Research Article

Regional and Intraseasonal Variation in Diet of Wintering and Staging Atlantic Brant

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ABSTRACT Regional and intraseasonal patterns of food use influence populations through impacts on breeding success, survival, and distribution of individuals. We used both traditional foregut content analysis and stable carbon and nitrogen isotopes in liver and leg muscle to determine intraseasonal patterns in the diet of Atlantic brant geese (*Branta bernicla hrota*) from early winter through spring staging (1 Dec–31 May 2007–2008) along the mid-Atlantic coast of the United States. Overall, brant diet consisted of macroalgae (52%), salt marsh cordgrass (22%), eelgrass (18%), and terrestrial grass and clover (8%). Mean δ^{13}C and δ^{15}N values differed among these 4 food sources. Therefore, we used an isotope mixing-model (SIAR) to estimate the relative contributions of each source to brant diet among regions and months. Wintering brant in northern and southern regions ate mostly macroalgae throughout the wintering period and ate more salt marsh and terrestrial grasses in spring. Brant in central regions had a more stable diet from December to May. Regional and intraseasonal patterns in brant diet are likely affected by several factors including variation in food source availability and quality due to synergistic effects of long-term annual and intraseasonal changes in abundance of submerged aquatic vegetation. Our estimates of diet combined with information on brant daily energy requirements and forage quality can be used to more accurately determine carrying capacity of wintering brant geese given established population objectives. © 2014 The Wildlife Society.

KEY WORDS Atlantic brant, *Branta bernicla hrota*, carbon, eelgrass, food, grass and clover, isotope mixing model, macroalgae, nitrogen, salt marsh cordgrass, stable isotopes.

Patterns in food resource use by animals have direct consequences for their breeding success, survival, and spatial distribution (Percival and Evans 1997, Rowcliffe et al. 2001, Drent et al. 2007, Tinkler et al. 2009). For example, arctic-nesting geese can be energy limited during winter and spring because of spatial and temporal variation in habitat quality and food availability (Owen et al. 1992, Clausen and Percival 1998, Inger et al. 2006a, Clausen et al. 2012) and this, in turn, can carry over to affect reproduction during the summer (Barry 1962, Raveling 1979, Ebbinge and Spaans 1995). Inger et al. (2010) found that dietary constraints in wintering European light-bellied brent geese (*Branta bernicla hrota*) inhibited their reproduction in the subsequent breeding season. In general, range-wide spatial and temporal patterns in food use and resulting body condition of wintering birds reflect varying intraseasonal energy requirements and food resource availability (Hassall et al. 2001, Mini and Black 2009, Ladin et al. 2011). Additionally, the foraging behavior of wintering geese may change with resource availability and enable their use of new food sources (Kirby and Obrecht 1980, Black et al. 2003, Jefferies and Drent 2006, Klaassen et al. 2006). Although food resource use and diet are not the only limiting factors for populations, this is an important area of research that will directly benefit the future habitat and population management of wintering brant.

Atlantic brant (*Branta bernicla hrota*, hereafter brant) winter along the central Atlantic coast between Massachusetts and North Carolina. Historically, brant were closely associated with eelgrass (*Zostera marina*), which provided a reliable and widely available food source during winter and spring staging (Reed et al. 1998). Large-scale reductions of eelgrass in 1930 and 1931 due to an acute disease outbreak

caused by the slime mold *Labyrinthula zosterae* (Rasmussen 1977) were linked with subsequent declines in the brant population in 1933–1934 (Cottam et al. 1944). Additionally, increasing anthropogenic pressures leading to habitat loss and degradation were also associated with brant population declines (Kirby and Obrecht 1982, Moore and Short 2006). Consequently, brant have used alternative food sources and habitats (Penkala 1976, Kirby and Obrecht 1980) including submerged aquatic vegetation, such as macroalgae (*Ulva* spp. and *Enteromorpha* spp.) during wintering periods (Penkala 1976, Kirby and Obrecht 1980, Ladin 2010). In spring (Mar–May), after submerged aquatic vegetation abundance generally declines, brant in the Mid-Atlantic have been documented eating new-growth salt marsh cordgrass (*Spartina alterniflora*), terrestrial grass (*Poa* spp.), and clover (*Trifolium* spp.; Kirby and Obrecht 1982, Ladin 2010). Although the Atlantic brant population has not fully recovered to historical levels, flexibility in foraging behavior seems to have enabled population stability over the past several decades. However, the extent to which individuals change their diets during winter has not yet been adequately explored. Understanding patterns of food resource use for brant is important for estimating wintering carrying capacity and guiding habitat management.

Over the past 50 years, foraging ecology and dietary trends of brant have been studied using traditional techniques that include analysis of foregut and fecal contents (Cottam et al. 1944, Penkala 1976, Rasmussen 1977, Kirby and Obrecht 1982). Although past studies have provided accounts of brant foraging ecology in relation to habitat and resource use, they have been limited in their spatial and temporal scope. Examining gross foregut contents provides only limited information (e.g., foods eaten within the past hour) about dietary patterns of organisms at a given time (Prop and Deerenberg 1991, Votier et al. 2003). Additionally, traditional dietary analyses may be biased if collected birds are from hunter-kills (Sheeley and Smith 1989, Heitmeyer et al. 1993).

In contrast, stable isotope analysis can be used to determine dietary shifts of individuals and provides less biased data because of the inherent disconnect between the proximate time and location of sampling and the food sources used by sampled individuals (Hobson et al. 1993, Wise et al. 2006). Differences in isotopic turnover rates among tissues such as liver and muscle allow a quantitative comparison of food resource use by individual ducks or geese within the past 3–5 days (liver) and 3–4 weeks (muscle), respectively (Hobson et al. 1993, Bauchinger and McWilliams 2009, Bauchinger et al. 2010).

