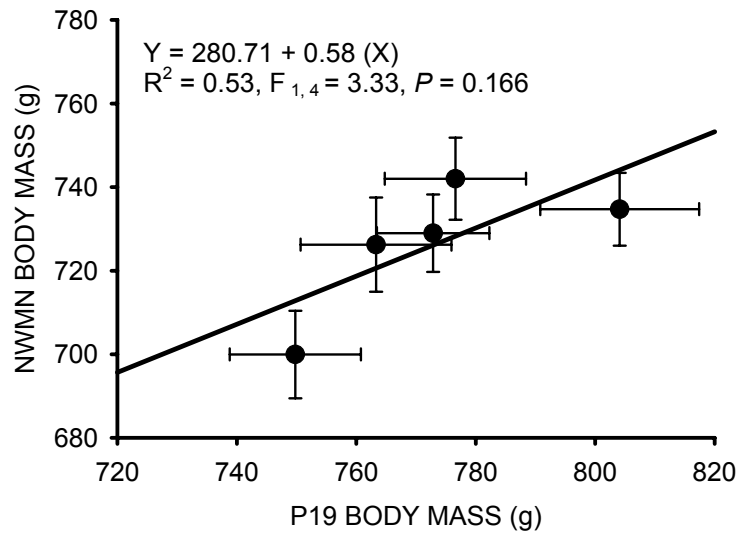
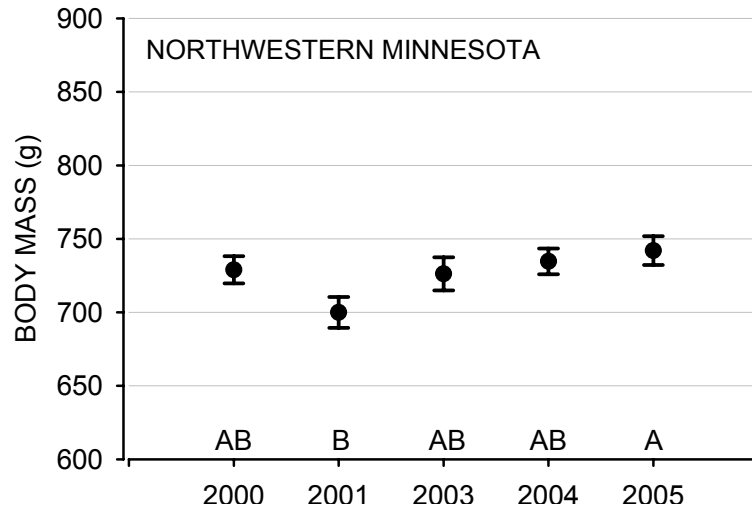
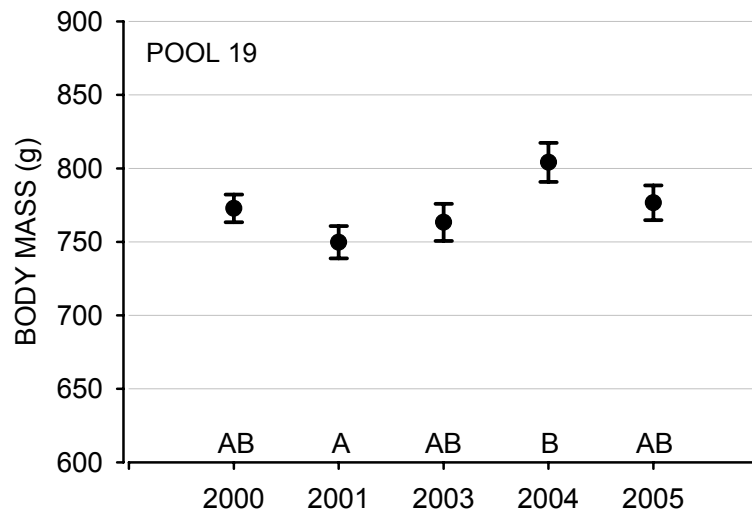
Annual Variation

In the principal component analysis of females collected at Pool 19 from 2000 – 2005, eigenvectors for PC1 ranged from 0.461 to 0.537; PC1 accounted for 41% of the variation in morphometrics. Body mass was positively correlated with PC1 (slope = 21.12; $F_{1, 130} = 27.06$; $P < 0.001$) at Pool 19. Body mass differed ($F_{4, 130} = 2.63$; $P = 0.037$) among years at Pool 19; females were heavier in 2004 than in 2001 (Figure 2.2).

In the principal component analysis for females collected in Northwestern Minnesota in 2000 – 2005, eigenvectors for PC1 ranged from 0.448 to 0.534; PC1 accounted for 53% of the variation in morphometrics. Body mass of females in Northwestern Minnesota was positively correlated with PC1 (slope = 24.43; $F_{1, 169} = 57.62$; $P < 0.001$), and differed among years ($F_{4, 169} = 2.45$; $P = 0.048$); females were heavier in 2005 than in 2001 (Figure 2.2).

Annual mean body mass of females at Pool 19 explained 53% of the variation in that of females in Northwestern Minnesota ($F_{1, 4} = 3.33$; $P = 0.166$; Figure 2.2).

Figure 2.2. Least-square mean plots and regression plot of least-square means of body mass (\pm SE) of female lesser scaup collected at Pool 19 (Mississippi River; P19) and in Northwestern Minnesota (NWMN) during spring migration for years 2000 – 2005. Capital letters are Tukey-Kramer adjusted mean grouping at $P < 0.05$.



Lipid Reserves and Body Mass in the Upper-Midwest

In the principal component analysis that included NW00 data, eigenvectors for PC1 ranged from 0.479 to 0.521; PC1 accounted for 51% of the variation in morphometrics.

Lipid reserves were positively correlated with PC1 (slope = 2.56; $F_{1,684} = 6.25$; $P = 0.013$) and varied among regions ($F_{7,684} = 3.45$; $P = 0.001$) and sub-regions within regions ($F_{18,684} = 2.35$; $P = 0.001$). Although lipid reserves varied among regions, *a priori* tests indicated that all regions were similar to NW00 (Figure 2.3).

Body mass was positively correlated with PC1 (slope = 18.36; $F_{1,684} = 129.51$; $P < 0.001$) and varied among regions ($F_{7,684} = 21.02$; $P < 0.001$) and sub-regions within regions ($F_{18,684} = 3.65$; $P < 0.001$). Body mass of females were lower in IAPP and Minnesota Morainal (MOR) than in NW00, but were similar between NW00 and other regions (Figure 2.3).

Protein and Mineral Reserves in the Upper-Midwest

In the principal component analysis, eigenvectors for PC1 ranged from 0.476 to 0.523; PC1 accounted for 50% of the variation in morphometrics.

Protein reserves were positively correlated with PC1 (slope = 3.88; $F_{1,617} = 167.44$; $P < 0.001$) and varied among regions ($F_{6,617} = 14.71$; $P < 0.001$) and sub-regions within regions ($F_{16,617} = 3.09$; $P < 0.001$), but did not vary annually ($P = 0.612$). Mean protein reserves of females were higher in North Dakota Missouri Coteau (COT), NDGP, the Red River Valley (RRV), and NWMN than those in MOR and IAPP (Figure 2.4).

Mineral reserves were positively correlated to PC1 (slope = 0.96; $F_{1,631} = 138.33$; $P < 0.001$) and varied among regions ($F_{6,631} = 2.43$; $P = 0.025$) and years ($F_{2,631} =$

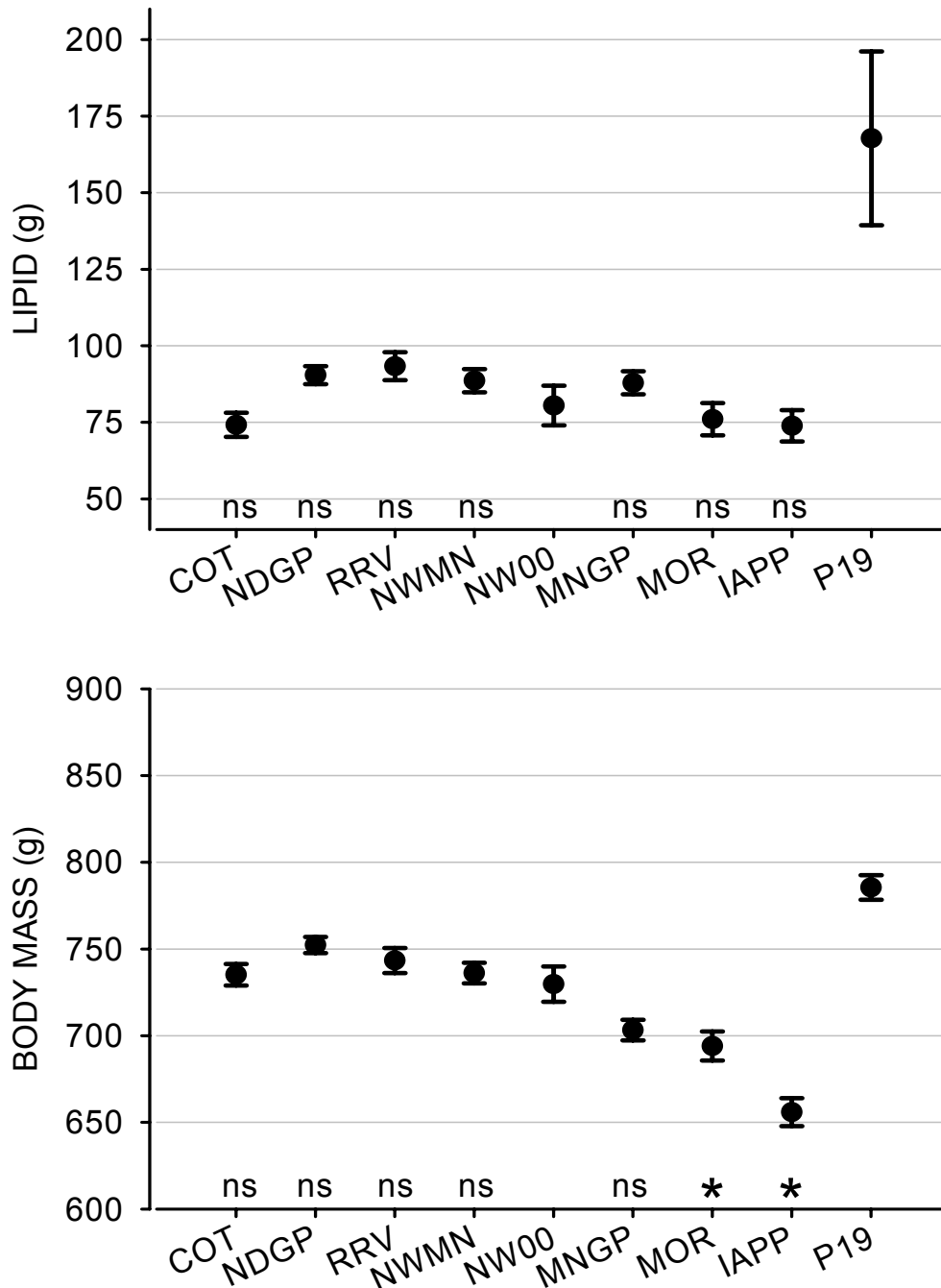


Figure 2.3. Least-square mean lipid reserves and body mass (\pm SE) of female lesser scaup collected during spring migration (years 2003 – 2005 pooled) by regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, NW00 = NWMN in 2000 – 2001 (Anteau and Afton 2004), MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole, and P19 = Pool 19 [included as a reference; for lipids P19 data from 2000 – 2001; Anteau and Afton 2004]). Asterisks indicate significance ($P < 0.05$) of the *a priori* contrasts between NW00 and each region; no statistical comparison made to P19.

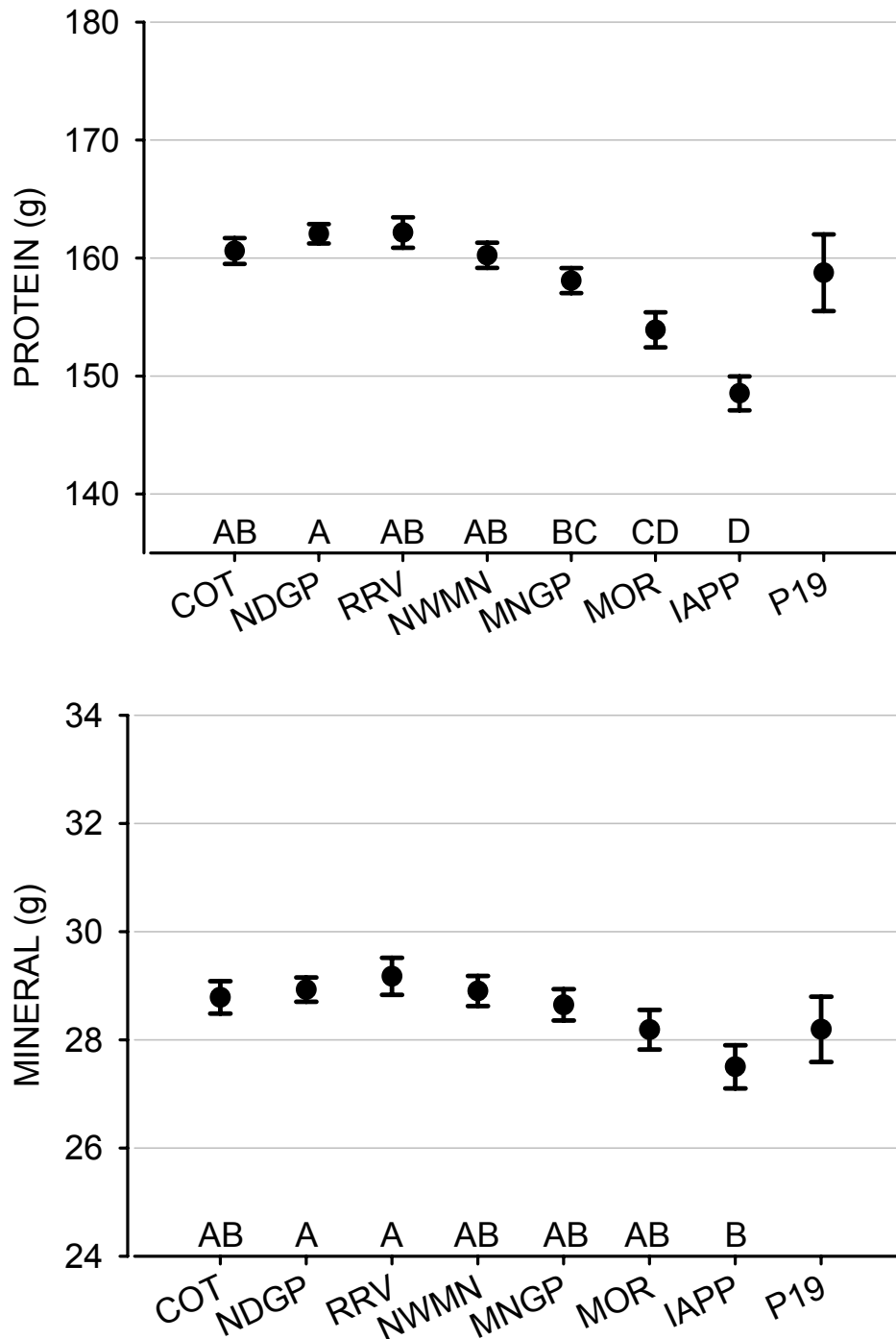


Figure 2.4. Least-square mean protein and mineral reserves (\pm SE) of female lesser scaup collected during spring migration (years 2003 – 2005 pooled) by regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole, and P19 = Pool 19 [from Anteau 2002; included as a reference]). Capital letters are Tukey-Kramer adjusted mean grouping at $P < 0.05$; no statistical comparison made to P19.

18.25; $P < 0.001$), but not among sub-regions within regions ($P = 0.134$). Mean mineral reserves (\pm SE) in 2004 and 2005 (28.7 ± 0.2 and 29.4 ± 0.2 , respectively) were higher than those in 2003 (27.7 ± 0.2). Mineral reserves of females in RRV and NDGP were higher than those in IAPP (Figure 2.4).

DISCUSSION

Annual Variation

Annual variation in environmental factors at Pool 19, or preceding stopover areas, may affect body mass variation of females in Northwestern Minnesota because females are catabolizing lipid reserves throughout the upper-Midwest, but not at Pool 19 (Chapter 4). Indeed, I found a correlation between mean body mass at Pool 19 and NWMN, which suggests that Pool 19 and proceeding migration stopover areas currently are critical for females to accumulate or maintain body mass and lipid reserves. I did not detect annual variation in body mass for years 2003 – 2005 thus it is unnecessary to consider such variations in subsequent nutrient reserve models for the upper-Midwest.

Macroinvertebrates are the predominant foods of scaup during spring migration in the upper-Midwest (Afton et al. 1991, Anteau and Afton 2006, Chapter 8); macroinvertebrate densities vary annually in a given wetland in response to varying water regimes and winter severity (Euliss et al. 1997). However, body mass and lipid and protein reserves of females did not vary annually in the upper-Midwest in 2003 – 2005. Scaup are highly mobile during spring migration and move relatively slowly across the upper-Midwest; the observed middle of spring migration is approximately 45 days later in Northwestern Minnesota than at Pool 19 (Anteau and Afton 2004). Therefore, scaup likely choose the best wetlands to forage on in any given year (Chapter 9), which might

make it difficult to detect annual variation in body mass or nutrient reserves of scaup during spring migration. Furthermore, my results strengthen the findings that lipid reserves of females have decreased from historical values (Anteau and Afton 2004) because it appears that annual variations in body mass and nutrient reserves of females migrating through the upper-Midwest are subtle.

Lipid Reserves and Body Mass in the Upper-Midwest

Anteau and Afton (2004) hypothesized that current low lipid-reserve levels of female scaup in NW00 were indicative of a landscape-scale decline in lipid reserves occurring somewhere between Pool 19 and Northwestern Minnesota. Observed lipid-reserve levels across Iowa, Minnesota, and North Dakota were similar to values reported by Anteau and Afton (2004; NW00) and thus are consistent with this hypothesis. Moreover, lipid reserves of female scaup collected in eastern South Dakota in 2003 and 2004 (Strand 2005) generally were similar to my data (Figure 2.3). In 2003 – 2005, lipid reserves of females throughout the upper-Midwest were 75 to 95 g lower, on average, than that of those at Pool 19 in 2000 – 2001 (Anteau and Afton 2004), which is consistent with findings that female scaup were catabolizing lipid reserves throughout spring migration in the upper-Midwest (Chapter 4). Moreover, regional rates of lipid catabolism (Chapter 4) generally are similar to regional lipid-reserve levels (Figure 2.3). Accordingly, my results generally are consistent with the Spring Condition Hypothesis and indicate that a large portion of the continental scaup population potentially is affected by the factor(s) causing the observed low levels of lipid reserves in females throughout the upper-Midwest.

Lovvorn and Barzen (1988) defined stress as "... a situation when demands of one event (physiological, behavioral, or otherwise) are great enough to interfere with desirable allocation of resources to other processes." Northern spring-stopover areas are important for accumulation and maintenance of lipid reserves subsequently used by breeding scaup, and females should be gaining lipid reserves in the upper-Midwest (Afton and Ankney 1991, Anteau and Afton 2004). Females currently are catabolizing lipids (Chapter 4) and have low lipid reserve levels throughout the upper-Midwest. Forage quality (nutritional value of forage consumed) of scaup in the upper-Midwest currently is low and probably has declined from historical values (Anteau and Afton 2006, Chapter 8). Moreover, scaup likely are spending more time searching for food (within and between wetlands) than they did historically (Chapter 9). Therefore, nutritional demands of female scaup during spring in the upper-Midwest (e.g., migration, courtship and pair formation, contour feather molt, and ovarian follicle development; Alisauskas and Ankney 1992, Anteau and Afton 2004) probably are interfering with the accumulation of nutrient reserves for breeding. Together, all of these results indicate that females currently are nutritionally stressed during spring migration.

Females in IAPP, MOR, and Minnesota Glaciated Plains (MNGP) generally had lower body masses than other regions; however, lipid reserves of these regions were similar to other regions. These differences in responses of body mass and lipid reserves are likely due to females in IAPP, MOR, and MNGP generally having lower protein and mineral reserves than other northerly regions (Figures 2.3, 2.4). As reported for lesser snow geese (*Chen caerulescens caerulescens*; Alisauskas 1988), protein and mineral reserves of female scaup generally increase with latitude of collection sites during spring

migration (Anteau 2002; this study). Accordingly, latitude also should be considered as an interacting factor when body mass is being used as an index for lipid reserves during spring migration.

The Spring Condition Hypothesis

Esler et al. (2001) reported that female scaup with non-developed ovaries in spring had smaller lipid and protein reserves than did those that had initiated rapid ovarian follicle development, which is consistent with a nutrient-reserve threshold that individuals must exceed before the initiation of ovarian follicle development (Reynolds 1972). Therefore, females arriving on breeding areas with small lipid reserves may be unable to quickly exceed their nutrient-reserve threshold and thus have decreased breeding propensities or must spend more time foraging on breeding areas prior to laying eggs (*cf.* Afton and Anderson 2001). However, little is known about the early stages of ovarian follicle development in waterfowl. In domestic fowl, this process begins more than 60 days before the initiation of rapid follicle development (Bluhm 1992). Based on 60-day early follicle development period, 6-day rapid follicle development (prior to laying; Alisauskas and Ankney 1992), and average nest initiation dates (Afton 1984, Austin et al. 1998, Brook 2002, Koons and Rotella 2003), scaup should be initiating early ovarian follicle development in early to mid-April, while migrating through the upper-Midwest. Unfortunately, it is not known at which stage of follicle development a nutrient threshold initiates or regulates the process. It is possible that nutritional stress during migration may delay nest initiation or decrease nesting propensity regardless of female body condition upon arrival on breeding areas.

Scaup currently are nesting markedly later than did those historically (Koons 2001, Brook 2002, Koons and Rotella 2003); whereas, other bird species, including some waterfowl, currently are nesting as much as 10 days earlier apparently due to global climate change effects (MacInnes et al. 1990, Crick et al. 1997, Wuethrich 2000, Both and Visser 2001). Nest success, duckling survival, and post-fledging survival generally are negatively correlated with nest initiation dates among northern nesting waterfowl (Rohwer 1992, Dzus and Clark 1998, Guyn and Clark 1999, Blums et al. 2002). Moreover, clutch size of scaup declines seasonally (Afton 1984, Esler et al. 2001, Brook 2002). Accordingly, females that arrive on breeding areas in poor body condition and do breed, probably nest later (Reynolds 1972, Esler et al. 2001) and concomitantly fledge fewer young. Alisauskas (2002) reported that body condition of lesser snow geese in spring was positively related to age ratios (immature/adult) later that fall, providing strong support that spring body condition is an important determinant of recruitment.

Female scaup arriving to breed in southwestern Manitoba in 2000 and 2001 were in poorer body condition than were those historically (Anteau 2002, Anteau and Afton 2004). Based on my results, I predict that females currently migrating to many northern breeding areas are arriving in poor body condition, arriving late, or not at all, because they have low lipid-reserve levels and are catabolizing lipid reserves in the northern portions of my study area (Chapter 4). If females nesting in the Boreal Forest are arriving in poor body condition, delays in nest initiation should have a greater effect on recruitment there than for those nesting in the Prairie Parklands because less time is available between arrival and egg laying to acquire nutrients for breeding in the Boreal Forest (Austin et al. 1998, Afton and Anderson 2001). Notably, Afton and Anderson (2001) reported that the steepest scaup population declines have occurred in the Boreal Forest of western Canada.

The most likely explanation for the observed low lipid reserves of females is reduced availability of preferred scaup foods (e.g., amphipods) on spring stopover areas in

the upper-Midwest (see Anteau and Afton 2006; Strand 2005; Chapters 6, 8, 9, 10).

Numbers of wetlands that scaup use, wetland quality, and amphipod densities currently are low in the upper-Midwest (Dahl 1990, Austin et al. 1998, Chapter 6). Aggregate percentage of amphipods in scaup diets were lower throughout Minnesota and Iowa than that had been reported historically, and scaup were consuming less food (49 – 52% dry mass) throughout the upper-Midwest than they did historically (Anteau and Afton 2006, Chapter 8).

Increased incidences of parasites or increases in environmental contaminants also could be contributing to the observed lipid catabolism. However, the abundance of intestinal cestodes were weakly positive correlated with lipid reserves or body mass in scaup during spring and fall migration (Vest 2002, Appendix D). Lipid reserves of scaup declined with increasing hepatic cadmium levels; however, current levels of cadmium contamination in scaup are too low in the Mississippi Flyway to explain the observed losses of lipid reserves of females (Custer et al. 2003, Chapter 5).

Implications for Conservation of Lesser Scaup

Several lines of evidence indicate that amphipods are in low abundance throughout the upper-Midwest and have decreased the ability of scaup to maintain and accumulate lipid reserves during spring migration (Anteau and Afton 2006; Strand 2005; Chapters 4, 5, 6, 8, 10). Conservation activities to stop the loss and degradation of scaup migration habitat and to restore and manage wetlands to increase amphipod densities throughout the upper-Midwest should improve lipid-reserve levels of females and may help reverse the continental population decline. Moreover, my results suggest that Pool 19 and subsequent migration stopover areas currently are critically important for scaup to maintain and

accumulate lipid reserves for migration through the upper-Midwest and to be used subsequently for breeding. Thus, efforts to better understand scaup ecology there and to protect these areas from potential habitat degradation is a priority.

Further tests of the Spring Condition Hypothesis are needed to better understand the scope of impact that the observed decline in lipid reserves of females throughout the upper-Midwest. Specifically, research needs is needed to: (1) examine migration corridors, distances of migration flights, stopover times, and breeding affinities of female scaup during spring migration; (2) understand at what point (if any) a nutrient reserve threshold initiates or regulates ovarian follicle development in female scaup; (3) examine nutrient-reserve levels and lipid metabolism of female scaup migrating through the Prairie Pothole and Parkland Regions of Canada; and (4) examine breeding propensity of female scaup.

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CHAPTER 3: ESTIMATING CHANGES IN LIPID RESERVES OF LESSER SCAUP FROM PLASMA-LIPID METABOLITES

INTRODUCTION

Nutrient reserves acquired during migration are important determinants of survival and influence reproductive success in some birds (Afton and Ankney 1991, Alisauskas and Ankney 1992, Pace and Afton 1999, Lindstrom 2003, Anteau and Afton 2004). Information on whether an individual is catabolizing or accumulating lipid reserves would be helpful in making inferences about habitat quality on specific migration stopover areas. However, traditional measures of body condition (e.g., size-adjusted body mass and lipid, protein, and mineral reserves) are influenced by a combination of environmental factors at collection sites and previous stopover areas (Anteau and Afton 2004). For example, birds collected from 2 stopover sites could have similar body mass and lipid reserves, but in 1 site they could be accumulating lipid reserves whereas in the other they could be catabolizing lipid reserves (Williams et al. 1999).

Plasma-lipid metabolites (triglycerides, glycerol, and β -hydroxybutyrate; hereafter TRIG, GLY, and BOHB, respectively) may be a useful tool for predicting lipid accumulation or catabolism in wild birds (Jenni-Eiermann and Jenni 1994, Williams et al. 1999). Fatty acids are the predominant form of energy storage in birds, and are composed of TRIG and GLY (Ramenofsky 1990). TRIG is utilized for energy through β -oxidation (catabolism of lipids), and GLY is used for storage and transport of TRIG (Ramenofsky 1990). Therefore, TRIG concentration is positively correlated with lipid deposition into adipose tissue; whereas, GLY is released into plasma when lipids are oxidized, but also may be released during deposition, potentially resulting in a “U”-

shaped curve in relation to lipid change (Ramenofsky 1990, Guglielmo et al. 2005).

BOHB is a ketone body and a byproduct of β -oxidation, thus it is positively correlated with rates of lipid catabolism (Ramenofsky 1990).

Analyses of the relationships between lipid reserve changes and TRIG, GLY, and BOHB generally have been conducted by (1) examining metabolite levels of captive birds in relation to changes in body mass (as an index for changes in lipid reserves; e.g., Le Maho et al. 1981, Boismenu et al. 1992, Jenni-Eiermann and Jenni 1994, Williams et al. 1999), (2) examining differences in metabolites of wild birds between habitats of differing quality and a single measure of body mass (e.g., Guglielmo et al. 2002, 2005), or (3) examining differences in metabolites of wild birds in relation to daily feeding patterns (Jenni and Jenni-Eiermann 1996). An evaluation of how plasma-lipid metabolites predict changes in lipid reserves of wild migratory birds would be useful because captive and wild birds have differing activity levels. I developed an index for detecting changes in lipid reserves (daily lipid change; hereafter DLC) in wild lesser scaup (*Aythya affinis*; hereafter scaup) by regressing plasma-lipid metabolite levels (TRIG, GLY, and BOHB) to known 1-day mass changes during spring migration.

METHODS

Study Area

In springs 2004 and 2005, I captured and banded wild scaup at Pool 19 of the Mississippi River between Hamilton and Dallas City, Illinois and Keokuk and Ft. Madison, Iowa as part of a larger study. Pool 19 is used extensively by scaup during spring migration and has been described in detail by Thompson (1973).

Capture, Recapture, and Bleeding

I captured scaup using swim-in and dive-in traps (Haramis et al. 1982) baited with corn. Captured scaup were held for approximately 2 hours (to minimize ingesta contribution to body mass), weighed (± 1 g), banded, and released. I excluded birds from this experiment that had noticeable amounts of food present in their crop, as determined by palpation.

I extracted 1 ml of blood from the brachial vein (25 gauge needle) of recaptured scaup soon after removal from trap. I transferred blood slowly into a 1.5 ml heparinized micro-centrifuge tube, and placed it in a cooler (not in direct contact with ice). I held all recaptured scaup for approximately 2 hours before they were reweighed (± 1 g) and released. Blood samples were centrifuged at 6,000 rpm (2,000 x G) for 5 – 10 minutes, and plasma was transferred into new vial and frozen within 2 – 3 hours of collection (-20°C ; Guglielmo et al. 2002). I recaptured, weighed, and collected blood from 111 different individuals, with 12 individuals recaptured 2 or more times.

Plasma-Lipid Metabolite Assays

Total triglycerides (TRIG + GLY) and GLY were measured by endpoint assay (Williams et al. 1999, Guglielmo et al. 2002; Appendix A). TRIG was calculated by subtracting GLY from total triglycerides (Williams et al. 1999, Guglielmo et al. 2002). BOHB was measured by kinetic assay (Guglielmo et al. 2005, Appendix B). All plasma-lipid metabolite assays were read on a microplate spectrophotometer (Thermo Lab Systems, Model 1500, Milford, Massachusetts; Williams et al. 1999, Guglielmo et al. 2002).

Statistical Analysis

I limited my analysis to birds recaptured within 1 day of previous capture (22 individuals [males]) because plasma-lipid metabolite levels change rapidly (Jenni and Jenni-Eiermann 1996) as do rates of scaup mass change (based on multiple captures of the same intervals; Appendix C). I calculated the mass change for each individual (recapture mass – mass from previous day). One individual that was recaptured twice (gained mass one day, lost the other); the latter observation was excluded to insure independence of samples.

I used a multiple regression to evaluate how well levels of TRIG, GLY, and BOHB predicted mass change of scaup (PROC REG; SAS Institute 2002). I initially included both linear and quadratic terms for GLY and examined residuals to determine whether transformations of the data were necessary; I subsequently natural-log-transformed (ln) BOHB because the relationship between non-transformed BOHB and DLC was curve-linear. I selected a final model using backwards elimination procedures (*alpha* 0.05; Zar 1996).

RESULTS

One-day mass changes ranged from -68 to 61 g, and 45% of scaup gained mass. The plasma-lipid metabolites had the following ranges (mmol*L⁻¹): GLY (0.263 – 2.303), TRIG (0.391 – 3.775), and BOHB (0.128 – 2.064).

TRIG and BOHB levels predicted mass change well ($R^2 = 0.75$; $F_{2,19} = 28.85$, $P < 0.001$). TRIG was positively correlated with mass change (estimate = 11.82, $t_{1,19} = 2.36$, $P = 0.029$), whereas, BOHB (ln) was negatively correlated with mass change (estimate = -28.65, $t_{1,19} = -4.29$, $P < 0.001$). Linear or quadratic terms for GLY were not

significant ($P > 0.05$) and were excluded. TRIG and the ln of BOHB appeared to be linearly related to mass change (Figure 3.1). Therefore, the final regression equation was as follows.

$$\text{DLC} = -54.49 + 11.82(\text{TRIG}) - 28.65(\text{BOHB}_{\ln})$$

DISCUSSION

My results for TRIG and BOHB generally were consistent with those from captive experiments on western sandpipers (*Calidris mauri*) and garden warblers (*Sylvia borin*; Jenni-Eiermann and Jenni 1994, Williams et al. 1999). Both of these experiments found that GLY increased with losses in body mass, whereas I found no evidence of a relationship between GLY and daily mass change. In domestic geese and captive greater snow geese (*Chen caerulescens atlantica*), BOHB was inversely correlated to body mass until lipid reserves were completely catabolized during starvation (Le Maho et al. 1981, Boismenu et al. 1992). Thus, captive studies may provide adequate reference to evaluate relationships of TRIG and BOHB with mass change for interpretations to wild bird populations.

Studies examining patterns of plasma-lipid metabolites among wild birds found that GLY did not vary with time since nightly fast or between locations of differing habitat quality (Jenni and Jenni-Eiermann 1996, Guglielmo et al. 2002), which is consistent with my results. GLY may be influenced by activity levels or confounded by some factor(s) that are not controlled in wild studies. Captive experiments and wild studies on the same species would be helpful to examine potential differences associated with activity or other confounding factors in the relationship between plasma-lipid metabolites and changes in lipid reserves.

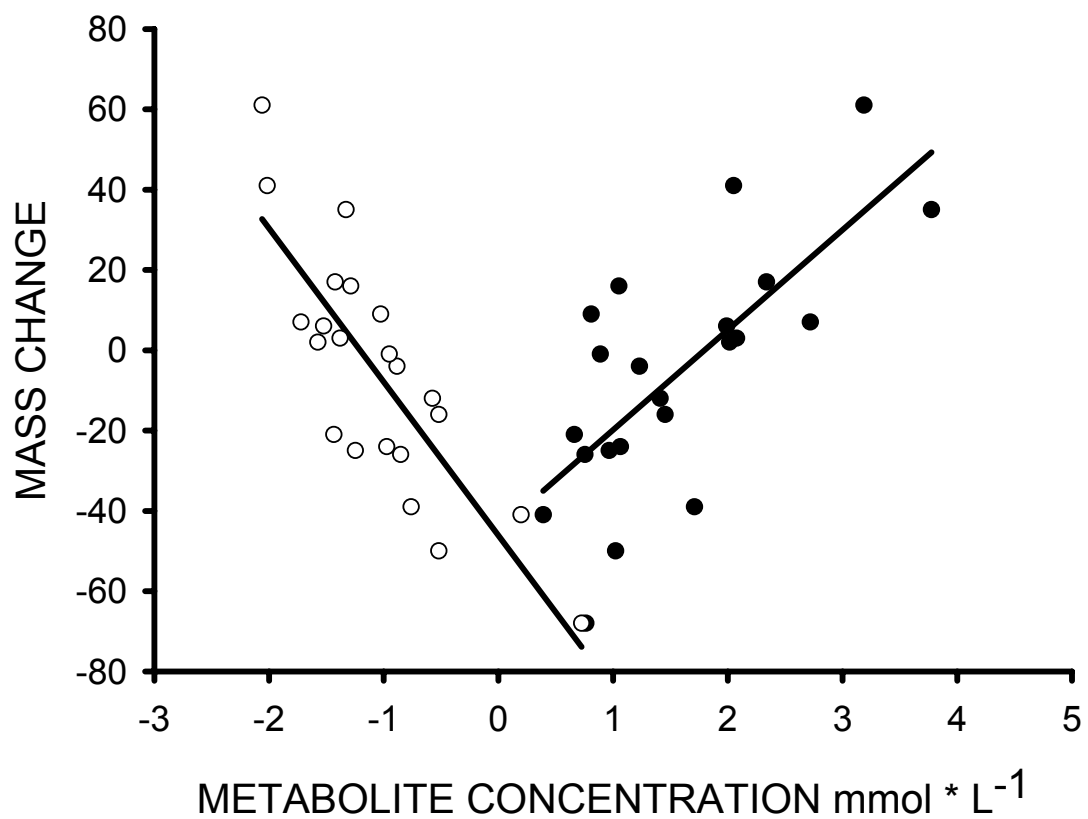


Figure 3.1. Relationships of triglycerides (TRIG) and natural-log β -hydroxybutyrate (BOHB) to 1-day mass changes of lesser scaup staging at Pool 19 of the Mississippi River during spring migration 2004 and 2005. Filled circles represent TRIG and unfilled circles represent BOHB.

