

ABUNDANCE OF WIGEONGRASS DURING WINTER AND USE BY HERBIVOROUS WATERBIRDS IN A TEXAS COASTAL MARSH

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Abstract: Wigeongrass (*Ruppia maritima*), a submerged aquatic plant inhabiting estuarine wetlands, is an important winter food for waterbirds along the Texas Gulf Coast. We examined availability of wigeongrass at Mad Island Wildlife Management Area, Texas, USA by estimating aboveground biomass from October through January, 1998–1999 and 2001–2002. We also used an enclosure experiment to determine the extent to which herbivory by waterbirds was responsible for depletion of wigeongrass. Aboveground biomass of wigeongrass declined an average of 189 g m⁻² and 71 g m⁻² between October and January each year. Aboveground biomass declined at a higher rate among plots exposed to herbivory compared to enclosures, and the loss of biomass attributable to foraging by waterbirds was 19%. In 1998, counts of gadwalls (*Anas strepera*), American wigeons (*A. americana*), and American coots (*Fulica americana*) using study ponds peaked in November and then followed a declining trend similar to availability of wigeongrass, suggesting that as wigeongrass was depleted herbivorous waterbirds moved to other habitats where food was more available.

Key Words: enclosure, food availability, herbivory, *Ruppia maritima*, waterfowl

INTRODUCTION

Interest in conserving and managing wetlands to produce food for migrating and wintering waterbirds increased rapidly in North America during the 1980s and 1990s. However, most research to date has concentrated on the production and use of seeds and asexual propagules (e.g., tubers, turions, rhizomes, etc.) as the primary plant food source in wetlands. Less attention has been directed toward understanding the potential for foliage production by selected aquatic plants as food for waterbirds. The leaves and stems of some submerged aquatic plants are relatively high in protein and important foods of many waterbird species adapted to a diet high in fiber (Knapton and Pauls 1994, McKnight and Hepp 1998).

Along the Texas Gulf Coast, wigeongrass (*Ruppia maritima* L.; Kantrud 1991) is an important submerged aquatic plant that provides forage for migrating and wintering waterbirds. The leaves and stems of wigeongrass are commonly consumed by American wigeons (*Anas americana* Gmelin, hereafter called wigeons; Landers et al. 1976, Swiderek et al. 1988), gadwalls (*A. strepera* L.; Paulus 1982), and American coots (*Fulica americana* Gmelin, hereafter called coots; Prevost et al. 1978). It occurs widely along the coasts of North America and is capable of

inhabiting shallow water in high-salinity bays and brackish wetlands. In the subtropical climate of the Gulf Coast, wigeongrass is capable of two annual peaks in biomass (Pulich 1985, Cho and Poirrier 2005), once in May and again in October just as migrating waterbirds begin to arrive. Annual production of wigeongrass is well documented in estuarine systems of the western Gulf Coast (Joanen and Glasgow 1965, Pulich 1985, Cho and Poirrier 2005); however, the amount of wigeongrass foliage available when waterbirds arrive at coastal wintering grounds in Texas is unknown. Further, there is a lack of information on the use of wigeongrass beds as foraging habitat by waterbirds wintering in Texas. Assessment of food production in Texas coastal marshes is needed by the Gulf Coast Joint Venture (Wilson and Esslinger 2002) to evaluate success of management actions and estimate carrying capacity of foraging habitats as part of implementing the North American Waterfowl Management Plan (Wilson 2003).

During 1998 and 2001, we investigated abundance of wigeongrass in a complex of brackish ponds at Mad Island Wildlife Management Area (MIWMA), Texas, USA. Specific objectives were to 1) estimate aboveground biomass of wigeongrass available to waterbirds in October 1998 and 2001; 2) estimate the amount of aboveground biomass lost during winter;

and 3) determine the extent of the loss that was attributed to exploitation by waterbirds. In addition, we observed abundance of herbivorous waterbirds (gadwalls, wigeons, and coots) between November 1998 and January 1999 to assess the relationship between availability of wigeongrass and waterbird use of brackish ponds at MIWMA.

