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Effects of Exotic Submerged Aquatic Vegetation on Waterfowl in the Mobile–Tensaw Delta

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Surveys conducted in the Mobile–Tensaw Delta, located in the Northern Gulf of Mexico, have documented a 96% decline in waterfowl populations from over 100,000 birds in 1939 to around 4,000 birds in 1999. Coincident with this decline has been the introduction and spread of nonnative Eurasian watermilfoil (*Myriophyllum spicatum*). Six surveys have documented the replacement of native wild celery (*Vallisneria americana*), the perceived preferred food for waterfowl, by *M. spicatum* as the dominant species of submerged aquatic vegetation (SAV) in this setting. Simple comparisons of SAV coverage and waterfowl surveys indicate that declines in waterfowl populations are not strongly related to invasion of *M. spicatum*. Stable isotope analysis of three species of waterfowl (*Anas strepera*, *Anas fulvigula*, and *Aix sponsa*) and their food sources show these waterfowl feed on both wild celery and milfoil. Isotopic signatures of animals living on these SAV were also in waterfowl tissues. Based on these two lines of evidence, it is unlikely that the invasion of milfoil, by itself, is responsible for waterfowl declines in this delta.

Human perturbations, including hydrographic alterations, eutrophication, and loss of vegetated habitat, are all known to negatively impact estuarine food webs (Vitousek et al., 1996; Mack et al., 2000). Equally pervasive, but less well understood, are the impacts of exotic species on these same food webs (Ruiz et al., 1999; Groshloz, 2002; Toft et al., 2003). Exotic species of submerged aquatic vegetation (SAV) now dominate soft bottoms in many estuaries. Although it is possible that the impact of such exotic species can be either positive or neutral, it is widely perceived to be negative, because they competitively displace native species (Aiken et al., 1979; Smith and Barko, 1990; Vitousek et al., 1996; Mack et al., 2000; Toft et al., 2003).

The Mobile–Tensaw Delta (hereafter the Delta; Fig. 1), located in the northern Gulf of Mexico, is one example of a dramatically impacted area. Located near a large metropolitan area (the city of Mobile), the Delta has experienced a host of anthropogenic insults to its structure and function. Among these challenges was the construction of an earthen causeway (in 1926–27), which reduced the frequency and intensity of tidal intrusion into the Delta (USACE, 2001). This hydrographic alteration has been hypothesized to have facilitated the spread of Eurasian watermilfoil (*Myriophyllum spicatum*) (hereafter referred to as milfoil), which until recently had displaced native species of SAV, including wild celery (*Vallisneria americana*), as the dominant species in many areas of the Delta (Baldwin, 1957; Beshears, 1979; Mullins et al., 2002).

The composition of SAV in the lower Delta is diverse, with 24 species known to occur here (Stout, 1979; Stout and LeLong, 1981; Vittor, 2003) and it may be that this diversity once sustained an abundance of migratory waterfowl (Pope and Polley, 1990; Mullins et al., 2002). Historical accounts from the 1940s reported a "seemingly inexhaustible supply of canvasbacks, mallards, gadwalls and wigeons" and that "there'd be such flights of ducks; the sky would almost look gray, like a cloud had come over" (Hodges, 1998; Lueth, 1963). Circumstances have changed and duck numbers have declined from their once historically abundant levels (Beshears, 1979; Borom, 1979; Mullins et al., 2002; Stout et al., 1982; Zolczynski, 1997). Coincident with reductions in waterfowl numbers was the proliferation of *M. spicatum* (Beshears, 1979; Duffy, 1998; Stout, 1982; Zolczynski, 1997). The impacts of the shift in dominance from native SAV towards milfoil for food web structure are undocumented. One native species, wild celery (*V. americana*), is considered to be the preferred food of waterfowl based on its perceived higher nutritional (i.e., nitrogen content) value (Martin and Uhler, 1939). As a result, the proliferation of milfoil throughout the Delta has been hypothesized to have negatively impacted waterfowl populations (Baldwin, 1957; Beshears, 1979 but see Perry and Deller, 1996; Benedict and Hepp, 2000).

Here we examine the effects of *M. spicatum* on waterfowl populations in the Delta via comparisons of historical changes in the coverage