Indexing lipid reserves with changes in body mass is problematic when ingesta mass is unknown. Uncontrolled-for changes in ingesta introduce variability into the mass change estimates. In a previous study, where ingesta mass was controlled, 1-day mass change in scaup during fall migration ranged from -15 to +30 g (A. D. Afton, US Geological Survey, unpublished data). My results may have been influenced by ingesta mass because body mass changes were relatively larger (up to 9% of body mass).

My model of TRIG and BOHB predicted 75% of the variation in mass change, despite the potential variability associated with ingesta mass. TRIG was positively correlated with amounts of ingesta (Jenni and Jenni-Eiermann 1996); thus, I assume that changes in ingesta mass were positively correlated to changes in lipid reserves. Therefore, my model should be reliable for predicting whether or not an individual is accumulating or catabolizing lipid reserves and making comparisons of DLC between areas, but probably is less reliable at predicting the actual rate of change in lipid reserves (g per day). Amounts of ingesta could be better controlled in captive study of scaup, through timing of meals and mass measurements or using alternative indexes of lipid reserves (e.g., total body electrical conductivity; Roby 1991).

I was unable to examine potential sexual differences in the relationship between plasma-lipid metabolites and DLC because males were easier to capture. However, males and females probably have a similar relationship between plasma-lipid metabolites and DLC until females initiate rapid ovarian follicle development, when females mobilize large amounts of lipids to reproductive tissue (Ramenofsky 1990).

Lipid metabolite concentrations change rapidly in plasma of birds; thus, mass changes can be predicted within a 2-hour to 2-day period (Jenni and Jenni-Eiermann

1996, Williams et al. 1999). Accordingly, my model should be valuable in assessing whether scaup are accumulating or catabolizing lipid reserves at particular stopover areas during migration based on concentrations of TRIG and BOHB. Such efforts would be valuable for identifying areas of high and low habitat quality specifically relative to the nutritional needs of migrating scaup.

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CHAPTER 4: ARE FEMALE LESSER SCAUP CATABOLIZING LIPID RESERVES DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST? A FURTHER TEST OF THE SPRING CONDITION HYPOTHESIS

INTRODUCTION

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly since 1978 (Austin et al. 1998, Afton and Anderson 2001); population estimates were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. Recruitment of lesser scaup apparently has declined since 1978, and female survival rates have declined relative to that of males (Afton and Anderson 2001). The segment of the scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through the upper-Midwest comprises a major component of the continental population and likely is experiencing the largest decline in numbers (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup (Afton 1984, Afton and Ankney 1991, Anteau 2002, Anteau and Afton 2004). The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas in lower body condition than in the past (Afton and Anderson 2001). Female scaup currently are migrating throughout the upper-Midwest and arriving to breed in southwestern Manitoba with fewer lipid reserves than did those historically (Anteau 2002, Anteau and Afton 2004, Chapter 2). Moreover,

females currently have markedly fewer lipid reserves throughout the upper-Midwest than do those on stopover areas in western Illinois, suggesting that females are catabolizing lipid reserves somewhere between western Illinois and northwestern Minnesota (Anteau and Afton 2004, Chapter 2).

Traditional measures of body condition (e.g., size-adjusted body mass and lipid, protein, and mineral reserves) of scaup likely are influenced by a combination of environmental factors at specific collection sites and at preceding migration stopover areas (Anteau and Afton 2004). For example, birds collected from 2 sites could have similar body mass and lipid reserves, but in they could be accumulating lipid reserves at 1 site and catabolizing lipid reserves at the other (Williams et al. 1999).

An assessment of where scaup are accumulating or catabolizing lipid reserves throughout the upper-Midwest is needed to further test and determine the scope of the Spring Condition Hypothesis. Specifically, areas where scaup are catabolizing lipid reserves need to be identified to help conservation activities aimed at population recovery. Scaup may be catabolizing lipid reserves in one area and then accumulating lipid reserves thereafter. Alternatively, scaup may be accumulating or catabolizing lipid reserves throughout the upper-Midwest.

Plasma-lipid metabolites (triglyceride and β -hydroxybutyrate; hereafter TRIG and BOHB, respectively) can predict daily lipid change (DLC) in scaup during spring migration (Chapter 3). I examined DLC of female scaup collected in western Illinois and throughout the upper-Midwest during spring migration to identify where females are accumulating or catabolizing lipid reserves.

METHODS

Study Area

My study area included Pool 19 of the Mississippi River (Figure 4.1; between Hamilton and Niota, IL; hereafter Pool 19). Pool 19 is extensively used by scaup during spring migration and has been described in detail by Thompson (1973).

My study area also included the Prairie Pothole Region in Iowa, Minnesota, and North Dakota (Figure 4.1), which comprises the most important spring migration stopover areas for scaup in the upper-Midwest, based on observations of wildlife biologists and managers, band-recovery data, sightings of color-marked scaup, and aerial surveys in spring (Low 1941, Afton and Hier 1985; Afton et al. 1991; Pace and Afton 1999; Minnesota Department of Natural Resources, unpublished data; North Dakota Game and Fish Department, unpublished data). I stratified the 3-state area into 7 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 4.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

Fixed collection sites.-In 2004 and 2005, I attempted to collect 25 females annually at Pool 19 to reference DLC of females prior to migrating through the upper-Midwest. I also attempted to collect 15 females from each of three fixed sites annually in Northwestern Minnesota (NWMN; Agassiz National Wildlife Refuge and Thief Lake and Roseau River Wildlife Management Areas) for another study (Chapter 2).

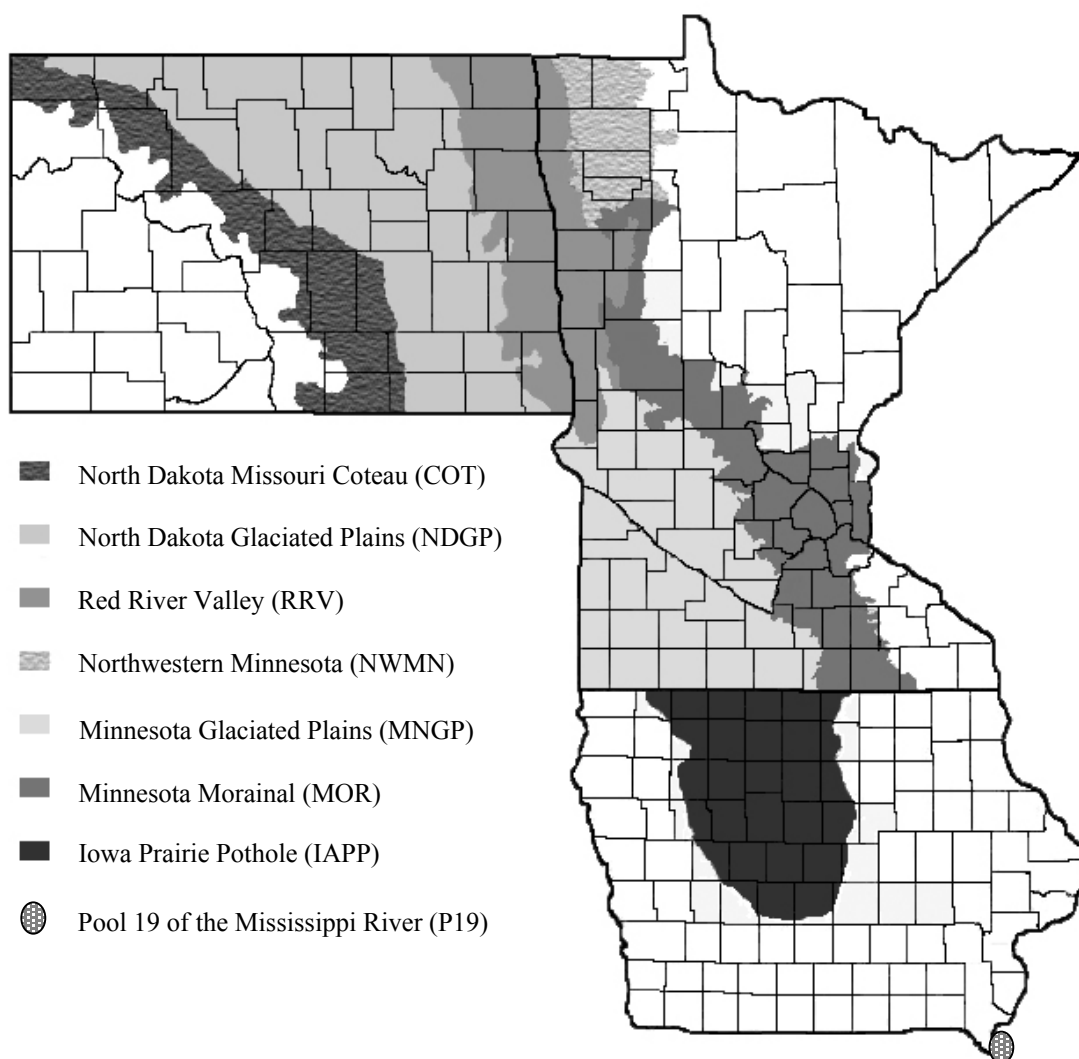


Figure 4.1. Map of the study area depicting 7 eco-physiographic regions for lesser scaup collections during spring migration in the upper-Midwest, 2004 – 2005. Areas in white were not sampled.

Random site selection.-I used constrained-random sampling techniques to select collection sites in all other regions. I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 4.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck North Dakota, unpublished data; S. Piepgras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or permanent wetlands. I then allocated numbers of collection sites among the 6 regions (3 to 6 sites per region; Table 4.1) based on region size and number of candidate townships available (Table 4.1, Figure 4.1). Each region was divided into equal-size sub-regions based on latitude, such that there was 1 collection site per sub-region each year (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 collection sites for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 4.1).

Random collection sites.-Each collection site (27,972 ha) was comprised of three 36-square-mile townships in order to insure adequate collection opportunities; however, in some instances (15% of townships where collections occurred), I randomly selected replacement townships because the initial selected township no longer had suitable scaup habitat (semipermanent or permanent wetlands) or had little or no current scaup use. I further constrained township selection so that the centrum of the second and third

Table 4.1. Regions, years, dates, and numbers of female lesser scaup (N) collected during spring migration in the upper-Midwest; including numbers collection sites (S) and numbers of candidate townships (T) for random selection of collection sites.

Region	Year	Dates	N	S	T
Iowa Prairie Pothole	2004	6 - 9 April	26	3	43 ^a
	2005	30 March – 4 April	22	3	
Minnesota Morainal	2004	10 - 15 April	12	4	348 ^b
	2005	8 - 16 April	30	4	
Minnesota Glaciated Plains	2004	8 - 19 April	30	4	285 ^b
	2005	10 - 15 April	33	4	
Northwestern Minnesota ^c	2004	4 - 13 May	44	3	n/a
	2005	23 - 28 April	33	3	
Red River Valley	2004	24 April - 2 May	16	3	66 ^b
	2005	17 - 21 April	25	3	
North Dakota Glaciated Plains	2004	20 April – 11 May	44	6	364 ^b
	2005	9 April - 2 May	63	6	
North Dakota Missouri Coteau	2004	15 - 22 April	27	3	208 ^b
	2005	7 April - 1 May	34	3	

^a Townships that contain at least 200 hectares total of semipermanent and permanent.

^b Townships that contain at least 200 hectares of semipermanent wetlands.

^c Fixed collection sites (same each year – see methods).

townships selected were within 50 km of the centrum of the first randomly selected township, to minimize travel by field crews. I attempted to collect 10 females from each collection site. I randomly selected new townships annually within each sub-region, from the list of candidate townships, to maximize representation of spatial variability in nutrient reserves of scaup.

Collection of Specimens

I collected female scaup randomly with a shotgun, without the use of decoys to avoid associated biases (Pace and Afton 1999); collections were conducted exactly as Afton et al. (1991) and Anteau and Afton (2004, 2006). In all regions, I attempted to collect females that were feeding during daylight hours (except at Pool 19). At Pool 19, I used a spotlight to collect females at night. I generally timed collections to occur during the middle of migration, coinciding with relatively large numbers of migrating scaup present on each collection site. I collected 459 female scaup with from across the upper-Midwest study in springs 2004 and 2005. At Pool 19, I also collected 19 and 25 female scaup in springs (March 21 – 27) 2004 and 2005, respectively.

Bleeding and Blood Handling

Immediately after specimens were collected, I took 1.5 ml of blood by cardiac puncture using a 3.8-cm-20-gauge needle. I transferred blood slowly into 1.5 ml heparinized micro-centrifuge tube and placed the filled tube in a cooler (not in direct contact with ice). Blood samples were centrifuged at 6,000 rpm (2,000 x G) for 5 to 10 minutes and plasma transferred into new vial within 2 – 3 hours of collection; plasma samples were frozen after returning from the field in the evening (-20°C; Guglielmo et al. 2002). In the laboratory, I conducted assays of TRIG and BOHB exactly as in Chapter 3.

Statistical Analyses

Twenty plasma samples were excluded from the dataset because they had exceptionally high levels of TRIG and BOHB suggesting problems with one or both metabolites (e.g., hemolysis prior to centrifuging; see Morris et al. 2002). Thus, I analyzed plasma-lipid metabolite data from 439 female scaup collected from across the upper-Midwest (Table 4.1) and 44 females collected from Pool 19. For each individual, I indexed DLC with the equation provided in Chapter 3.

I used analysis of variance (PROC MIXED; SAS Institute 2002) to test for regional variation in DLC, with region, year, and sub-region within region as class variables; I included data from Pool 19 as a region. I used t-tests within the LSMEANS statement to determine if regional estimates of DLC differed from zero (SAS Institute 2002). I also used the PDMIX800 macro (Saxton 1998) to get Tukey-Kramer adjusted least-square mean letter groupings for each region and year (if significant at *alpha* 0.05).

RESULTS

TRIG concentrations ($\text{mmol}\cdot\text{L}^{-1}$) for females collected at Pool 19 and in the upper-Midwest ranged from 0.196 – 6.927, and BOHB concentrations ($\text{mmol}\cdot\text{L}^{-1}$) ranged from 0.151 – 3.849.

Mean DLC varied among regions ($F_{7,458} = 12.56, P < 0.001$), among sub-regions within regions ($F_{16,458} = 2.59, P < 0.001$), and between years ($F_{1,458} = 12.83, P < 0.001$). Mean DLC differed from zero in all regions (all P s < 0.05); mean DLC of females were below zero in all regions of Iowa, Minnesota, and North Dakota (Figure 4.2). However, DLC was 16.8 g at Pool 19 and higher than in any other region (Figure 4.2). DLC was lower in Iowa Prairie Pothole (IAPP; -31.6 g) than in North Dakota Glaciated Plains and

Minnesota Glaciated Plains (-15.2 and -13.5 g, respectively; Figure 4.2). Overall mean DLC was lower in 2004 (-21.3 g, SE = 1.99) than in 2005 (-11.8 g, SE = 1.73).

DISCUSSION

Potential Sources of Variability and Error

Some levels of TRIG and BOHB (35 [7%] and 10 [2%], respectively) from collected scaup exceeded those in my calibrating model used to predict DLC (see Chapter 3). Exclusion of these observations could bias results because these observations represent extreme changes in lipid reserves. Conversely, if the relationship between metabolites and DLC and is not consistent at higher values of metabolite, the inclusion of these observations could decrease the accuracy estimates of DLC, however, there was no evidence that the relationships of TRIG and BOHB were not linear in the predictive model (Chapter 3). Thus, I included these observations in my model.

The calibration model I used to index DLC from TRIG and BOHB is reliable for predicting whether an individual is accumulating or catabolizing lipid reserves and indexing the rate of change in lipid reserves for relative comparisons among regions, but probably is less reliable at predicting the actual rate of DLC (g per day; Chapter 3). Accordingly, I limit further interpretations to whether females are catabolizing or accumulating lipid reserves and make regional comparisons of these indices.

Plasma-lipid metabolites in birds change rapidly (2-hours to 2-days) with energetic needs or surpluses (Jenni and Jenni-Eiermann 1996, Williams, Chapter 3). Scaup collected in the process of digesting food should exhibit a plasma-lipid metabolite profile indicating a high rate of lipid deposition (Jenni and Jenni-Eiermann 1996). Conversely, scaup collected soon after arrival from a long migration flight might have a

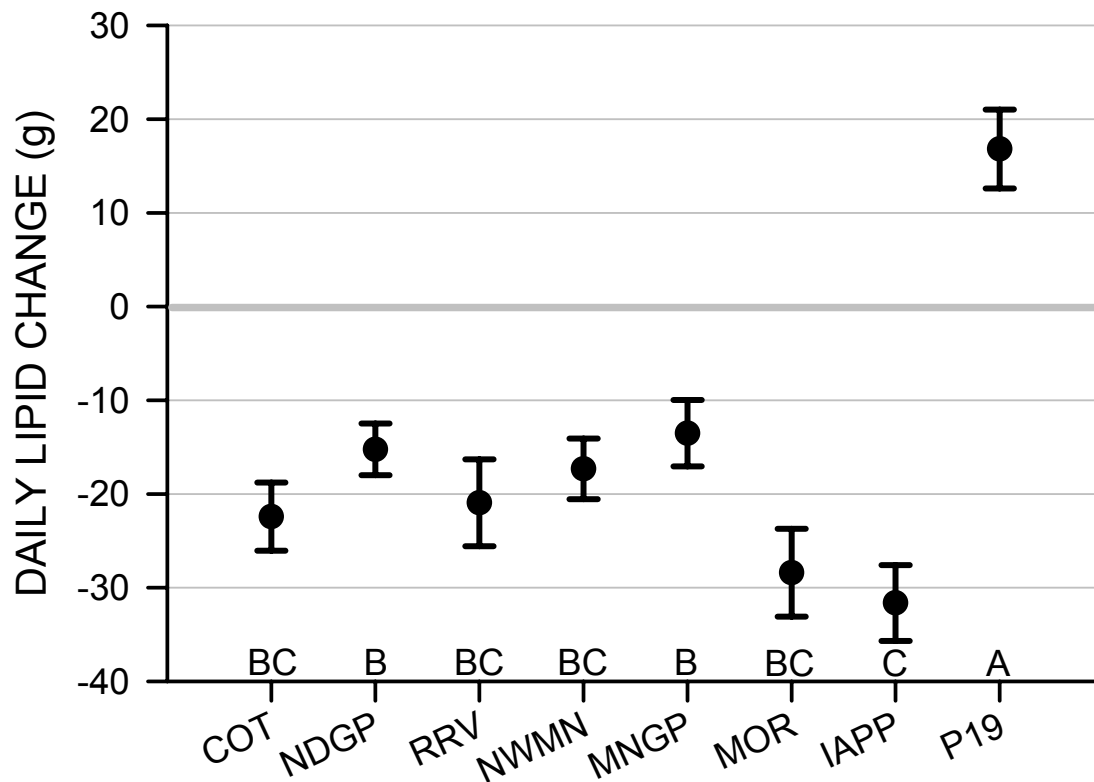


Figure 4.2. Least-square mean daily lipid change (DLC \pm SE) of female lesser scaup ($n = 483$) collected during spring migration 2004 and 2005 by regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole, and P19 = Pool 19). Asterisks indicate difference from zero; capital letters are Tukey-Kramer adjusted mean grouping at $P < 0.05$.

plasma-lipid metabolite profile indicating a high rate of lipid catabolism (Gannes et al. 2001). However, it is unlikely that scaup take long migration flights during spring migration in the upper-Midwest because the middle of spring migration at Pool 19 is approximately 45 days earlier than that in NWMN (only 1000 kilometers to the north; Anteau and Afton 2004). Thus, I conclude that factors relating to diets and activity levels of individuals just prior to collections are sources of variability rather than bias, and such variability should average out with large sample sizes and random collections in my study.

Pool 19

Large numbers of scaup are present at Pool 19 for a relatively long time (about 4 weeks) during spring migration (Thompson 1973, Havera 1999). Food resources of scaup currently are abundant at Pool 19 (Anteau 2002, Anteau and Afton 2004, M. J. Anteau, personal observations), and females currently have high body masses there (Anteau and Afton 2004, Chapter 2). My results were consistent with expectations that females collected at Pool 19 would be accumulating lipid reserves. However, I collected females at night and they may have been fasting because few had diet samples in their upper-digestive tract (15% of females collected 2000 – 2005; M. J. Anteau, Louisiana State University, unpublished data). Thus, if females were collected during the day, as they were for the rest of the collections, their TRIG and BOHB levels may have indicated even higher rates of lipid accumulation (Jenni and Jenni-Eiermann 1996).

Upper-Midwest

Anteau and Afton (2004) speculated that decreases in lipid reserves of female scaup in NWMN and southwestern Manitoba were indicative of a landscape-scale decline

in lipid reserves. Lipid reserves of females currently are low throughout the upper-Midwest (Chapter 2). My results here indicate that the observed low lipid reserves are the result of catabolism of lipids throughout the upper-Midwest and thus are consistent with the Spring Condition Hypothesis. Moreover, my results suggest that the large portion of the continental population that migrates through the upper Midwest (Bellrose 1980, Afton and Anderson 2001) likely is affected by the factor(s) causing females to catabolized lipid reserves there. Furthermore, Pool 19 and perhaps stopover areas to the south currently must be critically important for female scaup to accumulate lipid reserves for migration and breeding.

Scaup currently are nesting later than those historically on some breeding areas (Koons 2001, Brook 2002, Koons and Rotella 2003), whereas, other bird species, including some waterfowl, are nesting as much as 10 days earlier apparently due to global climate change effects (MacInnes et al. 1990, Crick et al. 1997, Wuethrich 2000, Both and Visser 2001). Nest success, duckling survival, and post-fledging survival generally are negatively correlated with nest initiation dates among northern nesting waterfowl (Rohwer 1992, Dzus and Clark 1998, Guyn and Clark 1999, Blums et al. 2002) and clutch size of scaup declines seasonally (Afton 1984, Esler et al. 2001, Brook 2002). Accordingly, female scaup that arrive on breeding areas in poor body condition and do breed, probably nest later (Reynolds 1972, Esler et al. 2001) and concomitantly fledge fewer young. Alisauskas (2002) reported that body condition of lesser snow geese (*Chen caerulescens caerulescens*) in spring was positively related to age ratios (immature/adult) later that fall, providing strong evidence that spring body condition is an important determinant of recruitment.

Female scaup arriving to breed in southwestern Manitoba in 2000 and 2001 were in poorer body condition than were those historically (Anteau 2002, Anteau and Afton 2004). My results suggest that females currently migrating to many northern breeding areas are arriving in poor body condition, arriving late, or not at all, because they have low reserve levels in the northern portions of my study area and probably are unable to accumulate lipid reserves there (Chapter 2). If females nesting in the Boreal Forest are arriving in poor body condition, delays in nest initiation should have a greater effect on recruitment than for those nesting in the Prairie Parklands because less time is available between arrival and egg laying to acquire nutrients for breeding in the Boreal Forest (Austin et al. 1998, Afton and Anderson 2001). Notably, Afton and Anderson (2001) reported that the steepest scaup population declines have occurred in the western Canadian Boreal Forest.

The most likely explanation for the observed widespread catabolism of lipid reserves by females is reduced availability of quality scaup food resources (e.g., amphipods) on spring stopover areas in the upper-Midwest (see Anteau and Afton 2006; Strand 2005; Chapters 6, 8, 9, 10). Numbers of wetlands that scaup use, wetland quality, and amphipod densities apparently have declined in the upper-Midwest (Dahl 1990, Austin et al. 1998, Chapter 6). Aggregate percentage of amphipods in scaup diets were lower throughout Minnesota and Iowa than that reported historically, and scaup were consuming 49 – 52% less food (dry mass of food) throughout the upper-Midwest than they did historically (Anteau and Afton 2006, Chapter 8). Moreover, it appears that amphipod densities currently are so low that scaup have to spend relatively more energy than that historically to procure amphipods throughout the upper-Midwest (Chapter 9).

Increased incidences of parasites or increases in environmental contaminants also could be contributing to lipid catabolism. However, the abundance of intestinal cestodes was positively correlated with lipid reserves or body mass in scaup during spring and fall migration (Vest 2002, Appendix D). Lipid reserves of scaup were negatively correlated with hepatic cadmium levels; however, current levels of cadmium contamination in scaup probably are too low in the Mississippi Flyway to explain the observed losses of lipid reserves of females (Custer et al. 2003, Chapter 5).

Scaup principally consume macroinvertebrate prey (75 – 98%) during spring migration (Afton et al. 1991, Anteau and Afton 2006, Chapter 8). Macroinvertebrate densities likely vary annually in a given wetland, in response to varying water regimes and winter severity (Euliss et al. 1997). Overall densities of *Hyalella azteca* (amphipods) in semipermanent and permanent wetlands across the upper-Midwest were higher in 2005 than those in 2004, which may have contributed to why scaup catabolized 44% fewer lipid reserves in 2005 than in 2004.

Northern spring stopover areas in the upper-Midwest are critical for accumulation and maintenance of lipid reserves used by breeding female scaup (Afton and Ankney 1991, Anteau and Afton 2004). Evaluating regional patterns in DLC should provide information about habitat quality for scaup because of the rapid turnover rates of the metabolites. Further, regional mean DLC can indicate which regions are in greatest need of conservation activities directed at improving migration habitat for scaup in the upper-Midwest. Based on results here, I conclude that conservation activities are needed throughout the upper-Midwest, but especially in IAPP and MOR (see Figure 4.2). Furthermore, conservation should be targeted to areas where scaup use of wetlands is

high and rates of lipid catabolism also are high (Chapter 9). Conservation activities could be more optimally prioritized if information on stopover times of individuals and numbers of scaup using each region of the upper-Midwest were available. For example, wetlands in MOR had lower probabilities of use by scaup than did those in the rest of the upper-Midwest (Chapter 9); it is unclear if this was due to low food availability/quality which caused individuals to spend less time there, or whether MOR is on the fringe of the spring migration corridor, thus receiving use by a smaller proportion of scaup migrating through the upper-Midwest (Chapter 9).

Implications for Conservation of Lesser Scaup

Several lines of evidence indicate that amphipod densities currently are low throughout the upper-Midwest and are preventing scaup from maintaining and accumulating lipid reserves during spring migration (Anteau and Afton 2006; Strand 2005; Chapters 2, 5, 6, 8, 10). Conservation activities to stop loss and degradation of scaup migration habitat and to restore and manage wetlands to improve amphipod abundances throughout the upper-Midwest should improve lipid-reserve levels of females and may help reverse the continental population decline. Moreover, Pool 19 and other preceding stopover areas currently are critically important stopover area for scaup to accumulate lipid reserves used for migration through the upper-Midwest and for breeding. Efforts to better understand scaup ecology there and to protect these areas from potential habitat degradation clearly are a priority.

Finally, further tests the Spring Condition Hypothesis are needed to understand the impact that the observed catabolism of lipid reserves by females migrating through the upper-Midwest has on a continental scale. Specifically, research is needed to: (1) examine

migration corridors, distances of individual migration flights, stopover times, and breeding affinities of female scaup during spring migration; (2) examine lipid metabolism and nutrient-reserve levels of female scaup migrating through the Prairie Pothole and Parkland regions of Canada; and (3) examine breeding propensity for female scaup.

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CHAPTER 5: INFLUENCES OF CADMIUM, MERCURY, AND SELENIUM ON NUTRIENT RESERVES OF FEMALE LESSER SCAUP DURING WINTER AND SPRING MIGRATION

INTRODUCTION

Declines in body condition have been linked to increasing levels of cadmium, mercury, and selenium in some captive and wild aquatic birds (e.g., Hoffman et al. 1992; Scheuhammer et al. 1998; Hoffman et al. 1998; Wayland et al. 2001, 2002, 2003).

Potential effects of trace elements on body condition of female ducks could be critical during spring migration because individuals are experiencing energetically costly events, such as migration, accumulating nutrient reserves for breeding, courtship and pair formation, contour feather molt, and ovarian follicle development (Afton and Ankney 1991, Alisauskas and Ankney 1992, Austin et al. 1998, Anteau and Afton 2004).

Trace-element contaminants may have direct and indirect effects on various aspects of a bird's physiology. Non-linear relationships may exist between trace elements and body condition; moreover, interactions between trace elements also may occur. Selenium is an essential nutrient (Puls 1994), but is toxic at high levels (Heinz 1996, Stanley et al. 1996, Hoffman 2002, Spallholz and Hoffman 2002). Thus, the relationship between selenium and body condition should be positive at lower concentrations of selenium and negative at higher concentrations (quadratic relationship). The presence of selenium may reduce deleterious effects of mercury (Heinz 1996, Heinz and Hoffman 1998, Scheuhammer et al. 1998).

An evaluation of trace-element contaminant levels and their affects on nutrient reserves is a priority for lesser scaup (*Aythya affinis*; Custer and Custer 2000, Custer et al. 2003, Anteau and Afton 2004). Elevated trace-element contaminants could increase

adult mortality or decrease egg viability and thus may be a factor in the recent combined continental population decline of greater and lesser scaup (Austin et al. 2000, Afton and Anderson 2001). Elevated trace-element contaminants have been found in lesser scaup (hereafter scaup) during spring migration in the Mississippi Flyway and the Great Lakes (Custer and Custer 2000, Custer et al. 2000, Custer et al. 2003). Anteau and Afton (2004) speculated that trace-element contaminants might be indirectly affecting scaup populations by inhibiting females from accumulating nutrient reserves during spring migration, ultimately decreasing reproductive success (see the Spring Condition Hypothesis; Afton and Anderson 2001). Information concerning effects of trace-element contaminants on the accumulation of nutrient reserves during spring migration, when females potentially are nutritionally stressed (Anteau 2002, Anteau and Afton 2004, Chapter 2), would be informative for directing conservation efforts for this species. Accordingly, I investigated the influence of hepatic cadmium, mercury, and selenium ($\mu\text{g/g}$ dry weight [dw]) on nutrient reserves (lipid, protein, and mineral) of female scaup during winter and spring migration in the Mississippi Flyway.

METHODS

Study Area, Collection of Specimens, and Body Composition Analyses

I used steel shot to collect scaup at four locations: (1) southern Louisiana (hereafter Louisiana), (2) Pool 19 of the Mississippi River between Hamilton and Niota, Illinois (hereafter Illinois), (3) Northwestern Minnesota (including collection sites at Thief Lake Wildlife Management Area, Agassiz National Wildlife Refuge, and Roseau River Wildlife Management Area; hereafter Minnesota), and (4) on a Prairie-Parkland breeding area west of Erickson, Manitoba (between Sandy Lake and Elphinstone,

Manitoba, and the area 35 km south of these towns; hereafter Manitoba). Detailed descriptions of these locations were provided in Rogers (1964), Thompson (1973), Hohman (1985), Afton et al. (1989), Pace and Afton (1999), and Anteau and Afton (2004). Collections and body composition analyses were described in Anteau (2002) and Anteau and Afton (2004).

Trace-Elements Estimation

Initially, I randomly selected 10 females from scaup collected at each of 4 locations (Louisiana, Illinois, Minnesota, and Manitoba) for trace element estimation (Custer et al. 2003) from specimens collected in 2000 (see Anteau 2002, Anteau and Afton 2004). Subsequently, I randomly selected 10 additional females from each location to improve estimates of trace-element effects. The second set of 40 samples was analyzed by Trace Element Research Laboratory, Texas A&M University using identical protocols as for the first set of 40 samples (Patuxent Analytical Control Facility contract and protocols; see Custer et al. 2003). Thus, my total sample size for this analysis was 80 collected females throughout the Mississippi Flyway (20 per collection location).

I classified trace-element concentrations as background, elevated, or potentially harmful based on available literature. I considered cadmium concentrations background at $< 3 \mu\text{g/g dw}$, elevated at $\geq 3 \mu\text{g/g dw}$, and potentially harmful at $\geq 7 \mu\text{g/g dw}$ (Di Giulio and Scanlon 1984, Scheuhammer 1987, Furness 1996, Custer et al. 2003). I considered mercury concentrations background at $< 3 \mu\text{g/g dw}$ and elevated at $\geq 3 \mu\text{g/g dw}$ (Fimreite 1974, Eisler 1987, Thompson 1996, Custer et al. 2003). Finally, I considered selenium concentrations background at $< 10 \mu\text{g/g dw}$, elevated at $\geq 10 \mu\text{g/g dw}$, and potentially harmful at $\geq 33 \mu\text{g/g dw}$ (Heinz et al. 1989, Heinz 1996).

Statistical Analyses

I first conducted a principal components analysis of the correlation matrix on 4 morphometrics (body length [total length – rectrix length], keel length, wing cord, and tarsus bone; PROC PRINCOMP; SAS Institute 2002). I then used the first principal component (PC1) to index body size (Ankney and Afton 1988, Afton and Ankney 1991). I natural-log-transformed all cadmium, mercury, and selenium concentrations ($\mu\text{g/g dw}$) to meet model assumptions of normality and homogeneity of variance (see Custer et al. 2003). I tested for a collection location effect on trace-element concentrations with a separate analysis of covariance (ANCOVA) for each trace element; I included body size and the concentrations of the other trace elements as covariates (PROC MIXED; SAS Institute 2002). I used backward elimination procedures ($\alpha = 0.05$) to select final models (Zar 1996). If the location effect was retained in the final model, I used the least squares means statement to estimate mean concentrations for each location (PROC MIXED; SAS Institute 2002); I also used the PDMIX800 macro (Saxton 1998) to group similar means for each location. However, overall means were estimated with the solution statement if the location effect was not retained in the final model (intercept model; SAS Institute 2002). Trace-element concentrations are presented as geometric means with a 95% confidence interval (CI; Custer et al. 2003).

The potential for non-linear relationships or interactions between trace elements requires testing *a priori* models based on physiological theory and using a single overall statistical model to test for effects of trace elements on each component of body condition (lipid, protein, and mineral reserves). Accordingly, I used a separate ANCOVA for lipid, protein, and mineral reserves to examine effects of trace-element concentrations

(cadmium, mercury, and selenium) on each nutrient reserve of female scaup while controlling for effects of location, liver mass, and body size (PROC GLM; SAS Institute 2002). I included a selenium-by-mercury interaction and a quadratic term for selenium in my initial models; while testing the quadratic term I used non-log-transformed selenium concentrations. I used backward elimination procedures ($\alpha = 0.05$) to select final models (Zar 1996). For each significant effect of interest (cadmium, mercury, or selenium), I plotted and examined the Type III partial relationship and calculated the Type III partial R^2 of that effect on the response of interest (lipid, protein, or mineral) solely by (1) rerunning the final model without that effect (exporting the response residuals; ANCOVA, PROC GLM; SAS Institute 2002), (2) conducting an analysis with that effect as a response and remaining variables from the final model as predictor variables (exporting the effect residuals; ANCOVA, PROC GLM; SAS Institute 2002), (3) regressing the residuals of the effect on the residuals of the response to calculate the Type III partial R^2 (PROC REG; SAS Institute 2002), and (4) plotting the results with SigmaPlot 8.02 (SPSS Inc., Chicago, IL, USA).