Our main objective was to examine dietary patterns of wintering and staging brant across their winter range to gain a better idea of within-season variation in food use. We predicted that brant diets would shift from mostly macro-algae in early winter (Dec–Feb) to greater percentages of salt marsh cordgrass, terrestrial grasses, and clover in late winter and spring (Mar–May). We based our prediction on past traditional dietary studies (Cottam et al. 1944, Penkala 1976, Rasmussen 1977, Kirby and Obrecht 1982), and patterns

found in European brent geese using both traditional methods (Rowcliffe et al. 2001, Spaans and Postma 2001) and stable isotope analysis (Inger et al. 2006b).

STUDY AREA

Our study took place on the United States Atlantic coast between Rhode Island and Virginia (Fig. 1) from December 2007 to May 2008. The mid-Atlantic coastal region is highly urbanized and densely populated by humans but provides an array of estuarine habitat types, and is the primary wintering region for brant. We defined 3 habitat types within the estuarine system (Cowardin et al. 1979): open water, estuarine, salt marsh, and 1 upland habitat. Open water habitat consisted of shallow sub-tidal embayments. Estuarine habitat contained intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. Salt marsh habitat consisted of both irregularly and regularly flooded intertidal emergent wetland dominated by salt marsh cordgrass. We defined upland habitat as terrestrial fields, lawns, or areas adjacent to or near estuarine habitat. These 4 habitats contained common brant foods, such as macroalgae, eelgrass, new-growth salt marsh cordgrass, and terrestrial grass and clover.

We designated 11 study sites (225 km^2 per site) along the winter range of brant (Fig. 1). We divided the winter range into 4 geographic regions based on latitude and known concentrations of brant from the mid-winter waterfowl survey throughout the Atlantic Flyway. Region 1 contained the 3 northern sites in Rhode Island and Connecticut, region 2 contained the 2 sites in New York, region 3 contained the 3 New Jersey sites, and region 4 contained 1 site each in Delaware, Maryland, and Virginia (Fig. 1).

METHODS

Analysis of Foregut Contents

We obtained brant carcasses using shotguns between December 2007 and May 2008 through hunter-harvested donations ($n = 192$), removal for aircraft collision abatement at John F. Kennedy (J.F.K.) Airport in New York ($n = 76$), or state-issued scientific collection permits ($n = 233$). We collected brant from varying locations and habitats within each of the 11 sites to provide a representative sample of the population (Table 1).

We first determined food sources in brant diet using gross analysis of foregut contents from brant carcasses. We dissected carcasses and removed the entire foregut (including the proventriculus and gizzard) and then froze the foregut at $-40°C$ until processing. In the laboratory, we sliced open thawed foreguts using a scalpel, and removed all contents and grit by flushing foreguts with de-ionized water over a 3-mm sieve. A sole observer identified all foregut contents through visual inspection and use of field identification guides where necessary (Hurley 1990, Gosner 1999). We broadly sorted contents into 4 food source categories (macroalgae, eelgrass, salt marsh cordgrass, or grass and clover). Macroalgae consisted of the phyla Phaeophyta, Rhodophyta, and
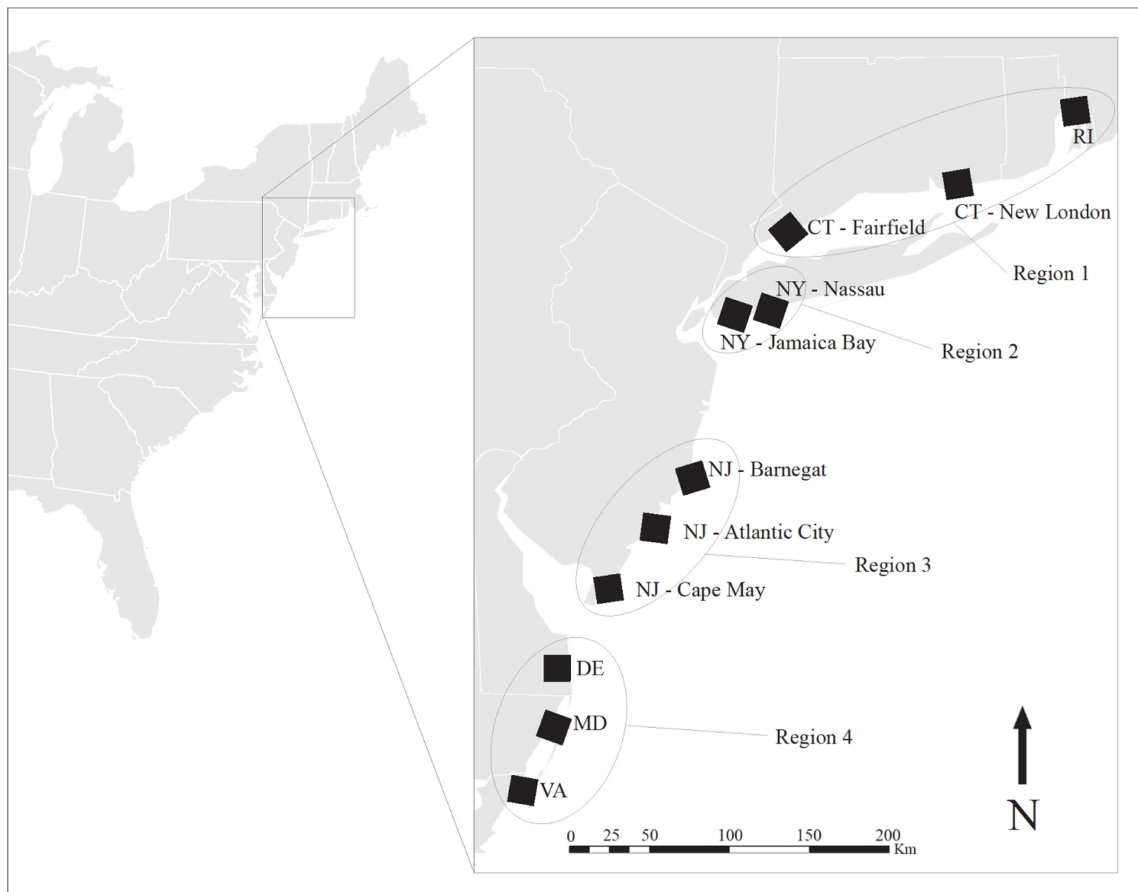
Figure 1. The 4 regions and 11 sampling sites (225 km^2 per site) distributed along the northeastern Atlantic coast, across the wintering range of Atlantic brant. Sampling sites included Narragansett Bay, Rhode Island (RI); New London, Connecticut (CT); Fairfield, CT; Point Lookout, New York (NY); Jamaica Bay, NY; Barnegat Bay, New Jersey (NJ); Atlantic City, NJ; Cape May, NJ; Indian River Bay, Delaware (DE); Sinepuxent Bay, Maryland (MD); and Chincoteague Bay, Virginia (VA), USA.