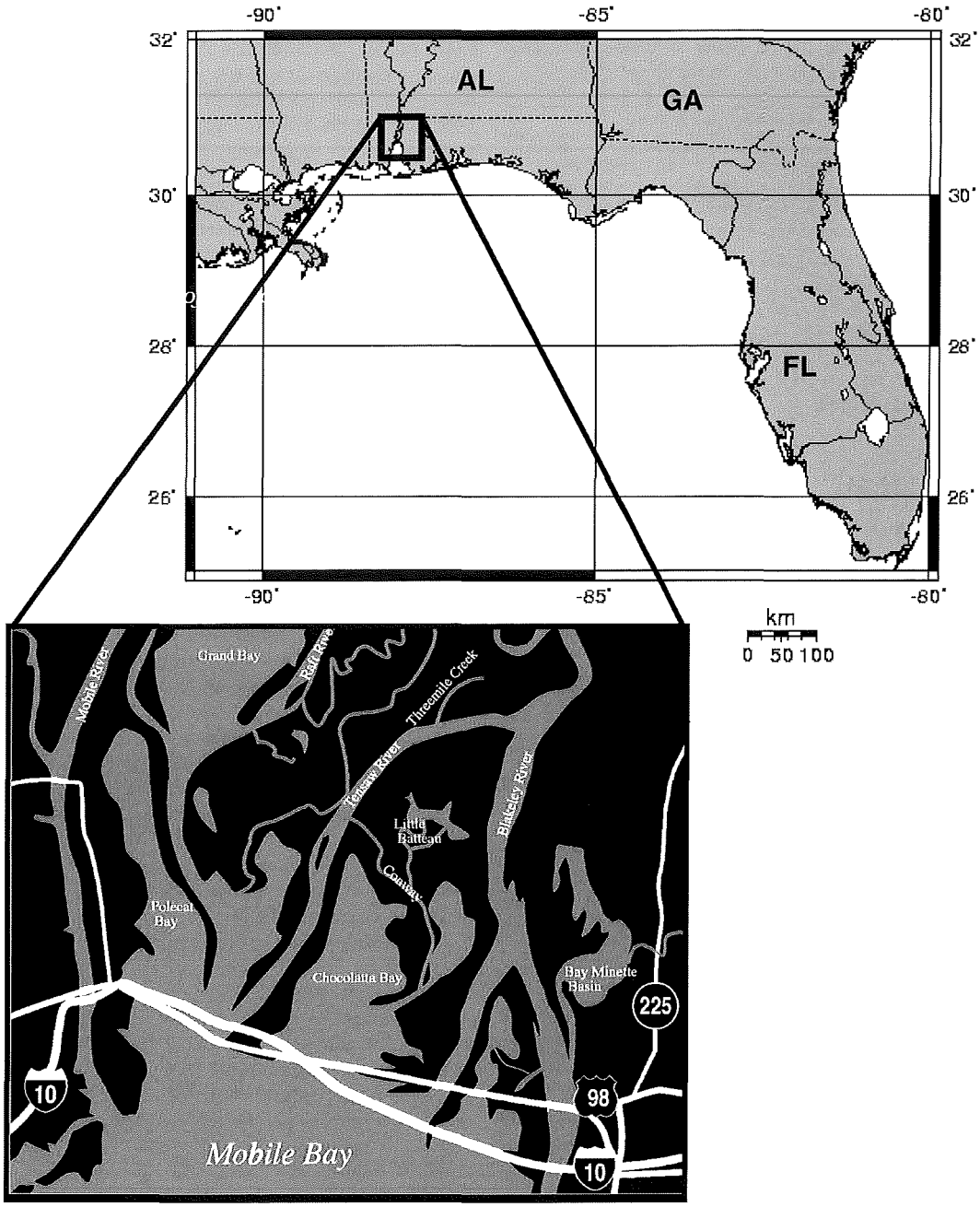

Fig. 1. Map of Mobile–Tensaw Delta, USA. Samples of SAV and invertebrates were collected from Chocolatta Bay.

of native and exotic SAV with changes in waterfowl densities over time. In addition, stable isotope analyses were used to determine if waterfowl feed on milfoil, native SAV, and their associated faunas, and we compare and contrast nutritional values of leaves of milfoil and wild celery in the Delta with the use of C/N analyses.

Methods

Waterfowl densities.—To determine if a negative relationship exists between milfoil and waterfowl abundance, we collected historical records of waterfowl density and SAV coverage for the Delta. The records from three separate waterfowl surveys were found. The oldest survey,

TABLE 1. Waterfowl species identified in mid-winter aerial surveys by the Alabama Wildlife and Freshwater Fisheries Department.

Waterfowl in Lower Mobile Delta	
Common Name	Species
Wood duck	*Aix sponsa*
Mottled duck	*Anas fulvigula*
Mallard	*Anas platyrhynchos*
Pintail	*Anas acuta*
Blue-winged teal	*Anas discors*
Green-winged teal	*Anas crecca*
Shoveler	*Anas clypeata*
Gadwall	*Anas strepera*
Widgeon	*Anas americana*
Ring-necked duck	*Aythya collaris*
Redhead	*Aythya americana*
Canvasback	*Aythya vallisineria*
Greater scaup	*Aythya mania*
Lesser scaup	*Aythya affinis*
Ruddy duck	*Oxyura jamaicensis*
Coot	*Fulica americana*

conducted by Leuth (1963) from 1939 to 1949, provided waterfowl counts and inventories made from either a boat or plane during migrations. The second survey period, from 1952 to 1978, was reported by Beshears in a 1979 symposium on natural resources in the Mobile Estuary, Alabama, although the methods used in this survey were not provided. The most complete surveys were conducted by the Alabama Wildlife and Freshwater Fisheries Department (AWFFD) from 1958 onwards. These surveys used aerial flyovers of the Delta in January to count waterfowl. Because this was the only study that separated counts by species, we standardized comparisons by pooling the 16 species of waterfowl recorded into a single estimate of waterfowl density (species list in Table 1).

Because methods used to collect these data were not standardized among studies, the data sets were analyzed separately. We assumed that methods used to count waterfowl in each survey remained constant over the duration of each survey. Because the AWFFD report indicated a change in survey personnel in 1988, these data were partitioned accordingly (1958–1986 and 1988–2004), and these components were analyzed separately. A simple linear regression of total waterfowl density on year was conducted to evaluate long-term changes in waterfowl density. A P value of < 0.05 was considered significant and a P value of < 0.10 was considered marginally significant in these analyses.

Historical SAV coverage.—Six SAV surveys documented abundances of both native and exotic species of SAV in the Delta (Baldwin, 1957; Lueth, 1963; Stout and Lelong, 1981; Vittor, 2003; Zolczynski, 1997; Zolczynski and Eubanks, 1990). As with the waterfowl surveys, SAV survey methods (i.e., boat versus aerial surveys) varied among studies (Stout et al., 1998) as did reporting methods (i.e., maps and/or written SAV distribution numbers). Because maps, when available, varied greatly in size, they were standardized areally to ensure consistent temporal comparisons. SigmaScanPro™ software was then used to estimate areal coverages of wild celery and milfoil, as well as total SAV coverage. In some cases milfoil or wild celery were reported in mixed SAV patches on maps. When this occurred, data were categorized as milfoil mixed or wild celery mixed. For studies that included only written data on SAV distributions, only those estimates that could be mapped were used.

These standardized estimates of native and exotic SAV coverage were reported on proportional bases (i.e., proportion of total SAV coverage contributed by wild celery, milfoil, wild celery mixed, or milfoil mixed; Table 2). Standardization allowed us to make comparisons of changes in abundances of native SAV and milfoil over time, independent of changes in total areal coverage (e.g., during drought years).

Stable isotopes.—Because gut contents reflect a consumer's last meal and not the full breadth

TABLE 2. Ratio of milfoil and wild celery bed coverage to the total SAV coverage reported that year (mono = monospecific beds; mixed = mixed beds of milfoil, wild celery, and other SAV).