RESULTS

In the principal components analysis, all correlations between morphometrics were positive; eigenvectors of PC1 ranged from 0.303 – 0.568. PC1 accounted for 51% of the observed variation in the morphometrics of female scaup.

Trace-Element Concentrations

Cadmium concentrations varied among locations (Table 5.1; $F_{3,74} = 3.92$; $P = 0.012$) after controlling for body size ($F_{1,74} = 6.38$; $P = 0.014$) and selenium concentration ($F_{1,74} = 50.72$; $P < 0.001$). Cadmium concentrations were higher in

Minnesota and Manitoba than in Louisiana and Illinois (Table 5.1). Overall, 7 of 80 females (9 %) had elevated cadmium levels ($\geq 3 \mu\text{g/g dw}$) and 1 female (1 %) had potentially harmful levels ($\geq 7 \mu\text{g/g dw}$).

Selenium concentrations also varied among locations (Table 5.1; $F_{3,74} = 5.01$; $P = 0.003$) after controlling for body size ($F_{1,74} = 4.32$; $P = 0.041$) and cadmium concentration ($F_{1,74} = 50.72$; $P < 0.001$). Selenium concentrations were higher in Louisiana and Illinois than in Minnesota and Manitoba (Table 5.1). Overall, 39 of 80 females (49 %) had elevated selenium levels ($\geq 10 \mu\text{g/g dw}$), and 2 females (3 %) had potentially harmful levels of selenium ($\geq 33 \mu\text{g/g dw}$).

Mercury concentrations did not differ among collection locations ($P > 0.05$). Mercury concentrations averaged $1.02 \mu\text{g/g dw}$ ($0.90 - 1.16$ 95% CI), with a range of 0.25 to $4.31 \mu\text{g/g dw}$; 4 of 80 females (5 %) had elevated mercury levels ($\geq 3 \mu\text{g/g dw}$).

Influence of Trace Elements on Nutrient Reserves

Lipid reserves.-My final lipid reserve model included effects of collection location, body size, cadmium, and selenium concentrations ($F_{6,73} = 20.03$; $P < 0.001$; $R^2 = 0.62$). The mercury main effect and selenium-by-mercury interaction effect were not retained in the final model ($P_s > 0.343$). There was no evidence that liver mass was correlated with lipid reserves ($P = 0.764$); thus, it was not included in the final model.

Table 5.1. Least-square geometric mean (\bar{u}), 95 % confidence interval (CI), and range (R), of cadmium and selenium concentrations ($\mu\text{g/g}$ dry) for female lesser scaup collected at 4 locations ($n = 20$ females per location) in the Mississippi Flyway during winter and spring migration. Numbers and percent of females with elevated (E) and potential harmful (H) levels of cadmium and selenium are noted (see text for criteria).

Location	Cadmium					Selenium				
	\bar{u}	CI	R	# E (%)	# H (%)	\bar{u}	CI	R	# E (%)	# H (%)
Louisiana	0.80 b ¹	0.61 - 1.05	0.26 - 6.57	2 (10)	0 (0)	11.81 a	9.94 - 14.03	6.04 - 52.29	12 (60)	1 (5)
Illinois	0.69 b	0.52 - 0.90	0.40 - 2.38	0 (0)	0 (0)	12.21 a	10.26 - 14.53	6.14 - 20.03	12 (60)	0 (0)
Minnesota	1.23 a	0.94 - 1.61	0.23 - 7.24	3 (15)	1 (5)	9.20 b	7.72 - 10.97	3.98 - 35.85	9 (45)	1 (5)
Manitoba	1.11 a	0.84 - 1.47	0.26 - 6.68	2 (10)	0 (0)	8.17 b	6.88 - 9.71	3.73 - 30.47	6 (30)	0 (0)

¹ Means with different letters (within a trace element) differed ($P < 0.05$).

There was weak evidence for a quadratic selenium effect (estimate = $6.70X - 0.07X^2$; $F_{1,72} = 3.06$; $P = 0.085$); however, this effect also was not retained in the final model. Collection location ($F_{3,73} = 16.43$; $P < 0.001$) and body size (estimate = 8.88; $F_{1,73} = 7.63$; $P = 0.007$) fit well in the model. Selenium concentrations were positively correlated with lipid reserves (estimate = 55.83; $F_{1,73} = 22.69$; $P < 0.001$; Figure 5.1), whereas cadmium was negatively correlated with lipid reserves (estimate = -19.64; $F_{1,73} = 6.92$; $P = 0.010$; Figure 5.1). Selenium concentration explained 24 % of the residual variation, after collection location, body size, and cadmium concentrations were included in the model. Cadmium concentration explained 9 % of the residual variation, after collection location, body size, and selenium concentration were included in the model.

Protein and mineral reserves.-Cadmium, mercury, and selenium were not correlated with mineral reserves of female scaup (all P s > 0.249), after controlling for body size, liver mass, and location.

DISCUSSION

Trace-Element Concentrations

Size-adjusted body mass and lipid reserves of female scaup during spring migration were lower in 2000 and 2001 than in 1986 – 1988 in Minnesota and in 1977 – 1980 in Manitoba (Anteau 2002, Anteau and Afton 2004); correspondingly, cadmium concentrations were highest in these 2 locations. My second data set contained more females with elevated or potentially harmful levels of cadmium and selenium than in the original sample, and my mean cadmium concentrations in Minnesota and Manitoba were qualitatively higher than the overall level reported in the original sample (Custer et al.

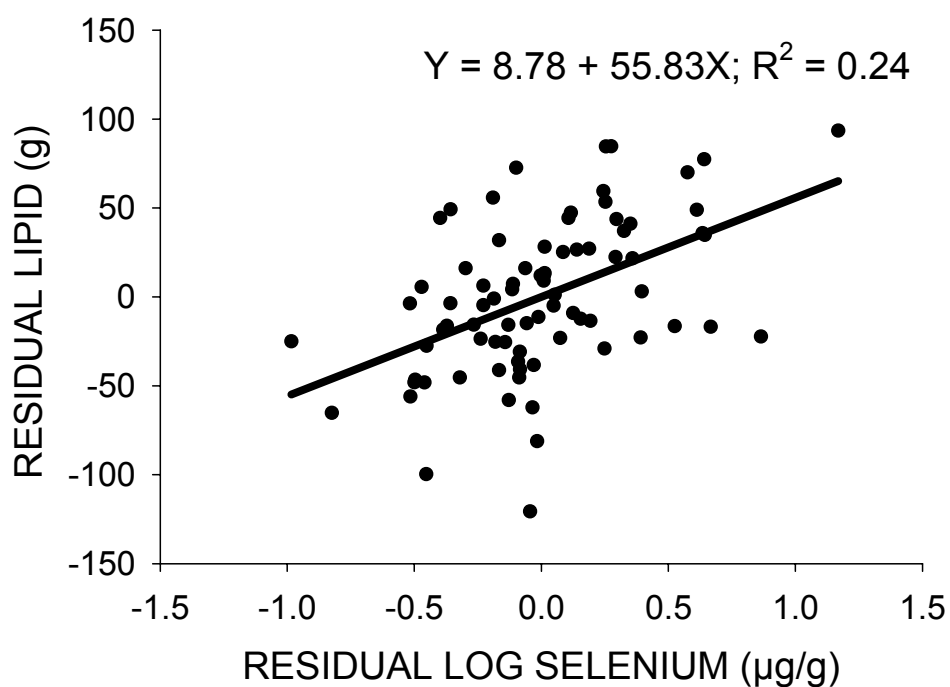
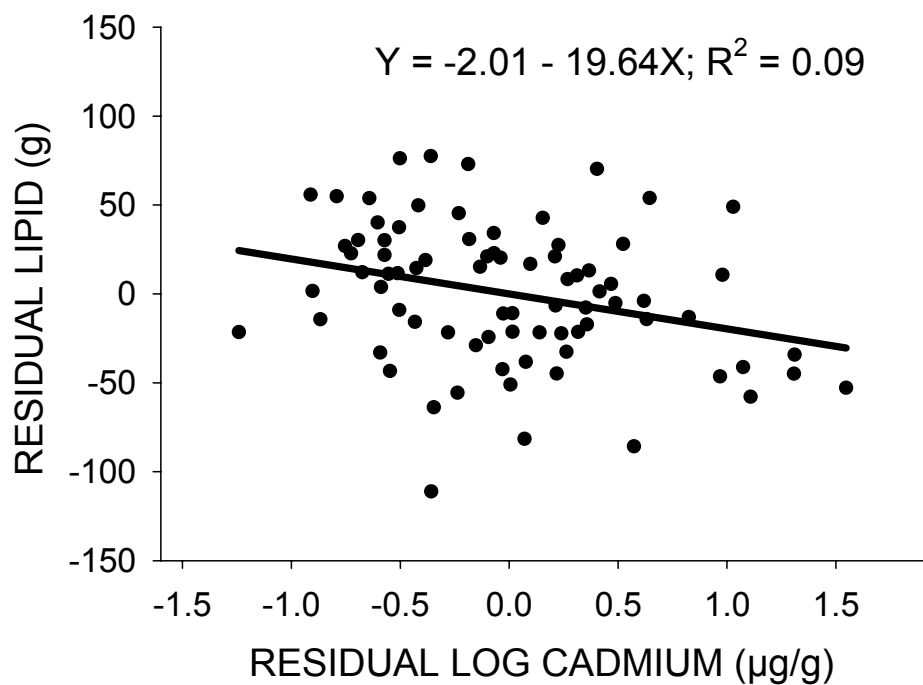


Figure 5.1. Type III partial relationships between lipid reserve residuals (see methods) and log cadmium and selenium concentration residuals (see methods) for 80 female lesser scaup collected from 4 locations within the Mississippi Flyway during winter and spring migration.

2003). Differences in percentages of females with elevated/harmful cadmium concentrations and mean cadmium concentrations between my original data and second data sets probably represent random sampling error and underscore the need for large sample sizes when evaluating trace-element concentrations in wild populations of migrating birds. However, my analyses of concentrations reported here are controlled for body size, which might have contributed to small differences in mean concentrations and increased precision of the location test.

Influence of Trace Elements on Nutrient Reserves

Lipid reserves.-Changes in liver mass, associated with changes in body condition, might influence hepatic concentrations of trace elements without a change in total hepatic trace-element levels. Thus, it was important to consider liver mass in models examining correlations between trace-element concentrations and nutrient reserves. However, the observed correlations between cadmium or selenium and lipid reserves of female scaup cannot be explained by variations in liver mass influencing hepatic concentrations of metals because liver mass was not correlated to lipid reserves.

Lipid reserves declined 55 g (47 %), on average, within the range of observed cadmium concentrations, even though 91 % of females had cadmium concentrations that were considered background. Cadmium concentrations were negatively correlated to body mass in wild common eiders (*Somateria mollissima*; Franson et al. 2000; Wayland et al. 2001, 2003). I found that cadmium concentration in scaup were 5 to 35 times lower than those in common eiders (Franson et al. 2000; Wayland et al. 2001, 2003). Despite the large amount of variation not explained by cadmium, I believe that the relatively large

observed effect size on lipid reserves of female scaup from low levels of cadmium is of concern, particularly if cadmium concentrations in scaup increase.

Effects of trace-element concentrations on body condition of captive and wild waterfowl often differ (Wayland et al. 2002, 2003). Captive studies indicated that cadmium had negligible effects on body condition of captive mallards (*Anas platyrhynchos*; White and Finley 1978, Di Giulio and Scanlon 1985, Bennett et al. 2000). However, higher levels of dietary cadmium increased energy stresses observed in captive mallards on a restricted diet (Di Giulio and Scanlon 1985), suggesting that cadmium influences lipid reserves indirectly (Wayland et al. 2002, 2003). Accordingly, cadmium and other trace elements may indirectly influence lipid reserves (e.g., decreasing foraging or energy metabolism efficiency). Furthermore, trace-element contaminants may affect nutrient reserves of active birds (e.g., during spring migration) more so than those of less active birds (e.g., captive, during winter, or incubation), if influences of trace-element effects are indirect and intermediated by a metabolic response. For example, selenium concentration was negatively correlated to blood-hemoglobin concentration in captive mallards (Hoffman 2002). Blood-hemoglobin concentrations in scaup may be important determinants of body condition during spring migration because scaup forage intensively in spring by diving (Austin et al. 1998).

Lovvorn and Barzen (1988) defined stress as "... a situation when demands of one event (physiological, behavioral, or otherwise) are great enough to interfere with desirable allocation of resources to other processes." Northern spring-stopover areas are important for accumulation and maintenance of lipid reserves subsequently used by breeding scaup, and females should be gaining lipid reserves in the upper-Midwest

(Afton and Ankney 1991, Anteau and Afton 2004). Females currently are catabolizing lipids (Chapter 4) and have low lipid reserve levels throughout the upper-Midwest (Chapter 2). Forage quality (nutritional value of forage consumed) of scaup in the upper-Midwest currently is low and probably has declined from historical values (Anteau and Afton 2006, Chapter 8). Scaup may be spending more time searching for food (within and between wetlands) than they did historically (Chapter 9). Thus, nutritional demands of female scaup during spring in the upper-Midwest (e.g., migration, courtship and pair formation, contour feather molt, and ovarian follicle development; Alisauskas and Ankney 1992, Anteau and Afton 2004) probably are interfering with the accumulation of nutrient reserves for breeding. Together, all of these results indicate that females are nutritionally stressed during spring migration, which also could explain why the relatively low levels of cadmium observed had the observed influence on lipid reserves.

Elevated selenium levels are a concern for scaup in the Great Lakes region and within the Mississippi Flyway (Custer and Custer 2000, Custer et al. 2000, Custer et al. 2003). Selenium is an essential nutrient, but in high levels it increases mortality, decreases body mass, impairs reproduction, reduces growth, and causes histopathological lesions, oxidative stress, and alterations in hepatic glutathione metabolism (Heinz 1996, Stanley et al. 1996, Hoffman 2002, Spallholz and Hoffman 2002). Selenium caused more physiological stress to captive mallard ducklings on a high (44%) protein diets than on a low protein diets (22%; Hoffman et al. 1992). Accordingly, scaup could be at particular risk of selenium toxicity because they consume foods that are rich in protein, especially in spring (Afton and Hier 1991, Afton et al. 1991, Anteau and Afton 2006).

The observed positive correlation between selenium and lipid reserves (Figure 5.1) is consistent with the idea of selenium (at levels observed) acting as a nutrient. However, this correlation also could occur if lipid reserves and selenium concentrations increase simply because females eat more food. In contrast to predictions, high levels of selenium were not associated with low levels of lipid reserves, at least at the levels observed in this study.

Hepatic selenium concentrations were not correlated with body mass or lipids in a combined sample of greater and lesser scaup during winter in California (Takekawa et al. 2002). Takekawa et al. (2002) attempted to fit a linear regression between selenium concentrations and body mass and lipids; however, a quadratic relationship might have been more appropriate (see above). I expected selenium and lipid reserves might be negatively correlated at higher concentrations of selenium particularly because females in Minnesota and Manitoba may be nutritionally stressed. I found weak evidence of a quadratic term for selenium ($P = 0.085$), suggesting that the effects of selenium in lipid reserves level-off at 47 $\mu\text{g/g dw}$ selenium and become negative thereafter, but my data are sparse at selenium concentrations over 33 $\mu\text{g/g dw}$ ($n = 2$). Regardless, the quadratic term for selenium was excluded from my final model, based on my *a priori* selection of alpha 0.05. If selenium influences lipid reserves negatively, this probably occurs at levels of selenium higher than those I observed in the Mississippi Flyway.

Implications for Conservation of Lesser Scaup

In springs 2000 and 2001, lipid reserves of female scaup migrating through Minnesota were 100 g lower than those in Illinois; historically, females likely gained lipid reserves as they migrated north through the upper-Midwest (Anteau 2002, Anteau

and Afton 2004). I found that increases in cadmium within the low range of concentrations observed were correlated with as much as 55 g (47 %) less lipid reserves of females, on average. However, the log of mean cadmium concentrations in Illinois and Minnesota (Table 5.1) only predict lipid reserves of females to be 11 g lower, on average, in Minnesota than those in Illinois (see Figure 5.1). Thus, cadmium concentrations could be a contributing factor to the recently documented decrease in lipid reserves for scaup migrating through the upper-Midwest (Custer et al. 2003, Anteau and Afton 2004); however, it seems unlikely that cadmium concentrations are the sole cause of the current low levels of lipid reserves in the upper-Midwest.

In conclusion, the negative correlation between cadmium and lipid reserves suggests that cadmium might be a conservation concern inhibiting lipid reserve accumulation by female scaup. Small declines in lipid reserves of females during spring migration could have large impacts on reproductive performance and ultimately on population size through declines in breeding propensity and delays in nest initiation, which in turn, causes declines in nest, duckling, and fledgling survival (Anteau and Afton 2004; Chapters 2, 4). However, observed cadmium concentrations seemingly do not explain the marked declines in lipid reserves of females observed throughout the upper-Midwest. Other mechanisms, in addition to the apparent cadmium related effects, probably are driving the decline in female scaup body condition during spring migration in the upper-Midwest. Scaup presently are faced with less habitat (Austin et al. 1998) and a decrease in the availability of quality foods (Anteau and Afton 2006; Chapters 6, 8) during spring migration in the upper-Midwest, which could result in decreases in lipid reserves. If levels of cadmium were to increase in scaup, cadmium potentially could

cause large decreases in female scaup lipid reserves levels during spring migration and have concomitant effects on the continental scaup population, especially when females apparently are nutritionally stressed.

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CHAPTER 6: AMPHIPOD DENSITIES AND INDICES OF WETLAND QUALITY ACROSS THE UPPER-MIDWEST

INTRODUCTION

A large proportion of wetlands in Iowa, Minnesota, and North Dakota has been drained or otherwise lost in the past 200 years, and the process of wetland drainage has the potential to degrade the quality of remaining wetlands (Dahl 1990). Factors influencing trophic structure and wetland quality have important implications for management of semipermanent and permanent wetlands in the upper-Midwest (Swanson and Nelson 1970, Bouffard and Hanson 1997, Hanson et al. 2005). Wetlands in this region may exist in either a clear-water state, which is dominated by submerged-aquatic vegetation (SAV), or a turbid state, which is primarily dominated by phytoplankton (Scheffer et. al 1993, Zimmer et. al 2002). Wetlands with clear water, abundant SAV, and higher macroinvertebrate densities provide more food for various wildlife species (Krull 1970, Dieter 1991, Gleason et al. 2003). Although the concept of wetland quality is poorly defined among wetland managers (La Peyre et al. 2001), I assume that clear wetlands with low sediment influxes, supporting more SAV and macroinvertebrates are higher quality, at least from a wildlife habitat perspective.

Amphipods are an important indicator of water quality, given their sensitivity to contaminants, pesticides, and pollution (Grue et al. 1988, Covich and Thorp 1991, Tome et al. 1995, Murkin and Ross 2000, Besser et al. 2004). Amphipod densities are positively correlated with submerged aquatic vegetation and negatively correlated with fish densities and high levels of suspended sediments (Chapter 10). Therefore, estimates

of amphipod densities across a landscape should index wetland and water quality at a landscape level.

Gammarus lacustris and *Hyaella azteca* (hereafter *Gammarus* and *Hyaella*, respectively) are the most abundant amphipod species in semipermanent and permanent wetlands of the upper-Midwest (Kantrud et al. 1989). These species are very productive and often flourish at high densities; *Gammarus* and *Hyaella* often are observed at densities in the thousands m⁻² and can produce multiple broods when the breeding season is relatively long (Covich and Thorp 1991, Wen 1992, Pickard and Benke 1996). Amphipods also are an important component of secondary production of prairie wetlands; they are detritivores and shredders of coarse particulate organic matter, but also forage on epibenthic algae and microbial bacteria (Murkin 1989, Wen 1992, Day et al. 1998, Dvorak et al. 1998, Murkin and Ross 2000).

Amphipods are important foods for fish and wildlife in prairie wetlands and lakes of the upper-Midwest, including fish ranging from fathead minnows (*Pimephales promelas*) to large northern pike (*Esox lucius*; > 50 cm; Peterka 1989, Dvorak et al. 1998, MacNeil et al. 1999; M. J. Anteau, Louisiana State University, unpublished data), tiger salamanders (*Ambystoma tigrinum*; Olenick and Gee 1981, Kantrud et al. 1989, MacNeil et al. 1999), migrating and breeding diving ducks (*Aythya* spp.), ruddy ducks (*Oxyura jamaicensis*), common goldeneye (*Bucephala clangula*), and several species of dabbling ducks during brood rearing (*Anas* spp.; Kantrud et al. 1989, Swanson and Duebbert 1989, Krapu and Reinecke 1992, Eadie et al. 1995).

Lesser scaup (*Aythya affinis*; hereafter scaup) are amphipod specialists, especially during spring migration in the upper-Midwest; however, they currently are consuming

fewer amphipods than did those historically (Afton et al. 1991; Anteau and Afton 2006; Chapters 8, 9). Female scaup migrating throughout the upper-Midwest currently are catabolizing lipids and have fewer lipid reserves than did those historically, likely due to a decline in availability and/or quality foods (Anteau and Afton 2004; Chapters 2, 4). Several nutritional and diet studies of scaup have suggested that there has been a landscape-scale decrease in amphipods on stopover areas in the upper-Midwest (Anteau and Afton 2004, 2006; Chapters 2, 4, 8). Accordingly, estimating spring amphipod densities in the upper-Midwest was identified as a research priority (Anteau 2002; Anteau and Afton 2004, 2006).

Other useful biotic and abiotic indices of wetland quality include specific conductivity, turbidity, chlorophyll *a*, SAV, and fish communities. Abiotic influences of water chemistry likely are important indicators of trophic communities in wetlands (Kantrud et al. 1989, Peterka 1989). Excessively high turbidity or phytoplankton density (indexed by chlorophyll *a*) may be indicative of agricultural sedimentation or influences of fish communities (Dieter 1991, Scheffer et al. 1993, Hanson et al. 2005). High abundances of SAV often are associated with abundant macroinvertebrate populations (Krull 1970, Chapter 10). Finally, fish communities, particularly fathead minnows (*Pimephales promelas*) and rough fish (e.g., common carp; *Cyprinus carpio*), have the potential to decrease macroinvertebrate abundance directly (through predation) and indirectly through trophic cascades (Scheffer et al. 1993, Bouffard and Hanson 1997).

I estimated densities of amphipods throughout the upper-Midwest and evaluated whether there has been a decline in amphipod densities by comparing current densities to historical published data on amphipod densities. I also described other indices of wetland

quality and make assessments of wetland quality based on available historical data and regional variations in these indices.

METHODS

Study Area

I sampled semipermanent and permanent wetlands within the Prairie Pothole Regions of Iowa, Minnesota, and North Dakota during springs 2004 and 2005. I stratified the 3-state area into 6 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 6.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

I used a constrained-random, clustered sampling approach to select wetlands to minimize travel time of field crews between wetlands and in areas with few wetlands. I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 6.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck North Dakota, unpublished data; S. Piegras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or permanent wetlands. Constraining township selection helped insure that there were enough semipermanent or permanent wetlands to sample within each township.

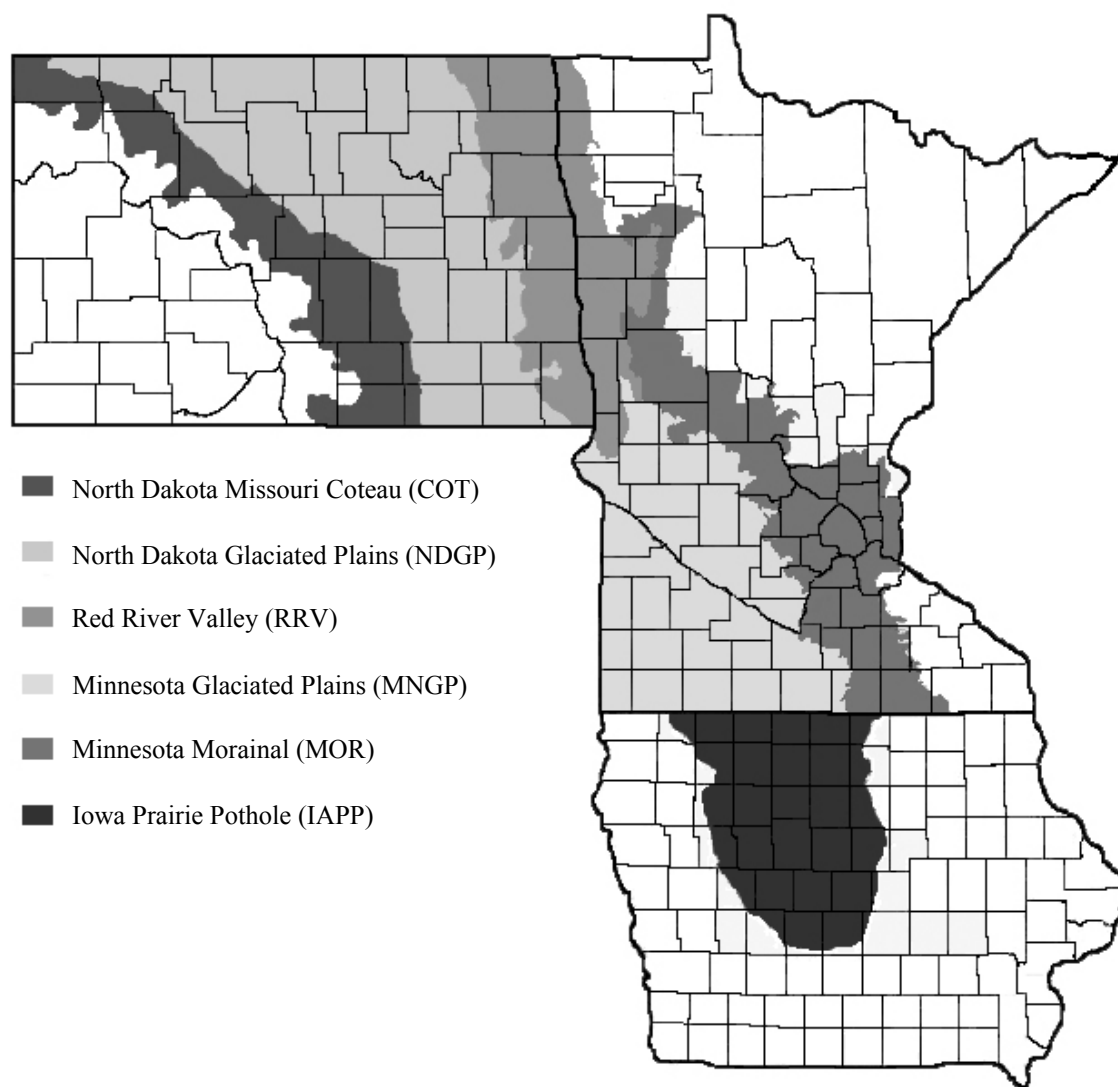


Figure 6.1. Map of the study area depicting 6 eco-physiographic regions for wetland sampling (2004 – 2005) during early spring in the upper-Midwest. Areas in white were not sampled.

Table 6.1. Numbers of sampling clusters, wetlands sampled for amphipod density (N_{Amph}), and a random subset of these wetlands sampled for water quality, submerged vegetation, and fish communities (N_{Complete}) by region and year; including numbers of candidate townships (T) available for random selection of sampling clusters.

Region	Clusters	N_{Amph}		N_{Complete}		T
		2004	2005	2004	2005	
North Dakota Missouri Coteau	3	27	26	9	26	208 ^a
North Dakota Glaciated Plains	6	42	50	15	50	364 ^a
Red River Valley	3	21	21	11	21	66 ^a
Minnesota Morainal	4	28	34	10	34	348 ^a
Minnesota Glaciated Plains	4	31	33	18	33	285 ^a
Iowa Prairie Pothole	3	20	23	17	23	43 ^b
Wetland Total		169	187	80	187	

^a Townships that contain at least 200 hectares of semipermanent wetlands.

^b Townships that contain at least 200 hectares total of semipermanent and permanent wetlands.

I allocated numbers of sampling clusters among the 6 regions (3 to 6 clusters per region; Table 6.1) based on region size and numbers of candidate townships available (Table 6.1, Figure 6.1). Each region was divided into sub-regions based on latitude, so that there was 1 sampling cluster per sub-region each year (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 sampling clusters for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 6.1). Each sampling cluster was comprised of 3 randomly selected 36-square-mile townships (27,972 ha total). The centurms of the second and third townships selected were constrained to be within 50 km of the centrum of the first randomly selected township. I subsequently randomly selected 3 semipermanent or permanent wetlands (> 4 ha) in each township for amphipod sampling. I randomly selected new townships and wetlands annually within each sub-region from the list of candidate townships to maximize representation of spatial variability in amphipod densities and indices of wetland quality. I conducted amphipod sampling on 356 wetlands in 2004 and 2005. However, complete wetland surveys were conducted on a random subset of the wetlands surveyed for amphipod densities in 2004 and on all wetlands in 2005, thus I conducted complete surveys on 267 wetlands (Table 6.1).

Wetland Sampling

I timed wetland sampling to occur with middle migration of scaup, when relatively large numbers of migrating scaup were present on my study area; thus, I started sampling in the southern portion of the study area and worked north. This approach insured that (1) my estimates of amphipod densities were representative for that available to scaup during spring migration, (2) sampling occurred at similar times relative to

phenology of spring, and (3) was prior to the first broods of amphipods (Wen 1992).

Sampling was conducted during 3 April – 16 May 2004 and 30 March – 3 May 2005.

Amphipod density.-For each wetland, I selected 4 transects on a map by randomly selecting a bearing (0 – 359) for each transect and then I used a protractor to draw each transect on the map from the center to the bank of the wetland. Maps then were used to locate transects in the field. Each transect had 2 sampling stations; the first station was 10 m past the ring of the emergent vegetation and the second was 50 m away from the first station along the transect (toward the center). However, I limited station locations to depths between 0.5 – 3 m for ease of sampling and because these are depths that scaup feed in spring (Austin et al. 1998). Thus, in some instances (< 5% of transects), station locations were adjusted along transects to accommodate depth requirements.

At each station, I measured water depth and sampled amphipod density with a D-shaped-sweep net (1,200 μm mesh, 0.072 m^2 opening, WARD's Natural Science, Rochester, New York). Each amphipod sample consisted of a bottom sample (skimming the net along the bottom for a distance equal to the depth at the sampling station) and an upward water column sweep. This pattern helped insure equal representation of bottom and water column in each sample. In the field, sweep-net samples ($n = 8$ per wetland) were combined into 1 composite sample per wetland, preserved in a 95% ethanol solution, and then transported to the laboratory for sorting.

In the laboratory, each composite sample was stained with Rose Bengal (Sigma # R3877, Sigma-Aldrich Corp., St. Louis, Missouri), sieved (500 μm mesh), and floated with sugar and water in a large dissecting tray. I sorted and counted all amphipods (i.e.,

Gammarus lacustris and *Hyalella azteca*) using a lighted magnifying glass and a stereomicroscope. I calculated the total water volume sweep (VS; m³) for each wetland with the equation:

$$VS = 2 (\Sigma D_i) \times SN$$

where D_i = depth (m) at each sampling station, and SN = sweep-net opening (0.072 m²).

I calculated densities of each species of amphipod for each wetland by dividing the count of each species by VS. I also calculated the frequencies that *Gammarus* and *Hyalella* occurred in wetlands of each region (percent occurrence; Swanson et al. 1974).

Estimation of submerged aquatic vegetation.-I used grab sampling (Nyman and Chabreck 1996) to estimate relative abundance of SAV along a sub-transect starting at each sampling station and running parallel to the bank. Each sub-transect had 10 grabs (1/meter) of a 36-tine Lake Rake[®] (Ben Meadows Co., Janesville, Wisconsin) gently dug into the bottom and pulled straight up (Nyman and Chabreck 1996). For each grab, presence/absence of vegetation was recorded. Relative abundance was estimated for each wetland by the proportion of grabs with SAV present (n/80).

Estimation of fish densities.-I estimated densities of various fish species with an experimental gill net (21 x 2 m with 7 – 3 m panels ranging in mesh size from 1.9 cm – 7.6 cm) set on a fifth transect. The end of the net with the smaller mesh sized panels was set about 10 m from the open water-emergent vegetation interface and extended along the transect toward the center of the wetland. I also set 5 minnow traps on each wetland to supplement data from the experimental gill net; one minnow trap per transect was placed at the transition between emergent vegetation and open water. Gill nets and minnow traps were set for 12 – 24 hours.

Fish caught in all 5 traps and in the gill net were enumerated by species. I calculated catch per unit effort (relative densities) of fish by dividing total numbers of fish in each species by the time that the net/traps were in the water. I then classified fish species into 1 of 4 categories: (1) fathead minnows, (2) rough fish (carp and buffalo [*Ictiobus spp.*]), (3) small fish (other minnows [*Cyprinidae*], darters [*Anhingidae*], sticklebacks [*Gasterosteidae*], and mudminnows [*Umbra spp.*]), and (4) large fish (e.g., northern pike, walleye [*Sander vitreus*], perch [*Perca spp.*], sunfish [*Lepomis spp.*], bullhead and catfish [*Ictaluridae*]). I also calculated the frequency that fish (all classes combined) occurred in wetlands of each region (percent occurrence; Swanson et al. 1974).

Water quality.-I measured turbidity (± 1 nephelometric turbidity unit [NTU]), chlorophyll *a* (± 1 mg/l), and specific conductance (± 1 μ S/cm) with portable water quality meters (YSI 6600 sonde with optical chlorophyll [YSI 6025] and turbidity [YSI 6136] probes; YSI Inc. Yellow Springs, Ohio) at the first 4 transects near the center of the wetland. All measurements were averaged for each wetland.

Statistical Analyses

I compared densities of *Gammarus* and *Hyalella* separately among regions and between years with analyses of variance (PROC MIXED; SAS Institute 2002). *Gammarus* and *Hyalella* densities were natural-log (+1) transformed to meet assumptions of normality (Devore 2000); I report back-transformed geometric means. I selected my final models using a backwards elimination procedure with *alpha* 0.05 (Zar 1996). For the each final model, I used the PDMIX800 macro (Saxton 1998) to get Tukey-Kramer adjusted mean letter groupings for each region.

I compared indices of wetland quality (SAV, specific conductance, chlorophyll *a*, turbidity, fathead minnows, rough fish, large fish, and small fish) among regions and between years with a multivariate analysis of variance (MANOVA; PROC GLM; SAS Institute 2002). Year was not significant in the model (*alpha* 0.05) and, thus was excluded. I then conducted contrasts to examine regional differences in all responses using Tukey-Kramer adjusted least-squares-mean groupings (pdiff-all option; *alpha* 0.05; PROC GLM; SAS Institute 2002).

RESULTS

Amphipod Densities

Gammarus and *Hyaella* were present in 19% and 54% of all wetlands surveyed, respectively; *Gammarus* and *Hyaella* densities ranged from 0 – 1147 and 0 – 1507 m⁻³, respectively (Figure 6.2). *Gammarus* occurred most frequently in wetlands of the Missouri Coteau of North Dakota (COT) and NDGP, and less so in other regions (Minnesota Glaciated Plains [MNGP], Minnesota Morainal [MOR], and Iowa Prairie Pothole [IAPP]); *Hyaella* occurred most frequently in COT, NDGP, and the Red River Valley (RRV), and less so in other regions (Table 6.2). *Gammarus* were not found in wetlands of IAPP and the occurrence of *Hyaella* also was low in this region (Table 6.2).

