

**BIOENERGETICS AND FOOD USE OF WINTERING AND STAGING
ATLANTIC BRANT**

by

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Ecology

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ABSTRACT

I conducted behavioral and food sampling of Atlantic brant (*Branta bernicla hrota*) across their winter range on the northeastern coast of the USA. I used time-activity budgets to estimate daily energy expenditure (DEE) of brant. Sampling occurred 1 Dec – 31 May 2006–2008 in eleven 225 km² sites between Rhode Island and Virginia containing important estuarine and upland habitat. Overall DEE for brant was 1,530±64 kJ/day. There was considerable variation in time-activity budgets between years, months, regions, habitat, tide, temperature, and time-of-day, and I detected no significant difference in DEE of brant between years or regions. However, DEE was significantly different between months and ranged from 2,018±173 kJ/day in January to 1,048±137 kJ/day in May. Brant spent most of their time feeding (32%), swimming (26%), resting (16%), and flying (15%). I also quantified diet of brant and energy density of food plants. Brant mostly ate macroalgae (*Ulva sp.*, *Enteromorpha sp.*) in early-mid winter and salt marsh cordgrass (*Spartina alterniflora*) and upland grass and clover (*Poa sp.* and *Trifolium sp.*) in late winter and spring. Energy density differed by vegetation type: macroalgae (12.6±0.1 kJ/g), eelgrass (*Zostera marina*) (14.1±0.1 kJ/g), salt marsh cordgrass (16.9±0.2 kJ/g), and upland grass and clover (17.7±0.1 kJ/g). I explored variation in the diet of brant between 1 November – 31 May 2007-2008. I determined dietary trends using stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes in four known food sources that brant eat. I predicted relative contributions from food sources would differ between months as food source availability shifted over time. I

sampled liver and leg muscle tissues from 525 individuals over a seven month winter period in four geographic regions. I measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in each of the tissues and food sources collected within each region. I detected significant differences between regional and monthly $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in both liver and leg tissues. Dietary trends were determined using Bayesian mixing-models to estimate relative contributions of food sources with the software package SIAR. I detected variation between regions and months in brant tissues and diet, reflecting population level responses to variation in food resource availability over the winter range.

Chapter 1

DAILY ENERGY EXPENDITURE AND FOOD USE OF WINTERING ATLANTIC BRANT

Introduction

Current research on wintering migratory waterfowl suggests that the primary factor limiting many populations is the availability of food (Haramis et al. 1986, Miller 1986, Conroy et al. 1989, Owen et al. 1992, Bergan and Smith 1993, Jeske et al. 1994, Clausen et al. 2003, Mini and Black 2009). As habitat loss and degradation affects coastal areas along the Atlantic Coast (Stewart et al 1988), there is concern that waterfowl energetic demands may not be met. Several joint ventures (JV; Arctic Goose JV, Central Valley Habitat JV, Mississippi Alluvial Valley JV, Gulf Coast JV) have adopted a bioenergetic approach to identify the amount of foraging habitat required to meet waterfowl population objectives, evaluate the extent to which these needs have been addressed on a regional scale, and to help identify areas for priority action (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986).

Atlantic brant (*Branta bernicula hrota*) (hereafter brant) populations changed considerably during the 1900s (Reed et al. 1998) in response to the disappearance of preferred foods at wintering and staging areas (Cottam et al. 1944). Brant once relied on eelgrass (*Zostera marina*) as a primary food plant (Reed et al. 1998). In 1931–1932 a wasting disease caused by the pathogenic slime mold *Labyrinthula zosterae*, extensively reduced eelgrass abundance on the North Atlantic

coast (Rasmussen 1977), and this coincided with drastic declines in the brant population (Cottam et al. 1944). The greatest effect on the population was likely due to reduced breeding effort and success by malnourished brant (Kirby and Obrecht 1982). A moratorium on brant hunting from 1933–1952 was put in place until populations of eelgrass and brant recovered (Rogers 1979). Since the 1970s, the brant population has fluctuated between 40,825–181,631 birds. A suite of factors including spatial and temporal variability in reproductive success, harvest, food availability, and severe weather are thought to be responsible for these population fluctuations (Nelson 1978, Rogers 1979, Kirby and Ferrigno 1980). In the past two decades, brant have exhibited some plasticity in foraging behavior and food preference enabling birds to exploit a variety of food resources throughout the winter (Penkala 1976, Kirby and Obrecht 1980). For example, eelgrass has not recovered to its former extent and brant switched to macroalgae (e.g. *Ulva sp.* and *Enteromorpha sp.*) while expanding to new wintering areas.

To inform population and management objectives, I estimate daily energy expenditure (DEE) calculated from time-activity budgets across the Atlantic coast wintering range. To potentially explain any observed variability in DEE, I also identified 1) peck rates to further quantify feeding behavior and food preference, 2) prevalence of disturbance due to natural and anthropogenic factors, 3) occurrence of consumed foods from harvested birds, and 4) nutritional quality of consumed foods.

Study Area

My study took place on the Atlantic coast of the United States between Rhode Island (RI) and Virginia (VA) (Figure 1.1) from December to May of 2006–2008. Eleven 225 km² sites (see Table 1.1 for abbreviations and location) were

designated in RI-Narragansett Bay, Connecticut (CT)-New London, CT-Fairfield, New York (NY)-Nassau, NY-Jamaica Bay, New Jersey (NJ)-Barnegat Bay NJ-Atlantic City, NJ-Cape May, Delaware (DE)-Indian River, Maryland, (MD)-Worcester, and Virginia (VA)-Accomack. This area coincides with the current wintering range of brant. I divided the winter range into four geographic regions based on latitude and known concentrations of brant from the Mid Winter Inventory (MWI, 1991-2005). Region 1 consisted of three northern sites in RI and CT, region 2 consisted of two sites in NY, region 3 consisted of the three NJ sites, and region 4 contained one site each in DE, MD, and VA.

Each of the 11 sites was subdivided into 225 1 km² plots and alpha-numerically coded (e.g. A1). For each site I *a priori* identified plots that contained both estuarine and upland habitat types where brant commonly occur that were accessible for observation. Plots from within this subset were selected randomly for behavioral data collection and vegetation sampling. I defined 4 habitat types including 3 habitat types within the Estuarine System (Cowardin et al. 1979) – open water, estuarine, salt marsh, as well as an upland habitat type. Open water habitat type consisted of shallow sub-tidal embayments. Estuarine habitat type contained intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. Salt marsh habitat type consisted of both irregularly and regularly flooded intertidal emergent wetland dominated by *Spartina spp.* The upland habitat type was defined as terrestrial fields, lawns, or areas adjacent to or nearby estuarine habitat. These 4 habitat types contained important brant foods (i.e. submerged aquatic vegetation (SAV) including macroalgae and eelgrass, new-growth salt marsh cord grass (*Spartina alterniflora*), and terrestrial grass (*Poa sp.*) and clover (*Trifolium sp.*).

Methods

Estimating Daily Energy Expenditure (DEE)

I reproduced the methods used by Albright et al. (1983) to estimate DEE using the following:

$$DEE = \sum_{i=1}^n [((BMR \times a_i) + C_T) \times T_i]$$

Equation 1

where BMR = average basal metabolic rate (kJ/hr), a_i = activity-specific multiple of BMR for the i^{th} behavioral activity, C_T = cost of thermoregulation (kJ/hr), and T_i = time engaged in the i^{th} behavioral activity (h). Estimates of DEE were calculated at two spatial and temporal scales. Overall mean DEE was calculated on a range wide and season wide scale. Additionally, I calculated DEE for each region and month separately.

I calculated BMR using values for brant geese (*Branta bernicla bernicla*) measured in the zone of thermoneutrality (Stahl 2001). Values were adjusted for wintering Atlantic brant with a mean mass of 1.390 ± 0.01 kg ($\bar{x} \pm \text{SE}$), yielding a BMR for brant of 17.98 kJ/hr. The energetic costs for each activity were calculated using multipliers (a_i) of BMR for feeding (1.7), resting (1.6), comfort (1.8), walking (1.9), and agonistic (1.9) provided by non-invasive heart rate telemetry calibrated with respirometry of semi-captive brant geese (Stahl 2001). I used metabolic multipliers for swimming (2.2) and courtship (2.4) derived from wintering black ducks (*Anas rubripes*) (Wooley and Owen 1978). Flight costs were calculated from the relationship $P_{\text{flight}} (\text{Watts}) = 52.6 \text{ mass}^{0.74}$ (Butler and Bishop 2000), using a mean mass of 1.390 ± 0.01 kg ($\bar{x} \pm \text{SE}$, $n=1,042$) from brant collected across the winter range

between December and May of 2006-2008. This allometric relationship predicted energy costs of 67.1 W (241.6 kJ/hr) for flapping flight and thus a multiplier of 13.4 for flight costs relative to BMR.

Given that ambient temperature from my data changed over time during Dec–May, I estimated C_T and DEE at two spatio-temporal scales: range wide (Dec–May 2006–08) and by region per month. All thermoregulatory costs were calculated using the inverse linear relationship between metabolic rate and ambient air temperature below the lower critical temperature (LCT) of 7.5 °C derived from respirometry studies of Pacific brant (*Branta bernicla nigricans*): $C_T = 1.5 - 0.0365(t)$ (L O₂/hr) calculated from (Morehouse 1974). I converted oxygen consumption of birds using the energy equivalent of 20.1 kJ/hr to 1 liter of O₂/hr (Carey 1996). When mean temperatures (temperature data collected during each behavioral observation period, this study) were above the LCT of 7.5 °C I assumed brant had no additional thermoregulatory costs. When calculating rangewide DEE estimates I used a mean temperature of 6.8 °C averaged from mean ambient air temperatures from each of the 11 sites between 1 Dec – 31 May 2006–2008 (NOAA, National Climatic Data Center) to derive a $C_T = 0.51$ kJ/hr.

To estimate the percent time brant engaged in different behavioral activities (T_i) throughout the day, instantaneous scan sampling of brant flocks were conducted at each of the 11 sites, generally once per week, during the study period (Altmann 1974), except that no data were collected at DE during 2006–07 since that site was added only in 2007–08. Observations were randomly distributed within *a priori* selected plots, and over 3 daytime periods: morning (30 minutes before sunrise – 1000 hr), midday (1000–1400 hr), and evening (1400 hr -30 minutes after sunset). I

was unable to collect any nocturnal observations because available night vision equipment proved ineffective under most field conditions. Given this limitation, I assumed that diurnal and crepuscular observations were representative of the entire 24-hour period to calculate DEE.

Observers in parked vehicles or on foot completed scans using a 20-60X spotting scope or 10X binoculars depending on the observer's proximity to birds. Once a group of birds was located, a 10-minute acclimation period followed. I scanned the group every 15 minutes for a one-hour period or until the group of birds left. I assumed that the scans collected every 15 minutes on the same group of birds (≤ 4 scans) were not independent of each other and averaged them together to avoid pseudoreplication. Activities were recorded as feeding, swimming, flying, walking, resting (sleeping and loafing), comfort (preening or bathing), agonistic, and courtship using micro-cassette and digital recorders, or hand counters. During each scan I also recorded if a disturbance event occurred. I defined disturbance events as times when birds became collectively alert and/or $\geq 50\%$ of birds took flight. Likely causes were categorized as 1) anthropogenic, people and dogs; 2) avian sources, raptors or large waders; 3) aircraft, planes, helicopters; 4) boats and jet skis; 5) autos, cars or trucks; and 6) unknown. I calculated the percent occurrence of disturbances due to each likely cause by dividing the number of disturbance events due to each likely cause by the total number of disturbance events. For each observation, I recorded plot number, date, habitat type (open water, estuarine, salt marsh, or upland), tidal stage (low, flood, full, and ebb), ambient air temperature ($^{\circ}\text{C}$), and time.

Additionally, I quantified peck rate in brant using focal sampling (Altmann 1974) to measure number of pecks per 15 seconds. Feeding birds were

randomly selected and observed using a stopwatch and voice recorder. Observations were randomly distributed across site, month, and time-of-day within the same plots where behavioral scan sampling also occurred. Habitat type was always recorded for each brant observation and food type was recorded when accurate visual identification of food was possible. All 15 second sampling periods (n=4,903) were averaged by sampling event. Values were converted from number of pecks per 15 seconds to pecks per minute.

I calculated a body condition index (BCI) for all individuals where I had complete body mass (g), un-flattened wing chord (mm), age, and sex data. I standardized body mass for structural differences between individuals by dividing body mass by wing chord (Baldasare and Bolen 1994).

I used univariate analysis of variance (ANOVA, $\alpha \leq 0.05$) to assess whether time-activity budgets differed between years, months, regions, habitat type, tidal stage, ambient air temperature categories ($< 0^{\circ}\text{C}$, $0-7.5^{\circ}\text{C}$, $> 7.5^{\circ}\text{C}$), and time-of-day (morning, midday, and evening, see above). All proportion data were arcsine transformed prior to analysis in order to meet underlying assumptions of normality (Zar 1974). I used ANOVA to test for differences in DEE between years, months, regions, and ambient air temperatures (listed above). I also used ANOVA to determine if peck rate differed by year, region, month, and habitat. To test for differences in BCI between years, months, regions, age, and sex, I used ANOVA. When I detected significant main effects and there were at least three levels of the independent variable, I used Tukey's post hoc tests ($\alpha \leq 0.05$) to determine level of significance.

Quantifying Brant Diet and Nutritional Quality

I estimated diet of brant using gross analysis of foregut contents from brant carcasses obtained through hunter-harvested donations, or state-issued scientific collection permits. Brant were collected in all 11 study sites, as well as in North Carolina during Dec – May 2006–08, and in James Bay on the staging grounds in May 2007 (Table 1.1). Carcasses were opened and the entire foregut (including the proventriculus and gizzard) was removed and frozen at -40 °C until processing. In the laboratory, foregut contents were thawed, sand and grit was removed by flushing with de-ionized water over a 50 µm sieve, and then each plant piece was sorted into one of four broad categories (macroalgae, eelgrass, new-growth *Spartina sp.*, and grass and clover). Vegetation samples were dried at 50 °C for 48 hrs, or until completely dry. The dry mass (g) of each sample was then recorded using a Mettler AE 100 balance to the nearest 0.0001g. I compared percent frequency of occurrence of food types for each month between years.

I also collected plant samples in areas where brant were observed foraging at all sites throughout the study period to measure food quality. Live vegetation was randomly collected once every month at each site and sorted into the same four categories used for foregut analysis (macroalgae, eelgrass, new-growth *Spartina alterniflora*, and grass and clover sp.). Upland grass and clover along with new-growth *Spartina alterniflora* were clipped at the soil line and SAV was collected by hand while wading in shallow water, or in some cases using a D-frame dip net, a metal rake, or by boat. Dead plant material and dirt was removed from all samples. Samples were rinsed in de-ionized water before being identified and dried for 48 h at 50 °C.

Dried samples were then homogenized using a Wiley-mill. All samples were analyzed using a Parr bomb calorimeter to determine energy density (kJ/g). Energy density values were analyzed using analysis of variance (ANOVA, $\alpha \leq 0.05$) to test for the main effects of year, month, region, and vegetation type.

Results

A total of 1,441 independent behavioral scans, after averaging by observation event, were completed across the study area. Using Equation 1, I estimated an overall mean DEE of $1,530 \pm 64$ kJ/day. DEE was different between months ($F_{5,102} = 2.44$, $P < 0.05$) but not between years, regions, or temperatures ($F_{1,102} = 2.59$, $P = 0.11$; $F_{3,102} = 0.03$, $P = 0.99$; and $F_{2,102} = 0.55$, $P = 0.58$ respectively; Appendices A and B). Energy expenditure peaked in January ($2,018 \pm 173$ kJ/day) and declined each month thereafter reaching the lowest energy expenditure in May ($1,049 \pm 137$ kJ/day) (Figure 1.2). To understand the possible mechanisms behind a monthly variable DEE, it is important to look at both intrinsic factors within the calculation as well as extrinsic factors that influence variables within the equation.

Intrinsically, DEE estimates are driven by the cost of thermoregulation and time spent in behavioral activities. Although energy costs associated with thermoregulation were relatively low throughout the study period, brant experienced greater thermoregulatory costs in Jan – Feb compared to other months. Thermoregulatory contributions to DEE when mean monthly temperatures were below the LCT of 7.5 °C were on average 4.5% of DEE or 64 kJ/day.

On average, brant were engaged in 32% feeding, 26% swimming, 14% flying, 3% walking, 16% resting, 8% comfort activity, and 0.7% agonistic activity (Table 1.2). Percent time brant spent in all activities except swimming and walking

differed between months with flight activity being significantly greater in January (24%) compared to all other months (Table 1.2). I further detected significant differences between years for all behaviors except comfort (Figure 1.3), regions (Table 1.3), and environmental factors including habitats, temperature, tide, and time-of-day (Table 1.4). Applying energetic costs to each of these behaviors produced relative contributions to yearly DEE of 14-19% feeding, 14-18% swimming, 50-58% flying, 1-2% walking, 6-11% resting, 4% comfort, and <1% agonistic (Appendix A).

I further examined 4 extrinsic factors that could have influenced monthly DEE including variability in food consumption behavior (as measured by peck rates), disturbance, foods consumption, and nutritional quality of consumed foods. First, the overall mean peck rate for brant was 29.3 ± 1.3 pecks/min. However, peck rate varied as a function of year, month, region, and habitat, but not of tide, temperature, or time-of-day (year: $F_{1,440} = 16.3, P < 0.01$; month: $F_{5,440} = 10.4, P < 0.01$; region: $F_{3,440} = 10.9, P < 0.01$; habitat: $F_{3,440} = 49.1, P < 0.01$; tide: $F_{3,440} = 0.55, P = 0.65$; temperature: $F_{2,440} = 0.21, P = 0.82$; and time-of-day: $F_{2,440} = 0.48, P = 0.62$). Focusing on monthly affects, peck rate of brant was significantly faster in May (54.5 ± 6.9) compared to all other months (Figure 1.4).

Disturbance impacts may also lead to higher energetic costs. I calculated the frequency of occurrence of disturbance events for each likely known cause over the entire winter range. I recorded a total of 374 unique disturbance events accounting for 26% of independent sampling events. Disturbances in January accounted for 31% of all scans; which was above the mean for all months. People and dogs caused 25% of disturbances (n=93), birds caused 14% of disturbances (n=53), automobiles caused 10% of disturbances (n=36), boats caused 9% (n=32), aircraft caused 6% (n=22), and

hunting was responsible for 2% of all observed disturbances (n=6). However, many causes of disturbance were unknown (36%, n=132) (Figure 1.5).

In addition to energetic costs associated solely with brant behavioral patterns, response to available food on the landscape may also greatly impact monthly DEE. Although I was not able to directly quantify food biomass and availability, I will assume foregut contents may act as an index to actual availability. Because brant are relative specialists on a few food sources, this assumption should be relatively robust. I estimated diet of brant using gross analysis of foregut contents from 1,057 carcasses. Macroalgae was consistently found in 40–60% of brant foreguts across all months and years (Figure 1.6). Eelgrass was commonly eaten by brant (45% of foregut samples) during November then declined in their diet during subsequent months. New-growth *Spartina* was not found in any brant foreguts during 2006–07, and was relatively rare in 2007-08 with a small amount of consumption during Feb. Grass and clover increased in frequency of occurrence over time especially in 2006–07 (67% of the brant diet by May) (Figure 1.6). Of note, 13 of 15 birds sampled on James Bay, a key staging area during migration, in May 2007 had full foreguts containing only terrestrial grasses (family Poaceae, alkalaigrass (*Puccinellia sp.*), and fescue (*Festuca sp.*)).