Chlorophyta, or brown, red, and green algae, respectively. We calculated frequency of occurrence (%) for each of the 4 food sources contained within foregut contents by dividing the number of detections of each food source by the total number of foreguts sampled for each month and region.

Table 1. Number of brant collected from 1 December 2007–31 May 2008 in 4 regions of the northeastern Atlantic coast including Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia, USA.

		Month						
Region	**State**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Total**
1	RI	17	14	11	13	12	0	67
	CT	5	8	12	11	16	13	65
2	NY	19	15	11	6	9	10	70
	NY[a]	0	19	18	20	0	19	76
3	NJ	12	12	13	14	15	15	81
4	DE	18	9	19	17	17	11	91
	MD	6	14	2	2	0	0	24
	VA	0	8	8	11	0	0	27
	Total	77	99	94	94	69	68	501

[a] Brant collected during bird hazard management at John F. Kennedy International Airport, New York.

Stable Isotope Analysis

We collected food sources for stable isotope analysis monthly at each of the 11 sites from December 2007 to May 2008. We subdivided each site into 225 1-km^2 plots. We sampled food sources within 179 1-km^2 plots that contained estuarine and upland habitat types where brant commonly occurred and were observed foraging. We collected macroalgae and eelgrass at 6 randomly selected plots per month at each site, either by hand while wading in shallow water, or from a boat with a D-frame dip net or metal rake. We collected salt marsh cordgrass at 2 randomly chosen plots within each site during months when it was available to brant. For example, we collected salt marsh cordgrass in region 4 in the southern portion of the study area from January to May, whereas in northern regions, we collected it only in April and May. We collected terrestrial grass and clover at 2 randomly selected plots per site each month by clipping live vegetation at the soil line with scissors. We placed all food sources in labeled plastic freezer bags and stored them at $-40°C$ until processing. We rinsed samples in de-ionized water before drying them for 48 hours at $50°C$. We ground dried samples using a Wiley-mill to pass a 1-mm sieve and measured 1.0–1.3 mg of each sample into tin capsules for stable isotope analysis.

For stable isotope analysis of brant tissues, we dissected liver and leg muscle samples, which were stored frozen, from brant collected from December 2007 to May 2008 at each of the 11 sites (Table 1). We freeze-dried liver and leg muscle samples from each individual, and then ground samples with a mortar and pestle. We placed a subsample (approx. 0.5 g) of each ground tissue sample in a cellulose thimble (exterior 12 mm × 55 mm) and refluxed the sample with petroleum ether for 6 hours in a Soxhlet apparatus to remove lipids (Dobush et al. 1985). We prepared samples for stable isotope analysis of carbon and nitrogen by weighing approximately 1.0–1.3 mg of the lipid-free dried liver or leg muscle into tin capsules.

We analyzed stable $\delta^{13}C$ and $\delta^{15}N$ isotopes of plant food sources and tissues using a Carlo-Erba NA 1500 series II elemental analyzer (Thermo Scientific, Waltham, MA) attached to a continuous flow isotope ratio Micromass Optima mass spectrometer (IsoPrime Ltd., College Station, TX). We report all stable isotope concentrations as δ-values expressed as parts per thousand (‰) derived from the equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1,000$, where X is ^{13}C or ^{15}N and R represents the associated $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio; $R_{standard}$ is the ratio of international references for carbon from the Vienna Peedee Belemnite (VPB) and atmospheric N_2 for nitrogen, both of which are assumed equal to 0.0‰. Replicate measures of internal laboratory standards resulted in a standard deviation of 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$.

We used the Stable Isotope Analysis models in R (SIAR) to estimate the relative contributions of the 4 distinct food sources to brant diet within 4 geographic regions by month from December 2007 to May 2008 (Jackson et al. 2008, Parnell et al. 2010). The SIAR package provides output from multiple-source concentration-dependent mixing models using a Bayesian approach that incorporates uncertainty in all model parameters (Parnell et al. 2010). The outputs from SIAR are true probability distributions of most-likely solutions (e.g., the estimated diet) that are amenable to statistical analyses (Inger and Bearhop 2008). Model parameters included 1) isotopic values of a mixture (brant liver or leg muscle by month and region), 2) isotopic values of sources (i.e., 4 food sources), 3) isotope discrimination values, and 4) carbon and nitrogen concentrations of each food source. Food source and consumer tissue inputs to the mixing models were $\delta^{13}C$ and $\delta^{15}N$ ratios measured in food sources and brant tissues sampled within each month and region. Ratios of stable $\delta^{15}N$ isotopes in consumer tissues are typically enriched 3–4‰ compared to food sources, whereas $\delta^{13}C$ isotopic ratios undergo relatively little enrichment during metabolic routing to consumer tissues (Minagawa and Wada 1984, Peterson and Fry 1987). Because discrimination factors (also known as trophic enrichment factors) have not been directly measured in brant, we used discrimination factors for liver ($\Delta^{13}C = 0.35$‰ and $\Delta^{15}N = 2.60$‰) and leg muscle ($\Delta^{13}C = 0.92$‰ and $\Delta^{15}N = 1.70$‰) derived from meta-analyses of values measured in several species of birds (Caut et al. 2009). We used mean values for total carbon and nitrogen