Gammarus and *Hyaella* densities differed among regions ($F_{5, 350} = 9.27, P < 0.001$ and $F_{5, 349} = 9.83, P < 0.001$, respectively; Figure 6.3). *Gammarus* densities did not vary annually; however, the overall *Hyaella* density was 3 m⁻³ higher in 2005 than in 2004 ($F_{5, 349} = 13.11, P < 0.001$). *Hyaella* generally were more abundant than were

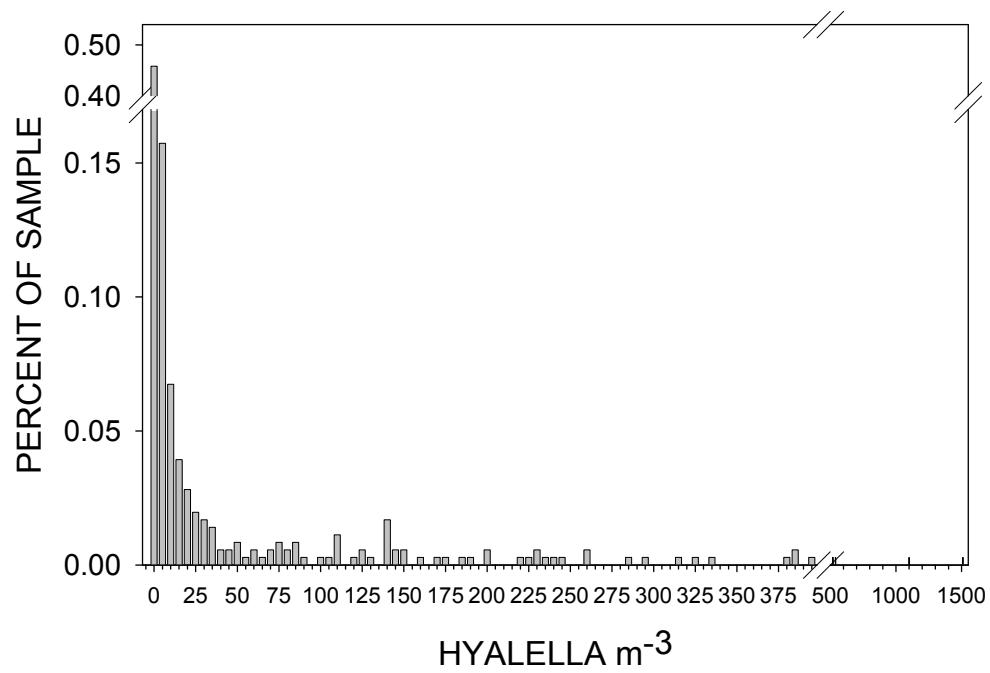
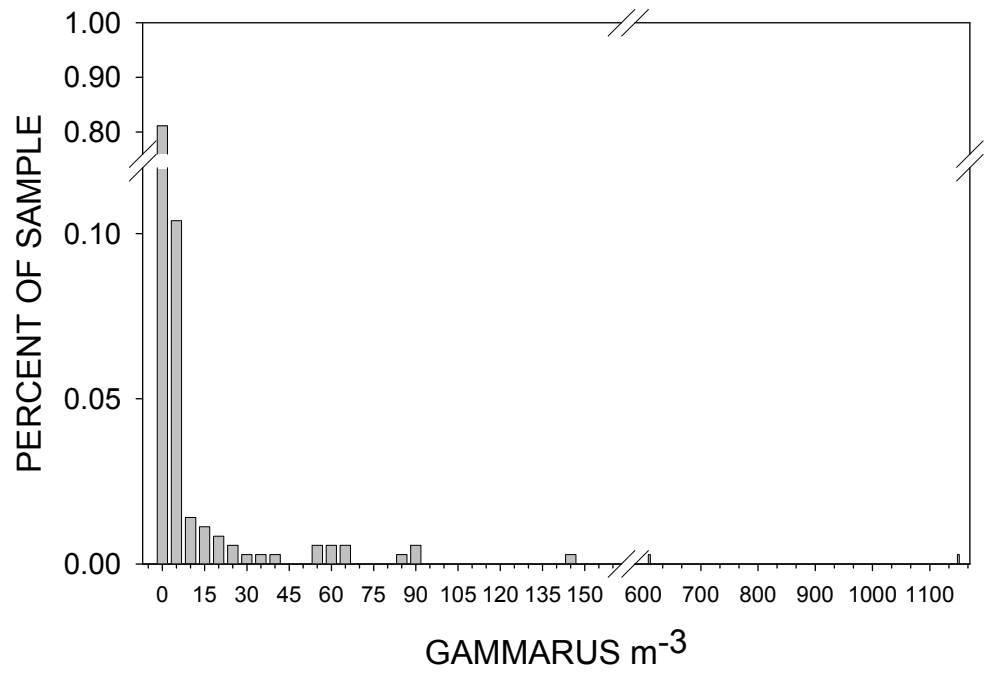


Figure 6.2. Distribution histograms of *Gammarus lacustris* and *Hyalella azteca* densities from wetlands sampled in the upper-Midwest in springs 2004 and 2005 combined.

Table 6.2. Percent occurrence of *Gammarus lacustris*, *Hyaella azteca*, and fish in wetlands sampled by eco-physiographic regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole) in springs 2004 and 2005.

Taxa	COT	NDGP	RRV	MNGP	MOR	IAPP
<i>Gammarus lacustris</i>	34	39	14	8	3	0
<i>Hyaella azteca</i>	64	78	60	41	48	16
Fish	31	45	84	78	84	74

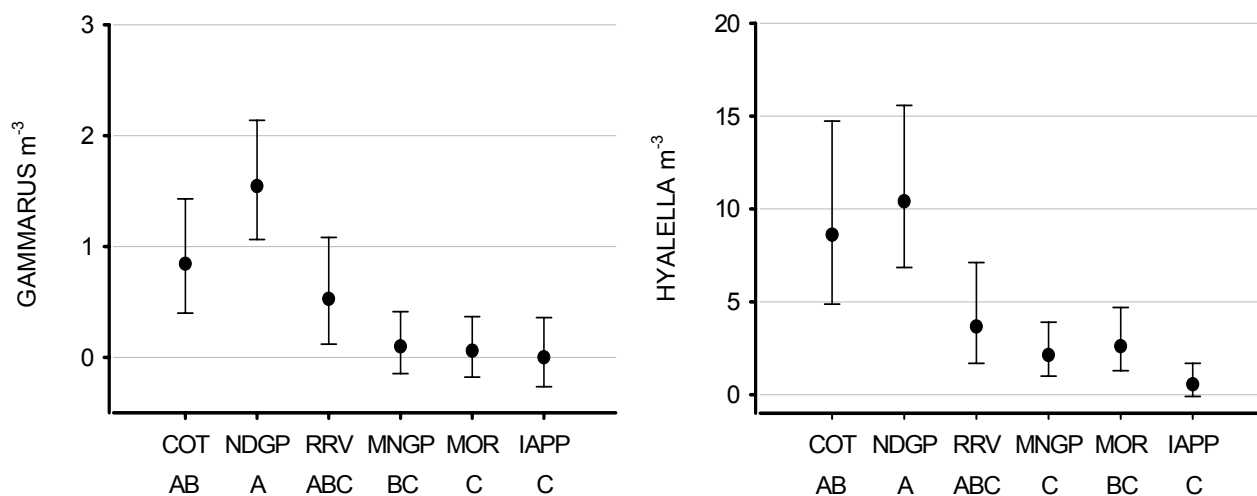


Figure 6.3. Geometric least-squares mean densities (\pm 95% CI) of *Gammarus lacustris* and *Hyalella azteca* by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at $P < 0.05$.

Gammarus in all regions (Figure 6.3). *Gammarus* and *Hyaella* densities were higher in NDGP than MOR, MNGP, and IAPP, whereas densities in RRV were intermediate between these two groups of regions (Figure 6.3). *Gammarus* density was higher in Missouri Coteau (COT) than that in MOR or IAPP (Figure 6.3); *Hyaella* density also was higher in COT than in MNGP and IAPP (Figure 6.3).

Wetland Quality

Indices of wetland quality also varied by region ($F = 9.54, P < 0.001$). Specific conductance was markedly higher in COT and NDGP than in RRV, MNGP, MOR, and IAPP (Figure 6.4). Turbidity was higher in IAPP, COT, NDGP, and MNGP than in RRV and MOR (Figure 6.4). Chlorophyll *a* was nearly 2 times higher in IAPP than any other region, but was significantly different (after Tukey-Kramer adjustments) from only RRV and MOR (Figure 6.4). SAV was lower in IAPP than that in MOR and RRV (Figure 6.4).

Fathead minnows were more abundant in wetlands of MNGP and NDGP than in those of COT and IAPP (Figure 6.5). Rough fish were more abundant in wetlands of IAPP than in those of any other region (Figure 6.5). Small fish were more abundant in wetlands of MOR than in those of IAPP, COT, and NDGP (Figure 6.5). Large fish were more abundant in wetlands of MNGP, MOR, and IAPP than in those of COT and NDGP; they were intermediate in RRV (Figure 6.5).

Regional fish percent occurrences ranged from 31 – 84, and generally occurred in wetlands of RRV, MNGP, MOR, and IAPP more frequently than those of COT and NDGP (Table 6.2).

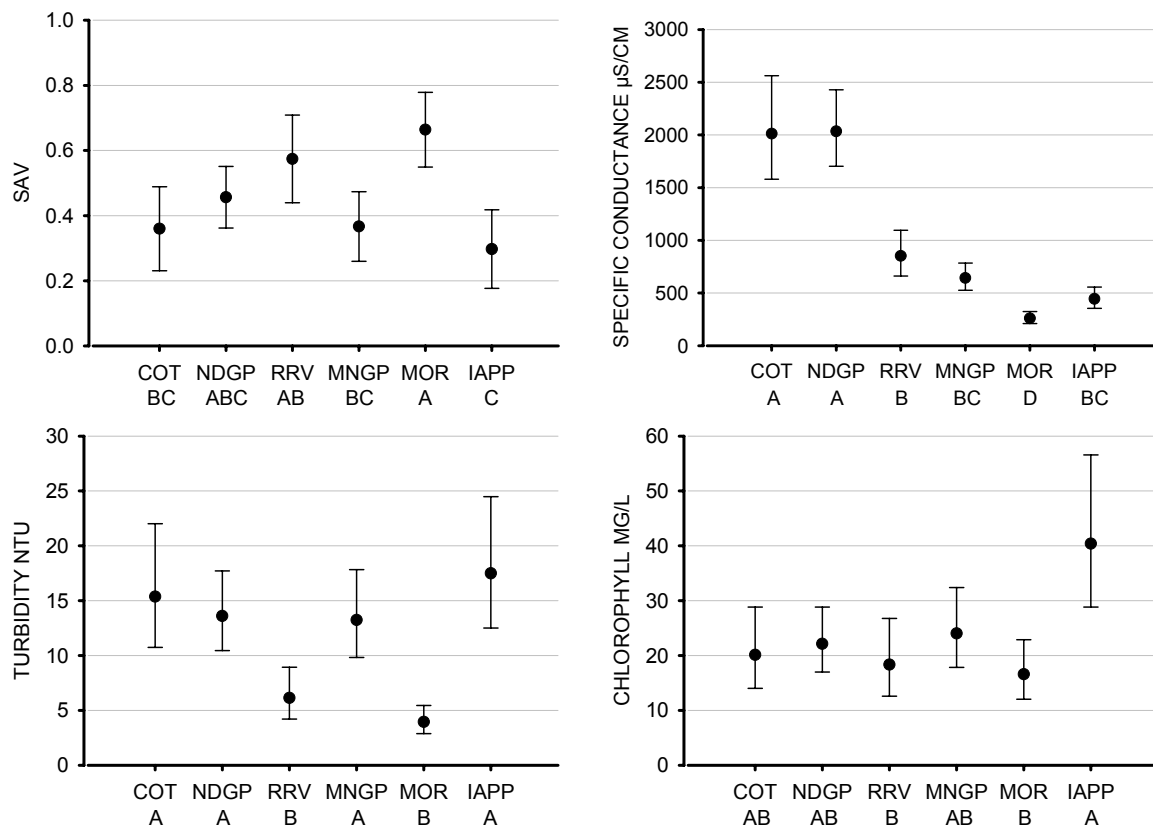


Figure 6.4. Geometric least-squares means (\pm 95% CI) of relative abundance of submerged aquatic vegetation (SAV), specific conductance, turbidity, and chlorophyll *a* by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at $P < 0.05$.

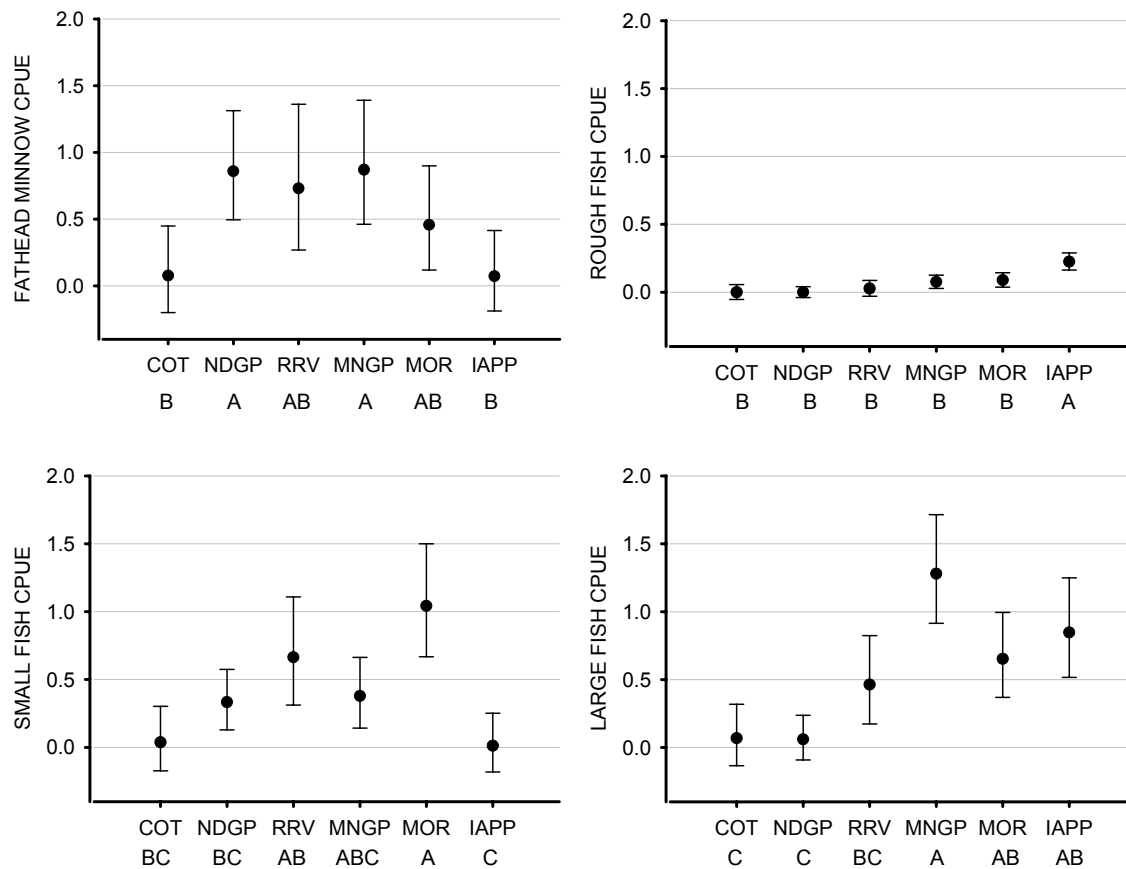


Figure 6.5. Geometric least-squares mean catch per unit effort (CPUE; \pm 95% CI) of fathead minnows, rough fish, small fish, and large fish by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at $P < 0.05$.

DISCUSSION

Amphipod Densities

Observed amphipod densities probably were driven by amphipod breeding productivity in the previous year and their winter survival, because I sampled prior to the first breeding event of the season (Wen 1992). Amphipods over winter as adults in prairie wetlands, and high survival is required for them to be abundant in early spring (Arts et al. 1995, Lindeman and Clark 1999, MacNeil et al. 1999). Amphipods generally are susceptible to fish predation year around, unlike other invertebrates which are more seasonally available (MacNeil et al. 1999). Thus, over-winter survival of amphipods and presence predatory fish may be major sources of annual variation in amphipod densities. However, I did not detect annual variation in *Gammarus* densities despite observations of widespread, severe winterkills of fish throughout MNGP and MOR in 2004 and few isolated winterkills observed there in 2005 (M. J. Anteau, Louisiana State University, personal observations; A. D. Afton, US Geological Survey, personal communication). *Hyaella* density was slightly higher in spring 2005 than in spring 2004, perhaps due to the severe winter 2003-2004 either directly by causing winterkills of *Hyaella*, or indirectly through the reduction of fish abundance. However, annual variation in *Hyaella* densities were relatively small in relation to that observed among regions and the range of observed densities from wetland to wetland.

Comparable estimates of historical spring amphipod densities generally are not available across my sampled area; however, one historical data set within NDGP and others from the Canadian portion of the Prairie Pothole Region are available (Table 6.3).

Table 6.3. Locations, years sampled, and numbers of wetlands sampled (W) for historical studies that presented *Gammarus lacustris* and *Hyalella azteca* densities (m^{-2} or m^{-3}) for mid-April to mid-June.

Location	Years	W	<i>Gammarus</i>	<i>Hyalella</i>
Southwestern Manitoba ^a	1976-1977	3	163	n/a
Southwestern Manitoba ^b	1977-1980	19	71	28
Southwestern Manitoba ^c	1979	1	1500	n/a
Southern Alberta ^d	1985-1986	1	n/a	1000 – 2000
Devil's Lake Chain, NDGP ^e	1986-1987	4	53	41

^a Salki (1981), mean density (m^{-3}).

^b Afton and Hier (1991), geometric mean density (m^{-3}), wetlands selected for lesser scaup diets study.

^c Mathias et al. (1982), mean density (m^{-2}) that clung to a net sent overnight.

^d Wen (1992), mean density (m^{-2}).

^e Brooks (1989), mean density (m^{-2}) from 4 bays within the Devil's Lake Chain.

Wetlands probably were not randomly selected in these studies, which may have resulted in high biased estimates. However, mean densities of amphipods that I observed (Figure 6.3) were extremely low compared to all other historical densities (Table 6.3). Furthermore, many landowners and local hunters indicated to me that they had observed a large decline in amphipods, particularly in Minnesota. Moreover, *Gammarus* were not found in wetlands sampled in IAPP and their occurrence and density were low in MNGP and MOR (Figure 6.3, Table 6.2), which is consistent with anecdotal and qualitative accounts.

Wetland Quality

Fish communities.—A total of 89, 42, and 49 % of wetlands in Iowa, Minnesota, and North Dakota, respectively, have been drained or otherwise lost between 1780 and 1980 (Dahl 1990). The process of wetland drainage has increased the connectivity of remaining wetlands and provided higher and more stable water regimes through increased drainage tile, ditches, and culverts that facilitate colonization and over-winter survival of fish into traditionally fish-free wetlands (Zimmer et al. 2000, 2001; Hanson et al. 2005). Moreover, connectivity of wetlands and the survivability of fish might have increased by the long, severe wet cycle during the end of the 20th century (Hanson et al. 2005); however, it appears that the wet cycle ended in the early 2000s (U.S. Fish and Wildlife Service 2005).

Historically, only about 10 – 20 % of northern prairie wetlands (1 – 5 m deep) supported over-wintering fish communities (Peterka 1989). Several studies speculated that natural invasions or introductions of fish have increased recently in semipermanent and permanent wetlands in the upper-Midwest (Hanson and Riggs 1995, Bouffard and Hanson

1997, Zimmer et al. 2002). I found high occurrences of fish throughout the upper-Midwest, especially in Minnesota and Iowa (Table 6.2), indicating a marked increase in fish occurrence.

Fish can decrease the abundance, biomass, activity, and size of amphipods and other macroinvertebrates directly through predation and indirectly by causing dramatic changes in the trophic structure of wetlands (Wellborn 1994; Hanson and Riggs 1995; Bouffard and Hanson 1997; Duffy 1998; Wooster 1998; Zimmer et al. 2001, 2002; Hanson et al. 2005; Chapter 10). Although, exact mechanisms are poorly understood, fish (especially fathead minnows and rough fish) can cause wetlands to remain in the turbid state, characterized by decreases in submerged-aquatic vegetation and macroinvertebrates (including amphipods; Hanson and Butler 1994; Zimmer et. al 2001, 2002). Accordingly, the high observed percent occurrence of fish in wetlands across the upper-Midwest probably has decreased wetland quality in this area.

Turbidity and chlorophyll *a*.-Anthropogenic influences (e.g., agriculture) accelerate wind and water facilitated erosion, and subsequently sedimentation into prairie wetlands, especially during high spring run-off over bare fields (Martin and Hartman 1987, Dieter 1991, Gleason and Euliss 1998). Such sedimentation causes loss of wetland depth and can fill wetlands in a single catastrophic event (Gleason and Euliss 1998). Suspended sediment and phytoplankton can reduce light to SAV on or near the bottom of the wetland and precipitation of sediment reduces SAV and invertebrate abundances (Dieter 1991, Gleason and Euliss 1998).

Measurements of turbidity in early spring should be a good index of mineral sedimentation in wetlands because sedimentation rates typically are highest during spring run-off (Dieter 1991, Gleason and Euliss 1998); however, turbidity, chlorophyll *a*, and fish communities should be considered together because fish can increase turbidity indirectly through increases in phytoplankton and directly by stirring sediments (Hanson and Butler 1994, Bouffard and Hanson 1997).

Turbidity levels in a large sample of fishless and non-agriculturally impacted boreal wetlands in north-central Alberta averaged 3.8 NTU (arithmetic mean; ranging 0.3 to 31.0; Bayley and Pranther 2003). Turbidity in wetlands of MOR was similar to that in north-central Alberta; however, wetlands of all other regions generally had much higher turbidity (Figure 6.4; ranging 1 to 297), suggesting that there may be high levels of sedimentation or fish influences in these regions.

Sedimentation into wetlands may be relatively high in COT and NDGP because relative levels of turbidity there were high, fish were low, and chlorophyll *a* was typical (relative to levels observed in other regions). Turbidity and chlorophyll *a* levels of wetlands were highest in IAPP; however, this region also had the highest abundance of rough fish, making it difficult to infer whether these high levels were due to fish and/or sedimentation. Factors influencing turbidity and phytoplankton levels in wetlands of the upper-Midwest clearly deserves future study.

Sedimentation may provide favorable conditions for monotypic stands of cattail (*Typha spp.*) that reduce or “choke out” the open-water zone of wetlands (Gleason and Euliss 1998, Gleason et al. 2003). Cattail was relatively rare in northern prairie wetlands in

the early part of the 20th century (Kantrud 1992). Cattail-choked semipermanent or permanent wetlands currently are widespread in parts of Iowa, Minnesota, and North Dakota (Kantrud 1992; M. J. Anteau, Louisiana State University, personal observation; A. D. Afton, U.S. Geological Survey, personal communication) and factors influencing cattail abundance should be investigated further.

Submerged aquatic vegetation.-Reductions in SAV are correlated with declines in invertebrate productivity (Krull 1970, Euliss and Grodhaus 1987, Neill and Cornwell 1992, Schriver et al. 1995, Gleason and Euliss 1998). Moreover, loss of vegetative structure in wetlands also increase susceptibility of macroinvertebrates to fish predation (MacNeil et al. 1999, Chapter 10). Wetlands of MOR and RRV had the highest SAV and also the lowest turbidity levels. However, I did not quantify species of vegetation; knowledge of species of SAV present in wetlands would be useful because different species support different densities of macroinvertebrates (Krull 1970).

Conclusions

My results here and other data concerning nutrition and diets of scaup (Anteau and Afton 2004, 2006; Chapters 2, 4, 8) together suggest that current densities of *Gammarus* and *Hyalella* are lower and the percent occurrence of fish is higher than historical values in wetlands throughout the upper-Midwest. Furthermore, turbidity levels of wetlands generally are high across most of the upper-Midwest and indicate that there may be problems with sedimentation into wetlands, especially in North Dakota. All of these relationships are consistent with landscape-wide declines in wetland quality in this region. Accordingly, conservation efforts to stop the degradation of wetlands and to improve

wetland quality should be considered in the upper-Midwest. However, before effective conservation can occur, several research and conservation issues need to be addressed, including (1) a clearly defined definition of wetland quality with standard metrics developed to allow evaluation of wetland quality before and after conservation activities; (2) specific research to determine what factors are contributing to turbidity levels in wetlands (e.g., sedimentation, fish communities, etc.); and (3) research to identify what factors regulate fish communities in wetlands.

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CHAPTER 7: DIET SHIFTS OF LESSER SCAUP DURING SPRING MIGRATION ARE CONSISTENT WITH THE SPRING CONDITION HYPOTHESIS

INTRODUCTION

The North American scaup population (lesser [*Aythya affinis*] and greater scaup [*Aythya marila*] combined) has declined markedly during the past 25 years (Austin et al. 1998, Afton and Anderson 2001). Annual population estimates of scaup have been below the population goal of the North American Waterfowl Management Plan since 1985 and were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. Recruitment of lesser scaup apparently has declined since 1978, and female survival rates have declined relative to that of males (Afton and Anderson 2001). The segment of the continental scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through Minnesota comprises a major component (40 %) of the continental population and is experiencing the largest decline (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup (Afton 1984, Afton and Ankney 1991, Pace and Afton 1999, Anteau 2002, Anteau and Afton 2004). Austin et al. (1999, 2000) and Afton and Anderson (2001) outlined several hypotheses explaining the scaup population decline, one of which was the Spring Condition Hypothesis. The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas with fewer lipid reserves than in the past, due to a decline in availability and/or quality of food resources

(Afton and Anderson 2001). Female scaup migrating through Northwestern Minnesota and arriving to breed in southwestern Manitoba had lower lipid reserves in the 2000s than did those in earlier decades (Anteau 2002, Anteau and Afton 2004). Two untested predictions of the Spring Condition Hypothesis are that forage availability and/or quality on northern stopover areas have declined. Investigations of forage resources on northern spring stopover areas are needed because forage quality (nutritional value of prey) or availability (abundance of prey) could have large effects on female lipid reserves and concomitant reproductive success (Anteau 2002, Austin et al. 2002, Anteau and Afton 2004).

Historically, scaup consumed macroinvertebrates almost exclusively in spring and amphipods were their single most consumed food during spring and summer in a variety of studies conducted throughout the Prairie Pothole Region (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Scaup use of individual wetlands is positively correlated with amphipod densities during spring migration in the upper-Midwest and breeding in prairie Canada (Lindeman and Clark 1999, Strand 2005, Chapter 9). Accordingly, I assume that amphipods are an important food for scaup during spring migration in the upper-Midwest and any decrease in amphipods in scaup diets would indicate a decrease in forage quality.

I tested one prediction of the Spring Condition Hypothesis that forage quality has declined for scaup during spring migration, by comparing current and historical diets. Specifically, I compared: (1) diets (mean aggregate percent dry mass of taxa) and mean individual prey mass (mean mass of individual taxa) of scaup at 2 important spring

stopover sites in Northwestern Minnesota in 2000 and 2001 to data from the same sites in 1986 – 1988 (Afton et al. 1991; hereafter 1980s), and (2) diets and mean individual prey mass of scaup upon arrival at a southwestern Manitoba breeding area in 2000 and 2001 to data from the same site in 1977 – 1980 (Afton and Hier 1991; hereafter 1970s).

METHODS

Study Areas

In springs 2000 and 2001, I collected diet data in: (1) Northwestern Minnesota at Thief Lake and Roseau River Wildlife Management Areas, and (2) southwestern Manitoba, on a Prairie-Parkland breeding area west of Erickson, Manitoba (between Sandy Lake and Elphinstone, Manitoba and the area 35 km south of these towns). Detailed descriptions of these locations are provided in Rogers (1959, 1964), Parker et al. (1980), and Hohman (1985).

Collection of Specimens

I collected scaup randomly with a shotgun, without decoys to avoid associated biases (Pace and Afton 1999); furthermore, collections were conducted exactly as in Afton et al. (1991). I generally collected scaup that were actively feeding; however, this was not always possible and a few scaup were collected without being observed prior to collection (Afton et al. 1991). Afton and Hier (1991) only collected actively feeding scaup, whereas collections by Afton et al. (1991) were similar to mine. In Northwestern Minnesota, I timed collections to coincide with the middle of migration, when relatively large numbers of migrating scaup were present. In southwestern Manitoba, I timed collections to begin when resident scaup (scaup attempting to breed locally) first arrived and began using small ponds and concluded before the start of rapid follicle growth in

females. I further limited collections to isolated pairs on smaller ponds, which insured a sample of resident breeding scaup (Anteau and Afton 2004).

Specimen Preparation

Immediately after collection, I preserved esophageal and proventricular contents by slowly injecting a 10% buffered formaldehyde solution down the esophagus with a syringe. Specimens then were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections. My procedures varied slightly from historical studies, in which esophageal and proventricular samples were removed and preserved prior to carcasses being frozen (Afton and Hier 1991, Afton et al. 1991).

In the laboratory, I thawed specimens and removed all food from the upper digestive tract (esophagus and proventriculus) and sorted it exactly as described in Afton and Hier (1991), and Afton et al. (1991). I weighed ($\pm 0.0001\text{g}$) sorted diet samples after being dried to a constant mass. For subsequent analyses, I grouped prey items into taxonomic groups (response variables) as in Afton and Hier (1991) and Afton et al. (1991); data were summarized by percent occurrence and aggregate percent dry mass (Swanson et al. 1974, Afton and Hier 1991, Afton et al. 1991). I calculated mean individual prey mass for each food taxon within each scaup by dividing the total mass of each taxon by the count of individual prey items in that taxon.

Statistical Analyses

I pooled samples collected in 2000 and 2001 into the 2000s decade and samples collected in 1977 – 1980 (Afton and Hier 1991) and 1986 – 1988 (Afton et al. 1991) into the 1970s and 1980s decades, respectively, because samples sizes were inadequate to test for annual variation in diets. I also pooled samples collected at Thief Lake and Roseau

River Wildlife Management Areas as in Afton et al. (1991) because of relatively small sample sizes at Roseau River WMA; however, similar proportions of specimens were collected from each of these sites in both decades. Finally, I pooled all samples over sex because current and historical diets were similar between sexes in Northwestern Minnesota and southwestern Manitoba (Afton et al. 1991, Afton and Hier 1991, 2000s data: $F_{7, 14} = 0.58, P = 0.764$; $F_{7, 53} = 0.87, P = 0.535$, respectively; multivariate analyses of variances [MANOVAs]).

Aggregate percent dry mass.-I compared aggregate percent dry mass of prey items between decades separately for Minnesota (1980s vs. 2000s) and Manitoba (1970s vs. 2000s) using MANOVA (PROC GLM, SAS Institute 2002). The response (dependent) variables were amphipods, bivalves, insects, gastropods, leeches, seeds, and vegetation (Tables 7.1 and 7.2). I also compared aggregate percent dry mass of insect sub-taxa (with > 1% aggregate percent dry mass in either decade) in scaup diets between decades (1970s vs. 2000s) in Manitoba with a MANOVA because this group was a diverse and large part of scaup diets in Manitoba (Table 7.2). The response variables were chaoborinae, chironomidae, corixidae, anisoptera, zygoptera, and trichoptera. For significant MANOVAs, I conducted an *a priori* test for a decadal effect on amphipods (except insect model); I then conducted *a posteriori* tests of other response variables using the pdiff option of the least-squares means statement on the decade effect (PROC GLM, SAS Institute 2002).

Table 7.1. Aggregate percentage dry mass and (percent occurrence) of taxa consumed by lesser scaup during spring migration in Northwestern Minnesota in decades of the 1980s (n = 57) and 2000s (n = 22).

Taxa	1980s ^a	2000s ^b
Amphipoda (<i>Gammarus</i> and <i>Hyaella</i> spp.; scuds) ^c	33.2 (51)	2.1 (32)
Bivalves (clams and mussels) ^c	6.0 (19)	26.3 (55)
<i>Musculium</i> spp. (fingernail clams)	6.0 (19)	21.4 (55)
Sphaeriidae (non- <i>Musculium</i> spp.; freshwater clams)	0 (0)	4.9 (23)
Insecta ^c	16.0 (63)	24.1 (91)
Chaoboridae (phantom midges)	0 (0)	2.8 (5)
Chironomidae (midges)	2.3 (23)	12.5 (59)
Coleoptera (water beetles)	1.9 (11)	0.1 (5)
Corixidae (water boatmen)	1.5 (14)	TR ^d (9)
Odonata (dragonflies and damselflies)	1.5 (7)	2.4 (5)
Anisoptera (dragonflies)	0.3 (4)	2.4 (5)
Zygoptera (damselflies)	1.2 (4)	0 (0)
Trichoptera (caddis flies)	8.8 (35)	6.2 (41)
Gastropoda ^c	32.0 (53)	23.1 (59)
Hydrobiidae (spire snails)	4.0 (7)	8.1 (50)
Lymnaeidae (pond snails)	2.7 (14)	0 (0)
Physidae (pouch snails)	0.4 (4)	0.5 (9)
Planorbidae (orb snails)	11.1 (26)	10.6 (36)
Valvatidae (round-mouthed snails)	11.0 (21)	3.9 (45)
Viviparidae (snails)	1.0 (4)	0 (0)
Hirudinea (leeches) ^c	1.3 (11)	6.2 (45)
Fish and fish parts <i>Culaea inconstans</i> (Kirtland, 1840)	3.5 (12)	0 (0)
Seeds ^c	6.0 (40)	6.8 (73)
Vegetation ^c	2.2 (26)	1.3 (23)
Invertebrate egg masses	0 (0)	6.8 (14)
Unidentified fragments	1.8 (5)	3.0 (9)

^a Collections conducted 1986–1987 (Afton et al. 1991).

^b Collections conducted in 2000 and 2001.

^c Response variable for overall MANOVA when testing for decadal effects.

^d Trace amounts (< 0.1 g)

Table 7.2. Aggregate percentage dry mass and (percent occurrence) of taxa consumed by lesser scaup soon after arrival on a breeding area in southeastern Manitoba in decades of the 1980s (n = 21) and 2000s (n = 61).

Taxa	1980s ^a	2000s ^b
Amphipoda (<i>Gammarus</i> and <i>Hyaletta</i> spp.; scuds) ^c	29.0 (48)	34.8 (51)
Bivalves (<i>Musculium</i> spp.; fingernail clams) ^c	0 (0)	0.9 (5)
Insecta ^c	50.3 (81)	44.5 (75)
Chaoboridae (phantom midges) ^d	1.7 (10)	TR ^e (2)
Chironomidae (midges) ^d	18.8 (38)	40.3 (66)
Coleoptera (water beetles)	0.6 (29)	0.2 (10)
Corixidae (water boatmen) ^d	4.9 (19)	0.2 (8)
Ephemeroptera (mayflies)	0.5 (10)	TR (2)
Odonata	9.6 (29)	3.0 (23)
Anisoptera (dragonflies) ^d	3.9 (5)	0 (0)
Zygoptera (damselflies) ^d	5.7 (29)	3.0 (23)
Tabanidae (horseflies)	0.1 (5)	0 (0)
Trichoptera (caddis flies) ^d	14.1 (43)	0.8 (10)
Gastropoda ^c	0.3 (5)	4.7 (20)
Hirudinea (leeches) ^c	17.4 (43)	8.6 (31)
Seeds ^c	2.8 (33)	4.5 (46)
Vegetation ^c	0.3 (5)	1.2 (23)
Unidentified fragments	0 (0)	0.9 (7)

^a Collections conducted 1977–1980 (Afton and Hier 1991; pre-rapid follicle growth).

^b Collections conducted in 2000 and 2001.

^c Response variable for overall MANOVA testing for decadal effects.

^d Response variable for insect MANOVA testing for decadal effects.

