LESSER SNOW GEESE (*ANSER C. CAERULESCENS*) AND AMERICAN THREE-SQUARE BULRUSH (*SCIRPUS AMERICANUS*) ON THE FRASER AND SKAGIT RIVER DELTAS

by

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LESSER SNOW GEESE (ANSER C. CAERULESCENS) AND
AMERICAN THREE-SQUARE BULRUSH (SCIRPUS AMERICANUS)
ON THE FRASER AND SKAGIT RIVER DELTAS

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Abstract

The number of Lesser Snow Geese (*Anser c. caerulescens*) overwintering on the Fraser and Skagit river deltas varied considerably from year to year, coinciding with large annual differences in recruitment. The Fraser/Skagit population was largely a closed one from December to March but at least half of all Wrangel Island geese wintering in California staged on the deltas in the fall of 1991.

The geese showed high site-fidelity and consistency in their distribution and movement patterns across years. These characteristics resulted in the development of largely distinct sub-populations on the deltas. I suspect that the traditional movement of Fraser birds to the Skagit delta in mid-winter developed because of trade-offs made between food quality/quantity and hunting disturbance.

Destructive sampling revealed that the net, annual change in rhizome mass of American three-square bulrush (*Scirpus americanus*) in the absence of grubbing was positive and constant across all patch densities. Also, both mean stem mass and rhizome mass per unit length increased as patch density decreased. These findings suggest that bulrush alters the way in which it allocates resources to different plant components as patch density declines due to grubbing.

All bulrush components responded positively to the application of commercial fertilizers, suggesting that growth is limited by nitrogen. Both rhizome mass and rhizome quality increased with increasing nitrogen level.

The annual growth and removal rates of bulrush rhizomes on the Fraser delta were similar between 1988 and 1992, resulting in a low level equilibrium. Both intrinsic and extrinsic factors were responsible for this steady-state. Non-destructive sampling confirmed that the annual change in rhizome mass in the absence of grubbing was positive and constant across all patch densities. In open plots, however, the annual removal rate of rhizomes decreased with decreasing patch density. Growth exceeded removal in patches with rhizome masses less than ca. 70 g m^{-2} but the opposite was true in patches with greater masses. A reserve of deep ($>$20 cm) rhizomes may also be important in maintaining bulrush growth when grubbing intensity is high. In addition, the existence of distinct sub-flocks on the Fraser delta, their consistent movement to the Skagit delta in mid-winter, and their elevated use of Alaksen National Wildlife Area fields with increasing abundance may have resulted in similar grubbing intensities each year.

Acknowledgements

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M. Davison, J. Garret, D. Kraege, and A. Lettenberger of the Washington State Dept. of Fish and Wildlife assisted with work on the Skagit delta. J. Takekawa of the U.S. National Biological Service provided advice and equipment for the radio-telemetry work. Russian biologists Y. Syroechkovskiy, K. Litvin, and V. Baranyuk allowed me to use their spring population estimates. B. Burton provided his 1974/75 weekly photo counts on the Fraser delta.

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Table of Contents

Chapter 1. General Introduction

Chapter 2. Abundance and Distribution of Lesser Snow Geese (*Anser c. caerulescens*) on the Fraser and Skagit River Deltas

Chapter 3. Growth Ecology of American Three-square Bulrush (*Scirpus americanus*) on the Fraser River Delta, B.C.

Chapter 4. Interaction Between Lesser Snow Geese (*Anser c. caerulescens*) and Three-square Bulrush (*Scirpus americanus*) on the Fraser and Skagit River Deltas

Chapter 5. Summary and Conclusions

List of Tables

List of Figures

Chapter 1

General Introduction

1.1 Introduction

Between 60,000-100,000 Lesser Snow Geese (*Anser c. caerulescens*) nest on Wrangel Island, Russia (Bousfield and Syroechkovskiy 1985, Anon. 1992). More than half of these geese overwinter on the Fraser River (B.C.) and Skagit River (Wash.) deltas (Anon. 1992, this study) where they grub (excavate) for rhizomes of American three-square bulrush (*Scirpus americanus*) (Burton 1977) and graze on farm crops such as rye, wheat, and pasture grasses. Snow Geese have caused "eat-outs" in Louisiana salt marshes (Lynch *et al.* 1947) and they have reduced the biomass and primary production of salt marshes on the Atlantic coast (Smith and Odum 1981, Smith 1983) and on the St. Lawrence River estuary (Giroux and Bedard 1987a, Reed 1989). The geese consumed about one-third of the below-ground mass of bulrush on the Fraser delta in 1974/75 (Burton 1977), a year when the Fraser/Skagit population was ca. 15,000 birds. Burton (1977) suggested that the marsh would be negatively affected if the number of geese doubled. The population increased by 3-4 fold in the late 1970s and it has remained high throughout the 1980s and early 1990s (Anon. 1992, this study). The geese began to forage on agricultural crops on the Alaksen National Wildlife Area on the Fraser delta in the early 1980s (Hatfield 1991; *pers. comm.* with local farmers and hunters). One explanation for this new foraging behaviour is that bulrush rhizomes were depleted to the point where the geese were unable to meet their requirements for some essential nutrient (e.g. energy, protein). Alternatively, the geese may be following some food-profitability gradient; cover crops may simply result in higher return rates compared to rhizomes (see Stephens and Krebs 1986, Krebs and Davies 1987). Whatever the reason, an understanding of the current interaction between the geese and bulrush will help predict the consequences to marsh integrity if goose numbers continue to increase. In this study, I describe the abundance and distribution patterns of Snow Geese on the deltas (Chapter 2), assess the seasonal and annual growth patterns of bulrush in patches at different stem densities (Chapter 3), and investigate the interaction between rhizome growth and removal rates (Chapter 4).

1.2 Plant-Herbivore Interaction

Both the consumption rate of a herbivore and the growth rate of its target plant are functionally related to plant biomass (Noy-Meir 1975, Crawley 1983, Begon and Mortimer 1986). When overlaid graphically, growth rate and consumption rate curves intersect at one or more points of equilibrium(ia). The status of any equilibrium (i.e. stable or unstable, high or low plant mass) is determined by the shape and magnitude of the growth rate and consumption rate functions. To illustrate this concept, growth functions G1 and G2 are plotted against consumption functions C1 and C2 in Figure 1. The growth functions differ only in terms of the plant mass where production is at a maximum. The consumption functions differ only in terms of the density of herbivores represented (C2>C1). C1 results in stable equilibria at high or medium plant biomass with G1 and G2, respectively. The interaction between C2 and G2 results in a stable

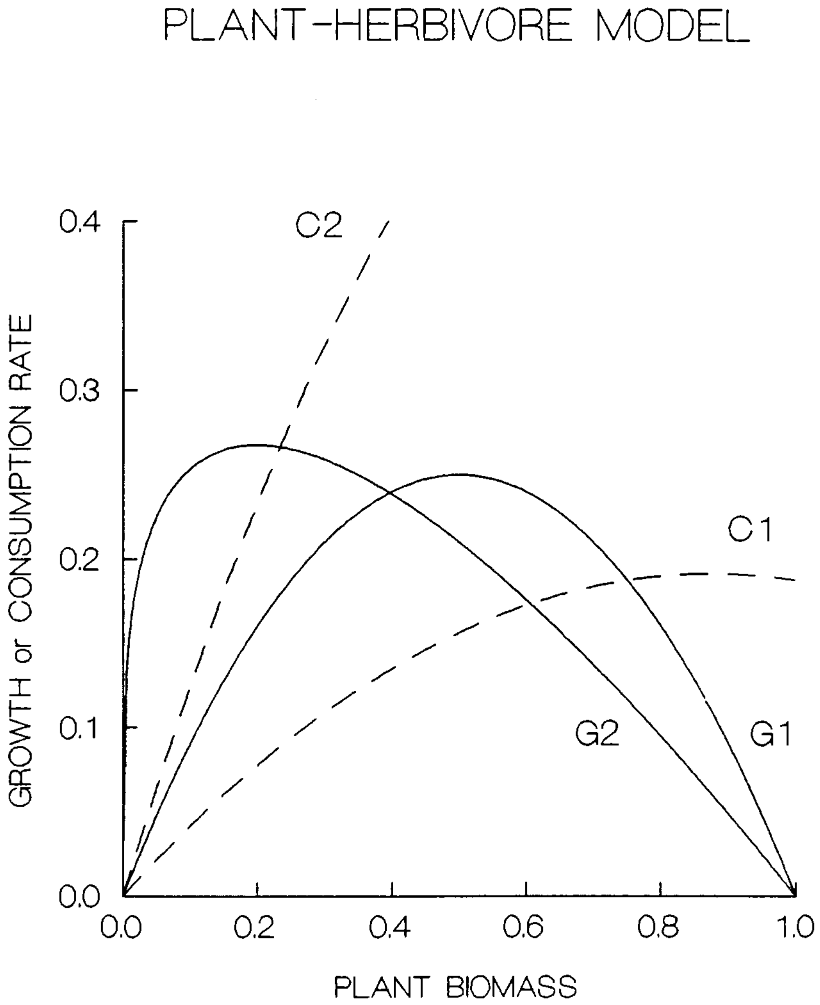


Figure 1. Noy-Meir's (1975) model describing the interaction between plant growth and herbivore consumption. C1 and C2 represent different consumption rate functions for the herbivore whereas G1 and G2 are different growth rate functions of the target plant.

equilibrium at low plant biomass but C2 overlaid with G1 results in extinction because consumption exceeds growth over all biomass values. These are only a few of the outcomes possible (see Noy-Meir 1975).

The model described above assumes a simple, artificial grazing system in which herbivore movement is restricted, herbivore density is constant, and consumption and plant growth are continuous and simultaneous. Most natural systems are open, herbivore densities fluctuate, and consumption and growth are often discrete and can occur at different times. Further, herbivores in an open system may shift to different foods if they are available and more profitable (Stephens and Krebs 1986, Krebs and Davies 1987). Except for freezing spells on the Fraser and Skagit deltas, when bulrush rhizomes are the primary or only food, Snow Geese usually have access to rye, wheat, and pasture grasses. Also, bulrush grows only in summer but foraging by geese occurs in winter. Although few of the assumptions of Noy-Meir's model are met, I used it as a framework to study the interaction between Snow Geese and bulrush on the deltas (Noy-Meir suggested that the qualitative results of the model should hold for a wide range of conditions). I modified the model as follows: First, annual rates of rhizome growth and removal were measured. I was concerned with the interaction over the long-term and the non-destructive technique I used required measurements to be made at one and the same point on bulrush's growth cycle each year. Second, the consumption rate measured was, in fact, an annual removal rate of rhizome mass; that is, the interaction was considered from the viewpoint of the plant rather than from that of the herbivore.

In this thesis, I test the prediction that the interaction between Snow Geese and bulrush rhizomes on the Fraser delta is at a low level steady-state as has been suggested for similar systems elsewhere (Smith and Odum 1981, Smith 1983, Giroux and Bedard 1987a, Reed 1989).

1.3 Study Area

Most of my research was conducted on the Fraser River delta in southwest British Columbia (Fig. 2). The delta covers about 680 km^2, extending from Sand Heads lighthouse in the west to New Westminster in the east and from Iona Island in the north to the Canada-US border in the south. Formerly, the delta flooded during the spring freshet of the Fraser River, but today much of the area is dyked. The remaining intertidal area is flooded by semi-diurnal tides, with 2 highs and 2 lows each day (Thomson 1981). The lowest tides occur near midnight in winter but around noon in summer. For a more detailed description of the Fraser delta, see Butler and Campbell (1987).

The tidal marshes of the delta are dominated by American three-square bulrush (*Scirpus americanus*), seacoast bulrush (*S. maritimus*), and Lyngbyei's sedge (*Carex lyngbyei*) (Burgess 1970, Yamanaka 1975, Burton 1977, Kistritz 1978, Moody 1978, Hutchinson 1982, and Karagatzides 1987). On Westham Island (including Reifel MBS), the three-square bulrush zone is homogeneous, 500-600 m wide, and bordered above by a pure sedge zone and below by mudflat. From October to April, waste potatoes, cover crops such as rye and wheat, and pasture grasses are present on dyked farmland adjacent to the tidal marshes at Westham Island.

Snow Geese use the marshes at Brunswick Point, Westham Island, Lulu Island,

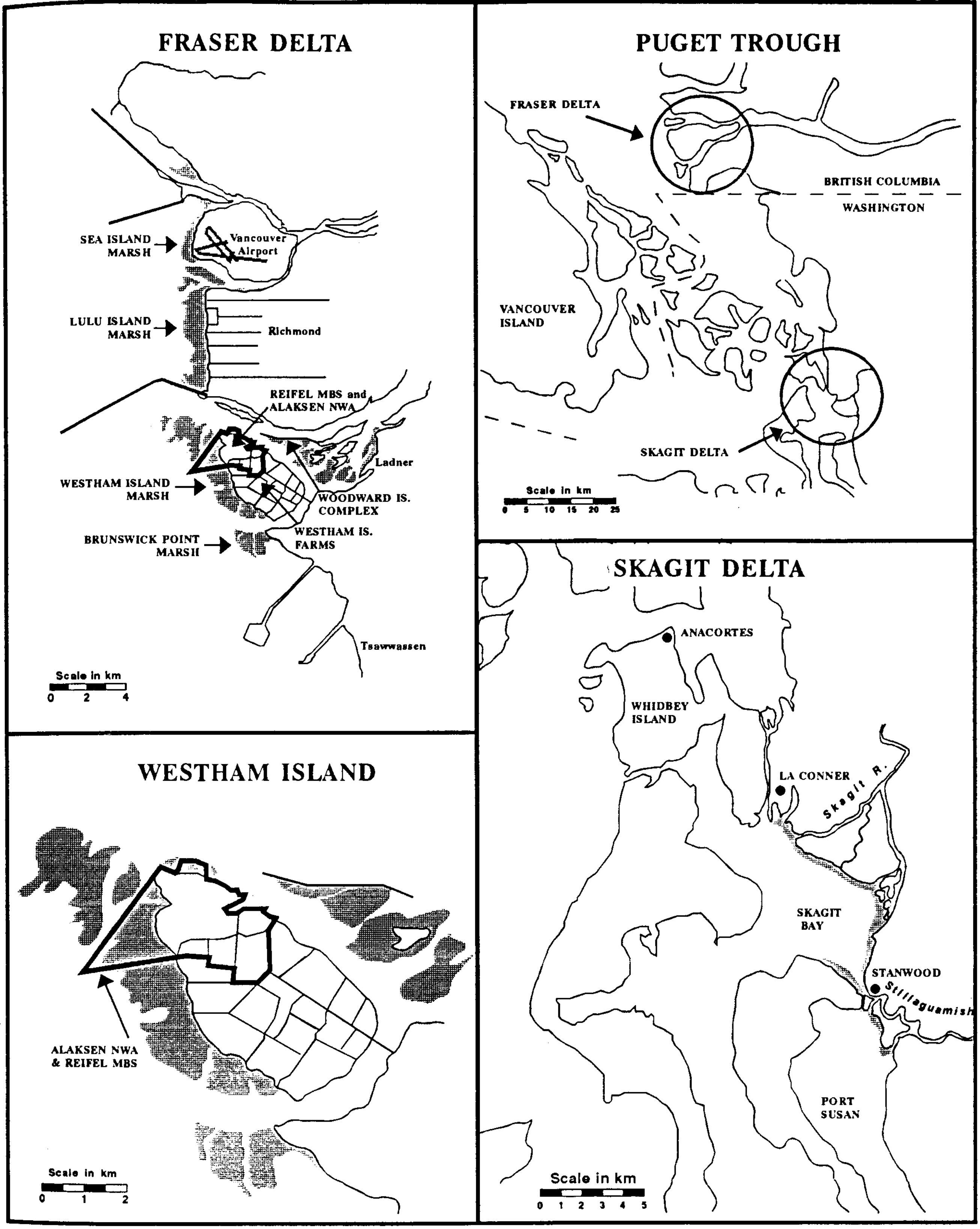


Figure 2. Map of the study area showing the Fraser River delta (British Columbia) and the Skagit River delta (Washington). Alaksen National Wildlife Area (NWA) and Reifel Migratory Bird Sanctuary (MBS) at Westham Island are also shown. Shaded areas are tidal marshes.

Sea Island, and Woodward Island, as well as farms on Westham Island (Fig. 2). The Reifel Migratory Bird Sanctuary (MBS) and Alaksen National Wildlife Area (NWA) have been closed to hunting since 1963 and 1972, respectively. Together, these areas contain about 400 ha of farms, old fields, and sloughs as well as 550 ha of tidal marsh and mudflat. In 1989, the foreshore of Sea Island was permanently closed to hunting.

Snow Geese also use the Skagit River delta in the State of Washington, 100 km to the south (Fig. 2). The Fraser and Skagit deltas are roughly the same size and they support the same dominant vegetation types (Ewing 1982, *pers. obs.*).

Chapter 2

Abundance and Distribution of Lesser Snow Geese (*Anser c. caerulescens*) on the Fraser and Skagit River Deltas

2.1 Introduction

Wrangel Island supports the last remaining population of Lesser Snow Geese (*Anser c. caerulescens*) in Russia. In contrast to other populations of Arctic geese in Europe (Madsen 1991, Ebbinge 1991) and Snow Geese in North America (Reed 1990), the number of Wrangel geese declined in recent decades (Bousfield and Syroechkovskiy 1985, Kalchreuter 1991, Anon. 1992). Many of these geese overwinter on the Fraser River (B.C.) and Skagit River (Wash.) deltas (Burton 1977, Jeffrey and Kaiser 1979, Anon. 1992). Little is known about their abundance and distribution patterns on the deltas or the ecological relationships between the geese and their winter habitat. My objectives were to examine: the size of the population in recent years compared to historical times; the importance of recruitment and harvest rates to changes in abundance across years and over the long-term; site fidelity and whether the population is a closed one; and distribution and movement patterns on the deltas. This information will help in the interpretation of the interaction between the geese and bulrush (*Scirpus americanus*) rhizomes (Chapter 4). It will also provide an ecological basis for the development of management prescriptions for the geese.

2.2 Methods

2.2.1 Abundance

Historical

Unpublished reports and occasional surveys were used to develop an historical perspective of Snow Goose abundance on the Fraser and Skagit deltas. Mid-winter aerial censuses (Anon. 1992) were used to describe population dynamics from 1948/49 to the present. Most of the censuses were airphoto counts but some were visual estimates. I corrected the visual estimates for observer bias using comparative data collected in a separate study (Boyd, unpubl. data). I then added harvest (Appendix 1) to estimate the size of the Fraser/Skagit population each winter. Population means were calculated for each decade and compared with a Tukey multiple comparison test.

Recent

The Snow Goose population on the Fraser and Skagit deltas was surveyed annually between 1987/88 and 1991/92 using an airphoto technique (Appendix 2). From early October to late April, ca. 25 weekly surveys were flown on the Fraser delta and between 4 and 12 total surveys were conducted on both the Fraser and Skagit deltas.

Goose-days were calculated using the following formula:

$$\text{Goose-days} = \sum N_i \frac{(D_{i+1} - D_{i-1})}{2}$$

where N_i = population at day i, D_{i+1} = next survey date (day), and D_{i-1} = previous survey date.

Proportional Changes

I used aerial census data collected since the late 1940s (Munro 1954, Morris and

Noble 1972, Burton 1977, McKelvey *et al.* 1985, and this study) to estimate the size of the fall population on the Fraser delta. The proportion of the Fraser/Skagit population on the Fraser delta in fall was then calculated and compared across periods.

Uspenskii (1965, 1968) estimated the number of breeding Snow Geese on Wrangel Island in the early 1960s and Y. Syroechkovskiy, K. Litvin, and V. Baranyuk counted the population annually from 1969 to the present (Bousfield and Syroechkovskiy 1985, unpubl. data). I used these estimates and 2 different indices of the abundance of wintering geese to calculate the proportion of the entire Wrangel Island population using the Fraser and Skagit deltas each year. I determined if this proportion changed over time by using linear regression analysis.

Recruitment and Harvest

I used high-quality, small-scale air-photos (see Appendix 2) to estimate the percent of immature (hatch year) birds in the population and a multiple comparison t-test to determine if this percent differed spatially across the Fraser delta in any year. Probability values were adjusted by the number of comparisons using Bonferonni's method (Zar 1974).

Existing data were used to determine recruitment and harvest rates during the period 1948/49-1991/92 (Anon. 1992). I used linear regression models to describe the relation between each rate and the magnitude of population change across years on the deltas.

2.2.2 Distribution

General Patterns

I investigated the general distribution and movement patterns of Snow Geese by dividing the Fraser delta into a grid (1.5 km x 1.5 km blocks) and plotting flock locations and sizes for each weekly census. For each census, I calculated the percent of the total Fraser population present in each grid block. Mean percents for different periods (fall/early winter versus spring, hunting versus non-hunting seasons in fall and spring) were then calculated and plotted on 3-dimensional maps (Wilkinson 1990).

I regressed the number of geese and the number of goose-days during the fall/early winter period on the Fraser delta against the size of the Fraser/Skagit winter population to assess the degree of consistency in distribution patterns across years. Unpublished airphoto counts collected in 1974/75 (Burton 1977) were also used. The same analysis was used for geese using the north half of the Fraser delta versus the south half against the total Fraser population in fall.

Specific Patterns

Movements and home ranges of individual geese on the deltas were determined using radio-telemetry. In late July 1991, 100 moulting geese were captured in 2 flocks on Wrangel Island. Forty geese were selected to carry conventional radio transmitters weighing 45 g. Thirty radios were mounted on neck-bands and 10 on backpacks. All radios were powered by battery but some also had solar power capability. Facial stains suggested that the geese had spent the previous winter on the Fraser/Skagit deltas (V. Baranyuk *pers. comm.*). An additional 30 geese, suspected to have wintered in California, were fitted with solar-powered, conventional radios on neck-bands as part of another study (J. Takekawa, unpubl. data).

Telemetry work on the Fraser delta began in early October 1991 and lasted until mid-April 1992. Tracking from the ground was done daily or every second day on Westham Island and Brunswick Point but less frequently on Lulu and Sea islands (Fig. 2). Two "around-the-clock" (24 h) telemetry surveys were also conducted on Westham Island and Brunswick Point each week. Compass direction and signal strength of each transmitter were recorded from several fixed stations using a receiver/scanner (ATS model 4000) equipped with a 4-element Yagi antenna. Telemetry was also done from an airplane once per week on the Fraser delta (ca. 20 times) and once every 2 weeks on the Fraser/Skagit complex (ca. 10 times). Finally, radio-marked birds were tracked on the Skagit delta from the ground periodically from mid-October to April (M. Davison, unpubl. data).

Only observations collected more than 2 h apart were used in the analysis to ensure independence. The location data were split into fall/early winter versus spring periods and daytime (0800 - 1700 h) versus nighttime hours (1800 - 0700 h). Locations were converted to UTM coordinates and plotted on a map of the Fraser delta. Harmonic mean core areas (statistical representations of the most intensely used areas; roughly 50-60% of all observations) were determined with the program HOMERANGE (Ackerman *et al.* 1990). I overlaid the plots visually to assess seasonal and day/night differences.

2.3 Results

2.3.1 Abundance

Historical

Snow Geese have likely been staging or overwintering in the study area for centuries. Snow Goose remains have been found in aboriginal bone middens on the Fraser delta dating to 1500 B.C. (Hobson and Driver 1987). Since at least the late 1700s, early explorers and settlers observed Snow Geese in the Pacific Northwest during winter (Coues [1893] in Jewett *et al.* 1953, Fannin 1891, Dawson and Bowles 1909, Pearse 1968). The geese were apparently rare on the Skagit delta during the late 1800s and early 1900s (Jeffrey and Kaiser 1979, M. Davison *pers. comm.*). However, Brown (in Jewett *et al.* 1953) noted at least 5,000 birds on the Skagit delta in late November 1922 and Hall (1936) reported between 5,000 and 12,000 in late January 1936. Snow Geese were present on the Fraser delta every winter from 1914 to 1946 (unpubl. reports by the B.C. Provincial Game Commission). They wintered in "large" numbers during the early 1920s (Munro 1921, Racey 1924, Butler 1924, Brooks and Swarth 1925, Cumming 1932). Racey (1924) estimated between 2,500 and 3,000 geese on Lulu Island in January 1924 and Cunningham and Cameron (in Butler 1924) estimated 3,500 geese off Lulu Island and 5,000 around south Westham Island and Brunswick Point all winter.

The mean size of the Fraser/Skagit population between 1948/49 and 1991/92 was estimated to be 37,400 ± 1,800 (SE) (n=38 years). The number of geese varied from a low of ca. 15,000 to a high of ca. 60,000 birds (Fig. 3A, Anon. 1992). The population declined abruptly in the early 1970s, coinciding with 4 consecutive breeding failures on

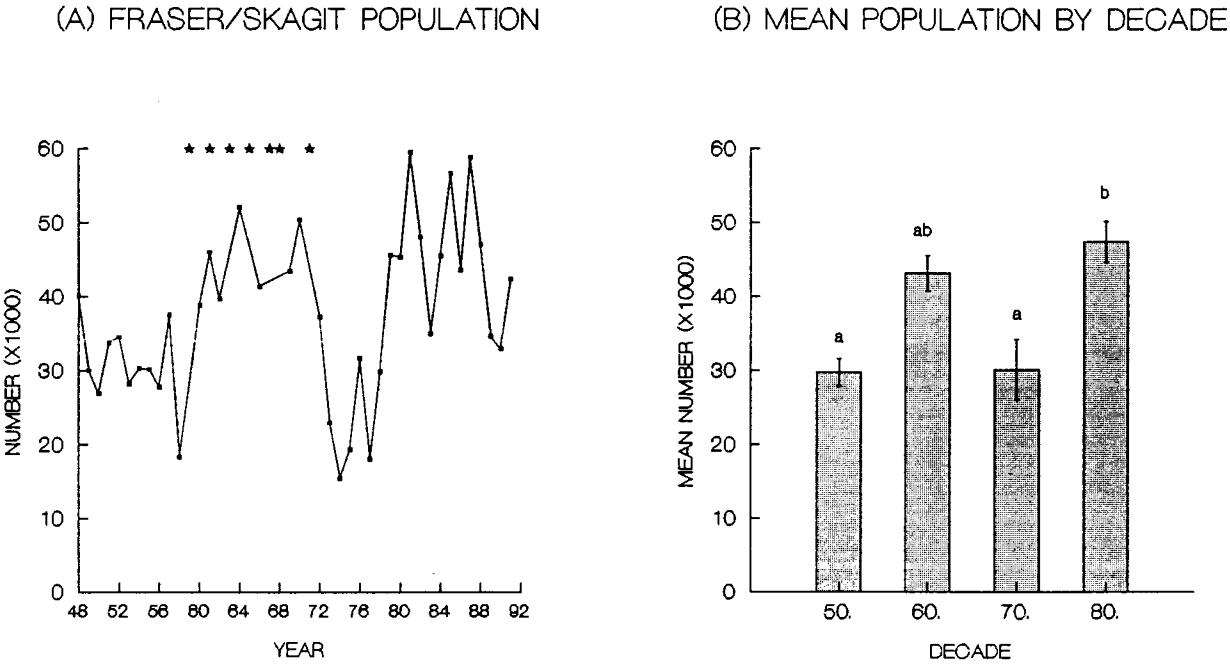


Figure 3. (A) Size of the wintering population of Snow Geese on the Fraser and Skagit deltas since 1948/49 (=48). Population size was estimated by correcting the mid-winter count for observer bias where necessary and adding fall/early winter harvest. Stars indicate years when data were not available. (B) Mean size (± 1SE) of the estimated population by decade. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

Wrangel Island (Bousfield and Syroechkovskiy 1985), but the population recovered by the late 1970s and remained high throughout most of the 1980s and early 1990s. The estimated population differed significantly across decades (ANOVA, $F_{3,29}=9.25$, $P<0.001$; Fig. 3B). Approximately 17,000 more geese were present on the deltas in the 1980s (47,400 ± 2,800) compared to the 1950s (29,700 ± 1,900) and 1970s (30,100 ± 4,100). Populations in the 1980s and 1960s (43,100 ± 2,400) did not differ but the data for the latter decade may not have been representative; only 5 years with complete counts were available and all censuses were visual estimates.

Recent

Snow Geese used the Fraser and Skagit deltas in a consistent manner each year from early October to late April (Figs. 4A-F but especially 4F, Appendix 3). Geese were present on the Skagit delta for the entire winter and on the Fraser delta only between early October and mid-January and again between late February and mid-April (Figs. 4A-F and 5A-E, Appendix 4). All geese were on the Skagit delta from mid-January to late February after which many moved north to the Fraser delta. Total counts for the deltas were constant from December to March and changes in abundance on the Fraser delta corresponded to equal but opposite changes on the Skagit delta (Figs. 4A-F). Hence, it appears that the deltas supported a largely closed population in winter.

Between 1987/88 and 1991/92, the mean size of the Fraser/Skagit population was 43,200 ± 4,700 (SE) birds (range = ca. 33,000-59,000). The deltas together supported about 7.5 million goose-days yr^{-1}. The Fraser delta had between 2.0 and 3.2 million goose-days yr^{-1} (mean = 2.5 ± 0.2 million, n=5 years) or about 33% of the total use.

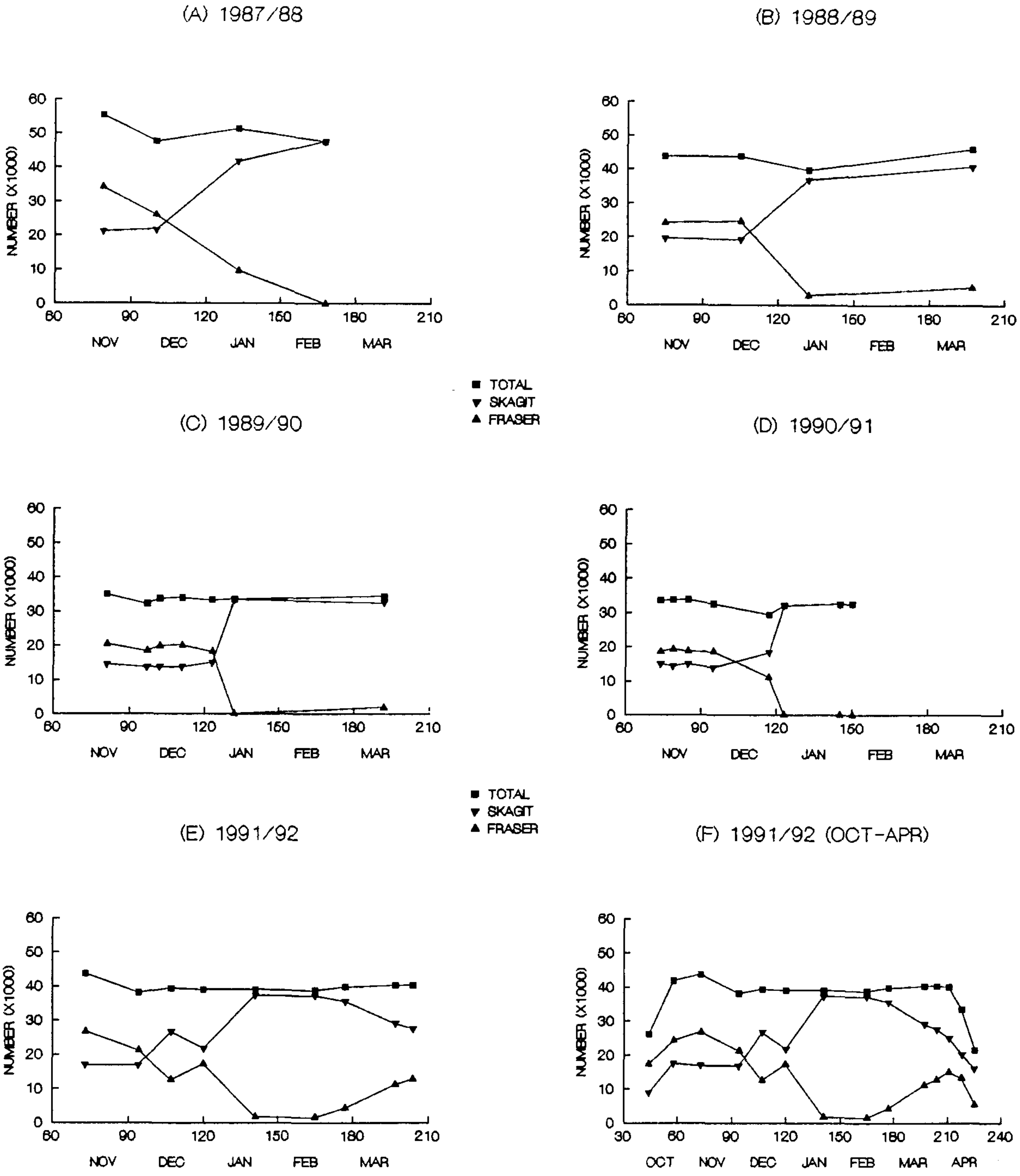


Figure 4. Number of Snow Geese on the Fraser and Skagit deltas as estimated from airphoto counts. (A-E) November to March, 1987/88 through 1991/92. (F) October to April, 1991/92. Months and Julian days are given on the horizontal axis.