A final extrinsic factor potentially influencing variability in behavior and associated DEE is variability in nutritional quality of certain foods over time. Average energy density of all vegetation samples (n= 796) collected during 2006–08 was 14.3 ± 0.1 kJ/g, although energy density differed between vegetation types (Figure 1.7), but not between year, month, or region (vegetation type: $F_{3,687} = 71.4$, $P < 0.01$; year: $F_{1,687} = 0.37$, $P = 0.54$; month: $F_{5,687} = 0.82$, $P = 0.54$; and region: $F_{3,687} = 0.35$, $P =$

0.79). All energy densities of each vegetation type were significantly different (Figure 1.6). Due to variation in energy density and seasonal availability between vegetation types, I subsequently analyzed variation due to main effects of year, month, and region for each vegetation type separately. Energy density of macroalgae was on average 12.6 ± 0.1 kJ/g, although it differed between months, but not between year or region (month: $F_{5,452} = 4.42$, $P < 0.01$; year: $F_{1,452} = 0.04$, $P = 0.85$; and region: $F_{3,452} = 0.52$, $P = 0.67$). Energy density of macroalgae was significantly greater in December (13.6 ± 0.3 kJ/g), January (13.3 ± 0.2 kJ/g), and February (13.3 ± 0.3 kJ/g) compared to April and May (11.3 ± 0.3 kJ/g and 11.8 ± 0.3 kJ/g, respectively). Overall mean energy density of eelgrass was 14.1 ± 0.1 kJ/g, however energy density of eelgrass varied only as a function of region, but not of year or month (region: $F_{3,35} = 4.63$, $P < 0.05$; year: $F_{1,35} = 0.68$, $P = 0.42$; and month: $F_{5,35} = 2.33$, $P = 0.06$). Pair-wise comparisons between regions were unable to detect any differences between regions. Overall mean energy density of new-growth *Spartina* was 16.9 ± 0.2 kJ/g and I detected no variation between years, months, or regions (model: $F_{10,52} = 0.25$, $P = 0.99$). Additionally, overall mean energy density of grass and clover was 17.7 ± 0.1 kJ/g (Figure 1.6), and I detected no variation between years, months, or regions (model: $F_{39,148} = 1.14$, $P = 0.28$).

Mean body condition index (BCI) of 1,040 brant was 4.29 ± 0.01 (mean \pm SE) (Appendix C). I detected differences between years, months, regions, ages, and sexes ($F_{1,866} = 28.9$, $P < 0.0001$, $F_{6,866} = 39.5$, $P < 0.0001$, $F_{3,866} = 12.0$, $P < 0.0001$, $F_{1,866} = 78.9$, $P < 0.0001$, and $F_{1,866} = 37.1$, $P < 0.0001$, respectively). I also detected a significant interaction between all terms ($F_{161,866} = 1.86$, $P < 0.0001$), indicating patterns of BCI between ages and sexes differed between regions, months,

and years. In 2006-07 brant had lower BCI (4.19 ± 0.02) compared to 2007-08 (4.37 ± 0.02). Values for BCI were greater in after hatch year (AHY) brant (4.42 ± 0.02) compared to hatch year (HY) brant (4.13 ± 0.03). Male brant had higher average BCI values compared to females (4.38 ± 0.02 , 4.20 ± 0.02 , respectively). Values for BCI were significantly lower in Jan, Feb, and Mar (4.16 ± 0.03 , mean \pm SE) compared to Nov, Dec, and APR (4.36 ± 0.04 , mean \pm SE), and BCI was greatest in May (4.86 ± 0.04). In region 4 brant had significantly lower BCI (4.20 ± 0.03) compared to region 1 (4.35 ± 0.03) and region 3 (4.42 ± 0.03).

Discussion

Wintering Atlantic brant, like other migratory waterfowl, were able to satisfy their energy requirements by adjusting overall time-activity budgets, foraging effort or intake rate, and by exploiting different types of available food (Madsen 1985, Prins and Ydenberg 1985, Owen et al. 1992, Rowcliffe et al. 1995, Hassall et al. 2001). The behavioral plasticity of brant allowed them to exploit different foods at different times during the winter and staging periods (Cottam et al. 1944, Kirby and Obrecht 1980, Percival and Evans 1997, Inger et al. 2006, Mason et al. 2007).

My estimate of DEE ($1,530 \pm 64$ kJ/day) was similar to that reported by Tinkler et al. 2009 (1326–1556 kJ/day), but higher than most other previous studies that used time-activity budgets to estimate DEE for brant geese (e.g., Riddington et al. 1996: 841.4 kJ/day, Stahl 2005: 842 ± 14 kJ/day, Inger et al. 2006: 1152 kJ/day, and Mini and Black 2009: 1013 ± 14 kJ/day). Similar to Tinkler et al. 2009, my study took place over the entire wintering period and included time-activity budget data from the entire wintering period, throughout which I detected significant seasonal variation. My estimate of DEE for brant also accounts for energy use of brant on a range-wide scale

over a large geographic area. Differences in estimates of DEE between European brent geese and Atlantic brant could also result from variation in energetic costs, habitat quality, spatial distribution of food resources between wintering regions, and nocturnal activity of geese.

I have documented that brant adjust their behavior in response to annual and monthly variation in potential food abundance and energy demands. In January, brant experienced the highest DEE of the winter period due to a combination of factors driven mostly by increased flying activity (Table 1.2). Increased flight behavior may allow brant to exploit relatively patchily distributed food resources, occur in response to increased competition for depleted food resources (Inger et al. 2006a), or result due to heightened frequency of disturbance (Riddington et al. 1995). Brant spent significantly less percent time flying (12%) and swimming (20%) in 2006–07, compared to percent time flying (16%) and swimming (30%) in 2007–08 (Figure 1.3). This variation in locomotive behavior alone corresponded to an increase of 176 kJ/day between years. When activity budgets were converted to energy budgets, flight behavior constituted 50% of DEE. Wintering European light-bellied brent geese have shown similar behavioral patterns in flight associated energy costs. Varying energetic requirements and shifts in food abundance for brent geese influenced foraging and habitat selection, and engagement in nighttime feeding that contributed to >50% of energy intake at times (Tinkler et al. 2009). Several previous studies have also found that waterfowl are active at night and vary their activity under different environmental and physiological stimuli (Morton et al. 1989, Anderson and Smith 1999, Guillemain et al. 2002, McWilliams and Ravelling 2004, Rizzolo et al. 2005).

Disturbance events occurred during 26% of all scans during 2006–08. Although I did not directly quantify flight time of brant in response to specific disturbance events I did include all flying brant in my behavioral observations to account for these energetic costs. Negative impacts due to disturbance have been documented in brant as well as other geese (Belanger and Bedard 1990, McWilliams et al. 1994, Ward et al. 1999, Desmots 2009). Additional energetic costs associated with increased flight due to disturbances have been documented in European brant geese in upland pasture and saltmarsh habitats where geese may recoup energetic costs associated with disturbance by feeding more at night (Riddington et al. 1996) or by increasing the percentage of time spent foraging in habitats where higher quality food is available (Inger et al 2008). This is a very important consideration, particularly in poor production years or during periods of severe winter weather when brant may be unable to meet their basic daily energetic requirements. Energetic costs due to disturbance in these situations can result in higher winter mortality (Kirby et al. 1986). Disturbance may also impede successful migration (Klaasen et al. 2006), and reduce localized reproductive success (Jefferies and Drent 2006). Although negative impacts from direct disturbance must be considered, broad-scale human impacts resulting in habitat degradation and loss may have an even greater impact on fitness (Desmots et al. 2009).

Seasonal dietary trends found from gross foregut content analysis indicate that brant used a combination of SAV species (macroalgae and eelgrass), salt marsh species (*Spartina* sp.), and upland grass and clover. My results were similar to brant wintering in New Jersey (Penkala 1976, Kirby and Obrecht 1980) that indicate brant eat mostly macroalgae in early winter months (Figure 1.5). Brant geese also select

foods based on quality and availability shifting from macroalgae and eelgrass in early winter to new-growth *Spartina alterniflora* and upland grass and clover as they become available in late winter (Rowcliffe et al. 2001, Inger et al. 2006). Seasonal variability in macroalgae abundance will impact brant feeding behavior and use of habitats. I observed brant using upland habitat more in 2006–07 (17%) compared with 2007–08 (9%). These habitat and food use shifts are most likely in response to seasonal variation in SAV abundance. These results support previous research indicating that brant may shift their diet based on energy content and availability (Hassal et al. 2001, Durant et al. 2004, Inger et al. 2006, Tinkler et al. 2009).

Energy density of foods that brant consume during the winter was similar to foods analyzed by Kirby and Obrecht (1980) including *Ulva* (14.6 kJ/g), eelgrass (14.6 kJ/g), and *Spartina* (17.9 kJ/g) (values converted from kcal/g). Interestingly, new-growth *Spartina* and grass and clover showed no difference in energy density across years, months, or regions. Conversely, I detected variation in energy density of SAV between months (for macroalgae) and regions (for eelgrass). As macroalgae nutritional quality decreases over the winter months, terrestrial grass and clover become an important dietary component for brant, particularly in late winter months prior to migration.

Management Implications

My study indicates that brant show behavioral plasticity thereby allowing modification of daily activity budgets to meet seasonally varying energetic requirements associated with wintering and spring staging. Recognizing a variable DEE can be used along with eventual estimates of food biomass and total

metabolizable energy on the landscape to calculate carrying capacity (goose use days) on state, region, or range-wide scales. Additionally with recognition of a variable DEE and seasonal carrying capacity estimates, adaptive management could inform annual harvest management decisions for brant throughout the Atlantic flyway. Future carrying capacity estimates should incorporate terrestrial field habitat acreage when calculating available biomass estimates. I also suggest that remote sensing and predictive modeling techniques be used to estimate seasonal abundances of SAV to aid in the future management of brant.

Table 1.1 List of site abbreviations and locations by state and local region.

Region	State	Site abbrev.	Location	GPS coordinates (deg. min.)
1	Rhode Island	RI	Narragansett Bay	41°39'N, 71°19'W
	Connecticut	CT-NL	New London County	41°18'N, 72°11'W
	Connecticut	CT-FF	Fairfield County	41°04'N, 73°23'W
2	New York	NY-NAS	Nassau County	40°36'N, 73°36'W
	New York	NY-JB	Jamaica Bay	40°36'N, 73°53'W
3	New Jersey	NJ-BAR	Barneгат Bay	39°39'N, 74°12'W
	New Jersey	NJ-ATL	Atlantic City	39°24'N, 74°25'W
	New Jersey	NJ-CM	Cape May	39°02'N, 74°48'W
4	Delaware	DE	Indian River Estuary	38°37'N, 75°07'W
	Maryland	MD	Worcester County	38°10'N, 75°14'W
	Virginia	VA	Accomack County	37°55'N, 75°25'W
	North Carolina*	NC	Roanoke Sound	35°25'N, 75°69'W
	Canada*		James Bay	52°24'N, 79°13'W

* sites where brant carcasses were collected but not included in behavioral and vegetation sampling

Table 1.2. Percent time ($\bar{x} \pm SE$) Atlantic brant spent in different activities along the northeastern Atlantic coast, USA, during Dec–May, 2006–2008.

Activity	Percent time spent per activity														ANOVA results		
	Dec		Jan		Feb		Mar		Apr		May		Overall		F	df	P
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
Feed	27.4	1.8	25.5	1.6	31.4	1.7	30.3	1.5	38.5 ^A	1.7	44.2 ^A	2.4	32.3	0.7	11.1	5, 1421	< 0.01
Swim	26.5	1.7	24.2	1.6	28.2	1.7	27.2	1.7	25.8	1.7	25.2	2.3	26.2	0.7	1.1	5, 1421	0.39
Fly	13.0 ^C	1.8	23.6 ^A	2.1	15.3 ^B	1.7	13.7	1.7	11.8 ^D	1.5	5.2 ^D	1.3	14.5	0.7	6.4	5, 1421	< 0.01
Walk	2.0	0.3	2.5	0.4	2.5	0.3	2.4	0.3	2.9	0.4	3.1	0.4	2.5	0.1	0.5	5, 1421	0.81
Rest	18.6 ^A	1.5	16.1	1.3	16.8	1.3	18.4	1.3	13.7 ^B	1.1	12.8	1.4	16.2	0.5	3.8	5, 1421	< 0.01
Comfort	11.8 ^A	1.2	7.4 ^B	0.8	5.3 ^B	0.7	7.0 ^B	0.7	6.7	0.6	8.7 ^A	1.2	7.6	0.3	10.0	5, 1421	< 0.01
Agonistic	0.8	0.1	0.7	0.1	0.5	0.1	0.9	0.2	0.7	0.1	0.8	0.3	0.7	0.1	3.2	5, 1421	< 0.01
Courtship	-	-	-	-	-	-	0.2	0.2	-	-	-	-	-	-	-	-	-
No. of scans	207		272		256		270		289		147		1441				

^{A, B, C, D} Post-hoc comparisons between months

Table 1.3. Percent of time ($\bar{x} \pm SE$) that Atlantic brant spent in different activities in 4 regions: region 1 (RI, CT-NL, CT-FF), region 2 (NY-NAS, NY-JB), region 3 (NJ-BAR, NJ-ATL, NJ-CM), and region 4 (DE, MD, and VA) along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

Activity	Region 1		Region 2		Region 3		Region 4		Overall		ANOVA results		
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	<i>F</i>	df	P
Feed	33.3	1.4	33.9	1.5	30.8	1.1	30.4	2.2	32.3	0.7	8.43	3, 1421	< 0.01
Swim	24.5 ^B	1.5	25.3 ^B	1.3	26.3	1.1	31.9 ^A	2.6	26.2	0.7	7.44	3, 1421	< 0.01
Fly	10.4 ^B	1.4	15.5 ^A	1.3	16.2 ^A	1.3	14.5	2.4	14.5	0.7	10.34	3, 1421	< 0.01
Walk	2.2 ^B	0.3	3.8 ^A	0.3	2.0 ^B	0.2	1.9	0.6	2.5	0.1	3.70	3, 1421	< 0.01
Rest	21.3 ^A	1.3	13.6 ^B	0.9	17.0 ^A	0.9	9.6 ^C	1.4	16.2	0.5	12.50	3, 1421	< 0.01
Comfort	6.8 ^B	0.6	7.3	0.6	7.3	0.5	11.0 ^A	1.5	7.6	0.3	10.30	3, 1421	< 0.01
Agonistic	1.3 ^A	0.2	0.6 ^B	0.1	0.5 ^C	0.1	0.7	0.2	0.7	0.1	12.40	3, 1421	< 0.01
Courtship	0.2	0.2	0.02	0.01	-	-	-	-	0.05	0.04	-	-	-
No. of scans	328		424		539		150		1441				

^{A, B, C} Post-hoc comparisons between regions

Table 1.4. Percent time ($\bar{x} \pm SE$) that Atlantic brant spent in activities between habitat, tide, temperature, and time-of-day factors along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

Factors	Activities	Categories								ANOVA results		
		Open water		Estuarine		Salt marsh		Upland		<i>F</i>	df	P
Habitat		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
	Feed	25.3 ^D	0.9	29.1 ^C	1.1	45.4 ^B	3.2	61.7 ^A	2.2	100.4	3, 1421	< 0.01
	Swim	31.2 ^A	1.1	30.4 ^A	1.2	9.1 ^B	1.7	3.8 ^C	0.9	101.4	3, 1421	< 0.01
	Fly	17.7 ^A	1.2	11.6 ^B	1.1	9.1	2.0	12.3	1.8	8.8	3, 1421	< 0.01
	Walk	1.4 ^C	0.2	2.3 ^B	0.2	2.5 ^B	0.5	7.9 ^A	0.7	75.0	3, 1421	< 0.01
	Rest	17.2 ^B	0.8	15.8 ^B	0.9	22.5 ^A	2.3	10.2 ^C	1.3	11.3	3, 1421	< 0.01
	Comfort	6.5 ^B	0.4	10.3 ^A	0.7	11.0 ^A	1.7	2.7 ^C	0.3	32.0	3, 1421	< 0.01
	Agonistic	0.7 ^B	0.1	0.5 ^B	0.1	0.4 ^B	0.1	1.4 ^A	0.3	12.2	3, 1421	< 0.01
	Courtship	-	-	-	-	-	-	-	-	-	-	-
	N	703		471		90		177				
Tide		Low		Flood		Full		Ebb		<i>F</i>	df	P
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
	Feed	35.8 ^A	1.6	29.8 ^B	1.4	30.6 ^B	1.8	33.3	1.2	11.2	3, 1421	< 0.01
	Swim	26.4 ^A	1.7	28.0 ^A	1.4	19.4 ^B	1.6	28.2 ^A	1.2	3.5	3, 1421	< 0.05
	Fly	9.7	1.3	18.0	1.6	14.1	1.7	14.2	1.2	2.4	3, 1421	0.07
	Walk	2.7	0.3	2.3	0.2	2.3	0.3	2.8	0.3	4.6	3, 1421	< 0.01
	Rest	17.3 ^B	1.3	14.2 ^B	0.9	23.8 ^A	1.6	13.3 ^B	0.8	10.9	3, 1421	< 0.01
	Comfort	6.7	0.6	7.3	0.7	8.8	0.9	7.6	0.5	2.4	3, 1421	0.07

Agonistic	1.1 ^A	0.1	0.4 ^B	0.1	1.1 ^A	0.2	0.6 ^B	0.1	7.7	3, 1421	< 0.01
Courtship	-	-	-	-	-	-	-	-	-	-	-
N	255		424		265		497				

Temperature (°C)	< 0		0 - 7.5		> 7.5		<i>F</i>	df	P
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
Feed	32.2	2.5	30.7	1.2	33.2	1.0	5.2	2, 1421	< 0.01
Swim	24.0	2.2	25.3	1.2	27.1	1.0	1.9	2, 1421	0.15
Fly	17.9	2.8	17.1	1.4	12.3	0.9	0.6	2, 1421	0.53
Walk	3.1	0.7	2.2	0.2	2.7	0.2	0.5	2, 1421	0.95
Rest	17.3	1.9	17.4	1.0	15.2	0.7	1.5	2, 1421	0.22
Comfort	4.9 ^B	0.7	6.7 ^B	0.5	8.6 ^A	0.5	8.2	2, 1421	< 0.01
Agonistic	0.6	0.2	0.6	0.1	0.8	0.1	8.8	2, 1421	< 0.01
Courtship	-	-	-	-	-	-	-	-	-
N	135		503		803				

Time-of-day	Morning		Midday		Evening		<i>F</i>	df	P
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
Feed	34.8	1.2	30.2	1.0	32.1	2.0	0.9	2, 1421	0.39
Swim	23.9	1.1	27.4	1.0	28.4	2.1	0.7	2, 1421	0.49
Fly	13.9	1.1	13.8	1.0	18.7	2.4	1.8	2, 1421	0.17
Walk	2.6	0.2	2.4	0.2	2.8	0.4	1.8	2, 1421	0.16
Rest	16.7 ^A	0.9	17.1 ^A	0.8	11.9 ^B	1.2	5.0	2, 1421	< 0.01
Comfort	7.4	0.6	8.3	0.5	5.7	0.8	7.3	2, 1421	< 0.01
Agonistic	0.8	0.1	0.7	0.1	0.6	0.1	0.8	2, 1421	0.46
Courtship	-	-	-	-	-	-	-	-	-
N	560		679		202				

^{A, B, C, D} Post-hoc comparisons between categories

Figure 1.1. Map of eleven 225 km² study areas distributed along the northeastern Atlantic coast.