	1947		1956		1980		1987		1994		2002	
	mono	mixed	mono	mixed	mono	mixed	mono	mixed	mono	mixed	mono	mixed
Vallisneria americana (wild celery)	0.14	—	0.11	0.85	0.03	0.39	0.03	0.05	0.16	0.15	0.22	0.37
Myriophyllum spicatum (Eurasian watermilfoil)	0.003	—	0.006	—	0.14	0.44	0.15	0.66	0.32	0.26	0.08	0.54

of their diet, stable isotope analyses were used to evaluate the extent to which native and exotic SAV, as well as their associated fauna, contributed to the diets of waterfowl in the Delta. The use of dual stable isotope analyses (carbon and nitrogen) is a powerful approach to identifying the probable sources of food for most consumers (Peterson and Howarth, 1987; Wada et al., 1991). The isotopic signature of carbon is considered to be indicative of basal sources of nutrition for most consumers (Peterson and Fry, 1987). The isotopic signature of nitrogen can also be used to identify food sources if consumers are feeding on different trophic levels within a region because the nitrogen stable isotope is enriched by 3–4% with each trophic level (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Owens, 1987; Vanderklift and Ponsard, 2003). Incorporation of such analyses in mixing models allowed us to estimate the probable contribution of known food sources to waterfowl diets (Phillips, 2001; Phillips and Gregg, 2001, 2003).

Waterfowl collection.—Waterfowl shot by hunters in the lower Delta in the 2003–04 season were used in this analysis. Waterfowl numbers were low during this study, and tissue collections were limited to three species of waterfowl [*Anas strepera*, gadwall (n = 2); *Anas fulvigula*, mottled duck (n = 1); and *Aix sponsa*, wood duck (n = 2)]. Muscle tissue was taken from the legs of waterfowl and prepared for analysis by grinding it (dried at 60 C for 24 hr) into a fine powder with a grinding mill.

Mottled ducks, wood ducks, and gadwalls feed primarily on aquatic plants, but are also reported to ingest animals, including insects, crustaceans, mollusks, and some fish (Bent, 1923, 1925; Beckwith and Hosford, 1957; Jarosz, 1960; Hester and Dermid, 1973; Terres, 1980; Ringelman, 1990). Both mottled and wood ducks are resident waterfowl; therefore their isotopic signatures should be reflective of feeding within the Delta. In the case of gadwalls, migration should have occurred in the fall, leaving sufficient time for assimilation of isotopic signatures of locally consumed foods prior to the winter opening of hunting season.

Food source collection.—To assess contributions of the dominant native and exotic SAV to the diets of the waterfowl, samples of both *Myriophyllum spicatum* and *Vallisneria americana* were collected by hand from Chocolatta Bay (30°40′N, 87°55′W; Fig. 1) in December 2003. In addition, numerically abundant epifaunal invertebrates (amphipods, *Gammarus* sp.; grass shrimp, *Palaeomonetes* spp.; and snails, *Neritina usnea*) were collected from the grass samples (Chaplin, 2001). Snails were removed from their shells before processing. Shrimp and amphipods were processed whole. Both the SAV and invertebrates were rinsed with distilled water, dried at 60 C for 24 hr, and then ground into a powder for stable isotope analysis.

Stable isotope analysis.—Samples were sent to the University of California–Davis Stable Isotope Facility for analysis. A continuous-flow isotope ratio mass spectrometer (IRMS) (Europa hydra 20/20) was used to determine the carbon and nitrogen isotope ratios in samples. Isotopic composition was quantified relative to standards (carbon = Pee Dee Belemnite; nitrogen = air). Stable isotope abundances are expressed as ratios of the two most abundant isotopes in the sample to their respective standards and are denoted by del (δ).

$$\delta X(‰) = [(R_{sample}/R_{standard}) 1] \times 1000$$

where X is either ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Higher values denote a greater proportion of the heavy isotope. Because differences in ratios in samples and standards are very small, results are expressed as parts per thousand (‰).

IsoSource version 1.1 software (provided by the U.S. Environmental Protection Agency) was used to estimate the probable contributions of food sources to waterfowl diets (Ben-David and Schell, 2001; Phillips, 2001; Phillips and Gregg, 2001, 2003). Because of trophic-level isotopic fractionation of nitrogen (Peterson and Howarth, 1987), 3‰ was subtracted from nitrogen isotope signatures in the waterfowl before running the model (Vanderklift and Ponsard, 2003). Carbon fractionation is assumed to be close to zero (Peterson and Fry, 1987); therefore, no adjustment was made.

Nutritional value.—Because herbivore feeding preferences are hypothesized to be determined by the nutritional content of their foods (expressed as either C/N or nitrogen content), the nutritional values of *Myriophyllum spicatum* and *Vallisneria americana* were assessed within the study area. Specifically, plants higher in nitrogen and lower in structural carbon content (low C/N values) are hypothesized to be preferred by herbivores (Goecker et al., 2005). To determine if there were significant differences in the nutritional content of *M. spicatum* and *V. americana*, proportions of carbon and nitrogen in these plants were measured.