^e Trace amounts (< 0.1 g)

Mean individual prey mass.—I compared mean individual prey mass between decades separately for Minnesota (1980s vs. 2000s) and Manitoba (1970s vs. 2000s) using separate analyses of variances (ANOVAs, PROC GLM, SAS Institute 2002) for each response variable (Tables 7.1 and 7.2). I could not use a MANOVA because not all response variables were represented in each individual diet sample. Vegetation was excluded from these analyses because I assumed that sizes of vegetation fragments varied randomly. I conducted decadal tests of mean individual prey mass on chironomids and zygoptera in Manitoba, but small sample sizes ($n \leq 15$ [both decades]) precluded me from conducting decadal tests in other insect sub-taxa.

RESULTS

Northwestern Minnesota

Overall, mean aggregate percentages of taxa differed between decades ($F_{7, 71} = 4.0$, $P < 0.001$). Mean aggregate percentage of amphipods in the 2000s (hereafter current) was 94% lower than that in the 1980s (hereafter historic); conversely, current mean aggregate percentage of bivalves was 77% higher than that of historical levels (Figure 7.1). Percent occurrence of amphipods in current diets was 19% lower than historical diets; however, 32% of current scaup diets contained amphipods despite their low aggregate percentage (Table 7.1). Aggregate percent of chironomids in current diets (12.5%, SE = 3.7) was 82% higher ($R^2 = 0.07$, $F_{1, 77} = 5.48$, $P = 0.022$; ANOVA) than that of historical diets (2.3%, SE = 2.3).

The current mean individual prey mass of amphipods (1.22 mg, SE = 1.64) was 87% ($R^2 = 0.35$, $F_{1, 34} = 18.59$, $P < 0.001$) lower than the historical mean prey mass (9.10

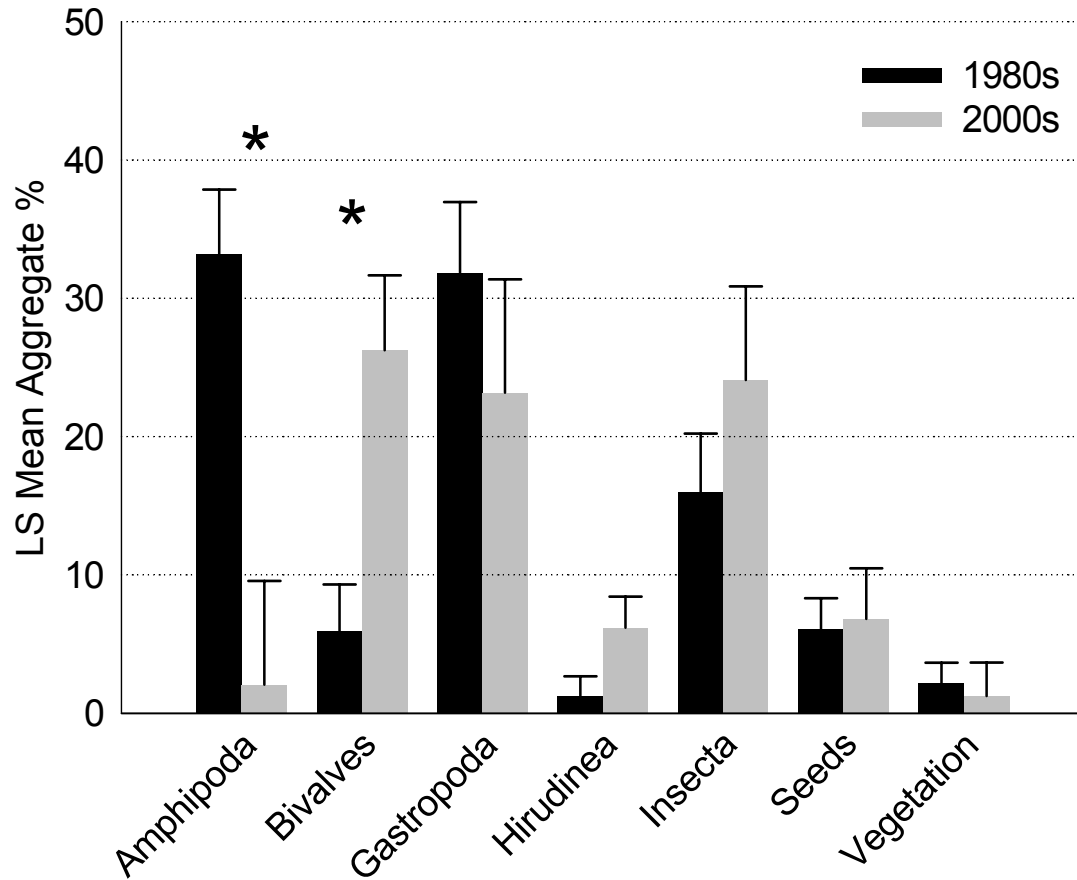


Figure 7.1. Least-square means (\pm SE) from MANOVA testing for decadal effects (1986 – 1988 versus 2000 and 2001) on foods (aggregate percent dry mass) consumed by lesser scaup in Northwestern Minnesota during spring migration. Asterisks above bar groups indicate significant differences (α 0.05) between decades.

mg, SE = 0.81). Similarly, current mean individual prey mass of bivalves (3.31 mg, SE = 8.73) was 85% (nearly one order of magnitude; $R^2 = 0.10$, $F_{1,21} = 2.24$, $P = 0.149$) lower than the historical mean prey mass (22.21 mg, SE = 9.12), although this difference was not statistically significant at *alpha* 0.05.

Southwestern Manitoba

Mean aggregate percentages of all taxa were similar between decades ($F_{7,74} = 0.99$, $P = 0.443$), but analysis of insect sub-taxa indicates that insect composition of diets has shifted between decades ($F_{7,74} = 5.24$, $P < 0.001$; Figure 7.2). Specifically, current aggregate percentages of trichoptera and chaoboridae in diets were 94% and 100% lower than historical diets (1970s), respectively; however, aggregate percent of chironomids in current diets was 53% higher than that of historical diets (Figure 7.2).

Current mean individual prey mass of all insects was 64% lower ($R^2 = 0.06$, $F_{1,61} = 3.99$, $P = 0.050$) than that of historical diets (Figure 7.3); current mean individual prey mass of chironomids and zygoptera were 44 ($R^2 = 0.23$, $F_{1,46} = 13.37$, $P < 0.001$) and 45% ($R^2 = 0.31$, $F_{1,18} = 7.92$, $P = 0.012$) lower than those of historical diets, respectively (Figure 7.3). Similarly, mean individual prey mass of seeds in current diets was 65% lower ($R^2 = 0.13$, $F_{1,33} = 5.06$, $P = 0.031$) than that of historical diets (Figure 7.3).

DISCUSSION

Northwestern Minnesota

Amphipods over-winter as adults in semipermanent and permanent wetlands, and their lipid reserves are highest in late fall and early spring (Mathias et al. 1982, Arts et al. 1995, Meier et al. 2000), whereas, lipid reserves in bivalves and insects generally peak in mid to late summer (Davis and Wilson 1983, Meier et al. 2000). Amphipods generally

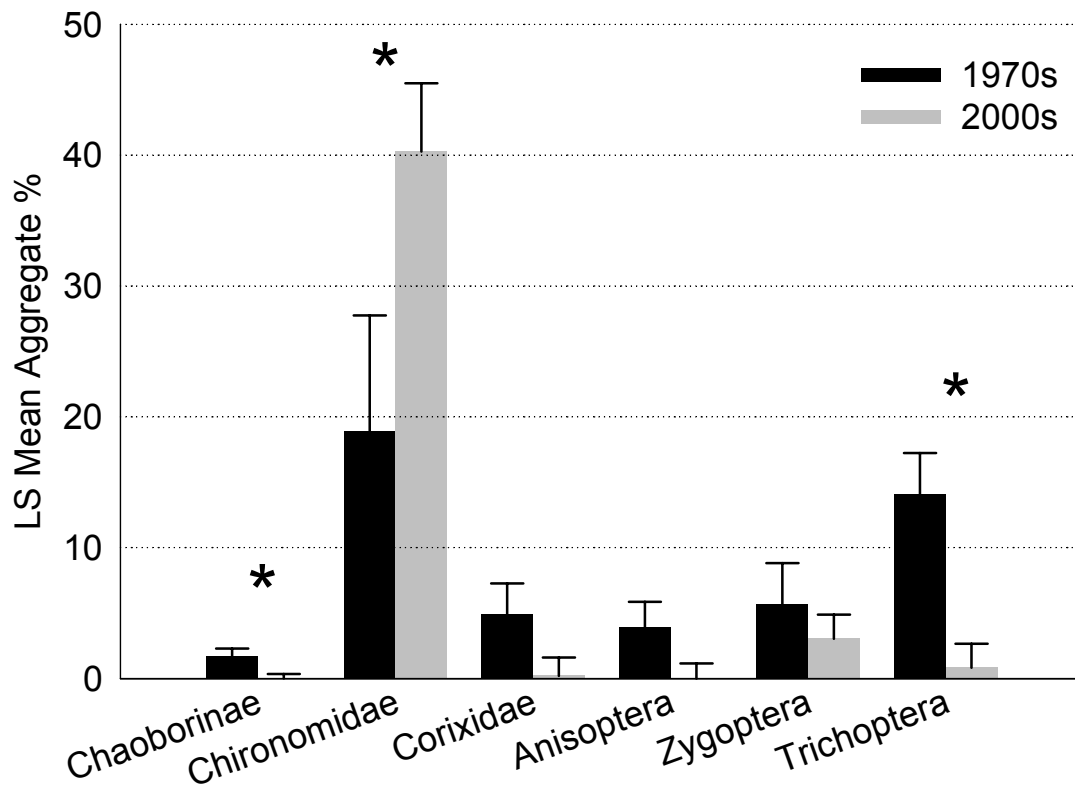


Figure 7.2. Least-square means (\pm SE) from MANOVA testing for decadal effects (1977 – 1980 versus 2000 and 2001) on insects (aggregate percent dry mass) consumed by lesser scaup soon after their arrival on a breeding area in southwestern Manitoba. Asterisks above bar groups indicate significant differences (α 0.05) between decades.

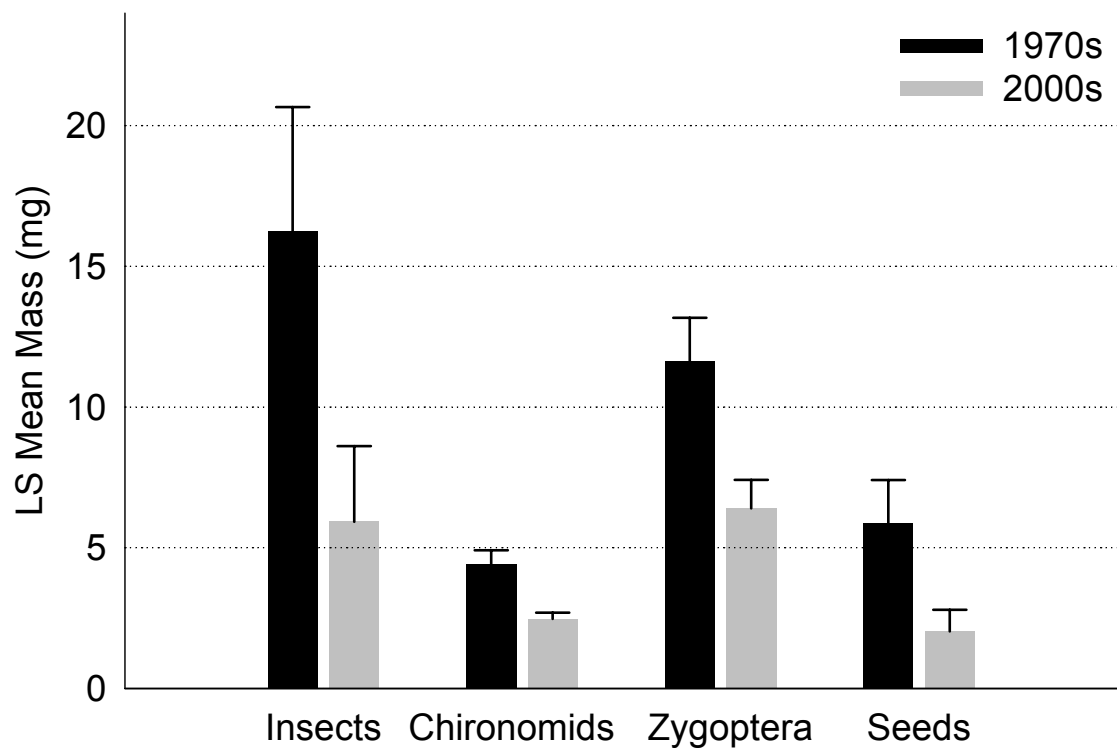


Figure 7.3. Least-square means ($\text{mg} \pm \text{SE}$) from significant ($\alpha 0.05$) ANOVAs testing for decadal effects (1977 – 1980 versus 2000 and 2001) on mean individual prey mass of foods consumed by lesser scaup soon after their arrival on a breeding area in southwestern Manitoba

have over 4 times higher gross energy, over 3 times higher protein, and over 4 times higher lipids than do bivalves or gastropods (Sugden 1978, Jorde and Owen 1988, Ballard et al. 2004). The relatively large lipid reserves of amphipods in spring probably facilitates accumulation of lipid reserves by scaup because scaup diets primarily are protein based (Afton and Hier 1991, Afton et al. 1991). In the absence of dietary lipids, scaup must synthesize endogenous lipid reserves from dietary protein or carbohydrate, which is less efficient than simply assimilating fatty acids from their diet to endogenous lipid reserves (Alisauskas and Ankney 1992).

Amphipods seemingly are the single most preferred food of scaup during spring migration and early summer in the Prairie Pothole Region because: (1) historically amphipods comprised a proportion of scaup diets (1960s – 1980s; Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991), (2) amphipod densities are a good predictor of wetland use by scaup (Lindeman and Clark 1999, Strand 2005, Chapter 9), but chironomid (another principal food) densities are not (Strand 2005, Chapter 9), (3) amphipods have relatively high nutritional values during spring, and (4) percent occurrence of amphipods observed in current scaup diets remained high, relative to the 94% decrease aggregate percentage of amphipods consumed. Accordingly, I argue that the observed shift from amphipods to bivalves in scaup diets during spring migration in Minnesota (between decades) has resulted in a decrease in forage quality consistent with the Spring Condition Hypothesis.

The observed decrease in mean individual prey mass of amphipods and bivalves between decades may be indicative of a decline in forage quality. Small prey items

require longer foraging and handling times to procure similar amounts of nutrients (Matthews et al. 1992, Lovvorn and Gillingham 1996, Richman and Lovvorn 2004). In addition, larger prey items within a given taxa (e.g., amphipods and bivalves) might be more nutritious because they have lower ratios of chitin or shell to meat due to the allometric relationship of surface area to volume (Ricklefs 1990). The percentage of shell was higher in bivalves 5 – 10 mm long than in those 10 – 15 mm long, but at longer lengths (> 15 mm) percentages of shell increase (Bustnes 1998); suggesting that meat to shell ratios follow a quadratic relationship. Diving ducks select against bivalves of large size (~ 260 – 570 mg or ~15 – 24 mm; De Leeuw and Van Eerden 1992, Hamilton et al. 1999, Richman and Lovvorn 2004). However, mean individual mass of bivalves observed in scaup diets (3.31 mg currently and 22.21 mg historically) were much smaller than those selected against in previous studies; thus, I assume that consuming larger bivalve prey is more nutritious, within the range of mass I observed.

Amphipods generally yield over 2 times higher true metabolizable energy (TME) than do bivalves and gastropods in black ducks (*Anas rubripes*; Jorde and Owen 1988) and 3 times higher TME than do bivalves and gastropods in northern pintails (*Anas acuta*; Ballard et al. 2004), and 3 times higher TME than gastropods in blue-winged teal (*Anas discors*; Sugden 1978). Scaup are more efficient at assimilating energy from amphipods than are blue-winged teal (Sugden 1978). The observed diet shift, from 33 % amphipods and 6 % bivalves historically to 2 % amphipods and 26 % bivalves currently, results in TME to be 65 and 94 % lower, based on TME estimates of amphipods and bivalves for black ducks and northern pintails, respectively (Jorde and Owen 1988, Ballard et al. 2004). However, these calculations are based on TME of similar prey taxa,

but for different duck species and do not account for changes in prey size and seasonal variation in nutritional values of prey.

The decadal decrease in amphipods in scaup diets in Minnesota parallels an earlier finding of a 28.8 g (30%; equivalent to 4.2 eggs) decadal decrease in lipid reserves of scaup (Anteau 2002, Anteau and Afton 2004). Together these results strongly suggest that there has been a decline in forage quality and/or availability in the upper-Midwest. The observed decreases in abundance and size of amphipods in scaup diets are consistent with increased fish predation on amphipods in wetlands (Matthews et al. 1992, Wellborn 1994; Wooster 1998, Hilton et al. 2002). However, global climate change, sedimentation, and agricultural runoff also could be contributing or interacting factors affecting the availability of amphipods and other foods for scaup (Anteau 2002, Anteau and Afton 2004).

Although consistent with the Spring Condition Hypothesis, my results are from only 2 sites in Northwestern Minnesota and sample sizes were relatively small in 2000 and 2001; however, effect sizes in diet differences are relatively large. Furthermore, diet data can be used to assess forage quality, but it cannot be used to directly assess availability of forage. Regardless, I surmise that amphipod abundance has declined because scaup shifted their diets from primarily amphipods (thought to be a highly preferred food) to bivalves (thought to be a lesser preferred food). Accordingly, landscape scale studies are clearly needed to determine the scope of this potential decline in forage quality and to estimate forage availability for scaup during spring migration in the upper-Midwest.

Female scaup arrived on the Manitoba breeding area in spring 2000 and 2001 with 3.2 g fewer mineral reserves than did those in the 1970s (equivalent to 0.8 eggs of minerals), but had similar amounts of mineral reserves between decades in Minnesota (Anteau and Afton 2004). Scaup currently may be deriving a calcium benefit from consuming larger amounts of bivalves than that historically. However, accumulation of calcium reserves probably is not driving the selection of dietary prey because unlike lipid reserves, calcium is largely acquired from exogenous sources on breeding areas (Afton and Ankney 1991, Esler et al. 2001), a pattern mirrored by the peak in consumption of bivalves and gastropods during rapid follicle development and egg laying (Afton and Hier 1991).

Southwestern Manitoba

Female scaup arrived on the Manitoba breeding area in springs 2000 and 2001 with 27.8 g fewer lipid reserves than did those in the 1970s (Anteau 2002, Anteau and Afton 2004). Anteau (2002) speculated that scaup in Manitoba had lower lipid reserves due to factors on preceding migration stopover areas because scaup were collected there soon after arrival. Thus, current diets of scaup probably had little influence on lipid-reserve levels observed by Anteau (2002) and Anteau and Afton (2004), but may influence lipid-reserve levels later in the breeding season.

Compositions of scaup diets in Manitoba were similar between decades, indicating no change in forage quality, but sample sizes were small for the 1970s. However, the observed decadal shift from trichoptera to chironomids in scaup diets may have affected forage quality (Figure 7.2). However, there appear to be no clear, marked, or consistent indications of differences in nutritional quality between chironomids and

trichoptera (Driver et al. 1974, Driver 1981, Sushchik et al. 2003). TME estimates of these prey for scaup would be informative for understanding how this shift affects forage quality for scaup.

The observed lower mean individual prey mass of insects in current diets was partly due to a shift from large taxa (anisoptera and trichoptera) to smaller taxa (chironomids; Table 7.2). However, mean individual prey mass of chironomids and zygoptera decreased 44.1 and 44.9 %, respectively between the 1970s and 2000s (Figure 7.3), indicating that these prey sub-taxa may currently be under more predation pressure (Matthews et al. 1992, Wellborn 1994; Hilton et al. 2002). Declines in mean individual prey mass probably result in a decrease in forage quality for scaup.

Mean individual prey mass of seeds in current diets also were lower than those historically, possibly due to a species shift in seeds consumed. However, I did not identify taxa of seeds because of their low fraction in scaup diets. Afton and Hier (1991) found that seeds were a preferred food of scaup during pre-rapid follicle growth and egg laying in Manitoba. A diet shift from larger to smaller seeds could influence the ability of scaup to accumulate lipid reserves because seeds are a good source of carbohydrates and lipids (Afton and Hier 1991, Ballard et al. 2004). However, the decadal differences in individual seed mass in scaup diets probably had a minimal effect on scaup lipid reserves, given the low percentage of seeds in scaup diets in both decades (Table 7.2).

Implications for Conservation of Lesser Scaup

Availability of highly nutritious forage for scaup on northern spring stopover areas could be one of the factors influencing the scaup population decline and deserves further research (Afton and Anderson 2001, Anteau 2002, Anteau and Afton 2004).

Restoring wetland quality to historical levels and increasing availability of nutritional foods, such as amphipods, at spring stopover areas in the upper-Midwest should help to increase lipid reserves of female scaup and may help to reverse the population decline. Finally, several research questions should be addressed to further test the Spring Condition Hypothesis and provide for effective scaup conservation: (1) Are decreases in scaup lipid reserves and in forage quality and availability widespread on northern spring stopover areas in the upper-Midwest?; (2) Are decreases in scaup lipid reserves causing reduced reproductive success or survival of females?; (3) Are factors other than forage quality and availability involved in declines in scaup lipid reserves?; (4) What factors influence the availability of quality scaup forage in the upper-Midwest?; and (5) What management strategies and techniques are effective in preventing further losses in forage and wetland quality and for restoring critical spring stopover habitat for scaup and other species?

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CHAPTER 8: DIETS OF LESSER SCAUP DURING SPRING MIGRATION THROUGHOUT THE UPPER-MIDWEST ARE CONSISTENT WITH THE SPRING CONDITION HYPOTHESIS

INTRODUCTION

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly since 1978 (Austin et al. 1998, Afton and Anderson 2001); population estimates were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. The segment of the scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through the upper-Midwest comprise a major component of the continental population, and likely is experiencing the largest decline in numbers (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup, and northern spring stopover areas are important for the accumulation of these reserves (Afton 1984, Afton and Ankney 1991, Pace and Afton 1999, Anteau and Afton 2004). The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas in lower body condition than in the past (Afton and Anderson 2001). Female scaup currently migrating throughout the upper-Midwest have fewer lipid reserves (Anteau and Afton 2004, Chapter 2) and catabolize lipid reserves as they migrate throughout the upper-Midwest (Chapter 4).

Two predictions of the Spring Condition Hypothesis is that forage availability (abundance of prey) and/or quality (nutritional value of prey) in northern stopover areas

have declined. Historically, scaup consumed macroinvertebrates almost exclusively in spring, and amphipods were predominant food during spring and summer in the upper-Midwest (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Densities of amphipods are positively correlated with use of particular wetlands by scaup in spring and summer (Lindeman and Clark 1999, Strand 2005, Chapter 9). Moreover, fewer amphipods in scaup diets indicate lower forage quality (Anteau and Afton 2006). The percentage of amphipods in scaup diets decreased markedly from historical values in Northwestern Minnesota (2000 – 2001; hereafter NW00), and amphipod densities in wetlands across the upper-Midwest in 2004 – 2005 were low, suggesting that there has been a landscape-scale decline in amphipods (Anteau and Afton 2006, Chapter 6). Accordingly, I conducted a landscape-scale investigation of scaup diets on northern spring stopover areas because forage quality or availability could have large effects on female body condition and concomitant reproductive success (Anteau 2002, Austin et al. 2002, Anteau and Afton 2004, Anteau and Afton 2006).

Specifically, I tested a prediction of the Spring Condition Hypothesis by comparing percentages of *Gammarus lacustris* (hereafter *Gammarus*) and *Hyaella azteca* (hereafter *Hyaella*) amphipods in diets (mean aggregate percent dry mass of taxa) of scaup during spring migration collected throughout the upper-Midwest in 2003 – 2005 to those of scaup in NW00. A decrease in amphipods in scaup diets likely results in a decrease in forage quality (Anteau and Afton 2006), thus amphipod consumption in the upper-Midwest similar to decreased levels observed in NW00 would indicate a decrease in forage quality in scaup diets there. Furthermore, I explored potential regional

differences in diet composition, feeding success (proportion of females with food present), and food mass (mass of entire food sample).

METHODS

Study Area

I collected scaup in the Prairie Pothole Regions of Iowa, Minnesota, and North Dakota (Figure 8.1). This area comprises the most important spring migration stopover areas for scaup within the upper-Midwest, based on observations of wildlife biologists and managers, band-recovery data, sightings of color-marked scaup, and aerial surveys in spring (Low 1941; Afton and Hier 1985; Afton et al. 1991; Pace and Afton 1999; Minnesota Department of Natural Resources, unpublished data; North Dakota Game and Fish Department, unpublished data). I stratified the 3-state area into 7 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 8.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

Sampling design and allocation.—I used constrained-random sampling techniques to select collection sites in all regions except Northwestern Minnesota. I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 8.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service,

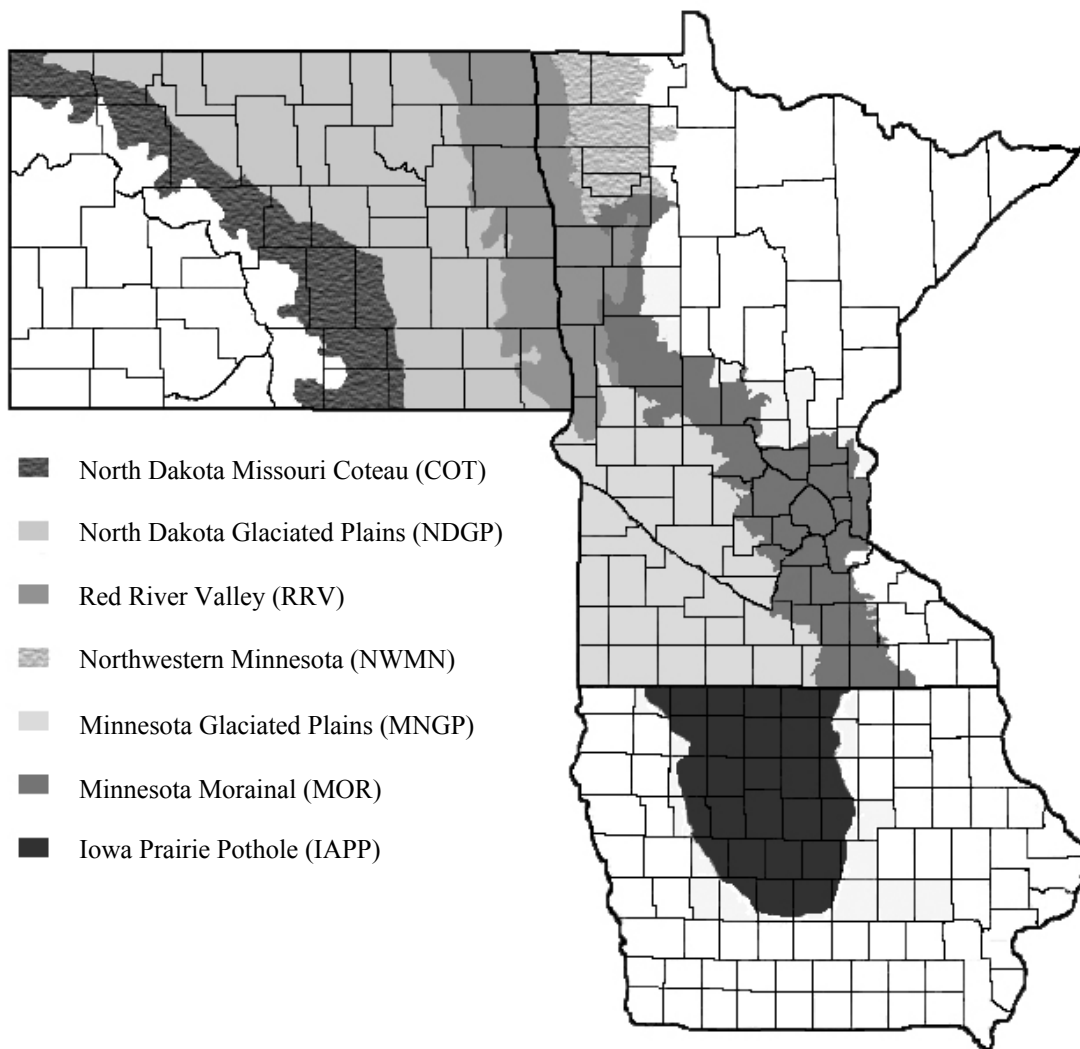


Figure 8.1. Map of the study area depicting 7 eco-physiographic regions for lesser scaup collections (2003 – 2005) during spring migration in the upper-Midwest. Areas in white were not sampled.

Table 8.1. Numbers of randomly selected collection sites each year, numbers of lesser scaup diet samples (N), and candidate townships (T) available for random selection of collection sites by eco-physiographic region.

Region	Sites	N ^a	T
North Dakota Missouri Coteau	3	49	208 ^b
North Dakota Glaciated Plains	6	73	364 ^b
Red River Valley	3	25	66 ^b
Northwestern Minnesota	3 ^c	37	n/a
Minnesota Glaciated Plains	4	41	285 ^b
Minnesota Morainal	4	25	348 ^b
Iowa Prairie Pothole	3	13	43 ^d

^a Includes 20 males collected in 2003 – 2005.

^b Townships that contain at least 200 hectares of semipermanent wetlands.

^c Fixed collection sites (see methods).

^d Townships that contain at least 200 hectares total of semipermanent and permanent wetlands.

Bismarck North Dakota, unpublished data; S. Piepgras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or permanent wetlands. I then allocated numbers of collection sites among the 6 regions (3 to 6 sites per region; Table 8.1) based on region size and number of candidate townships available (Table 8.1, Figure 8.1). Each region was divided into equal-sized sub-regions based on latitude, such that there was 1 collection site per sub-region each year (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 collection sites for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 8.1).

Collection sites.-Each collection site (27,972 ha) was comprised of three 36-square-mile townships in order to insure adequate collection opportunities; however, in some instances I had to replace townships with another randomly selected township because the original selected township no longer had suitable scaup habitat (semipermanent or permanent wetlands) or had little or no scaup use (17% of townships where collections occurred). I attempted to collect 10 females from each collection site. I randomly selected new townships annually within each sub-region from the list of candidate townships to maximize representation of spatial variability in scaup diets. In 2004 and 2005, I further constrained township selection so that the centrum of the second and third townships selected were within 50 km of the centrum of the first randomly selected township to minimize travel by field crews. In Northwestern Minnesota, collections were conducted on the same sites annually (Agassiz National Wildlife Refuge and Thief Lake and Roseau River Wildlife Management Areas; Table 8.1) thus, data

were comparable to other data sets (Afton et al. 1991, Anteau and Afton 2006). I attempted to collect 15 females from each of these fixed sites annually in 2003 – 2005 (hereafter NWMN).

Collection of Specimens

I collected female scaup randomly with a shotgun, without the use of decoys to avoid associated biases (Pace and Afton 1999); collections were conducted exactly as in Afton et al. (1991) and Anteau and Afton (2004, 2006). In all regions, I attempted to collect females that were feeding, so that feeding success and food mass would be comparable among regions. I generally timed collections to occur during the middle of migration, coinciding with relatively large numbers of migrating scaup present. I obtained diet samples from 263 scaup in springs 2003 – 2005 (Table 8.1); diet samples from 20 male scaup were included in my data set (collected in 2003 – 2005) because scaup diets in spring are similar between sexes (Afton et al. 1991, Afton and Hier 1991, Anteau and Afton 2006). In Iowa Prairie Pothole (IAPP) region, I only collected scaup and diet samples in 2004 – 2005.

Specimen Preparation

Immediately after collection, I preserved esophageal and proventricular contents by slowly injecting a 10% buffered formaldehyde solution down the esophagus with a syringe. Specimens then were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections.

In the laboratory, I thawed specimens and removed all food from the upper-digestive tract (esophagus and proventriculus) and sorted it exactly as described in Afton and Hier (1991), and Afton et al. (1991). I occasionally detected a reflux or reverse

movement of ingesta from the gizzard into the upper-digestive tract (when food was absent in the upper-digestive tract). This resulted in the upper-gut containing seeds, shell fragments, and pebbles. I minimized this potential bias by excluding samples from the analysis that only had shell fragments, seeds, and pebbles in the upper-gut, if this ingesta matched that of the gizzard. I weighed ($\pm 0.0001\text{g}$) and sorted foods after being dried to a constant mass at 60°C . For subsequent analyses, I grouped foods into taxonomic groups (response variables) as in Afton et al. (1991) and Anteau and Afton (2006); data were summarized by aggregate percent dry mass and percent occurrence (Swanson et al. 1974, Afton et al. 1991).

Statistical Analyses

I included diet data from 22 scaup collected in 2000 – 2001 at Thief Lake and Roseau River (Anteau and Afton 2006) for reference; those data were included into subsequent analyses as a separate region (Northwestern Minnesota 2000 – 2001 [NW00]). I pooled samples over years and assumed that annual variation was less important than spatial variability (Afton and Hier 1991, Afton et al. 1991, Anteau and Afton 2006, Chapter 6). Furthermore, the variable year could have a spatial element because I randomly selected collection sites annually without replacement to maximize spatial representation.

I compared aggregate percent dry mass of foods (*Gammarus*, *Hyalella*, bivalves, insects, gastropods, leeches, seeds; Table 8.2) among regions with a MANOVA (PROC GLM; SAS Institute 2002). I conducted *a priori* tests for regional differences in *Gammarus* and *Hyalella* least-squares means between each region and NW00 (Dunnett adjusted pdiff-control option; $\alpha 0.05$; PROC GLM; SAS Institute 2002). I then

Table 8.2. Aggregate percentage dry mass of taxa consumed by lesser scaup (n = 263) during spring migration in 2003 – 2005 by eco-physiographic regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole).

Taxa	COT	NDGP	RRV	NWMN	MNGP	MOR	IAPP
Amphipoda (scuds)	55.4	48.6	19.5	20.4	7.9	23.4	2.7
<i>Gammarus lacustris</i> ^a	37.4	26.3	15.8	17.5	4.3	16.0	0
<i>Hyaella azteca</i> ^a	18.0	22.3	3.7	2.9	3.6	7.4	2.7
Bivalves (<i>Musculium</i> sp.; fingernail clams) ^a	0.3	TR ^b	1.1	2.6	1.3	1.6	0
Anostraca (fairy shrimp)	1.0	0	0	0	0	0	0
Ostracoda (mussel or seed shrimp)	0	0	3.0	0	6.7	1.5	0.6
Insecta^a	31.3	33.9	54.2	49.0	45.8	49.3	63.6
Ceratopogonidae (biting midges)	0	0	TR	0	0.3	TR	2.5
Chaoboridae (phantom midges)	0	0	4.0	0	0.2	0.5	2.2
Chironomidae (true midges)	26.4	25.3	43.2	46.8	42.7	34.4	50.8
Coleoptera (water beetles)	0.1	1.2	0	TR	0.1	0	0
Corixidae (water boatmen)	1.9	1.3	TR	0.1	1.3	4.3	0
Ephemeroptera (mayflies)	0	0	0	0	0.3	9.5	0
Trichoptera (caddis flies)	1.5	1.2	7.0	2.0	0.4	0.1	2.4

continued ...