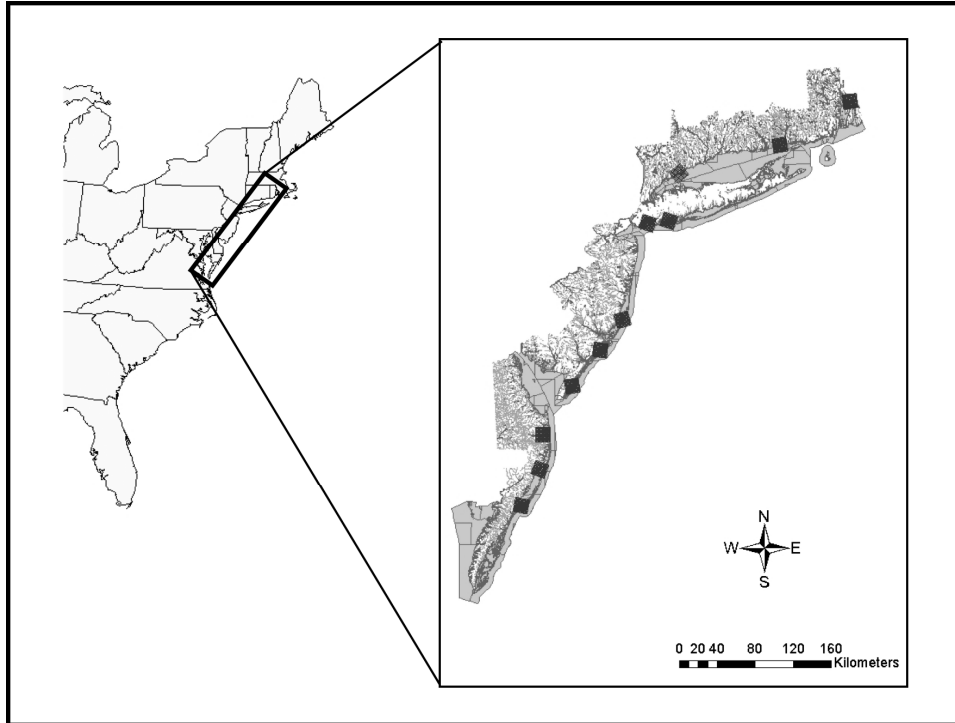


Figure 1.2. Daily energy expenditure (DEE, kJ/day \pm SE) of Atlantic brant by month along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

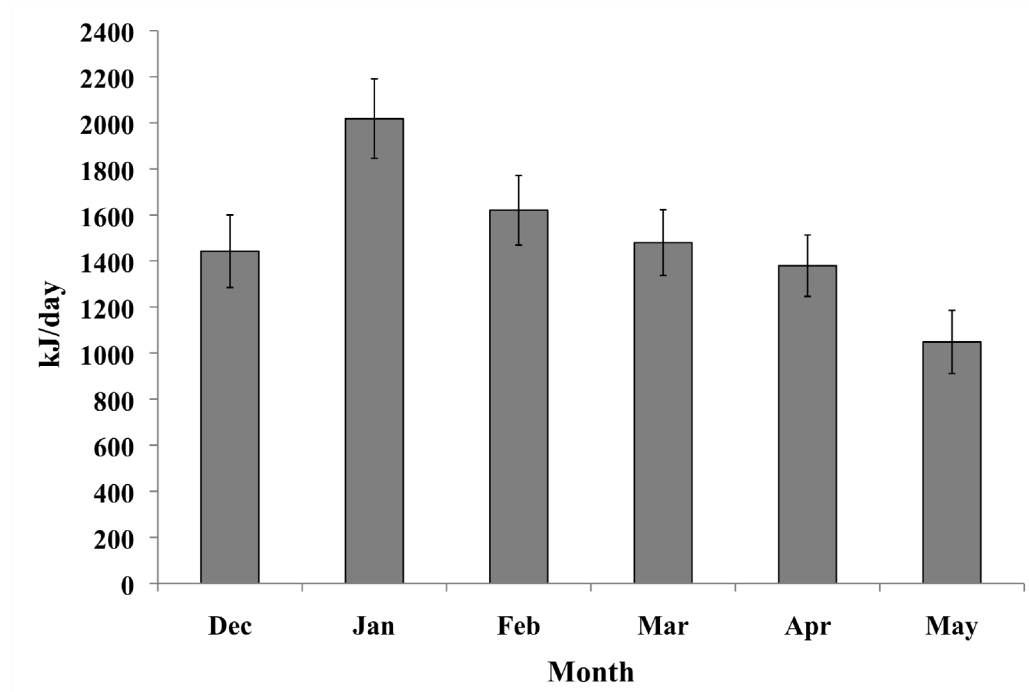


Figure 1.3. Percent time Atlantic brant spent in different activities ($\bar{x} \pm SE$) along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

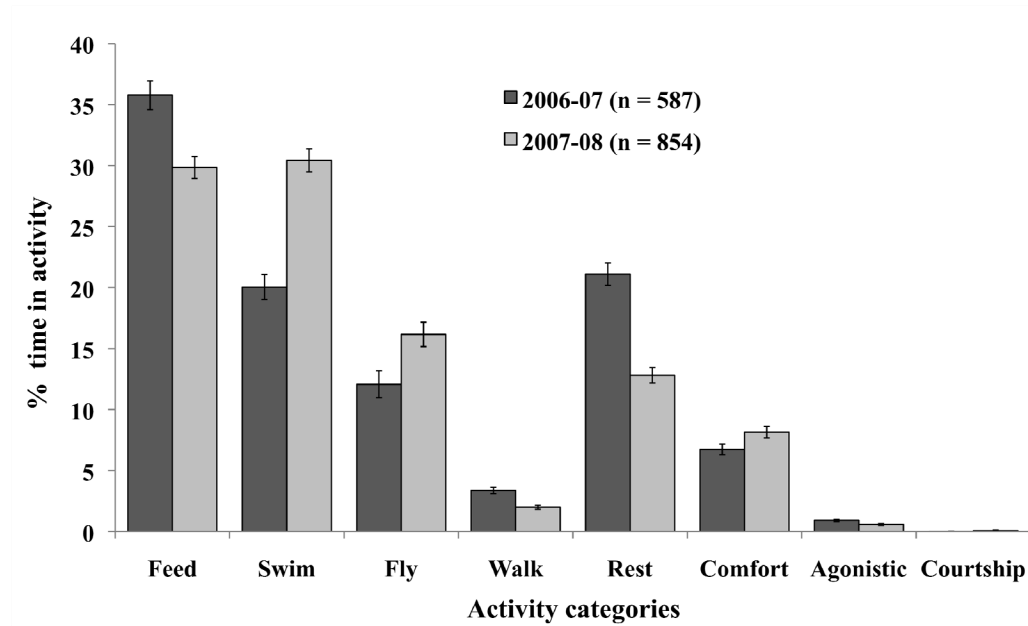


Figure 1.4. Peck rate (pecks/min) ($\bar{x} \pm SE$) of brant actively feeding on four vegetation types along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

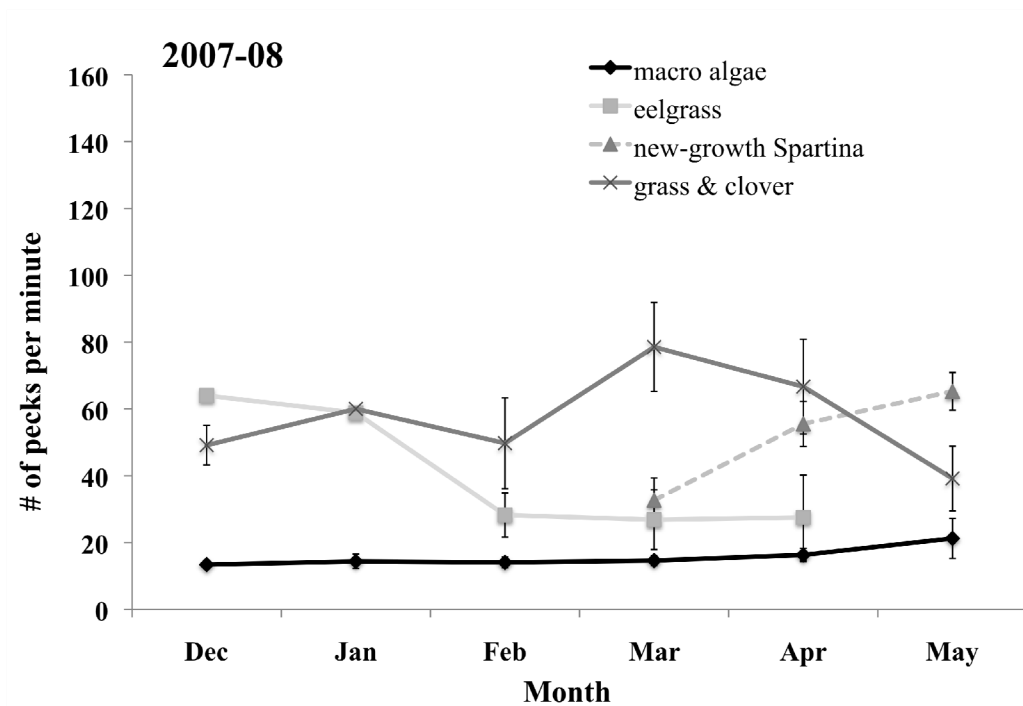
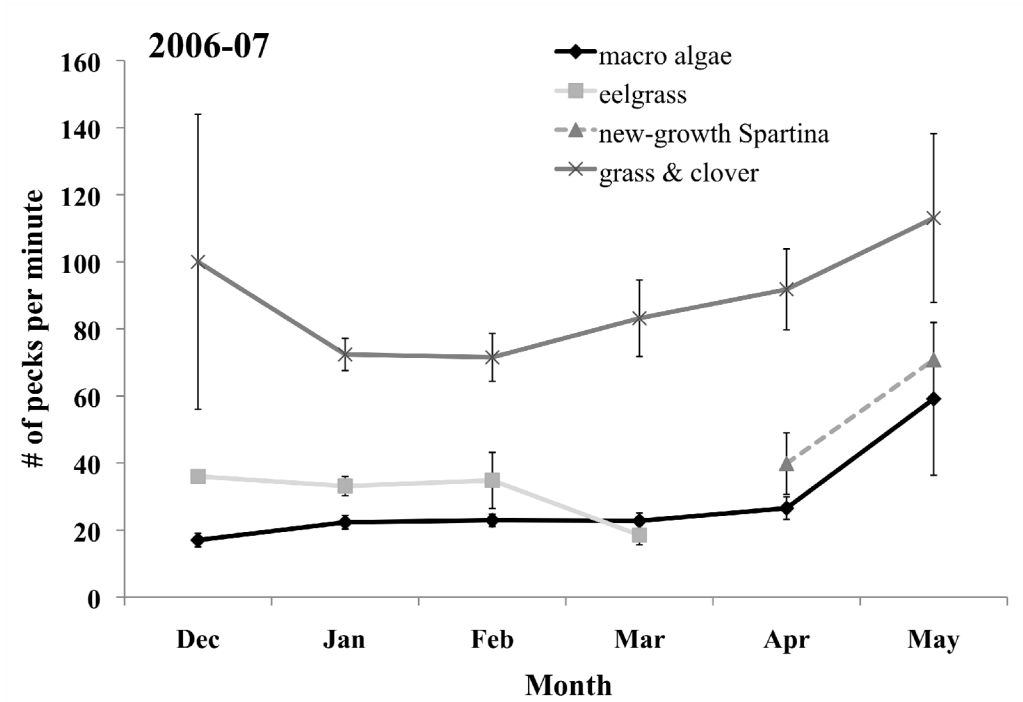


Figure 1.5. Percent of likely causes of disturbance ($\bar{x} \pm SE$) of Atlantic brant wintering on the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

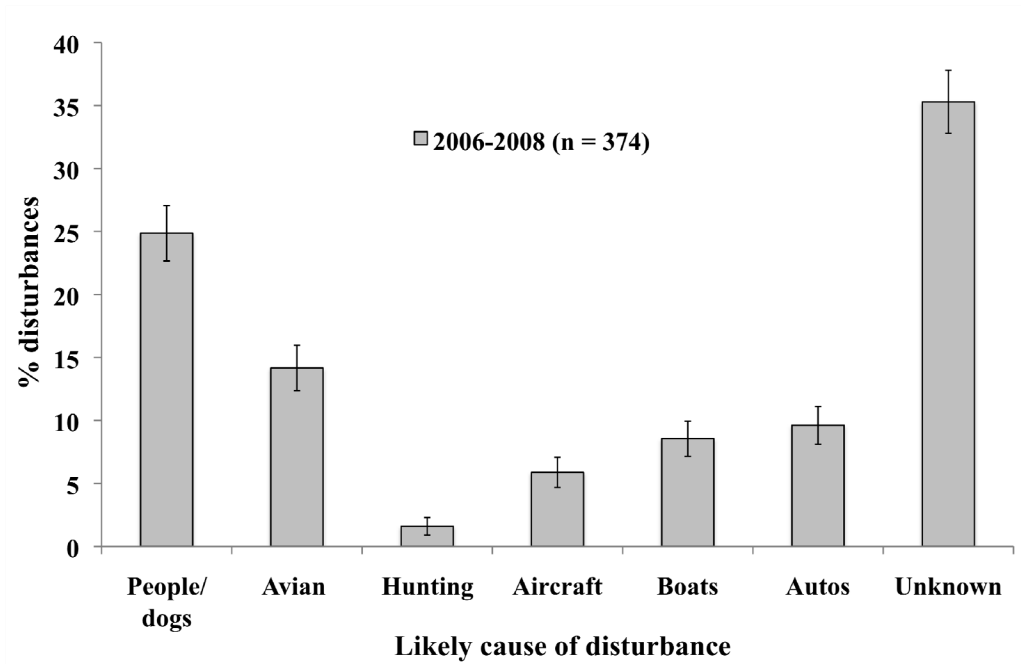


Figure 1.6. Percent of Atlantic brant foregut samples with different food types along the northeastern Atlantic coast, USA, during Nov-May 2006–2008.

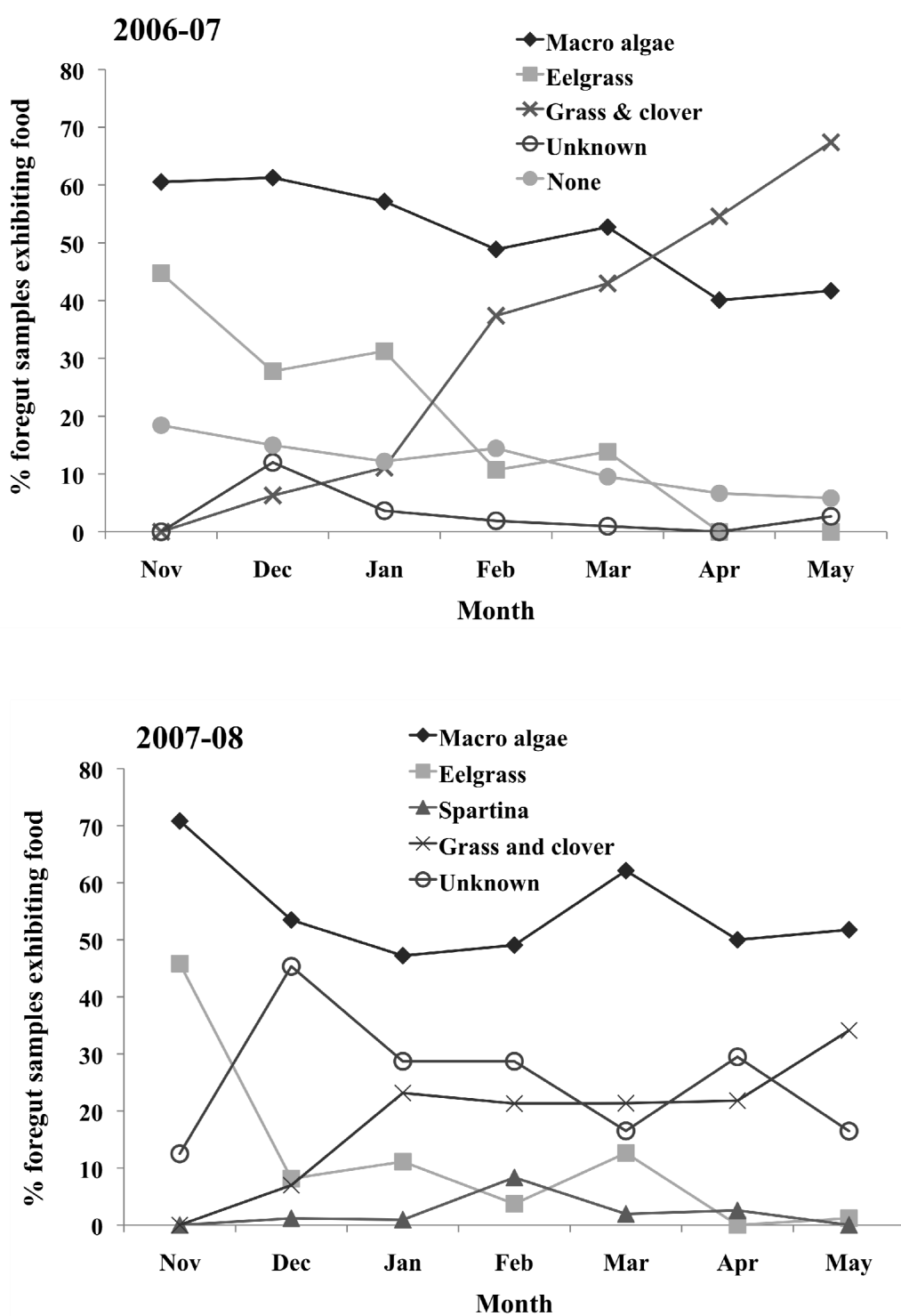
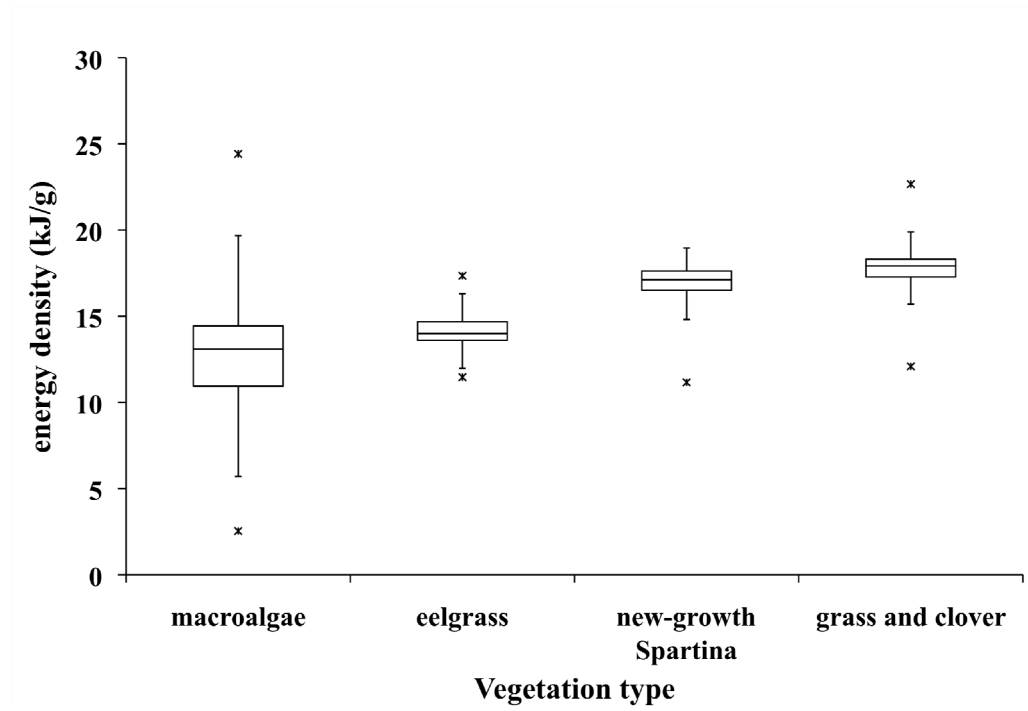


Figure 1.7 Energy density (kJ/g) of preferred Atlantic brant forage samples (n = 796) collected along the northeastern Atlantic coast, USA, during Nov–May 2006–2008.