Milfoil and wild celery shoots (n = 3) were

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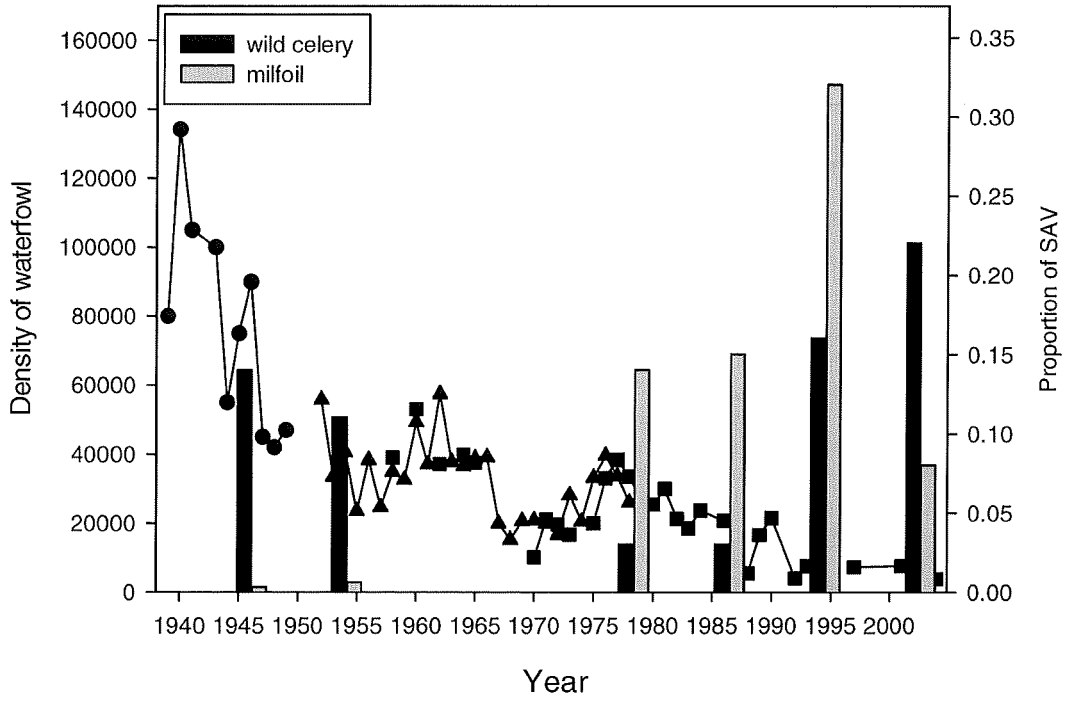

Fig. 2. Line graphs represent the total number of waterfowl reported from 1939–2004 in the Mobile–Tensaw Delta. Circles represent data reported by Lueth (1963), 1939–1949. Triangles represent data reported by Beshears (1979), 1952–1978. Squares represent data collected by Alabama Wildlife and Freshwater Fisheries Department (1956–2004). The bar graph represents the relative proportions of milfoil and wild celery reported from SAV surveys conducted in the Delta [1947, Lueth (1963); 1956, Baldwin (1957); 1980, Stout and LeLong (1981); 1987, Zolczynski and Eubanks (1990); 1994, Zolczynski (1997); and 2002, Vittor (2003)].

collected from Chocolatta Bay, dried at 60 C for 24 hr, and ground into a powder; then the C and N contents were measured with the use of a Costech CNS analyzer. A one-way ANOVA was used to compare the arcsin-transformed percent nitrogen, carbon, and C/N ratios of wild celery and milfoil.

Results

Long-term data set.—Although the proportion of the variance in waterfowl counts explained by separate regression analyses varied greatly among surveys, results showed significant declines in waterfowl density over time (Fig. 2). In surveys done by Lueth (1963), a significant decrease in waterfowl populations occurred from 1939–49 ($r^2 = 0.57$; F = 10.77; df = 9; $P = 0.01$). Similar analysis of Beshear's (1979) data, indicated that these decreases continued through the late 1970s ($r^2 = 0.19$; F = 5.86; df = 26; $P = 0.02$). The AWFFD survey conducted between 1958 and 1986 showed that this decreasing trend continued through the mid 1980s ($r^2 = 0.32$; F = 8.47; df = 19; $P = 0.01$) and into the present ($r^2 = 0.29$; F = 3.31; df = 9; $P = 0.10$).

Historical SAV coverage.—Lueth (1963) showed that milfoil coverage was low, only ~ 0.3% (~ 0.17 km^2) of surveyed SAV habitats in 1947, and was limited to a small embayment on the eastern side of the Delta (Bay Minette Basin; Fig. 1). Wild celery coverage, in contrast, was substantial (~ 7.8 km^2), mostly in the largest basin in the Delta, Chocolatta Bay, where it covered ~ 14% of surveyed SAV habitats (Table 2). Milfoil coverage remained low in the Delta over the next 10 yr (0.18 km^2), covering ~ 0.6% of SAV habitats surveyed and was still limited to Bay Minette Basin (Baldwin, 1956). Wild celery remained wide spread, covering 11% of the SAV habitats surveyed as well as being present in 85% of the mixed beds examined (Baldwin, 1957).

Stout and Long (1981) and Stout et al. (1982) documented the spread of milfoil to the southernmost reaches of the Delta in the