Table 8.2 continued

Taxa	COT	NDGP	RRV	NWMN	MNGP	MOR	IAPP
Zygoptera (damselflies)	1.4	4.7	TR	0.1	0.5	0.3	0
Insect fragments	0	0.2	0	0	0	0.2	5.7
Isopoda (freshwater hoglouse)	0	0	0	0	0	0.1	0
Gastropoda^a	4.9	4.5	14.8	12.5	7.7	11.2	0
Hydrobiidae (spire snails)	0.1	1.6	7.3	0	0	0.4	0
Physidae (pouch snails)	1.5	0.4	2.9	0.1	0.8	0.7	0
Planorbidae (orb snails)	3.3	2.5	4.6	9.2	4.5	10.1	0
Valvatidae (round-mouthed snails)	0	0	0	2.7	2.4	0	0
Unidentified parts	0	0	0	0.5	0	0	0
Oligochaeta (aquatic worms)	TR	0	0.2	0	0	0	1.1
Hirudinea (leeches) ^a	1.4	4.9	4.0	3.6	6.3	4.7	7.4
Hydrachnidae (water mites)	TR	TR	0	0	0.1	TR	0
Fish and fish fragments	0	1.2	0.1	0	0	0	7.6
Seeds (seeds, nutlets, achenes) ^a	5.4	5.0	2.1	11.9	22.0	6.6	15.1
Vegetation fragments	TR	0.3	TR	0	0	1.2	1.9
Tubers	0	1.3	0	0	0	0	0
Algae (filamentous)	0	0	0	0	2.4	0	0

^a Response variable for MANOVA testing for regional effects^b Trace amounts (< 0.1%).

conducted *a posteriori* contrasts for regional differences in bivalves, insects, gastropods, leeches, and seeds using Tukey-Kramer adjusted least-squares-mean groupings (pdiff-all option; α 0.05; PROC GLM; SAS Institute 2002).

I examined regional variation in feeding success (number of females with diet samples over the total females collected in each region) with a logistic regression (binomial distribution, logit link; PROC GENMOD; SAS Institute 2002). I also compared diet sample mass (dry mass of total food sample) of scaup that had diet samples among regions with an ANOVA (PROC MIXED; SAS Institute 2002); diet sample mass were log-transformed to conform residuals to normality.

RESULTS

The overall composition of diets differed among regions ($F = 4.42$; $P < 0.001$). Aggregate percentages of *Gammarus* and *Hyalella* in NW00 were similar to those of IAPP, Minnesota Morainal (MOR), Minnesota Glaciated Plains (MNGP), Red River Valley (RRV), and NWMN; however, aggregate percentages of *Gammarus* and *Hyalella* in North Dakota Missouri Coteau (COT) and NDGP were higher than those in NW00 (Figure 8.2). Aggregate percentage of leeches did not vary among regions ($F = 0.42$, $P = 0.891$). Aggregate percentages of insects also were similar among regions after Tukey-Kramer adjustment for multiple comparisons (Figure 8.2). Aggregate percentages of gastropods in NDGP, and COT were lower than those in NW00 (Figure 8.2). Scaup consumed more bivalves in NW00 than in all other regions (Figure 8.2). Aggregate percentages of seeds in scaup diets were higher in MNGP than that of those in RRV, NDGP, and COT. Scaup migrating through IAPP consumed primarily insects (63.6%) and seeds (15.1%; Figure 8.2).

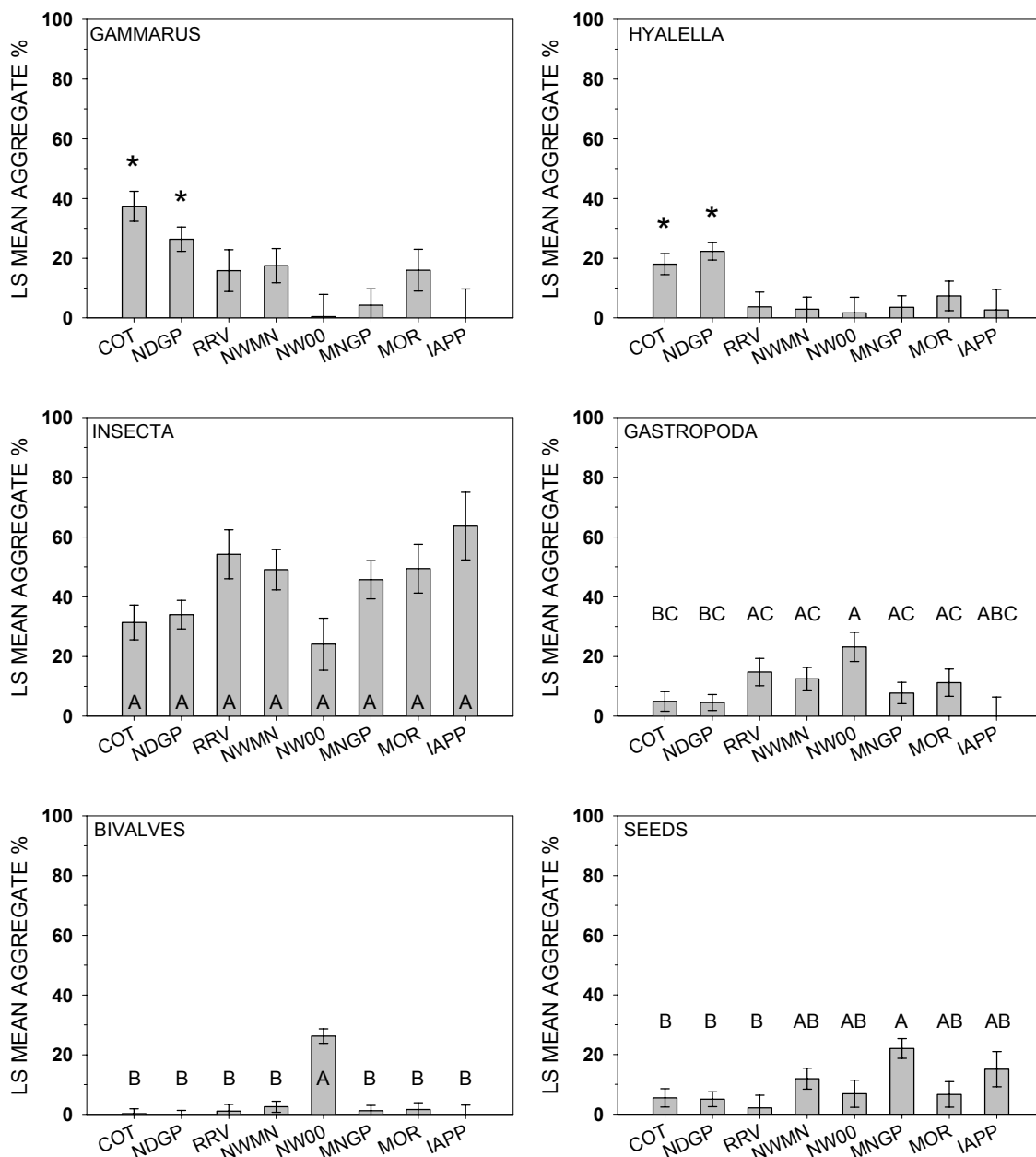


Figure 8.2. Least-square mean aggregate percent dry mass (\pm SE) of foods consumed by lesser scaup collected during spring migration in 2003 – 2005 (unless otherwise stated) by region. Regions are depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, NW00 = Northwestern MN (Thief Lake and Roseau River WMAs) in 2000 – 2001 (see Anteau and Afton 2005), MNGP = MN Glaciated Plains, MOR = MN Morainial, and IAPP = IA Prairie Pothole. Asterisks indicate significance ($P < 0.05$) of Dunnett adjusted *a priori* contrasts between each region and NW00 within *Gammarus* and *Hyalella* plots. Capital letters at bottom are Tukey-Kramer adjusted mean grouping ($P < 0.05$) for *a posteriori* contrasts of each taxa between regions.

Percent occurrences of amphipods generally were higher and seeds were lower in COT, NDGP, and RRV than those in NWMN, MNGP, MOR, and IAPP (Table 8.3).

Percent occurrences of bivalves generally were low in all regions, but highest in NWMN (Table 8.3).

Feeding success varied among regions ($\chi^2_{6, 634} = 17.97, P = 0.006$; Figure 8.3). Females in IAPP were 3.9 ($\chi^2 = 11.72, P < 0.001$) and 3.0 ($\chi^2 = 8.44, P = 0.004$) times less likely to have consumed food prior to collection than had those in COT and NDGP, respectively. Similarly, females in NWMN were 2.3 ($\chi^2 = 7.61, P = 0.006$) and 1.7 ($\chi^2 = 4.25, P = 0.039$) times less likely to have acquired food prior to collection than those in COT and NDGP, respectively. Food mass were similar among regions ($F = 1.37; P = 0.227$) for scaup that had consumed food (overall geometric mean = 79 mg [dry]).

DISCUSSION

Several lines of evidence indicate that scaup strongly prefer amphipods as food during spring migration in the upper-Midwest. First, amphipods historically were the predominate food in a variety of locations and years during spring and early summer (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Second, scaup use of wetlands is positively correlated to amphipod densities (Lindeman and Clark 1999, Strand 2005, Chapter 9), but not correlated to chironomid densities, another frequently consumed food (Strand 2005, Chapter 9). Third, scaup continue to consume amphipods at high aggregate percentages in NDGP and COT (Table 2, Figure 8.2) despite apparent declines in their availability across the upper-Midwest (Chapter 6). Fourth, percent occurrences of amphipods in scaup diets generally were high in all regions (Table 8.3).

Table 8.3. Percent occurrence of major taxa consumed by lesser scaup (n = 263) during spring migration in 2003 – 2005 by eco-physiographic regions (COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, NWMN = Northwestern MN, MNGP = MN Glaciated Plains, MOR = MN Morainal, IA = IA Prairie Pothole).

Taxa	COT	NDGP	RRV	NWMN	MNGP	MOR	IAPP
Amphipoda (scuds)	76	68	60	37	29	44	15
<i>Gammarus lacustris</i>	53	40	28	22	7	16	0
<i>Hyaella azteca</i>	37	47	52	22	27	28	15
Bivalves (<i>Musculium</i> sp.; fingernail clams)	2	1	12	31	2	8	0
Insecta	63	66	80	85	73	68	92
Gastropoda	24	18	36	46	29	28	0
Hirudinea (leeches)	14	22	16	25	17	16	8
Seeds (seeds, nutlets, achenes)	27	29	28	56	54	48	46

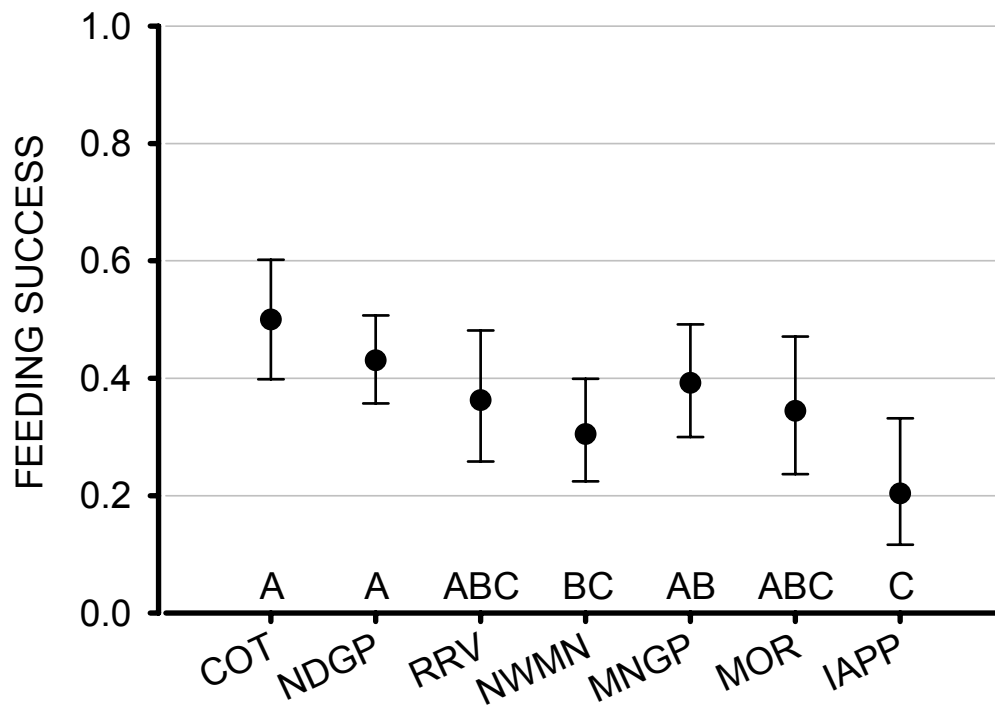


Figure 8.3. Least-squares mean probability of scaup collected had consumed food (feeding success; \pm 95% CI) by regions in the upper-Midwest in springs 2003 - 2005. The regions are depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Means with same letter beneath region labels are similar ($P > 0.05$).

Amphipods have higher gross energy, protein, and lipids than do bivalves and gastropods (Jorde and Owen 1988, Ballard et al. 2004); amphipods also have higher true metabolizable energy than do bivalves and gastropods when consumed by ducks (Sudgen 1978, Jorde and Owen 1988, Ballard et al. 2004). Furthermore, scaup are more efficient at assimilating energy from amphipods than other ducks (see Sugden 1978, Jorde and Owen 1988, Ballard et al. 2004) suggesting that scaup are highly adapted to a diet of amphipods.

Amphipods over-winter as adults in semipermanent and permanent wetlands and their lipid reserves are highest in late fall and early spring (Mathias et al. 1982, Arts et al. 1995, Meier et al. 2000); whereas, lipid reserves in bivalves and insects generally peak in mid to late summer (Davis and Wilson 1983, Meier et al. 2000). Relatively large lipid reserves of amphipods in spring may facilitate accumulation of lipid reserves by scaup because scaup diets, otherwise, are mainly protein based (Afton and Hier 1991; Afton et al. 1991). In the absence of dietary lipids, scaup must synthesize endogenous lipid reserves from dietary protein or carbohydrate, which is less efficient than simply assimilating fatty acids from their diet to endogenous lipid reserves (Alisauskas and Ankney 1992). Thus, the apparent decreases in the percentage of amphipods in scaup diets during spring migration in Iowa and Minnesota probably reflects a decrease in forage quality for scaup there (Anteau and Afton 2006).

In the 1960s, aggregate percentages of amphipods in scaup diets, during spring and early summer throughout the Prairie Pothole Region, ranged from 46 – 67 (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson

and Duebbert 1989). In the 1980s, aggregate percentages of amphipods ranged from 29 – 33 (Afton and Hier 1991, Afton et al. 1991) and aggregate percentages were much lower in Northwestern Minnesota in 2000 – 2001 (Anteau and Afton 2006). Thus, historical data and my results are consistent with a decreased in aggregate percentages of *Gammarus* and *Hyaella* amphipods consumed by scaup in Iowa and Minnesota (Table 8.2, Figure 8.2); aggregate percentage of amphipods in Northwestern Minnesota in 2000 – 2001 were similar to those across Minnesota and Iowa in 2003 – 2005. Unfortunately, historical quantitative data for amphipod consumption are not available for regions other than NWMN, thus precluding more rigorous tests. However, the current low percentages of amphipods consumed throughout Iowa and Minnesota coupled with evidence that amphipod densities in the upper-Midwest likely have decreased (Chapter 6) strongly suggests that there has been a landscape scale decrease in the availability of amphipods, which is consistent with the Spring Condition Hypothesis.

Aggregate percentages of amphipods in scaup diets in NDGP and COT were similar to that of historical scaup diets. However, females migrating throughout the upper-Midwest (including NDGP and COT) had low lipid-reserve levels (Anteau and Afton 2004, Chapter 2) and were catabolizing of lipids reserves (Chapter 4); thus, scaup apparently are not meeting their dietary requirements in these regions. Foraging efficiency of scaup (intra- and inter-wetland) probably has decreased because amphipod densities are currently low across the upper-Midwest, and anthropogenic influences on wetlands may be interfering with cues that scaup use to find wetlands with abundant amphipods (Chapters 6, 9). Consequently, females in NDGP and COT might be expending more energy to procure similar percentages of amphipods.

Moreover, apparently are consuming lower mass of amphipods throughout the upper-Midwest than they did historically because my observed geometric means of diet sample mass were 77 mg (49%) and 87 mg (52%) lower than those of historical studies in Minnesota and Manitoba, respectively (Afton and Hier 1991, Afton et al. 1991), despite similar collection procedures used among studies (see Anteau and Afton 2006). Unfortunately, diet sample mass were not reported for other historical studies and some were measured by volume. The observed differences in aggregate percentages of a taxa among regions are indicative of differences in mass of that taxa consumed because diet sample mass were similar among regions.

Female scaup migrating through IAPP in 2004 and 2005 were catabolizing lipid reserves at higher rates than for any other region (Chapter 4). Females collected in IAPP were over 3 times less likely to have consumed food than those collected in NDGP or COT (Figure 8.3); however, the probability that scaup were observed feeding on wetlands in IAPP was similar to those in NDGP and COT (Chapter 9). I conclude that the energetic costs feeding exceeded energy gained through diets in IAPP. Concomitantly, the lower likelihood of females having consumed food in IAPP resulted in small sample size of scaup diets there, which made precision of tests between IAPP and other regions low.

Duck diets are influenced by relative availability of foods and preferences for particular food items; preference is driven by a number of factors including: energetic or nutritional requirements, foraging adaptations (e.g., bill morphology, diving vs. dabbling), and niche competition (Afton and Hier 1991, Alisauskas and Ankney 1992, Krapu and Reinecke 1992). Spatial variation in availability of macroinvertebrate foods is

large among wetlands in spring (Chapter 6; M. J. Anteau, unpublished data). Thus, collecting diet samples over a large landscape should allow inferences about diet preference, based on mean percentages of foods consumed because relative availability is essentially averaged-over at a large landscape-scale. However, if there are landscape-wide decreases in the availability of a particular food item this may not hold true.

My results are consistent with the hypothesis that bivalve consumption by scaup in the upper-Midwest is a result of lack the of availability of other preferred foods (Anteau and Afton 2006). Aggregate percentages and percent occurrences of bivalves in scaup diets generally were low in all regions, except NWMN in 2000 – 2001 where amphipod consumption was low (Anteau and Afton 2006). My results also suggest that gastropods are a less preferred than amphipods because regional aggregate percentages of gastropods consumed generally were low and inversely correlated to that of *Gammarus* ($r = -0.15$, $P = 0.01$; MANOVA partial correlation). Regional percentages of insects consumed generally were high (except NWMN in 2000 – 2001; Figure 8.2), and overall percentages were negatively correlated to that of bivalves ($r = -0.16$, $P = 0.01$; partial correlation) and gastropods ($r = -0.29$, $P < 0.001$; partial correlation), suggesting that bivalves and gastropods generally were less preferred foods than are insects. Regional percent occurrences of seeds appear inversely correlated with those of amphipods. In MNGP, seed consumption was high and *Gammarus* and *Hyaella* consumption was low. Thus, seeds may be consumed by scaup, in the absence of amphipods, to accumulate lipid reserves because seeds can be a good source of carbohydrates and lipids (Afton and Hier 1991, Ballard et al. 2004).

In conclusion, my results generally were consistent with the Spring Condition Hypothesis because forage quality apparently has declined in Iowa and Minnesota and perhaps declines in overall mass of foods consumed throughout the upper-Midwest; moreover, my results are constant with the hypothesis that the observed decline in body condition of scaup in the upper-Midwest was caused by a decline in availability and/or quality forage (Anteau 2002, Anteau and Afton 2004, Anteau and Afton 2006, Chapter 5, Appendix D). Accordingly, increasing availability of amphipods at spring stopover areas in the upper-Midwest should help to increase body condition of female scaup and may help to reverse the population decline.

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CHAPTER 9: WETLAND USE AND FEEDING BY LESSER SCAUP DURING SPRING MIGRATION ACROSS THE UPPER-MIDWEST

INTRODUCTION

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly since 1978 (Austin et al. 1998, Afton and Anderson 2001); population estimates were lowest on record in 2005 (Wilkins et al. 2005). The segment of the scaup population that winters in states bordering the Gulf of Mexico and migrates along the Mississippi River valley and through the upper-Midwest comprises a major component of the continental population and likely is experiencing the largest decline in numbers (Afton and Anderson 2001).

The Spring Condition Hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving on breeding areas in lower body condition than in the past, due to a decline in availability and/or quality of food resources (Afton and Anderson 2001). Food availability, forage quality, and lipid reserves of female scaup are low or have decreased recently during spring migration in the upper-Midwest (Anteau 2002; Anteau and Afton 2004; Anteau and Afton 2006; Strand 2005; Badzinski and Petrie 2006; Chapters 2, 4, 5, 6, 8); moreover, there has been an apparent concomitant decline in breeding success of scaup (Afton and Anderson 2001, Koons 2001, Koons and Rotella 2003). Accordingly, conservation, restoration, and management of wetland habitats used by scaup during spring migration is the goal of a major conservation plan in the upper-Midwest (Ducks Unlimited 2004). Three important questions need to be addressed to target types of wetlands that scaup use and regions of greatest need.

First, what are the preferred foods of scaup during spring migration? Amphipods and chironomids are two principal foods consumed scaup during spring migration (Afton et al. 1991, Anteau and Afton 2006, Chapter 8). Amphipod densities are positively correlated with scaup use on breeding areas, but it is unclear if this is a direct link or only because amphipod densities are correlated with densities of other scaup foods (Chapter 6). Therefore, I simultaneously examined influences of amphipod and chironomid densities on wetland use and feeding of scaup to better determine how particular foods influence wetland use and feeding.

Second, what characteristics of wetlands might scaup use to select wetlands for feeding? The size and class of wetlands used by scaup during spring migration must be identified so that conservation efforts can be efficiently targeted. Moreover, an understanding of how wetland vegetation structure or water clarity may function as visual cues used by scaup to select wetlands used for feeding. Consequently, I examined how wetland characteristics (e.g., turbidity, depth, size of open-water zone, water regime, and amount and species of emergent vegetation; in addition to principle food densities) influenced wetland use and feeding by scaup.

Third, what areas or regions in the upper-Midwest are in most need of conservation efforts? Accordingly, I examined inter-regional variation in the probabilities that wetlands would be used by scaup and whether feeding activity occurred in relation to nutritional and dietary data from these same areas (Chapters 4, 8).

METHODS

Study Area

I sampled wetlands and observed scaup within the Prairie Pothole Regions of Iowa, Minnesota, and North Dakota. This area encompasses the most important spring migration stopover areas for scaup in the upper-Midwest, based on observations of wildlife biologists and managers, band-recovery data, sightings of color-marked scaup, and aerial surveys in spring (Low 1941; Afton and Hier 1985; Afton et al. 1991; Pace and Afton 1999; Iowa Department of Natural Resources, unpublished data; Minnesota Department of Natural Resources, unpublished data; North Dakota Game and Fish Department, unpublished data). I stratified the 3-state area into 6 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 9.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

I used a constrained-random clustered sampling approach to select survey wetlands to minimize travel time of field crews. I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 9.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck North Dakota, unpublished data; S. Piepgras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or

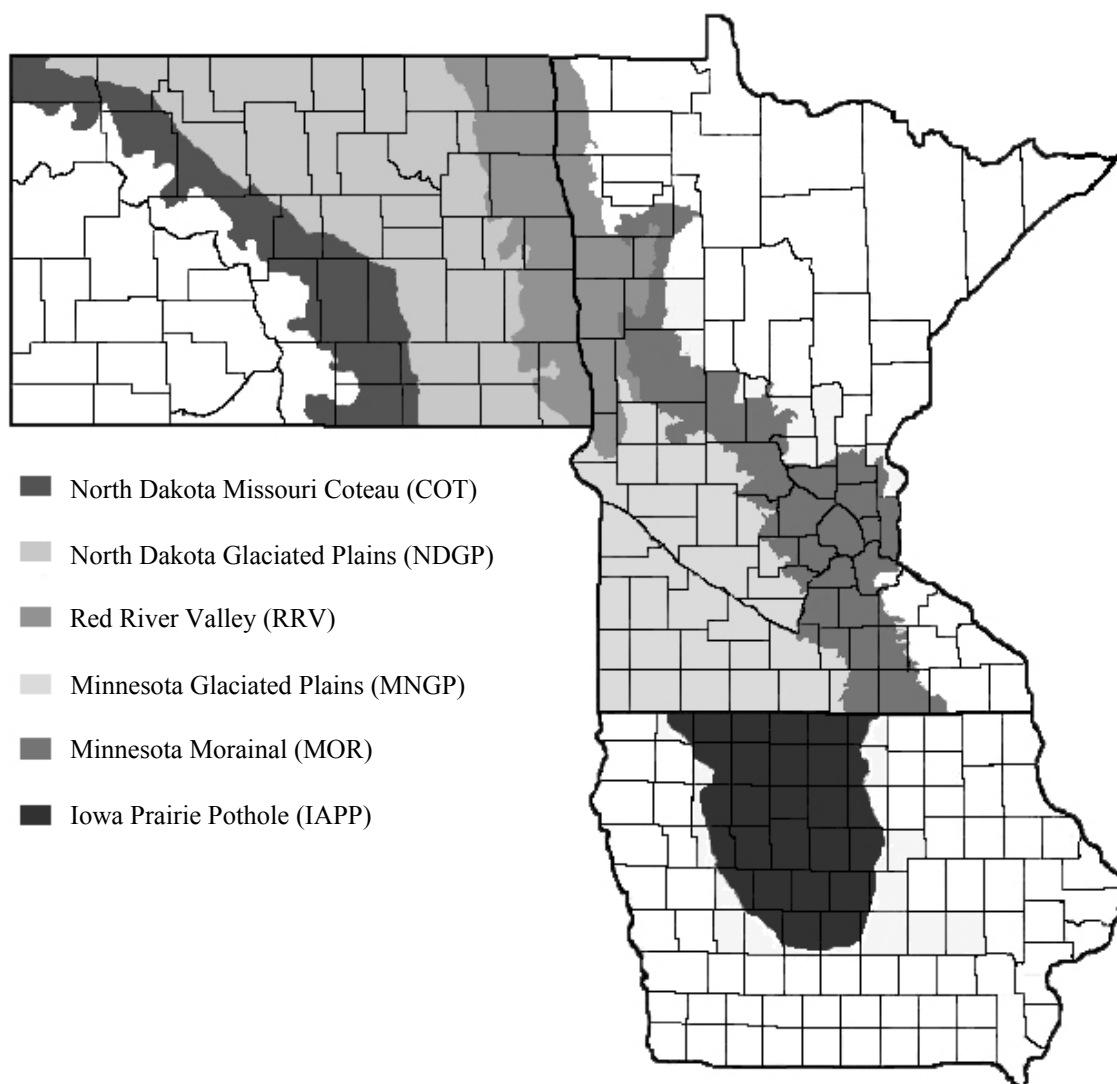


Figure 9.1. Map of the study area depicting 6 eco-physiographic regions for observations of lesser scaup wetland use and feeding during spring migration (2004 and 2005) in the upper-Midwest. Areas in white were not sampled.

Table 9.1. Numbers of sampling clusters (C), randomly selected wetlands observed for lesser scaup use and feeding (N_{Random}), wetlands with complete wetland surveys (N_{Complete}) by region in springs 2004 and 2005, and candidate townships (T) available for random selection of sampling clusters.

Region	C	N_{Random}		N_{Complete}		T
		2004	2005	2004	2005	
North Dakota Missouri Coteau	3	27	26	9	26	208 ^a
North Dakota Glaciated Plains	6	42	50	15	50	364 ^a
Red River Valley	3	21	21	11	22 ^b	66 ^a
Minnesota Morainal	4	28	34	17	39 ^b	348 ^a
Minnesota Glaciated Plains	4	31	33	18	36 ^b	285 ^a
Iowa Prairie Pothole	3	20	23	20	23	43 ^c
Annual wetland totals		169	187	90	196	

^a Townships that contain at least 200 hectares of semipermanent wetlands.

^b Numbers include supplemental wetlands surveyed (see method).

^c Townships that contain at least 200 hectares total of semipermanent and permanent wetlands.

permanent wetlands. Constraining township selection helped insure that there were adequate numbers of wetlands to sample within each township.

I then allocated numbers of sampling clusters among the 6 regions (3 to 6 clusters per region; Table 9.1) based on region size and number of candidate townships available (Table 9.1, Figure 9.1). Each region is divided into sub-regions based on latitude, such that there was 1 sampling cluster per sub-region each year (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 sampling clusters for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 9.1).

Each sampling cluster was comprised of 3 adjacent 36-square-mile townships (27,972 ha total). The centruns of the second and third townships selected were constrained within 50 km of the centrum of the first randomly selected township. I randomly selected 3 semipermanent or permanent wetlands (> 4 ha) in each township for wetland sampling. New townships and wetlands were selected annually within each sub-region from the list of candidate townships to maximize representation of spatial variability in wetland characteristics.

In springs 2004 and 2005, I observed wetland use and behavior of scaup on 356 wetlands and conducted complete wetland sampling on a random subset of wetlands ($n = 286$; Table 9.1). In spring 2005, the latter sample was supplemented with 9 wetlands in Minnesota that had relatively high scaup use because preliminary analyses indicated that modeling would be improved if more wetlands with high scaup use were included in Minnesota (Anteau et al. 2004).

I timed wetland sampling to occur with the middle of scaup migration, when relatively large numbers of scaup were present; thus, I initiated sampling in the southern portion of the study area and worked north. This approach insured a relatively equal probability of scaup being present within each sub-region, and that sampling occurred at similar times relative to phenology of spring. Sampling was conducted from 3 April – 16 May 2004 and 30 March – 3 May 2005.

Determination of Wetland Use and Feeding

I assessed wetland use and feeding by scaup on each selected wetland with 4 visits (twice a day for 2 days; each visit was at least 4 hours apart). During each visit wetland use was scored as scaup present (1) or absent (0); scaup feeding also was scored as at least one scaup feeding (1) or none-feeding (0). I also scored feeding as zero if wetland use was zero to allow examination of probabilities of scaup feeding among regions independently of wetland use and because wetlands where scaup use was not detected still represent opportunities for scaup to feed, thus should be incorporated in models examining what factors influence scaup feeding. Lesser and greater scaup can be difficult to differentiate at long distances; however, misidentification of these species should be minimal because: (1) observers were experienced with duck identification, (2) my study area primarily was lesser scaup migration habitat (Bellrose 1980, Austin et al. 1998), and (3) indeed very few greater scaup were observed (< 1% of total scaup observed; M. J. Anteau, Louisiana State University, personal observations; A. D. Afton, US Geological Survey, personal communication; S. Stephens, Ducks Unlimited, Inc., personal communication).

Wetlands Sampling

Macroinvertebrate sampling.—For each wetland, I selected 5 transects on a map by randomly selecting a bearing (0 – 359) for each transect and then drawing each transect on the map from the center to the bank of the wetland using a protractor. Maps then were used to locate transects in the field. Transects 1 – 4 had 2 sampling stations each, the first was 10 m past the ring of the emergent vegetation and the second was 50 m away from the first station along the transect (toward the center). However, station locations were limited to depths between 0.5 – 3 m for ease of sampling and because scaup feed at these depths in spring (Austin et al. 1998). Thus, in some instances (< 5% of transects), station locations were adjusted along transects to accommodate depth requirements. At each station, I measured water depth and sampled macroinvertebrate density with a D-shaped-sweep net (1,200 μm mesh, 0.072 m^2 opening, WARD's Natural Science, Rochester, New York). Each macroinvertebrate sample consisted of a bottom sample (skimming the net along the bottom for a distance equal to the depth at the sampling station) and an upward water column sweep. This sampling method helped insure equal representation of bottom and water column. In the field, all sweep-net samples ($n = 8$ per wetland) were combined into 1 composite sample per wetland, preserved in a 95% ethanol solution, and then transported to the laboratory for sorting.

In the laboratory, each composite sample was stained with Rose Bengal (Sigma # R3877, Sigma-Aldrich Corp., St. Louis, Missouri), sieved (500 μm mesh), and floated with sugar and water in a large dissecting tray. I sorted and counted all amphipods (i.e., *Gammarus lacustris* and *Hyaella azteca*) and chironomids (*Chironomidae*) using lighted magnifying glass and stereomicroscopy.

Estimation of aquatic vegetation, open water zone, and water quality.-I

visually categorized the width (0, 1-4, 5-10, 11-30, 31-60, and >60m) of the emergent vegetation ring (distance from the edge of the emergent vegetation to the bank) at all 5 transects in each wetland. I also visually categorized (<100, 100-200, 201-500, and >500m) the size of open water zone of each wetland (distance along the transect from each side of the emergent vegetation ring or bank) at all 5 transects in each wetland. I indexed emergent vegetation width and size of open water zone by attaching “dummy” variables (0 – 5 and 1 – 4, respectively) to the levels of to each measurement and averaging all of the dummy variables for each wetland, thus creating separate covariates for emergent vegetation and open water. Lastly, I classified the dominant plant species in the emergent vegetation ring for each wetland as cattail (*Typha* spp.), bulrush (*Scirpus* spp.), other, or no emergent vegetation. I measured turbidity (± 1 nephelometric turbidity unit [NTU]) with portable water quality meters (YSI 6600 sonde with an optical turbidity [YSI 6136] probe) at the first 4 transects near the center of the wetland; turbidity measurements were averaged for each wetland.

Statistical Analyses

Factors influencing wetland use and feeding.- I calculated the total water volume sweep with sweep nets (VS; m³) for each wetland with the equation:

$$VS = 2 (\sum D_i) * SN$$

where D_i = depth (m) at each sampling station, and SN = sweep-net opening (0.072 m²).

I calculated densities (m⁻³) of each species of amphipod by dividing the count of each species by VS. I classified the water regime of each wetland as either semipermanent or permanent using converged basin National Wetland Inventory data (Johnson and Higgins

1997; HAPET, US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck, North Dakota, unpublished data). I used maximum depth (deepest measurement of 8 amphipod-sampling stations) to index the depth of each wetland.

I examined factors that influence wetland use and feeding by scaup with separate logistic regressions (PROC GENMOD; SAS Institute 2002). In both models, I specified year, region, water regime, and emergent vegetation species as nominal class variables (in class statement), amount of emergent vegetation and open water, amphipod and chironomid density, turbidity, and maximum depth as continuous variables; both models had a binomial distribution and a logit link function. I included quadratic terms for turbidity and maximum depth and interaction terms for region-by-year, region-by-amphipod density, and region-by-chironomid density. Amphipod and chironomid density, turbidity, and maximum depth were log transformed to improve model fit. In the feeding model, I included quadratic terms for amphipod and chironomid densities because density of quality foods (foods with high nutritional value; see Anteau and Afton 2006) may not be linearly correlated to feeding. In the wetland use model, I scaled the standard errors (scale = 1.69) for all tests with the DSCALE option (SAS Institute 2002) to insure a conservative model because the deviance/DF (2.78) indicated slight problems with overdispersion. I selected a final models for scaup use and feeding using backwards elimination procedures on the type III likelihood ratio statistic with *alpha* 0.05 (Zar 1996).

Regional patterns of wetland use and feeding.-I compared wetland use and feeding among regions with separate logistic regressions (PROC GENMOD; SAS

Institute 2002). In both models, I specified region as a class variable, using a binomial distribution and a logit link function. I used the LSMEANS statement to calculate least-squares mean probabilities of wetland use and feeding with 95% confidence intervals (CI), and the DIFF option to conduct contrasts between regions (SAS Institute 2002). I subsequently assigned letters to similar means ($P > 0.05$) based on contrasts of the DIFF option. In the wetland use model, I scaled the standard errors (scale = 1.83) for all tests with the DSCALE option (SAS Institute 2002) to insure a conservative model because the deviance/DF (3.36) indicated slight problems with overdispersion.

RESULTS

Factors Influencing Wetland Use and Feeding

My final model for wetland use included region ($\chi^2_{5, 276} = 24.75, P < 0.001$), amphipod density (estimate = 0.22, $\chi^2_{1, 276} = 13.42, P < 0.001$), amount of open water (estimate = 0.28, $\chi^2_{1, 276} = 5.60, P = 0.018$), and a quadratic term for turbidity (estimates = $1.71X - 0.22X^2$; $\chi^2_{1[X], 276} = 20.71, P < 0.001$; $\chi^2_{1[X^2], 276} = 10.53, P < 0.001$). I found no evidence that year-by-region, region-by-amphipod density, and region-by-chironomid density interactions, maximum depth (linear or quadratic), chironomid density, year, amount of emergent vegetation, species of emergent vegetation, and water regime influenced scaup use of wetlands (all P s > 0.05). Amphipod density and amount of open water were positively correlated with wetlands use; turbidity was positively correlated to wetland use at levels up to 45 NTU and then negatively correlated at higher levels (holding all other variables constant).