Chapter 2

DETERMINING DIET OF WINTERING ATLANTIC BRANT USING STABLE ISOTOPES

Introduction

Availability of food has direct consequences on breeding success, survival, and spatial distribution of animals (Rowcliffe et al. 2001, Drent et al. 2007, Tinkler et al. 2009). Wintering migratory geese can be limited by energy intake due to changes in food source availability (Owen et al. 1992, Clausen et al. 1998, Inger et al. 2006a). Individuals should respond to potential negative impacts on fitness according to optimal foraging theory (Krebs 1978) by maximizing energy intake rates and foraging efficiency (Percival and Evans 1997, Hassal et al. 2001, Mini and Black 2009). Behavioral plasticity in response to shifting food availability has enabled migrating and wintering geese to exploit novel food sources, and has benefited populations world wide (Kirby and Obrecht 1980, Black et al. 2004, Jefferies and Drent 2006, Klaassen et al. 2006). Hence, dietary trends of individuals or groups reflect direct responses to spatial and temporal variation in food availability.

Recent studies that have explored factors affecting dietary trends in geese suggest that nutritional quality and digestibility play important roles in food resource quality and thus food use (Prop and Deerenberg 1991, Hassal et al. 2001, Durant et al. 2004). Additional constraints on dietary trends involve energy costs and habitat selection associated with heightened disturbance (Riddington et al. 1996, Ferét et al. 2003) and predation risk (Inger et al. 2006a). Dietary trends are also largely driven by shifting food availability on the landscape (Rowcliffe et al. 2001, Tinkler et al. 2009).

The light-bellied Atlantic brant (*Branta bernicla hrota*) population spends the winter on the central Atlantic coast between Massachusetts and North Carolina. Over the past 50 years foraging ecology and dietary trends of Atlantic brant (hereafter brant) have been studied using traditional forage analysis techniques relying on examination of foregut and fecal contents

(Cottam et al. 1944, Penkala 1976, Ramussen 1977, Kirby and Obrecht 1982). Historically, brant were closely associated with eelgrass (*Zostera marina*), which provided a reliable and widely available food source supporting the population wintering along the northeastern Atlantic coast of the United States (Reed et al. 1998). Major shifts in availability of this food source due to widespread disease, habitat loss or degradation, and increased anthropogenic pressures (e.g. fishing and marine recreation) have resulted in correlated population declines in brant (Cottam et al. 1944, Kirby and Obrecht 1982, Moore and Short 2003). Although populations have not recovered to historical levels, brant have been able to exploit novel food sources and habitats exhibiting plasticity in foraging behavior (Penkala 1976, Kirby and Obrecht 1980). Upon arrival in early winter (Nov – Dec) brant have been observed to feed on abundant submerged aquatic vegetation (SAV) including macroalgae (*Ulva sp.* and *Enteromorpha sp.*) and eelgrass (Penkala 1976, Kirby and Obrecht 1980). In late winter (Mar – May), after SAV abundance generally declines, brant exploit available new-growth salt marsh cord grass (*Spartina alterniflora*) and terrestrial grass (*Poa sp.*) and clover (*Trifolium sp.*) (Kirby and Obrecht 1982).

These past studies provide an important foundation for the understanding of brant foraging ecology in aspects of food preference, nutritional quality, and habitat use. However, studies that have used these traditional techniques may only provide limited information into accurately describing complex trophic dynamics (Votier et al. 2003). In recent years many ecological studies have been greatly aided by using an integrative approach combining traditional techniques with stable isotope analysis to determine dietary trends, track animal movements and distributions, and to study population and community responses to the environment (Alisauskas and Hobson 1993, Inger et al. 2006b, Inger and Bearhop 2008, Moreno et al. 2010).

Advances in our ability to measure stable isotopes in consumer foods and tissues have provided alternative approaches to studying feeding ecology and dietary trends (Hobson et al. 1993, Podledak et al. 2005, Inger and Bearhop 2008). Stable isotope analysis and the use of simple linear mixing models (e.g. ISOSOURCE) have been widely used to estimate relative

contributions when several food sources make up a consumer's diet (Post 2002, Phillips and Koch 2002, Phillips and Gregg 2003). Recent improvements in isotopic mixing models using Bayesian inference now allow for the incorporation of uncertainty associated with model inputs, and provide much more robust results compared to past linear mixing model approaches (Parnell et al. 2010). Bayesian mixing models can be simply run and analyzed using the open source software package SIAR (Stable Isotope Analysis in R) (Parnell et al. 2008). Resulting outputs from SIAR provide true probability distributions of most likely solutions that can be used to calculate measures of central tendency useful in downstream statistical analyses (Parnell et al. 2010).

Here I determine dietary trends of wintering and staging brant using stable carbon and nitrogen isotopes (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) in brant tissues against four known consumed food sources from Nov 2007 – May 2008. First I determine spatial and temporal variation of brant dietary trends using a stable isotope analysis. Second, I compare stable isotope results to gross foregut content analysis. Using the software package SIAR, I was able to determine mean relative contributions of food sources to brant diet within four geographic regions by month.

Study Area

My study took place on the Atlantic coast of the United States between Rhode Island (RI) and Virginia (VA) (Figure 1.1) from Nov 2007 – May 2008. Eleven 225 km² sites (see Table 1.1 for abbreviations and location) were designated in RI-Narragansett Bay, Connecticut (CT)-New London, CT-Fairfield, New York (NY)-Nassau, NY-Jamaica Bay, New Jersey (NJ)-Barnegat Bay NJ-Atlantic City, NJ-Cape May, Delaware (DE)-Indian River, Maryland, (MD)-Worcestor, and Virginia (VA)-Accomack. This area coincides with the primary current wintering range of brant. I divided the winter range into four geographic regions based on latitude and known concentrations of brant from the Mid Winter Inventory (MWI, 1991-2005, ($\bar{x} \pm \text{SE}$) 145,605 \pm 6,491). Region 1 consisted of three northern sites in RI and CT, region 2 consisted of 2

sites in NY, region 3 consisted of the three NJ sites, and region 4 contained the DE, MD, and VA sites.

Each of the 11 sites were subdivided into 225 1 km² plots and alpha-numerically coded (e.g. A1). For each site I *a priori* selected plots that contained both estuarine and upland habitat types where brant commonly occur. Plots from within this subset were selected randomly for vegetation sampling. I defined 4 habitat types including 3 habitat types within the Estuarine System (Cowardin et al. 1979) – open water, estuarine, salt marsh, as well as an upland habitat type. Open water habitat type consisted of shallow sub-tidal embayments. Estuarine habitat type contained intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. Salt marsh habitat type consisted of both irregularly and regularly flooded intertidal emergent wetland dominated by salt marsh grasses (*Spartina spp*). The upland habitat type was defined as terrestrial fields, lawns, or areas adjacent to or nearby estuarine habitat. These 4 habitat types contained important brant foods (i.e. submerged aquatic vegetation (SAV) including macro algae (*Ulva sp.* and *Enteromorpha sp.*), eelgrass (*Zostera marina*), new-growth salt marsh cord grass (*Spartina alterniflora*), and terrestrial grass (*Poa sp.*) and clover (*Trifolium sp.*).

Methods

Sample Collection

I randomly sampled live brant food sources monthly at each site and sorted them into the four broad plant food sources (macroalgae, eelgrass, new-growth *Spartina alterniflora*, and grass and clover). Terrestrial grass and clover along with new-growth *Spartina alterniflora* were clipped at the soil line and SAV was collected by hand while wading in shallow water, or in some cases using a D-frame dip net, a metal rake, or by boat. Dead plant material and dirt was removed from all samples. Samples were rinsed in de-ionized water before being identified and dried for 48 h at 50 °C. Dried samples were then homogenized using a Wiley-mill, weighed out to between 1.0-1.3 mg using a Mettler AE 100 balance and placed in tin capsules. I attempted to collect birds monthly between Nov 2007 – May 2008 in each state throughout the study area via

hunter-harvest donations and late winter and spring collections. Birds were aged, sexed, and morphometric data were recorded. Liver and leg muscle samples were removed from each individual and stored frozen.

Stable Isotope Analysis

Differences in isotopic turnover rates in liver and leg muscle tissue allow us to compare isotopic values in food sources at two temporal scales. Liver is a metabolically active tissue and has a relatively high turnover rate and provides a record of recent diet in consumers (days to weeks), compared to muscle tissue's low turnover rate used to infer diet over a longer period of time (months) (Hobson et al. 1993). Therefore, by comparing mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in both tissues of groups of individuals I can discern dietary shifts in groups when they occur.

Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes of tissues and plant food sources were analyzed using a Carlo-Erba NA 1500 series II elemental analyzer attached to a continuous flow isotope ratio Micromass Optima spectrometer. Liver and leg muscle tissue samples were freeze-dried and then homogenized using a Wiley mill. A soxhlet extraction was then performed on all tissue samples to remove lipids. Analysis took place at the Environmental Protection Agency Atlantic Ecology Division in Narragansett, RI. I report all stable isotope concentrations as δ -values expressed as parts per thousand (‰) derived from the equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ where X is ^{13}C or ^{15}N and R represents the associated $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio, and R_{standard} is the ratio of international references for carbon from the Peedee Belemnite (PDB) and atmospheric N_2 for nitrogen both of which are assumed equal to 0.0‰. Replicate measures of internal laboratory standards resulted in standard deviation of 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Isotopic Mixing Models

I used mixing models to estimate the relative contributions of four distinct food sources to consumers' diets by determining isotopic contributions of food sources to consumers'

tissues (Inger and Bearhop 2008). When considering n stable isotopes I am able to calculate a unique solution for up to $n + 1$ sources. In this study where I determine the relative contributions of four food sources using $n=2$ stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), this constraint is violated and so I estimate a most-likely solution (Phillips and Gregg 2003). I used the software package SIAR in the open-source statistical program R to calculate proportion of contributions of food sources to tissues in birds (Jackson et al. 2009, Parnell et al. 2010). SIAR provides output from multiple source mixing models using a Bayesian approach allowing for the incorporation of uncertainty of all model parameters to determine relative contributions of food sources to a consumer's diet (Parnell et al. 2010). The outputs from SIAR are true probability distributions representing most-likely solutions that are then able to undergo statistical analyses (Inger and Bearhop 2008). I averaged $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from brant liver and leg muscle tissue by month and region so all groups had adequate sample sizes ($n \geq 10$). Ratios of stable $\delta^{15}\text{N}$ isotopes in consumer tissues is typically enriched between 3-4‰ compared to food sources, whereas $\delta^{13}\text{C}$ isotopic ratios relatively little enrichment during metabolic routing to consumer tissues (Miagwa and Wada 1984, Peterson and Fry 1987). I used discrimination factors (also known as trophic enrichment factors) for liver ($\Delta^{13}\text{C} = 0.35\text{‰}$ and $\Delta^{15}\text{N} = 2.6\text{‰}$) and leg muscle ($\Delta^{13}\text{C} = 0.92\text{‰}$ and $\Delta^{15}\text{N} = 1.7\text{‰}$) derived through meta-analyses from the literature (Caut et al. 2009). I used mean values for total carbon and nitrogen concentration within each food type from the literature for macroalgae (%N = 1.66, %C = 19.70), eelgrass (%N = 2.97, %C = 36.00), terrestrial grass (%N = 3.55, %C = 40.30) (Inger et al. 2006a), and *Spartina* (%N = 1.7, %C = 41.00) (Osgood and Zieman 1993). For food source inputs to the mixing models I used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios measured in vegetation samples to calculate source means from the four food sources sampled within each region. Resulting outputs from SIAR will allow us to quantify the relative contributions and hence proportion of different food sources in brant diets within four geographic regions for each month over the course of the wintering period.

Since trophic enrichment of nutrients between food sources and consumers can vary within and between species, and to evaluate the robustness of mixing model estimates (Post

2002, Inger and Bearhop 2008), I conducted a sensitivity analysis on trophic enrichment factors by adjusting values for both liver tissue and leg muscle tissue $\delta^{15}\text{N}$ between 0‰ and 5‰, and values of $\delta^{13}\text{C}$ between 0‰ and 2‰. Overall, the relative contributions from the grass and clover sources were more sensitive to shifts in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of enrichment factors compared to other food sources. Relative contributions from all food sources to consumer $\delta^{15}\text{N}$ experienced variable sensitivity between months in liver tissue with ranges falling between 0.14% in December and 20% in March, and in leg muscle tissue with ranges falling between 0.6% in January and 18% in December. Relative contributions from all food sources to consumer $\delta^{13}\text{C}$ was less sensitive, yet also experienced variable sensitivity between months in liver tissue with ranges falling between 0.1% in January and 12% in May, and in leg muscle tissue with ranges falling between 1.6% in January and 12% in May. Lower sensitivity of mixing models in early winter months provide us with greater confidence in early winter estimates compared to estimates in late winter that experienced wider variation due to changes in trophic enrichment factors. I additionally performed a sensitivity analysis on the food source values by varying both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios for each food source between $\pm 1‰$ and $\pm 5‰$. Source sensitivity impacted relative contributions which also varied between months and were comparatively lower in $\delta^{15}\text{N}$ where ranges fell between 0.2% in December and 20% in March for liver tissue, and 2% in January to 17% in April for leg muscle tissue. Relative contribution to consumer $\delta^{13}\text{C}$ in liver tissue ranges fell between 3% in December and 35% in May, and 15% in December and 37% in May for leg muscle tissue. This pattern in sensitivity of mixing models between early winter and late winter is most likely due to the increasing number of food sources available to brant throughout the winter. As more food sources become available on the landscape allowing for more complex mixtures of sources contributing to consumer tissues, mixing models provide less robust estimates and must be interpreted more cautiously.

Gross Analysis of Foregut Contents

I estimated diet of brant using gross analysis of foregut contents from brant carcasses obtained through hunter-harvested donations, or state-issued scientific collection permits. Carcasses were opened and the entire foregut (including the proventriculus and gizzard) was removed and frozen at -40 °C until processing. In the laboratory, foregut contents were thawed, sand and grit was removed by flushing with de-ionized water over a 50 µm sieve, and then each plant piece was sorted into one of four food source categories (macroalgae, eelgrass, new-growth *Spartina sp.*, and grass and clover). Vegetation samples were dried at 50 °C for 48 hrs, or until completely dry. The dry mass (g) of each sample was then recorded using a Mettler AE 100 balance to the nearest 0.0001g. I compared percent frequency of occurrence of food sources averaged by month between the four regions.

Statistical Analysis

I used SPSS Version 17.0 to run all statistical tests (SPSS Inc., Chicago, IL). I used the Kolmogorov-Smirnov test of normality for all data, and non-Gaussian distributions underwent either log, rank, or squared transformations prior to analysis (Zar 1974, Conover and Iman 1981, Martin and Bateson 1986). I used univariate analysis of variance (ANOVA) with $\alpha = 0.05$ and protected Tukey's HSD post hoc tests to detect significance levels between pairs when more than three groups were present ($\alpha = 0.05$).

Results

Stable Isotope Analysis

Food Sources

I collected and analyzed 373 vegetation samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios. Mean $\delta^{15}\text{N}$ values were greatest for macroalgae (8.59, SE = 0.16), followed by *Spartina* (6.50, SE = 0.52), eelgrass (6.55, SE = 0.40), and were lowest in grass and clover (3.37, SE = 0.28).

Mean $\delta^{13}\text{C}$ values were lowest for grass and clover (-30.17, SE = 0.14), and increased from macroalgae (-17.10, SE = 0.20), to *Spartina* (-13.58, SE = 0.07), to eelgrass (-10.97, SE = 0.30).

I detected highly significant differences between food sources for both $\delta^{15}\text{N}$ ($F_{3,298} = 67.7$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{3,298} = 312.6$, $P < 0.01$). I found significant variation between geographic regions for $\delta^{15}\text{N}$ ($F_{3,298} = 3.86$, $P < 0.05$), but not for $\delta^{13}\text{C}$ ($F_{3,298} = 1.49$, $P = 0.22$). I also detected significant interactions between region and food sources for $\delta^{15}\text{N}$ ($F_{6,298} = 6.73$, $P < 0.01$). The interaction between region and food type indicates that the patterns of variation in $\delta^{15}\text{N}$ between food sources differs between regions. No significant differences were found between months for $\delta^{15}\text{N}$ ($F_{5,298} = 0.64$, $P = 0.67$) or $\delta^{13}\text{C}$ ($F_{5,298} = 1.34$, $P = 0.25$).

Atlantic brant tissues

I collected 592 individuals, of which, 525 were used for stable isotope analysis from all 11 study sites between Nov 2007 – May 2008 (Table 2.1). Individuals with missing tissue data and spurious outliers were removed. Collected brant were comprised of 45% males and 55% females, and 62% adults and 38% juveniles, however, these percentages varied between months and states (Table 2.1). I sampled liver and leg muscle tissues from all individuals and analyzed each for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios. I detected highly significant differences between regions for liver tissue $\delta^{15}\text{N}$ ($F_{3,427} = 46.4$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{3,427} = 29.7$, $P < 0.01$), as well as for leg muscle tissue $\delta^{15}\text{N}$ ($F_{3,427} = 102.7$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{3,427} = 45.7$, $P < 0.01$) (Figure 2.1). Mean liver and leg tissue $\delta^{15}\text{N}$ values were heterogeneous between all regions with region 1 having the greatest value, followed by region 4, region 3, and region. Mean liver and leg tissue $\delta^{13}\text{C}$ was significantly lower in region 2 compared to regions 4, region 3, and 1 (liver tissue only) while mean leg tissue $\delta^{13}\text{C}$ in region 1 was significantly greater than all other regions.