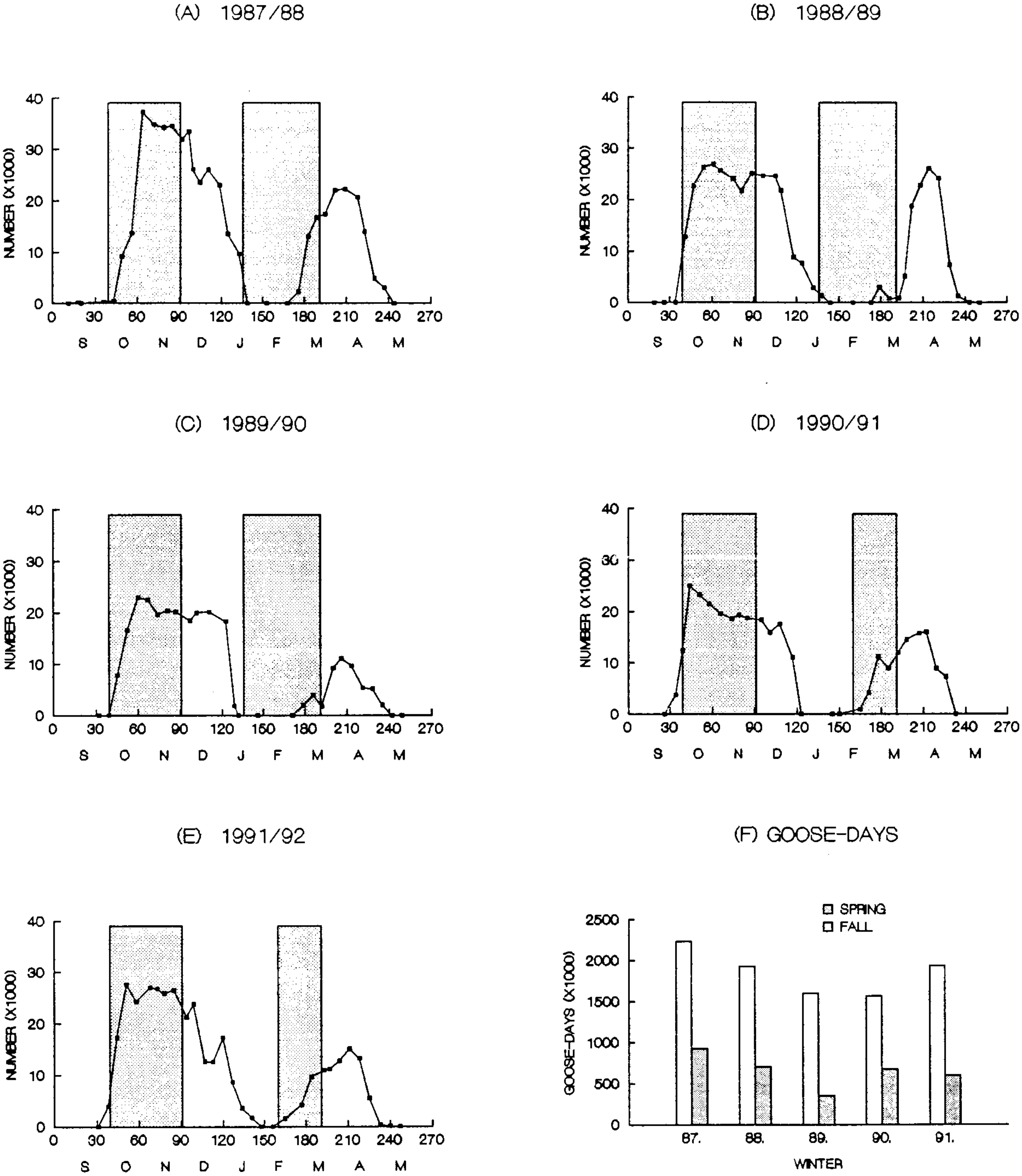


Figure 5. (A-E) Number of Snow Geese on the Fraser delta from September to May, 1987/88 through 1991/92. Months and Julian days are given on the horizontal axis. Hunting seasons for Snow Geese are represented by the shaded bars; the spring hunting season was reduced by one month starting in 1990/91. (F) Number of goose-days on the Fraser delta in fall/early winter (fall) and in spring for the above years (87 = 1987/88).

Most goose-days on the Fraser delta (ca. 75%) were in the fall/early winter period (Fig. 5F).

Proportional Changes

The relative proportions of Wrangel Island geese wintering on the Fraser/Skagit deltas (versus in California) and on the Fraser delta (compared to the Skagit delta) changed substantially in recent times. The proportion of the Fraser/Skagit population using the Fraser delta in fall increased from 30-40% in the period 1950-1970, to 50-60% in the early 1980s, to 60-65% in the late 1980s-early 1990s, and to >65% at present (based on data from Munro 1954, Morris and Noble 1972, Burton 1977, McKelvey *et al.* 1985, this study and more recent surveys). Also, between the late 1960s and early 1990s, the proportion of Wrangel geese wintering on the Fraser and Skagit deltas doubled (Figs. 6A,B). Linear models were significant for both the actual mid-winter population as a proportion of the following spring population on Wrangel Island (Fig. 6A; $r^2=0.74$, $F_{1,20}=56.83$, $P<0.001$) and the estimated mid-winter population as a proportion of the previous spring population on Wrangel Island (Fig. 6B; $r^2=0.44$, $F_{1,19}=15.24$, $P=0.001$). Based on the regressions, the deltas should have held approximately 15-20% of all Wrangel geese in the early 1960s. This proportion is close to one calculated using the estimated mid-winter population and Uspenskii's (1965, 1968) estimates of the size of the breeding population.

Recruitment and Harvest

The first geese to arrive on the deltas in early October were non-breeders or failed-breeders (*pers. obs.*). The percent of immature birds in the population peaked by

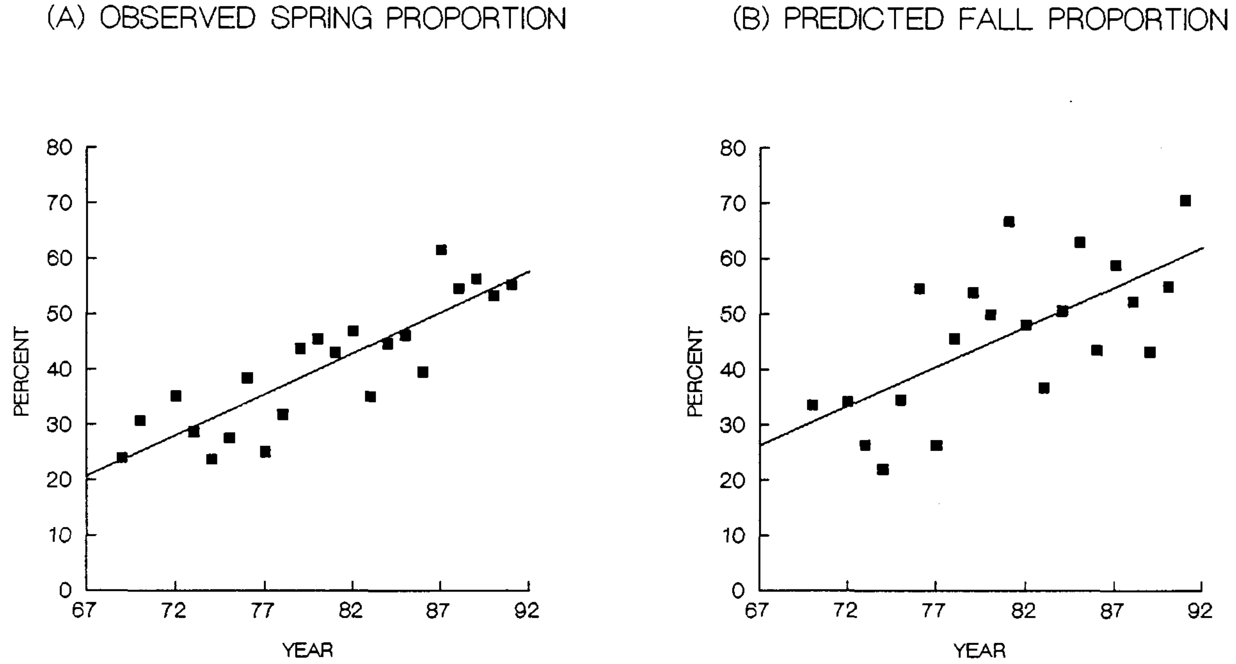


Figure 6. (A) Linear regression between the mid-winter count of Snow Geese on the Fraser and Skagit deltas (corrected for visual estimates only) as a percent of the following spring population on Wrangel Island plotted against year (1969/70 to 1991/92; 67 = 1967/68) ($Y=-78.3+1.48X$; $r^2=0.74$, $P<0.001$, $n=22$). (B) Linear regression between the predicted number of Snow Geese wintering on the Fraser and Skagit deltas as a percent of the previous spring population on Wrangel Island plotted against year (1969/70 to 1991/92; 67 = 1967/68) ($Y=-69.8+1.43X$; $r^2=0.44$, $P=0.001$, $n=21$).

late October and remained constant to at least late December (Figs. 7A-D). This percent did not differ between the Fraser and Skagit deltas in 1990/91 and 1991/92 and there were no spatial differences across the Fraser delta within any year ($P>0.05$ for all comparisons and all years; Appendix 5).

Both recruitment and harvest influenced the dynamics of the Fraser/Skagit population from year-to-year and over the long-term. Between 1987/88 and 1991/92, the percent of immature birds in the fall population varied between 0-30% (mean = 13.6 ± 5.5% (SE), n=5 years; Figs. 7A-E). No young were present in 1989/90 because of freezing conditions on Wrangel Island shortly after hatch (V. Baranyuk *pers. comm.*). Between 1948/49 and 1991/92, the number of immatures varied from zero to 30,000 (0-50% of the population) with a mean of 8,000 ± 1,200 (SE) or 19.6 ± 2.4% (SE) of the population (n=36 years; Fig. 8A).

The number of geese harvested between 1948/49 and 1991/92 on the deltas varied from ca. 700 to 16,400 per year. Mean harvest was 5,200 ± 600 (SE) geese or 14.1 ± 1.2% (SE) of the population (n=37 years; Fig. 8B).

Separate linear models describing the change in the number of geese on the deltas from Year t to Year t+1 (dependent variable) versus the number of immature birds or the number of geese harvested (independent variables) were significant ($Y=-9.9+1.21X$: $r^2=0.61$, $F_{1,27}=41.85$, $P<0.001$ for immatures and $Y=-8.4+1.63X$: $r^2=0.29$, $F_{1,28}=11.47$, $P=0.002$ for harvest). The amount of variance explained by harvest was lower compared to immatures (29% versus 61%). Also, when both indices were entered into a multiple linear regression, only recruitment was significant ($P<0.001$). Harvest

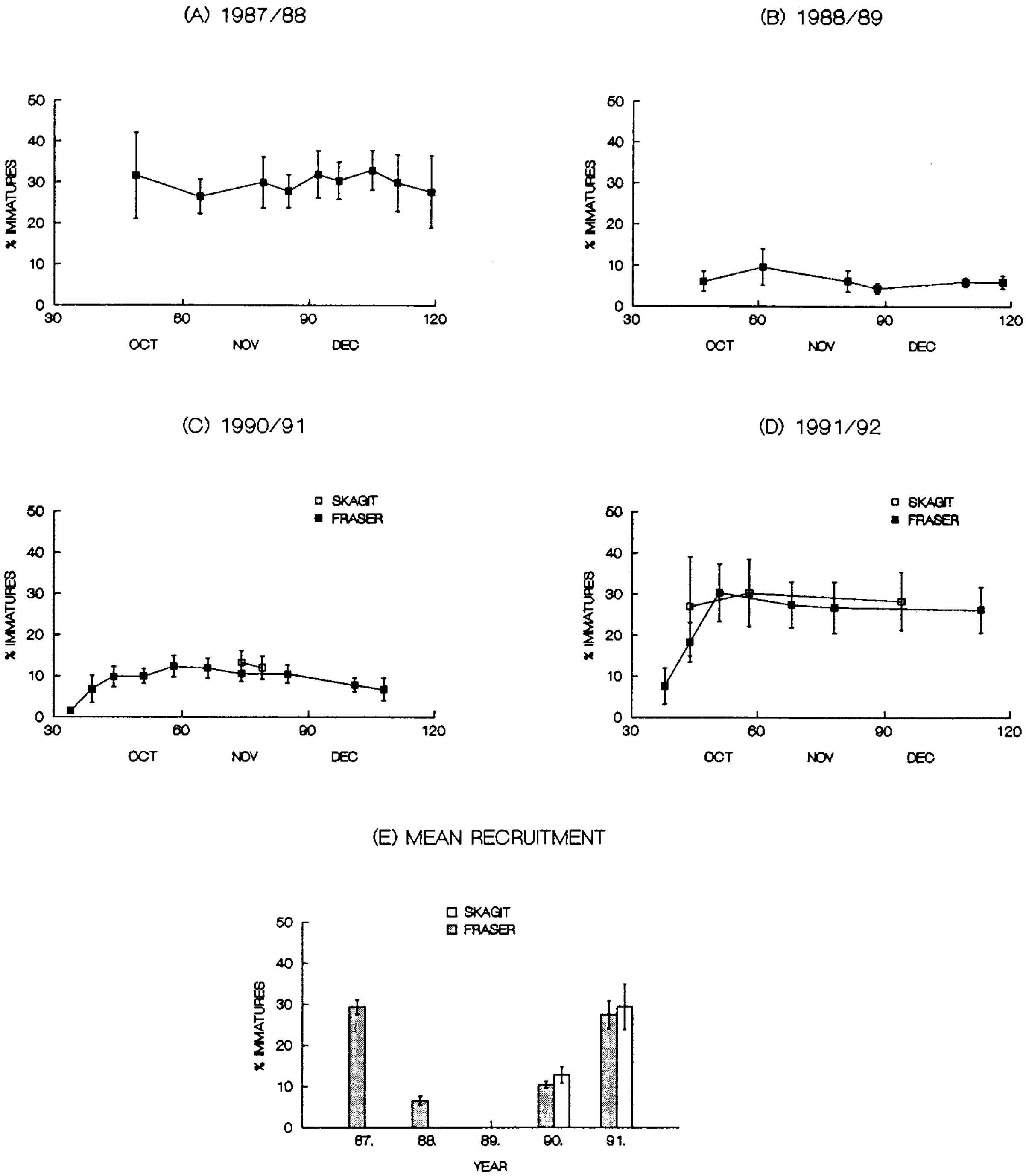


Figure 7. (A-D) Mean (± 1SE) percent of immature birds in the Fraser/Skagit Snow Goose population from October to December, 1987/88 through 1991/92, as estimated from air-photos. Data for the Skagit delta were available only for 1990/91 and 1991/92. Recruitment was zero in 1989/90. Months and Julian days are given on the horizontal axis. (E) Mean values (± 1SE) for the percent of immature birds by year (87 = 1987/88).

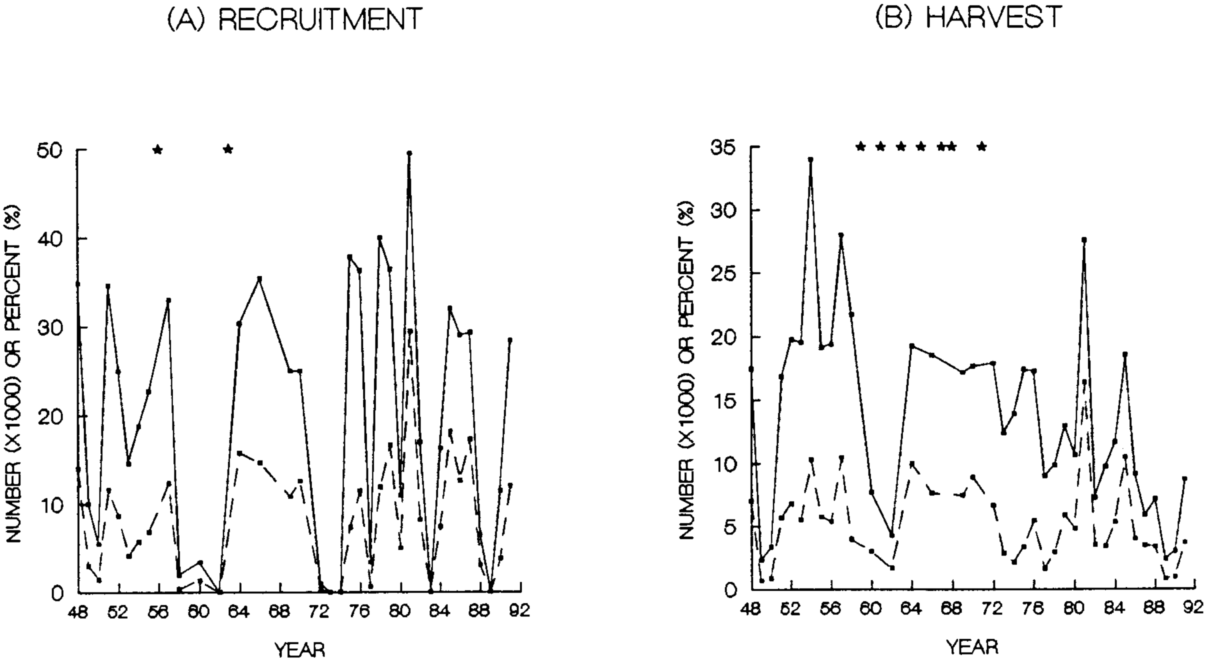


Figure 8. (A) Estimated recruitment rate in terms of the number of immature birds (dashed line) or the percent of immature birds (solid line) in the Fraser/Skagit Snow Goose population each year since 1948/49 (= 48). Stars indicate years when data were not available. (B) Estimated harvest rate in terms of the number of geese (dashed line) or percent of the population (solid line) taken by hunters each year since 1948/49 (= 48). Stars indicate years when data were not available.

($P=0.75$) did not improve the final model results ($r^2=0.61$, $F_{2,26}=20.28$, $P<0.001$) but its importance may have been masked because it was correlated with the number of immatures in the population ($r^2=0.53$, $F_{1,34}=38.60$, $P=<0.001$).

The percent of immatures in the population varied considerably across years but it did not change over the long-term. Mean percent before 1980 (19.8 ± 3.0% (SE), n=24 years) did not differ from that after 1980 (19.2 ± 4.3% (SE), n=12 years). Although not significant (t-test: P=0.30), the number of immatures in the population increased from a mean of 7,100 ± 1,200 (SE) before 1980 to a mean of 9,700 ± 2,500 (SE) after 1980. The percent of the Fraser/Skagit population harvested each year declined over the long-term: from 15.9 ± 1.4% (SE) (n=25 years) before 1980 to 10.2 ± 2.0% (SE) (n=12 years) after 1980 (t-test: P=0.03). The number harvested per year, however, remained constant (5,300 ± 600 (SE) before 1980 versus 5,000 ± 1,300 (SE) after 1980).

The above analysis suggests that both the short- and long-term dynamics of the Fraser/Skagit population were influenced mostly by recruitment and, thus, by conditions (especially weather) on Wrangel Island. Harvest also affected abundance but to a lesser extent.

2.3.2 Distribution

General Patterns

Reifel MBS and Alaksen NWA supported most of the Fraser geese delta during the daytime between 1987/88 and 1991/92 (fall and spring seasons and hunting and non-hunting periods pooled; see also Appendix 6).

During the fall hunting period, Reifel MBS and Alaksen NWA supported ca. 47% of all geese on the Fraser delta (n=5 years; Fig. 9A). The marshes at Sea Island, Lulu Island, Westham Island, and Brunswick Point supported much lower percents (11-16%). Percents were roughly the same in the fall non-hunting period except that Lulu Island held ca. 28% of all geese (Fig. 9B).

Distribution changed dramatically in spring (Figs. 9C,D). Reifel MBS and Alaksen NWA together held only ca. 4% of the geese during the spring hunting period and 6% during the non-hunting period whereas percents at Lulu Island (mostly the northern and southern parts) rose to ca. 53% and 31% for the same periods.

Figure 10 shows the diurnal distribution pattern of geese on the delta in each of the 5 years of study. In fall/early winter (Fig. 10A), most geese were concentrated in Alaksen NWA and Reifel MBS. The marshes at the north half of Lulu Island and Sea Island were also important but not nearly to the same extent. Most geese in spring were on the marshes at Woodward Island, on the south half of Westham Island and Brunswick Point, the Outer Island, and the extreme north and south parts of Lulu Island (Fig. 10B).

Both the mean number of geese and number of goose-days on the Fraser delta in fall increased linearly with the total Fraser/Skagit population (Figs. 11A,B; $r^2=0.96$, $F_{1,4}=103.02$, $P=0.001$ and $r^2=0.97$, $F_{1,4}=145.98$, $P<0.001$, respectively). Also, both the mean number of geese and number of goose-days on the south half of the Fraser delta in fall increased linearly with the size of the fall population on the delta (Figs. 11C,D; $r^2=0.90$, $F_{1,4}=36.92$, $P=0.004$ and $r^2=0.89$, $F_{1,4}=31.41$, $P=0.005$, respectively). These

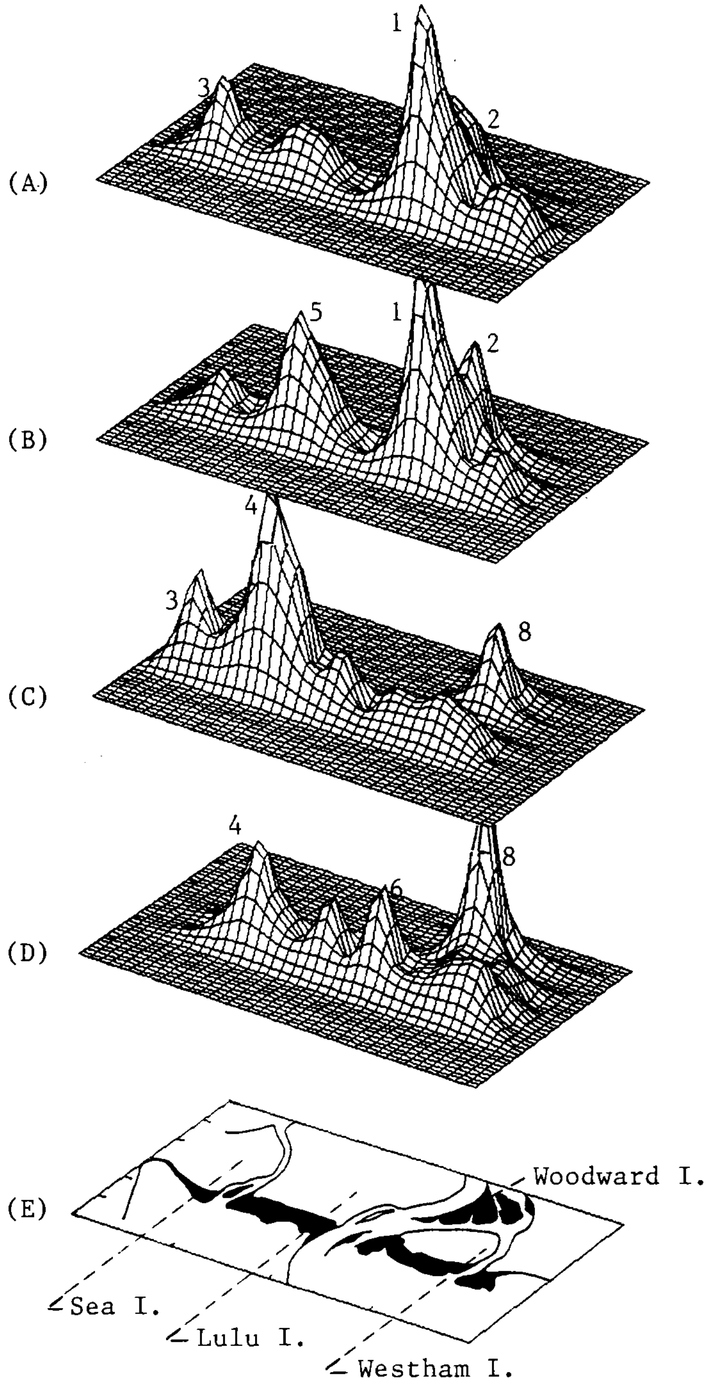


Figure 9. Spatial variation in the Fraser delta goose population during a given period. Data from 1987/88-1991/92 were pooled. (A) Fall hunting season (about 10 October to 30 November each year). (B) Fall non-hunting season (1 December to about 15 January). (C) Spring hunting season (from 1987/88 to 1989/90: 15 January to 10 March; in 1990/91 and 1991/92: 15 February to 10 March. (D) Spring non-hunting season (after 10 March). (E) Map of the Fraser delta corresponding to the above plots (tidal marsh shaded). For reference, numbers adjacent to the peak percents correspond to the following locations: (1) Reifel MBS marsh, (2) Alaksen NWA fields, (3) Sea Island marsh, (4) marsh at the north half of Lulu Island, (5) marsh at the south half of Lulu Island, (6) Outer Island marsh, (7) marshes at the south half of Westham Island and Brunswick Point, and (8) Woodward Island marshes.

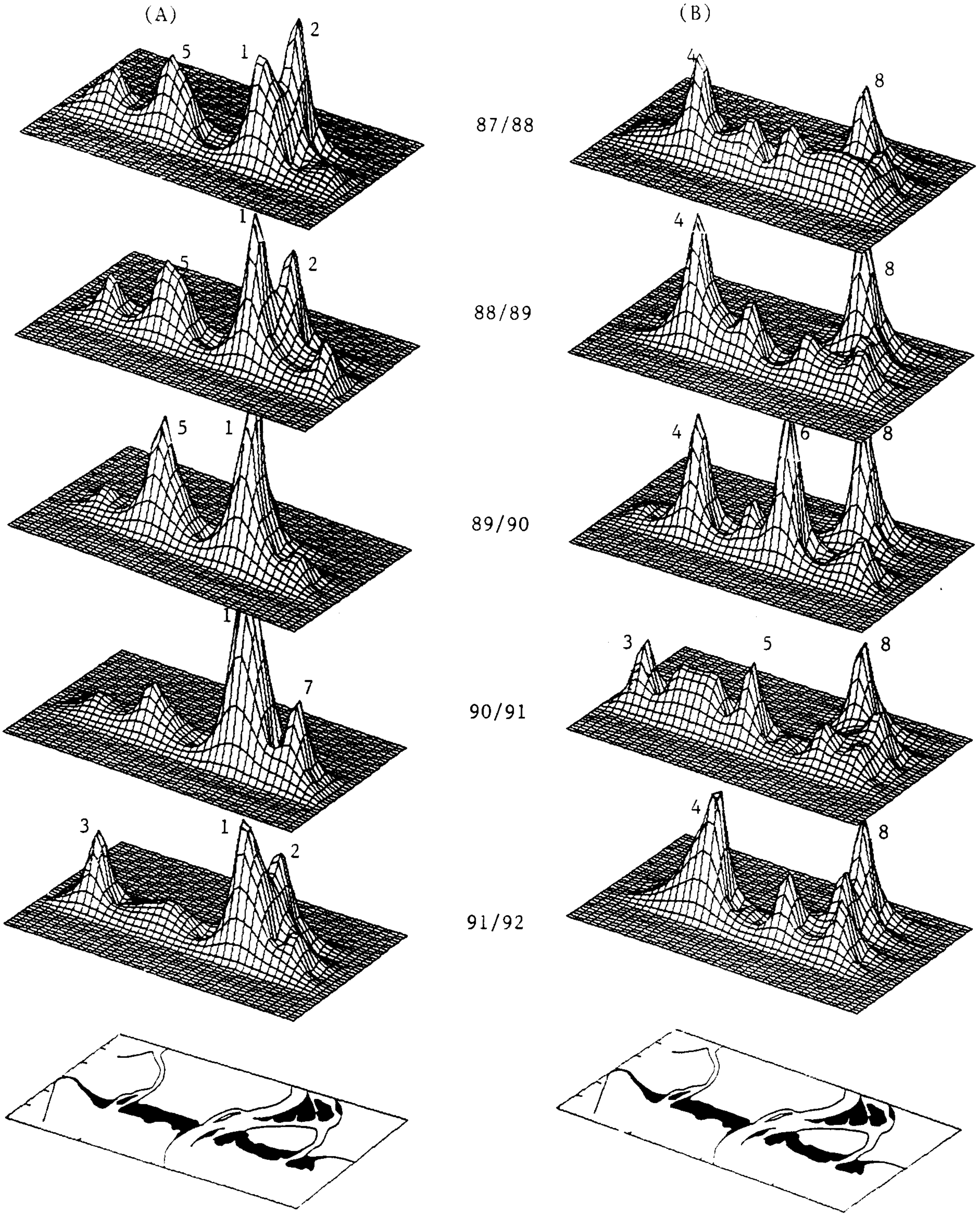


Figure 10. Spatial variation in the Fraser delta goose population in each year of the study from 1987/88 to 1991/92 during (A) the fall/early winter period and (B) the spring period. Maps of the Fraser delta are shown at the bottom of each sequence (tidal marsh shaded). For reference, numbers adjacent to the peak percents correspond to the following locations: (1) Reifel MBS marsh, (2) Alaksen NWA fields, (3) Sea Island marsh, (4) marsh at the north half of Lulu Island, (5) marsh at the south half of Lulu Island, (6) Outer Island marsh, (7) marshes at the south half of Westham Island and Brunswick Point, and (8) Woodward Island marshes.

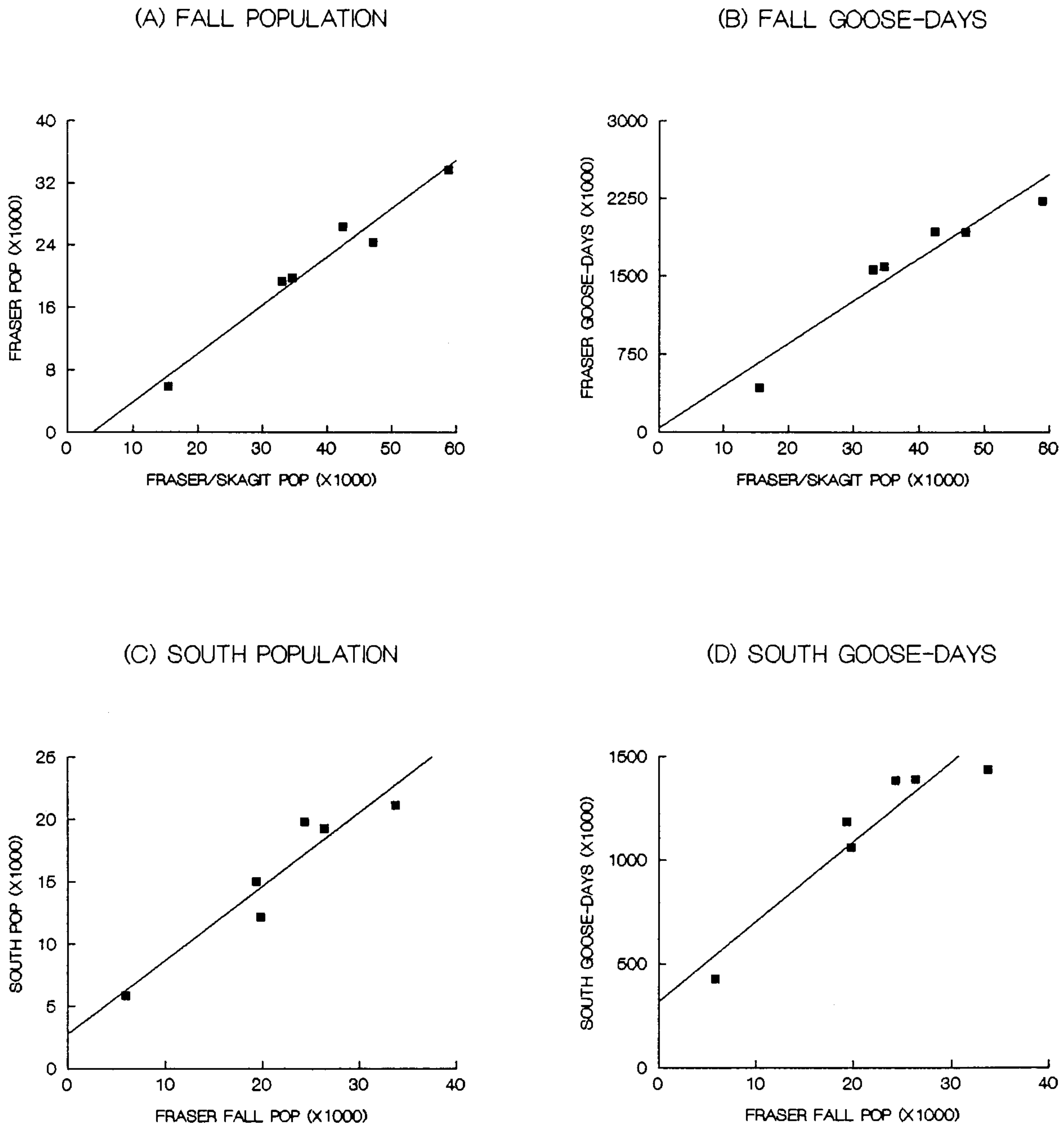


Figure 11. (A and B) Linear regressions between the number of geese and goose-days in fall on the Fraser delta and the total mid-winter population on the Fraser and Skagit deltas. Burton's (1977, unpubl.) airphoto counts for 1974/75 were also used. (C and D) Linear regressions between the numbers of geese and goose-days on south half of the Fraser delta (including Alaksen NWA) in fall and the mean fall population on the Fraser delta. The following equations describe the linear regressions: (A) $Y=2.4+0.62X$ ($r^2=0.96$, $P=0.001$, $n=6$); (B) $Y=35+40.9X$ ($r^2=0.91$, $P=0.003$, $n=6$); (C) $Y=2.7+0.59X$ ($r^2=0.90$, $P=0.004$, $n=6$); and (D) $Y=316+38.6X$ ($r^2=0.89$, $P=0.005$, $n=6$).

relationships (in conjunction with the radio-telemetry data presented below) suggest that largely distinct groups of birds with consistent habitat use patterns were present on the Fraser and Skagit deltas; non-significant results would have occurred had the geese used the deltas in a random way.

Specific Patterns

Twelve of the 26 radio-marked geese that wintered in California (J. Takekawa, unpubl. data) were tracked on the Fraser and Skagit deltas in fall. Most of the radio-marked geese moved through the deltas between 12 and 16 October, 1991. Therefore, based on the percent of radios (12/26 = 45%) and the fraction of the Wrangel Island population suspected to winter in California (ca. 40%), at least 12,000 California-bound geese used the deltas during fall migration. Telemetry did not begin on the Skagit delta until after most of the radio-marked geese had moved through so the true number may have been higher.