concentration within each food source 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. 2006b), and salt marsh cordgrass (%N = 1.7, %C = 41.00; Osgood and Zieman 1993). To determine how discrimination factors and carbon and nitrogen concentrations affected our mixing model results, we conducted a sensitivity analysis by independently varying discrimination factors for values of tissue $\delta^{15}N$ between 0‰ and 5‰, and values of tissue $\delta^{13}C$ between 0‰ and 2‰. The degree of model sensitivity varied depending on food source and month. For example, the relative contributions from grass and clover to the diet compared to other food sources were more sensitive to varying $\delta^{15}N$ and $\delta^{13}C$ values in late winter and spring months than during early winter months. However, all model estimates of mean relative dietary contributions under all scenarios fell within 95% credibility intervals, showing no significant differences from the null model.

To delineate the time frame over which liver and leg muscle tissues incorporate carbon, we estimated fractional rates of carbon incorporation (k) for brant liver and leg muscle tissue using the allometric equations based on the log(body mass) (x) (Bauchinger and McWilliams 2009):

$$\log(k_{liver}) = -0.2758(\pm 0.0676) \times x - 0.4224(\pm 0.1684)$$

and

$$\log(k_{leg}) = -0.2793(\pm 0.0055) \times x - 1.0788(\pm 0.0149)$$

We used mean body mass of all brant collected for this study (1,390 g; $n = 501$). We calculated median retention time, or carbon half-life ($C_{t1/2}$), for both tissues using $C_{t1/2} = \ln(2)/k$. We multiplied carbon half-lives for liver (13.5 days) and leg muscle (63 days) by 2.3 to estimate the duration of days required for approximately 90% of the carbon in the initial diet to be replaced within tissues (Bauchinger and McWilliams 2009). Hence, we used the duration of days for 90% carbon replacement within tissues to indicate the carbon turnover rates in brant liver (34 days) and leg muscle (145 days) tissues to define the temporal windows in which food sources are metabolically routed to tissues.

Statistical Analysis
We analyzed stable isotopic ratios of food sources and brant tissues using general linear models (type III sums of squares). We used univariate analysis of variance (ANOVA; $\alpha = 0.05$) to determine effects of food type, region, month, and their respective interaction terms on the $\delta^{15}N$ and $\delta^{13}C$ values of the 4 food sources. We used a nested ANOVA design to determine effects of region, months nested within region, sex, age, and interactions on $\delta^{15}N$ and $\delta^{13}C$ values for both liver and leg muscle tissue. We sampled every tenth percentile from posterior SIAR mixing model distributions for use in downstream ANOVA to determine differences among mean relative contributions of food sources to diet, and present these results in online supplemental materials (see Table S1, available online at www.onlinelibrary.wiley.com). All proportion data were arcsine-square root transformed before analysis to improve normality. We used a

nested ANOVA to determine differences in mean relative contributions of each source to diet among months. Subsequently, we determined pair-wise differences between months within regions for each food type independently using ANOVA and Tukey's post-hoc test ($\alpha = 0.05$). We used Levene's test to assess homoscedasticity, and tested all data for departures from normality by assessing residual plots, symmetry, and kurtosis. Consequently, we used Fisher's Z transformation on leg muscle $\delta^{13}C$ values. We used SPSS Version 17.0 (SPSS, Inc., Chicago, IL) to run all statistical tests.

RESULTS

We collected 501 brant between December 2007 and May 2008 (Table 1). Overall, the brant collected were 54% female and 61% adults. We identified 4 main food sources by gross foregut analysis, and estimated percent frequency of occurrence (mean $\pm$ SE): macroalgae ($52 \pm 2\%$), eelgrass ($12 \pm 4\%$), salt marsh cordgrass ($3 \pm 1\%$), and grass and clover ($18 \pm 4\%$). Foreguts containing macroalgae were largely dominated by sea lettuce (*Ulva lactuca*); however, we also regularly documented other genera including *Enteromorpha*, *Chaetomorpha*, *Cladophora*, and *Ceramium*. Patterns in the mean frequency of occurrence of food sources provide qualitative evidence of dietary differences among regions (Fig. 2).

We measured $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios in 373 food source samples: macroalgae ($n = 245$), eelgrass ($n = 29$), salt marsh cordgrass ($n = 27$), and grass and clover ($n = 72$). Because eelgrass was not present at all sites, we collected it only in regions 3 and 4. Both $\delta^{15}N$ ($F_{3,298} = 67.7$, $P < 0.01$) and $\delta^{13}C$ ($F_{3,298} = 312.6$, $P < 0.01$) values differed among the 4 food sources (Fig. 3). We found no differences in $\delta^{15}N$ ($F_{5,298} = 0.64$, $P = 0.67$) or $\delta^{13}C$ ($F_{5,298} = 1.34$, $P = 0.25$) among months. The combined differences in $\delta^{13}C$ and $\delta^{15}N$ values among the 4 food sources provided unique mean isotopic signatures (Fig. 3) that we used, along with

respective standard deviations, in isotopic mixing models (SIAR).