My final model for scaup feeding included region ($\chi^2_{5, 276} = 27.18, P < 0.001$), a quadratic term for amphipod density (estimates = $0.57X - 0.09X^2$; $\chi^2_{1[X], 276} = 14.07, P <$

0.001; $\chi^2_{1[X^2], 276} = 10.06, P = 0.002$), and a quadratic term for turbidity (estimates = $1.44X - 0.21X^2$; $\chi^2_{1[X], 276} = 24.57, P < 0.001$; $\chi^2_{1[X^2], 276} = 16.21, P < 0.001$). I found no evidence that year-by-region, region-by-amphipod density, and region-by-chironomid density interactions, maximum depth (linear or quadratic), chironomid density (linear or quadratic), year, amount of open water and emergent vegetation, species of emergent vegetation, and water regime influenced scaup feeding (all P s > 0.05). Amphipod density was positively correlated with scaup feeding up to 26 m^{-3} , but was negatively correlated at higher densities (holding all other variables constant). Turbidity was positively correlated with scaup feeding up to 30 NTU, but was negatively correlated at higher levels (holding all other variables constant).

Regional Patterns of Wetland Use and Feeding

Wetland use varied among regions ($\chi^2_{5, 350} = 55.89, P < 0.001$). Wetlands in Missouri Coteau of North Dakota (COT) and NDGP had a higher probability of being used than those in Minnesota Glaciated Plains (MNGP), Minnesota Morainal (MOR), and Iowa Prairie Pothole (IAPP); wetlands in MOR had a lower probability of being used than any other region (Figure 9.2).

Feeding also varied among regions ($\chi^2_{5, 350} = 29.25, P < 0.001$). Scaup had higher probabilities of feeding on wetlands within the Red River Valley (RRV) and IAPP than within MNGP and MOR; scaup had a lower probability of feeding on MOR than any other region (Figure 9.2).

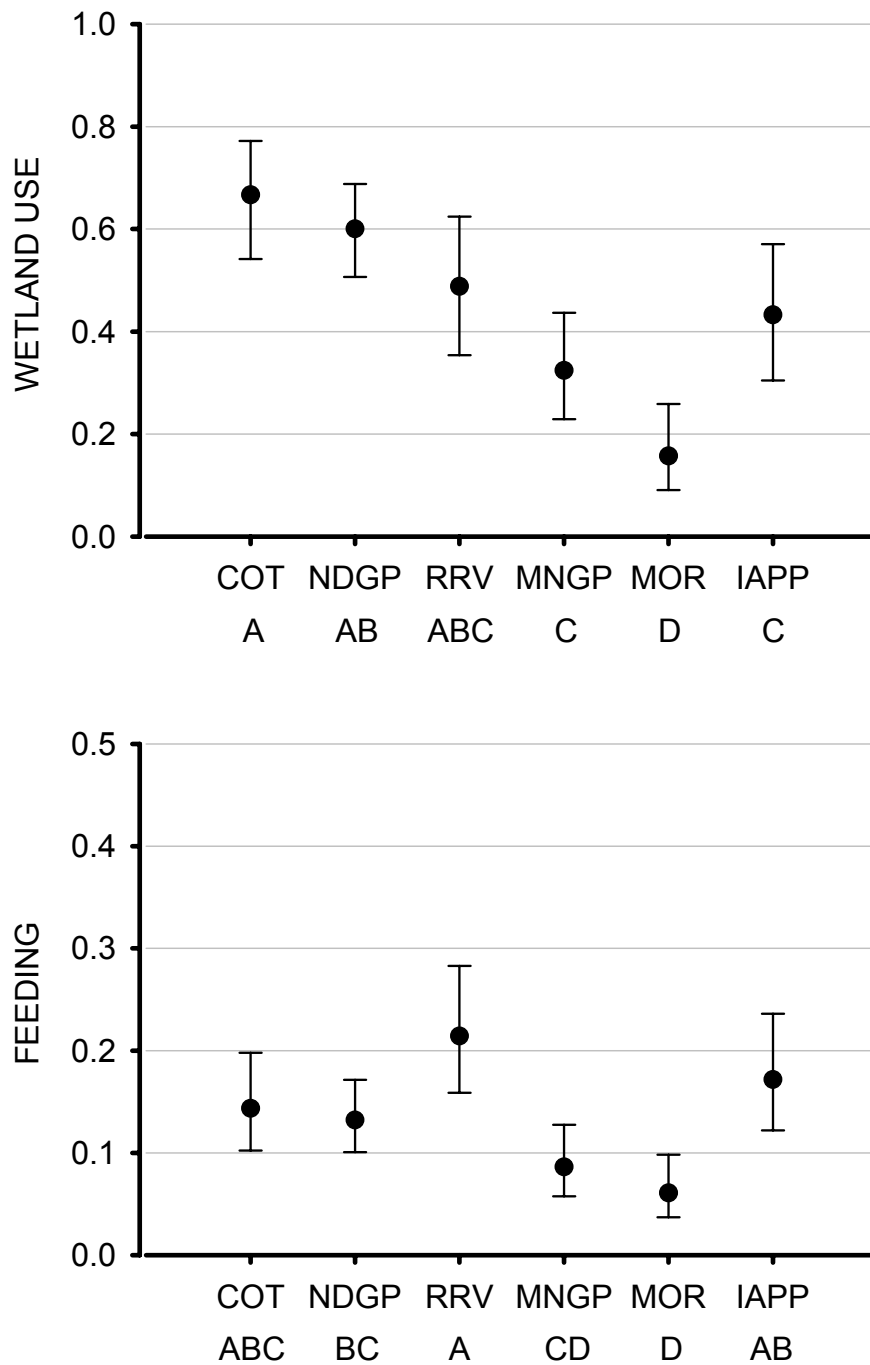


Figure 9.2. Least-squares mean probabilities of wetland use (\pm 95% CI) and feeding (\pm 95% CI) by lesser scaup among regions in the upper-Midwest in springs 2004 and 2005 combined. The regions are depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Means with same letter beneath region labels were similar ($P > 0.05$).

DISCUSSION

Factors Influencing Wetland Use and Feeding

Amphipod densities.-Scaup are highly mobile during spring migration and move relatively slowly across the upper-Midwest; the observed middle of spring migration was approximately 45 days later in Northwestern Minnesota than in western Illinois (Anteau and Afton 2004). Thus, scaup potentially can sample food resources in numerous wetlands across this large landscape. Wetland use by scaup was positively correlated with relative abundance of amphipods on breeding areas in southern Saskatchewan (Lindeman and Clark 1999) and in the boreal forest near Yellowknife, Northwest Territories (Fast et al. 2004). However, amphipods are reasonably good indicators of wetland and water quality (Chapter 6); thus, correlations between amphipod densities and scaup use could be driven by high availability of alternate foods.

Chironomids currently are the predominant food consumed by scaup in RRV, MNGP, MOR, IAPP, and Northwestern Minnesota (Chapter 8). However, Strand (2005) and I found no evidence that chironomid density influenced wetland use by scaup, whereas amphipod densities were positively correlated to wetland use in both studies. These results indicate that scaup prefer amphipods more than chironomids during spring migration in the upper-Midwest. Moreover, amphipods historically were the predominant food of scaup during spring and early summer throughout the Prairie Pothole Region (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991).

In springs 2004 and 2005, amphipod densities throughout the upper-Midwest averaged between 0 and 12 m⁻³, whereas historical average densities generally were over

100 m⁻³ (Chapter 6). Therefore, odds ratios from my analysis, on these amphipod densities, can be informative about the magnitude of the correlation between amphipods and wetland use. If amphipod density is 100 m⁻³ in a given wetland, then scaup are 2.8 times more likely to use that wetland than a wetland with no amphipods; if amphipod density is 10 m⁻³ then scaup are 1.7 times more likely to use that wetland.

Optimal foraging theory and the optimality hypothesis imply that feeding efficiency increases with the abundance of quality foods in a given patch, and that if forage efficiency is low then animals should move to a different patch or discontinue feeding (Krapu and Reinecke 1992, Alcock 1993). Considering wetlands as patches, time spent feeding on a wetland generally should follow a \cap -shaped quadratic curve in relation to abundance of quality foods. My results for amphipods are consistent with these predictions. Therefore, intra-patch (within wetland) forage efficiency of scaup on amphipods must be low across the upper-Midwest because amphipod densities currently are far below the levels in which feeding probabilities begin to decrease (26 m⁻³ [point of zero slope in quadratic line]; Chapter 6).

Wetland characteristics.—The observed positive correlation between wetland use and size of the open-water zone of wetlands is consistent with that found by Lindeman and Clark (1999) and Strand (2005). Lindeman and Clark (1999) speculated that scaup might use wetland area as a cue for predicting dense populations of amphipods. However, larger wetlands or wetlands with a larger open-water zone also may provide better refuge from disturbances near wetland margins (Korschgen et al. 1985, Kahl 1991). I found no evidence that the species or amount of emergent vegetation influenced wetland use by scaup; however, there could be an indirect-negative effect of amount of

emergent vegetation, if the size of the emergent vegetation ring reduces the size of the open-water zone in the wetland.

Interestingly, amphipod densities were positively correlated with turbidity at lower levels, but negatively correlated at higher levels (30 to 40 NTU [with none to average chlorophyll *a*]; Chapter 10). Moreover, my results indicate that wetland use and feeding by scaup were highest at 30 – 45 NTU. Wetland use and feeding by scaup might be high on wetlands that have moderate turbidity levels because of a coincidence, and scaup ultimately use wetlands that have the highest present amphipod densities.

Alternatively, scaup may have evolved using turbidity as a cue for which wetlands have high amphipod densities. My results indicated the latter because I included turbidity and amphipod densities in my models and interpreted the type III likelihood ratio tests of coefficients; both were significant independent predictors of wetland use and feeding by scaup. For example, my models predict that if a number of wetlands had the same amphipod densities, wetland use and feeding by scaup would be highest on the wetlands with moderate turbidity levels.

If scaup use turbidity as a cue for amphipod abundance, now this cue may be less effective because other new factors currently influencing turbidity in wetlands of the upper-Midwest (e.g., agricultural sedimentation and detritivorous fish communities; Swanson and Duebbert 1989, Gleason et al. 2003). Thus, inter-patch foraging efficiency also may have decreased because the presence of anthropogenic turbidity may cause scaup to spend more time stopping and attempting to feed on wetlands that contain little food.

Regional Patterns of Wetland Use and Feeding

Mean amphipod densities currently are higher in NDGP and COT than in MNGP, MOR, and IAPP (Chapter 6); similarly, wetlands use in NDGP and COT was higher than that in MNGP, MOR, or IAPP. Use of wetlands in Iowa appeared high relative to amphipod densities there (Chapter 6), perhaps because few wetlands remain in Iowa; 89% of all wetlands in Iowa were drained or lost from 1780 to 1980 (Dahl 1990). Wetland use was lowest in MOR, perhaps due to poor availability or quality of foods there (Chapter 6) or if MOR is a less used spring migration corridor. I did not record scaup abundance data, and stopover durations for scaup are unknown; thus, inferences to numbers of scaup using each region are not possible. Studies of marked female scaup (e.g., satellite transmitters) are needed to determine migration corridors, flight distances, and stopover durations; such data could be used to better interpret observational data of wetland use to target conservation activities to geographic areas of greatest need.

Feeding probabilities alone cannot directly indicate what areas have better forage availability and/or quality because feeding probabilities follow a \cap -shaped-quadratic curve in relation to availability of quality forage (i.e., amphipods). For example, feeding might be low if high quality food is highly available or if food is so scarce that birds use more energy feeding than they gain from the food acquired. Fortunately, interpreting regional feeding probabilities in relation to diet and nutritional data of scaup from these regions (Chapters 4, 8) is much more informative in relating how foods influence behavior and energetics.

For example, lower feeding probabilities in MOR and MNGP may indicate that energetic costs of diving for food (Lovvorn and Jones 1994) were higher than what scaup

were acquiring from food consumed because diets in these regions had lower quality foods (see Anteau and Afton 2006, Chapter 8). Conversely, in NDGP and COT, feeding probabilities were intermediate in relation to other regions, but more scaup were acquiring higher quality foods there (primarily amphipods; Chapters 8). Female scaup collected in IAPP were over 3 times less likely to be collected with food present in their upper digestive tract than were those collected in NDGP or COT (Chapter 8); however, feeding probabilities of scaup were similar between these regions. Similarly, females in IAPP were catabolizing lipid reserves at a higher rate than other regions and (Chapters 4, 8). Accordingly, low abundances of quality foods (amphipods) for scaup across IAPP, MNGP, and MOR (Chapter 6) apparently have reduced forage efficiency and concomitantly lipid reserves of scaup.

Implications for Migration Habitat Conservation

Conservation activities to restore and manage spring migration habitat in the upper-Midwest should target high-priority regions most beneficial to scaup. Data on food availability, feeding behavior, diets, and energetics of scaup indicate that management activities to provide preferred foods during migration are needed throughout the upper-Midwest (Anteau and Afton 2006; Chapters 2, 4, 6, 8), but are especially needed in IAPP and MNGP. My results indicate that large semipermanent or permanent wetlands with open-water zones > 500 m (diameter) should be targeted by managers, and that emergent vegetation should be prevented from “choking-out” the open water zones of wetlands.

Numerous lines of evidence indicate that amphipods are important foods for scaup in the upper-Midwest. My results indicate that an absolute minimum target mean

(geometric) density of amphipods should be 26 m^{-3} for semipermanent and permanent wetlands within this landscape. Amphipod densities were positively correlated to submerged aquatic vegetation, and width of upland vegetation buffer/filter strip, but were strongly-negatively correlated to fish abundances (Chapter 10). Accordingly, to increase amphipod density, managers should target restoration/conservation effort to wetlands that are deep enough to support over-wintering populations of amphipods and possible to manage fish communities; further, managers should provide abundant submerged aquatic vegetation, and a thick buffer of upland vegetation around the wetland.

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CHAPTER 10: FACTORS INFLUENCING SPRING *GAMMARUS* AND *HYALELLA* (AMPHIPODA) DENSITIES ACROSS THE UPPER-MIDWEST

INTRODUCTION

Gammarus lacustris and *Hyaella azteca* (hereafter *Gammarus* and *Hyaella*, respectively) are the most abundant amphipod species in semipermanent and permanent wetlands of the upper-Midwest (Kantrud et al. 1989). *Gammarus* and *Hyaella* can be very productive and often flourish at high densities; they frequently are observed at densities in the thousands m⁻² and can produce multiple broods when the breeding season is relatively long (Covich and Thorp 1991, Wen 1992, Pickard and Benke 1996).

Amphipods also are an important component of secondary production of prairie wetlands in the upper-Midwest; they are detritivores and shredders of coarse particulate organic matter, but also forage on epibenthic algae, periphyton, and microbial bacteria (Murkin 1989, Wen 1992, Day et al. 1998, Dvorak et al. 1998, Murkin and Ross 2000).

Amphipods are important foods for fish and wildlife in prairie wetlands and shallow lakes of the upper-Midwest, including fish ranging from fathead minnows (*Pimephales promelas*) to large northern pike (*Esox lucius*; > 50 cm; Peterka 1989, Dvorak et al. 1998, MacNeil et al. 1999; M. J. Anteau, Louisiana State University, unpublished data), tiger salamanders (*Ambystoma tigrinum*; Olenick and Gee 1981, Kantrud et al. 1989, MacNeil et al. 1999), migrating and breeding diving ducks (*Aythya* spp.), ruddy ducks (*Oxyura jamaicensis*), common goldeneye (*Bucephala clangula*), and several species of dabbling ducks during brood rearing (*Anas* spp.; Kantrud et al. 1989, Swanson and Duebbert 1989, Krapu and Reinecke 1992, Eadie et al. 1995).

Gammarus and *Hyalella* densities throughout the upper-Midwest currently are low (Chapter 6). Lesser scaup (*Aythya affinis*; hereafter scaup) are amphipod specialists, especially during spring migration in the upper-Midwest (Afton et al. 1991, Anteau and Afton 2006, Chapters 8, 9). Several lines of evidence suggest that the decline in the continental scaup population is linked to the decline in amphipods on spring migration stopover areas in the upper-Midwest (Anteau and Afton 2004; Strand 2005; Chapter 2, 4, 9). Accordingly, an understanding of factors influencing current amphipod densities in the upper-Midwest is a research priority (Afton et al. 1991; Anteau 2002; Anteau and Afton 2004, 2006; Chapter 6).

Anteau (2002) and Anteau and Afton (2004) hypothesized that amphipod populations may have declined across the upper-Midwest, due to landscape-scale increases in (1) abundance or foraging effectiveness of fish and/or (2) anthropogenic caused sedimentation. Fish may cause marked decreases in abundance, biomass, and size of amphipods directly through predation and indirectly by causing changes in the trophic structure of wetlands (Wellborn 1994; Bouffard and Hanson 1997; Duffy 1998; Zimmer et al. 2001, 2002; Hanson et al. 2005). Anthropogenic disturbance of surface cover (e.g., by agriculture) accelerate wind and water facilitated erosion, and subsequently increase sedimentation into prairie wetlands, especially during high spring run-off over bare fields (Martin and Hartman 1987, Dieter 1991, Gleason and Euliss 1998, Gleason et al. 2003). Suspended sediment can reduce light penetration into wetlands and precipitation of sediment reduces submerged-aquatic vegetation (SAV) and invertebrate abundances (Dieter 1991, Gleason and Euliss 1998). Other important factors influencing or interacting with spring amphipod densities likely are vegetation structure (SAV and

emergent vegetation), water chemistry, and the likelihood of winterkill of adult amphipods.

I examined potential factors influencing densities of *Gammarus* and *Hyalella* in semipermanent and permanent wetlands throughout the upper-Midwest. Specifically, I explored factors relating to fish communities and densities, sedimentation (indexed with turbidity, surrounding landscape impacts, and the width of the upland vegetation buffer/filter strip), depth, water chemistry, and SAV.

METHODS

Study Area

In springs 2004 and 2005, I sampled wetlands within the Prairie Pothole Regions of Iowa, Minnesota, and North Dakota. I stratified the 3-state area into 7 eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Figure 10.1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data).

I used a constrained-random, clustered sampling approach to select wetlands to minimize travel time of field crews in all regions except Northwestern Minnesota (NWMN). I first estimated numbers of townships within each region that had at least 200 hectares of semipermanent wetlands (candidate townships for random selection; Table 10.1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (Habitat and Population Evaluation Team [HAPET], US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and

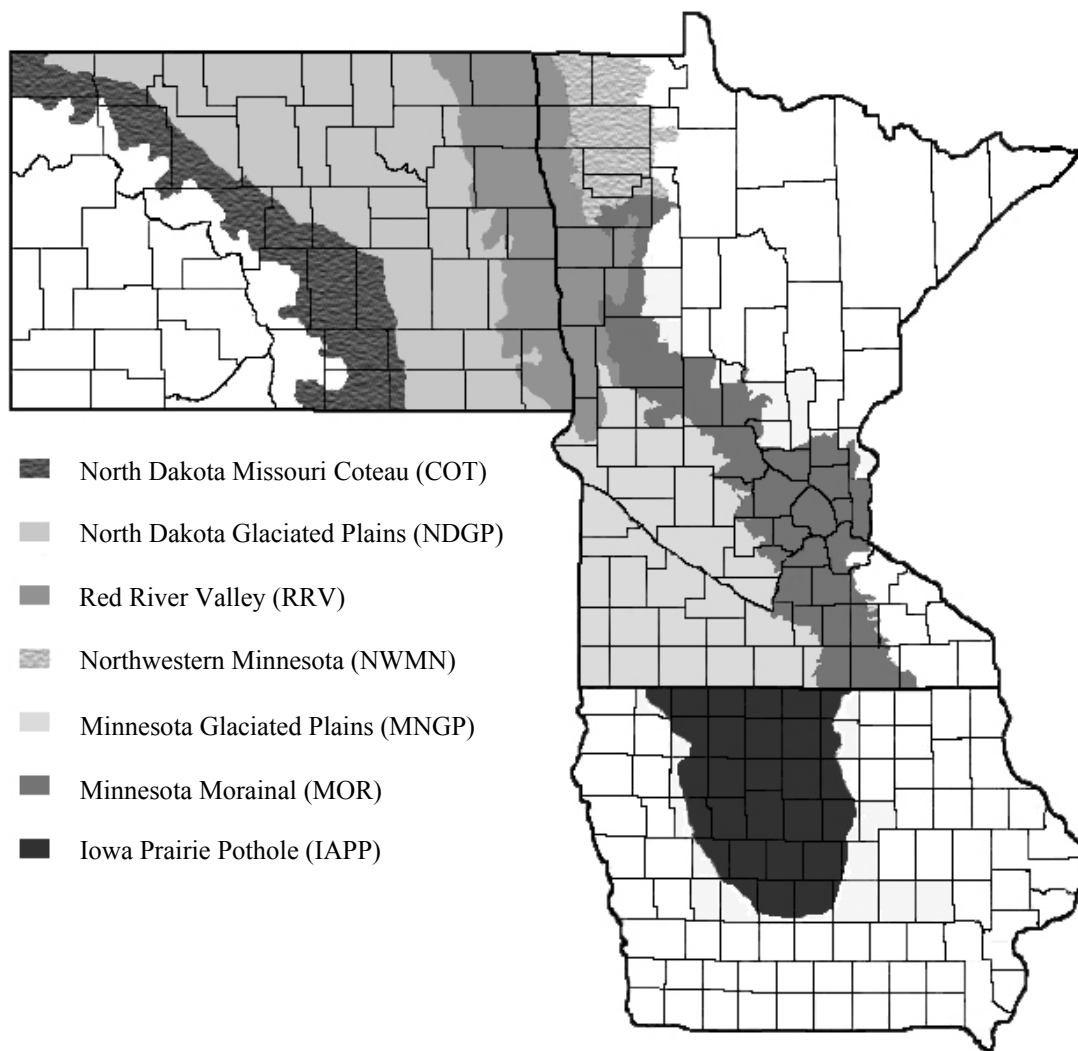


Figure 10.1. Map of the study area depicting 7 eco-physiographic regions for wetland sampling (2004 – 2005) during early spring in the upper-Midwest. Areas in white were not sampled.

Table 10.1. Numbers of sampling clusters (each year), wetlands sampled (N), and candidate townships (T) available for random selection of sampling clusters by eco-physiographic region in the upper-Midwest.

Region	Clusters	N	T
North Dakota Missouri Coteau	3	35	208 ^a
North Dakota Glaciated Plains	6	65	364 ^a
Red River Valley	3	33	66 ^a
Northwestern Minnesota ^b	n/a	7	n/a
Minnesota Morainal	4	49	348 ^a
Minnesota Glaciated Plains	4	54	285 ^a
Iowa Prairie Pothole	3	40	43 ^a
Wetland Total		283	

^a Townships that contain at least 200 hectares of semipermanent wetlands.

^b Fixed sampling locations (see methods).

^c Townships that contain at least 200 hectares total of semipermanent and permanent wetlands.

Wildlife Service, Bismarck North Dakota, unpublished data; S. Piepgras, Minnesota Department of Natural Resources, unpublished data; T. Bishop, Iowa Department of Natural Resources, unpublished data). In Iowa, I broadened the constraint to include townships with 200 hectares of semipermanent or permanent wetlands. Constraining the township selection helped insure that there were enough semipermanent or permanent wetlands to sample within each township.

I allocated numbers of sampling clusters among 6 regions (3 to 6 clusters per region; Table 10.1) based on region size and numbers of candidate townships available (Table 10.1, Figure 10.1). Each region was divided into sub-regions based on latitude, so that there was 1 sampling cluster per sub-region each year (except in North Dakota Glaciated Plains [NDGP]). In NDGP, I assigned 2 sampling clusters for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 10.1). Each sampling cluster was comprised of 3 randomly selected 36-square-mile townships (27,972 ha total). The centruns of the second and third townships selected were constrained to be within 50 km of the centrum of the first randomly selected township. I subsequently randomly selected 3 semipermanent or permanent wetlands (> 4 ha) in each township for amphipod sampling. I randomly selected new townships and wetlands annually within each sub-region from the list of candidate townships to maximize representation of spatial variability numbers of different wetlands sampled. I included 16 non-randomly selected wetlands from across Minnesota: 7 in NWMN and 9 from the other regions in Minnesota. The former were selected because of prior research on these areas and the latter because they appeared to have relatively high amphipod densities; preliminary analyses indicated that modeling would be improved if more

wetlands with high amphipod densities were included in Minnesota (Anteau et al. 2004). I sampled a total of 283 wetlands in 2004 and 2005 (Table 10.1).

Wetland Sampling

I timed wetland sampling to occur prior to the first reproductive event of amphipods (Wen 1992). I started sampling in the southern portion of the study area and worked north following the timing of middle spring migration of scaup, when relatively large numbers of migrating scaup were present on my study area. This approach insured that sampling occurred at similar times relative to phenology of spring. Sampling was conducted during 3 April – 16 May 2004 and 30 March – 3 May 2005.

Amphipod density.-For each wetland, I selected 4 transects on a map by randomly selecting a bearing (0 – 359) for each transect and then drew each transect on the map from the center to the bank of the wetland using a protractor. I used maps to locate transects in the field. Each transect had 2 sampling stations, the first was 10 m past the ring of the emergent vegetation and the second was 50 m away from the first station along the transect (toward the center). However, station locations were limited to depths between 0.5 – 3 m for ease of sampling. Thus, in some instances (< 5% of transects), station locations were adjusted along transects to accommodate depth requirements.

At each station, I measured water depth and sampled amphipod density with a D-shaped-sweep net (1,200 μm mesh, 0.072 m^2 opening, WARD's Natural Science, Rochester, New York). Each amphipod sample consisted of a bottom sample (skimming the net along the bottom for a distance equal to the depth at the sampling station) and an upward water column sweep. This pattern helped insure equal representation of bottom

and water column in each sample. In the field, sweep-net samples ($n = 8$ per wetland) were combined into 1 composite sample per wetland, preserved in a 95% ethanol solution, and then transported to the laboratory for sorting.

In the laboratory, each composite sample was stained with Rose Bengal (Sigma # R3877, Sigma-Aldrich Corp., St. Louis, Missouri), sieved (500 μm mesh), and floated with sugar and water in a large dissecting tray. I sorted and counted all amphipods (i.e., *Gammarus* and *Hyalella*) using a lighted magnifying glass and stereomicroscope. I calculated the total water volume sweep (VS ; m^3) for each wetland by the equation:

$$VS = 2 (\Sigma D_i) \times SN$$

where D_i = depth (m) at each sampling station, and SN = sweep-net opening (0.072 m^2).

Estimation of submerged aquatic vegetation.-I used grab sampling (Nyman and Chabreck 1996) to estimate relative density of SAV along a sub-transect starting at each sampling station ($n = 8$ per wetland) and running parallel to the bank. Each sub-transect had 10 grabs (1/meter) of a 36-tine Lake Rake[®] (Ben Meadows Co., Janesville, Wisconsin) gently dug into the bottom and pulled straight up (Nyman and Chabreck 1996). For each grab, presence/absence of vegetation was recorded. Relative density was calculated for each wetland by the proportion of grabs with SAV present ($n/80$).

Estimation of emergent vegetation and open water zone.-I visually categorized the width (0, 1-4, 5-10, 11-30, 31-60, and $>60\text{m}$) of the emergent vegetation ring (distance from the edge of the emergent vegetation to the bank) at all 5 transects in each wetland. I also visually categorized (<100 , 100-200, 201-500, and $>500\text{m}$) the size of open water zone of each wetland (distance along the transect from each side of the emergent vegetation ring or bank) at all 5 transects in each wetland. I indexed emergent

vegetation width and size of open water zone by attaching “dummy” variables (0 – 5 and 1 – 4, respectively) to each measurement and averaging all of the dummy variables for each wetland, thus creating separate covariates for emergent vegetation and open water.

Surrounding land-use.-Agricultural impacts surrounding each wetland were characterized as “low” (1), “moderate” (2), or “severe” (3) using criteria established in Tangen et al. (2003). I estimated the width of the ring of upland vegetation (buffer/filter strip; hereafter upland vegetation) immediately surrounding the wetland (0, 1-4, 5-10, 11-50, >50m) and assigned “dummy” variables (0 – 4) to each level.

Estimation of fish densities.-I estimated densities of various fish species with an experimental gill net (21 x 2 m with 7 – 3 m panels ranging in mesh size from 1.9 cm – 7.6 cm) set on a fifth transect. The end of the net with the smaller mesh sized panels was set about 10 m from the open water-emergent vegetation interface and extended along the transect toward the center of the wetland. I also set 5 minnow traps (Gee, #G40M, Memphis Net and Twine Co., Memphis, Tennessee) on each wetland to supplement data from the experimental gill net; one minnow trap per transect was placed at the transition between emergent vegetation and open water. Gill nets and minnow traps were set for 12 – 24 hours.

Fish caught in all 5 traps and in the gill net were enumerated by species. I calculated catch per unit effort (relative densities) of fish by dividing total numbers of fish in each species by the time that the net/traps were in the water. I then classified fish species into 1 of 4 categories: (1) fathead minnows, (2) rough fish (carp [*Cyprinus spp.*] and buffalo [*Ictiobus spp.*]), (3) small fish (other minnows [*Cyprinidae*], darters [*Anhingidae*], sticklebacks [*Gasterosteidae*], mudminnows [*Umbra spp.*]), and (4) large

fish (e.g., northern pike, walleye [*Sander vitreus*], perch [*Perca spp.*], sunfish [*Lepomis spp.*], bullhead and catfish [*Ictaluridae*]).

Water quality.—I measured turbidity (± 1 nephelometric turbidity unit [NTU]), chlorophyll *a* (± 1 mg/l), pH (± 0.1), and specific conductance (± 1 μ S/cm) with portable water quality meters (YSI 6600 sonde with optical chlorophyll [YSI 6025] and turbidity [YSI 6136] probes; YSI Inc. Yellow Springs, Ohio) at the first 4 transects near the center of the wetland. All water quality measurements were averaged for each wetland.

Statistical Analyses

Measurements of chlorophyll *a* in early spring probably do not predict those later in the year (see Wen 1992, Hanson and Butler 1994), but chlorophyll *a* is a component of turbidity. Accordingly, I used chlorophyll *a* measurements to control for its variability in the observed turbidity measurements because I was interested in evaluating correlations between amphipod densities and organic or mineral suspended solids (OMSS). I indexed OMSS with a regression on the natural logs (ln) of turbidity (dependent) and chlorophyll *a* (independent). Turbidity and chlorophyll *a* were positively correlated ($Y = 0.32 + 0.66[X]$; $P < 0.001$), chlorophyll *a* accounted for 38% of the variation in turbidity. I calculated OMSS by adding the residuals of the regression to the overall mean of ln turbidity (2.45).

I classified the water regime of each wetland as either semipermanent or permanent using converged basin (Johnson and Higgins 1997) National Wetland Inventory data (HAPET, US Fish and Wildlife Service, Fergus Falls, Minnesota, unpublished data; HAPET, US Fish and Wildlife Service, Bismarck, North Dakota,

unpublished data). I used maximum depth (deepest measurement of 8 amphipod-sampling stations) to index the depth of each wetland.

I examined factors that potentially influenced *Gammarus* and *Hyaella* densities with separate generalized linear regressions (PROC GENMOD; SAS Institute 2002). In both models, counts of amphipods (*Gammarus* or *Hyaella*) were used as the dependent variable and the full models included all effects listed in Table 10.2; both models had a negative binomial distribution, a ln link function, and ln of VS was used as an offset variable (controls counts for the amount of water swept). I included quadratic effects for fathead minnows and small fish because these fish may have similar tolerances to water quality and over-winter survival requirements as do amphipods. I included a quadratic effect for maximum depth because amphipods must survive over-winter in wetland, but if wetlands are too deep then they might be less productive for amphipods. I also included a quadratic term for OMSS because I noticed (in the field) that wetlands with high amphipod densities generally had moderate turbidity levels. I ln-transformed all covariates (Table 10.2) to improve model fit (based on ln likelihood), except OMSS, which was already in ln form. However, I excluded data from the Iowa Prairie Pothole (IAPP) region from the *Gammarus* analysis because none were not found in samples there. I selected final models for *Gammarus* and *Hyaella* using backwards elimination procedures on the type III likelihood ratio statistic with *alpha* 0.05 (Zar 1996).

RESULTS

My final model for *Gammarus* (Table 10.3) fit the data well (deviance/DF = 0.55). *Gammarus* densities varied among regions and were positively correlated with the relative density of SAV, but negatively correlated with relative density of large fish

Table 10.2. List of effects used in full models examining factors influencing *Gammarus lacustris* and *Hyalella azteca* densities in wetlands throughout the upper-Midwest.

Effect	Type
Region	Class
Regime	Class
Organic and Mineral Suspended Solids (OMSS)	Covariate
Width of Upland Vegetation	Ordinal Class
Agricultural Impacts	Ordinal Class
Fathead Minnows	Covariate
Rough Fish	Covariate
Large Fish	Covariate
Small Fish	Covariate
Submerged Aquatic Vegetation (SAV)	Covariate
Size of Open-Water Zone	Ordinal Class
Width of Emergent Vegetation	Ordinal Class
Specific Conductivity	Covariate
PH	Covariate
Maximum Depth	Covariate
Region-by-Fish ^a	Interactions
Region-by-SAV	Interaction
Region-by-OMSS	Interaction
Agricultural Impacts-by-Width of Upland Vegetation	Interaction
Large Fish-by-Width of Emergent Vegetation	Interaction
Large Fish-by-SAV	Interaction
OMSS ²	Quadratic
Maximum Depth ²	Quadratic
Fathead Minnows ²	Quadratic
Small Fish ²	Quadratic

^a Interaction for each category of fish (fathead minnows and rough, large, and small fish).

Table 10.3. Effects, numbers of numerator DF (N_{DF}) and denominator DF (D_{DF}), parameter estimates (E), Type III-likelihood ratio χ^2 -values (χ^2), and P -values for final model examining factors influencing *Gammarus lacustris* densities in the upper-Midwest.

Effect	N_{DF}	D_{DF}	E	χ^2	P
Region	5	231	n/a	36.58	< 0.001
Submerged Aquatic Vegetation	1	231	2.80	11.10	< 0.001
OMSS ^a	1	231	5.14	15.92	< 0.001
OMSS ²	1	231	-0.77	11.45	< 0.001
Large Fish	1	231	-1.73	6.70	0.01
Fathead Minnows	1	231	4.74	33.45	< 0.001
Fathead Minnows ²	1	231	-1.18	21.23	< 0.001

^a Organic and mineral suspended solids (see methods).

(Table 10.3). *Gammarus* densities were positively correlated with OMSS up to 3.37, and then negatively correlated at higher levels of OMSS (Table 10.3, Figure 10.2; holding all other variables constant). OMSS of 3.37 is roughly equal to turbidity of 30 or 40 NTU with none or mean levels of chlorophyll *a*, respectively. *Gammarus* densities were positively correlated with relative density of fathead minnows up to 1.6 fatheads caught per-trap-per-hour, and then negatively correlated at higher relative densities (Table 10.3, Figure 10.2; holding all other variables constant).

My final model for *Hyaella* (Table 10.4) also fit the data well (deviance/DF = 1.03). *Hyaella* densities varied among regions and were positively correlated with SAV and width of upland vegetation; however, they were negatively correlated with small, rough, and large fish relative densities (Table 10.4). *Hyaella* densities were positively correlated with relative density of fathead minnows up to 0.8 fatheads caught per-trap-per-hour, and then negatively correlated at higher relative densities (Table 10.4, Figure 10.2; holding all other variables constant).