The distribution of radio-marked geese on the deltas varied over space and time. I classified the geese as either Fraser or Skagit birds depending on the amount of time spent on each delta in the fall/early winter period (Fig. 12). Seventeen radio-marked geese used the Fraser and Skagit deltas. Two of these 17 geese (5830 and 5322) were a pair (*pers. obs.*). Nine of the 16 "independent" geese (i.e. 56%) were classified as Fraser birds. This proportion is close to one based on the number of geese on the deltas (mean = ca. 60%). Radio-marked geese, therefore, were divided equally between the deltas and each probably represented the movements of 2,000-3,000 birds.

Fraser radio-marked geese used the Fraser delta from mid-October 1991 to about

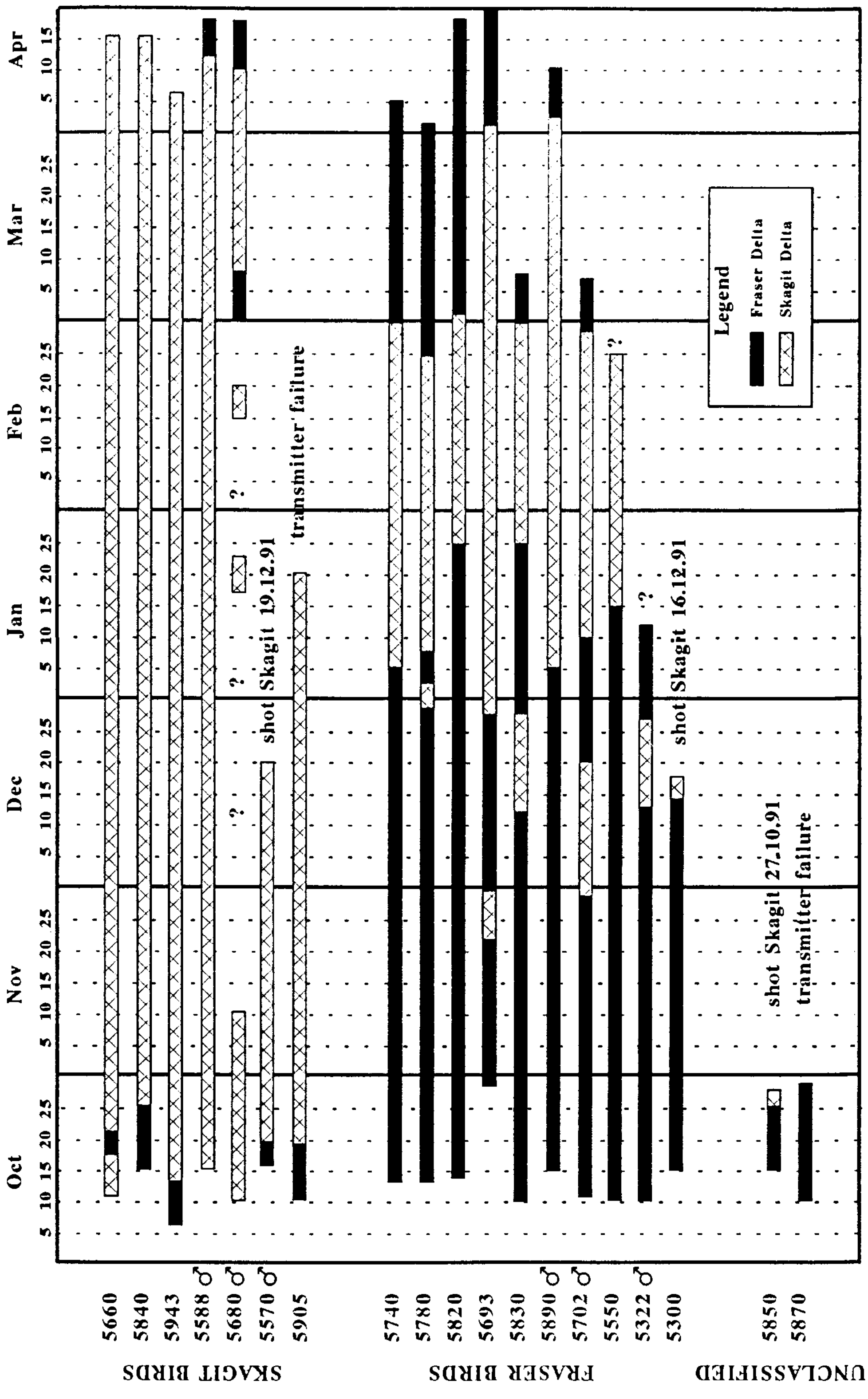


Figure 12. Distribution of radio-marked Snow Geese on the Fraser delta (cross-hatched) and on the Skagit delta (solid) between October 1991 and April 1992. The geese were classified as either "Fraser" or "Skagit" birds (or unclassified). All geese were female except as indicated.

mid-January 1992 and again from early March to mid-April 1992 (Fig. 12). These geese were on the Skagit delta from mid-January to early March 1992. Seven of the 9 Fraser geese returned to the Fraser delta in spring. I suspect that the radios on the other 2 geese failed in mid-winter. The above movement sequence corresponded to the temporal pattern of abundance on the deltas in 1991/92 (Fig. 4F). Skagit radio-marked geese used the Skagit delta from mid-October 1991 through to mid-April 1992. Five of the 7 Skagit geese stopped briefly at the Fraser delta in fall and 2 of 5 Skagit geese stopped at the Fraser delta in spring. These findings suggest that Snow Geese were split into 2 largely distinct groups. One group used the Skagit delta almost exclusively from October through April. The second group was mostly confined to the Fraser delta in fall and spring but was on the Skagit delta in mid-winter.

Several radio-marked geese moved between the deltas outside of the pattern described above. Between November 1991 and January 1992, 4 of the 9 independent Fraser birds (5780, 5693, 5830, and 5702) moved from the Fraser delta to the Skagit delta, remained there for several weeks, and then moved back to the Fraser delta (Fig. 12). This coincided with a movement of about 9,000 geese from the Fraser delta to the Skagit delta in early December 1991 followed by a return flight of about 4,500 birds to the Fraser delta within 2 weeks (Fig. 4F); the pair 5830 and 5322 were involved in both moves. One Skagit bird (5660) moved from the Skagit delta to the Fraser delta in fall and another (5680) did the same in spring.

Figure 13 is an example of telemetry observations collected for a radio-marked goose (5890) in the fall/early winter period 1991/92. Throughout this period, all radio-

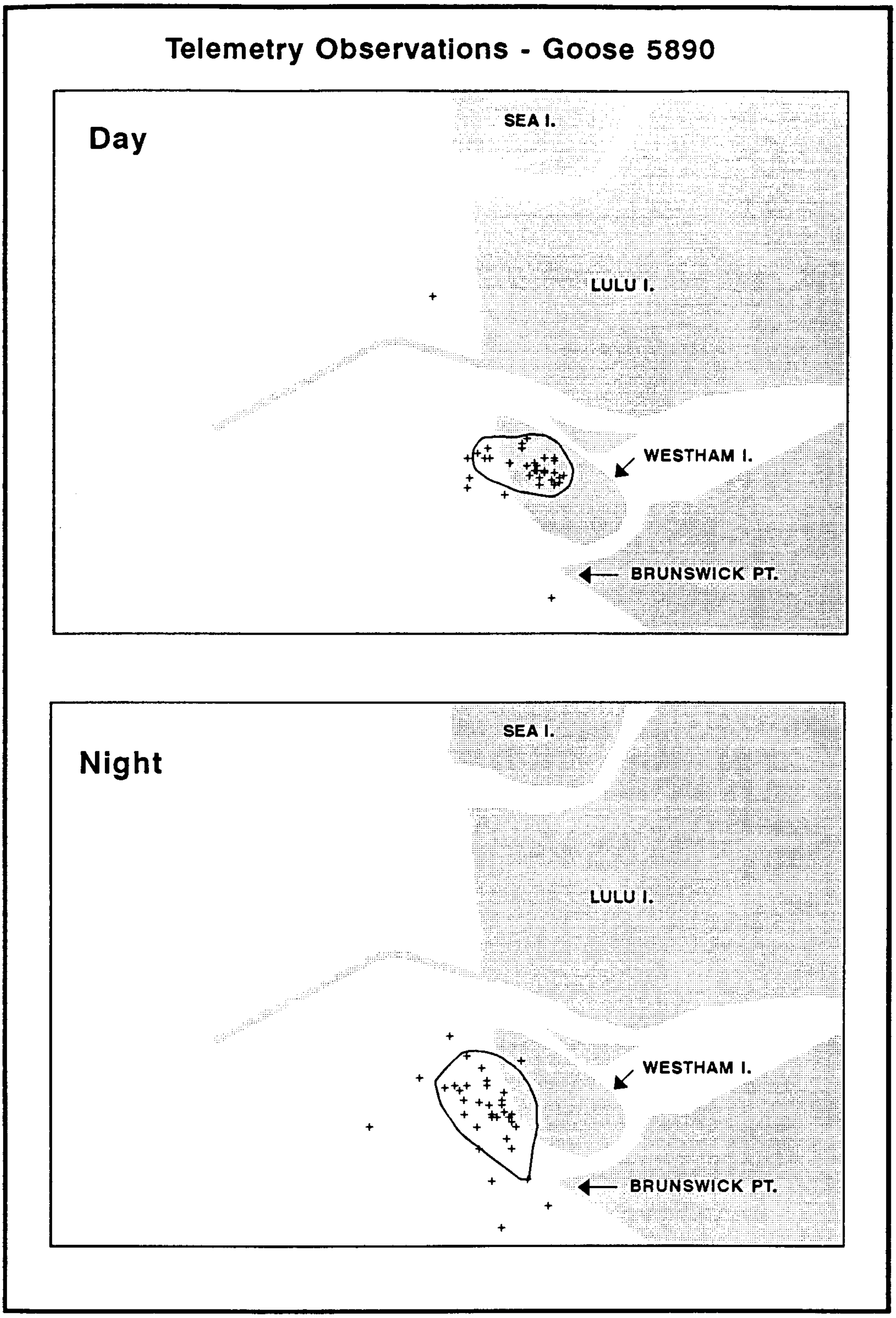
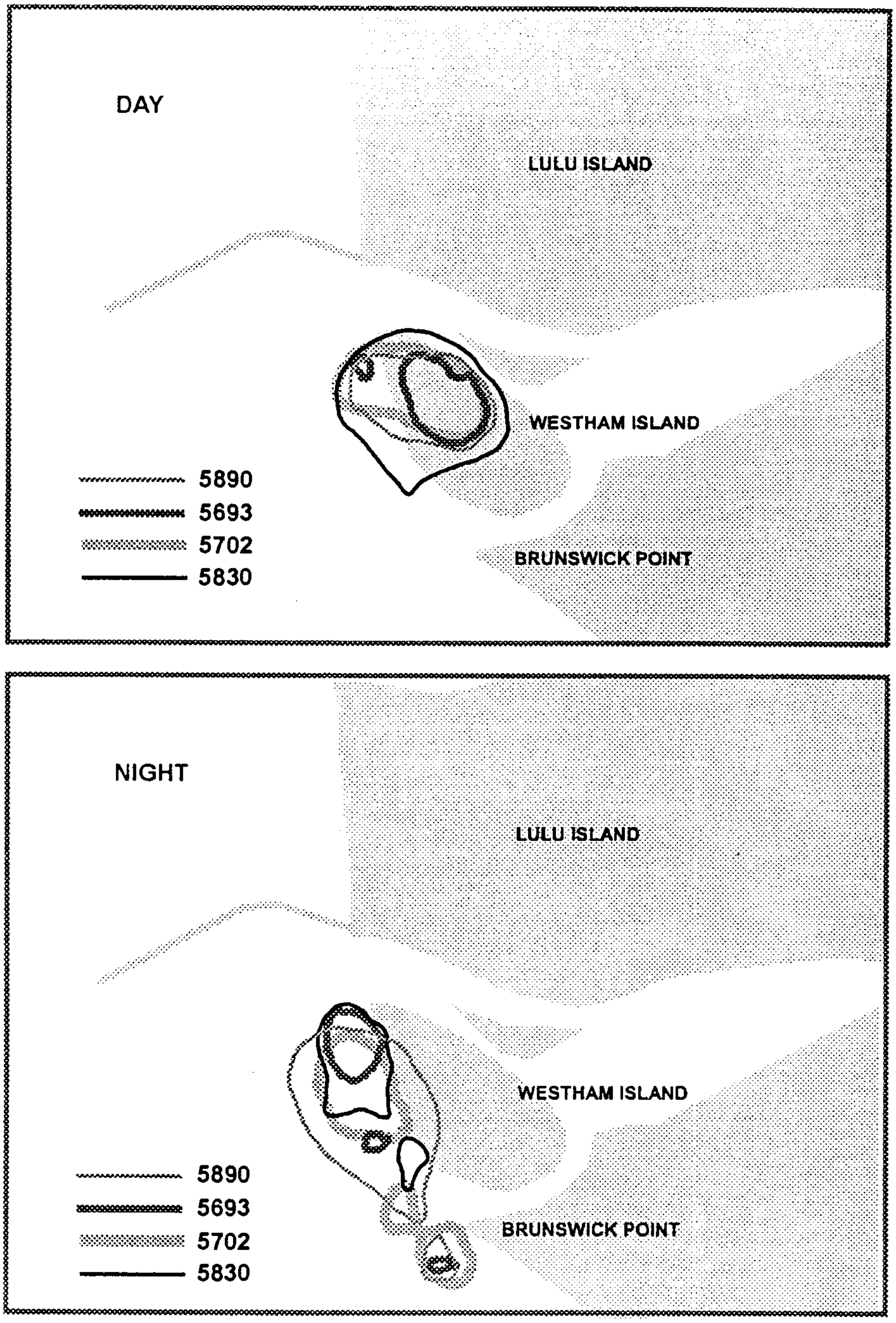


Figure 13. Example of telemetry observations for goose 5890 on the Fraser delta. Such data were used to determine daytime and nighttime home ranges of individual radio-marked Snow Geese on the Fraser delta in fall/early winter. Each cross corresponds to a location estimated by bi- or triangulation. Polygons represent harmonic mean core areas.

marked geese had home ranges that included to a large extent Alaksen NWA fields and Reifel MBS marsh (Figs. 14 and 15). Marked geese did not use Sea Island although several thousand birds were present there in fall/early winter (Appendix 4). Alaksen NWA fields were used only during the daytime by most marked geese. At night, between 1800-0700 h, almost all marked birds were on the tidal marshes close to the Westham Island dykes.

Two home range patterns were apparent on the Fraser delta in the fall/early winter period. Four geese (5693, 5702, 5890, and 5830) used the Alaksen NWA fields and Reifel MBS marsh during the day and the marshes of Westham Island and Brunswick Point at night (Fig. 14). Three other geese (5300, 5850, and 5870) showed the same pattern but their data sets were small. The other home range pattern (exhibited by geese 5550, 5740, 5780, and 5820) coincided with the Alaksen NWA fields and, to a lesser extent, the marsh at the south half of Lulu Island during the day (Fig. 15). At night, these birds were mostly on the marshes at Reifel MBS or the south half of Lulu Island. The above home ranges did not vary between the hunting season (early October to late November 1991) and the non-hunting season (early December 1991 to late January 1992). Also, the 4 birds that moved between the deltas in fall/early winter returned to their same home ranges on the Fraser delta, showing a high level of site-fidelity.

Several Fraser geese returned to the Fraser delta in spring. Goose 5820 was the only one to use Alaksen NWA and Reifel MBS to the same extent as in the fall/early winter period. It also used the marsh at Woodward Island. The spring home range of goose 5693 was largely within its fall home range on the marshes at Westham Island and



HOME RANGE TYPE 1 (FALL)

Figure 14. Harmonic mean core areas describing the Type 1 home ranges of 4 radio-marked Snow Geese on the Fraser delta during the fall/early winter period of 1991. Alaksen NWA fields and Reifel MBS marsh were used during the day and the tidal marshes of Westham Island and Brunswick Point were used at night.

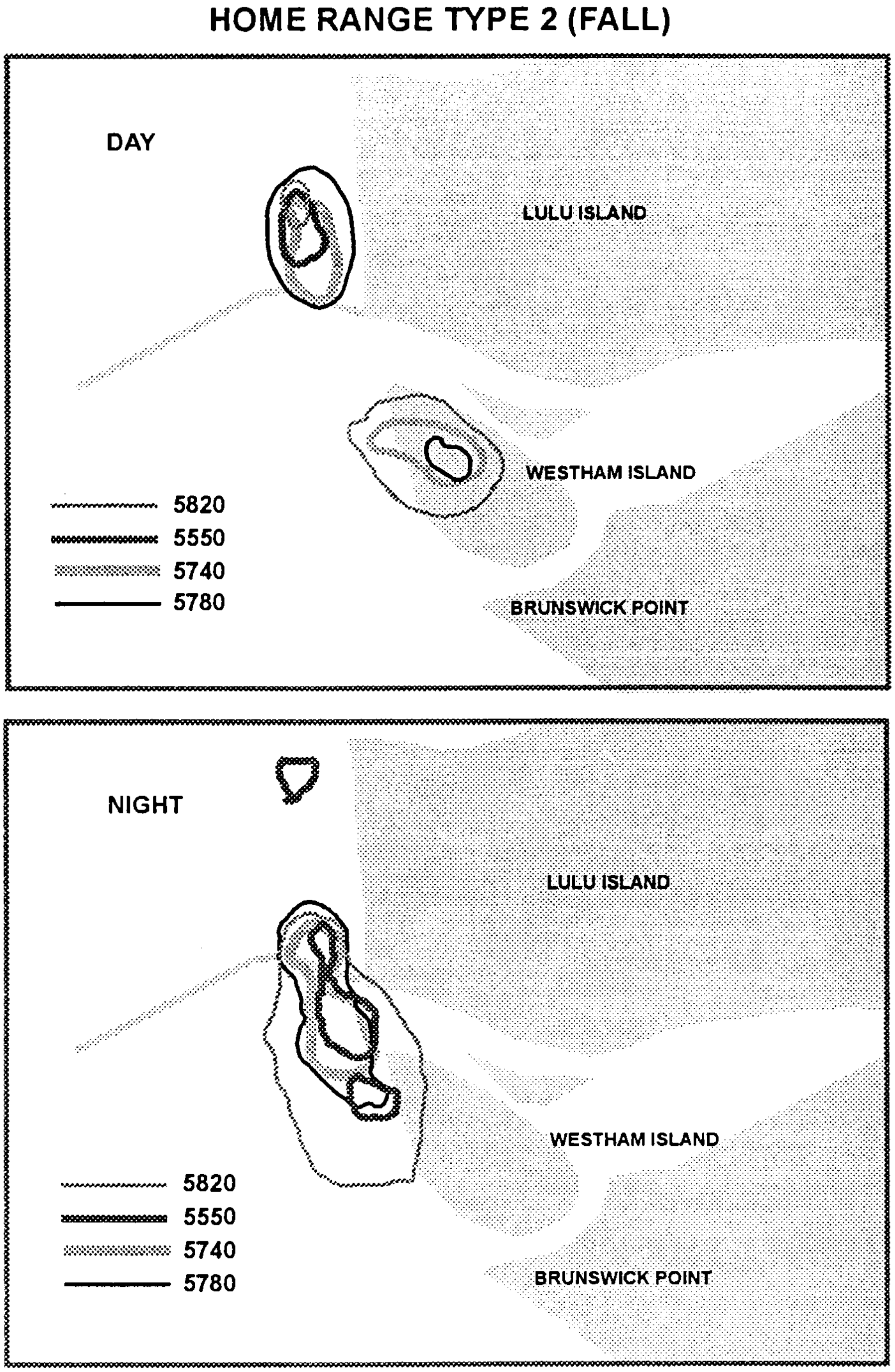


Figure 15. Harmonic mean core areas describing the Type 2 home ranges of 4 radio-marked Snow Geese on the Fraser delta during the fall/early winter period of 1991. Alaksen NWA fields, Reifel MBS marsh, and the marsh at the south half of Lulu Island were used during the day and the tidal marshes of Westham Island and at the south half of Lulu Island were used at night.

Brunswick Point but it did not use Alaksen NWA fields to the same extent as in fall. Geese 5740 and 5780 used only a portion of their previous fall home range, an area centered on the marsh at the south part of Lulu Island.

One radio-marked goose (5780) returned to the Fraser delta in the fall of 1992. It used the same areas during daytime as it did in the fall of 1991 until at least early December 1992 when its radio failed.

I conclude from the above that individual Snow Geese exhibit strong site-fidelity on the Fraser and Skagit deltas and that this tradition results in the formation of largely distinct groups of birds.

2.4 Discussion

2.4.1 Abundance

Annual fluctuations in the size of the Snow Goose population wintering on the Fraser and Skagit deltas were mostly due to a variable recruitment rate. The coefficient of variation for the percent of immature birds in the fall population (80%) was equal to or higher than that for several other populations of Arctic geese with long-term data sets (Ebbinge 1985, 1992, Reed 1990). This reflects the inter-annual variability and severity of conditions on Wrangel Island. Breeding failures were common: 13 of 41 years had <5% immature birds in the fall population and 8 of 41 years were complete failures (0% immature birds). Four consecutive failures in the early 1970s coincided with severe declines in the Wrangel population (from ca. 150,000 to 60,000 birds) and the Fraser/Skagit population (from ca. 50,000 to 15,000 birds).

Recent increases in Arctic goose populations in Europe (Madsen 1991, Mooij 1991, Prokosch 1991, Meire and Kuijken 1991) have been attributed to reductions in harvest (Amat 1986, Ebbinge 1985, 1991). However, the growth of the Fraser/Skagit population after 1980 coincided with a greater (albeit non-significant) number of immatures in the population each year while the number of geese harvested remained relatively constant. My analysis suggests that recruitment was more important than harvest to both the short- and long-term dynamics of this wintering population.

Differential harvest rates likely influenced the spatial distribution of the geese over the long-term. During the last 4 decades, approximately 7 times more geese were harvested on the Skagit delta each year compared to the Fraser delta (from Anon. 1992). Also, more Wrangel Island geese were shot in Oregon and California in the past compared to the Fraser and Skagit deltas combined (Teplov and Shevareva 1965, unpubl. data from J. Bartonek). These differences in harvest on largely distinct groups of birds may account for the increase in the proportion of the Fraser/Skagit population on the Fraser delta in fall and the increase in the proportion of the Wrangel population on the Fraser and Skagit deltas in winter.

Geese using Alaksen NWA have access to an abundance of high quality food in fall/early winter. As a result, they may be in better physical condition and experience higher natural survival rates compared to geese using other parts of the Fraser delta or the Skagit delta. Also, Alaksen NWA on the Fraser delta may attract and retain some birds that otherwise would move on to the Skagit delta or to California in fall. These factors may have contributed to the proportional shifts in goose distribution noted above.

A detailed analysis of banding records would help clarify this issue.

Abundance and telemetry data suggested that the Fraser and Skagit deltas support a largely closed population in winter. Airphoto counts could be used with a conservative return rate (75% based on 6 years when immature birds made up <5% of the population) to predict the minimum number of geese returning the following year (pre-harvest estimate). Hunting regulations could then be adjusted to help maintain the population within desired limits (see Middleton *et al.* 1993).

2.4.2 Distribution

My study concurs with several others which showed that Arctic geese are site-faithful and consistent in their distribution and movement patterns (Raveling 1979, St. Joseph 1979, Owen and Black 1990, Wilson *et al.* 1990, Ebbinge 1992). Radio-marked geese could be classified as either Fraser or Skagit birds based on their movement and occupancy patterns and individual birds on the Fraser delta had distinct home ranges throughout the fall/early winter period. Also, the large-scale movement of Fraser geese to the Skagit delta in mid-winter was consistent across years.

Site-fidelity results in the development of distinct groups, each with their own survival and recruitment rates. The Wrangel population divides into largely discrete California and Fraser/Skagit components (Anon. 1992, this study) and the Fraser/Skagit population also splits into largely distinct Fraser and Skagit components in fall. Separate flocks may even be present on the Fraser delta for part of the year.

Estuarine deltas are relatively stable environments across years. Traditional patterns of habitat use are probably adaptive for long-lived birds such as Snow Geese

(Owen and Black 1990). Tradition means that habitat use patterns change slowly but once a new pattern emerges it becomes entrenched. As an example of this, Snow Geese did not use Alaksen NWA until the early 1980s even though it was established in 1972 (Hatfield 1991), and they have used it every year since. Also, marshes at Woodward Island began to develop in the 1950s but Snow Geese were not observed there until the late 1970s (Burton 1977, J. Hatfield and R. Young *pers. comm.*); the marshes were used every spring during this study. Finally, despite the fact that farmland on the Skagit delta was flooded with 1-2 m of water and cover crops were unavailable during the entire winter of 1990/91, all Fraser birds moved to the Skagit delta in mid-winter and remained there for 6-7 weeks.

I suspect that the traditional distribution and movement patterns observed today reflect compromises made historically by the geese between food quality/quantity and hunting disturbance. Cover crops have higher concentrations of nitrogen and carbohydrates compared to bulrush rhizomes (unpubl. data) and grazing is probably less energy-expensive than grubbing. Hence, cover crops should be a more profitable food (Stephens and Krebs 1986, Krebs and Davies 1987) and Snow Geese should graze them whenever and wherever it is safe to do so. This appears to be the general pattern. Geese use agricultural fields on the Skagit delta but usually only in large numbers after the fall/early winter hunting season has closed. Fields used prior to this time are those in which hunting has been prohibited. On the Fraser delta, farms are used in fall/early winter only on Alaksen NWA where hunting is prohibited. The geese often move onto other farmland on Westham Island but only during non-hunting periods. Further, all

Fraser geese move to the Skagit delta in mid-winter. At this time, cover crops are available and hunting is prohibited on the Skagit delta but hunting has traditionally occurred on the Fraser delta. The movement occurs despite the fact that rhizome quality (nitrogen and carbohydrate levels) improves from September to January (Chapter 3) and rhizomes are still relatively abundant in the lower half of the bulrush zone on Westham Island (Chapter 4). The above observations suggest that the geese exploit a food-profitability gradient (Drent *et al.* 1978/79, Charman 1979, Boudewijn 1984, Madsen 1985) within the contraints imposed by hunting disturbance (Ebbinge 1991). This pattern of exploitation continues in spring when the geese return to the Fraser delta and graze on high quality shoots of sedge (*Carex lyngbyei*).

2.5 Conclusions and Recommendations

The Fraser and Skagit deltas support a largely closed population of Snow Geese in winter. Both the short- and long-term dynamics of the population appear to be mostly influenced by recruitment which, in turn, is largely affected by weather conditions on Wrangel Island. The size of the Fraser/Skagit population after 1980 was greater than in the previous 3 decades and this coincided with an increase in the mean number of immature geese. The proportion of Fraser/Skagit geese on the Fraser delta in fall and the proportion of Wrangel geese on the deltas in winter increased in recent years. Differential harvest rates on largely distinct groups of birds may explain these increases. Snow Geese showed high site-fidelity and consistency in their distribution and movement patterns on the deltas. These traditional patterns may reflect compromises that have developed over time with respect to spatial and temporal differences in food quality/quantity and hunting disturbance.

The Wrangel Island population of Snow Geese is unique. It is the last remaining one of its kind in Russia and the only wintering population of Snow Geese in Canada. Because it is highly traditional and largely closed on the Fraser and Skagit deltas in winter, relatively accurate estimates of abundance, recruitment, and harvest can be achieved. Within the constraints imposed by recruitment on Wrangel Island, it may be possible to maintain this population within desired limits by manipulating harvest and by intensively managing refuges. The following demographic data should continue to be collected for management purposes: annual estimates of the size of the wintering population on the Fraser and Skagit deltas, the percent of immature birds and family sizes in the fall population, and the number of geese (including immature birds) harvested.

The following studies would help improve our understanding of the population ecology and foraging ecology of the geese: an analysis of existing banding records and, if necessary, additional marking and re-sighting of geese to determine harvest rates and interchange rates between wintering areas; development of a simulation model, with sensitivity analyses, to determine the importance of factors such as recruitment and harvest on population and sub-population dynamics; and an assessment of seasonal differences in intake rates, energy expenditures, biomass and nutrient concentrations of different foods, and disturbance levels to assess the proximate reasons behind the movement patterns of the geese.

Chapter 3

Growth Ecology of American Three-square Bulrush (*Scirpus americanus*) on the Fraser River Delta, B.C.

3.1 Introduction

Snow Geese (*Anser c. caerulescens*) on the Fraser River and Skagit River deltas forage in the foreshore marsh by grubbing (excavating) rhizomes of American three-square bulrush (*Scirpus americanus*) (Burton 1977). Snow Geese have been shown to decrease the biomass and production of different marsh macrophytes in North America (Lynch *et al.* 1947, Burton 1977, Smith and Odum 1981, Smith 1983, Giroux and Bedard 1987a, Reed 1989). On the Fraser delta, Snow Geese removed about one-third of the below-ground mass of bulrush in 1974/75 when the Fraser/Skagit population was ca. 15,000 geese (Burton 1977). The population increased in the late 1970s and is now between 35,000-50,000 geese (Chapter 2). The Fraser delta currently supports ca. 2.5 million goose-days yr^{-1} (Chapter 2) which is more than 3 times that in 1974/75. If the number of geese and their total foraging pressure continue to increase, rhizome mass may be depressed to a point where the geese are unable to meet their energy requirements. This could affect survival rates and patterns of habitat use. Other herbivorous birds (e.g. swans) and input to the estuarine detrital food chain may also be negatively affected. Virtually nothing is known about the growth ecology of bulrush to predict the impact of grubbing.

In Chapter 2, I described the abundance and distribution of Snow Geese on the

Fraser and Skagit deltas. Here, I describe the growth dynamics of bulrush. I begin by investigating the seasonal and annual growth patterns of all plant components in patches at different stem densities, with special emphasis on rhizomes. I then determine if nitrogen limits bulrush growth and describe the levels of selected plant constituents in different plant components. Results will improve our knowledge of bulrush ecology and help in the interpretation of the interaction between Snow Geese and bulrush on the Fraser and Skagit deltas (Chapter 4).

3.2 Methods

3.2.1 Growth Pattern

Two small grids, each 10 m x 10 m, were established in the bulrush zone of Reifel MBS in May 1989. Grid 1 was in a patch with high stem density in the lower half of the zone whereas Grid 2 was in a patch with low stem density. Density was more uniform in Grid 2 than in Grid 1; the latter contained several small craters and channels. Each grid contained 100 plots spaced at 1 m intervals. Once each month, from May to October, I counted the number of live stems in a 25 cm x 25 cm quadrat placed in the middle of each plot in both grids (n = 200 plots total). I also clipped all stems at the mud surface and excavated 2 adjacent substrate cores in 12 or 13 randomly selected plots in each grid (no replacement). The cores (12.5 cm diameter x 30 cm deep) were sampled using a steel cylinder with a serrated cutting edge. All samples were labelled, bagged, and transported to the lab within a few hours. On 4 July and 31 July 1989, 6 additional plots were sampled from a high density area immediately adjacent to Grid 1.

Mud was cleaned from the below-ground plant components using a pressure washer and 2 mm sieve. The samples were rinsed a second time by hand through a 0.5 mm sieve. Roots, rhizomes, and below-ground stem parts were sorted into live and dead material. The latter material was discarded. Some fine root material escaped through the 2 mm sieve so I had to adjust weights with a correction factor (unpubl. data). Above-ground stems were hand-rinsed and sorted into live (green, vigorous) and dead (brown, flaccid) material. All plant components were dried at 70°C for 48 h in a forced-air oven and weighed to the nearest 0.001 g. Weights were converted to g m^{-2} dry mass.

The above sampling scheme was repeated on 29 May, 3 July, and 9 August in 1990. The second sampling date was close to that in 1989 (4 July) but the first and last dates were chosen to be about one week earlier and later than their corresponding 1989 dates to encompass the entire growth period of rhizomes. Sampling procedure was also the same except for the following: cores were split into top (0 to 15 cm) and bottom (> 15 cm) portions and processed separately, cumulative length of all rhizomes was measured to the nearest cm, and 6 extra plots were sampled from an area near Grid 1 on 3 July 1990.

Stainless steel wire (68 kg test) was strung at 25 to 30 cm height around and over the top of metal poles surrounding each grid. The wire was present from late September 1989 to early May 1990 to prevent grubbing by Snow Geese. I checked and repaired the wire several times throughout the winter.

3.2.2 Nitrogen

Experiments were conducted in 2 different patches of bulrush at low but uniform stem density to determine if nitrogen was limiting to growth. Slow release OSMOCOTE 40-0-0 (in pellet form) was used in the first experiment. It was applied on 7 May 1990 and again on 29 April 1991 to 1.5 m x 1.5 m plots in the following concentrations: 0 (control), 150, 300, and 450 kg ha^{-1} nitrogen. A randomized block design was used and each treatment was replicated 10 times. The pellets were spread evenly across each plot and worked into the substrate to a depth of about 2 cm.

Stem densities and maximum stem lengths were measured in 2 quadrats (each 25 cm x 25 cm and systematically located) in each plot on 5 July 1990 and 24 June and 29 July 1991. Two substrate cores (also systematically located) were excavated from each plot on 21 September 1991. Sampling and laboratory procedures for the cores were the same as those described previously. Wire was strung around and over the top of all plots throughout the winter of 1990/91 to prevent grubbing by Snow Geese.

Commercial urea 40-0-0 (in pellet form) was used in the second experiment. It was applied on 29 April 1991 to 1 m x 1 m plots in the following concentrations: 0 (control), 250, 500, 750, and 1,000 kg ha^{-1} nitrogen. A Latin square design was used and each treatment was replicated 5 times. Stem densities and maximum stem lengths were measured in 50 cm x 50 cm quadrats positioned in the middle of each plot on 24 June and 29 July 1991. Two cores were systematically sampled from each plot on 21 September 1991.