We found no differences between sexes in liver $\delta^{15}N$ ($F_{1,468} = 0.003$, $P = 0.97$) and $\delta^{13}C$ ($F_{1,468} = 0.03$, $P = 0.86$), or in leg muscle $\delta^{15}N$ ($F_{1,468} = 1.65$, $P = 0.20$) and $\delta^{13}C$ ($F_{1,468} = 2.56$, $P = 0.11$). However, after-hatch-year birds had greater liver $\delta^{15}N$ ($12.6 \pm 0.1‰$) than hatch-year birds ($12.0 \pm 0.2‰$; $F_{1,468} = 7.41$, $P < 0.01$), and leg muscle $\delta^{13}C$ was greater in after-hatch-year birds ($-15.4 \pm 0.2‰$) than in hatch-year birds ($-15.8 \pm 0.2‰$; $F_{1,468} = 5.24$, $P = 0.02$).

Regional and monthly isotope values differed for liver and leg muscle (Fig. 4). Liver $\delta^{15}N$ values differed among regions ($F_{3,21} = 7.38$, $P < 0.01$), and post hoc tests showed liver $\delta^{15}N$ values were greatest in region 1, followed by region 4, region 3, and region 2 (Fig. 4). Liver $\delta^{13}C$ values were greater in regions 1 and 3 compared to region 4 and region 2 ($F_{3,21} = 3.79$, $P = 0.03$; Fig. 4). Leg muscle $\delta^{15}N$ values also differed among all regions ($F_{3,21} = 16.5$, $P < 0.01$), and post hoc tests revealed values for leg muscle $\delta^{15}N$ were greatest in region 1, followed by region 4, region 3, and region 2 (Fig. 4a–d). Leg muscle $\delta^{13}C$ values were greater in region 1 compared to both regions 3 and 4, and region 2 ($F_{3,21} = 6.57$, $P < 0.01$; Fig. 4). Within each region, we found differences among months ($P < 0.01$ in all cases) for both liver and leg $\delta^{15}N$ ($F_{20,468} = 10.9$ and 8.0, respectively) and $\delta^{13}C$ ($F_{20,468} = 11.4$ and 7.3, respectively; Fig. 4).

Overall, the estimated relative contribution of each food source to brant diet differed consistently for liver ($F_{3,956} = 205.3$, $P < 0.01$) and leg muscle ($F_{3,956} = 418.6$, $P < 0.01$), and indicated that dietary contributions differed among food sources (based on liver and leg muscle, respectively): macroalgae ($51 \pm 2\%$, $58 \pm 2\%$), salt marsh cordgrass ($23 \pm 1\%$, $19 \pm 1\%$), eelgrass ($18 \pm 1\%$, $14 \pm 1\%$), and grass and clover ($8 \pm 1\%$, $9 \pm 1\%$). Although macroalgae was generally the predominant food source in brant diet, mixing model results depicted variation among regions for
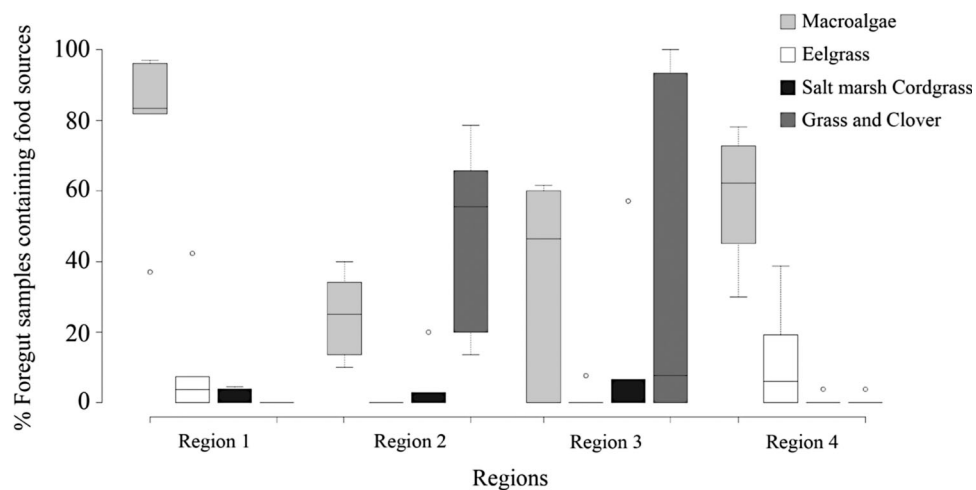

Figure 2. Frequency of occurrence of food sources in the foregut of brant ($n = 501$) collected from 4 regions along the northeastern Atlantic coast, USA, from December–May 2007–2008. Boxplots by region show macroalgae (light gray), eelgrass (white), salt marsh cordgrass (black), and grass and clover (dark gray). Boxes represent first and third quartiles, dark lines within boxes indicate median values, whiskers are 1.5 times the interquartile range, and circles depict outliers.
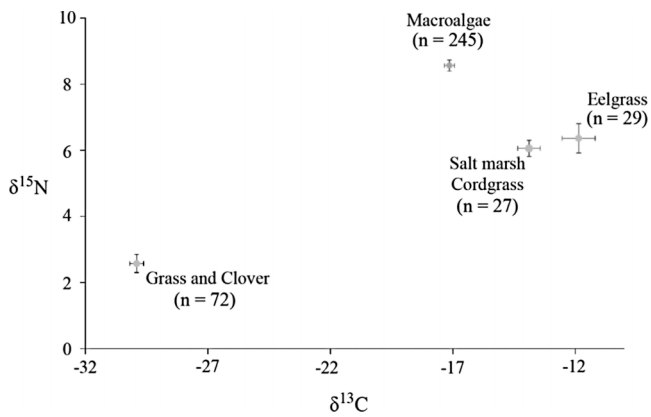
Figure 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values ($\pm$SE) of 4 food sources eaten by Atlantic brant. We collected plants from December–May 2007–2008 from 4 regions along the northeastern Atlantic coast, USA.

each food source across winter months (Fig. 5 and see online supplemental material).