STUDY AREA

The 2,940 ha MIWMA is located in the Matagorda Bay estuary system on the central coast of Texas, a major wintering area for waterbirds (Stutzenbaker and Weller 1989). Primary wetland habitats (1,722 ha) at MIWMA were freshwater (42%) and brackish (38%) emergent marshes, freshwater and brackish ponds (16%), and seasonally flooded impoundments (4%) during this study. Salinity of brackish wetlands at MIWMA ranges from < 1 to 20 ppt during the year, but is typically < 15 ppt during the growing season. We collected data from five (3–4 each year) shallow brackish ponds (\bar{x} = 8 ha, range = 3–21 ha) where most wigeongrass production occurred.

METHODS

Data Collection

We selected four ponds in 1998 and three ponds in 2001 for sampling in autumn and winter. Sampling was not conducted in 1999 and 2000 because below average precipitation and excessive salinities limited production of wigeongrass at MIWMA. In October, before large numbers of waterbirds arrived, we selected sample sites (n = 13 in 1998; n = 12 in 2001) at random in monoculture wigeongrass beds and clipped aboveground vegetation of wigeongrass (stems, leaves, and seeds) within a 1-m² plot at each site. Immediately after collecting initial samples, 1-m² exclosures (n = 40 in 1998; n = 36 in 2001) were placed randomly in wigeongrass beds. Exclosures were square fences (50–60 cm high) constructed of rigid wire mesh (2.5 cm mesh), secured to the surface of the sediment with steel rods. In November, we visited a random subset of exclosures (n = 13 in 1998; n = 12 in 2001) and clipped aboveground vegetation of wigeongrass within each exclosure and within a 1-m² open plot immediately adjacent to each exclosure. We returned to a new random subset of exclosures in December (n = 13 in 1998; n = 12 in 2001) and January (n = 14 in 1999; n = 12 in 2002) and repeated the sampling procedure each month. Clipped samples of wigeongrass were taken to the laboratory, washed to remove algae and debris, and

dried in an oven (50°C) to a constant mass. After drying, samples of aboveground vegetation (including seeds) were weighed to the nearest 0.5 g. We considered herbivorous waterbirds as the primary forager on wigeongrass because muskrat (*Ondatra zibethicus*) and nutria (*Myocastor coypus*) were absent from brackish ponds at MIWMA (personal observations) and fish seldom consume large amounts of wigeongrass (Kantrud 1991).

A waterbird census was conducted three to four times each month in November and December 1998 and January 1999 on the ponds sampled for wigeongrass. Because hunting is allowed at MIWMA on a limited basis, we scheduled waterbird counts on days when the area was closed to hunting. We counted numbers of wigeons, gadwalls, and coots because they are herbivores, feeding primarily on aboveground parts of submerged aquatic plants, they frequently use the coastal ponds at MIWMA, and they accounted for nearly half (\bar{x} = 48%, n = 17 counts) of all waterbirds counted on wigeongrass beds at MIWMA in winter 1998–1999. Observations were made from an elevated blind at different locations on land using a spotting scope. During each census period, we attempted to count birds once in the morning and again in the afternoon; and averaged those two counts.

Statistical Analysis

We developed an *a priori* set of candidate models (Table 1) to explain variation in aboveground biomass (*ABM*) of wigeongrass during late fall and winter. We included the effect of month (m ; October, November, December, January) in all models because monthly variation in biomass of wigeongrass is well documented (Pulich 1985, Cho and Poirrier 2005). Variation between years (y ; 1998–1999, 2001–2002) was included in models as an additive and interactive effect with month. The most complex model (full) considered represented the full extent of temporal variation in the data (y , m , $y*m$). We used Akaike's information criterion (AIC_c ; corrected for small sample size) to select the most parsimonious model (Burnham and Anderson 2002). The model with the lowest AIC_c is the best approximating model given the data. We computed ΔAIC_c (the increase over the lowest observed value of AIC_c) to compare and rank the candidate models. Generally, models with $\Delta AIC_c \leq 2$ have substantial empirical support, whereas models with $\Delta AIC_c = 4-7$ have limited support, and models with $\Delta AIC_c > 10$ have essentially none (Burnham and Anderson 2002:70). We used the best model and the ESTIMATE option of PROC GLM (SAS Institute 2004) to estimate