3.2.3 Constituents

Plant samples from Grids 1 and 2 were analysed for ash, acid-detergent fibre, soluble carbohydrate, and total nitrogen content. Rhizome samples from the 2 fertilization experiments were analysed for soluble carbohydrate and nitrogen content. Analyses were done at the Dept. of Animal Science, University of British Columbia, using standard methods.

3.2.4 Statistical Analysis

I used ANOVAs with Tukey multiple comparison tests to determine if dry weights varied across grids, months, and years. Paired sample t-tests were used to compare plant components in the top substrate layer versus the bottom layer in 1990. Numbers were transformed with log (x+1) if variances were unequal (Bartlett's test) or the data were non-normal (Kolmogorov-Smirnov test). This transformation helped normalize the data because the standard deviations tended to be proportional to the means, and data, if skewed, were skewed to the right. All tests had a significance level of 0.05. Means (± 1SE) are presented throughout the text.

Linear regression analysis was used to study the relation between rhizome mass and patch stem density. The grids had overlapping densities so I pooled their data. Stem density at the time of sampling was used as the independent variable to establish the consistency of the relationship across years. Stem density adjusted to 4 July 1989 was used to assess changes in rhizome mass across sampling dates, years, and patches. Regressions were compared with F-tests.

I compared constituent levels in roots versus rhizomes with t-tests and temporal differences in rhizome nutrients with ANOVAs. I also compared the level of carbohydrates and nitrogen in rhizomes from Grids 1 and 2 using paired t-tests. Percents were transformed using Arcsine.

3.3 Results

3.3.1 Growth Pattern

1989

Stem density in Grid 1 (the high stem density patch) was 2.5 times greater but live stem mass was only 1.4 times greater than in Grid 2 (the low stem density patch) (Figs. 16A,B, Appendix 7). Shoots in Grid 2 were longer and had larger basal diameters than those in Grid 1 (*pers. obs.*) and these characteristics resulted in greater mean stem masses (Fig. 16C). Live stem mass peaked later in Grid 2 compared to Grid 1 (Fig. 16B) and both live and dead stem masses were greater in Grid 2 by late summer (Figs. 16B,D), perhaps because of their more vigorous stems.

Roots made up 80% and 75% of the total below-ground mass in Grids 1 and 2, respectively. Root mass in Grid 1 did not vary from June to October (Table 1) but real changes may have been masked by high variability in the samples (Fig. 17A). In Grid 2, root mass increased significantly by 111% during August and remained high to mid-October (Fig. 17A).

Rhizome mass changed in the same way in both grids (Fig. 17B). Mass was constant throughout June but it almost doubled between early July and early August (Table 1). It remained high and constant from early August to mid-October.

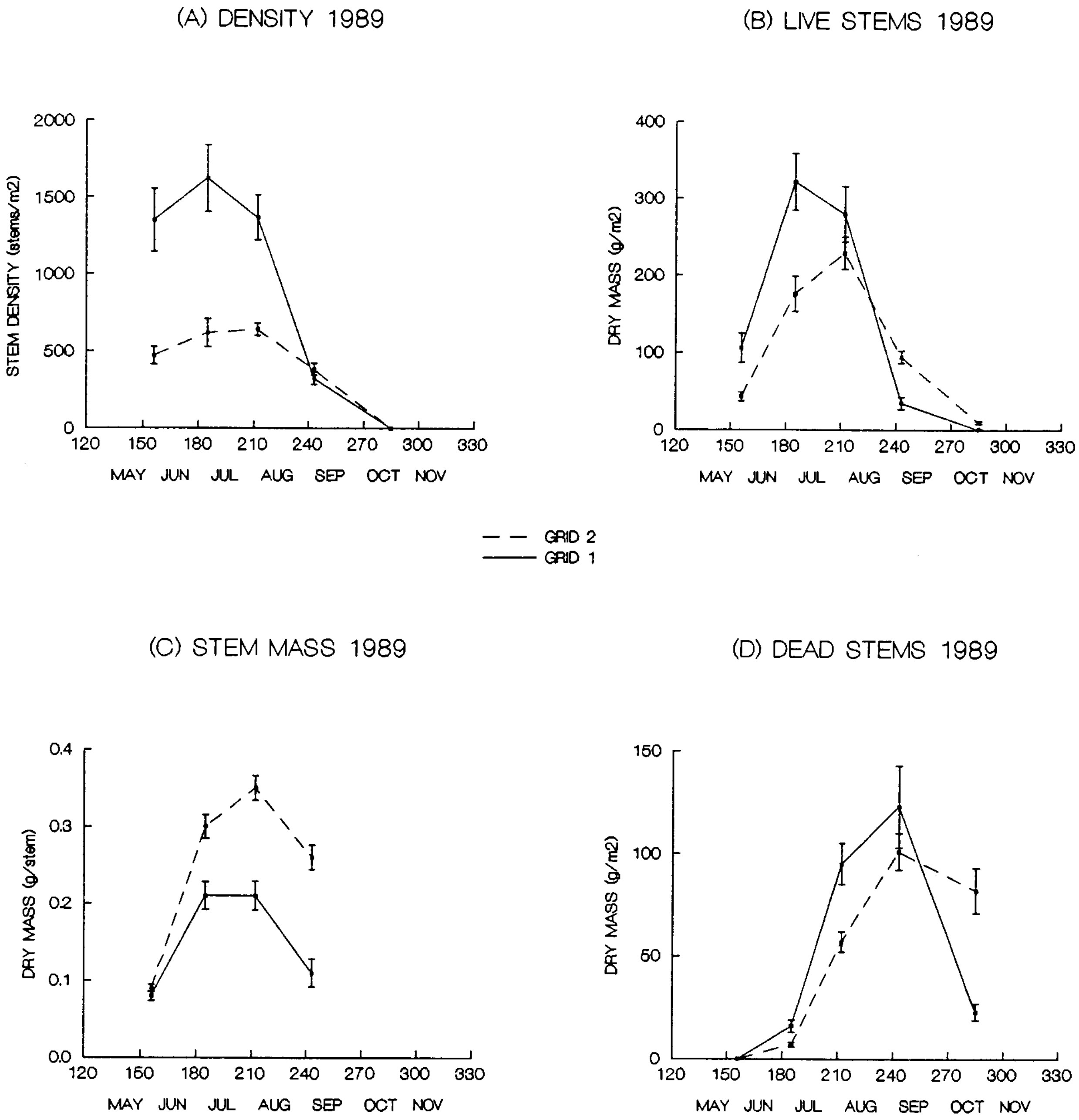


Figure 16. Above-ground components (mean ± 1SE) of bulrush (*Scirpus americanus*) in Grid 1 (high stem density patch) and Grid 2 (low stem density patch) in 1989. (A) Stem density (live stems). (B) Live stem mass. (C) Mean mass per stem. (D) Dead stem mass. Months and Julian days are given on the horizontal axes.

Table 1. Change in bulrush (*Scirpus americanus*) below-ground components in Grid 1 (high density patch) and Grid 2 (low density patch) across 5 months in 1989 and across 3 months in 1990 (1-way ANOVAs). F = F ratio. P = probability.

Component	1989				1990			
	Grid 1		Grid 2		Grid 1		Grid 2	
	$F_{4,58}$	P	$F_{4,58}$	P	$F_{2,34}$	P	$F_{2,34}$	P
Rhizome mass (g m$^{-2)}$	4.43	**0.003**	10.93	**<0.001**	11.04	**<0.001**	9.88	**<0.001**
Root mass (g m^{-2})	0.95	0.439	37.21	**<0.001**	1.17	0.322	4.69	**0.016**
Below-ground mass (g m^{-2})	0.90	0.465	31.80	**<0.001**	0.87	0.425	7.12	**0.003**

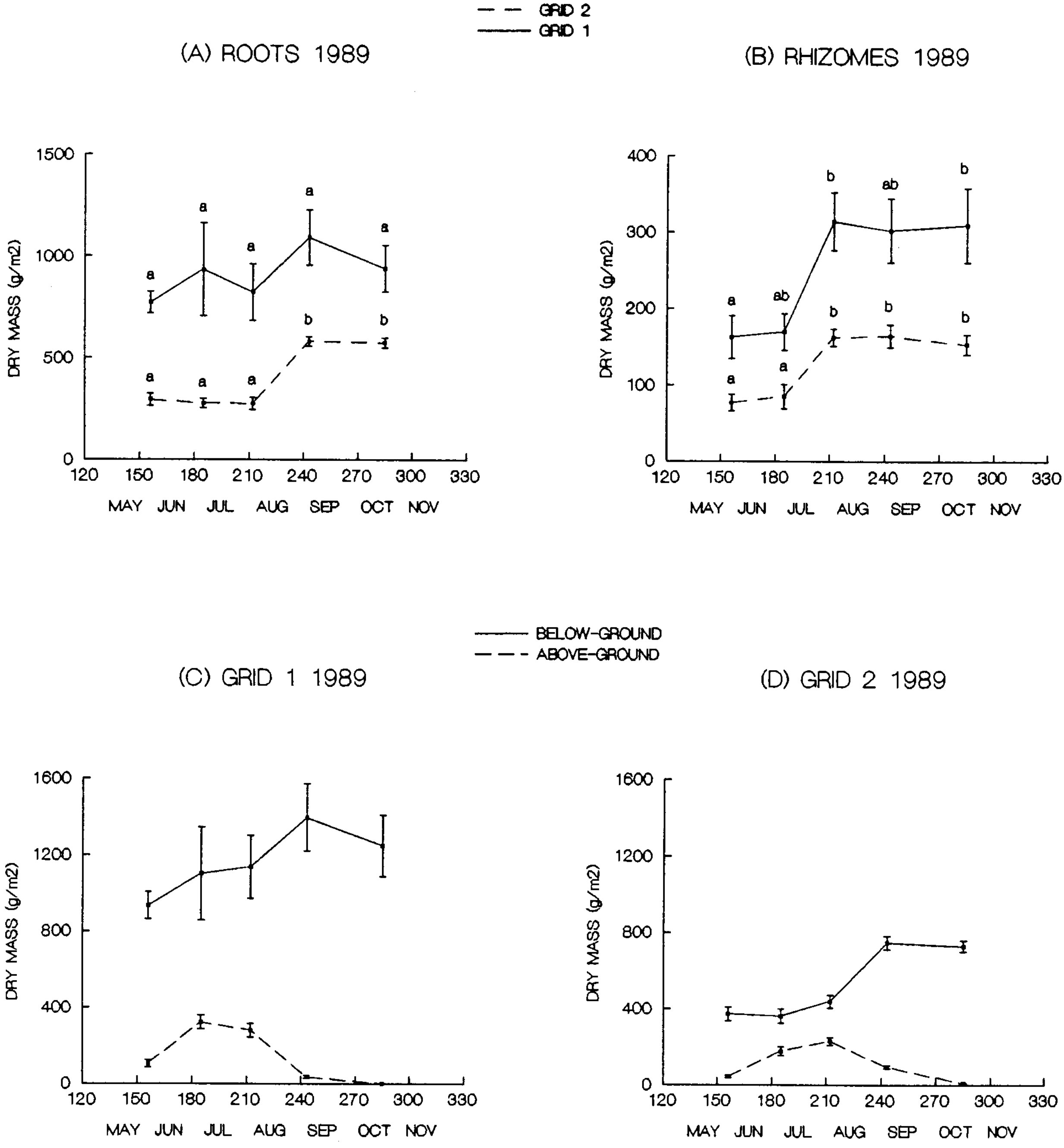


Figure 17. Below-ground and above-ground components (mean ± 1SE) of bulrush (*Scirpus americanus*) in Grid 1 (high stem density patch) and Grid 2 (low stem density patch) in 1989. (A) Root mass. (B) Rhizome mass. (C and D) Below-ground mass (roots plus rhizomes) and above-ground mass (live stems plus below-ground stem material). Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test). Months and Julian days are given on the horizontal axes.

A significant increase in total below-ground mass occurred only in Grid 2 (Table 1, Appendix 7). When live stem mass was at its peak, below-ground mass constituted 77% of the total plant mass in the high stem density patch (Grid 1) and 66% in the low stem density patch (Grid 2).

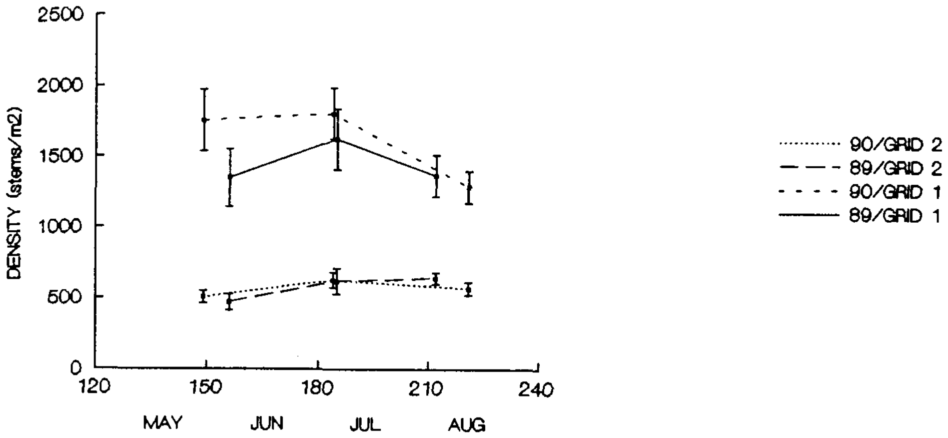
1989 and 1990

All plant components experienced the same growth pattern in 1990 as in 1989 in both grids, at least between early June and early August (Figs. 18 and 19). All components varied across grids (Table 2, Figs. 18 and 19). Above-ground indices (stem density, live and dead stem masses) did not vary across years but below-ground indices (root, rhizome, and below-ground masses) increased significantly. Live stem, dead stem, and rhizome masses were the only components to vary across months (only June, July, and August were considered).

I pooled the data for June and early July (i.e. prior to stem senescence) to investigate resource allocation to the below-ground components over the annual cycle (see Appendix 7). Root mass increased by only 32% in Grid 1 (high stem density patch) but by 104% in Grid 2 (low stem density patch). Rhizome mass increased by only 17% (28 g m^{-2}) in Grid 1 but by 36% (29 g m^{-2}) in Grid 2. Over the annual growth cycle, then, bulrush allocated proportionally more resources to below-ground components in the low stem density patch.

In Grid 2, root mass from August to October 1989 (ca. 600 g m^{-2}) was approximately the same as that present between late May and early August 1990 (Figs. 17A and 19B). This suggests that root growth occurred predominantly in August. From

(A) DENSITY 1989/1990



(B) LIVE STEMS 1989/1990

(C) DEAD STEMS 1989/1990

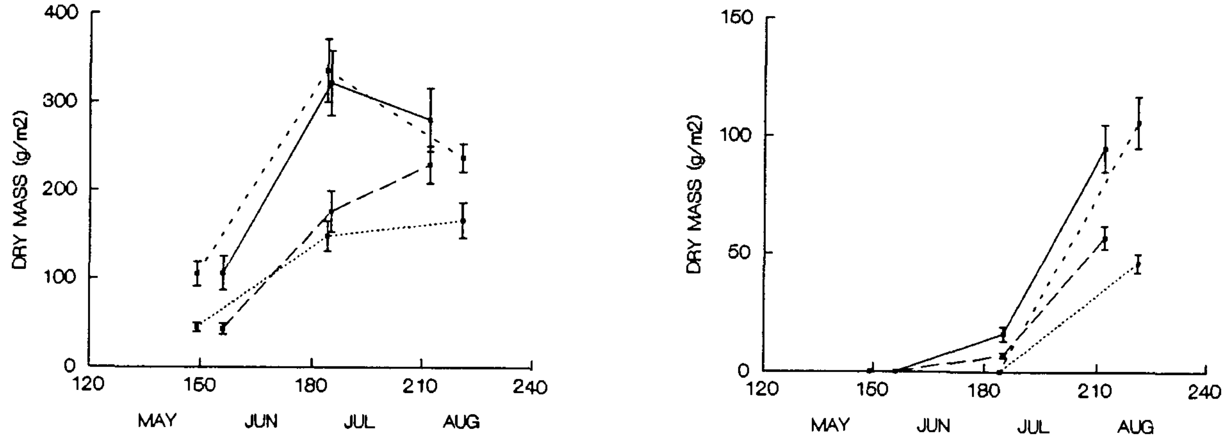


Figure 18. Above-ground components (mean ± 1SE) of bulrush (*Scirpus americanus*) across years (1989 and 1990), patches (Grid 1 and Grid 2), and months (June, July, and August). (A) Stem density (live stems). (B) Live stem mass. (C) Dead stem mass. Months and Julian days are given on the horizontal axes. Grid 1 = high stem density patch. Grid 2 = low stem density patch.

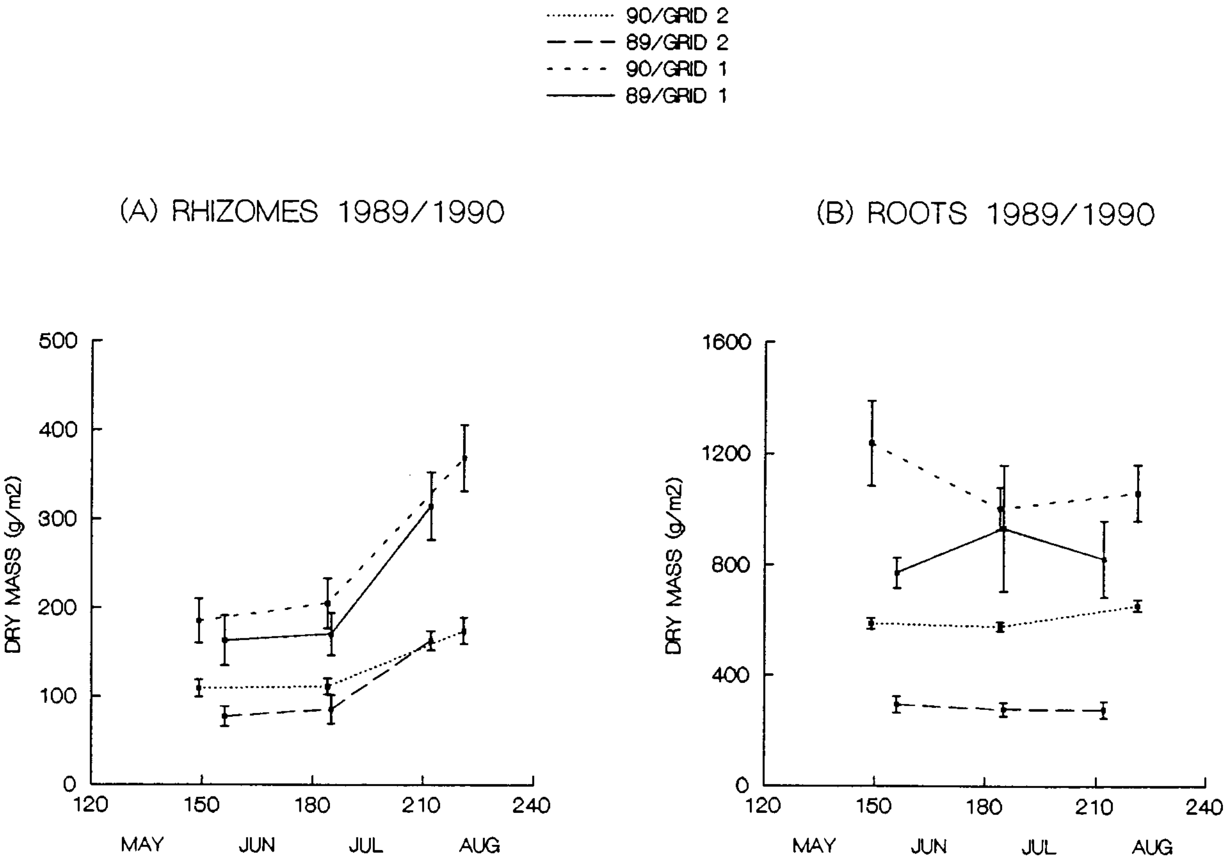


Figure 19. Below-ground components (mean ± 1SE) of bulrush (*Scirpus americanus*) across years (1989 and 1990), patches (Grid 1 and Grid 2), and months (June, July, and August). (A) Rhizome mass. (B) Root mass. Months and Julian days are given on the horizontal axes. Grid 1 = high stem density patch. Grid 2 = low stem density patch.

Table 2. ANOVAs comparing bulrush (*Scirpus americanus*) components across years (1989 versus 1990), patches (Grid 1 versus Grid 2), and months (June, July, and August). df = degrees of freedom. F = F ratio. P = probability.

Source of Variance		Live Stem Mass ($g\ m^{-2}$)		Dead Stem Mass ($g\ m^{-2}$)		Root Mass ($g\ m^{-2}$)		Rhizome Mass ($g\ m^{-2}$)		Below-ground Mass ($g\ m^{-2}$)		Stem Density (stems m^{-2})	
	df	F	P	F	P	F	P	F	P	F	P	F	P
Year	1,138	2.15	0.145	1.99	0.160	27.18	**<0.001**	5.08	**0.026**	24.87	**<0.001**	1.03	0.312
Grid	1,138	50.81	**<0.001**	42.80	**<0.001**	88.70	**<0.001**	73.50	**<0.001**	98.89	**<0.001**	148.63	**<0.001**
Month	2,138	64.48	**<0.001**	320.32	**<0.001**	0.07	0.926	34.20	**<0.001**	1.31	0.273	2.39	0.095
Year x Grid	1,138	0.52	0.468	0.71	0.399	0.33	0.562	0.27	0.603	0.15	0.693	1.30	0.255
Year x Month	2,138	1.52	0.222	1.94	0.146	1.03	0.360	0.01	0.984	0.75	0.474	1.18	0.308
Grid x Month	2,138	6.72	**0.002**	33.66	**<0.001**	0.21	0.806	4.90	**0.009**	0.00	0.992	2.28	0.105
Year x Grid x Month	2,138	0.23	0.789	2.76	0.067	1.18	0.308	0.32	0.720	0.77	0.463	0.48	0.617

fall 1989 to early summer 1990, rhizome mass decreased by 37% (114 g m^{-2}) in Grid 1 and by 32% (51 g m^{-2}) in Grid 2 (data pooled for each period) (Figs. 17B and 19A). Snow Geese were excluded from the grids so these declines occurred in the absence of grubbing.

Substrate Depth

All below-ground components varied significantly across substrate layer (Table 3, Appendix 8). Root mass, rhizome mass, rhizome length, and rhizome linear density (mass per unit length) varied across grids. Only rhizome mass and rhizome linear density varied across months.

In the high stem density patch (Grid 1; 3 months pooled), the top 15 cm layer of substrate contained significantly more root mass and below-ground stem mass than the bottom 15 cm layer (Table 4). However, rhizome mass, length, and linear density did not differ across layers. All indices differed across layers in the low stem density patch (Grid 2). The bottom substrate layer in Grid 2 contained almost 2 times more rhizome mass than the top layer. Recent grubbing in Grid 2 and decreased grubbing intensity with substrate depth would have caused these differences.

All plant indices experienced the same pattern of change over time, regardless of substrate layer (Figs. 20A-E). Root mass and below-ground stem mass remained constant from early June to early August and rhizome mass increased significantly between early July and early August. The change in rhizome mass was due mostly to a significant increase in its mass per unit length rather than length (Figs. 20D,E).

Table 3. ANOVAs comparing bulrush (*Scirpus americanus*) below-ground components across substrate layers (top 15 cm versus bottom 15 cm), patches (Grid 1 versus Grid 2), and months (June, July, and August 1990). df = degrees of freedom. F = F ratio. P = probability.

Source of Variance		Root Mass (g m^{-2})		Rhizome Mass (g m^{-2})		Rhizome Length (m m^{-2})		Rhizome (linear) Density (g m^{-1})		Below-ground Stem Mass (g m^{-2})	
	df	F	P	F	P	F	P	F	P	F	P
Layer	1,136	3.89	**0.050**	13.81	**<0.001**	4.79	**0.030**	7.28	**0.008**	223.78	**<0.001**
Grid	1,136	86.40	**<0.001**	60.71	**<0.001**	78.16	**<0.001**	10.58	**0.001**	3.29	0.072
Month	2,136	1.81	0.168	25.61	**<0.001**	2.17	0.118	12.90	**<0.001**	1.72	0.183
Layer x Grid	1,136	6.86	**0.010**	2.68	0.104	0.73	0.394	0.03	0.847	2.32	0.129
Layer x Month	2,136	0.73	0.480	1.25	0.289	0.54	0.584	0.03	0.964	0.79	0.455
Grid x Month	2,136	2.11	0.124	5.54	**0.005**	0.98	0.378	0.25	0.773	1.63	0.198
Layer x Grid x Month	2,136	0.62	0.535	0.02	0.979	0.26	0.769	0.24	0.785	2.08	0.128

Table 4. Paired-sample t-tests comparing bulrush (*Scirpus americanus*) below-ground components across substrate layers (top 15 cm versus bottom 15 cm) in Grid 1 and Grid 2. Data for 29 May, 3 July, and 9 August 1990 were pooled. Degrees of freedom for each comparison were 36. T = t-test value. P = probability.

Component	Patch Density			
	High (Grid 1)		Low (Grid 2)	
	T	P	T	P
Root Mass (g m^{-2})	3.40	**0.002**	-2.54	**0.015**
Rhizome Mass (g m^{-2})	-1.53	0.134	-7.43	**<0.001**
Rhizome Length (m m^{-2})	-1.05	0.299	-5.22	**<0.001**
Rhizome Linear Density (g m^{-1})	-2.06	0.050	-2.65	**0.012**
Below-ground Stem Mass (g m^{-2})	11.76	**<0.001**	9.25	**<0.001**

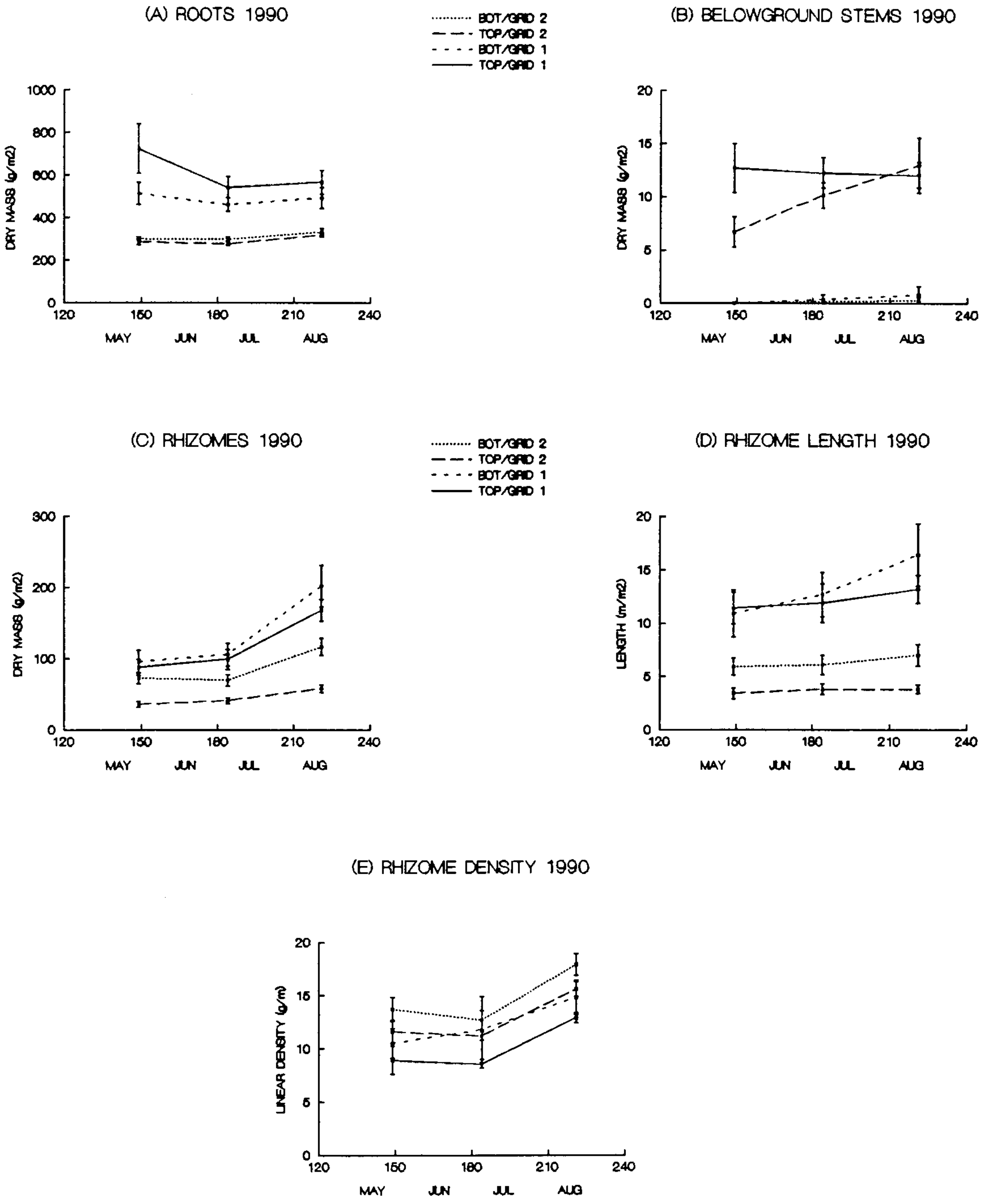


Figure 20. Below-ground components (mean ± 1SE) of bulrush (Scirpus americanus) across substrate layers (top 15 cm [TOP] and bottom 15 cm [BOT]), patches (Grid 1 and Grid 2), and months (June, July, and August) in 1990. (A) Root mass. (B) Below-ground stem mass. (C) Rhizome mass. (D) Rhizome (cumulative) length. (E) Rhizome (linear) density. Months and Julian days are given on the horizontal axes. Grid 1 = high stem density patch. Grid 2 = low stem density patch.

Rhizome Linear Density

The mass per unit length (linear density) of rhizomes increased with decreasing patch stem density. Linear density in the low stem density patch (Grid 2) was 23% greater than in the high density patch (Grid 1) when substrate layers and all months in 1990 were pooled (Fig. 20E). I investigated this relation further by regressing rhizome linear density against stem density (on 4 July 1989) for all plots in Grids 1 and 2 (pooled) for 3 July and 9 August 1990 (Fig. 21). The regressions for both dates were significant ($r^2=0.53$, $F_{1,24}=26.82$, $P<0.001$ and $r^2=0.45$, $F_{1,22}=18.28$, $P<0.001$, respectively) and different ($F_{2,46}=38.54$, $P<0.001$). This result, and the finding that mean mass per stem increases with declining patch density (see Fig. 16C), suggests that the resource allocation strategy of bulrush changes considerably with patch density.

Rhizomes Versus Stem Density

I used linear regression analysis to compare the relationships between rhizome mass and current stem density across years at similar Julian dates (Table 5). Only the regressions for 31 July 1989 and 9 August 1990 were different. Stem senescence was more advanced and destructive sampling occurred one week later in 1990 compared to 1989; hence, fewer stems were present per unit mass of rhizomes on 9 August 1990 compared to 31 July 1989, resulting in the former having a regression with a relatively steep slope. The results suggest that rhizome growth could be compared across sampling dates and patch stem densities if the latter could be adjusted to some common point on the annual growth cycle. I explored this possibility by using densities present on 4 July 1989 as the independent variable (Figs. 22A-F and Figs. 23A-D) and then comparing

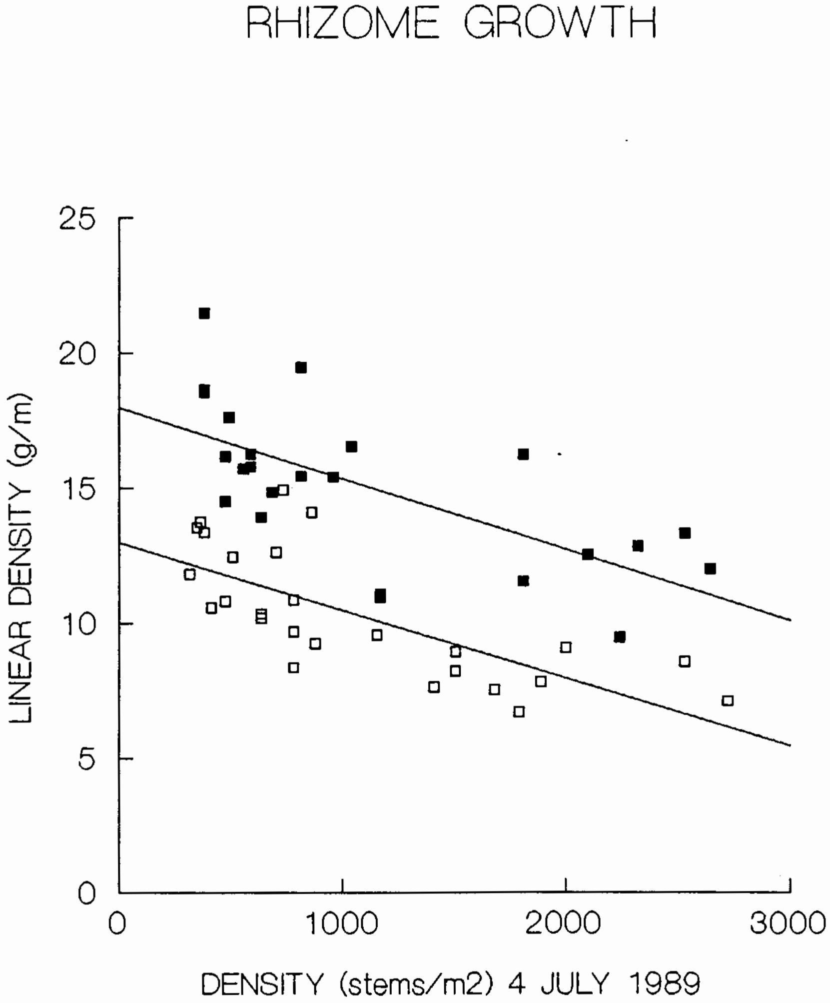
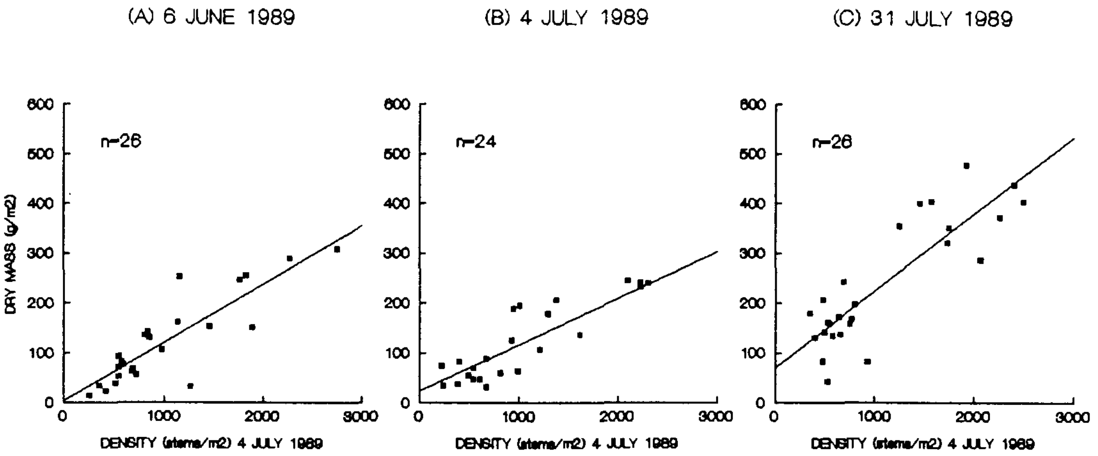


Figure 21. Linear regressions between rhizome (linear) density and stem density (adjusted to 4 July 1989). Grid 1 and Grid 2 data were pooled. Open symbols represent data for 3 July 1990 ($Y=12.9-0.003X$; $r^2=0.53$, $P<0.001$, $n=26$). Closed symbols are for 9 August 1990 ($Y=17.9-0.003X$; $r^2=0.45$, $P<0.001$, $n=24$).