The relative dietary contribution of macroalgae based on leg muscle was greater in region 1 ($76 \pm 0.7\%$) compared to regions 2, 3, and 4 ($60 \pm 0.4\%$, $36 \pm 0.6\%$, $62 \pm 0.6\%$, respectively; $F_{3,20} = 4.67$, $P = 0.01$, but did not differ among regions based on liver ($F_{3,20} = 2.62$, $P = 0.08$; Fig. 5). Relative contributions of eelgrass to diet based on both liver ($F_{3,20} = 0.81$, $P = 0.50$) and leg muscle ($F_{3,20} = 2.73$, $P = 0.07$) were similar among regions. Liver and leg muscle-based relative dietary contributions of salt marsh cordgrass ($F_{3,20} = 5.82$, $P < 0.01$; $F_{3,20} = 5.19$, $P < 0.01$, respectively) were greater in region 3 ($39 \pm 1\%$, $28 \pm 0.5\%$) compared to other regions (Fig. 5). Similarly, grass and clover contributions to both liver and leg muscle differed among regions ($F_{3,20} = 10.32$, $P < 0.01$; $F_{3,20} = 13.0$, $P < 0.01$, respectively), and were greater in region 2 ($18.2 \pm 0.4\%$, $18 \pm 0.1\%$) than other regions (Fig. 5). We detected differences among months nested within region, based on both liver and leg muscle tissue, for all 4 food source contributions to diet ($F_{20,216} \geq 9.32$, $P < 0.01$ in all cases; Fig. 5; see Table S1, available online at www.onlinelibrary.wiley.com).

DISCUSSION

Our results generally support previous studies of wintering brant diet showing that brant predominantly ate macroalgae, yet also consumed eelgrass and salt marsh cordgrass throughout wintering and staging periods, and terrestrial grass and clover in late-winter (Cottam et al. 1944, Penkala 1976, Kirby and Obrecht 1982). However, we found that brant diets differed among regions and months, which has important implications for habitat and food resource management across their winter range.

We predicted that brant would shift their diet from submerged aquatic vegetation in early-winter to salt marsh cordgrass and terrestrial grass and clover in late-winter and spring. Although this prediction was generally supported in regions 1 and 4, we did not find this pattern in regions 2 or 3, where we found higher relative use of eelgrass, as well as continued use of both salt marsh cordgrass and terrestrial

grass and clover throughout the wintering period. This contrasting pattern to our prediction suggests that central regions of the wintering range may have had a greater availability of all 4 food sources compared to regions 1 and 4 (Fig. 5). If availability of all food sources were greater in central regions, we would expect brant to consume greater proportions of higher quality foods (e.g., salt marsh cordgrass and terrestrial grass) over the winter months, which may explain why we did not observe our predicted pattern in regions 2 and 3.

Brant ate multiple food sources during the winter, similar to other migratory goose species (Rowcliffe et al. 2001, Jefferies and Drent 2006, Klaassen et al. 2006). The use of multiple foods, including both terrestrial and aquatic food sources, may allow brant to respond to variation in food availability throughout the winter and spring months. The Eastern Canadian High Arctic population of brent geese (*Branta bernicla hrota*) that winter in northern Ireland had similar food resource use patterns as determined using stable isotope analysis. These brent ate eelgrass and macroalgae in early and mid-winter months and then ate more terrestrial grass in late winter months (Inger et al. 2006*b*). In general, dietary patterns observed in wintering and staging geese can be driven by food source availability and quality, so changes in brant diet over time and among sites are likely due to a synergy of effects including weather and tidal patterns (Carter et al. 1994), long-term changes in submerged aquatic vegetation abundance (Moore et al. 2000), seasonal variation in submerged aquatic vegetation abundance (Valiela et al. 1997, Villares and Carballeira 2003), nutrient loading and eutrophication (Hurley 1990, Krause-Jensen et al. 2007), and local depletion by consumers (Therkildsen and Madsen 1999, Inger et al. 2006*c*). Furthermore, drivers of food source availability may act across different spatial and temporal scales that could give rise to observed differences in diet patterns among regions and months. For example, where eelgrass beds have been largely depleted and slow to recover in region 1 (Orth and Moore 1983) and in region 4 (Short et al. 1993), brant ate greater percentages of macroalgae and less eelgrass (Fig. 5). Additionally, brant in region 3 ate more salt marsh cordgrass, which corresponds with New Jersey's greater area of salt marsh habitat compared to other regions (U.S. Environmental Protection Agency 2010).