Table 1. Candidate models for explaining variation in aboveground biomass (g m^{-2}) of wigeongrass during late autumn and winter in 1998–1999 and 2001–2002 at Mad Island Wildlife Management Area, Texas, USA. Models were ranked using Akaike's information criterion corrected for small sample size (AIC_c); ΔAIC_c is the increase in AIC_c over the lowest observed value of AIC_c , w_i is the model weight, and K is the number of parameters.

Model structure ^a	K	AIC_c	ΔAIC_c	w_i
<i>ABM</i> (<i>y m y*m</i>)	9	772.12	0.00	1.00
<i>ABM</i> (<i>y m</i>)	6	792.58	20.45	0.00
<i>ABM</i> (<i>m</i>)	5	792.91	20.79	0.00

^a *ABM* is aboveground biomass; *y* is year (1998–1999 or 2001–2002); *m* is month (October, November, December, January); and * indicates the interaction between model parameters.

effects of selected variables on aboveground biomass of wigeongrass in late fall and winter.

We used a general linear model (PROC GLM) to assess the influence of herbivory on wigeongrass with a single interactive effect between month and the enclosure experiment. We used the ESTIMATE option of PROC GLM to estimate effects of the enclosure experiment on aboveground biomass of wigeongrass. We acknowledge that annual variation also may interact with waterbird herbivory; however, we were interested in examining the influence of herbivory on wigeongrass averaged across years. All estimates generated from the entire analysis are reported as arithmetic means unless noted otherwise.

RESULTS

Among three candidates (Table 1), the best model included the effects of year, month, and their interaction. The remaining models were more than 20 AIC_c units (Table 1) from the best model. Thus, we used the top ranked model to predict effects of selected variables on biomass of wigeongrass.

Estimates from that model indicated that aboveground biomass of wigeongrass varied among months within each year. In October before large numbers of waterbirds arrived, mean biomass at MIWMA was 202 ± 22 (SE) g m^{-2} in 1998 and 107 ± 15 g m^{-2} in 2001 (Table 2). By January, mean biomass was < 1 g m^{-2} in 1999 and 11 ± 8 g m^{-2} in 2002 (Table 2). Between October and January, the average decrease (least-squares means) in wigeongrass was 189 ± 17 g m^{-2} in the first year and 71 ± 18 g m^{-2} in the second year.

Between October and January, estimates (least-squares means) from our herbivory model indicated that aboveground biomass decreased 123 ± 12 g m^{-2} inside enclosures and 151 ± 12 g m^{-2} among plots exposed to foraging by waterbirds ($F_{6,170} = 36.15$, $P < 0.001$; Table 3). The loss of biomass attributable to foraging by waterbirds was 19% between October and January. The largest decline in wigeongrass during the enclosure experiment was between October and November (Table 3). On average (least-squares means), aboveground biomass decreased 65 ± 12 g m^{-2} inside enclosures and 87 ± 12 g m^{-2} on adjacent control plots between October and November. The loss of biomass attributable to foraging by waterbirds was 25% between October and November.

During the first year of the study, abundance of herbivorous waterbirds using coastal ponds at MIWMA exhibited a trend similar to aboveground biomass of wigeongrass. Between November 1998 and January 1999, the number of wigeons, gadwalls, and coots declined at the study ponds (Figure 1). The monthly average abundance for the three species combined peaked in November at 396 (range 247–701) and dropped 96% by January ($\bar{x} = 15$, range 4–31). The peak in abundance of herbivorous waterbirds preceded a 34% decline in wigeongrass aboveground biomass (Figure 1, Table 2).