I detected significant differences between months for liver tissue $\delta^{15}\text{N}$ ($F_{6,427} = 4.75$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{6,427} = 16.7$, $P < 0.01$) as well as for leg muscle tissue $\delta^{15}\text{N}$ ($F_{6,427} = 4.1$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{6,427} = 11.4$, $P < 0.01$) (Figure 2.1). Mean liver tissue $\delta^{15}\text{N}$ was significantly greater in December compared to all other months while $\delta^{13}\text{C}$ was also significantly greater in December and significantly lower in March compared to all other months. Mean leg muscle

tissue $\delta^{15}\text{N}$ was significantly greater in December and April compared to May and November while $\delta^{13}\text{C}$ was significantly greater in December, January, February, and April compared to November, March, and May.

Additionally, I detected significant interactions between region and month terms for liver $\delta^{15}\text{N}$ ($F_{16,427} = 7.6$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{16,427} = 3.1$, $P < 0.01$), as well as for leg muscle tissue $\delta^{15}\text{N}$ ($F_{16,427} = 7.7$, $P < 0.01$) and $\delta^{13}\text{C}$ ($F_{16,427} = 4.7$, $P < 0.01$). These interactions between regions and months indicate that regional patterns in liver and leg muscle tissue $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differ between months and are most likely due to the combination of spatial and temporal variation in food source availability across the winter range.

I detected significant differences between age classes for liver tissue $\delta^{15}\text{N}$ ($F_{1,427} = 4.77$, $P = 0.029$) and $\delta^{13}\text{C}$ ($F_{1,427} = 4.92$, $P = 0.027$), as well as for leg muscle tissue $\delta^{13}\text{C}$ ($F_{1,427} = 8.93$, $P < 0.01$). However, no differences between age classes were detected for leg muscle and $\delta^{15}\text{N}$ ($F_{1,427} = 0.2$, $P = 0.89$). Liver tissue $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively was greater for after hatch year birds ($12.5 \pm 0.1\text{‰}$, $-15.4 \pm 0.1\text{‰}$) compared to hatch year birds ($12.0 \pm 0.2\text{‰}$, $-15.7 \pm 0.2\text{‰}$). Leg muscle tissue $\delta^{13}\text{C}$ was similarly greater in after hatch year birds ($-15.7 \pm 0.2\text{‰}$) than in hatch year birds ($-16.2 \pm 0.2\text{‰}$).

I detected no significant differences between sexes for liver tissue $\delta^{15}\text{N}$ ($F_{1,427} = 0.12$, $P = 0.73$) and $\delta^{13}\text{C}$ ($F_{1,427} = 0.56$, $P = 0.45$), and leg muscle $\delta^{15}\text{N}$ ($F_{1,427} = 3.17$, $P = 0.08$). However, I did detect significant differences between sexes for leg muscle $\delta^{13}\text{C}$ ($F_{1,427} = 4.06$, $P < 0.05$) where female birds ($-16.18 \pm 0.1\text{‰}$) had lower mean leg muscle $\delta^{13}\text{C}$ than males ($-15.60 \pm 0.1\text{‰}$).

Isotopic Mixing Models and Gross Foregut Analysis

Mean values for brant grouped by region and month were used in SIAR mixing models. The output from these models shows most likely contributions from four food sources to brant diet including credibility intervals for those estimates (Figure 2.2). Overall trends from the four regions indicate macroalgae made up 51% to brant diet, *Spartina* and eelgrass contributed

23% and 19%, respectively to brant diet, and grass and clover contributed 8% to the diet. Macroalgae contributed a greater proportion to the diet compared to other sources in both regions 1 and 4 between Feb and Apr (Figures 2.2a and 2.2d). In regions 1, 2, and 4 macroalgae contribution generally increased in early winter reaching its peak in February. However, in region 3 contributions from macroalgae increased from December to January, but then decreased in February (Figure 2.2). Examining gross foregut contents, I found the overall mean frequency of occurrence for macroalgae was 55%, eelgrass was 12%, *Spartina* was 2%, grass and clover was 18%, and an unknown category was 25%.

In Region 1 (RI and CT), SIAR mixing models estimated macroalgae contributions ranged between 12% - 93% over the sampling period. Liver tissue samples indicated macroalgae contributions increased in early winter from Dec to Feb (Figure 2.2a). Contributions from macroalgae to leg muscle tissue peaked in April; however, since leg muscles have a relatively slower rate for metabolic routing of nutrients, this would support the finding that macroalgae consumption peaked in Jan – Feb. Gross foregut analysis (n=162) showed a similar increase through the winter but peak consumption occurred in Mar – Apr (Figure 2.3a). Mixing models indicated Eelgrass contributed a greater amount in Dec compared to all other food sources but declined in Jan (Figure 2.2a) while gross foregut analysis indicated preference from early winter months, peaking in Mar, and then declining in Apr and May (Figure 2.3a). Lastly, both mixing models and gross foregut analysis estimated relative low consumption of new-growth *Spartina* and grass and clover sources.

In region 2 (NY) SIAR mixing models predicted macroalgae contributed 26%-78% throughout the winter, peaking in Dec and May according to liver tissue (Figure 2.2b). Macroalgae contributions were greater than grass and clover sources in Dec. In May, macroalgae contribution to diet was greater than all other food sources combined. Patterns in food source contributions to leg muscle tissue indicate that a decrease in contributions from macroalgae and an increase in grass and clover contributions in Feb – Mar correspond with a similar trend in liver tissue in Dec – Jan (Figure 2.2b). Foregut analysis (n=166) found macroalgae was prevalent

10%-40% during the winter with mean frequency increasing between Dec – Jan, steadily declining until Apr, and then increasing again in May (Figure 2.3b). SIAR mixing models predicted eelgrass contributed 6%-24% and *Spartina* contributed 10%-24% to brant diet. Foregut frequency of occurrence of *Spartina* was relatively low in early winter but increased through Apr (Figure 2.3b). Last, mixing models predicted grass and clover sources contributed 4%-38% to diet, increasing through Mar and then declining in Apr – May (Figure 2.2b). Interestingly, foregut analysis, showed a greater dominance for grass and clover ranging between 14% in Dec to 79% in Mar (Figure 2.3b).

In region 3 (NJ), SIAR estimates from liver tissue indicated a relatively equal contribution from *Spartina* (37%), macroalgae (32%), and eelgrass (25%), followed by a lower contribution from grass and clover (6%). Contributions from *Spartina* ranged between 22%-62% throughout the winter with peak contributions occurring in Dec and Feb (Figure 2.2c). A decrease in contributions from *Spartina* to leg muscle tissue in Feb – Mar corresponds to a decrease from Dec – Jan contributions to liver tissue (Figure 2.2c). Generally supporting this, frequency of *Spartina* occurrence in foreguts increased from Jan to Feb, and then declined in Mar (Figure 2.3c). According to liver tissue, macroalgae contributed between 14% - 57% between Nov – May and a peak in Apr (Figure 2.2c). Trends in macroalgae contributions to leg muscle from Jan – Mar correspond with contributions to liver tissue in Nov – Jan (Figure 2.2c). Foregut analysis found macroalgae peaked in Nov – Dec and then declined throughout the winter with a second small peak in Apr (Figure 2.3c). SIAR estimates and foregut analysis of dietary contributions from eelgrass were relatively stable and ranged between 16% - 39% and 0-8% respectively (Figure 2.2c and Figure 2.3c). While SIAR estimates of grass and clover contributions to diet were relatively stable and low (3% - 10%), gross foregut analysis showed a greater overall preference and a massive increase in Apr (100%) and May (93%) (Figure 2.3c).

In Region 4 (DE, MD, and VA), SIAR mixing models estimated macroalgae was the major contributory source to brant making up 64% of the winter diet. The next largest contribution to diet was from *Spartina* (21%), followed by eelgrass (12%), and grass and clover

(3%). While macroalgae contributions to diet ranged between 31% - 80%, they reached their peak between Feb – Apr (Figure 2.2d). Macroalgae frequency of occurrence in foreguts was relatively steady during early winter months (51%) before peaking in Feb (78%) (Figure 2.3d). Mixed model estimates of contributions from *Spartina* to brant diet ranged between 11% - 38% between Nov – May and peaked in May (38%) and eelgrass contributions to diet ranged between 6% - 24% reaching peak contributions in May. Foreguts showed a low prevalence of *Spartina*; however interestingly, I observed a prevalence of eelgrass in Nov (91%) before declining throughout the rest of the winter months (Figure 2.3d). Both SIAR models and foregut analysis found grass and clover contributions to diet were relatively low ranging between 1% – 11% in May (Figure 2.2d). Both grass and clover and *Spartina* food sources were exhibited in 4% of foreguts in Dec (Figure 2.3d).

Discussion

Stable isotopic analysis of liver and leg muscle tissues in addition to gross foregut content analysis were used to explore spatial and temporal variation in wintering and staging brant feeding ecology. Past studies of brant foraging ecology relying on traditional techniques have provided important foundations into understanding food use and how the wintering population responds to shifts in food availability (Cottam et al. 1944, Penkala 1976, Kirby and Obrecht 1982). Brant, like other migratory species of geese have exhibited plasticity in foraging behavior by exploiting novel food sources and habitats such as agricultural and terrestrial grass fields (Rowcliffe et al. 2001, Jefferies and Drent 2006, Klaassen et al. 2006).

My study using stable isotope analysis confirms that wintering and staging brant eat mostly macroalgae food sources throughout the winter months across the entire winter range. In addition to contributions from macroalgae to brant diet, I detected important proportions of eelgrass and *Spartina* in the diet. The grass and clover food source, although contributing a relatively smaller proportion to brant diet was found to be an important part of the diet,

particularly in region 2 (NY), as well as in late winter (April-May) across all regions (Figure 2.2).

When comparing overall contributions of food sources to diet from stable isotope analysis and gross foregut content analysis I detect only broad similarities at best. Overall estimates of proportions of the diet consisting of macroalgae (51%), *Spartina* (23%), eelgrass (19%), and grass and clover (8%) determined through stable isotope analysis cannot be directly compared to frequency of occurrence of food sources identified in foreguts sampled. However, broad trends from gross foregut analysis support frequency of detection of macroalgae (55%) a dominant food source, in addition to detection of eelgrass (12%), but do not correspond as well to detection of *Spartina* (2%), and grass and clover (18%) within foregut samples. One of the major biases of gross foregut analysis lies in when and where individuals are harvested since foregut contents can provide only limited information into a small temporal period of feeding activity prior to harvest (Votier et al. 2003). For example, in region 2 (NY) individuals were sampled through hunter-harvest as well as depredation efforts at JFK airport, where individuals were known to feed heavily on grass and clover fields on the premises (Figure 2.3b). When comparing these results to stable isotope analysis estimates of proportion of grass and clover contributions to brant diet there are similar heightened contributions in region 2 compared to other regions (Figure 2.2b). However, estimates based on liver tissue reflect a more accurate picture of the contribution of grass and clover (4% -38%) of the overall diet around the time of harvest (several days prior) for brant in region 2. I additionally remove bias around when and where individuals were sampled using estimates of the proportion of contribution of food sources to diet based on leg muscle tissue that reflects the diet of individuals several months prior to harvest. In region 2 estimates of grass and clover contributions to diet based on leg muscle tissue indicate birds harvested in March had been feeding on grass and clover during early winter months in January and February. Since estimated mean values are similar between March (31%) for leg muscle tissue and January (26%) for liver tissue, I can conclude that brant in region 2 have experienced little or no dietary shifts during early winter.

Spatial and temporal variation detected in brant liver and leg muscle tissues correspond with SIAR mixing model estimates of food source contributions to diet. Mean isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in both liver and leg muscle tissues showed significant differences between regions and months (Figure 2.1). Greater mean values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in tissues indicate a diet rich in macroalgae, eelgrass, and *Spartina*, which contain relatively greater corresponding isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, compared to grass and clover which have significantly lower isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. I detected similar patterns in variation between regions for mean brant liver and leg tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 2.1) and proportions of food source contributions (Figure 2.2). Significant differences between months in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in tissues with greater mean values in early winter months (Figure 2.1) correspond with a general trend of a relatively greater proportion of macroalgae and potentially eelgrass contributing to the diet in early winter months across all regions (Figure 2.2).

Recent studies using stable isotope analysis to determine relative contributions of food sources to consumer diets have the enhanced ability to detect spatial and temporal variation in feeding ecology in complex food webs where consumers use several types of food sources that shift in their availability in space and time (Ainley et al. 2003, Wise et al. 2006, Moreno et al. 2010). Dietary trends of Eastern Canadian High Arctic population of light-bellied brent geese (*Branta bernicla hrota*) wintering in northern Ireland were determined using stable isotope analysis and exhibited similar dietary patterns to Atlantic brant relying heavily on eelgrass and macroalgae in early and mid winter months and then shifting to increased use of a terrestrial grass food source in late winter months (Inger et al. 2006b).

Although stable isotope analysis coupled with recent advances in Bayesian mixing models has provided ecologists with a highly valuable technique for disentangling trophic relationships between multiple food sources and polyphagous consumers there are limitations to this approach when studying dietary trends of animals. These methods are ideally employed in biological situations where food sources exhibit highly distinct isotopic signatures and enable meaningful interpretation of estimates of relative contributions of those sources to consumer diet

provided by source partitioning mixing models (Alisauskas and Hobson 1993, Inger et al. 2006a, Inger and Bearhop 2008). Stable isotope analysis is able to deal with increased trophic complexity from a greater number of potential food sources, relative distinction between food source isotopic signatures, or a combination of the two by increasing the number of isotopes used in the analysis (Phillips and Gregg 2003). In determining spatial variation in diet of yellow-legged gulls (*Larus michahellis*) the use of three isotopes ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$) enabled a more accurate depiction of dietary trends based on increased distinction between food sources when compared to models relying only on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes (Moreno et al. 2010).

In my study isotopic signatures of macroalgae, eelgrass, and *Spartina*, although distinct, showed overlap due to variance of food sources sampled. All three, however, were highly distinct from terrestrial grass and clover. Therefore, I interpret estimates of relative contributions of these three food sources cautiously, whereas I have greater confidence in estimates of proportion of grass and clover in brant diet. For example, in region 3 (NJ) during December SIAR mixing models estimate relatively large proportions of *Spartina* in the diet (Figure 2.2c). Although this may be an accurate estimate of contributions from *Spartina* to brant diet, based on gross foregut analysis of brant in region 3 during December I detected no occurrence of *Spartina* in foreguts of brant during that time (Figure 2.3c).

One other limitation of using stable isotope analysis to estimate diet lies in the dependence of models on assumptions associated with model inputs of trophic enrichment factors (Caut et al. 2009) and C:N concentrations in plant food sources (Phillips and Koch 2002, Robbins et al. 2002). My sensitivity analysis performed on trophic enrichment factors for both liver and leg muscle tissues revealed that slight changes in these model inputs can have important impacts on estimates of food source contributions to diet, particularly in late winter compared to early winter months. This emphasizes yet another need to interpret results with caution. However, since both trophic enrichment factors and food source C:N concentrations remain constant throughout all mixing models they have little or no affect on the relative contributions of food sources to diet between regions or months.

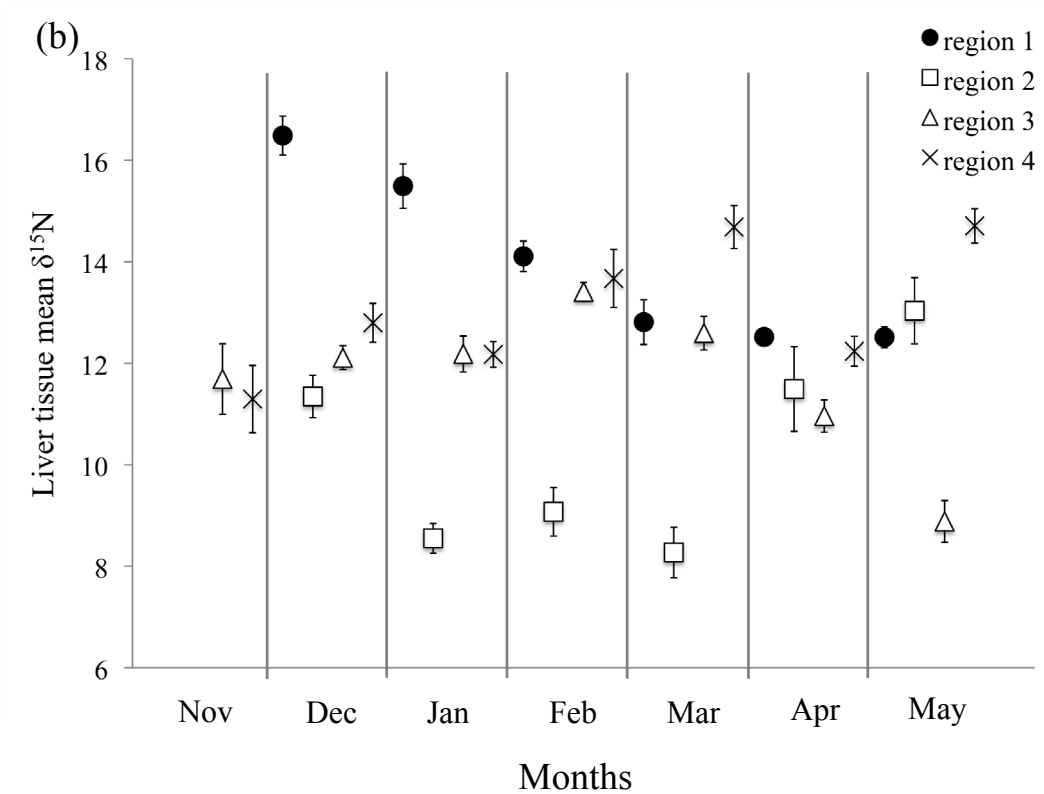
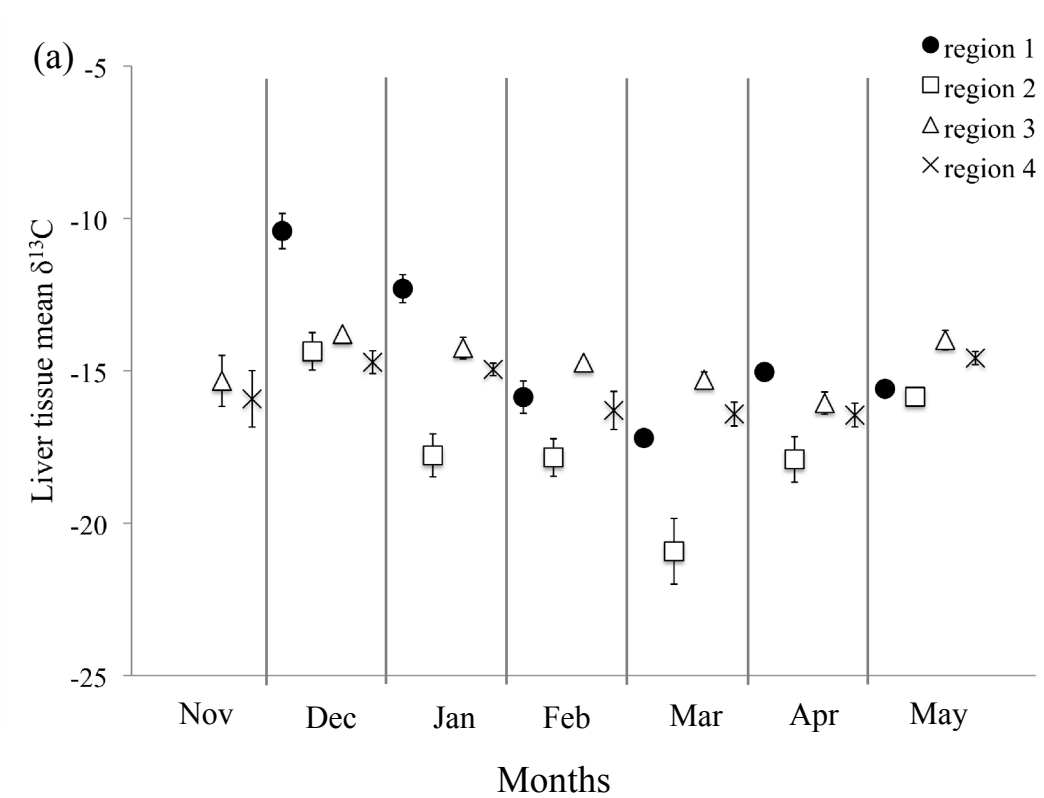
When appropriately used, stable isotope analysis is a powerful technique to explore dietary trends in complex trophic systems confounded by shifting spatial and temporal availability of food resources (Inger and Bearhop 2008). In conclusion, my results from stable isotope analysis of brant tissues and food sources provide robust support of previous evidence of dietary trends of wintering brant derived using traditional feeding ecology techniques (Cottam et al. 1944, Penkala 1976, Kirby and Obrecht 1982). Use of stable isotope analysis in conjunction with traditional foraging ecology techniques enhances an overall understanding of consumer use of food resources. These techniques provide an important tool for the future management of wintering and staging brant, and associated population level responses to spatial and temporal variation in food availability.