In addition to the amount of available food on the landscape, several studies suggest food quality and energy content play an important role in food and habitat selection (Prop and Deerenberg 1991, Hassall et al. 2001, Durant et al. 2004). Experimental studies on European free-living brent geese suggest that geese select foods having greater nitrogen and energy content (Bos et al. 2005, Tinkler et al. 2009). Differing patterns in brant diet among regions may be influenced in part by differences in availability of relatively energy-rich foods, such as terrestrial grass and clover. Ladin et al. (2011) found that energy densities (kJ/g dry) differed among foods collected across the winter range of brant during December–May 2006–2008 and were greater in grass and clover compared to salt marsh cordgrass, eelgrass, and macroalgae. Similar to previous studies, we found that brant
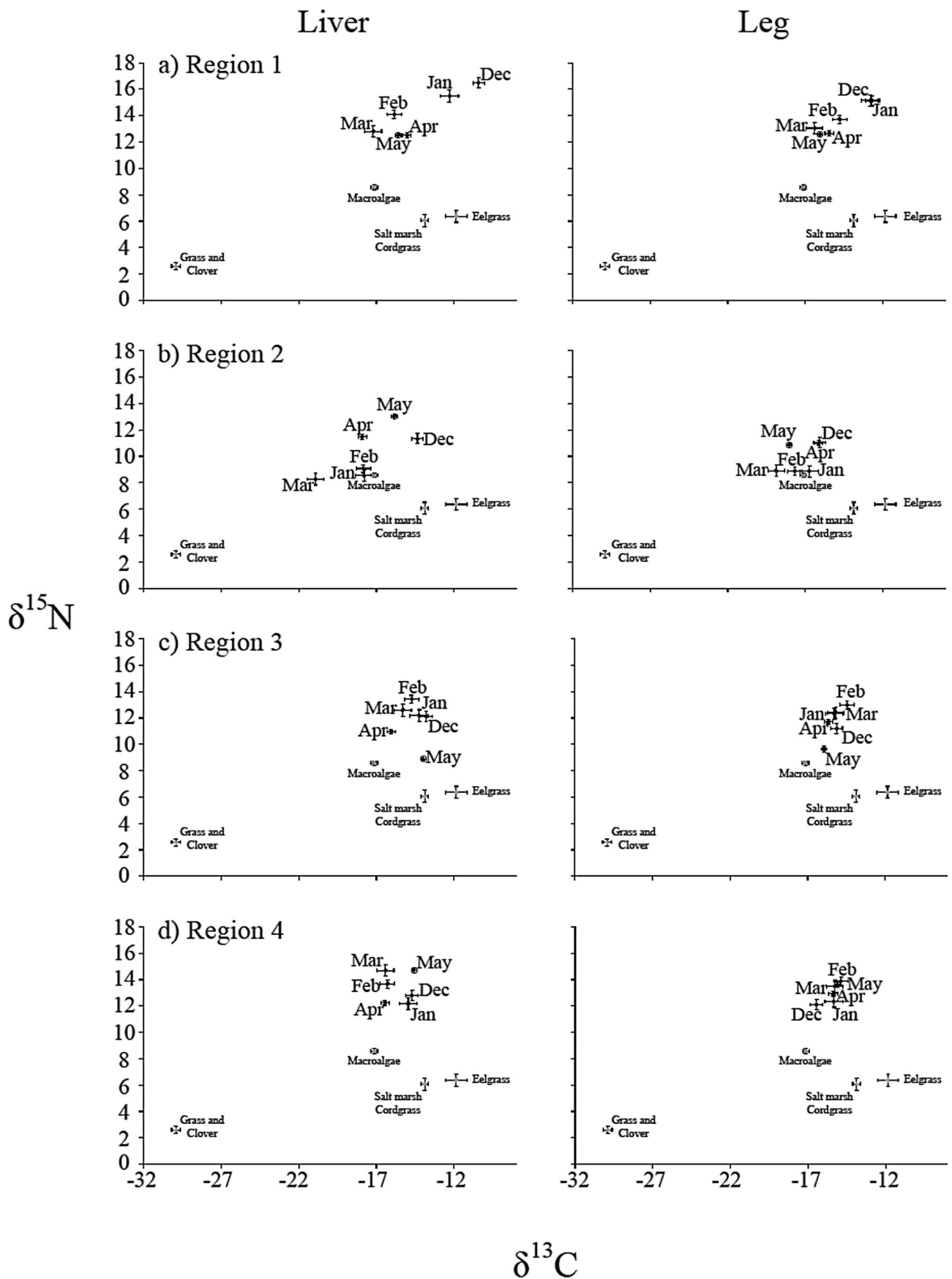
Figure 4. Mean δ¹³C and δ¹⁵N values (±SE) of 4 food sources (gray filled circles) and brant liver and leg muscle (black filled circles) collected from December–May 2007–2008 from 4 regions: a) region 1 (RI, CT), b) region 2 (NY), c) region 3 (NJ), and d) region 4 (DE, MD, VA).
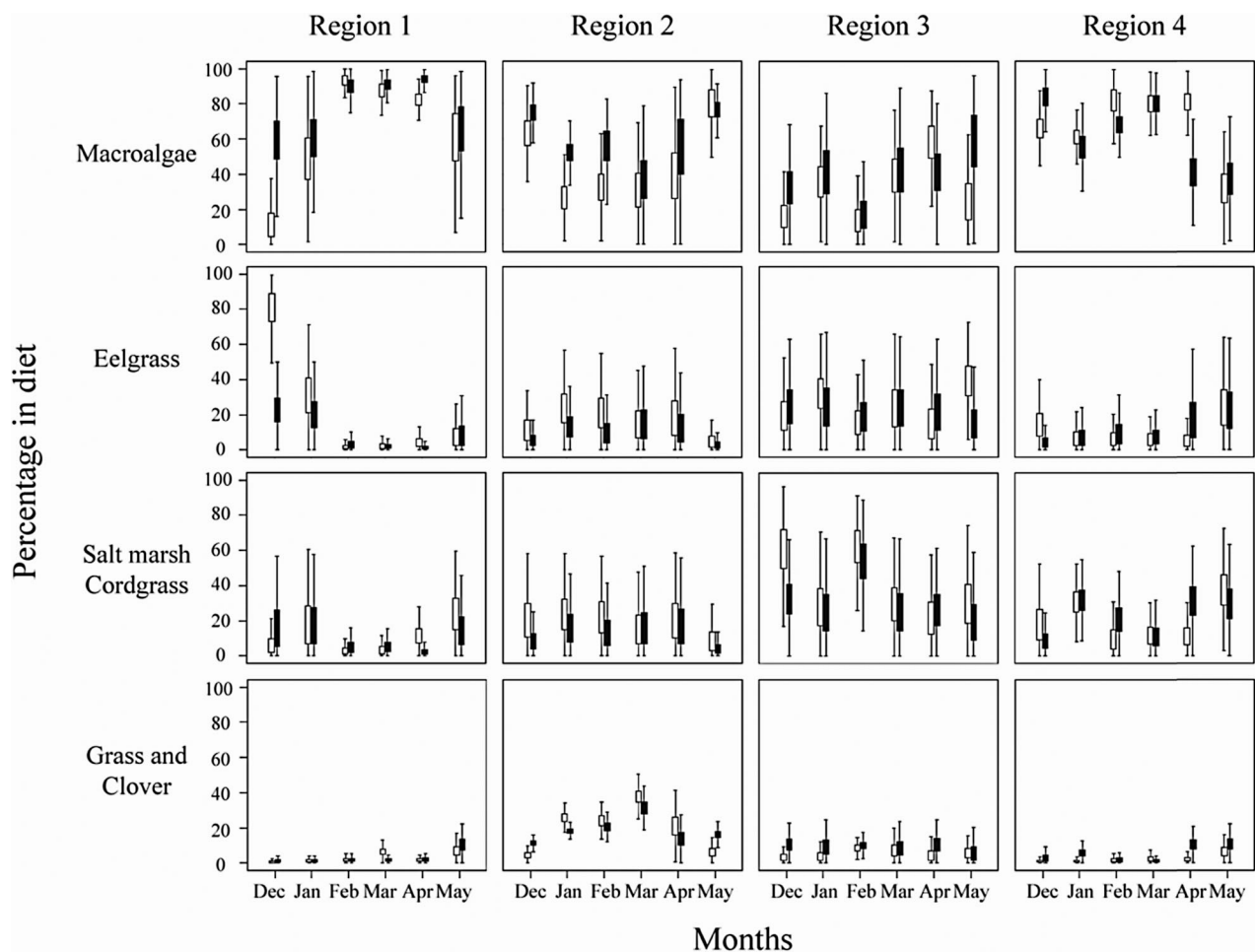
Figure 5. Relative contributions of 4 food sources to liver and leg muscle of brant from 4 regions along the northeastern Atlantic coast, December–May 2007–2008. Food sources include: macroalgae, eelgrass, salt marsh cordgrass, and grass and clover. Boxes indicate inter quartile ranges and whiskers represent the range of possible solutions estimated using the package SIAR. Relative contributions to diet for liver and leg muscle are represented by white and black boxes, respectively.