Table 2. Mean aboveground biomass (g m^{-2}) of wigeongrass from October to January in 1998–1999 and 2001–2002 at Mad Island Wildlife Management Area, Texas, USA.

Year	Month	n	\bar{x}	SE	95% LCL	95% UCL
1998–1999						
	October	13	202.31	21.58	155.28	249.34
	November	13	69.69	6.71	55.07	84.31
	December	13	13.38	6.16	−0.04	26.81
	January	14	0.96	0.48	−0.08	2.00
2001–2002						
	October	12	107.33	14.72	74.93	139.73
	November	12	69.50	16.92	32.26	106.74
	December	12	36.33	9.97	14.39	58.28
	January	12	10.92	7.78	−6.21	28.04

Table 3. Mean aboveground biomass of wigeongrass (g m^{-2}) for each month in plots unprotected and protected from foraging by waterbirds during 1998–1999 and 2001–2002 at Mad Island Wildlife Management Area, Texas, USA. Initial samples collected in October represented a baseline estimate of biomass, and samples from the enclosure experiment were not collected until November.

Month	Enclosure experiment					
	Outside			Inside		
	n	\bar{x}	SE	n	\bar{x}	SE
October	25	156.72	16.21	-	-	-
November	25	69.60	8.64	25	92.00	8.77
December	25	24.40	6.10	25	48.70	4.83
January	26	5.56	3.65	26	33.23	4.61

DISCUSSION

At MIWMA, mean aboveground biomass of wigeongrass in October 1998 and 2001 (202 and 107 g m^{-2} , respectively) was similar to previous estimates from the west Gulf Coast region. Dunton (1990) reported mean shoot biomass in early autumn nearly reached 200 g m^{-2} in San Antonio Bay, Texas, approximately 80 km southeast of MIWMA. More recent estimates of aboveground biomass in autumn were between 100 and 150 g m^{-2} among four sites in Lake Pontchartrain, Louisiana (Cho and Poirrier 2005). However, availability of wigeongrass in autumn can be reduced by competition from other submerged aquatic plants and unfavorable weather. At two sites on the south Texas coast, where wigeongrass coexisted with shoalgrass (*Halodule wrightii* Aschers.), aboveground biomass of wigeongrass in autumn (Pulich 1985) was less than estimates at MIWMA. Cho and Poirrier (2005)

reported reduced biomass in autumn at one sample site because of wave action associated with strong summer storms. At MIWMA, drought conditions persisted during the growing season in 1999 and 2000 so that by October, wigeongrass was nearly absent from ponds (personal observations).

Our enclosure experiment indicated wigeongrass exposed to waterbird foraging decreased at a higher rate compared to wigeongrass inside enclosures, with foraging representing 19% of total biomass lost between October and January. The greatest effect of foraging by waterbirds occurred between October and November (25% biomass loss). Verhoeven (1980) reported exploitation of *Ruppia cirrhosa* (Petag.) Grande by Eurasian coots (*Fulica atra* L.) contributed up to 22% of total biomass loss from a coastal pond in The Netherlands. However, enclosure experiments in brackish impoundments of South Carolina did not detect an effect of foraging on wigeongrass availability (Prevost *et al.* 1978, Swiderek *et al.* 1988). Prevost *et al.* (1978) observed a dense growth of algae covering wigeongrass beds by autumn, which reduced biomass both inside and outside enclosures. Dunton (1990) also documented a negative relationship between wigeongrass and algae at two estuaries in south Texas; where algae reached two times the biomass of wigeongrass during summer, wigeongrass was absent during winter (Dunton 1990). Competition from algae can have a negative impact on seagrasses by shading plants and retarding growth (Hauxwell *et al.* 2001, Hays 2005). However, at MIWMA, algal biomass in vegetation samples was negligible (unpublished data).