Table 2.1. Birds collected in RI, CT, NY, NY (JFK airport), NJ, DE, MD, and VA between 1 Nov 2007 - 31 May 2008.

State	Month	Collected	% Adult	% Female
RI	Dec	17	76	44
	Jan	14	100	71
	Feb	11	73	36
	Mar	13	69	31
	Apr	12	67	58
	May	-	-	-
CT	Dec	5	80	60
	Jan	8	38	88
	Feb	12	75	83
	Mar	11	73	64
	Apr	16	63	44
	May	13	54	54
NY	Dec	19	47	68
	Jan	15	60	47
	Feb	11	100	45
	Mar	6	0	50
	Apr	9	100	44
	May	10	60	50
NY (JFK airport)	Dec	-	-	-
	Jan	19	42	53
	Feb	18	67	39
	Mar	20	70	50
	Apr	-	-	-
	May	19	84	42
NJ	Nov	13	69	62
	Dec	12	75	50
	Jan	12	50	50
	Feb	13	77	31
	Mar	14	64	50
	Apr	15	100	47
	May	15	53	40
DE	Dec	18	56	56
	Jan	9	67	78
	Feb	19	42	47
	Mar	17	59	53
	Apr	17	41	47
	May	11	27	55
MD	Nov	11	73	55

	Dec	6	33	67
	Jan	14	43	57
	Feb	2	50	50
	Mar	2	50	100
	Apr	-	-	-
	May	-	-	-
VA	Dec	-	-	-
	Jan	8	63	75
	Feb	8	38	50
	Mar	11	73	55
	Apr	-	-	-
	May	-	-	-
Total		525		
Mean			62	55

Figure 2.1. Brant liver tissue $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) and leg muscle $\delta^{13}\text{C}$ (c) and $\delta^{15}\text{N}$ (d) isotopic values ($\bar{x} \pm \text{SE}$) in four regions. No birds were sampled in November in regions 1 and 2.



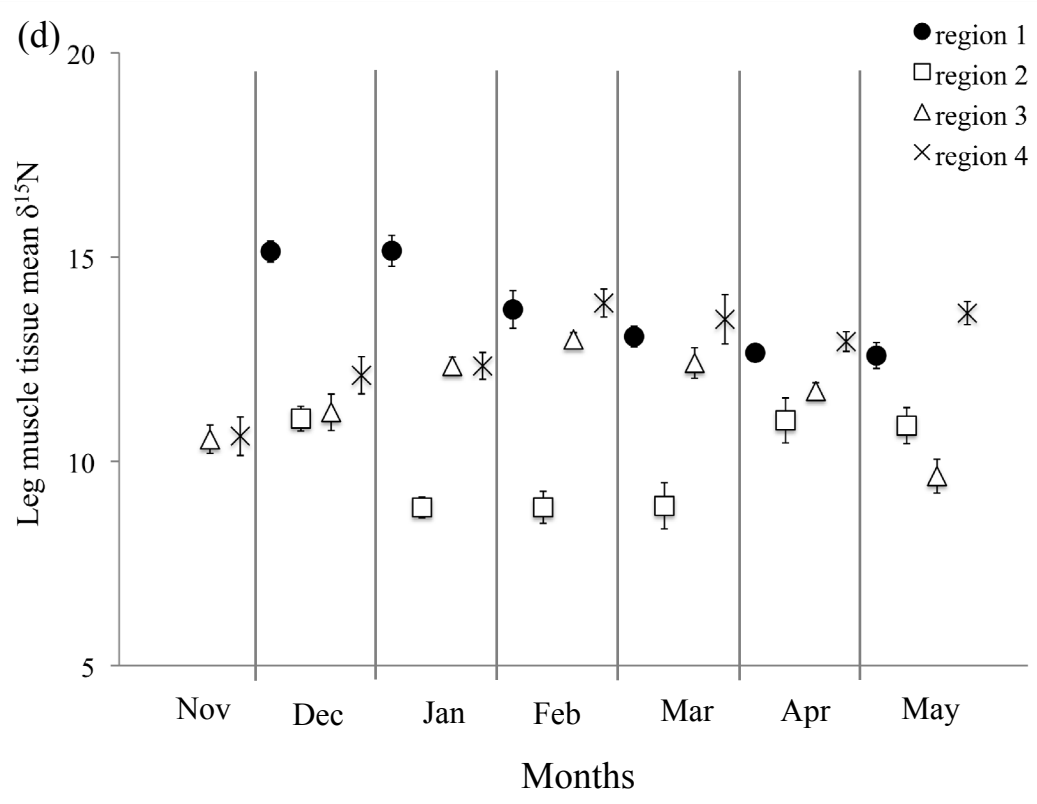
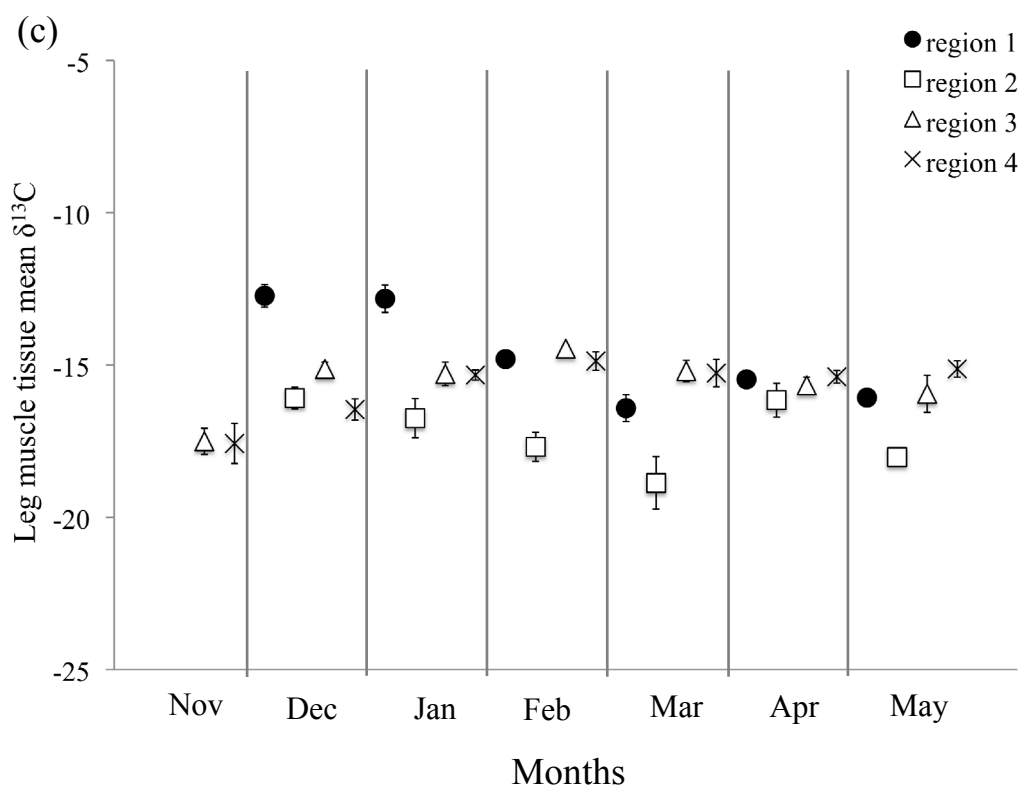
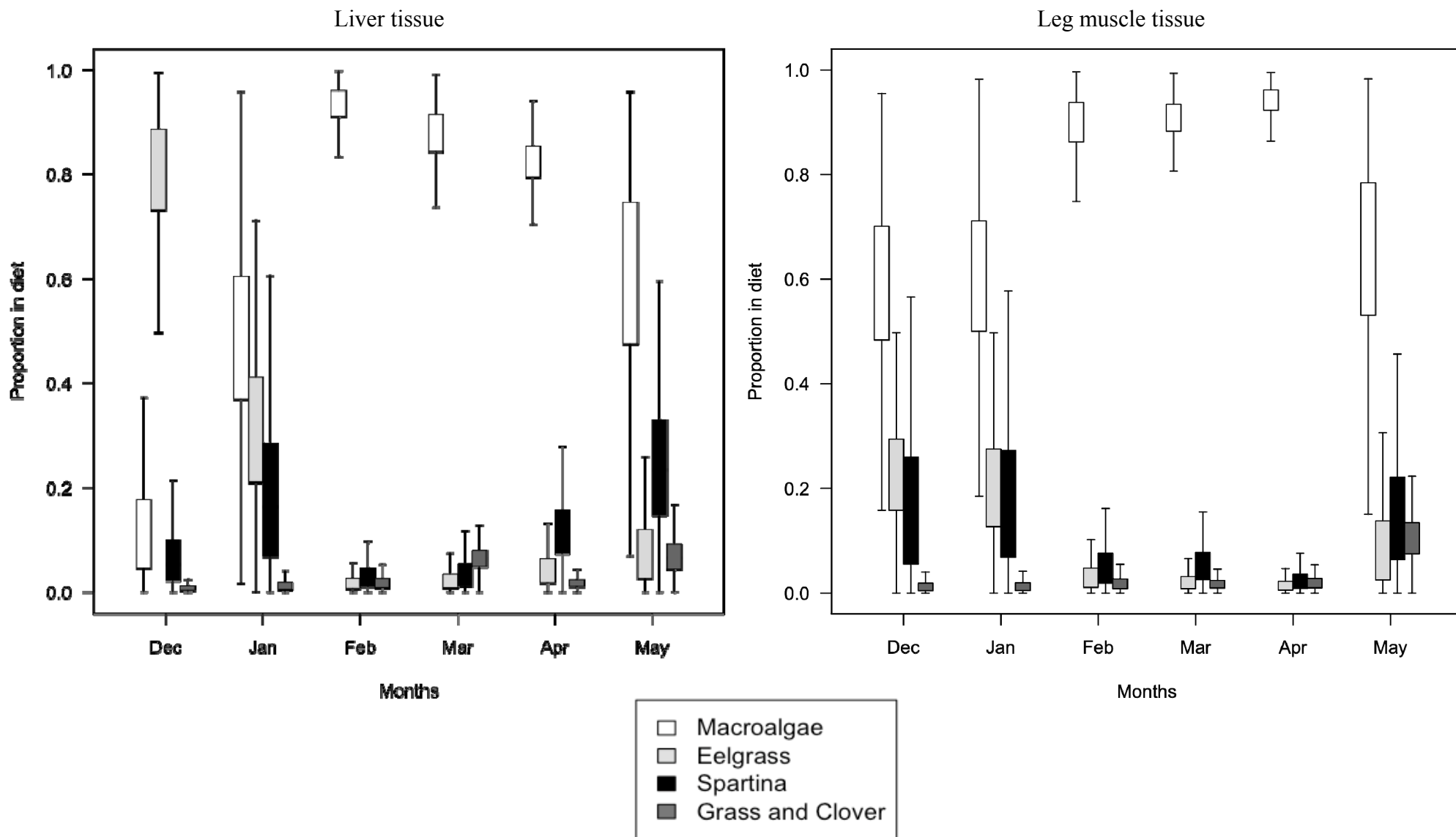


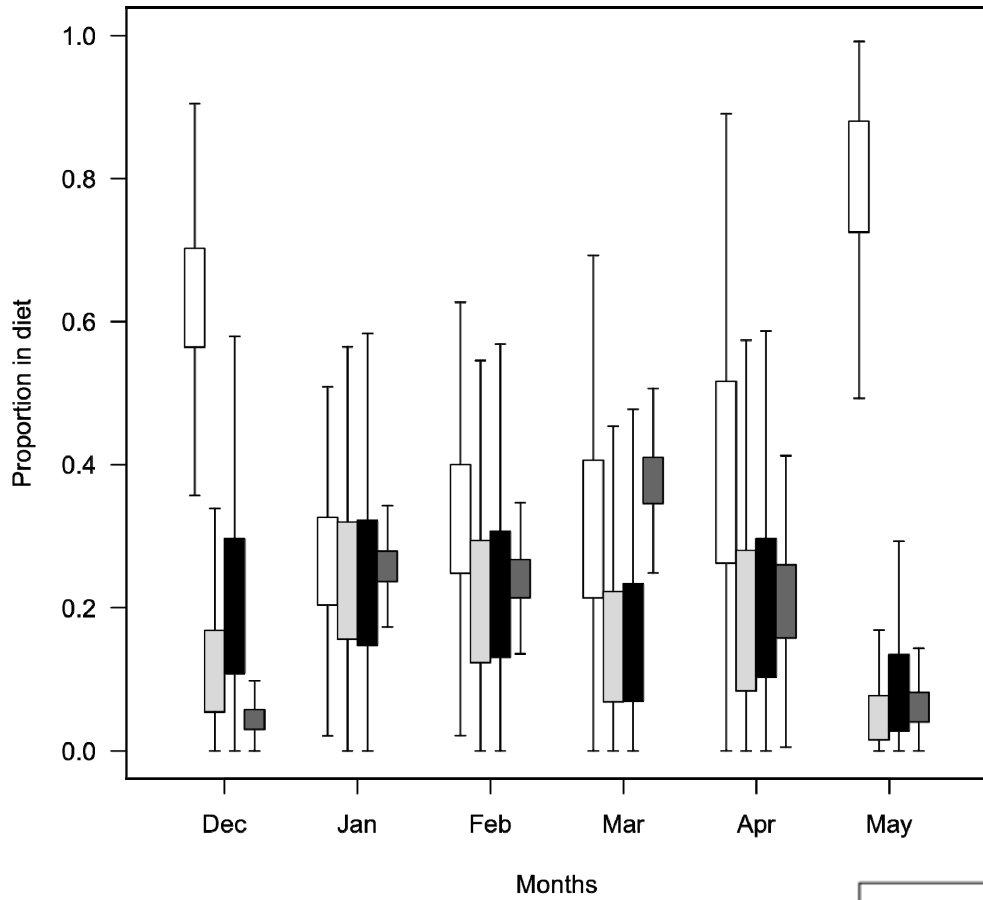
Figure 2.2. Box plots representing ranges of relative contributions of macroalgae, eelgrass, *Spartina*, and grass and clover to brant diet in (a) Region 1, (b) Region 2, (c) Region 3, and (d) Region 4 throughout the winter (Nov – May 2007-08). Boxes indicate inter quartile ranges and whiskers represent the range of possible solutions calculated by the program SIAR.