in regions 1 and 4 consumed foods with higher energy content (i.e., salt marsh cordgrass and terrestrial grass and clover) in late winter and spring when birds were increasing fat stores needed for migration. However, in contrast to predicted patterns, brant in regions 2 and 3 consumed relatively greater amounts of salt marsh cordgrass and terrestrial grass and clover throughout the wintering period compared to regions 1 and 4 (Fig. 5). The greater area of salt marsh and adjacent upland grass habitats within these central regions give brant increased opportunities to forage on higher quality food sources.

Indirect evidence suggests annual changes in forage availability also seem likely to affect intraseasonal and regional patterns in brant diet. In our study, dietary patterns of brant may have been influenced by above-average macroalgae production and availability. Although we did not directly measure food source availability, vegetation sampling within our study area during the previous winter and spring 2006–2007 to estimate energy density (kJ/g) of brant food sources (Ladin et al. 2011) qualitatively revealed reduced macroalgae abundance compared to 2007–2008. Additionally, differences in habitat use, time-energy

budgets, and body condition of brant between the winters of 2006–2007 and 2007–2008 provide indirect evidence for how seasonal variation in forage availability may affect brant diet (Ladin et al. 2011). Previous studies have also documented the influence of food availability on habitat use and time-energy budgets in European brant geese (Clausen and Percival 1998, Bos et al. 2005, Tinkler et al. 2009, Clausen et al. 2012). Given the known potential for annual variation in food source abundance and availability, intraseasonal patterns in brant diets may be dampened, particularly in regions 2 and 3, informing why our results only generally supported predictions of significant dietary shifts that would be more likely to occur in winters with reduced submerged aquatic vegetation availability.

MANAGEMENT IMPLICATIONS

Our findings can be used to build more accurate carrying capacity models for wintering brant at regional scales and have implications for the continued sustainable management of the brant population. Estimating wintering carrying capacity for brant is now a major research priority established by the Arctic Goose Joint Venture because of known links

between food distribution and abundance, winter body condition, survival, and breeding success (Arctic Goose Joint Venture Technical Committee 2008). Carry-over effects that influence survival and reproduction have been well documented for arctic-breeding geese (Barry 1962, Ankney and MacInnes 1978, Raveling 1979, Ebbinge and Spaans 1995, Sedinger et al. 1995, Bêty et al. 2003). Our estimates of diet combined with information on brant daily energy requirements and forage quality (Ladin et al. 2011) can now be used to estimate food requirements for brant across the winter range in light of established population objectives. Given monthly differences in mean energy requirements for brant (Ladin et al. 2011), we recommend developing conservative carrying capacity models based on peak energetic requirements during overwintering within a particular region. Carrying capacity or goose-use-days for wintering brant can then be determined by geographic region with estimates of available habitat area. Improved accuracy of carrying capacity models will be important for evaluating and predicting whether adequate resources are available on the landscape in accordance with brant population objectives, helping to prioritize adaptive habitat management strategies for wintering brant. Sustainable management of the brant population must consider potentially limiting factors throughout the annual cycle, including wintering carrying capacity, to inform and guide annual harvest regulations and habitat management in both Canada and the United States.

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