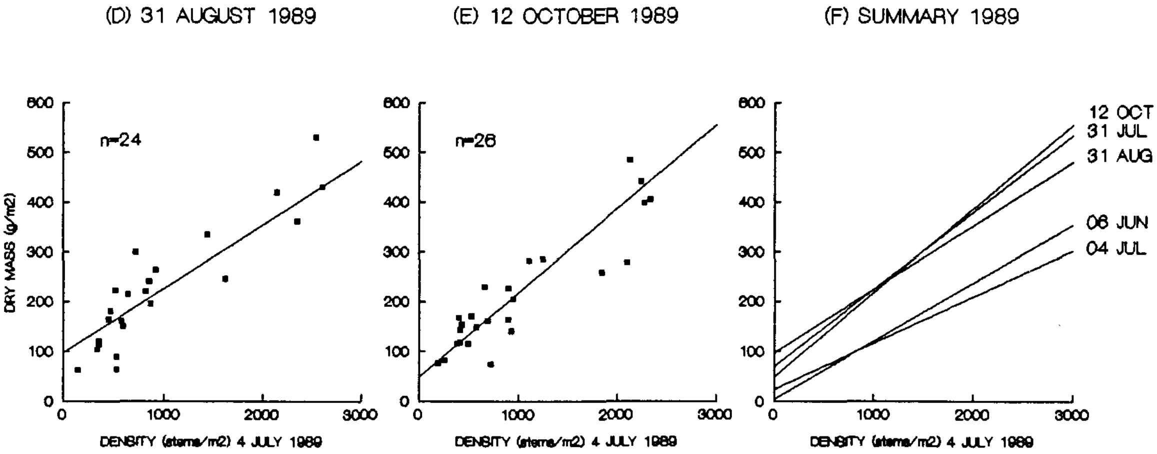
Table 5. Linear regressions of bulrush (*Scirpus americanus*) rhizome mass against current stem density for common dates in 1989 and 1990 plus results of F-tests comparing regression pairs across years.

Date	Linear Regressions				F-test Comparisons		
	r^2	df	F	P	df	F	P
6 June '89	0.75	1,24	72.66	<0.001	2,46	2.32	>0.10
29 May '90	0.60	1,22	33.47	<0.001			
4 July '89	0.88	1,28	205.55	<0.001	2,58	2.23	>0.10
3 July '90	0.64	1,30	54.49	<0.001			
31 July '89	0.71	1,30	74.01	<0.001	2,52	13.31	<0.001
9 August '90	0.84	1,22	118.48	<0.001			


(A) 6 JUNE 1989

(B) 4 JULY 1989

(C) 31 JULY 1989


(D) 31 AUGUST 1989

(E) 12 OCTOBER 1989

(F) SUMMARY 1989

Figure 22. Linear regressions between bulrush (*Scirpus americanus*) rhizome mass and adjusted stem density for 5 dates in 1989. Density was that present on 4 July 1989. Densities >3000 stems m^{-2} were not included in the plots. (A) 6 June. (B) 4 July. (C) 31 July. (D) 31 August. (E) 12 October. (F) Summary regressions for 1989.

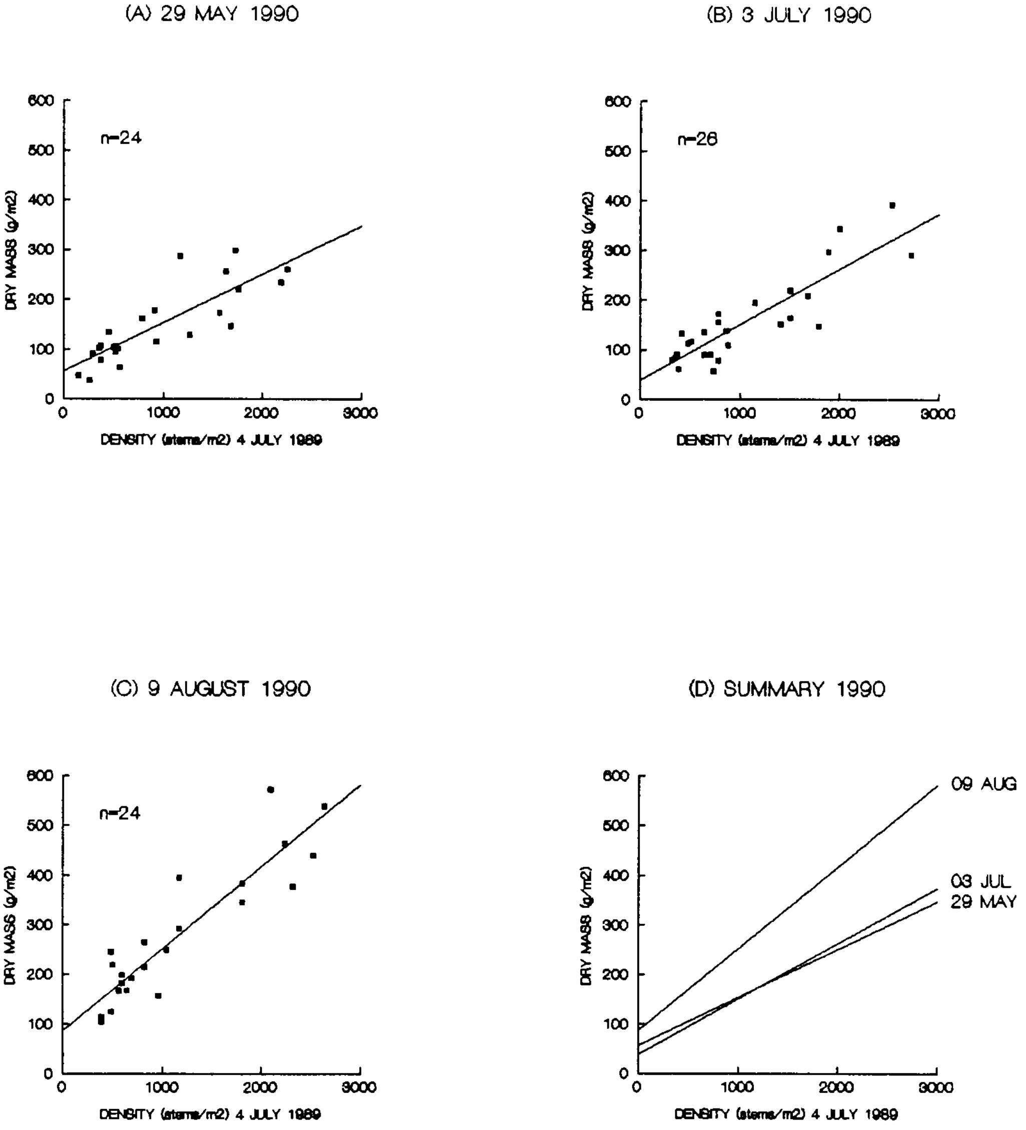


Figure 23. Linear regressions between bulrush (*Scirpus americanus*) rhizome mass and adjusted stem density for 3 dates in 1990. Density was that present on 4 July 1989. Densities >3000 stems m^{-2} were not included in the plots. (A) 29 May. (B) 3 July. (C) 9 August. (D) Summary regressions for 1990.

regressions for consecutive dates (Table 6). Only the regressions for early July and early August differed in both years, suggesting that rhizome mass increased significantly and consistently between these dates across all patch densities.

I investigated rhizome growth across years by pooling data for dates before the July growth phase and for dates after this phase for both years and then comparing the resulting regressions for the same periods across years (Table 7, Fig. 24). The early 1989 and early 1990 regressions were different, suggesting that the net increase in rhizome mass was significant across years and across all patch stem densities. The net increase was relatively constant, varying only between 32-38 g m^{-2} yr^{-1} in patches from zero density to 3,000 stems m^{-2}. The late 1989 and late 1990 regressions did not differ; low sample size may have been the reason (sampling occurred only once in late 1990).

3.3.2 Nitrogen

OSMOCOTE

On 5 July 1990, 1.5 months after fertilization, the 450 kg ha^{-1} nitrogen application of OSMOCOTE resulted in a 75% increase in stem density over the controls (Table 8, Fig. 25A). Even greater responses were recorded in 1991; by 24 June and 29 July, concentrations as low as 300 and 150 kg ha^{-1} resulted in 92% and 68% increases, respectively. Maximum stem length responded in the same way, with significant increases occurring at lower concentrations in the second year (Fig. 25B).

The 450 kg ha^{-1} nitrogen treatment of OSMOCOTE resulted in a 50% increase in rhizome mass over the controls by September 1991 (Fig. 26A). Rhizome masses at the 150 and 300 kg ha^{-1} treatment levels increased by ca. 40% over the controls but these

Table 6. Linear regressions of bulrush (*Scirpus americanus*) rhizome mass against adjusted stem density for different dates in 1989 and in 1990 plus results of F-tests comparing consecutive regression pairs within each year. Densities were those estimated on 4 July 1989.

Date	Linear Regressions				F-test Comparisons		
	r^2	df	F	P	df	F	P
6 June '89	0.75	1,24	72.45	**<0.001**			
					2,46	1.06	>0.25
4 July '89	0.78	1,22	77.92	**<0.001**			
					2,46	31.75	**<0.001**
31 July '89	0.73	1,24	67.98	**<0.001**			
					2,46	0.68	>0.50
31 August '89	0.79	1,22	87.65	**<0.001**			
					2,46	2.23	>0.10
12 October '89	0.86	1,24	148.42	**<0.001**			
29 May '90	0.69	1,22	48.86	**<0.001**			
					2,46	0.36	>0.50
3 July '90	0.76	1,24	78.46	**<0.001**			
					2,46	30.10	**<0.001**
9 August '90	0.83	1,22	107.42	**<0.001**			

Table 7. Linear regressions of bulrush (*Scirpus americanus*) rhizome mass against adjusted stem density for pooled dates in 1989 and 1990 plus results of F-tests comparing regression pairs across years. Densities were those estimated on 4 July 1989.

Date	Linear Regressions				F-test Comparisons		
	r^2	df	F	P	df	F	P
6 June & 4 July '89	0.75	1,48	146.72	<0.001	2,96	8.08	<0.001
29 May & 3 July '90	0.73	1,48	131.07	<0.001			
31 July, 31 August & 12 October '89	0.79	1,74	287.68	<0.001	2,96	2.63	>0.05
9 August '90	0.83	1,22	107.42	<0.001			

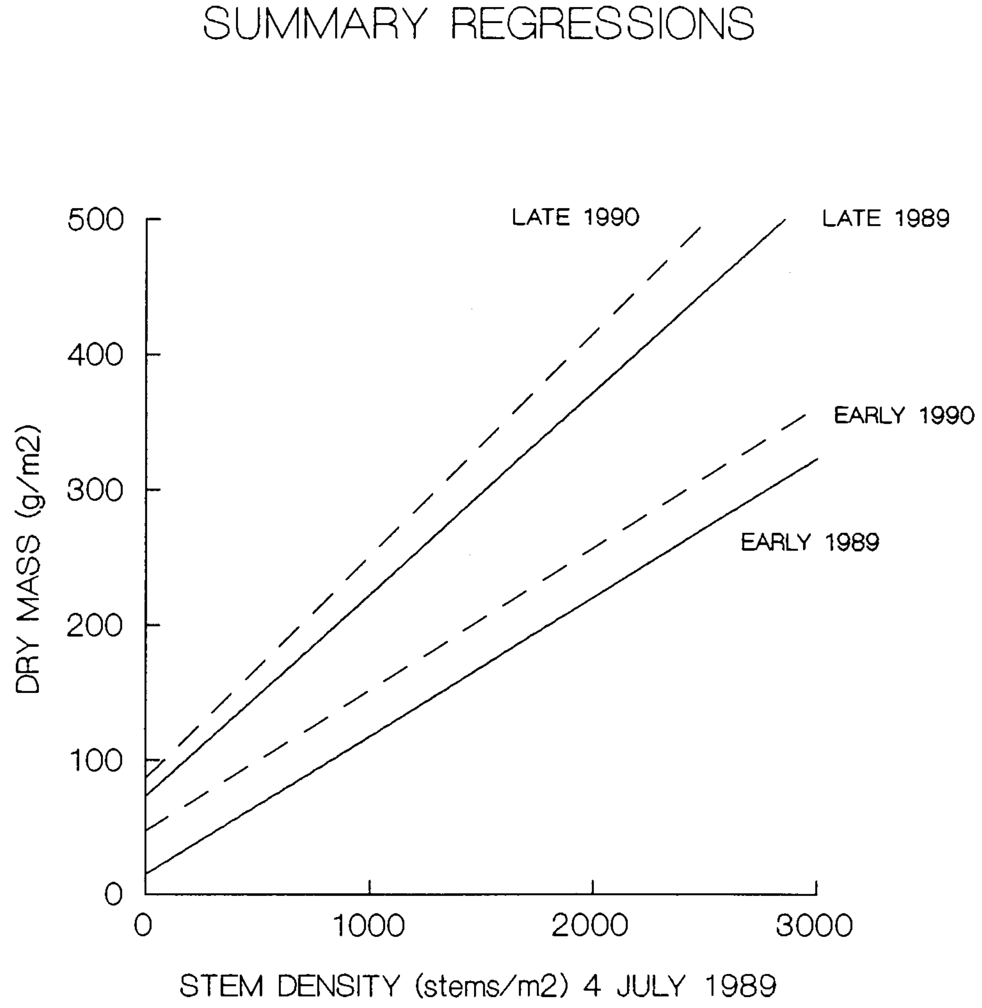
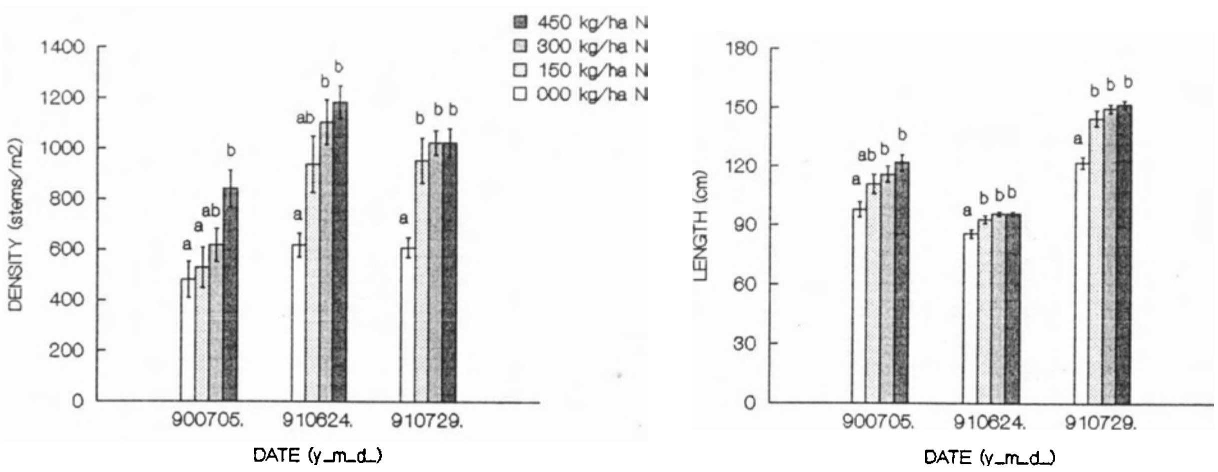


Figure 24. Bulrush (*Scirpus americanus*) rhizome growth across seasons, years, and patch densities. Regression lines were derived by pooling the data for the following dates: 6 June and 4 July (early 1989); 31 July, 31 August, and 12 October (late 1989); 29 May and 3 July (early 1990); 9 August (late 1990).

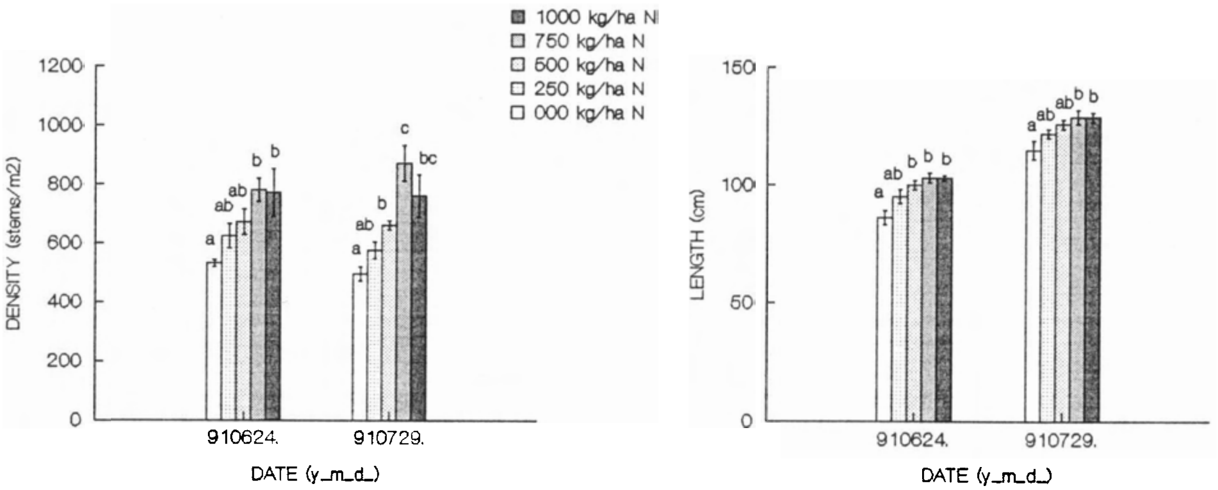
Table 8. ANOVAs testing the effect of nitrogen addition on bulrush growth. Rhizomes and roots were sampled in September 1991. OSMOCOTE was applied in the springs of 1990 and 1991 whereas urea was applied only in the spring of 1991.

Component	OSMOCOTE		UREA	
	$F_{3,36}$	P	$F_{4,20}$	P
Stem Density (stems m^{-2})				
- 5 July 1990	4.84	**0.006**	-	-
- 24 June 1991	9.04	**<0.001**	5.21	**0.005**
- 29 July 1991	10.30	**<0.001**	12.30	**<0.001**
Max. Stem Length (cm)				
- 5 July 1990	5.92	**0.002**	-	-
- 24 June 1991	7.16	**0.001**	9.39	**<0.001**
- 29 July 1991	24.86	**<0.001**	5.19	**0.005**
Rhizomes				
- Mass (g m^{-2})	3.64	**0.021**	3.85	**0.018**
- Length (m m^{-2})	2.35	0.088	3.29	**0.032**
- Linear Density (g m^{-2})	0.96	0.420	1.39	0.270
Root Mass (g m^{-2})	0.38	0.764	3.16	**0.036**



(A) OSMO/STEM DENSITY

(B) OSMO/STEM LENGTH



(C) UREA/STEM DENSITY

(D) UREA/STEM LENGTH

Figure 25. Effect of OSMOCOTE (A and B) and urea (C and D) on bulrush (*Scirpus americanus*) stem density and stem length in 1990 and 1991 (for each sampling date, n = 10 plots per OSMOCOTE treatment and n = 5 plots per urea treatment). OSMOCOTE was applied in the spring of both 1990 and 1991 whereas urea was applied only in the spring of 1991. Mean response values (± 1SE) are presented. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

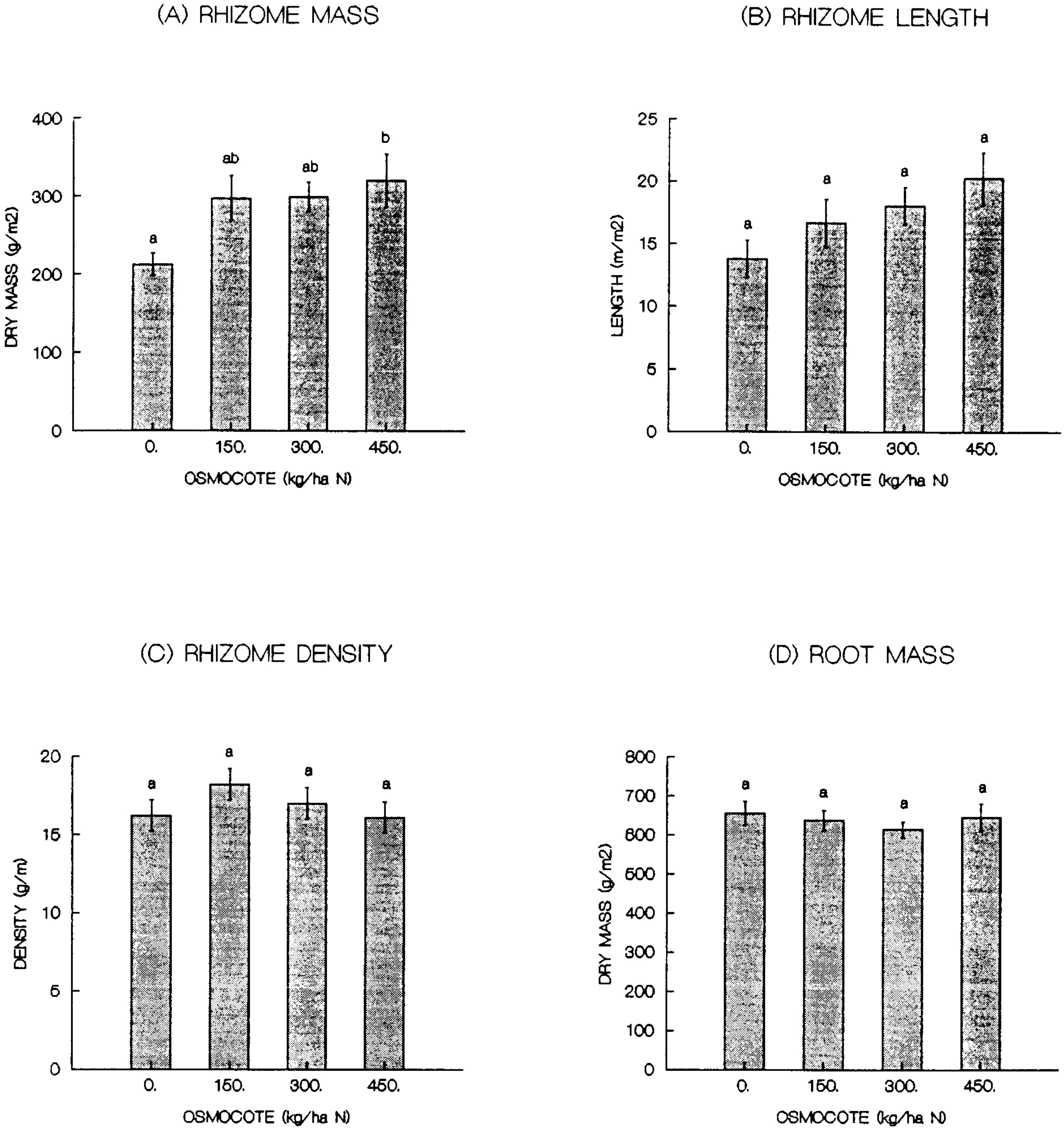


Figure 26. Effect of OSMOCOTE on bulrush (*Scirpus americanus*) below-ground components in September 1991 (n = 10 plots per treatment). OSMOCOTE was applied in the spring of both 1990 and 1991. (A) Rhizome mass. (B) Rhizome (cumulative) length. (C) Rhizome (linear) density. (D) Root mass. Mean response values (± 1SE) are presented. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

increases were not significant. Although a positive trend in rhizome length occurred, neither length nor linear density varied significantly with OSMOCOTE treatment (Figs. 26B,C). Root mass showed no response to any treatment (Fig. 26D).

Urea

In the urea experiment, the 750 kg ha^{-1} nitrogen treatment caused a significant increase in stem density 1.5 months after application (24 June 1991) and the effective concentration decreased to 500 kg ha^{-1} by 29 July 1991 (Table 8, Fig. 25C). Maximum stem length on 24 June and 29 July 1991 increased significantly over the controls at concentrations of 500-750 kg ha^{-1} (Fig. 25D).

Rhizomes and roots responded positively and significantly to almost the entire range of urea treatments (Figs. 27A-D). Rhizome mass increased significantly by 500 kg ha^{-1} nitrogen (80% increase over controls; Fig. 27A). Most of the increase in mass was caused by an increase in rhizome length, significant at 750 kg ha^{-1} but positive over lower concentrations (Fig. 27B). Rhizome linear density did not vary across treatments. Roots responded significantly only at the 1000 kg ha^{-1} level but the response was positive over all concentrations (Fig. 27D).

3.3.3 Constituents

Rhizomes are a much higher quality food for Snow Geese compared to roots. Rhizomes contained 2.6 times less ash, 1.7 times less fibre, 6.3 times more soluble carbohydrates, and 1.6 times more total nitrogen than roots (t-tests: $P<0.001$; Figs. 28A-D). Live stems had the highest soluble carbohydrate and total nitrogen levels whereas dead stems had low carbohydrate but relatively high nitrogen levels (Figs. 28C,D).

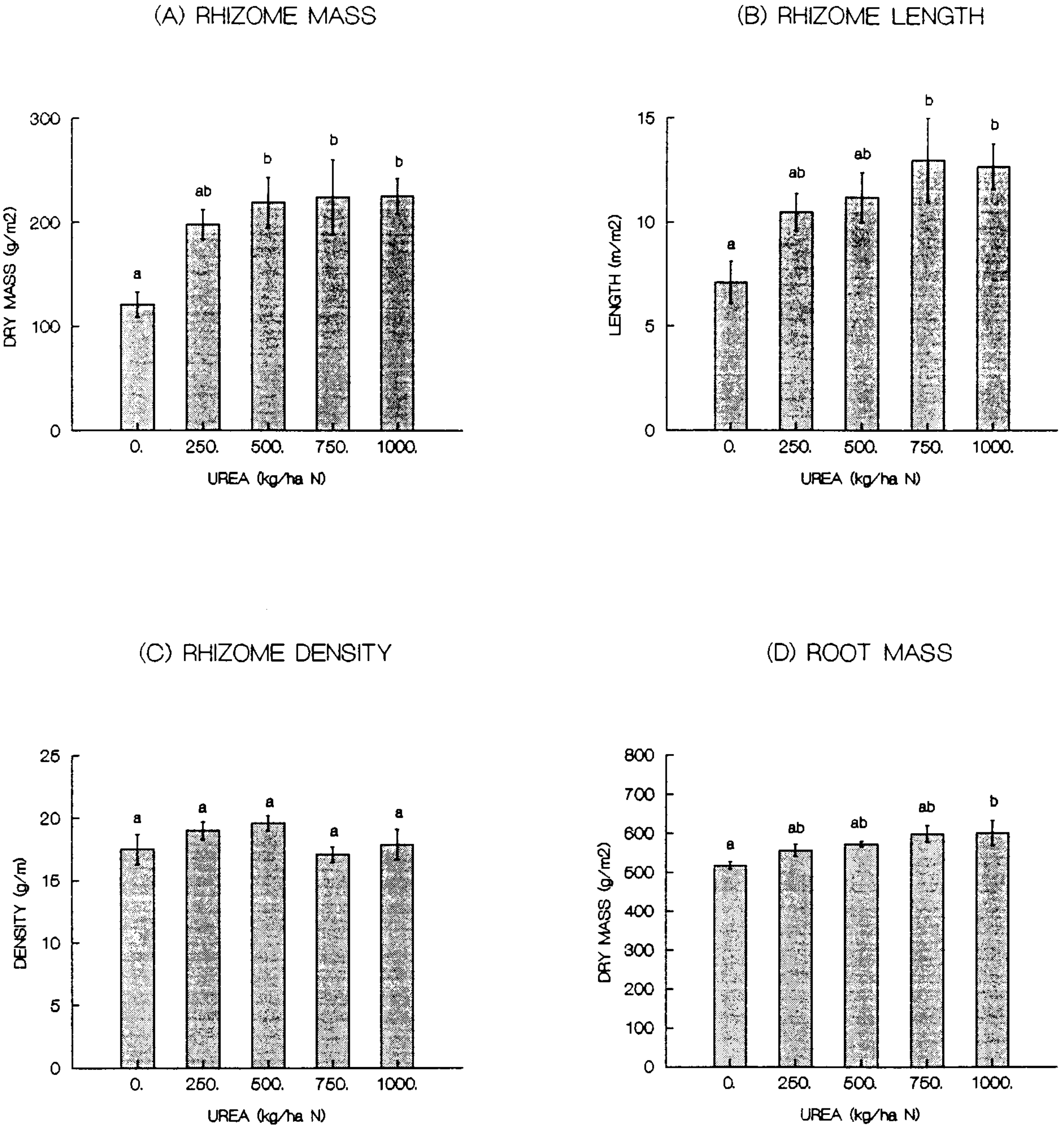


Figure 27. Effect of urea on bulrush (*Scirpus americanus*) below-ground components in September 1991 (n = 5 plots per treatment). Urea was applied in the spring of 1991. (A) Rhizome mass. (B) Rhizome (cumulative) length. (C) Rhizome (linear) density. (D) Root mass. Mean response values (± 1SE) are presented. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

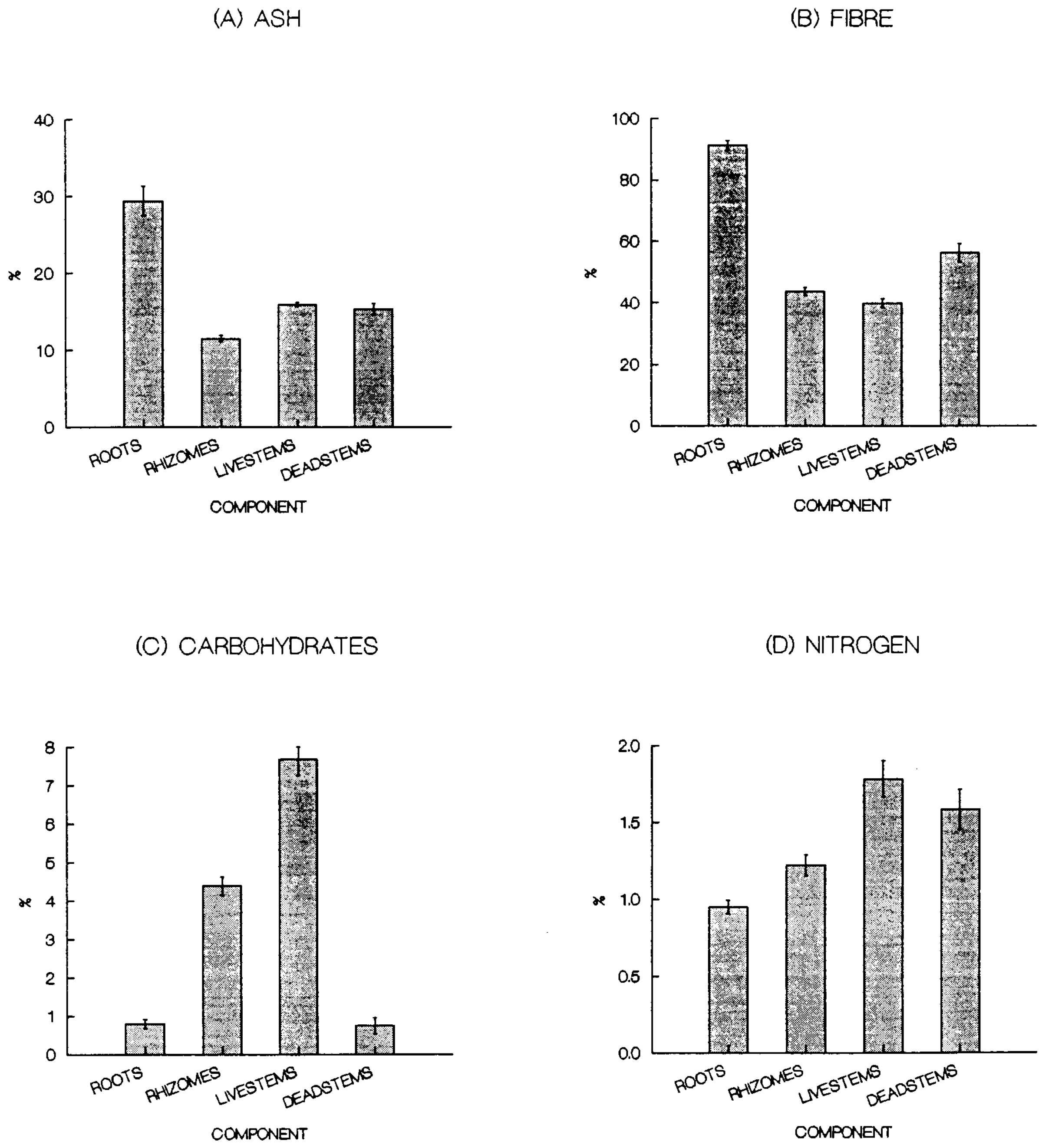


Figure 28. Mean percent (± 1SE) of (A) Ash, (B) Acid detergent fibre, (C) Soluble carbohydrates and (D) Nitrogen in bulrush (*Scirpus americanus*) roots, rhizomes, live stems, and dead stems. Data for 1989 and 1990 were pooled (n=38 for both roots and rhizomes, n=30 for live stems, and n=5 for dead stems). Ash content was based on dry mass (DM) whereas the other constituents were based on ash-free dry mass (AFDM).