(a) Region 1 (RI & CT)

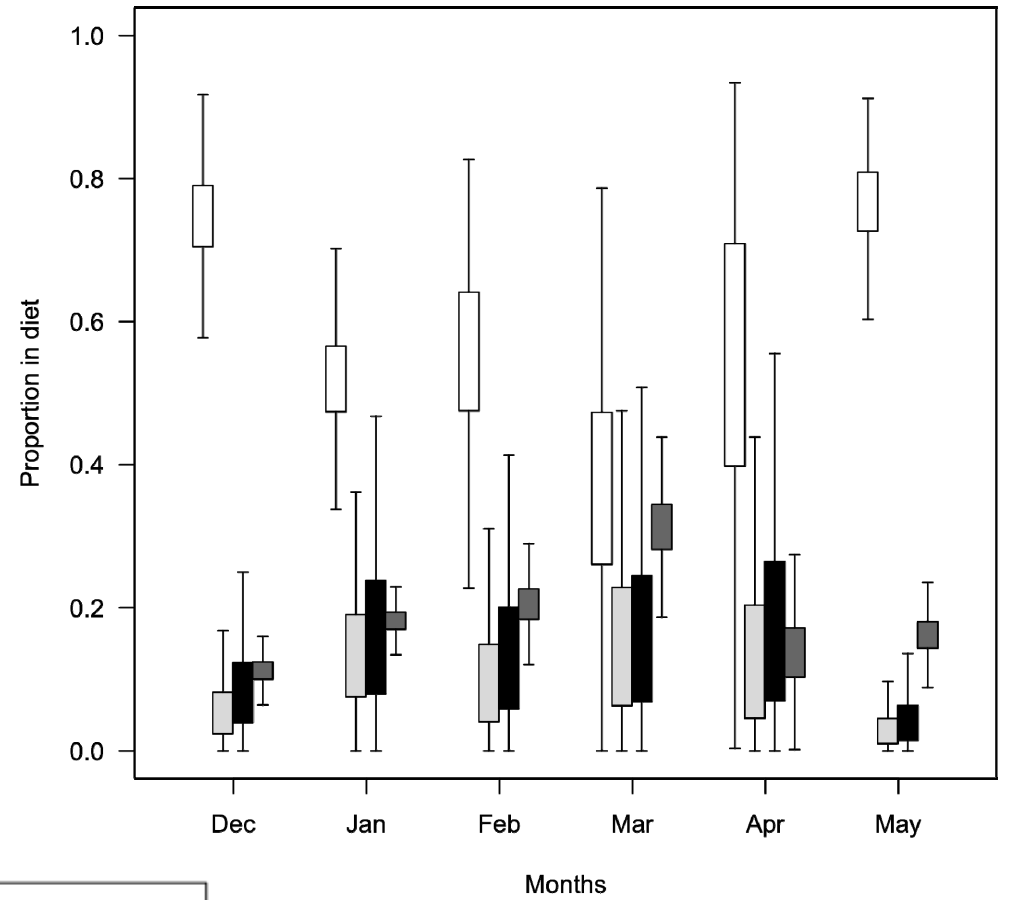


(b) Region 2 (NY)

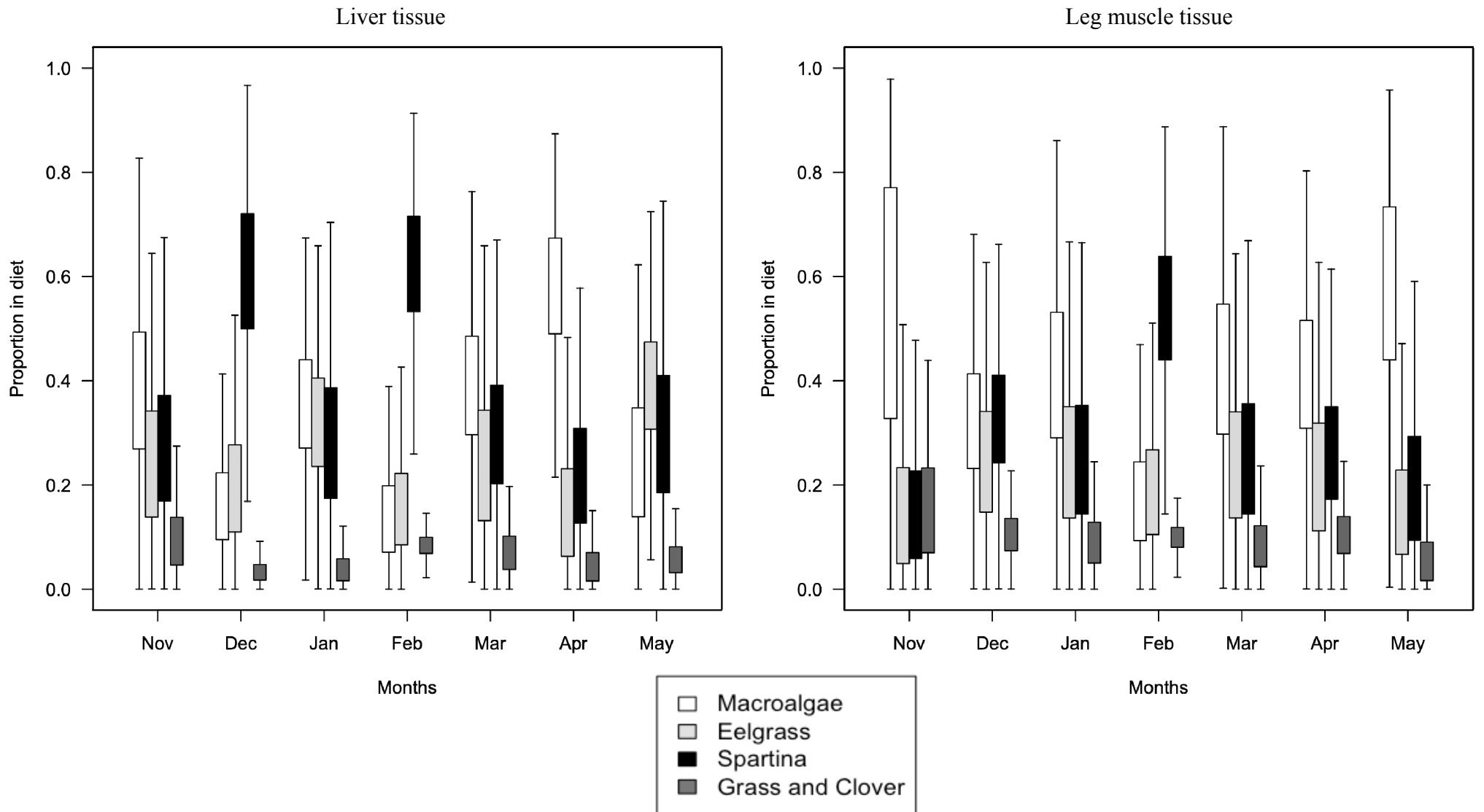
Liver tissue



Leg muscle tissue



(c) Region 3 (NJ)



(d) Region 4 (DE, MD, & VA)

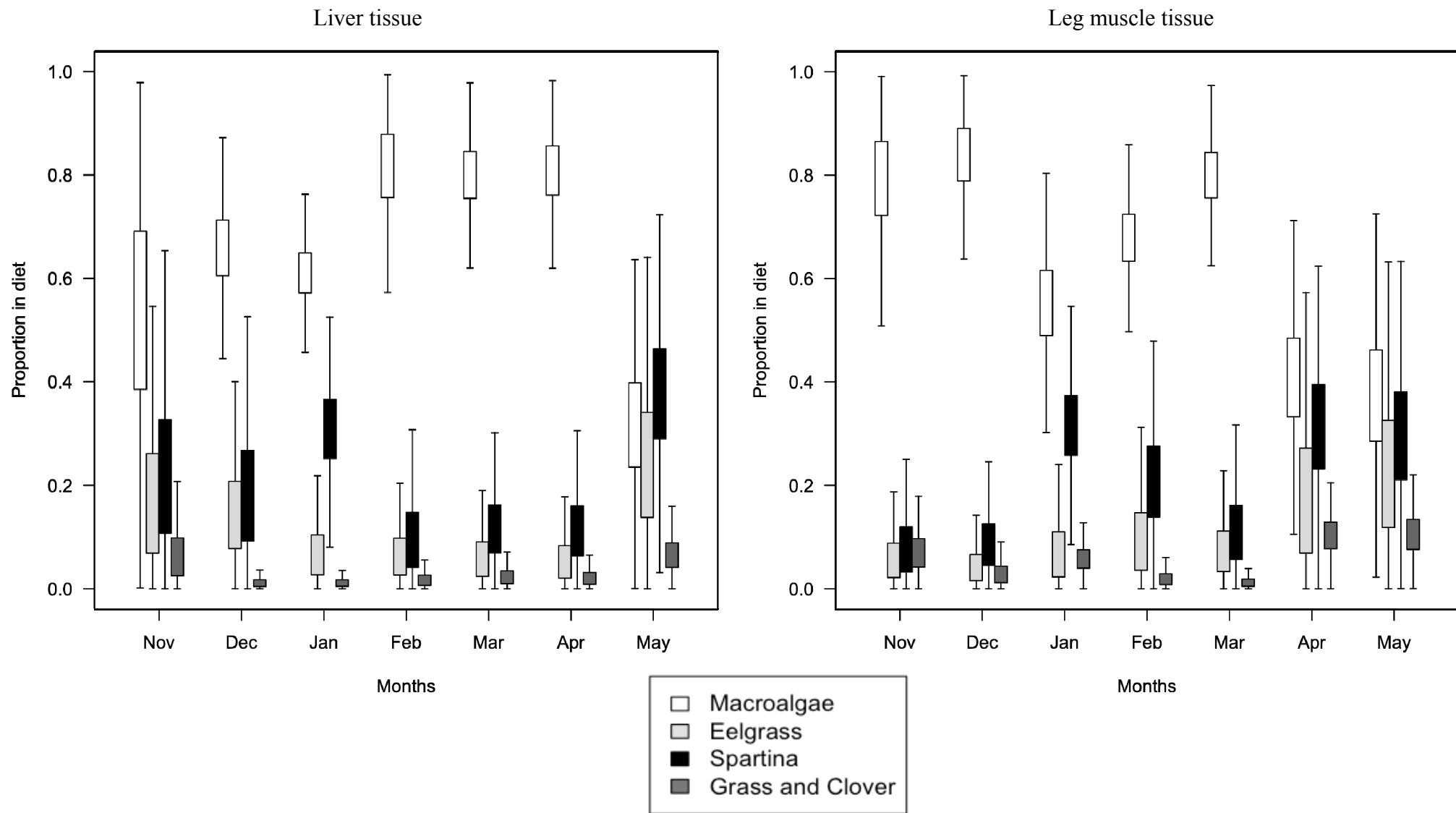
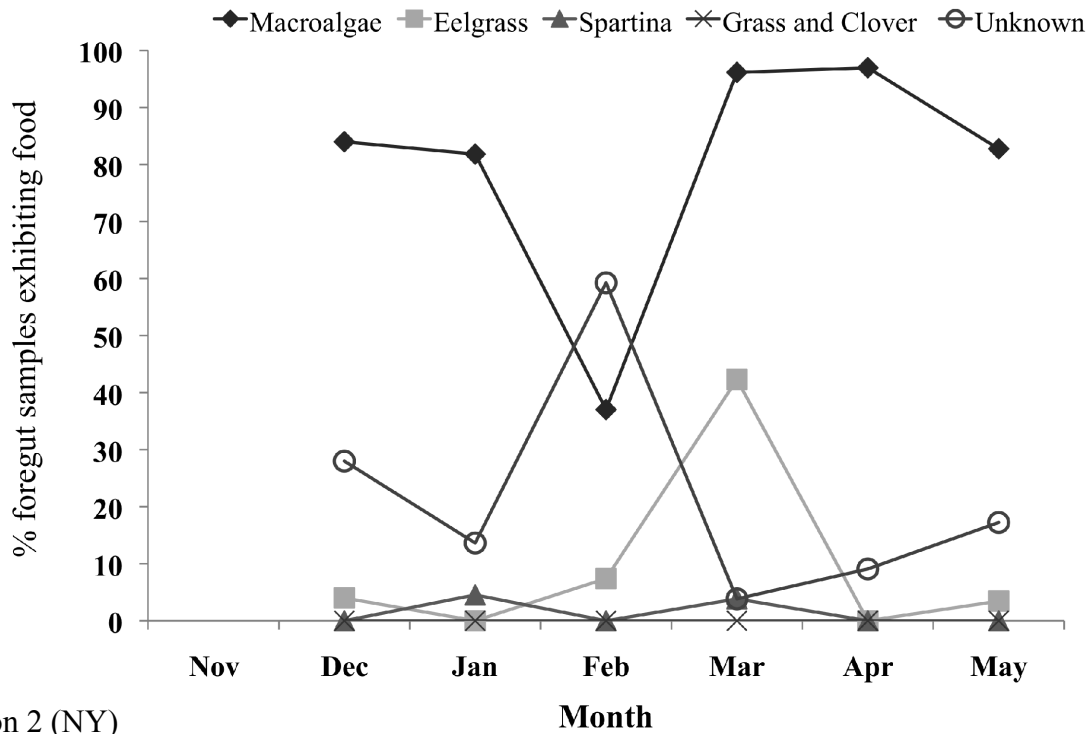
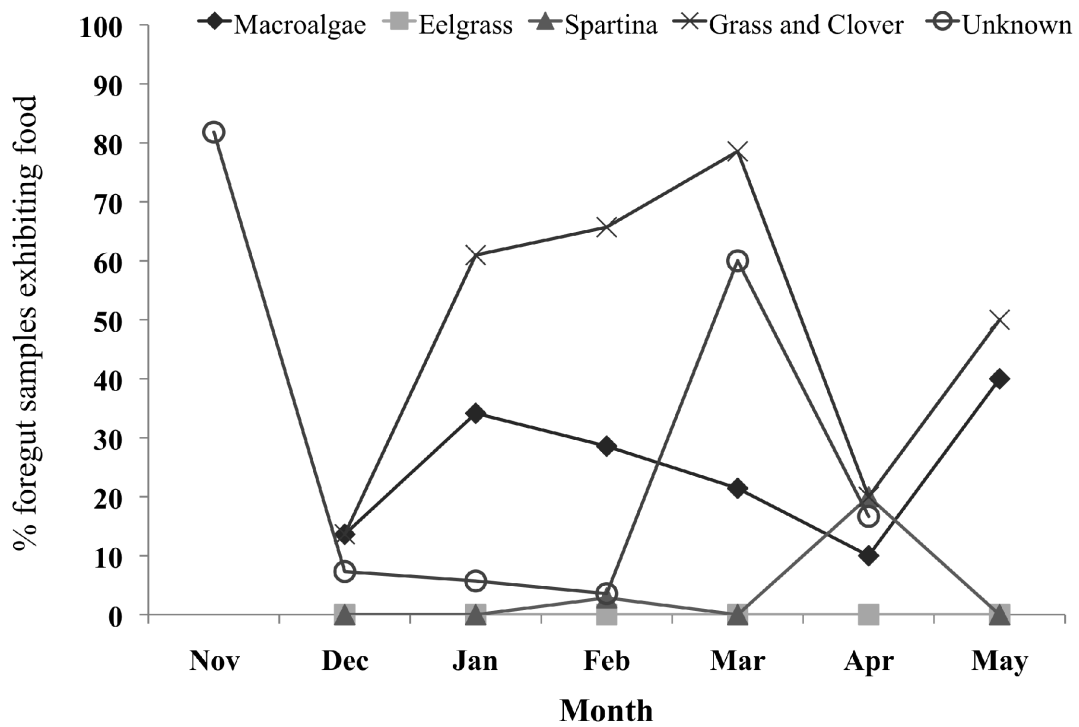


Figure 2.3. Frequency of occurrence of food sources in from gross analysis of foregut contents from four regions (a) Region 1 (RI, CT), (b) Region 2 (NY), (c) Region 3 (NJ), and (d) Region 4 (DE, MD, VA) between November – May 2007-08.

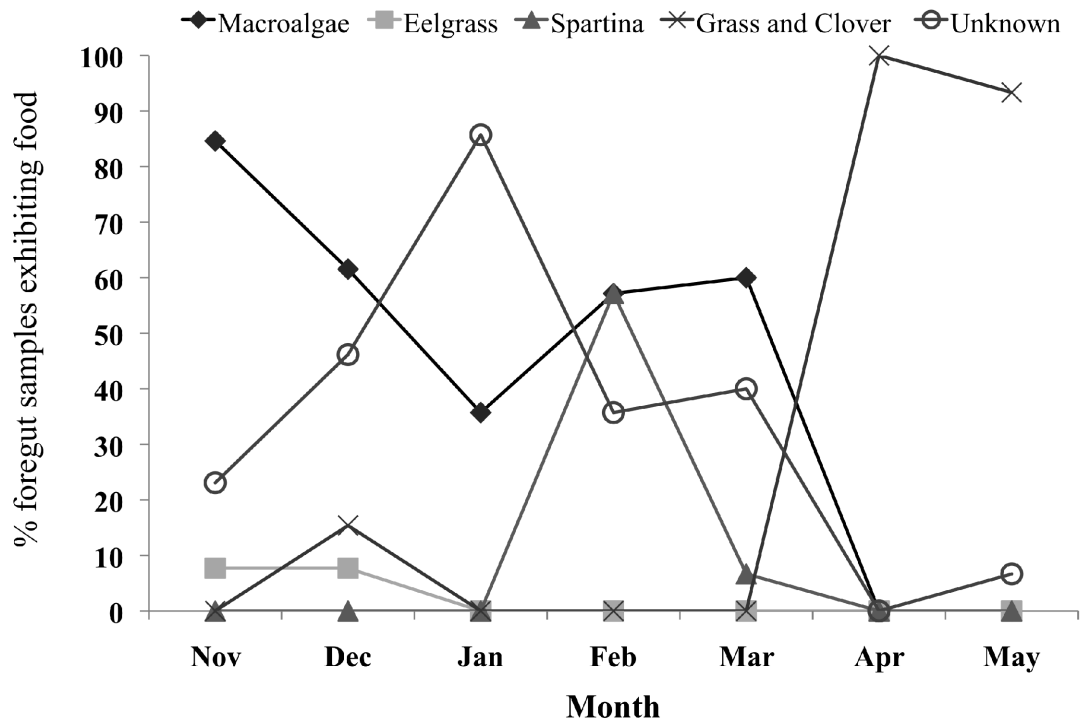
(a) Region 1 (RI, CT)



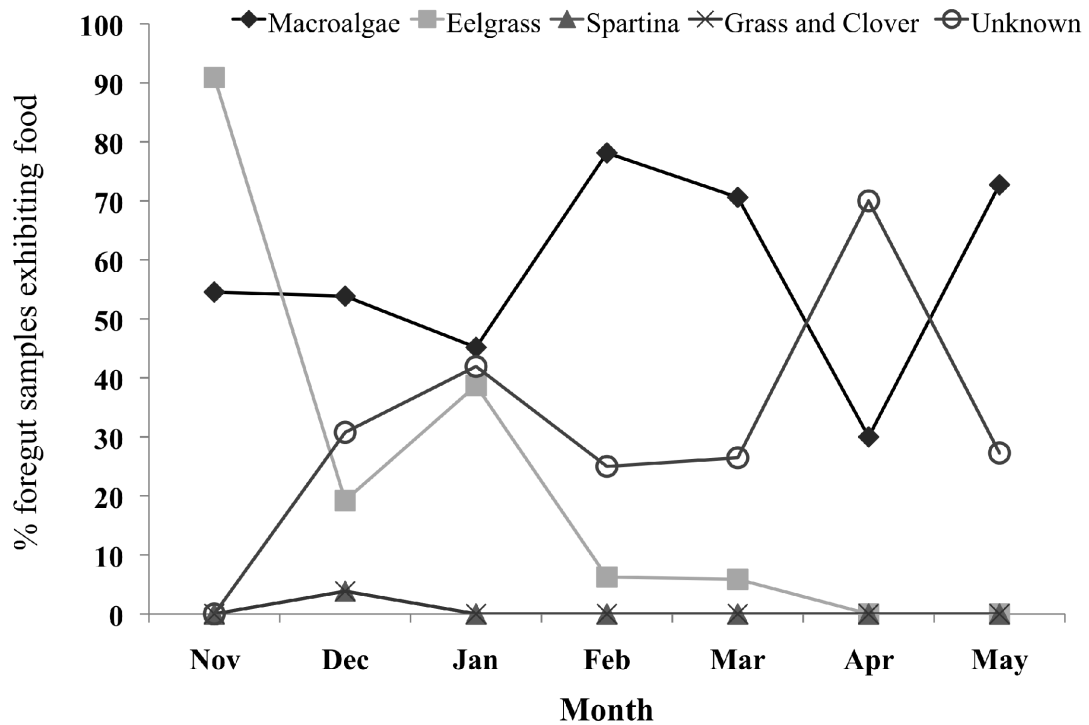
(b) Region 2 (NY)



(c) Region 3 (NJ)



(d) Region 4 (DE, MD, VA)



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Appendix A

ENERGY EXPENDITURE BY SITE AND ACTIVITY

Energy expenditure (kJ/day, $x \pm SE$) associated with specific activities of Atlantic brant and total diurnal energy expenditure (DEE, kJ/day, $\sum x \pm SE$) at 11 sites along the northeastern Atlantic coast, USA, during Dec–May 2006–2007.