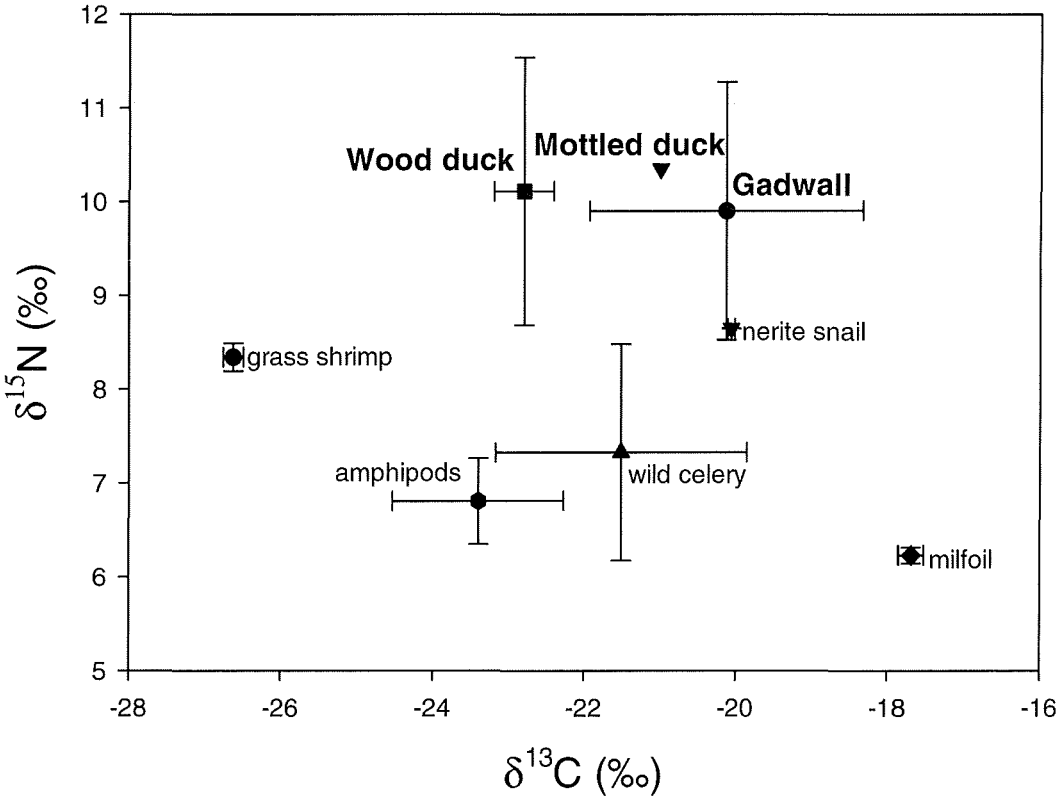

Fig. 3. Mean (± SE) carbon and nitrogen stable isotope signatures for gadwall (n = 2), mottled duck (n = 1), and wood duck (n = 2) and their potential food sources (n = 3 for each) in the Delta.

late 1970s. In these studies, milfoil comprised over 50% of surveyed SAV beds. Wild celery covered ~ 40% of surveyed SAV beds. A subsequent survey by Zolczynski and Eubanks (1990) conducted in 1987 found that the spread of milfoil continued, with its coverage exceeding 80% of all the Delta's SAV habitats. Wild celery coverage declined and by the late 1980s covered just 7% of the SAV beds.

Milfoil coverage declined to < 60% of all surveyed SAV habitats in early 1990s, and wild celery coverage increased to ~ 30% (Zolczynski, 1997). This shift in dominance continues to this day, as a recent survey (Vittor, 2003) showed that 2002 milfoil coverage declined to ~ 8% of surveyed SAV habitats. Wild celery coverage has remained low, covering over 22% of SAV habitats surveyed (Table 2; Fig. 2).

Stable isotope analyses.—Nitrogen signatures in the waterfowl obtained for this study were similar to one another (~ 10‰). As such, collected waterfowl were feeding on foods found on approximately the same trophic levels in the Delta. Carbon signatures in their tissues, however, differed from one another (ranging from −22.79 to −20.13‰), indicating that they were feeding on different food (Fig. 3; Table 3). Among the possible foods for these waterfowl, isotopic signatures (both carbon and nitrogen) of milfoil and wild celery were well separated (Fig. 3). Grass shrimp were most depleted in $\delta^{13}C$ and milfoil was the most enriched. Milfoil was most depleted in $\delta^{15}N$ and nerite snails were the most enriched (Fig. 3; Table 3).

The results provided by the mixing model indicate that milfoil, wild celery, and animals living on these SAV species were all important sources of food for waterfowl. The probable contribution of milfoil to waterfowl diets ranged from 33–73% for gadwall, to 6–53% for mottled ducks, to 0–34% for wood ducks. Model analysis also showed that the probable contributions of wild celery to the diets of these waterfowl was similar, ranging from 0–66% for gadwall, to 0–87% for mottled ducks, to 0–50% for wood ducks.

Epifaunal invertebrates were also important food sources for waterfowl (Figs. 4–6). The

TABLE 3. $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) (±SE) values for waterfowl and their possible food sources.

Waterfowl	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Anas strepera (gadwall)	2	−20.12 ± 1.80	9.91 ± 1.38
Anas fulvigula (mottled duck)	1	−21.01	10.36
Aix sponsa (wood duck)	2	−22.79 ± 0.39	10.11 ± 1.43
Possible Food sources [Scientific name (common name)]			
Plant			
Myriophyllum spicatum (Eurasian watermilfoil)	3	−17.69 ± 0.17	6.23 ± 0.08
Vallisneria americana (wild celery)	3	−21.51 ± 1.66	7.33 ± 1.15
Crustaceans			
Gammarus sp. (amphipods)	3	−23.40 ± 1.12	6.81 ± 0.46
Paleomonetes sp. (grass shrimp)	3	−26.63 ± 0.13	8.34 ± 0.15
Mollusks			
Neritina usnea (nerite olive)	3	−20.06 ± 0.05	8.65 ± 0.001

model estimated that amphipod contributions to the diets of gadwalls, mottled ducks, and wood ducks ranged from 0 to 38%, 0 to 46%, and 27 to 86%, respectively. Grass shrimp are important to the diets of both gadwalls (ranging from 0 to 28%), and mottled ducks (between 0 and 34%), but less so for wood ducks (between 0 and 39%). Nerite snails also contributed to the diets of gadwalls (0–24%), mottled ducks (4–41%), and wood ducks (0–20%).

Nutritional value.—Milfoil contained significantly less nitrogen ($F = 123.95$; df = 1; $P < 0.01$) and more carbon than wild celery ($F = 778.9$; df = 1; $P < 0.01$) (Fig. 7). Accordingly, C/N ratios for wild celery in this study were significantly lower than that of milfoil ($F = 146.67$; df = 1; $P < 0.01$).

DISCUSSION

Surveys used in this evaluation strongly show that waterfowl populations have declined in the Delta over the past 60 yr. This decline is similar to those observed in other estuaries in North America (Perry and Deller, 1996). Although many hypotheses have been advanced to explain the loss of waterfowl in this delta, replacement of native species of SAV by exotic SAV has been considered to have played a key role in their decline in the Mobile–Tensaw Delta (Beshears, 1979; Borom, 1979; Stephenson et al., 1984).

Although milfoil rapidly expands once it becomes established, its dominance does not persist for long (Smith and Barko, 1990). For reasons that remain unknown, its coverage declined from 58% of the SAV in 1994 (Zolczynski, 1997) to only 40% of the SAV coverage in 2002 (Vittor, 2003) in the Delta. Large intervals between surveys and differing methodological approaches to documenting SAV coverage among studies may account for the wide variance in estimates. As such, some caution should be used in interpreting shifts in milfoil and wild celery abundances in the Delta. Clearly milfoil abundance has varied greatly over time and these fluctuations in milfoil coverage were not matched by similar fluctuations in waterfowl density, as would have been expected if these two variables were tightly correlated. This alone suggests that factors other than milfoil proliferation have contributed to the historical decline in waterfowl density in the Delta.