DISCUSSION

Submerged Aquatic Vegetation

My results were similar to that of others who reported reductions in SAV were correlated with declines in invertebrate productivity (Krull 1970, Euliss and Grodhaus 1987, Neill and Cornwell 1992, Schriver et al. 1995, Gleason and Euliss 1998). The amount of SAV in a wetland likely is positively correlated with the amount of food for amphipods because SAV produces coarse particulate organic matter and provides structure on which periphyton grow (Covich and Thorp 1991). Moreover, vegetative structure in wetlands also may make amphipods less susceptible to predation by fishes

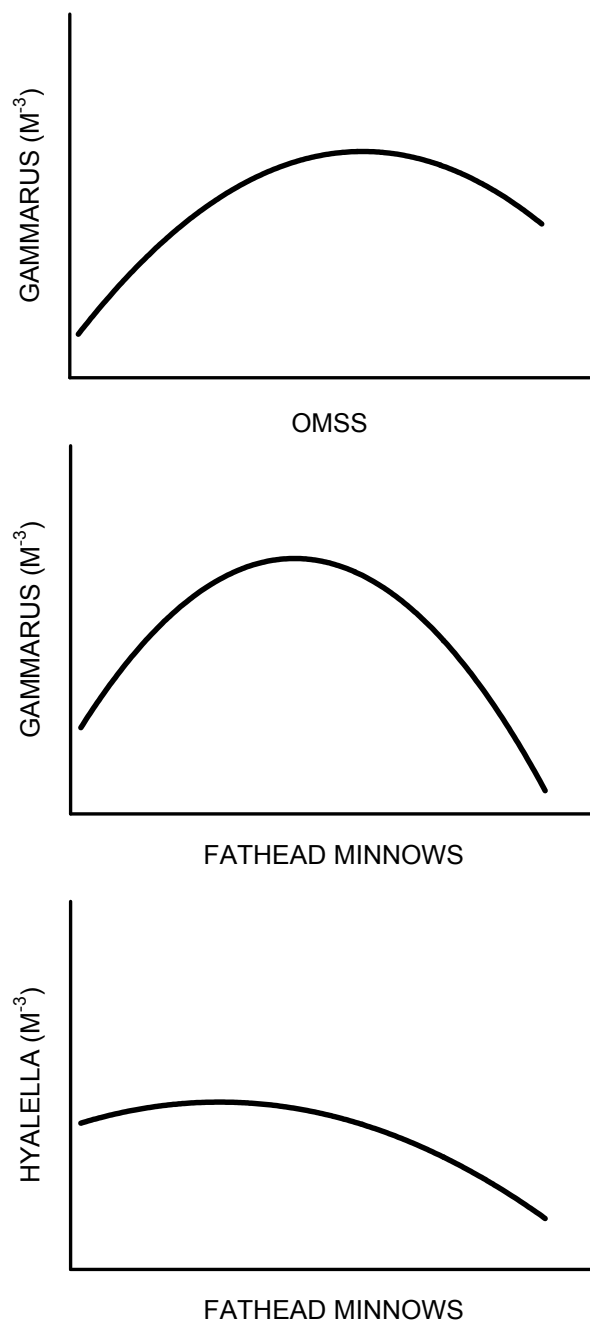


Figure 10.2. Shape of quadratic-effect curves of the correlations between: *Gammarus lacustris* densities and organic and mineral suspended solids; *Gammarus lacustris* densities and relative densities of fathead minnows; and *Hyaella azteca* densities and relative densities of fathead minnows.

Table 10.4. Effects, numbers of numerator DF (N_{DF}) and denominator DF (D_{DF}), parameter estimates (E), Type III-likelihood ratio χ^2 -values (χ^2), and P -values for final model examining factors influencing *Hyaella azteca* densities in the upper-Midwest.

Effect	N_{DF}	D_{DF}	E	χ^2	P
Region	5	269	n/a	36.58	< 0.001
Submerged Aquatic Vegetation	1	269	1.81	17.81	< 0.001
Width of Upland Vegetation	1	269	0.32	8.30	0.004
Small Fish	1	269	-0.43	3.92	0.048
Large Fish	1	269	-0.68	6.17	0.013
Rough Fish	1	269	-4.82	5.21	0.022
Fathead Minnows	1	269	1.13	3.87	0.049
Fathead Minnows ²	1	269	-0.40	4.54	0.033

(Covich and Thorp 1991, MacNeil et al. 1999) and concomitantly may allow amphipods to maintain high activity levels in the presence of predators (Wooster 1998).

Fish Communities

Fish communities have the potential to decrease amphipod density directly (through predation) and indirectly through trophic cascades (Swanson and Nelson 1970, Scheffer et al. 1993, Bouffard and Hanson 1997). Percent occurrence of fish in semipermanent and permanent wetlands throughout the upper-Midwest has increased markedly from historic estimates, especially in Minnesota and Iowa (Chapter 6). I found strong negative correlations between relative fish densities and *Gammarus* and *Hyaella* densities, consistent with the hypothesis that an increase in fish abundance has contributed to a decline in amphipod densities in the upper-Midwest (*c.f.*, Anteau 2002, Anteau and Afton 2004).

My results indicate that, when amphipod densities are low or zero, fathead minnow densities also are low or zero, suggesting that amphipods and fathead minnows have similar requirements and tolerances that limit which wetlands they can occur. Amphipods and fathead minnows both must survive during winter in wetlands to be present in spring (Peterka 1989, Arts et al. 1995, Lindeman and Clark 1999, MacNeil et al. 1999), and might have similar tolerances to salinity and dissolved oxygen (Swanson et al. 1989, Peterka 1989). Moreover, fathead minnows and amphipods generally are abundant in the same regions in the upper-Midwest (Chapter 6).

Fathead minnows may influence *Gammarus* and *Hyaella* densities through both direct and indirect mechanisms. Fathead minnows typically consume zooplankton,

amphipods, and other macroinvertebrates when those foods are abundant in wetlands (Held and Peterka 1974, Price et al. 1991, Duffy 1998). However, unlike other small fishes fathead minnows consume detritus and periphyton when abundances of macroinvertebrates and zooplankton are low (*c.f.* Zimmer et al. 2002, Hanson et al. 2005). Therefore, fathead minnows can be competitors with *Gammarus* and *Hyaella* for the same foods. Moreover, alternate equilibria theory (Scheffer et al. 1993) predicts that because fathead minnows sustain their densities by eating detritus, they (1) can continually depress zooplankton abundance and (2) reduce SAV abundances through increases in turbidity, both of which may cause eventual shifts to a phytoplankton dominated trophic structure (Scheffer et al. 1993, 2001; Zimmer et al. 2002), which probably would result in less food and cover for amphipods.

Rough fish can increase turbidity through the consumption of detritus and SAV (Bouffard and Hanson 1997). I found that relative density of rough fish was negatively correlated with *Hyaella* densities, but unrelated to *Gammarus* densities. Only 1 wetland in my sample had rough fish and *Gammarus*; thus the model likely could not fit a slope to a single non-zero result. However, *Gammarus* and rough fish probably are negatively correlated because they rarely occurred in the same wetlands.

Hanson et al. (2005) hypothesized that the ecological influences of fish in wetlands increases from northwest to southeast in the Prairie Pothole Region. Relative densities of fish in wetlands generally increase from northwest to southeast (Chapter 6). However, I found that the ecological influences of fish on amphipods were similar across the Prairie Pothole Region, contrary to this hypothesis.

Sedimentation

Sedimentation into wetlands has the potential to reduce amphipod densities through reduction of SAV seed emergence and by covering the coarse particulate organic matter, epibenthic algae, and periphyton that amphipods feed upon (Gleason and Euliss 1998, Gleason et al. 2003). Spring turbidity measurements likely are a good index of sedimentation in wetlands because of high spring runoff over bare fields (Dieter 1991, Chapter 6). Current levels of turbidity in the upper-Midwest are high in relation to boreal wetlands not impacted by agriculture (Bayley and Prather 2003, Chapter 6). My results of a positive relationship between *Hyalella* and width of upland vegetation, coupled with the negative correlation between high levels of OMSS and *Gammarus* densities, are constant with the hypothesis that an increase in sedimentation has contributed to a decline in amphipod densities in the upper-Midwest (*c. f.*, Anteau 2002, Anteau and Afton 2004).

I expected that the variable, agricultural impacts, would index the amount of sedimentation into wetlands, but I found no evidence of a correlation between agricultural impacts and amphipod densities. Tangen et al. (2003) found a weak relationship between macroinvertebrate assemblages and the same classification of agricultural impacts; they speculated that high spatial variability was a potential reason for the lack of precision in their tests. However, I suspect that this classification was not detailed or accurate enough because I had much larger sample sizes and spatial representation, but I still did not detect a relationship between amphipod densities and agricultural impacts. Moreover, the landscape that drains into a wetland likely is larger than can be evaluated by observations made at or immediately surrounding the wetland,

particularly with the increasing connected character of wetlands in many parts of the upper-Midwest (Hanson et al. 2005; Chapter 6).

The observed quadratic relationship between OMSS and *Gammarus* (Figure 10.2) suggests that *Gammarus* is sensitive to high levels of sedimentation. The positive correlation observed at lower levels of OMSS could be caused by a number of mechanisms. For example, (1) *Gammarus* may be less susceptible to predation in more turbid water or (2) high densities of *Gammarus* (e.g., hundreds or thousands m⁻³) in wetlands may increase OMSS by their consumption of coarse particulate organic matter (Murkin 1989, Day et al. 1998, Dvorak et al. 1998, Murkin and Ross 2000) and release of fine particulate organic matter (Murkin and Ross 2000).

Wetland Depth

I expected that amphipods would be correlated with wetland depth because amphipods over-winter in wetlands as adults to be present in spring and typically have been associated with deeper wetlands (Arts et al. 1995, Lindeman and Clark 1999, MacNeil et al. 1999). However, I found that maximum depth was not correlated to amphipod density; my measurement of depth may have been inadequate to index wetland depth. Furthermore, the presence of fathead minnows may have been a better predictor of wetland depth necessary to over-winter amphipods than maximum depth. Wetland depth must be an important factor related to the presence or absence of amphipods, despite the lack of an observed direct correlation between maximum depth and amphipod densities.

Conclusions

Several lines of evidence suggest that there has been a landscape-wide decrease in wetland quality in the upper-Midwest: (1) Current low densities of *Gammarus* and *Hyalella*, (2) current high percent occurrence of fish, and (3) relatively high current turbidity levels in wetlands (Chapter 6). My results suggest that the low densities of amphipods were caused by increases in presence or density of fish, and increases in sedimentation into wetlands. Further research and experimentation is needed to more clearly understand the mechanisms driving the observed correlations between amphipod densities and fish communities, indices of sedimentation, and SAV.

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CHAPTER 11: GENERAL CONCLUSIONS

THE SPRING CONDITION HYPOTHESIS

Scope of the Spring Condition Hypothesis

Anteau and Afton (2004) speculated that decreases in lipid reserves of female lesser scaup (*Aythya affinis*; hereafter scaup) in Northwestern Minnesota and southwestern Manitoba were indicative of a landscape-scale decline in lipid reserves. I found that lipid-reserve levels of females across Iowa, Minnesota, and North Dakota in 2003 – 2005 were similar to low values reported by Anteau and Afton (2004), and thus are consistent with this hypothesis (Chapter 2). Moreover, lipid reserves of female scaup collected in eastern South Dakota in 2003 and 2004 (Strand 2005) generally were similar to my data from across the rest of the upper-Midwest (Chapter 2).

In 2003 – 2005, lipid reserves of female scaup throughout the upper-Midwest were 75 to 95 g, on average, lower than that of those at Pool 19 in 2000 – 2001 (Anteau and Afton 2004), which is consistent with my other findings that female scaup were catabolizing lipid reserves throughout spring migration in the upper-Midwest (Chapter 4). Moreover, regional rates of lipid catabolism (Chapter 4) generally are similar to regional lipid-reserve levels (Chapter 2). Accordingly, my results are consistent with the Spring Condition Hypothesis and indicate that a large portion of the continental scaup population that migrates through the upper-Midwest (Bellrose 1980, Afton and Anderson 2001) potentially is affected by factor(s) that are causing the observed catabolism and low levels of lipids.

Female scaup continue to have high lipid reserves at Pool 19 (Anteau and Afton 2004, Chapter 2) and this was the only area that females were accumulating lipids

(Chapter 4). Therefore, Pool 19 and previous stopover areas currently are critically important for female scaup to accumulate lipid reserves for migration and breeding. Historically, female scaup likely accumulated lipid reserves for breeding further north (Anteau and Afton 2004).

Scaup currently are nesting markedly later than that historically (Koons 2001, Brook 2002, Koons and Rotella 2003); whereas, other bird species, including some waterfowl, are nesting as much as 10 days earlier due to global climate change effects (MacInnes et al. 1990, Crick et al. 1997, Wuethrich 2000, Both and Visser 2001). Nest success, duckling survival, and post-fledging survival generally are negatively correlated with nest initiation dates among northern nesting waterfowl (Rohwer 1992, Dzus and Clark 1998, Guyn and Clark 1999, Blums et al. 2002) and clutch size of scaup declines seasonally (Afton 1984, Esler et al. 2001, Brook 2002). Accordingly, females that arrive on breeding areas in poor body condition and do breed, probably nest later (Reynolds 1972, Esler et al. 2001) and concomitantly fledge fewer young. Alisauskas (2002) reported that body condition of lesser snow geese (*Chen caerulescens caerulescens*) in spring was positively related to age ratios (immature/adult) later that fall, providing strong support that spring body condition is an important determinant of recruitment.

Female scaup arriving to breed in southwestern Manitoba in 2000 and 2001 were in poorer body condition than were those historically (Anteau 2002, Anteau and Afton 2004). Based on my results, I predict that females migrating to many northern breeding areas currently are arriving in poor body condition, arriving late, or not at all, because they have low lipid-reserve levels and are catabolizing lipid reserves in the northern portions of my study area (Chapter 2, 4). If females nesting in the Boreal Forest are

arriving in poor body condition, delays in nest initiation should have a greater effect on recruitment there than for those nesting in the Prairie Parklands because less time is available between arrival and egg laying to acquire nutrients for breeding in the Boreal Forest (Austin et al. 1998, Afton and Anderson 2001). Notably, Afton and Anderson (2001) reported that the steepest scaup population declines have occurred in the western Boreal Forest.

Mechanisms of the Spring Condition Hypothesis

The most likely explanation for the observed low lipid reserves of females is reduced availability of preferred scaup foods (e.g., amphipods) on spring stopover areas in the upper-Midwest (see Anteau and Afton 2006; Strand 2005; Chapters 6, 8, 9, 10). Numbers of wetlands that scaup use, wetland quality, and amphipod densities currently are low in the upper-Midwest (Dahl 1990, Austin et al. 1998, Chapter 6). Wetland use of scaup was positively correlated with amphipod densities throughout the upper-Midwest, but was not related to chironomid densities (highly consumed food), indicating that amphipods are a preferred food for scaup during spring migration in the upper-Midwest (Chapter 9). Aggregate percentage of amphipods in scaup diets were lower throughout Minnesota and Iowa than what had been reported historically, and scaup were consuming less food (49 – 52% dry mass) throughout the upper-Midwest than they did historically (Anteau and Afton 2006, Chapter 8). Feeding probabilities increased with amphipod density up to 26 m^{-3} , but then declined at higher amphipod densities, suggesting that scaup spend less time searching for food within a wetland to procure adequate amounts of amphipods at densities above 26 m^{-3} ; however, mean amphipod densities in the upper-Midwest currently are much lower (range $1 - 12 \text{ m}^{-3}$; Chapter 9).

Increased incidences of parasitism or increases in environmental contaminants could also be contributing to the observed lipid catabolism. However, the abundance of intestinal cestodes was positively correlated with lipid reserves or body mass in scaup during spring and fall migration (Vest 2002, Appendix D). Lipid reserves of scaup declined with increasing hepatic cadmium concentrations; however, current levels of cadmium contamination in scaup are too low in the Mississippi Flyway to explain the observed losses of lipid reserves of females (Custer et al. 2003, Chapter 5).

Migration Habitat Conservation

Conservation activities to restore and manage scaup spring migration habitat in the upper-Midwest should target high-priority regions that would be most beneficial to scaup. Data on food availability, feeding behavior, diets, and energetics of scaup indicate that management activities to provide preferred foods during migration are needed throughout the upper-Midwest, but are especially needed in Iowa and southern Minnesota (Anteau and Afton 2006; Chapters 2, 4, 6, 8, 9). My results indicate that large semipermanent or permanent wetlands with open-water zones > 500 m (diameter) should be targeted by managers, and that emergent vegetation should be prevented from “choking-out” the open water zones of wetlands.

Numerous lines of evidence indicate that amphipods are important foods for scaup in the upper-Midwest (see Anteau and Afton 2006; Chapters 8, 9). My results indicate that an absolute minimum target mean (geometric) density of amphipods should be 26 m^{-3} for all semipermanent and permanent wetlands within this landscape. Amphipod densities were positively correlated to submerged aquatic vegetation, but were strongly-negatively correlated to fish abundances and sedimentation into wetlands

(Chapter 10). Accordingly, to increase amphipod densities, managers should target restoration/conservation to wetlands that are deep enough to support over-wintering populations of amphipods and possible to manage fish communities; further, managers should provide abundant submerged aquatic vegetation, and a thick buffer of upland vegetation around the wetland or other land management to prevent sedimentation.

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APPENDIX A: GLYCEROL AND TRIGLYCERIDE PROTOCOL

Glycerol and Total Triglycerides Endpoint Assay ^a

Overview:

Triglycerides and glycerol are lipid metabolites, which can indicate if a bird is accumulating or catabolizing lipid reserves. This assay is run on a 96-well microplate and read on a microplate spectrophotometer. This protocol instructs the measure of free glycerol and total triglycerides of blood plasma samples on the same microplate. To calculate triglyceride levels then simply subtract the glycerol values from the total triglyceride values.

Required Supplies:

Standard: Triglyceride standard (Sigma #G7793)

Reagent 1: Free Glycerol reagent, 40 ml (Sigma #F6428) – one bottle fills ~125 wells

Reagent 2: Triglyceride reagent, 10 ml (Sigma #T2449) – one bottle fills ~125 wells

Microplate: Clear polystyrene 96-well flat-bottom with 400 µl capacity

Standard:

The Sigma Trig. standard straight from the bottle is 2.82 mmol, so prepare a serial dilution of the standard so you have tubes of standards at the following levels: 2.82, 1.41, 0.705, 0.353, and 0. However, the top standard for the standard curve is 5.64, which is attained by adding twice the amount (10 µl) to the microplate well.

Standards should keep in the refrigerator for about a month, if tightly capped.

Loading samples and standards in the plate:

Samples and standards should be run in duplicate or triplicate; insure that only one of the samples/standards is located on an edge row/column of the plate.

Pipetting: Draw up – one stop, Expel – two stops (touch tip on side wall and drag the tip up the edge while expelling).

Load each standard at 5 µl, except load 10 µl of the 2.82 standard into a separate well (in addition to the well for the 2.82 standard), this is the top standard (5.62).

Vortex all samples (especially if they were frozen), and load 5 µl of sample in each well.

Reagent 1 - Glycerol:

Load Glycerol reagent (240 µl) to each well (Draw up – one stop, Expel – one stop; do not touch well).

Reading:

Incubate plate for 10 min at 37° C (insert plate, a turn on plate warmer, and time for 10 min).

Shake 10 sec. (low; once incubated you can open and run existing protocol titled “trig”, which will shake and read).

Read at 540 nm (absorbance reading) and 750 nm (reference reading).

Reagent 2 – Triglyceride:

Load Triglyceride reagent (60 µl) to each well of the same plate (Draw up – one stop, Expel – one stop; do not touch well).

Reading:

Same as above.

Calculations:

Calculate a standard curve and use the regression equation to calculate the levels (mmol/L) of each lipid. If the calculated concentration is higher than the top standard the sample must be diluted and run again, multiply the new calculated concentration by the dilution factor.

^a Michael J. Anteau – Adapted from Chris Guglielmo (University of Western Ontario, protocol).

APPENDIX B: β -HYDROXYBUTYRATE PROTOCOL

β -OHButyric Acid Kinetic Assay ^a

Overview:

β -Hydroxybutyrate is a type of ketone in lipid metabolism. It is a byproduct of β metabolism (catabolism of lipids), which can indicate if a bird is catabolizing lipid reserves. This assay is run on a 96-well microplate and read on a microplate spectrophotometer. This protocol instructs the measure of β -Hydroxybutyrate of blood plasma samples. Standard curve linear to 3.2 mmol.

Required Supplies:

Standard: Stanbio TDM/ β -Hydrox. standards set (Fisher # SB 2450-604)

Kit: r-biopharm D-3-Hydroxybutyric Acid kit (E0907979; www.r-biopharm.com) one kit does 140 samples in triplicate. Mix reagents as per kit instructions.

Microplate: Clear polystyrene 96-well flat-bottom with 400 μ l capacity

Loading standards and samples:

- Samples and standards should be run in duplicate or triplicate; insure that only one of the samples/standards is located on an edge row/column of the plate.
- Pipetting: Draw up – one stop, Expel – two stops (touch tip on side wall and drag the tip up the edge while expelling).
- Load the following standards: 0 mmol = 5 μ l of standard 1; 0.25 mmol = 2.5 μ l of standard 2; 0.5 mmol = 5 μ l of standard 2; 1.0 mmol = 5 μ l of standard 3; 1.5 mmol = 7.5 μ l of standard 3; 2.0 mmol = 5 μ l of standard 4; 3.0 mmol = 7.5 μ l of standard 4.
- Vortex all samples (especially if they were frozen), and load 5 μ l of sample in each well.

Working solution and activator enzyme:

- After samples and standards are loaded, prepare a working solution of reagents (must be used right away).
- 22.5 ml working solution is enough for one 96-well microplate.
- Mix gently: 15 ml dH₂O, 4.5 ml of solution 1, 1.5 ml solution 2 (must mix first – see kit instructions), 1.5 ml solution 3 (must dilute first – see kit instructions).
- Load 200 μ l working solution into each well of the same plate (Draw up – one stop, Expel – one stop; do not touch well).
- Incubate room temperature (20 – 25° C) for 2 minutes.
- Add 4 μ l of activator enzyme (solution 4) to each well. This has to be done very quickly so use a multi-channel pipette or a repeater pipette. This can be a source of error in the assay so, it is best to practice this before you load samples and use the enzyme.

Reading:

- Shake plate (low – 10 seconds).
- Read plate immediately (t=0), 492 nm.
- Read plate every 1 minute for 40 minutes (41 reads). Can use existing protocol on computer titled “B-OH”, this is set up to read every minute.

Calculations:

- Export the reading data (one file has data from all readings), open in Excel. Subtract three times the change in absorbance between t=30 and t=40 (background) from the change in absorbance between t=0 and t=30. net absorbance = $(t_{30} - t_0) - 3(t_{40} - t_{30})$.
- Use the net absorbencies of the standards and standard mmol to calculate the standard curve, and then use the regression equation to calculate the mmol of the samples.
- If the calculated concentration is higher than the top standard the sample must be diluted and run again, multiply the new calculated mmol by the dilution factor.

^a Michael J. Anteau – Adapted from Chris Guglielmo (University of Western Ontario, protocol).

APPENDIX C: MASS CHANGES OF RECAPTURED LESSER SCAUP

Listing of band numbers, sex, month (M), day (D), year (Y), mass, mass change (C), days between captures (D), and mass change per day (CPD) for lesser scaup recaptured multiple times during staging at Pool 19 of the Mississippi River; footnotes (1) and (2) denote previous capture and recapture, respectively. Not all individuals were bled on each capture and individuals captured and recaptured only once are not included in list.

BAND	SEX	M ₁	D ₁	Y	M ₂	D ₂	MASS ₁	MASS ₂	C	D	CPD
108666716	M	3	25	2004	3	28	647	611	-36	3	-12
	M	3	28	2004	3	29	611	587	-24	1	-24
	M	3	29	2004	3	30	587	596	9	1	9
	M	3	30	2004	4	1	596	590	-6	2	-3
108666683	M	3	24	2004	3	25	630	663	33	1	33
	M	3	25	2004	3	26	663	651	-12	1	-12
	M	3	26	2004	3	29	651	758	107	3	36
	M	3	29	2004	3	30	758	775	17	1	17
	M	3	30	2004	4	1	775	768	-7	2	-4
108666653	M	3	24	2004	3	26	638	595	-43	2	-22
	M	3	26	2004	3	28	595	589	-6	2	-3
	M	3	28	2004	3	30	589	615	26	2	13
108666664	M	3	24	2004	3	26	608	601	-7	2	-4
	M	3	24	2004	3	27	601	587	-14	3	-5
	M	3	24	2004	3	28	587	528	-59	4	-15
108666521	M	3	21	2004	3	23	627	614	-13	2	-7
	M	3	23	2004	3	24	614	624	10	1	10
108666569	M	3	22	2004	3	24	680	608	-72	2	-36
	M	3	24	2004	3	25	608	567	-41	1	-41
	M	3	25	2004	3	27	567	521	-46	2	-23
108666650	M	3	24	2004	3	28	738	658	-80	4	-20
	M	3	28	2004	3	30	658	659	1	2	1
108665694	M	3	19	2004	3	24	860	727	-133	5	-27
	M	3	24	2004	3	30	727	808	81	6	14
108665793	M	3	20	2004	3	25	713	608	-105	5	-21
	M	3	25	2004	3	28	608	559	-49	3	-16
108665809	F	3	16	2004	3	19	600	570	-30	3	-10
	F	3	19	2004	3	21	570	530	-40	2	-20

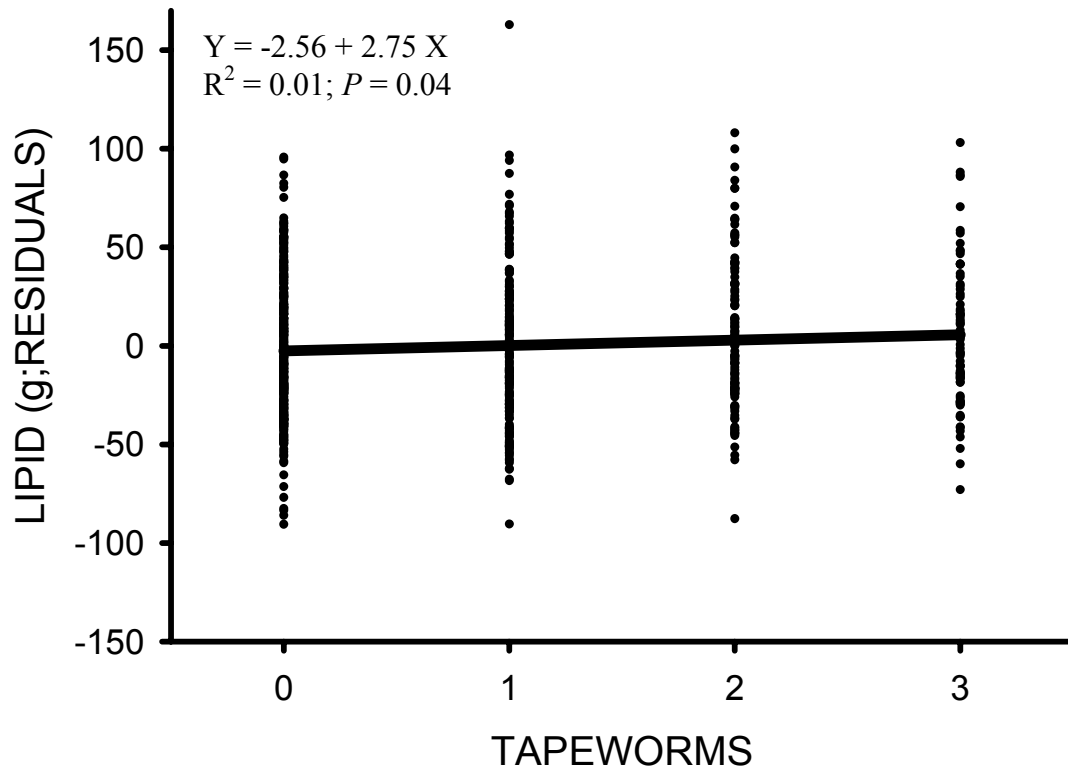
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Appendix C
continued

BAND	SEX	M1	D1	YEAR	M2	M3	MASS1	MASS2	C	D	CPD
108665922	F	3	20	2004	3	23	610	566	-44	3	-15
	F	3	23	2004	3	24	566	528	-38	1	-38
	F	3	24	2004	3	25	528	539	11	1	11
	F	3	25	2004	3	26	539	533	-6	1	-6
	F	3	26	2004	3	27	533	536	3	1	3
108666015	M	3	17	2004	3	21	769	691	-78	4	-20
	M	3	21	2004	3	27	691	766	75	6	13
108666045	M	3	17	2004	3	26	740	662	-78	9	-9
	M	3	26	2004	3	28	662	632	-30	2	-15
	M	3	28	2004	3	30	632	635	3	2	2
	M	3	30	2004	4	5	635	628	-7	5	-1
108666136	M	3	19	2004	3	23	790	680	-110	4	-28
	M	3	23	2004	3	25	680	720	40	2	20
	M	3	25	2004	3	27	720	720	0	2	0
108666141	M	3	19	2004	3	23	910	760	-150	4	-38
	M	3	23	2004	3	26	760	790	30	3	10
108666240	M	3	19	2004	3	23	760	663	-97	4	-24
	M	3	23	2004	3	25	663	655	-8	2	-4
108667486	M	3	15	2005	3	16	669	617	-52	1	-52
	M	3	16	2005	3	18	617	643	26	2	13
	M	3	18	2005	3	19	643	645	2	1	2
108667527	M	3	15	2005	3	17	727	745	18	2	9
	M	3	17	2005	3	19	745	731	-14	2	-7
108667661	M	3	15	2005	3	17	780	764	-16	2	-8
	M	3	17	2005	3	21	764	774	10	4	3
108667855	M	3	16	2005	3	17	773	764	-9	1	-9
	M	3	17	2005	3	18	764	696	-68	1	-68
108668504	M	3	20	2005	3	21	660	675	15	1	15
	M	3	21	2005	3	22	675	716	41	1	41

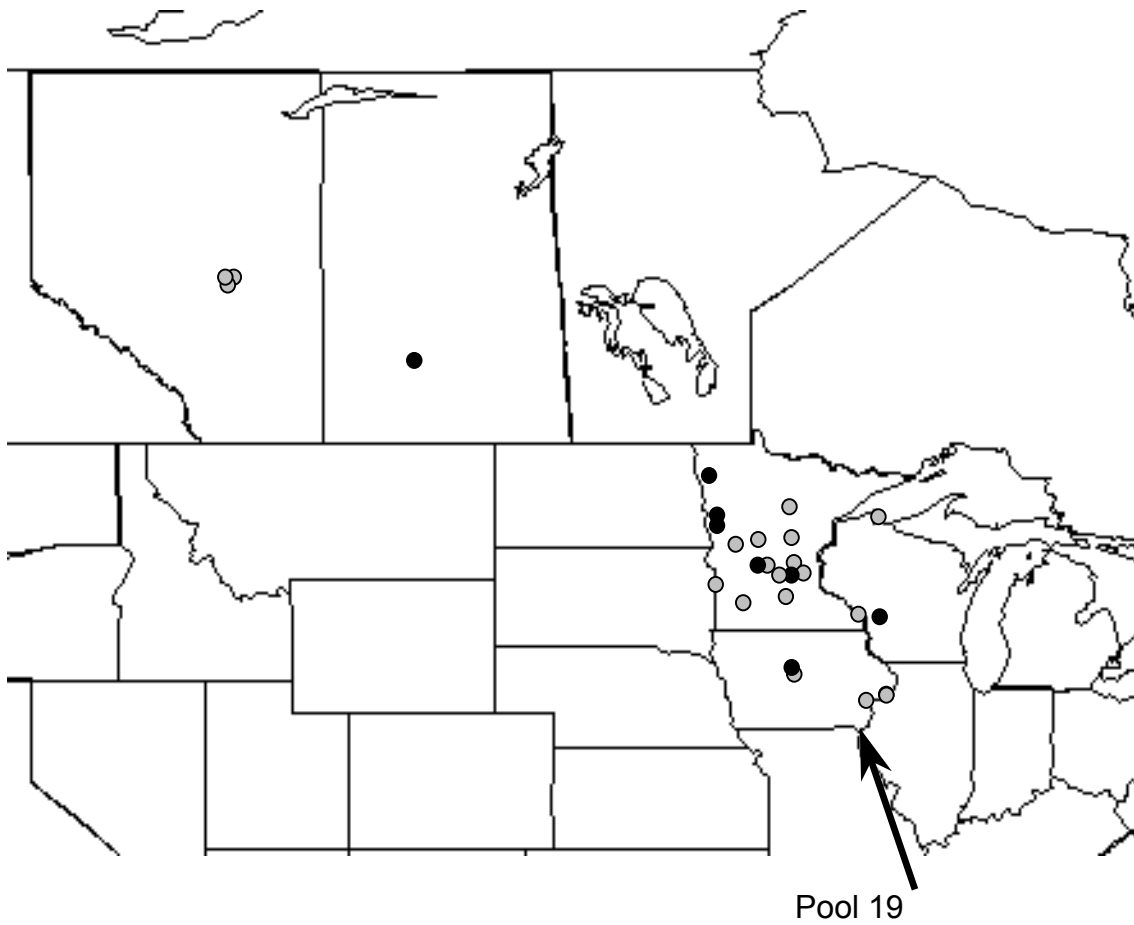
APPENDIX D: CORRELATION BETWEEN TAPEWORM ABUNDANCE AND LIPID RESERVES OF FEMALE LESSER SCAUP.

Regression of tapeworm (cestode) abundance (classified as 0 – 3 [none to high]) on lipid reserves residuals from of female lesser scaup collected during spring migration in the upper-Midwest (see Chapter 2 for details of lipid-reserve analysis).



APPENDIX E: SIGHTINGS OF COLOR-MARKED SCAUP DURING SPRING MIGRATION

Map of confirmed sightings (n = 29) of lesser scaup color-marked while staging at Pool 19 of the Mississippi River in springs 2004 – 2005 (years pooled). Grey circles indicate that the scaup were lighter than average at marking (females ≤ 760 and males ≤ 838) and black circles indicate heavier than average.



VITA

Michael J. Anteau grew up in Alaska with moose and ducks in his back yard, which taught him to appreciate nature, the outdoors, and wildlife. Michael has been interested in waterfowl since his early childhood and his father Thomas J. Anteau, a Michigan native, helped instill in him a special fondness for lesser scaup.

Michael graduated from University of Alaska Fairbanks in 1997 with 2 Bachelor of Science degrees (Wildlife Biology and Biological Sciences). At the University of Alaska Fairbanks, Michael studied under Dr. James S. Sedinger as well as worked for him on the Yukon-Kuskokwim Delta studying the breeding ecology of black brant. After graduating from University of Alaska Fairbanks, Michael set off to see the rest of North America. He worked as an environmental consultant in New Mexico, studied songbird breeding distributions on the north rim of the Grand Canyon, worked on a mourning dove telemetry study in South Carolina, studied the wintering ecology of black brant in Baja California, Mexico, and worked on a mottled duck breeding study in Cameron Parish, Louisiana.

Michael's interest in lesser scaup took him to Louisiana State University to study under Dr. Alan D. Afton, where he became a Master of Science student in August of 1999. Michael finished his Master of Science and started a doctoral program at Louisiana State University in August 2002. Michael defended his dissertation in December 2005, and is now working as a Research Scientist at the USGS Northern Prairie Wildlife Research Center in Jamestown, North Dakota.