Rhizome carbohydrate and nitrogen levels did not differ between the high and low density grids (paired t-tests: $P>0.5$; mean values for different dates were used as the sample units). Rhizome nitrogen content in September 1991 increased positively with OSMOCOTE and urea concentration but the response was significant only with OSMOCOTE (a 35% increase by the 300 kg ha^{-1} nitrogen treatment; Figs. 29A,B). The lack of significance with urea was probably due to the small sample size per treatment ($n=2$). Rhizome nitrogen concentration increased significantly between September 1991 and April 1992 in the control and 150 kg ha^{-1} OSMOCOTE plots (Fig. 29C). Carbohydrate content increased significantly between September 1991 and January 1992 and remained constant to April 1992 for both treatments (Fig. 29D).

3.4 Discussion

3.4.1 Growth

Bulrush rhizome mass increased only during July in both years and in both patches studied. This growth coincided with the lowest tides during daylight, the warmest and sunniest weather, and peaks in stem density and live stem mass. All of these factors probably contributed to high photosynthetic rates. Some of the photosynthate, surplus to the maintenance and growth requirements of the plant, would have been translocated to the rhizomes for storage, similar to the mobilization patterns of other marsh macrophytes (Kistritz *et al.* 1983, Schubauer and Hopkinson 1984, Bellis and Gaither 1985, Hackney and de la Cruz 1986, Groenendijk and Vink-Lievaart 1987, and Giroux and Bedard 1988).

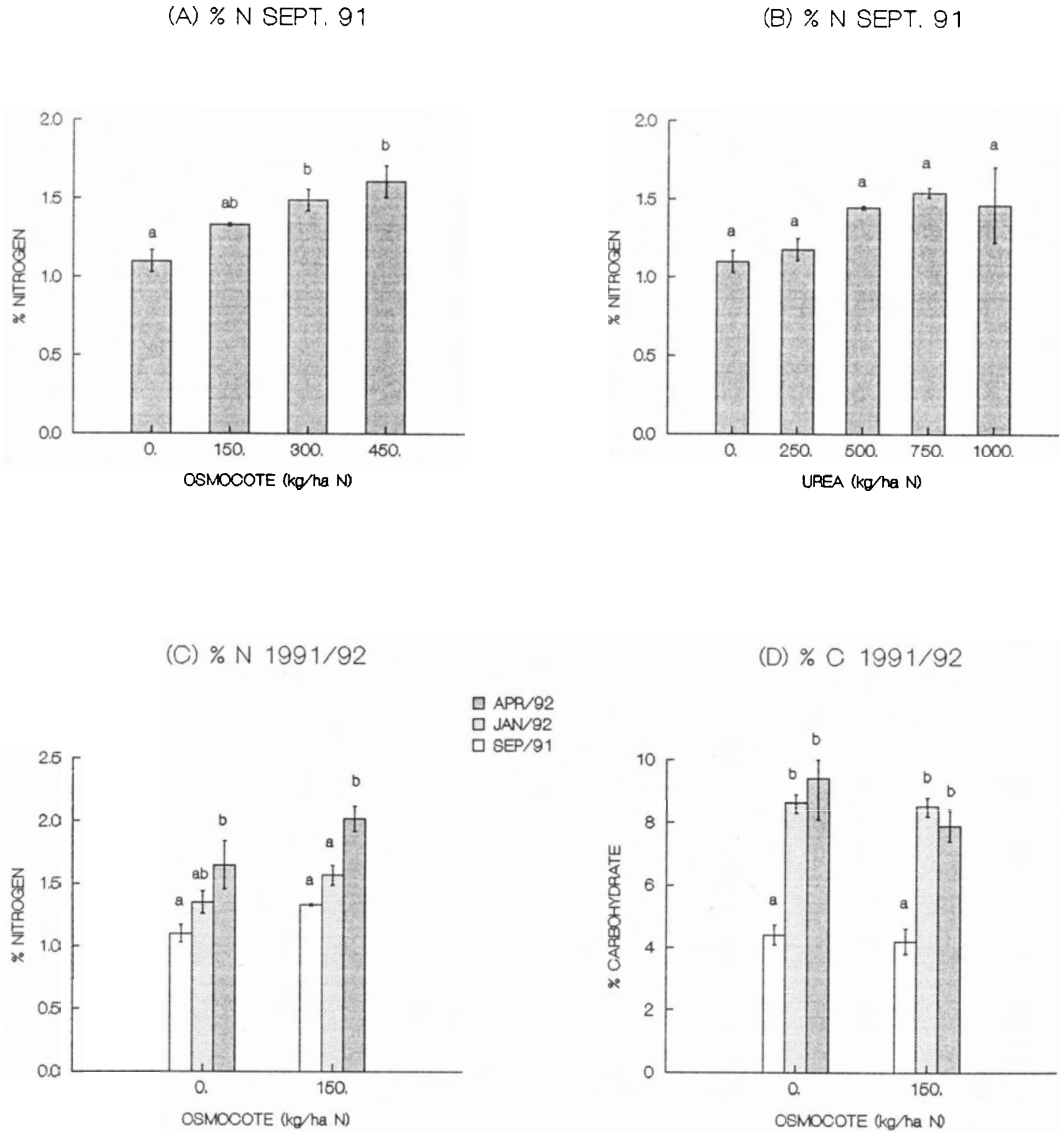


Figure 29. (A and B) Effect of OSMOCOTE and urea on nitrogen concentrations in bulrush (*Scirpus americanus*) rhizomes in September 1991 (n=5 for each OSMOCOTE treatment and n=2 for each urea treatment). OSMOCOTE was applied in the spring of both 1990 and 1991 whereas urea was applied only in the spring of 1991. (C and D) Rhizome nitrogen and soluble carbohydrate concentrations in September, January, and April of 1991/92. The rhizomes were previously exposed to no (control) or 150 kg ha^{-1} nitrogen treatments of OSMOCOTE (n=5 per date for each treatment). Mean percents (± 1SE) are presented. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

In the high stem density patch (Grid 1), rhizome mass increased by 142 g m^{-2} during the summer but declined by 114 g m^{-2} during the following fall-spring period for a net annual increase of 28 g m^{-2} yr^{-1}. In the low stem density patch (Grid 2), rhizome mass increased by 80 g m^{-2} in July and declined by 51 g m^{-2} for a net annual increase of 29 g m^{-2} yr^{-1}. Hence, the production of rhizome mass within a single growing season was considerably greater in the high density patch but, when considered over the annual growth cycle, the net change in rhizome mass was the same for both patches. Also, both mean mass per stem and rhizome linear density increased (see above) and seed production decreased (*pers. obs.*) as patch density decreased. These results suggest that bulrush alters how it allocates resources to different plant components as patch density changes. Other factors, such as a decline in rhizome mortality/leaching rates or a decrease in competition for limiting resources (light, nitrogen) with declining patch density, may also contribute to the constant, annual growth function. These mechanisms should be studied in more detail.

Reed (1989) suggested that rhizomes growing beyond the probing depth of Greater Snow Geese (*Anser caerulescens atlantica*) may have been partially responsible for maintaining bulrush growth in Cap Tourmente marshes on the St. Lawrence River estuary in spite of heavy grubbing pressure. This may also be true on the Fraser delta. In the low stem density patch (Grid 2; uniformly grubbed in recent years), substrate below 15 cm depth contained ca. 66% of all rhizome mass throughout the summer of 1990. Also, in the upper part of the bulrush zone in Reifel MBS where grubbing intensity is high, substrate below the estimated probing depth of Lesser Snow Geese (>20 cm) contained ca. 10% of all rhizome mass in spring (unpubl. data collected over 2 years). This inaccessible reserve may be important to the stability of the goose-bulrush interaction on the Fraser delta.

In summary, a constant net, annual increase in rhizome mass across all patch densities and the presence of deep rhizomes should help maintain bulrush growth irrespective of grubbing pressure. These factors are likely important to the current low level steady-state of bulrush on the Fraser delta (Chapter 4).

3.4.2 Nitrogen

Nitrogen is limiting to bulrush growth on the Fraser delta. Two commercial fertilizers had positive effects on all plant components, including the mass and quality of bulrush rhizomes. These results are consistent with the findings of other studies (Sullivan and Daiber 1974, Valiela and Teal 1974, Gallagher 1975, Patrick and DeLaune 1976, Buresh *et al.* 1980, Smart and Barko 1980, Loveland and Unger 1983, Cargill and Jefferies 1984, Covin and Zedler 1988). Senescent stems, with their relatively high levels of nitrogen (Fig. 28D), are exported from the marsh every autumn (*pers. obs.*) and geese remove large amounts of rhizomes and attached roots every winter (Chapter 4). These mechanisms may be responsible for keeping nitrogen at a low and limiting level.

Based on the results of my experiments, an application of 200-300 kg ha^{-1} nitrogen (urea) to the mid-upper half of the bulrush zone on Westham Island in May would increase rhizome mass in September by ca. 75% over its normal level. The total amount of rhizome soluble carbohydrate and nitrogen in the treated area would increase by ca. 75% and 100%, respectively. These levels may increase further if fertilization was conducted over several, consecutive years. Such an enhancement would have positive benefits for both the estuarine grazing and detrital food chains. Documenting the response of Snow Geese to the enhancement would improve our understanding of their foraging requirements. For example, the geese may reduce their foraging time or foraging intensity on Alaksen NWA fields or they may remain on the Fraser delta in mid-winter instead of moving to the Skagit delta. Such changes in behaviour would suggest that rhizome mass may have been previously at a level where the geese were unable to meet their requirements for some essential nutrient.

3.5 Conclusions and Recommendations

The growth pattern of bulrush is typical of tidal marsh macrophytes throughout the temperate zone of North America: photosynthate is translocated from shoots to storage structures in summer and most plant mass is concentrated below-ground. Although rhizome mass in the high stem density patch increased more than in the low density patch in summer, both patches experienced the same net increase in mass over the annual cycle. This constant growth function, along with significant changes in stem and rhizome vigour, suggest that the resource allocation strategy of bulrush changes with patch density. This, and the presence of deep (>20 cm) rhizomes, may be important to the low level steady-state on the Fraser delta (Chapter 4). These mechanisms should be studied in more detail.

All bulrush components responded positively to commercial fertilizers, suggesting that nitrogen is limiting to growth on the Fraser delta. The upper part of the bulrush zone at Westham Island could be fertilized and the response of Snow Geese studied. This would improve our understanding of their foraging requirements.

Chapter 4

Interaction Between Lesser Snow Geese (*Anser c. caerulescens*) and Three-square Bulrush (*Scirpus americanus*) on the Fraser and Skagit River Deltas

4.1 Introduction

In Chapters 2 and 3, I described the abundance and distribution of Snow Geese on the Fraser and Skagit deltas and the growth ecology of one of their principal foods, bulrush rhizomes. In this chapter, I investigate the dynamic interaction between goose-grubbing and rhizome-growth. The intent is to assess the stability of the interaction and to predict the outcome should the goose population continue to grow.

Grubbing (excavating) of below-ground plant components by Snow Geese can substantially reduce the biomass and production of coastal macrophytes (Lynch *et al.* 1947, Burton 1977, Smith and Odum 1981, Smith 1983, Giroux and Bedard 1987a, and Reed 1989). The number of Greater Snow Geese staging on the St. Lawrence estuary increased dramatically in recent decades (Reed 1990) but bulrush below-ground mass has remained at a low level equilibrium (Giroux and Bedard 1987a, Reed 1989). Lesser Snow Geese (*Anser c. caerulescens*) removed about one-third of the below-ground mass of bulrush (*Scirpus americanus*) on the Fraser delta in 1974/75 (Burton 1977). The Fraser/Skagit population increased in the late 1970s and remained high throughout the 1980s to the present (Anon. 1992). Between 1987 and 1992, the Fraser delta supported ca. 2.5 million goose-days yr^{-1} (Chapter 2) or 3-4 times that in 1974/75. Snow Geese began to forage on Alaksen NWA farms in the early 1980s and this behaviour has intensified in recent years (Hatfield 1991, *pers. obs.*). The reason for this new foraging behaviour is unknown but it may have something to do with the grubbing pressure exerted by the geese versus the regrowth potential of bulrush. In this chapter, I describe the current status of rhizome mass on the deltas, estimate growth and removal rates of rhizomes, determine the temporal and spatial patterns of grubbing, and assess the impact of grubbing on substrate dynamics. I also generate rhizome growth and removal rate functions (Noy-Meir 1975) and compare these functions over time and space.

4.2 Methods

4.2.1 Rhizome Growth and Removal Rates

RRI and RRO Grids

In 1988, I established 2 large (100 m x 250 m) grids in the monotypic bulrush zone of Westham Island (Fig. 2). One grid (RRI) was located inside the Reifel Migratory Bird Sanctuary (MBS). The other (RRO) was 350 m south of the sanctuary boundary. Both grids were positioned in the middle of the bulrush zone at the same substrate elevation (unpubl. data).

The first corner plot in each grid was located randomly and all other plots were placed relative to it. Each grid had 3 rows oriented in a north-south direction, perpendicular to the direction of the tide. The rows were 50 m apart and each contained 11 plot pairs positioned at 25 m intervals. The plot pairs were 15 m apart with the "off-row" plot perpendicular to the direction of the row. Exclosures were erected around the odd-numbered "on-row" plots and the even-numbered "off-row" plots. Hence, 11 closed and 11 open plots were staggered along each row. In 1990, I added 5 rows to the RRI grid to include most of the elevation gradient of the bulrush zone. Three rows were added above the grid and 2 rows were added below, increasing the total size of the RRI grid to 350 m x 250 m. The top row was ca. 50 m away from the sedge zone whereas the bottom row ended before the bulrush became discontinuous with mudflat.

Two 5 cm x 5 cm x 1 m long stakes marked each "on-row" plot; only one stake was used for each "off-row" plot. The stakes were driven into the substrate until only 10-15 cm protruded. Exclosure (closed) plots (1.25 m x 2.25 m) consisted of a strand of stainless-steel wire (68 kg test) wrapped around and crossed over the top of 4 metal poles. The poles (2.5 cm diameter x 1.5 m long) protruded only 30 cm above the mud surface. The wire was strung at 25-30 cm height from late September to early May each year.

Stem Density Measurements

Between mid-June and mid-July each summer, live stems were counted in a 25 cm x 75 cm quadrat placed in the middle (same location) of each plot. The quadrat was positioned by lining up plot stakes with range poles and measuring 1 m off one stake.

The exclosures were checked several times each winter and repaired if necessary. If an exclosure was damaged and stem density decreased by more than 10% across years (maximum decrease measured in ungrubbed, permanent plots in a related study), the plot was excluded from the data set. Snow Geese, being the predominant grubbing herbivore, probably caused the reduction in density. It was assumed that Snow Geese were successfully excluded from the remaining closed plots but swans (because of their longer necks) could have grubbed inside.

Stem densities were adjusted for date of sampling and converted to rhizome dry mass using an allometric equation (Appendix 9).

4.2.2 Seasonal Differences in Rhizome Mass

Control Plots

I used 5 different types of controls (3 in 1990/91 and 2 in 1991/92) to determine the change in rhizome mass in the absence of grubbing during the fall/early winter period and again during spring. All controls were inside the Reifel MBS (Fig. 2). In 1990/91, one core (systematically located) was excavated from each "on-row" exclosure in Rows 1, 2, 4, 5, 7, and 8 in the large RRI grid. Thirty-six plots were sampled on each date.

Two small patches used in a related study (Grids 1 and 2; see Chapter 3) were also sampled in 1990/91. Sixteen cores (randomly located) were taken from each patch on each sampling date. I also collected 16 cores (randomly chosen) from open plots adjacent to these patches to determine the extent of grubbing in the immediate area.

In 1991/92, I sampled from a patch of bulrush that had been previously used in a nitrogen enhancement experiment (Chapter 3). Two cores (systematically chosen) were taken from each of 10 control and 10 treatment (150 kg ha^{-1} OSMOCOTE) plots. The mean of the 2 cores per plot was used as the sample unit.

All control plots were wired at 25-30 cm height to exclude Snow Geese from September to May. Wire was strung around and over the top of metal poles at the corners and sides of the plots. The plots were monitored each winter for evidence of grubbing and to repair the wires.

Open Plots

For the open plot samples, 2 cores (randomly located within 5 m of each "on-row" exclosure) were excavated along the same 6 rows used for the controls in the large RRI grid. The mean of the 2 cores was used as the sample unit (n=36 plots per date). In 1991/92, the number of random cores near each exclosure was increased to 6 (again, the mean was used as the sample unit) and all except Rows 1 (top) and 8 (bottom) were used (n=36 plots per date).

Sampling Procedure

Cores were taken in mid-September, late January, and late April during both years. Control samples in both years and open samples in 1990/91 were excavated using a 12.5 cm diameter steel cylinder with a serrated cutting edge. A different cylinder (5 cm diameter) was used for the open samples in 1991/92. All cores were 25-30 cm long and processed using the same technique described in Chapter 3.

4.2.3 Spatial Differences in Rhizome Mass

Fraser Delta, 1989-1992

In 1989, I established 5 permanent transects throughout the southern half of the Fraser delta (Fig. 2). The Brunswick Point transect contained 3 parallel rows (25 m apart) whereas Outer Island and Westham South had 2 rows each (also 25 m apart). Reifel MBS and a site just south of the sanctuary contained only one transect each. Transects ran in the direction of tidal flow, from the sedge zone to the mudflats. Plots were marked with single stakes (10 cm protruding) at 25 m intervals along each transect.

Stem densities were determined with a procedure similar to that used for the exclosure grids except that 2 quadrats (25 cm x 75 cm) were used at each plot, 1 m on either side of each stake. The mean density for the 2 quadrats was used as the sample unit. The procedure meant that the same locations were sampled each year. Stem densities were adjusted for date of sampling and then converted to rhizome dry mass (Appendix 9).

Fraser and Skagit Deltas, 1989

Stem densities were measured throughout the Fraser and Skagit deltas in July 1989. Six locations were sampled on the Fraser delta. Each location contained 4 to 11 transects (spaced at 100 m intervals) running in the direction of tidal flow. Shoots were counted in 3 quadrats (25 cm x 25 cm) randomly tossed every 25 m along each transect. The quadrats were scattered over a small area (radius < 10 m) so I used their mean value as the sample unit. Stem densities were converted to rhizome dry mass.

The above procedure was followed on the Skagit delta with the following exceptions: 9 locations, each with only one transect, were distributed evenly throughout Skagit Bay and Port Susan Bay; 4 quadrats (25 cm x 75 cm) were randomly sampled at sites every 25-50 m along each transect; and the quadrats at each site were scattered over a relatively large area (radius > 10 m) so each was treated as a sample unit.

4.2.4 Substrate Dynamics

I used a laser level (Laserplane Eagle) to determine substrate elevations across the bulrush zone along transects established in the direction of tidal flow (east-west). Three transects were used for each of the RRI and RRO grids in mid-September 1988 but only one transect per grid was used in mid-September 1989. In 1988, elevation was measured once every 10 m along each transect. In 1989, 4 measurements (randomly chosen) were made at 25 m intervals along each transect; I used the mean of the 4 measurements as the sample unit. I adjusted substrate elevations relative to bench marks on 2 poles (5 m high x 30 cm diameter) at the south boundary of the Reifel MBS. Cross-sectional profiles through the bulrush zone were plotted with lines of best fit using a distance weighted least squares function (Wilkinson 1990).

The "on-row" open and closed plots in the RRI and RRO grids were used to determine changes in substrate elevation over time. In early May and in early September from 1990 to 1992, a rigid, aluminium pole was laid across the 2 stakes marking each plot, flush with the corner of one stake. Vertical distances between 3 marks on the pole and the mud surface were measured to the nearest mm. I used the mean of the 3 measurements as the sample unit. The number of plots sampled were 48 closed and 40 open in RRI and 18 closed and 15 open in RRO.

4.2.5 Statistical Analysis

ANOVAs with Tukey multiple comparison tests were used to determine if rhizome mass differed across locations and years and if changes in substrate elevation differed across grids, years, and plot types. Differences in rhizome mass from Year t to Year t+1 were regressed against rhizome mass in Year t to develop functions describing the net, annual change in rhizome mass in open and closed plots. I used F-tests to compare the regressions across locations and years. For reasons outlined in Chapter 3, numbers were transformed with log $(x+1)$ if variances were unequal (Bartlett's test) or the data were non-normal (Kolmogorov-Smirnov test). All tests had a significance level of 0.05. Means

(± 1SE) are presented throughout the text.

4.3 Results

4.3.1 Rhizome Growth and Removal Rates

Open Versus Closed Plots

Rhizome mass was derived from stem density so both indices varied across years in the same way (Figs. 30A-D); only rhizomes are considered further. From 1988 to 1992, rhizome mass in open plots in the original RRI and RRO grids (n=33 plots over 3 rows in each grid) varied between 50-70 g m^{-2}. Rhizome mass in the open plots did not vary across grids or years (Table 9, Figs. 30C,D) but the latter was close to being significant (P=0.053). I analysed the data for each grid separately using linear regressions. Rhizome mass did not decrease significantly over time in RRI (r^2=0.00, $F_{1,163}$=0.49, P=0.48) but this was not the case in RRO (r^2=0.05, $F_{1,163}$=7.82, P=0.006). The slope for the latter regression suggested a decrease in mass of ca. 6 g m^{-2} yr^{-1}.

Rhizome mass in the closed plots varied across grids and years (Table 9). Mass increased consistently from 1988 to 1992, by 2.3 times in RRI and by 2.5 times in RRO (Figs. 30C,D) but 2-3 years were required before the increases were significant.

In RRI, rhizome mass in the open plots varied across all 8 rows but not across years (Table 10, Fig. 31). Mass in the closed plots varied significantly across rows and years but increases across years were significant only in the upper half of the grid (Rows 1 to 4; Figs. 31A-D).

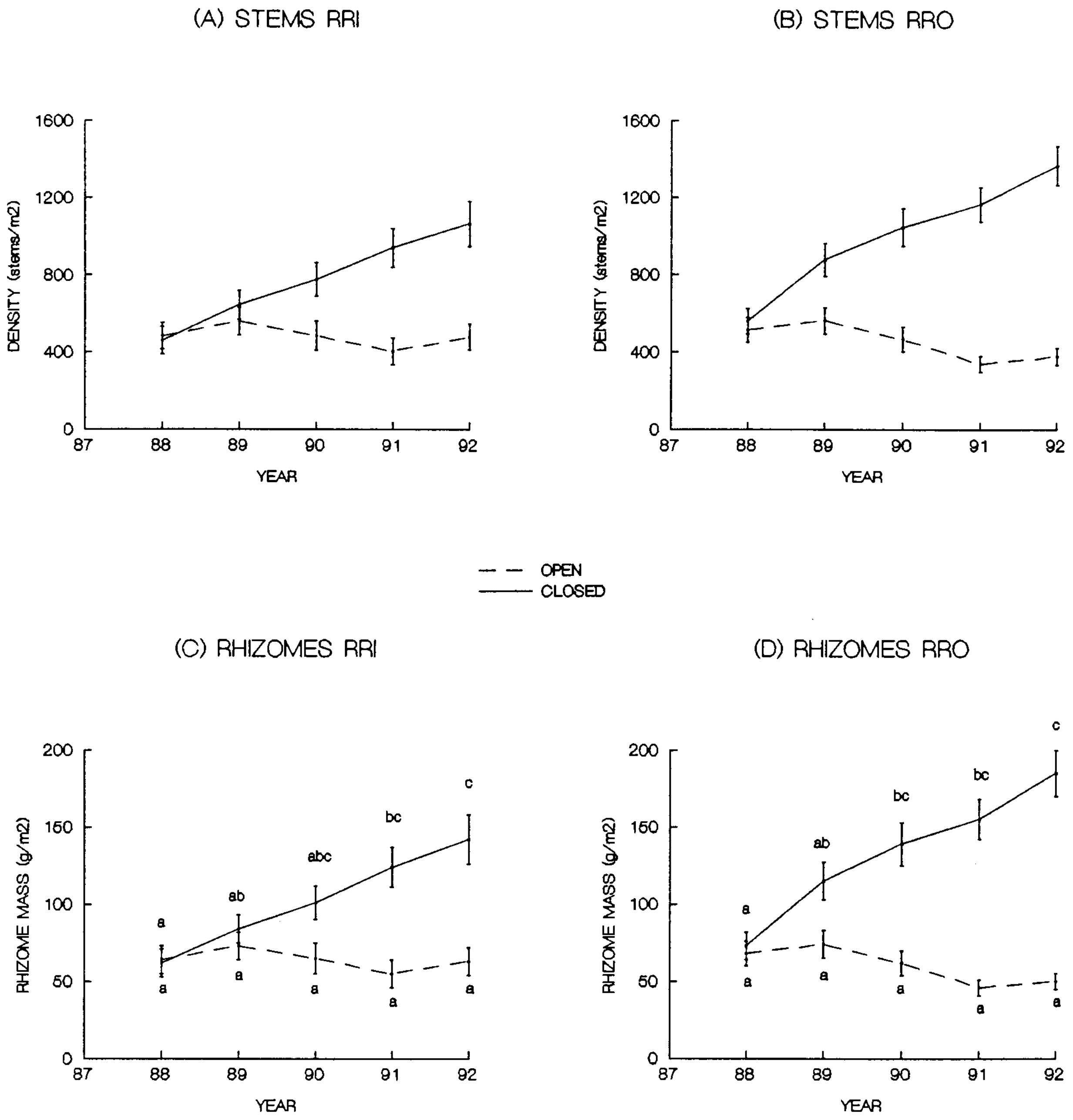


Figure 30. Stem density and rhizome mass (mean ± 1SE) of bulrush (*Scirpus americanus*) in early July in open and closed plots in Reifel MBS (RRI) and just south of the sanctuary (RRO). (A,B) Stem densities in RRI and RRO. (C,D) Rhizome masses in RRI and RRO. Sample sizes in each grid for both plot types started at 33 in 1988 but by 1992 the closed plots declined to 24 in RRI and 30 in RRO. Means with the same superscript do not differ at $P=0.05$ (Tukey multiple comparison test).

Table 9. ANOVAs comparing bulrush (*Scirpus americanus*) rhizome mass across grids (RRI versus RRO) and years (1988 to 1992) for open and closed plots. df = degree of freedom, F = F ratio, P = probability. Data from only the original 3 rows in RRI and RRO were used.

Source of Variance	Open Plots			Closed Plots		
	df	F	P	df	F	P
Grid	1,320	0.71	0.399	1,288	16.16	**<0.001**
Year	4,320	2.36	0.053	4,288	18.78	**<0.001**
Grid x Year	4,320	0.35	0.838	4,288	0.51	0.726

Table 10. ANOVAs comparing bulrush (*Scirpus americanus*) rhizome mass across rows (1 to 8) and years (1990 to 1992) in RRI for open and closed plots. df = degrees of freedom, F = F ratio, P = probability.

Source of Variance	Open Plots			Closed Plots		
	df	F	P	df	F	P
Year	2,240	0.50	0.608	2,213	22.93	**<0.001**
Row	7,240	6.72	**<0.001**	7,213	6.57	**<0.001**
Year x Row	14,240	0.19	0.999	14,213	0.40	0.975

(A) ROW 1 (B) ROW 2 (C) ROW 3 (D) ROW 4

(E) ROW 5 (F) ROW 6 (G) ROW 7 (H) ROW 8

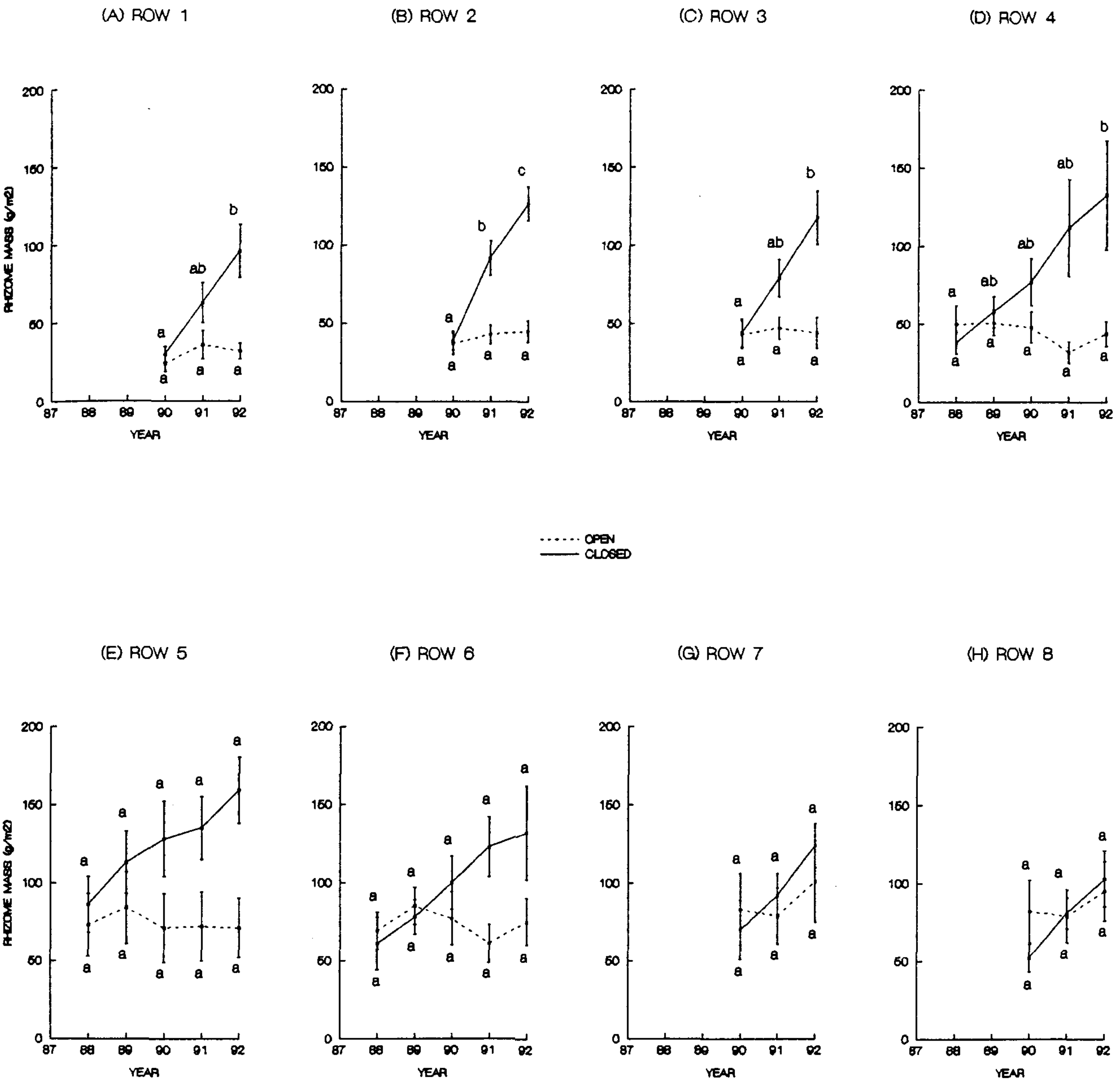


Figure 31. Rhizome mass (mean ± 1SE) of bulrush (*Scirpus americanus*) in early July in open and closed plots in different rows in Reifel MBS (RRI). Row 1 (A) was located at the top of the bulrush zone whereas Row 8 (H) was near the bottom. Data were available from 1988 to 1992 for Rows 4, 5, and 6 but only from 1990 to 1992 for the remaining rows. Each row contained 11 open plots throughout the study. Each row started with 11 closed plots in 1988 or 1990 but ended with the following number in 1992: Row 1: 11, Row 2: 10, Row 3: 11, Row 4: 8, Row 5: 9, Row 6: 7, Row 7: 9, and Row 8: 10. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

I estimated the mean, annual change in rhizome mass in the absence of grubbing in RRI and RRO (3 rows and 4 years each) by averaging the changes in closed plots across years (Table 11). These were ca. 20 and 28 g m^{-2} yr^{-1} for RRI and RRO, respectively. I also estimated the mean, annual removal of rhizome mass due to grubbing by averaging the differences between the annual change in the open plots from the annual increase in the closed plots. These were ca. 20 and 32 g m^{-2} yr^{-1} for RRI and RRO, respectively.