The results from the mixing model support the contention that the proliferation of milfoil alone is not responsible for decreasing waterfowl density. Model results show evidence that both native and exotic SAV figure prominently in the diets of the waterfowl studied here, with milfoil representing 0–73% of diet and wild celery representing 0–87%. This is despite the fact that wild celery was found to have greater nitrogen content and a lower C/N ratio than milfoil (this study). If these ducks preferred wild celery over milfoil, large differences in diets should have been seen rather than the high degrees of overlap estimated by the model.

Compensatory feeding (i.e., consuming greater quantities of low nutritional quality foods to meet nutritional requirements) may be one reason for the high percentage of milfoil in waterfowl diets. Alternatively, the consumption of low nutritional quality foods could be supplemented by the consumption of protein-rich invertebrates living in the SAV. Based

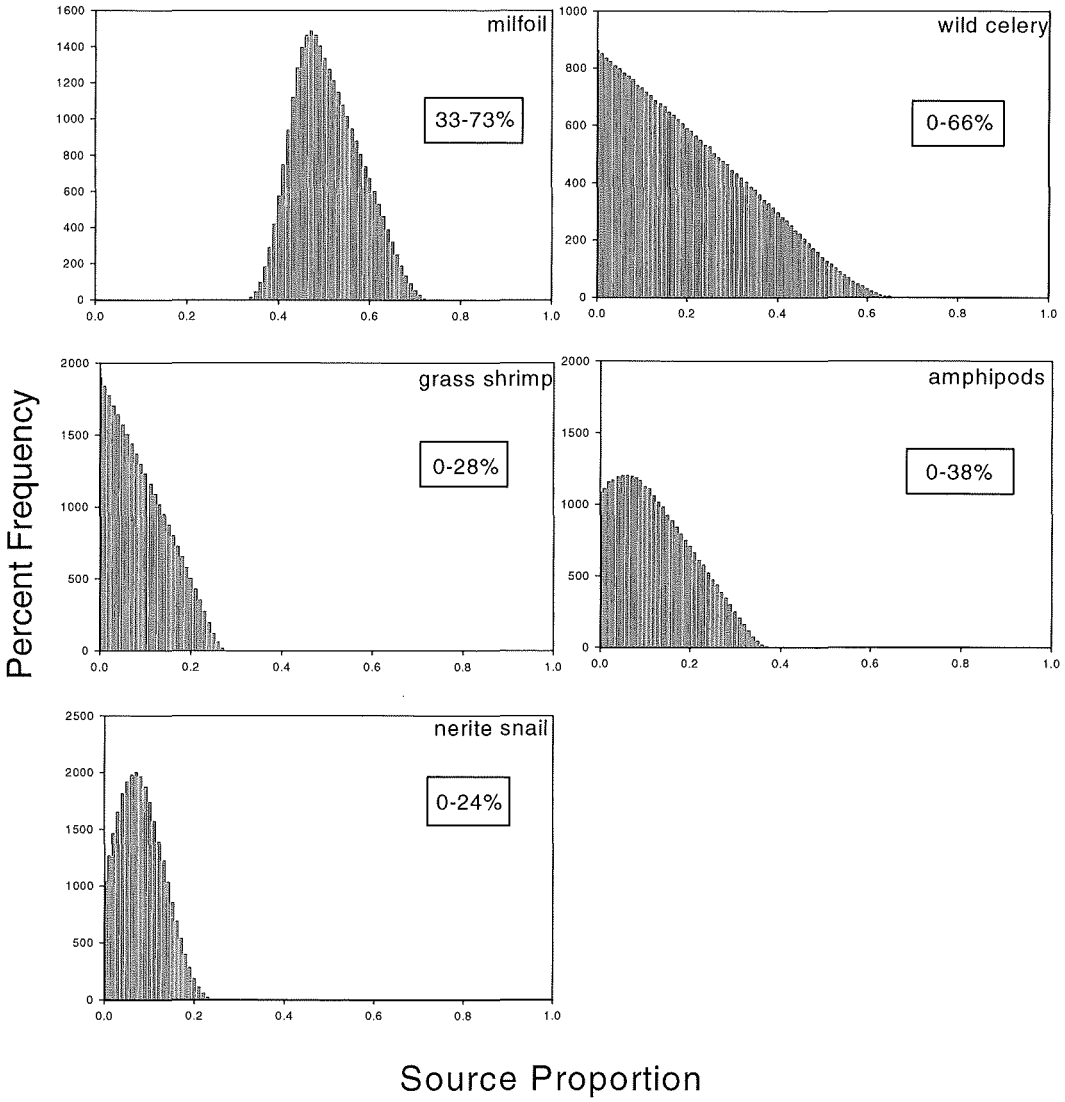

Fig. 4. Distribution of possible food sources for gadwall. Percentages report the probable contributions of the individual food sources to gadwall diets.

on the model analysis, both invertebrates, particularly amphipods, and SAV were important to waterfowl diets. Locally, milfoil supports extremely high secondary production of up to 1,250 g AFDW/m^2/yr, of which ~ 1,070 g of this production comes from amphipods (Chaplin, 2001). Comparatively, only 17 g AFDW/m^2/yr of amphipod production was estimated for wild celery (Chaplin, 2001). Ringelman (1990) reported that the diet of the gadwall in the fall and winter consists of 95% plant material including milfoil, but in the spring and summer months half of their diet changes to small invertebrates such as shrimp.