Energy expenditure (kJ/day) of specific activities																			
Site	N	Feed		Swim		Fly		Walk		Rest		Comfort		Agonistic		Courtship		DEE	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	$\sum x$	SE
RI	94	305.4	16.0	8.9	3.7	178.5	53.0	20.8	5.3	253.6	16.0	103.6	9.5	23.8	3.1	0.0	0.0	894.7	106.6
CT-NL	29	284.7	39.0	313.7	46.4	199.8	199.8	2.1	1.7	155.4	32.4	26.3	11.1	0.2	0.2	0.0	0.0	982.2	330.7
CT-FF	28	212.6	42.5	200.5	40.3	2021.0	492.8	23.0	5.7	58.9	22.4	31.8	10.3	0.7	0.6	0.0	0.0	2548.5	614.5
NY-NAS	102	238.4	21.3	207.6	22.3	1014.6	140.9	22.5	3.5	137.8	16.7	43.8	7.1	4.5	0.8	0.4	0.4	1669.6	213.1
NY-JB	108	328.7	26.5	188.3	26.5	629.6	147.6	40.7	5.9	82.4	12.2	60.3	11.3	2.5	0.4	0.3	0.2	1332.8	230.6
NJ-BAR	46	244.2	29.7	269.0	36.5	1180.5	320.9	14.1	4.3	96.0	17.0	21.2	5.3	4.8	1.7	0.0	0.0	1829.7	415.5
NJ-ATL	71	214.2	21.8	258.9	26.1	446.3	126.0	18.8	3.4	180.8	18.1	58.2	8.4	7.4	1.5	0.0	0.0	1184.6	205.3
NJ-CM	62	245.3	25.9	234.0	31.7	663.3	214.9	27.8	5.2	153.3	17.5	36.0	6.2	8.5	3.3	0.0	0.0	1368.0	304.7
DE	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MD	26	322.4	40.6	181.5	50.1	888.3	345.2	25.7	15.1	117.4	25.5	15.2	4.6	2.4	1.2	0.0	0.0	1552.9	482.4
VA	21	172.6	24.0	322.7	60.4	502.0	295.6	7.1	4.9	185.2	38.0	50.3	22.4	7.5	6.3	0.0	0.0	1247.4	451.4
Overall	587	266.8	8.8	192.8	9.9	699.1	63.4	23.6	1.9	148.3	6.5	53.1	3.5	7.6	0.8	0.1	0.1	1391.5	94.8

Energy expenditure (kJ/day, $x \pm SE$) associated with specific activities of Atlantic brant and total diurnal energy expenditure (DEE, kJ/day, $\sum x \pm SE$) at 11 sites along the northeastern Atlantic coast, USA, during Dec–May 2007–2008.

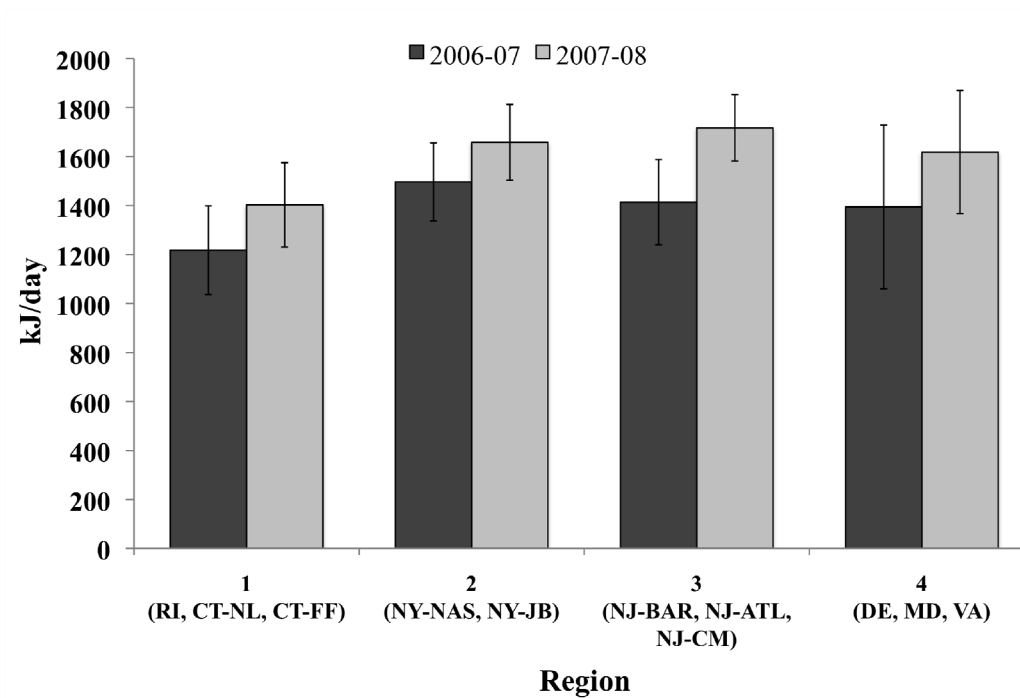
Energy expenditure (kJ/day) of specific activities

Site	N	Feed		Swim		Fly		Walk		Rest		Comfort		Agonistic		Courtship		DEE	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	$\sum x$	SE
RI	92	174.0	17.9	357.0	30.0	838.1	175.2	21.2	4.0	109.7	16.5	39.1	7.5	7.6	1.6	6.2	5.7	1552.9	258.5
CT-NL	55	261.4	22.3	336.9	32.0	254.8	133.1	5.5	3.2	143.4	20.1	26.3	6.4	8.2	3.0	0.0	0.0	1036.6	220.0
CT-FF	30	273.0	37.4	347.3	50.1	904.4	309.8	2.0	1.4	36.0	12.2	42.7	25.7	5.9	4.4	1.6	1.1	1612.8	442.1
NY-NAS	110	232.8	17.6	277.1	21.5	793.3	108.6	20.7	2.8	101.8	11.7	61.9	7.8	8.6	3.7	0.0	0.0	1496.1	173.8
NY-JB	104	210.2	20.7	299.7	28.6	1168.4	182.5	23.8	3.8	60.8	10.0	63.6	8.5	3.3	0.7	0.0	0.0	1829.8	254.8
NJ-BAR	121	222.1	20.3	230.7	24.0	1605.1	209.7	10.9	3.3	69.0	10.2	54.3	11.2	2.3	1.8	0.1	0.1	2194.5	280.7
NJ-ATL	120	196.9	16.1	256.7	22.3	1032.9	158.6	7.6	1.8	133.7	15.7	68.4	9.8	2.7	1.0	0.0	0.0	1698.8	225.4
NJ-CM	119	266.7	17.9	273.5	22.5	512.2	96.9	12.6	1.9	109.9	10.8	73.6	9.4	1.8	0.7	0.0	0.0	1250.2	160.1
DE	74	206.4	23.6	383.2	36.8	371.4	83.0	14.6	6.8	28.3	9.0	149.7	21.7	8.2	2.5	0.0	0.0	1161.9	183.4
MD	25	204.5	48.5	216.0	57.8	2640.1	527.3	2.4	1.3	17.4	7.4	13.3	4.2	0.5	0.2	0.0	0.0	3094.2	646.7
VA	4	340.4	33.3	339.1	34.7	174.6	166.4	6.3	3.3	68.8	17.4	33.6	8.4	9.5	1.8	0.1	0.1	972.3	265.4
Overall	854	222.6	6.7	292.6	9.2	936.4	57.8	14.0	1.1	89.9	4.5	64.2	3.8	4.8	0.7	0.7	0.6	1625.2	84.4

Appendix B

ENERGY EXPENDITURE BETWEEN REGIONS AND YEARS

Daily energy expenditure (DEE, kJ/day \pm SE) of Atlantic brant by region along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.



Appendix C

BODY MASS, WING CHORD, AND BODY CONDITION INDEX OF ATLANTIC BRANT

Body mass (g), wing chord (mm), and body condition index (BCI) of Atlantic brant collected between October 2006 – May 2008, all values are mean \pm SE.

Year	Region	Month	Age ^a	Sex ^b	N	Body mass (g)		Wing Chord (mm)		BCI	
						\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
2006-07	1 (RI, CT)	Dec	HY	M	1	1230	-	302	-	4.07	-
				F	2	1315	15	303	2	4.35	0.01
		Jan	AHY	M	4	1450	54	321	5	4.52	0.11
				F	5	1446	61	320	7	4.51	0.17
			HY	M	1	1540	-	330	-	4.67	-
				F	4	1210	60	318	5	3.81	0.19
		Feb	AHY	M	8	1478	33	337	2	4.39	0.08
				F	7	1397	51	334	5	4.19	0.15
			HY	F	2	1200	20	305	0	3.93	0.07
		Mar	AHY	M	12	1463	38	344	5	4.25	0.09
				F	12	1345	29	330	2	4.08	0.10
			HY	M	14	1487	30	341	3	4.36	0.07
		Apr	AHY	M	13	1362	32	331	3	4.11	0.09
				F	13	1345	29	330	2	4.08	0.10
			HY	M	4	1308	38	319	7	4.11	0.19
				F	3	1113	41	309	6	3.61	0.21
AHY	M	17	1536	54	339	2	4.53	0.15			
	F	16	1517	30	325	3	4.66	0.06			

2 (NY)	May	HY	F	3	1447	119	305	0	4.74	0.39
		AHY	M	6	1663	41	337	5	4.95	0.17
	Nov		F	2	1600	160	324	6	4.93	0.40
		HY	M	1	1140	-	314	-	3.63	-
	Feb	AHY	M	5	1416	37	338	2	4.18	0.09
			F	7	1289	55	322	4	4.01	0.17
		HY	M	6	1075	59	314	3	3.42	0.17
			F	2	1148	13	303	8	3.79	0.14
		AHY	M	10	1322	30	330	5	4.00	0.05
			F	16	1193	27	318	3	3.74	0.07
	Mar	HY	M	2	1155	145	328	9	3.52	0.35
			F	1	1070	-	315	-	3.40	-
AHY		M	5	1438	61	338	4	4.26	0.16	
Apr		F	7	1251	35	326	5	3.84	0.10	
	HY	F	1	1030	-	296	-	3.48	-	
	AHY	M	3	1473	67	338	9	4.36	0.13	
May		F	7	1283	34	323	3	3.97	0.09	
	HY	M	1	1380	-	305	-	4.52	-	
		F	1	1390	-	317	-	4.38	-	
	AHY	M	11	1635	35	333	2	4.91	0.10	
		F	8	1440	40	320	2	4.50	0.12	
	Nov	AHY	M	4	1625	40	338	6	4.82	0.10
Dec		F	3	1377	123	318	7	4.32	0.31	
	AHY	M	5	1442	62	319	2	4.52	0.18	
		F	9	1331	33	312	4	4.27	0.09	
Jan	HY	M	1	1120	-	309	-	3.62	-	
		F	4	1198	57	309	4	3.87	0.13	
	AHY	M	2	1435	65	329	16	4.37	0.02	
		F	10	1387	51	327	3	4.24	0.14	
Feb	HY	M	1	1280	-	320	-	4.00	-	
	AHY	M	2	1510	50	328	2	4.61	0.12	

4 (MD, VA, NC)	Mar		F	9	1384	28	327	3	4.24	0.08	
		HY	M	4	1206	40	297	2	4.06	0.12	
			F	5	1147	43	305	4	3.76	0.09	
		AHY	M	3	1397	78	332	5	4.20	0.18	
			F	3	1215	6	317	0	3.84	0.02	
		Apr	AHY	M	5	1572	48	336	4	4.67	0.10
			F	2	1485	5	323	1	4.60	0.00	
		May	AHY	M	4	1545	97	338	6	4.57	0.26
			F	1	1640	-	320	-	5.13	-	
		Nov	HY	M	4	1448	26	323	8	4.49	0.03
			F	3	1267	86	307	4	4.13	0.30	
			AHY	M	6	1433	35	320	3	4.48	0.12
			F	6	1242	44	298	5	4.17	0.15	
		Dec	HY	M	2	1350	150	306	4	4.41	0.43
			F	5	1118	38	308	7	3.64	0.15	
			AHY	M	4	1328	66	321	6	4.13	0.14
			F	10	1299	22	319	5	4.07	0.07	
		Jan	HY	M	9	1353	55	321	4	4.22	0.17
			F	11	1083	54	300	4	3.60	0.16	
			AHY	M	28	1384	24	332	3	4.16	0.06
			F	21	1315	33	322	2	4.08	0.10	
		Feb	HY	M	8	1239	35	302	3	4.10	0.09
			F	5	1090	14	298	6	3.67	0.10	
			AHY	M	24	1416	19	327	2	4.34	0.06
		F	14	1300	30	319	2	4.09	0.11		
	Mar	HY	M	1	1200	-	307	-	3.91	-	
		F	1	1080	-	281	-	3.84	-		
		AHY	M	6	1450	29	339	4	4.28	0.10	
		F	5	1328	28	315	5	4.22	0.10		
	2006-07 Overall			480	1341	7	320	1	4.19	0.02	

2007-08	1 (RI, CT)	Dec	HY	M	1	1410	-	334	-	4.22	-
				F	3	1357	35	320	6	4.24	0.19
			AHY	M	9	1526	54	342	2	4.46	0.15
				F	9	1536	41	333	2	4.61	0.11
		Jan	HY	M	1	1000	-	335	-	2.99	-
				F	2	1210	30	334	3	3.62	0.06
			AHY	F	3	1353	111	335	3	4.04	0.32
			Feb	HY	M	2	1175	15	299	1	3.93
				F	4	1191	58	312	12	3.82	0.15
				AHY	M	10	1474	45	336	2	4.38
		Mar		F	11	1268	37	320	4	3.96	0.10
			HY	M	5	1366	38	317	5	4.32	0.13
			F	3	1308	22	321	5	4.07	0.05	
			AHY	M	10	1482	23	342	3	4.33	0.06
	Apr		F	8	1429	25	327	4	4.37	0.06	
		HY	M	7	1385	30	310	3	4.47	0.12	
			F	3	1393	121	312	10	4.45	0.29	
			AHY	M	10	1601	24	333	5	4.81	0.07
	May		F	12	1454	37	327	3	4.45	0.11	
		HY	M	7	1638	44	319	3	5.13	0.10	
			F	4	1631	26	319	6	5.11	0.10	
			AHY	M	12	1771	31	341	3	5.19	0.08
	Dec	2 (NY)		F	8	1721	35	329	3	5.23	0.11
			HY	M	4	1355	77	312	8	4.34	0.14
	F		7	1256	25	294	3	4.28	0.13		
	AHY		M	3	1570	15	324	8	4.84	0.07	
			F	8	1466	58	323	3	4.54	0.14	
Jan	HY		M	11	1330	47	313	2	4.25	0.14	
			F	5	1256	58	299	4	4.19	0.15	
	AHY		M	8	1598	50	333	4	4.80	0.12	
			F	10	1387	33	316	2	4.39	0.10	
Feb	HY		M	5	1274	24	310	4	4.11	0.07	

		F	1	1100	-	315	-	3.49	-	
	AHY	M	16	1497	36	332	3	4.51	0.12	
		F	12	1280	40	314	3	4.08	0.13	
Mar	HY	M	7	1259	31	314	3	4.01	0.10	
		F	7	1257	43	304	3	4.13	0.13	
	AHY	M	7	1371	37	334	4	4.10	0.10	
		F	7	1264	27	323	2	3.91	0.07	
Apr	HY	M	6	1360	72	327	5	4.16	0.22	
		F	4	1373	11	317	2	4.33	0.05	
May	AHY	M	5	1510	43	306	4	4.93	0.12	
		F	3	1253	111	297	10	4.21	0.25	
	HY	M	12	1634	64	332	3	4.92	0.18	
		F	10	1556	31	318	2	4.89	0.09	
3 (NJ)	Nov	AHY	M	1	1200	-	305	-	3.93	-
		F	2	1180	130	295	5	4.02	0.52	
	HY	M	4	1508	64	327	4	4.62	0.23	
		F	6	1443	70	315	2	4.58	0.21	
Dec	AHY	M	1	1220	-	283	-	4.31	-	
		F	2	1500	220	308	13	4.85	0.51	
	HY	M	6	1510	56	328	7	4.61	0.22	
		F	4	1335	73	314	7	4.26	0.23	
Jan	HY	M	3	1355	145	312	2	4.34	0.44	
		F	3	1263	27	309	5	4.08	0.04	
	AHY	M	5	1644	47	331	4	4.97	0.12	
		F	3	1447	13	319	3	4.53	0.08	
Feb	HY	M	4	1405	75	310	4	4.55	0.27	
	AHY	M	5	1570	38	323	6	4.87	0.11	
		F	4	1360	64	311	4	4.38	0.19	
Mar	HY	M	3	1363	47	310	6	4.40	0.07	
		F	3	1207	30	301	5	4.01	0.04	
	AHY	M	4	1578	64	329	4	4.79	0.19	
		F	5	1272	59	310	2	4.10	0.20	

4 (DE, MD, VA)	Apr	AHY	M	8	1668	39	336	4	4.96	0.09	
			F	7	1394	51	323	2	4.32	0.17	
	May	HY	M	4	1480	27	308	2	4.81	0.06	
			F	4	1388	29	303	3	4.58	0.09	
	Nov	AHY	M	5	1670	41	333	3	5.02	0.13	
			F	2	1590	90	317	1	5.02	0.30	
		HY	F	3	1160	29	291	4	3.99	0.07	
			AHY	M	5	1417	43	323	4	4.39	0.12
		Dec	HY	F	3	1320	59	304	6	4.34	0.11
				M	4	1363	85	309	7	4.41	0.20
	AHY		F	8	1250	45	302	4	4.14	0.16	
			M	7	1507	26	338	5	4.47	0.08	
	Jan	HY	F	7	1370	46	320	7	4.29	0.11	
			M	4	1230	47	305	9	4.03	0.11	
		AHY	F	8	1221	59	298	7	4.10	0.15	
			M	4	1420	88	325	11	4.35	0.14	
	Feb	HY	F	12	1323	30	322	5	4.11	0.09	
			M	7	1359	54	319	3	4.25	0.14	
		AHY	F	11	1263	35	310	4	4.07	0.08	
			M	7	1487	27	336	4	4.43	0.07	
	Mar	HY	F	5	1282	30	327	1	3.92	0.09	
			M	5	1310	40	320	5	4.09	0.15	
		AHY	F	8	1215	34	305	5	3.99	0.13	
			M	10	1413	31	334	4	4.24	0.11	
Apr	HY	F	11	1362	17	322	3	4.23	0.07		
		M	6	1300	32	311	4	4.19	0.14		
	AHY	F	6	1192	24	309	2	3.87	0.10		
		M	4	1400	29	342	5	4.09	0.07		
May	HY	F	4	1188	29	314	6	3.78	0.03		
		M	4	1505	89	308	4	4.89	0.25		
	AHY	F	4	1490	23	293	4	5.10	0.12		
		M	2	1510	340	321	9	4.69	0.94		

		F	1	1580	-	311	-	5.08	-
	2007-08 Overall		560	1390	6	318	1	4.37	0.02
Total	2006-08		1040	1368	5	319	0.4	4.29	0.01

^a Age (HY = hatch year, AHY= after hatch year)

^b Sex (M=male, F=female)