Most (81%) of the biomass lost between October and January could not be explained by waterbird foraging. A substantial reduction (56%) in aboveground biomass of wigeongrass occurred between October and November, of which only 25% of the loss was attributed to foraging by waterbirds. Wigeongrass in the western Gulf Coast naturally

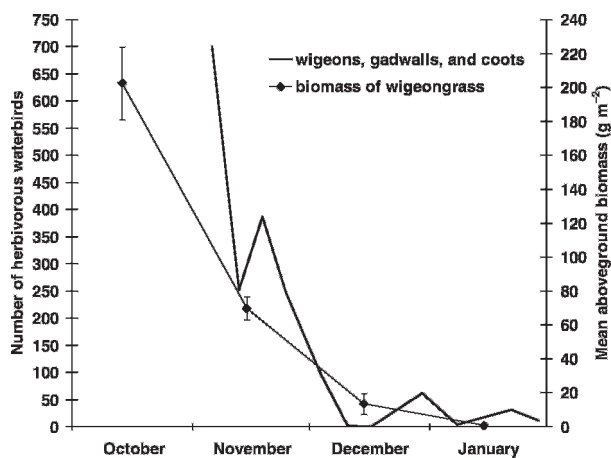


Figure 1. Relationship between number of herbivorous waterbirds and mean aboveground biomass of wigeongrass (g m^{-2} , SE) in four brackish ponds at Mad Island Wildlife Management Area, Texas, USA, October 1998 to January 1999.

declines via senescence during winter (Dunton 1990, Cho and Poirrier 2005) with shorter day length and cooler water temperatures. In addition, hydrology in the Matagorda Bay system is substantially influenced by wind driven tides, and during winter it is not uncommon for submerged vegetation of associated brackish ponds to be completely exposed when northern winds prevail (Ward et al. 1980). Desiccation stress from tidal exposure can cause seasonal losses of aboveground biomass in seagrasses (Björk et al. 1999, Boese et al. 2005).

In our study, abundance of herbivorous waterbirds (gadwalls, wigeons, and coots) using brackish ponds at MIWMA peaked in November, coinciding with the period when nearly two-thirds of the initial aboveground biomass was lost. Subsequently, counts of herbivorous waterbirds observed on study ponds declined dramatically. Use of wetland habitats by migratory waterbirds during winter is generally linked to availability of food. However, hunting pressure also is an important variable in selection and use of habitats (Cox and Afton 1997). At MIWMA, hunting of waterfowl and coots was allowed 28 out of 86 days between late October 1998 and mid January 1999, and generally followed a seven-day pattern of two consecutive days of hunting followed by five days of no hunting. It is likely that disturbance from hunting also influenced use of wigeongrass beds by herbivorous waterbirds.

Exclusive of disturbance, quality of foraging habitat declines as abundance of food declines, and approaches a threshold level that limits efficient feeding. At some point, waterbirds will abandon a habitat (Reinecke et al. 1989, Nolet et al. 2006). Verhoeven (1980) observed that Eurasian coots abandoned a pond dominated by *R. cirrhosa* when above- and belowground biomass declined to 9 g m^{-2} . Counts of herbivorous waterbirds using wigeongrass beds at MIWMA were negligible in January 1999 when mean aboveground biomass reached 1 g m^{-2} .

Coastal wetland managers concerned with providing food resources for herbivorous waterbirds should try to maintain a complex of brackish and freshwater wetlands to provide alternative sources of submerged aquatic vegetation. As availability of wigeongrass is depleted from brackish wetlands, foraging waterbirds can switch to adjacent freshwater habitats where food may be more abundant. In addition, biologists interested in modeling carrying capacity of coastal marsh as winter foraging habitat for waterbirds need to consider factors that may reduce overall availability of submerged aquatic vegetation.

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