Other studies have produced findings that are similar to those reported here. A study in Guntersville Reservoir, Alabama, for example, has reported that native SAV and milfoil contribute equally to the diets of ducks and coots (Benedict and Hepp, 2000). Perry and Deller (1996) reported that coots and gadwalls fed predominantly in areas dominated by milfoil in Chesapeake Bay. When SAV abundances were low, coots were observed to dive in deeper water to feed on milfoil (McKnight and Hepp, 1998). Even so, the spread of exotic SAV species has been shown to lead canvasbacks to change their migration routes to find and feed

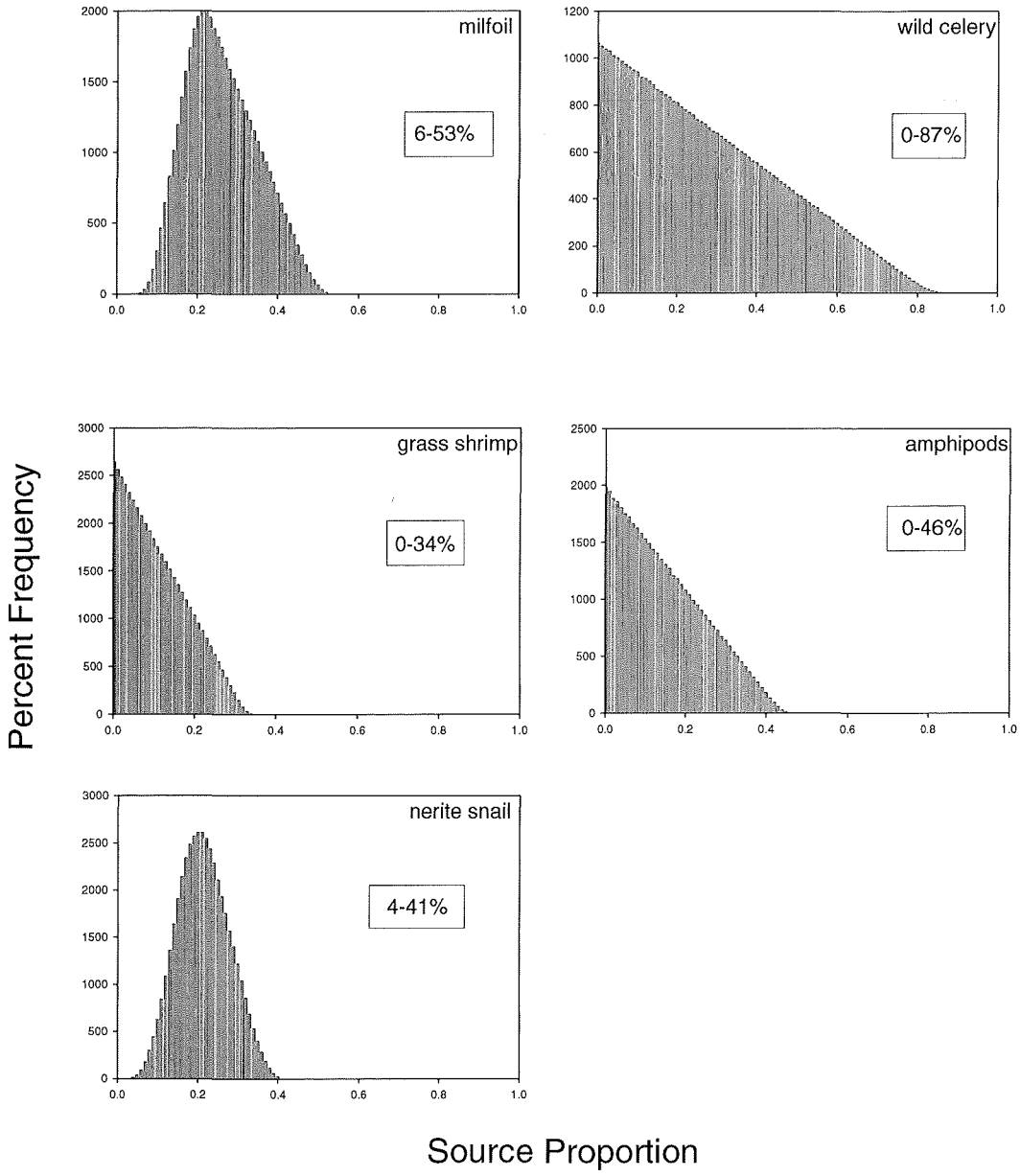

Fig. 5. Distribution of possible food sources for mottled duck. Percentages report the probable contributions of the individual food sources to mottled duck diets.

on *Vallisneria* and that 75% of the canvasback population uses this food resource along three eastern flyways (Korschgen et al., 1988).

Stable isotope analysis of three common waterfowl species collected in the Delta and lack of solid correlative data based on comparisons of historical SAV and waterfowl records do not support the contention that the spread of milfoil has had a large negative effect on waterfowl populations in the Delta. There are other alternative factors that could have played a leading role in the declines of waterfowl populations in the Mobile–Tensaw Delta. These include: (1) loss of breeding habitats (Dindo, 2003); (2) meteorological events (i.e., warmer winters, drought; Beshears, 1979); (3) intense hunting (Baldwin, 1957); (4) increasing levels of contaminants (lead poisoning, herbicides; Digiulio and Scanlon, 1984; Peachey, 2003); (5) drowning of fields (Beshears, 1979; Perry