Functional Responses

I regressed the change in rhizome mass from Year t to Year t+1 against mass in Year t to develop functional responses for the closed and open plots. Differences in the functions across years and locations were investigated using F-tests (Tables 12 and 13, Figs. 32 to 37). Data were not possible in the following domains: (A) where negative annual changes were greater than the initial standing crop and (B) below 12 g m^{-2} (due to the Y-intercept in the allometric equation in Appendix 9). These biases do not affect the model results discussed below because they were common to both closed and open plots. Further, my analyses are based on data that extend between ca. 12-300 g m^{-2} (see Appendix 9). I do not know how the system would respond if it is moved beyond this range.

The functional responses for the closed plots exhibited only minor temporal and spatial variability. Regressions for both RRI (original 3 rows) and RRI (all 8 rows) did not differ across years (Table 12, Figs. 32A-F). Regressions for RRO (3 rows) differed across years (Table 12, Figs. 32G-J) but no directional trend was apparent. Regressions

Table 11. Summary of growth and removal rates of bulrush (*Scirpus americanus*) rhizomes in the RRI and RRO grids, Westham Island. Values are means ± 1SE.

Grid	Annual Change ($g\ m^{-2}\ yr^{-1}$)	Removal Rate ($g\ m^{-2}\ yr^{-1}$)
RRI (3 rows, 4 years)	20.0±1.5	20.3±5.3
RRO (3 rows, 4 years)	28.0±5.5	32.0±2.4
RRI (8 rows, 2 years)	28.0±1.0	25.5±5.5

Table 12. Linear regressions describing the relationship between the change in rhizome mass from Year t to Year t+1 versus rhizome mass in Year t. F-tests were used to determine differences between selected regressions. Temporal and spatial differences were investigated for closed plots only. df = degrees of freedom. F = F ratio. P = probability.

Comparisons	Linear Regressions				F-test Comparisons		
	r^2	df	F	P	df	F	P
Temporal Differences							
RRI (3 rows pooled):							
1988-89	0.01	1,29	0.42	0.52			
1989-90	0.00	1,28	0.06	0.81			
1990-91	0.00	1,22	0.00	0.97			
1991-92	0.16	1,22	4.05	0.06	6,101	0.94	>0.25
RRI (8 rows pooled):							
1990-91	0.00	1,75	0.18	0.68			
1991-92	0.00	1,73	0.27	0.60	2,148	1.40	0.25
RRO (3 rows pooled):							
1988-89	0.16	1,30	5.85	0.02			
1989-90	0.00	1,29	0.00	0.97			
1990-91	0.14	1,28	4.68	0.04			
1991-92	0.00	1,28	0.04	0.85	6,115	3.21	<0.01
Spatial Differences							
1988-89 to 1991-92 (3 rows pooled):							
RRI	0.00	1,107	0.19	0.66			
RRO	0.01	1,121	1.61	0.21	2,228	1.30	>0.25
1990-91 to 1991-92 (RRI):							
Rows 1 & 2	0.01	1,40	0.40	0.53			
Rows 3 & 4	0.09	1,36	3.47	0.07			
Rows 5 & 6	0.01	1,30	0.16	0.70			
Rows 7 & 8	0.01	1,38	0.48	0.49	6,144	2.11	0.05

Table 13. Linear regressions describing the relationship between the change in rhizome mass from Year t to Year t+1 versus rhizome mass in Year t. F-tests were used to determine differences between selected regressions. Temporal and spatial differences were investigated for open plots only. df = degrees of freedom. F = F ratio. P = probability.

Comparisons	Linear Regressions				F-test Comparisons		
	r^2	df	F	P	df	F	P
Temporal Differences							
RRI (3 rows pooled):							
1988-89	0.01	1,31	0.32	0.58			
1989-90	0.11	1,31	3.91	0.06			
1990-91	0.25	1,31	10.21	0.003			
1991-92	0.11	1,31	3.78	0.06	6,124	2.08	0.05
RRI (8 rows pooled):							
1990-91	0.28	1,86	33.13	<0.001			
1991-92	0.00	1,86	0.24	0.63	2,172	7.48	<0.001
RRO (3 rows pooled):							
1988-89	0.08	1,31	2.57	0.12			
1989-90	0.22	1,31	8.63	0.006			
1990-91	0.62	1,31	51.21	<0.001			
1991-92	0.21	1,31	8.21	0.007	6,124	3.44	<0.005
Spatial Differences							
1988-89 to 1991-92 (3 rows pooled):							
RRI	0.12	1,130	18.02	<0.001			
RRO	0.25	1,130	42.42	<0.001	2,260	2.56	>0.05
1990-91 to 1991-92 (RRI):							
Rows 1 & 2	0.43	1,42	32.01	<0.001			
Rows 3 & 4	0.42	1,42	30.02	<0.001			
Rows 5 & 6	0.17	1,42	8.87	0.005			
Rows 7 & 8	0.03	1,42	1.50	0.25	6,168	5.32	<0.001

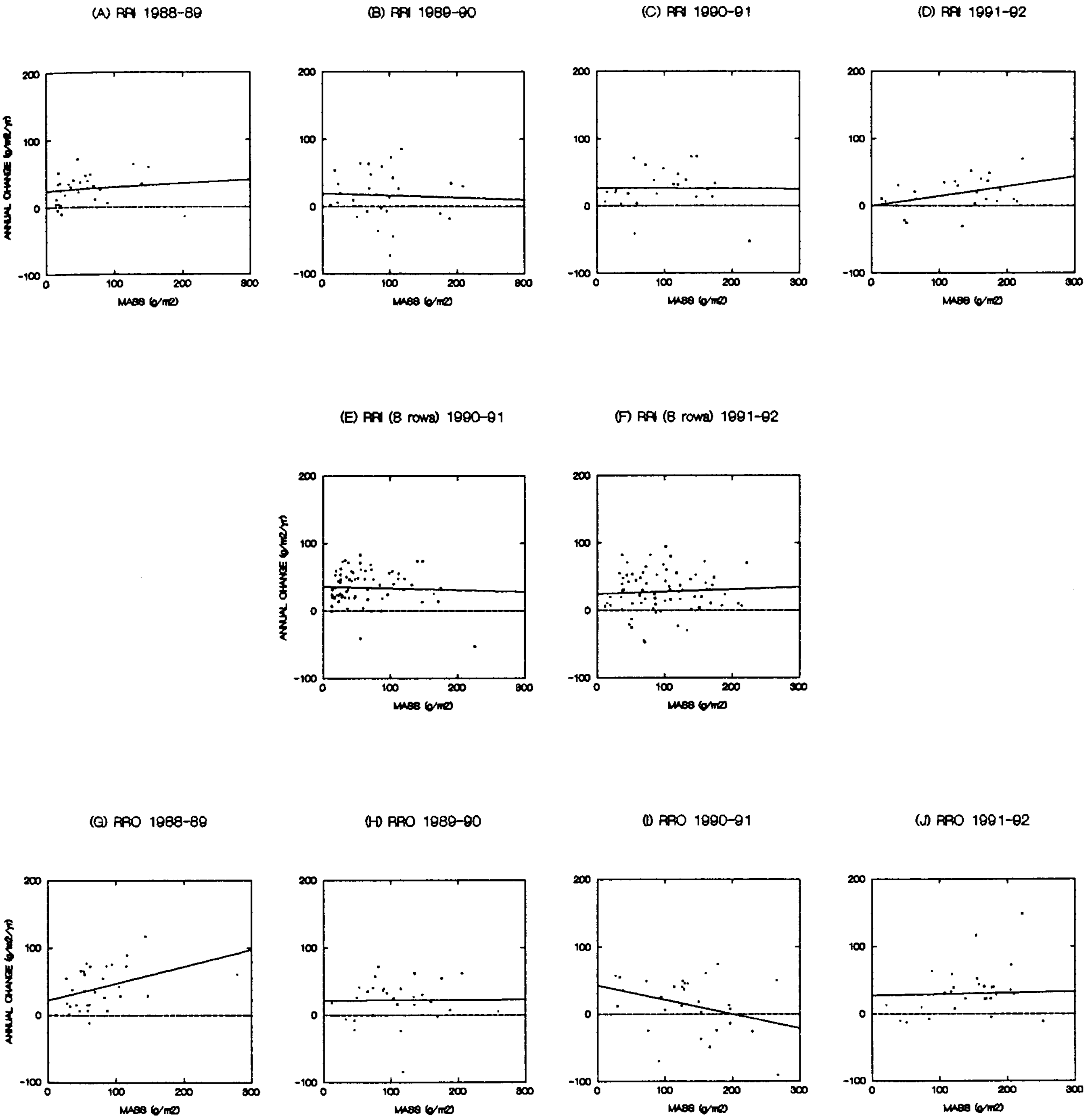


Figure 32. Temporal differences in linear regressions describing the change in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t in closed plots. (A-D) RRI grid (3 original rows): 1988-89 versus 1989-90, 1990-91, and 1991-92. (E,F) RRI (all 8 rows): 1990-91 versus 1991-92. (G-J) RRO grid (3 original rows): 1988-89 versus 1989-90, 1990-91, and 1991-92.

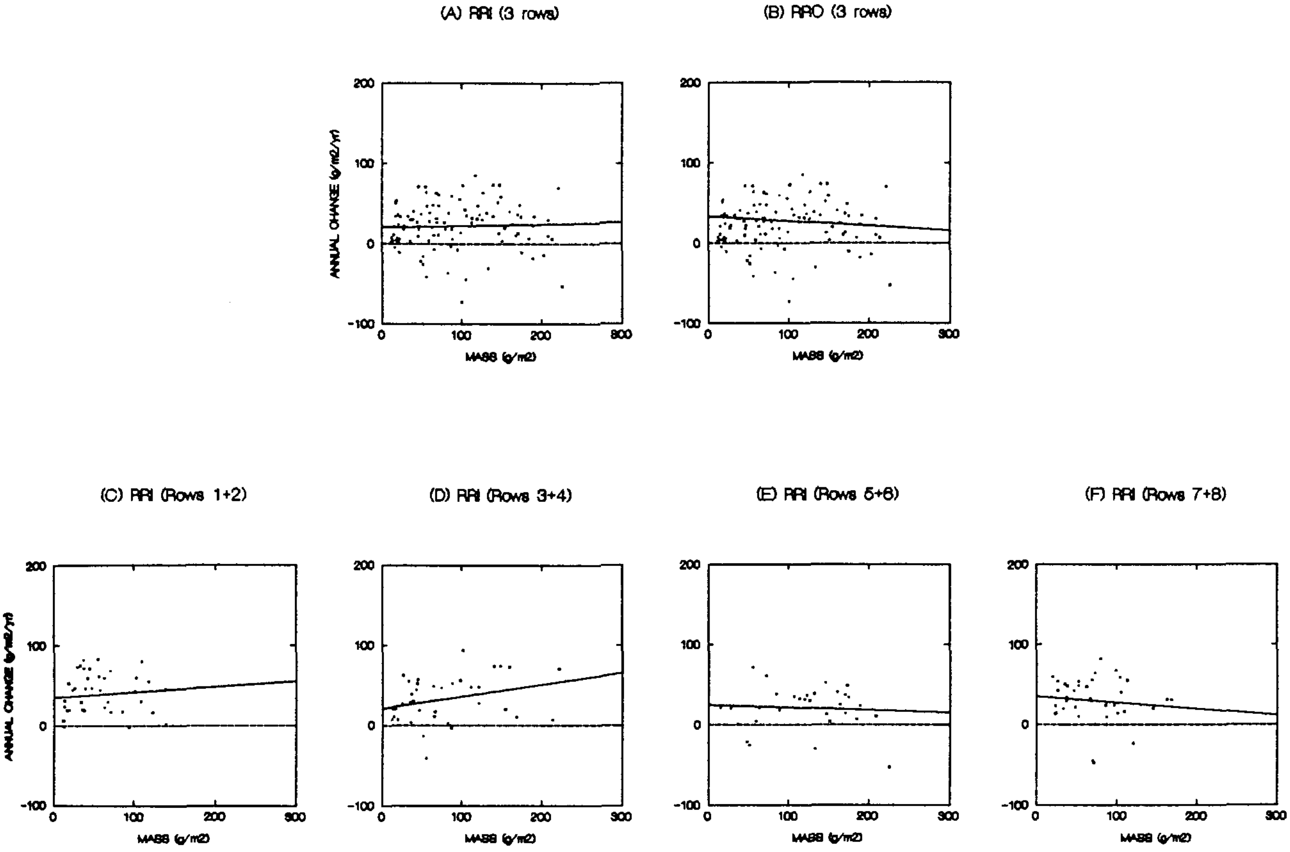


Figure 33. Spatial differences in linear regressions describing the change in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t in closed plots. (A,B) RRI grid versus RRO grid (3 original rows and 4 years each). (C-F) RRI grid (Rows 1+2 versus Rows 3+4, Rows 5+6, and Rows 7+8).

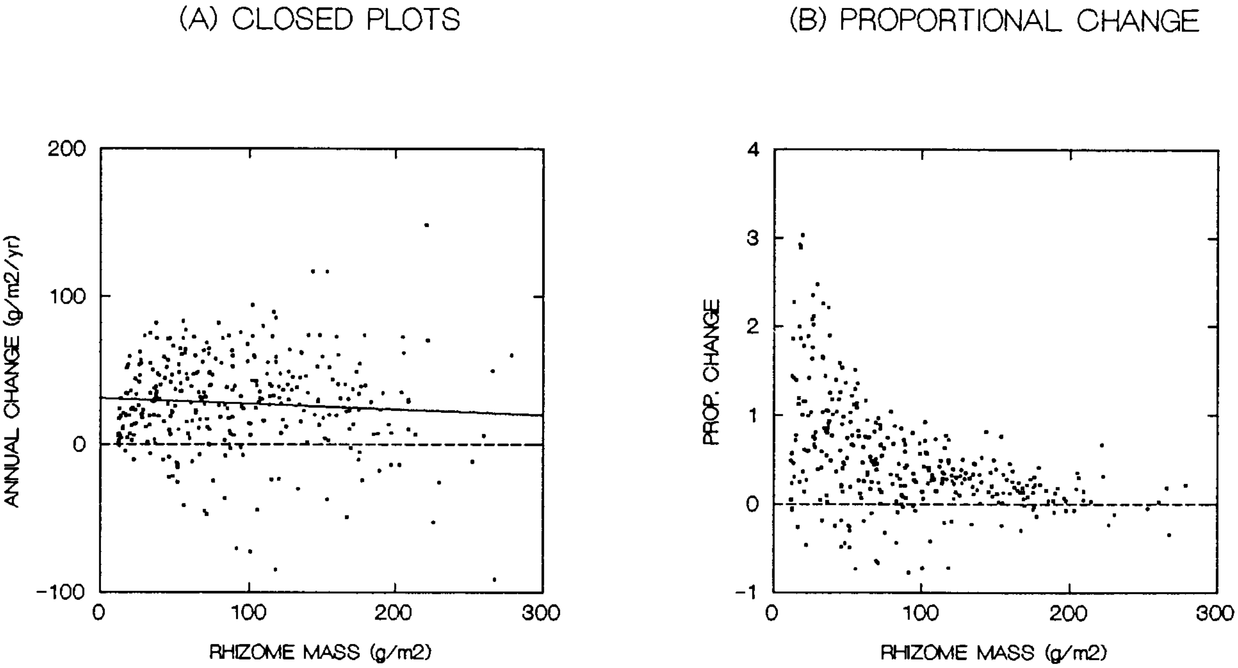


Figure 34. Actual (A) and proportional (B) changes in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t (all locations and years pooled) in closed plots. The following equation describes the linear regression: $Y=31.2-0.038X$ ($r^2=0.01$, $P=0.16$, $n=336$).

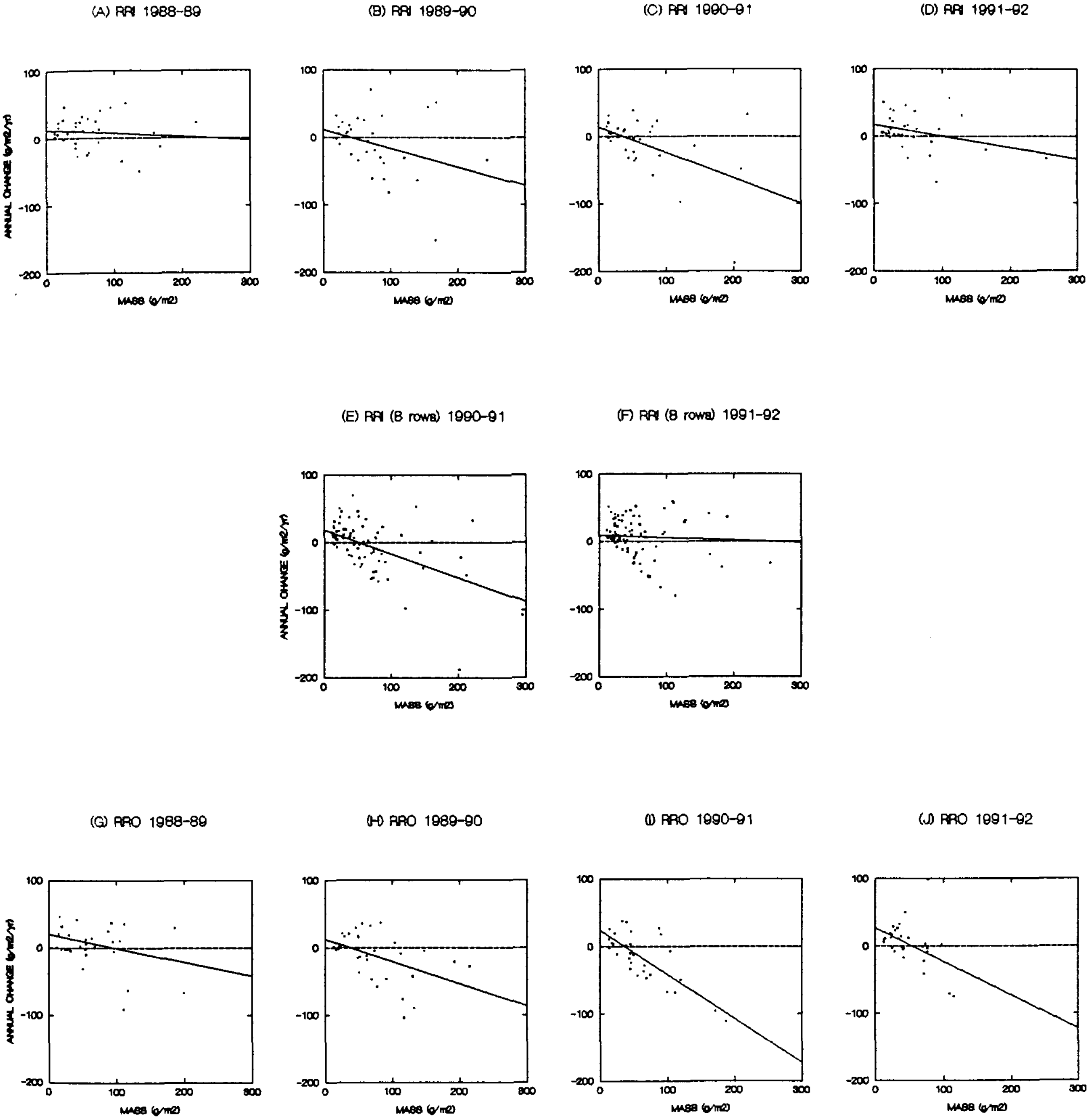


Figure 35. Temporal differences in linear regressions describing the change in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t in open plots. (A-D) RRI grid (3 original rows): 1988-89 versus 1989-90, 1990-91, and 1991-92. (E-H) RRO grid (3 original rows): 1988-89 versus 1989-90, 1990-91, and 1991-92. (I,J) RRI (all 8 rows): 1990-91 versus 1991-92.

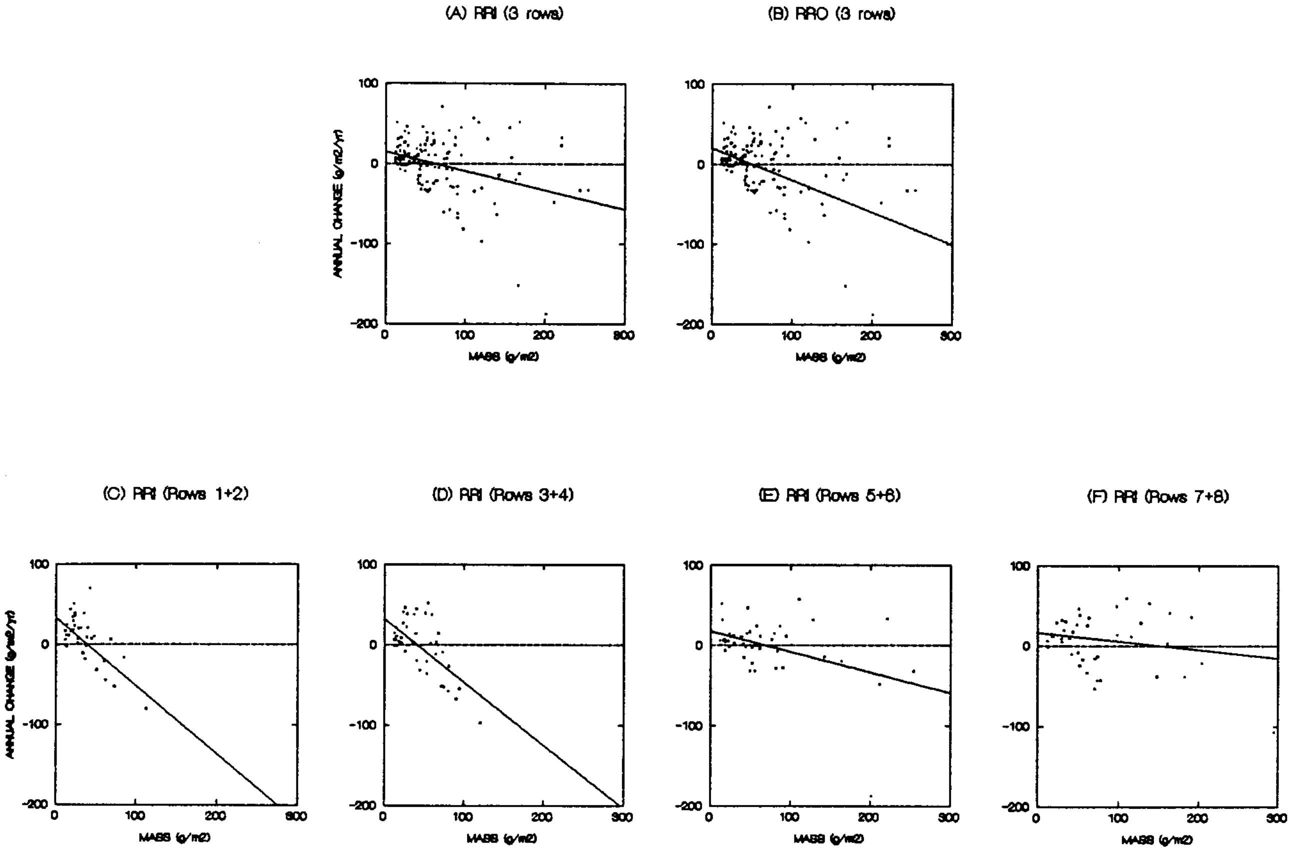
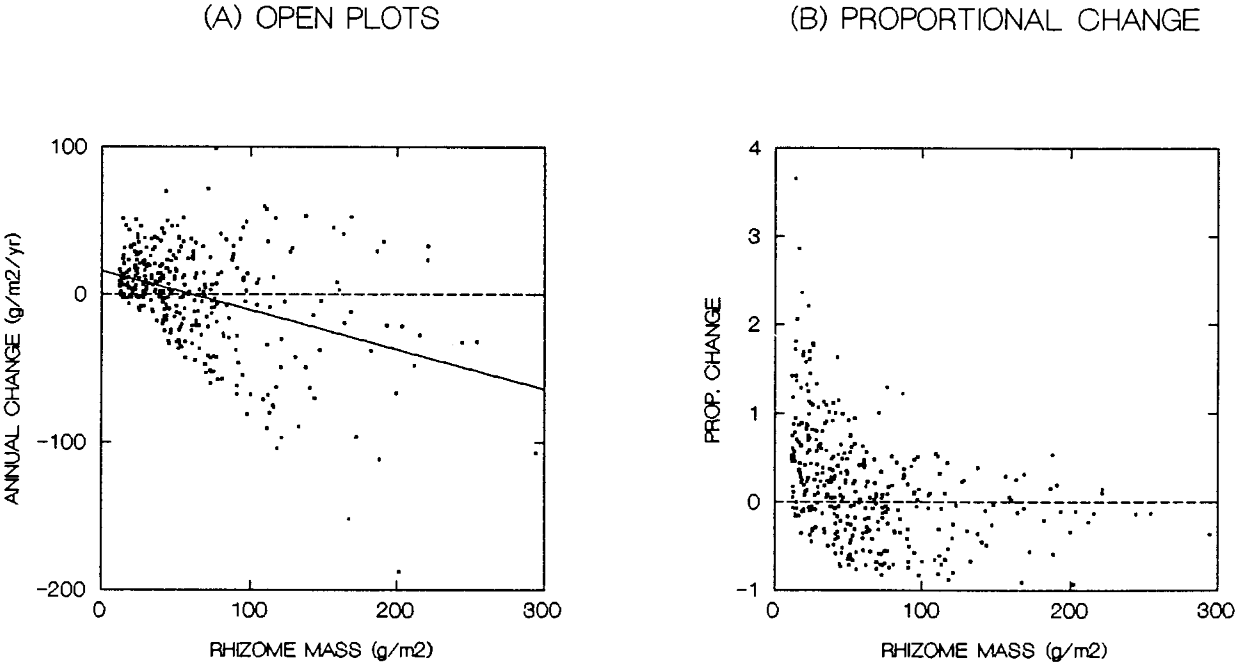


Figure 36. Spatial differences in linear regressions describing the change in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t in open plots. (A,B) RRI grid versus RRO grid (3 original rows and 4 years each). (C-F) RRI grid (Rows 1+2 versus Rows 3+4, Rows 5+6, and Rows 7+8).


(A) OPEN PLOTS

(B) PROPORTIONAL CHANGE

Figure 37. Actual (A) and proportional (B) changes in bulrush (*Scirpus americanus*) rhizome mass from Year t to Year t+1 versus mass in Year t (all locations and years pooled) in open plots. The following equation describes the linear regression: $Y=16.0-0.226X$ ($r^2=0.14$, $P<0.001$, $n=374$).

for RRI and RRO (years pooled; original 3 rows each) did not differ (Table 12, Figs. 33A,B) and those describing the pooled rows in RRI (Table 12, Figs. 33C-F) were only barely different ($P=0.05$) and no directional trend was apparent. When I pooled the data, the overall regression did not differ from one with zero slope (Fig. 34A; $r^2=0.01$, $F_{1,334}=1.93$, $P=0.16$) and there was no apparent, non-linear trend in the residuals. This constant function corresponds to an inverse relationship between net production per unit weight and rhizome mass (Fig. 34B).

In closed plots with rhizome masses <25 g m^{-2}, the annual change in rhizome mass varied between 0 and ca. 60 g m^{-2} yr^{-1}. Some of this variability was due to sampling error and variation associated with the allometric equation relating rhizome mass to stem density (Appendix 9). Differences in initial rhizome density in and around each plot probably also contributed to the variability. I investigated this by calculating the mean annual change in rhizome mass for plots with initial masses <25 g m^{-2}. The result was ca. 6 g m^{-2} yr^{-1} or 5 times less than the rate predicted using the above regression model. Hence, the net annual change in rhizome mass approaches zero when density over a large area approaches zero.

Almost all regressions for the open plots differed across years and locations (Table 13, Figs. 35A-J and Figs. 36A-F), likely due to differential grubbing intensities by Snow Geese. All regressions had negative slopes and most crossed the horizontal axis at low mass. The pooled regression differed from one with zero slope (Fig. 37A; $r^2=0.14$, $F_{1,372}=58.84$, $P<0.001$). Again, proportional change per unit weight was inversely correlated with rhizome mass (Fig. 37B).

No trends were apparent in the regressions for the open plots across years (Figs. 35A-D and Figs. 35G-J) but a spatial trend was conspicuous in RRI (Figs. 36C-F). The slope of the function remained negative but consistently decreased from the upper part of the bulrush zone (Rows 1+2) to the lower part (Rows 7+8), reflecting a decrease in grubbing pressure with distance down the zone.

I estimated a removal rate function by subtracting the regression function for the open plots (Fig. 37) from that for the closed plots (Fig. 34). When superimposed, this removal function intersected with the growth rate function (closed plots) at ca. 70 g m^{-2} (Fig. 38). Growth exceeded loss when rhizome mass was below this value whereas the opposite occurred in patches with greater masses.

4.3.2 Seasonal Differences in Rhizome Mass

Control Plots

I found no evidence of grubbing inside any of the wired control plots. Also, rhizome mass in open plots adjacent to the 2 small control plots in 1990/91 did not change over the winter period (ANOVAs: $F_{2,44}=1.43$, $P=0.25$ and $F_{2,45}=3.09$, $P=0.06$). Therefore, I suspect that any changes in the controls were due to rhizome death, leaching, or reallocation of stored constituents for shoot initiation.

Rhizome mass in the controls decreased from September to April but, because of high variation and small sample sizes, none of the declines was significant (ANOVAs: $P>0.05$). Despite these non-significant results, I weighted the decreases by sample size and arrived at mean declines in rhizome mass of ca. 5% for the September-January period and ca. 15% for January-April period.

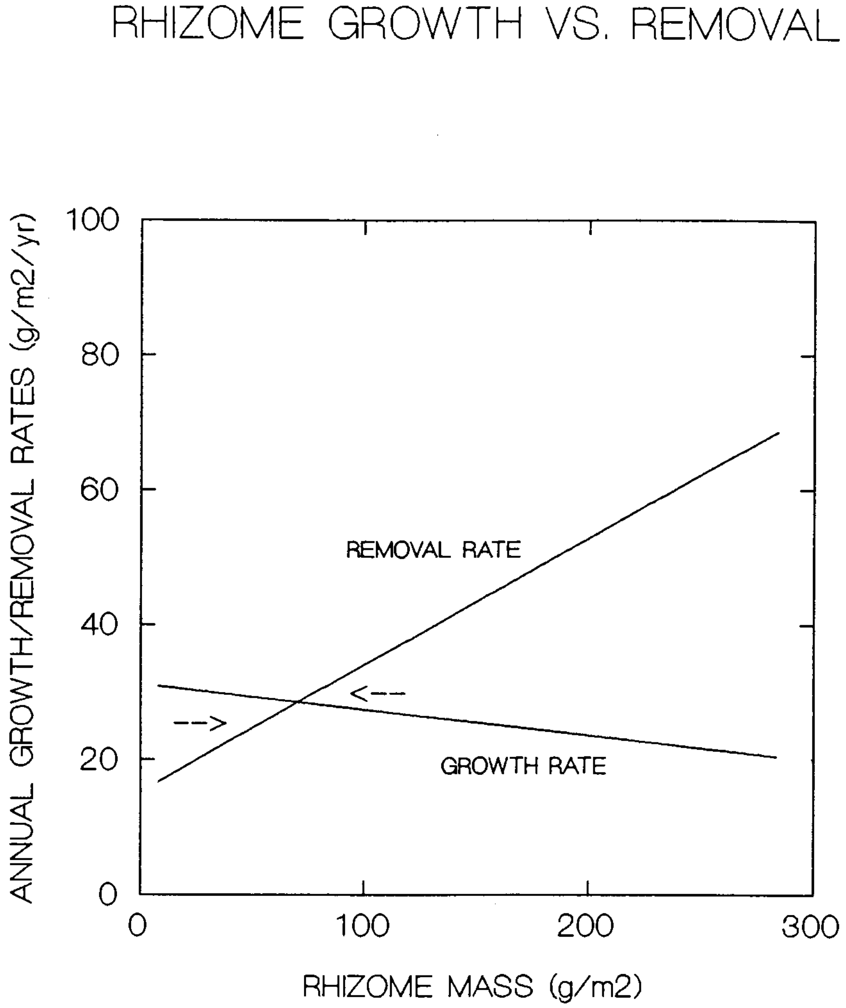


Figure 38. Growth rate and removal rate functions for bulrush (*Scirpus americanus*) rhizomes. The regressions intersect at a low level equilibrium mass around 70 g m^{-2}. The arrows show the likely direction of annual change in a plot given its current mass.

Open Plots

Rhizome mass in the open plots in Reifel MBS decreased over the winter in both years (ANOVAs: $F_{2,105}=4.85$, $P=0.01$ for 1990/91 and $F_{2,105}=14.11$, $P<0.001$ for 1991/92) but the declines were significant only for the September-January period (32%; Figs. 39A,B). Hence, grubbing caused a ca. 27% decrease in rhizome mass in the fall/early winter period (after accounting for the change in controls) but it had no measurable effect in spring.

4.3.3 Spatial Differences in Rhizome Mass

Fraser Delta, 1989-1992

Stem density measurements on the Fraser delta suggested that rhizome mass in early July varied significantly across locations ($F_{4,792}=24.31$, $P<0.001$) but not across years ($F_{3,792}=1.52$, $P=0.21$). Mean mass (years pooled) ranged from 47.4 ± 1.7 g m^{-2} at Westham South to 86.6 ± 3.4 g m^{-2} at Outer Island (Fig. 40A). I pooled the data despite the differences across locations and arrived at a mean rhizome mass of 66.2 ± 1.9 g m^{-2} (Fig. 40B). This estimate is similar to the mean value in the open plots in the large RRI grid (64.5 ± 2.9 g m^{-2}) and in the RRO grid (60.0 ± 5.3 g m^{-2}). With the exception of Westham South ($F_{3,213}=7.52$, $P<0.001$), rhizome mass was consistent across years at all locations ($P>0.05$) suggesting that rhizome growth was balanced by removal over a large part of the Fraser delta during this study (Fig. 40C,D).