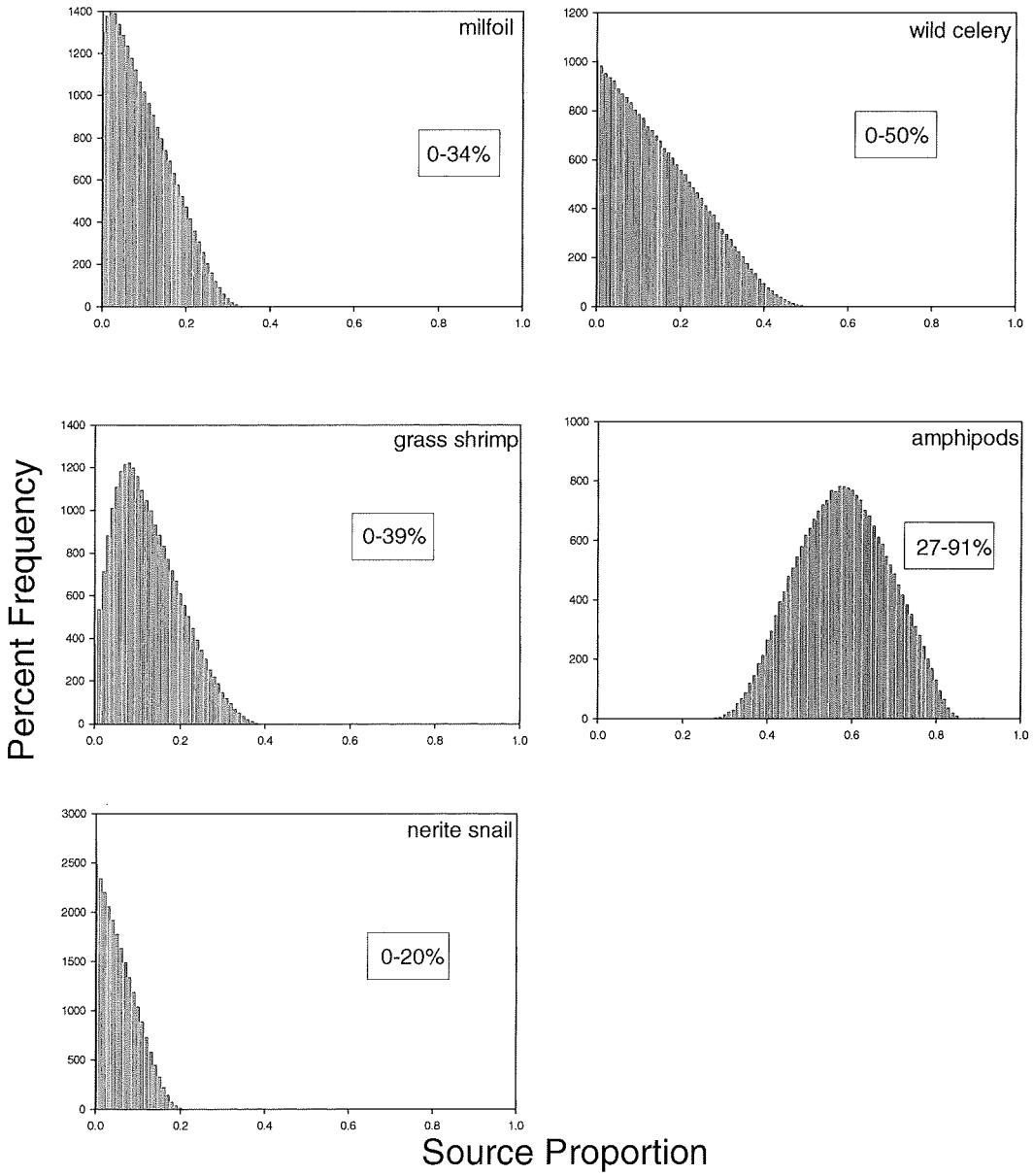

Fig. 6. Distribution of possible food sources for wood duck. Percentages report the probable contributions of the individual food sources to wood duck diets.

and Deller, 1996); and (6) increased boating activity (Perry and Deller, 1996; Mullins et al., 2002; Formicella et al., 1999).

In conclusion, midwinter surveys have provided a valuable resource for detecting shifts in the size of waterfowl populations. However, the underlying causes of these changes remain poorly understood. To understand the importance of various factors in the decline of waterfowl populations, further studies need to incorporate rigorous experimental evaluations encompassing many of the suspected factors. Such studies would provide data that are critical to future management and conservation of waterfowl populations.

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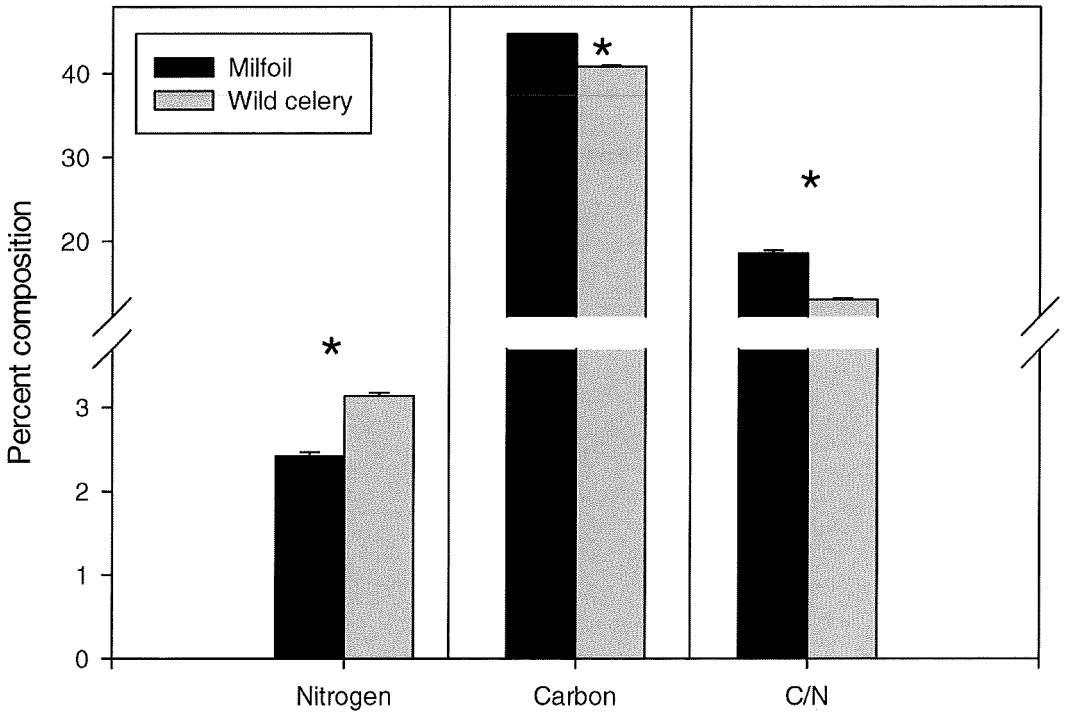

Fig. 7. Percent nitrogen and carbon composition and the carbon/nitrogen ratio (± SE) of milfoil (*Myriophyllum spicatum*) and wild celery (*Vallisneria americana*). The asterisk denotes a significant difference between milfoil and wild celery.

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