Fraser and Skagit Deltas, 1989

As above, rhizome mass in early July 1989 varied across the Fraser delta ($F_{5,607}=5.88$, $P<0.001$; Table 14) and across the Skagit delta ($F_{8,416}=28.83$, $P<0.001$).

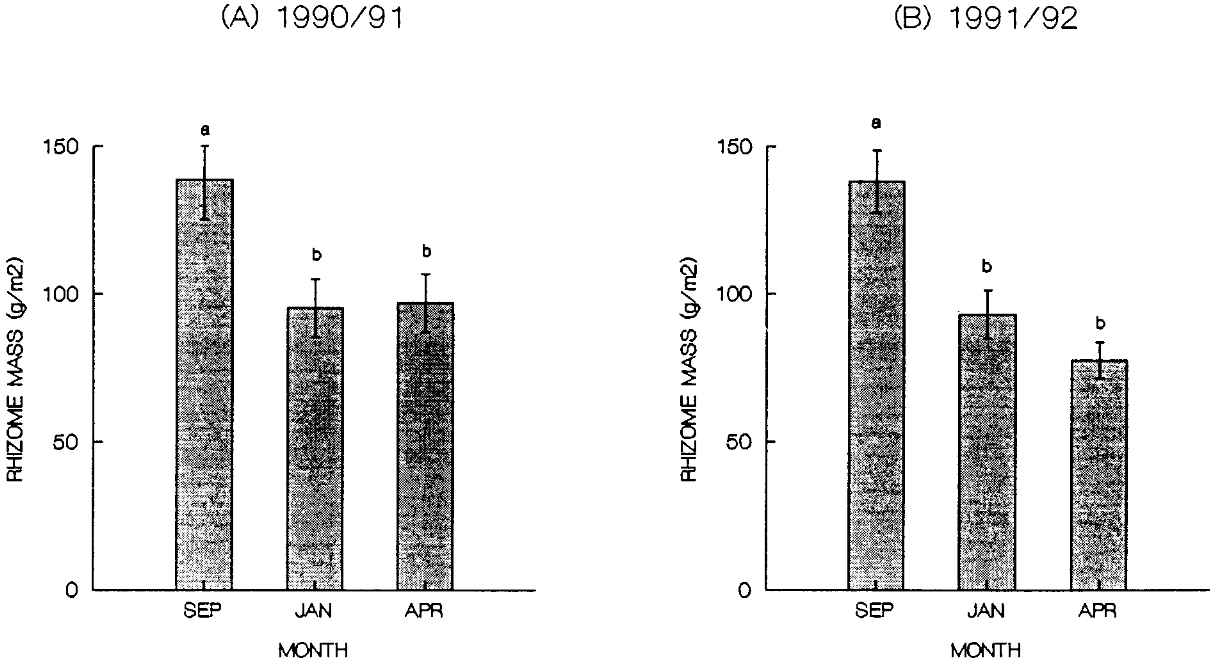
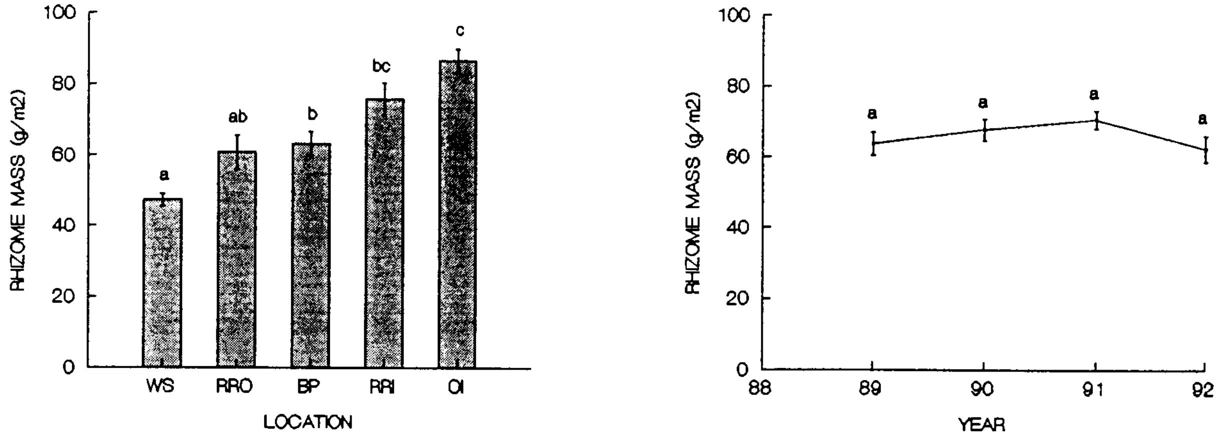
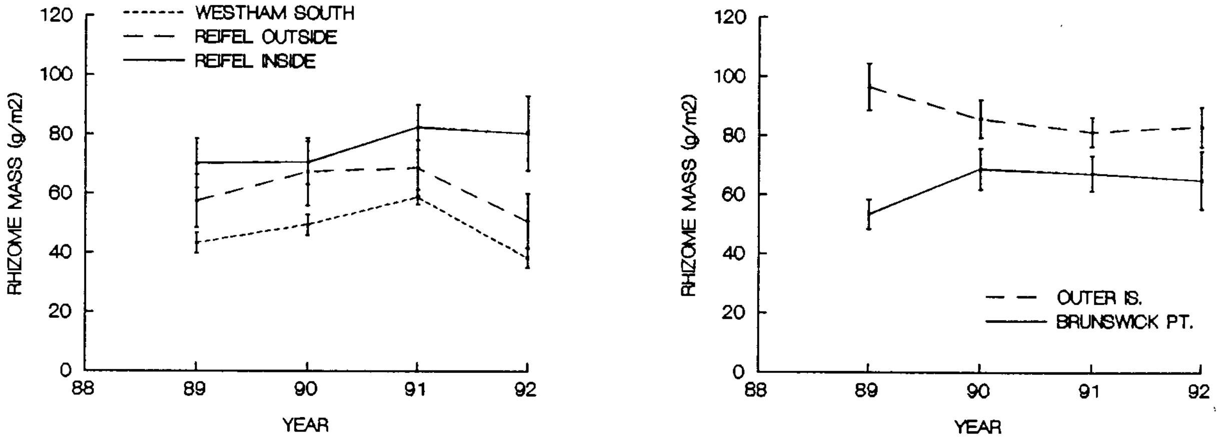


Figure 39. Bulrush (*Scirpus americanus*) rhizome mass (mean ± 1SE) in September, January, and April in Reifel MBS (RRI). (A) 1990/91 (n=36). (B) 1991/92 (n=36). Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).



(A) LOCATIONS

(B) YEARS



(C) WESTHAM ISLAND

(D) OTHER LOCATIONS

Figure 40. Rhizome mass (mean ± 1SE) of bulrush (*Scirpus americanus*) in early July in open plots at different locations on the Fraser delta. (A) Rhizome mass across locations (4 years pooled). Data are presented in order of increasing mass. Symbols: WS = south Westham Island (n=56 plots), RRO = just south of RRO grid (n=27), BP = Brunswick Point (n=51), RRI = just north of RRI grid (n=27), and OI = Outer Island (n=52). (B) Rhizome mass across years (locations pooled). (C) and (D) Rhizome mass at each of the 5 locations across years. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

Table 14. Stem density and rhizome mass of bulrush (*Scirpus americanus*) sampled at different locations on the Fraser delta in 1989. Values are means ± 1SE. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

Location	Number of Transects	Mean Transect Length (m)	Sample Size	Density (stems m^{-2})	Rhizomes (g m^{-2})
Brunswick Point	11	320	142	398±40	56.5±5.1^{abc}
Westham South	4	725	116	358±29	49.0±3.6^{ab}
Westham North	7	500	141	465±29	61.7±3.6^{bc}
Outer Island	4	420	67	544±45	71.7±5.6^{c}
Lulu South	8	200	65	309±36	43.6±4.2^{a}
Lulu North	5	410	82	340±28	46.2±3.0^{ab}

Mean rhizome mass on the Fraser delta (transects pooled) was 1.7 times higher than on the Skagit delta (t-test: $T_{1036}=8.60$, $P<0.001$): 55.2 ± 1.8 versus 32.8 ± 0.9 g m^{-2} rhizomes (or 405 ± 15 versus 223 ± 8 stems m^{-2}). The lower mass on the Skagit delta may reflect the fact that it has historically been subjected to more goose-days and perhaps higher grubbing intensities than the Fraser delta (Chapter 2).

The highest rhizome masses recorded on the Fraser delta in early July were ca. 400 g m^{-2}. Hence, assuming equal growth capability, mean rhizome masses on the Fraser delta and Skagit delta were only at ca. 15% and 10% of their potential maximum levels, respectively.

Reifel MBS

Data from the plots that were sampled non-destructively in RRI (5 years pooled) showed that mean rhizome mass increased with distance from the top of the bulrush zone to the mudflat zone (Fig. 41). A linear regression model describing the relation was significant ($r^2=0.92$, $F_{1,6}=65.22$, $P<0.001$) although an abrupt change in mass occurred at about mid-zone. Assuming equal growth potential over the marsh, rhizome mass was only at ca. 20% of its maximum potential in the lower half of the bulrush zone and only at ca. 10% in the upper half.

4.3.4 Substrate Dynamics

Some of the substrate elevation profiles in the upper half of the bulrush zone on Westham Island were concave (Fig. 42). Also, vertical distances between bulrush and sedge substrate at the top of the transects were between 30-50 cm and relict sedge patches were present as far down as the middle of each transect (*pers. obs.*). These observations

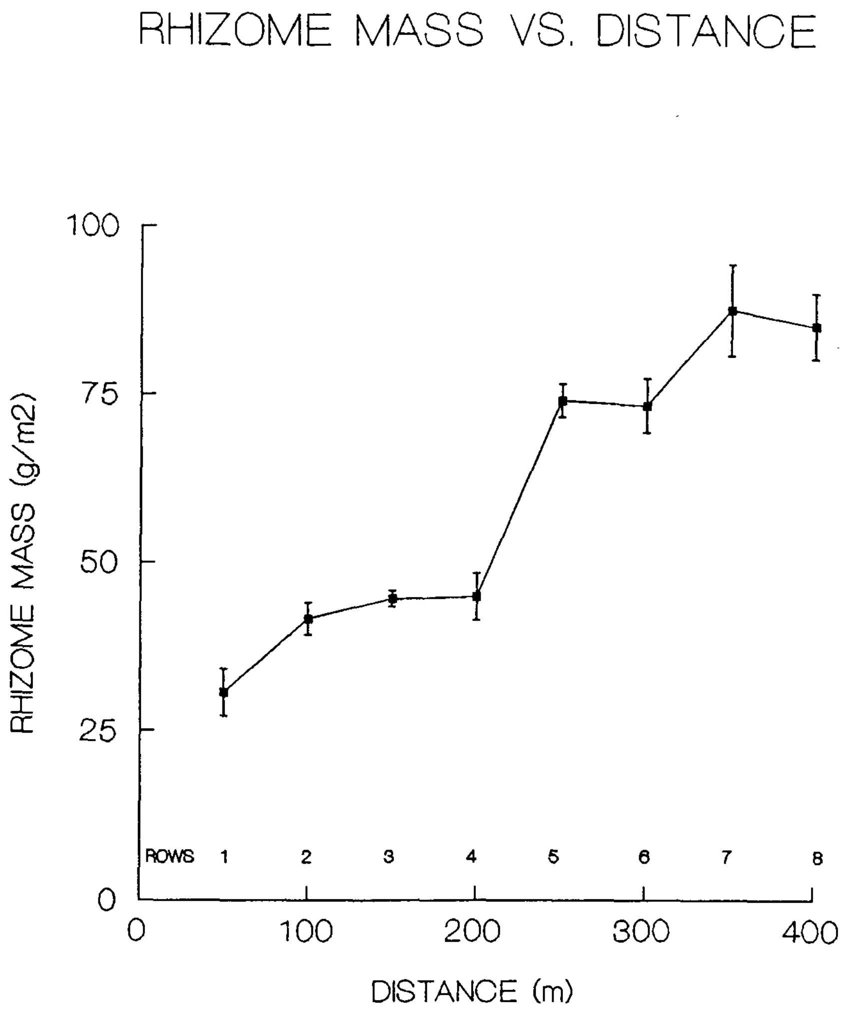


Figure 41. Rhizome mass (mean ± 1SE) of bulrush (*Scirpus americanus*) in early July in open plots versus distance from the top of the bulrush zone to the mudflat zone (non-destructive sampling). Each mean (= Row) value was based on 11 open plots (n=3 years for Rows 1, 2, 3, 7, and 8; n=5 years for Rows 4, 5, and 6). Row numbers are shown above the horizontal axis.

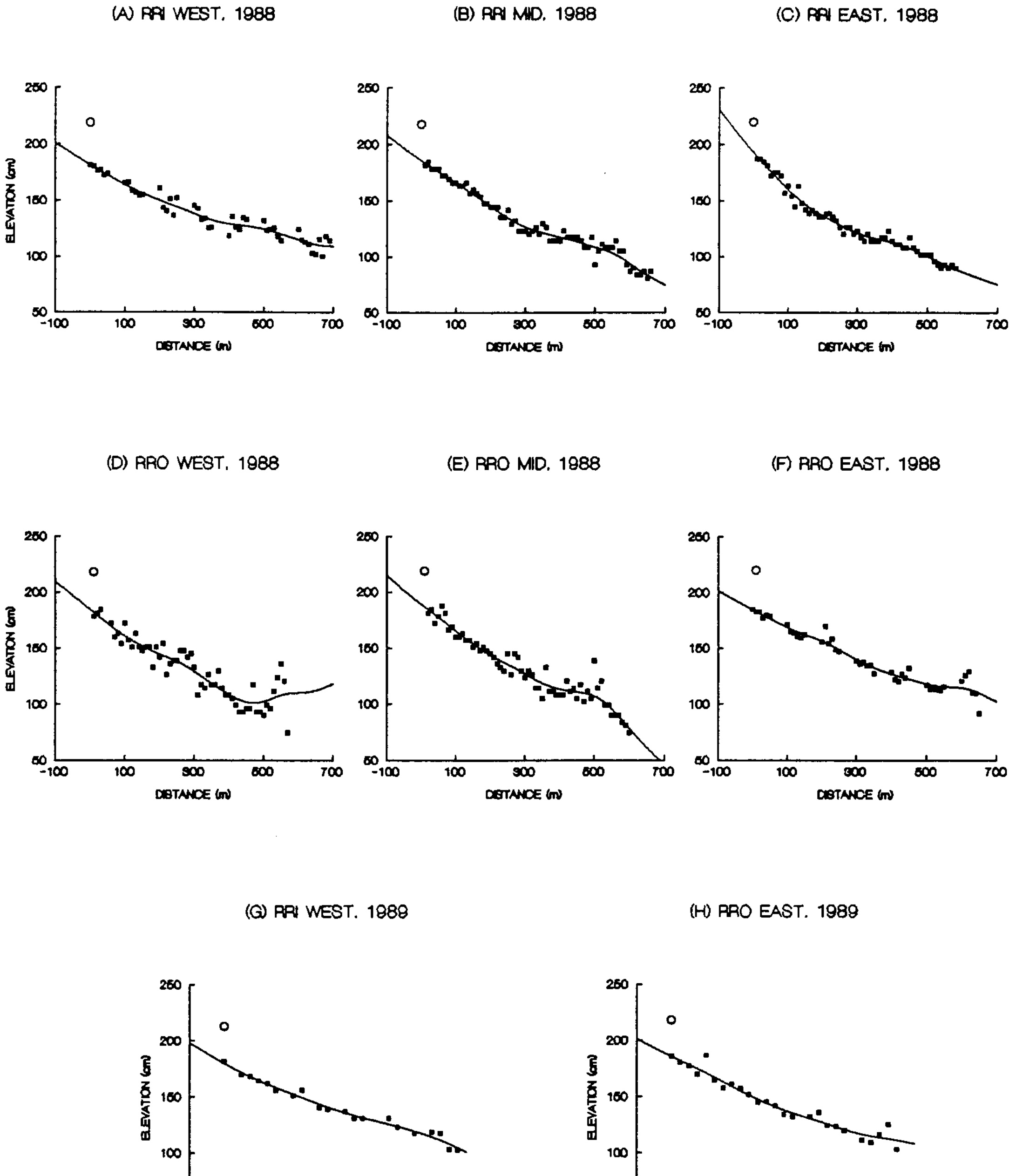


Figure 42. Topographic profiles along transects through the bulrush (*Scirpus americanus*) zone in September 1988 and 1989. Filled squares represent substrate elevations along the transects. The open circle represents the mean substrate elevation at the bottom of the sedge zone (n=5). A distance weighted least squares function was used to plot the line of best fit for each profile. (A to C) West, mid, and east transects through the RRI grid in 1988. (D to F) West, mid, and east transects through the RRO grid in 1988. (G) West transect through the RRI grid in 1989. (H) East transect through the RRO grid in 1989. Distance is from the top of the bulrush zone to the mudflat zone. Elevation is relative to established bench marks.

suggest that changes have occurred to marsh succession at Westham Island and that grubbing by Snow Geese may have been an important factor.

Measurements in permanent plots showed that substrate elevation increased in summer and decreased in winter (Figs. 43A-D). Sediment accumulation varied only across years in summer and only across plot types (open versus closed) in winter. The finding that accretion in summer was largely consistent across grids suggests that sediment was deposited evenly over a large part of the bulrush zone on Westham Island each year.

I pooled the data by year and computed the mean change in substrate elevation across seasons, grids, and plot types. In the small RRO grid, mean elevation increase in summer was the same in the open and closed plots but mean decrease in winter was 3.0 times greater in the open plots. The net result was a decrease of 1.3 cm yr^{-1} in the open plots and an increase of 1.5 cm yr^{-1} in the closed plots for an overall grubbing impact of 2.8 cm yr^{-1}.

In the large RRI grid (8 rows), mean elevation increase in summer was similar in the open and closed plots but mean decrease in winter was 2.1 times greater in the open plots. The net result was a decrease of 0.3 cm yr^{-1} in the open plots and an increase of 1.1 cm yr^{-1} in the closed ones for an overall grubbing impact of 1.4 cm yr^{-1}, or half of that estimated for the small RRO grid.

The large RRI grid spanned most of the entire bulrush zone so I split it into upper and lower halves (locations) and analysed for differences. As above, substrate accretion in summer varied only across years and substrate loss in winter varied only across plot

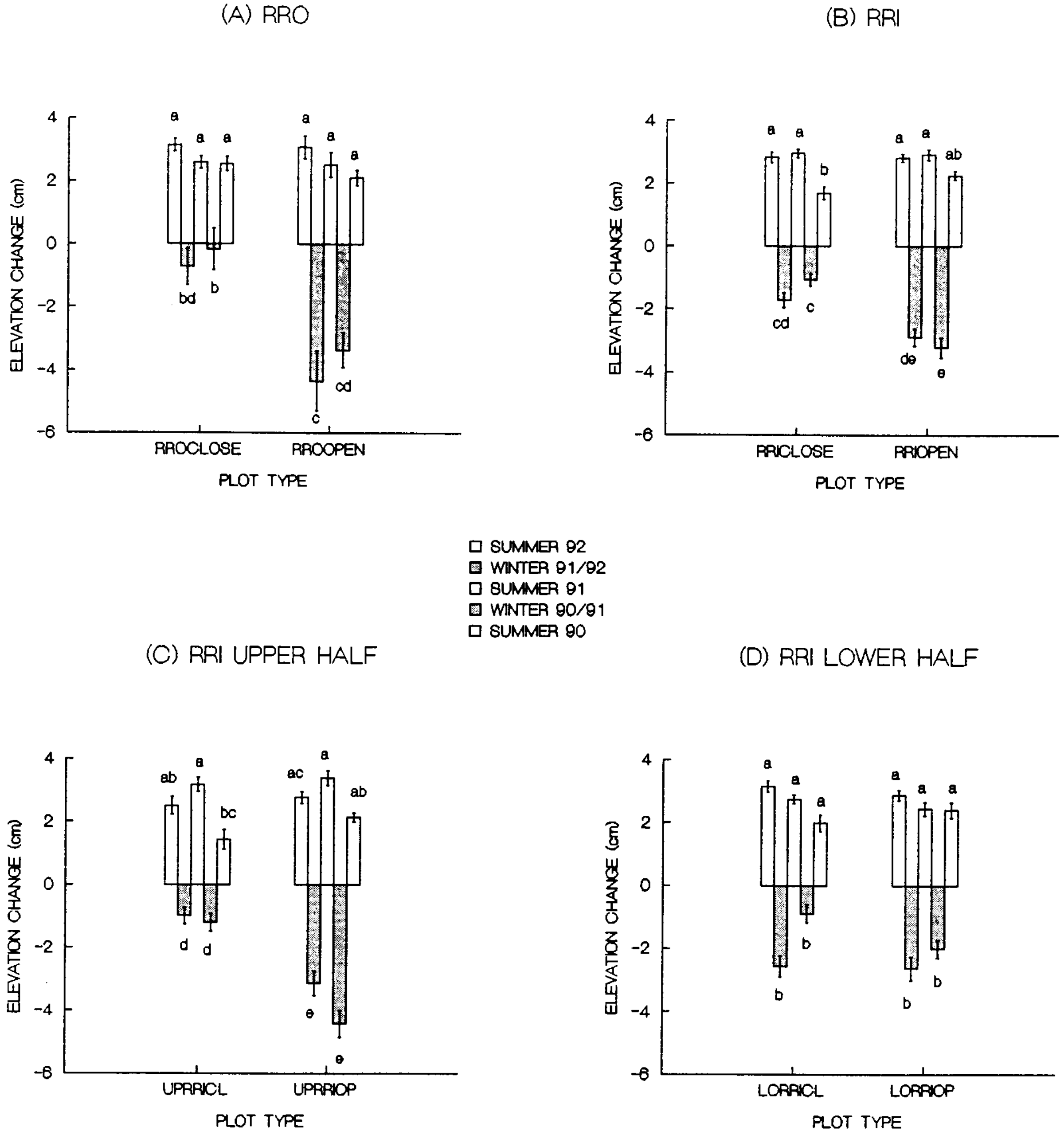


Figure 43. (A) Change in substrate elevation (mean ± 1SE) in open (RROOPEN) and closed (RROCLOSE) plots in summer (May to September; open bars) and winter (September to May; closed bars) in the RRO grid. Bars represent consecutive summers or winters from left to right. (B) Same as above for the RRI grid; RRIOPEN = open plots and RRICLOSE = closed plots. (C) Change in substrate elevation (mean ± 1SE) in open (UPRRIOP) and closed (UPRRICL) plots in summer and winter in the upper half of the RRI grid. (D) Same as above for the lower half of the RRI grid; LORRIOP = open plots and LORRICL = closed plots. Means with the same superscript do not differ at P=0.05 (Tukey multiple comparison test).

types. Accretion rates in summer were largely similar across location and plot type (Figs. 43C,D). In winter, substrate elevation decreased significantly more in open plots in the upper half of RRI than in the lower half. Mean elevation decrease during winter in the open plots was 3.5 times greater than in the closed plots in the upper half of RRI. The net result was a decrease of 1.0 cm yr^{-1} in the open plots, an increase of 1.3 cm yr^{-1} in the closed plots, and an overall grubbing impact of 2.3 cm yr^{-1}. In the lower half, mean elevation decrease during winter was only 1.4 times greater in the open plots compared to the closed plots. The net result was an increase of 0.3 cm yr^{-1} in the open plots, an increase of 0.8 cm yr^{-1} in the closed plots, and an overall grubbing impact of only 0.5 cm yr^{-1}.

Mean elevation change in the open plots (years pooled) versus distance down the bulrush zone showed that accretion during summer was consistent across the gradient but substrate loss during winter was greatest in the upper 4 rows (Fig. 44). These results confirm that most grubbing occurred in the top half of the bulrush zone.

4.4 Discussion

4.4.1 Rhizome Equilibrium

Bulrush rhizome mass on the Fraser delta remained relatively constant from 1988 to 1992 and only at 50-70 g m^{-2} or about 15% of its maximum potential level (Fig. 38). This low level equilibrium between Snow Geese and bulrush is qualitatively consistent with Noy-Meir's (1975) model (Fig. 1) and with the results of other studies that have investigated the relationship between Greater Snow Geese and marsh macrophytes on the

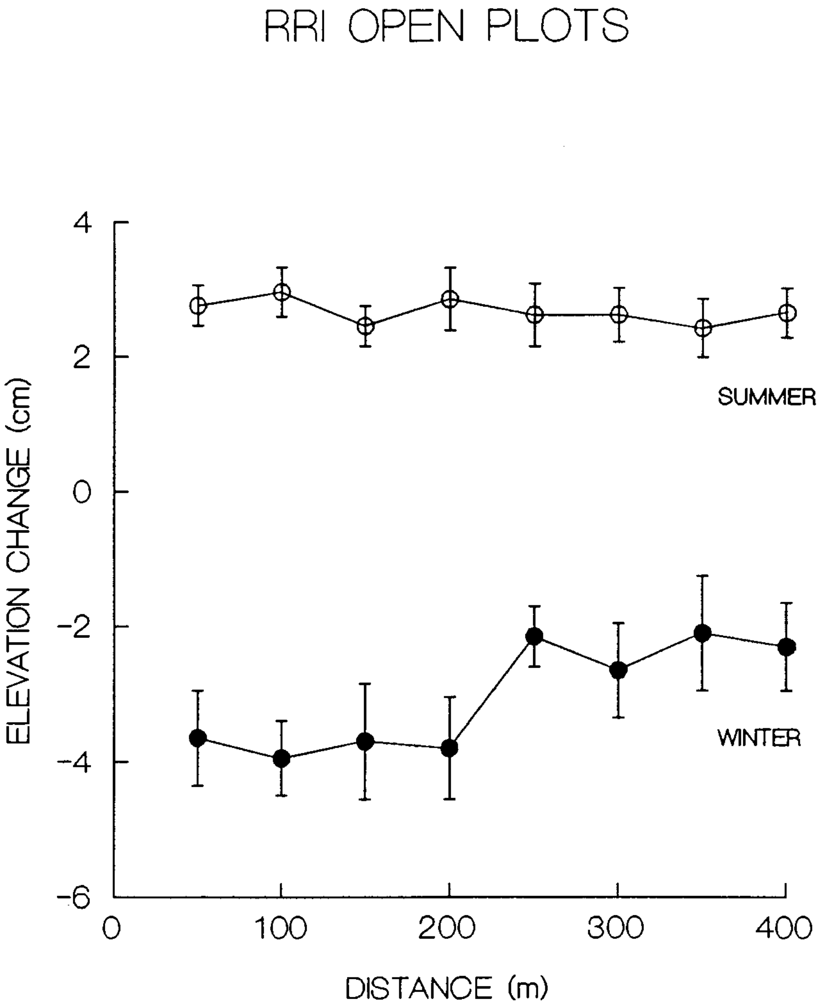


Figure 44. Change in substrate elevation (mean ± 1SE) in summer (open circles; n=3) and in winter (closed circles; n=2) across the bulrush zone in RRI open plots. Distance is from the top of the bulrush zone to the mudflat zone. Each mean (= Row) value was based on 11 open plots.

St. Lawrence River (Giroux and Bedard 1987a, Reed 1989) and in North Carolina (Smith and Odum 1981, Smith 1983). Intrinsic and/or extrinsic factors were responsible for the equilibrium.

Intrinsic Factors

The net, annual increase in rhizome mass in the absence of grubbing was constant across all patch densities but the net removal rate of rhizomes declined with decreasing patch density. On average, growth exceeded loss in patches below ca. 70 g m^{-2} and, as a result, rhizome mass increased from one year to the next. The opposite occurred in patches at higher masses. The constant growth rate function may result from changes in the resource allocation strategy of bulrush as patch density changes. Both mean mass per stem and rhizome linear density increased (Chapter 3) whereas seed production decreased (*pers. obs.*) as patch density decreased. Other factors, such as a decline in rhizome mortality/leaching rates or a decrease in competition for limiting resources (light, nitrogen), also may have been important.

The foraging returns of geese may decline as rhizome density decreases, at least below some threshold (Belanger and Bedard 1994a). Patches with very low masses may be avoided altogether because of their low returns compared to the energy needed to extract them. Whatever the mechanism responsible, the removal rate of rhizomes declined with decreasing rhizome density and this contributed to the low level steady-state.

Deep rhizomes may be important to the regrowth potential of bulrush. Reed (1989) suggested that rhizomes growing beyond the probe depth of Snow Geese were partially responsible for the low level equilibrium at Cap Tourmente NWA marshes on the St. Lawrence estuary. This may also be true for the Fraser delta. In Chapter 3, I showed that substrate at >15 cm depth in a recently grubbed, low stem density patch contained 66% of all rhizome mass in summer. In spring, substrate at >20 cm depth in the upper part of the bulrush zone in Reifel MBS where grubbing intensity is high contained ca. 10% of all rhizome mass (unpubl. data collected over 2 years).

Seeds appear to be relatively unimportant for new bulrush growth, especially in areas that have been grubbed severely. Less than 1% of mature plants on the St. Lawrence estuary result from seedlings (Giroux and Bedard 1987a) and this appears to be the case on the Fraser delta (*pers. obs.*).

Extrinsic Factors

Snow Geese were present in largely distinct groups on the Fraser delta and their mid-winter movement to the Skagit delta was consistent across years (Chapter 2). Coefficients of variation for the number of goose-days on the entire Fraser delta and on the south half of the delta in the fall/early winter period were only ca. 16% and 12%, respectively. I regressed the annual decrease in rhizome mass against the number of goose-days on the Fraser delta between 1987/88 and 1991/92 (Chapter 2). I used all combinations of age classes (adults only, total birds), time periods (fall only, total winter), and areas (south half of delta only, the entire Fraser delta) but none of the regressions was significant ($P>0.05$). Further, Alaksen NWA was used in the fall/early winter period in proportion to the abundance of geese present: when I regressed the number of goose-days on Alaksen NWA against the total number of goose-days on the south half of the delta in fall, the result was positive and significant ($b=1.3$, $r^2=0.77$,

$F_{1,3}=10.25$, $P=0.05$). Hence, the presence of distinct groups of birds, their consistent habitat use patterns and regular movement to the Skagit delta in mid-winter, and their elevated use of Alaksen NWA with increasing abundance may have altogether resulted in similar grubbing intensities each year.

4.4.2 Grubbing Effects

Urbanization and the establishment of protected areas probably caused Snow Geese to concentrate at the northwest part of Westham Island since the turn of the century. Also, the number of geese on the deltas increased in recent years (Chapter 2). I suspect that the associated increase in grubbing pressure contributed to a reversal in marsh succession as suggested by the concave substrate profiles and remnant sedge patches in the middle of the bulrush zone.

Grubbing intensity was greater in the upper half of the bulrush zone compared to the lower half. This pattern may be due to an increased amount of time available to forage or to increased foraging returns. The upper edge of the bulrush zone is exposed and available for grubbing for about twice as many hours as the lower edge (unpubl. data). Rhizome quality (nitrogen and carbohydrate content) does not vary with patch stem density (Belanger *et al.* 1990, Chapter 3) but both rhizome linear density (mass per unit length) and substrate penetrability are inversely proportional to patch density (Chapter 3, unpubl. data). Hence, returns per bite should increase and energy costs should decrease as patch stem density declines, at least down to some low level (see also Giroux and Bedard 1988, Belanger and Bedard 1994a). In a simulated grubbing experiment, I found that return rates (in g min^{-1} rhizomes excavated) were twice as high in low-medium stem density patches compared to patches near maximum density (unpubl. data). Thus, the mid-upper part of the bulrush zone may be the most profitable place for geese to grub.

The Skagit delta supported twice as many goose-days as the Fraser delta during the study period (Chapter 2). The deltas are approximately the same size and Snow Geese on the Skagit delta in fall/early winter foraged mostly only on the marsh. Hence, the Skagit delta may have experienced twice as much grubbing pressure as the Fraser delta historically and this may explain why mean rhizome mass there is much lower than on the Fraser delta (see also Boyd 1988).

Most grubbing occurred in the fall/early winter period within the Reifel MBS and this is probably true for rest of the delta. Snow Geese graze heavily on new sedge shoots in spring (*pers. obs.*). Compared to bulrush rhizomes, sedge shoots contain greater levels of nitrogen and carbohydrates in spring (unpubl. data) and grazing is probably less energetically costly compared to grubbing. I suspect that the geese are tracking a food-quality gradient at this time.

4.5 Conclusions and Recommendations

Bulrush rhizome mass on the Fraser delta was at a low level steady-state throughout the study period. I suspect that both intrinsic and extrinsic factors were responsible for the equilibrium. Rhizome mass increased at a constant, annual rate across all patch densities but mass was removed at a decreasing rate as patch density declined. Growth exceeded loss in patches with rhizome masses <70 g m^{-2} but the opposite was true in patches at higher masses. The constant growth rate function may be a result of changes in the resource allocation strategy of bulrush as patch density changes. Both mean mass per stem and rhizome linear density increased whereas seed production decreased as patch density decreased. Other factors, such as a decline in rhizome mortality/leaching rates or a decrease in competition for limiting resources, also may be important. A growth reserve of deep (>20 cm) rhizomes likely contributed to the regrowth potential of bulrush in heavily grubbed patches. In addition, the existence of distinct sub-flocks on the Fraser delta, their consistent movement to the Skagit delta in mid-winter, and their elevated use of Alaksen NWA with increasing abundance may have resulted in the same grubbing intensities in the study area each year.

Bulrush rhizomes will always be an important food for Snow Geese. The geese depend exclusively on the marsh during extended freezing periods that occur almost every winter (*pers. obs.*). On the Skagit delta and in parts of the Fraser delta, the geese forage heavily on the marsh during the fall/early winter period. Also, farmland is gradually disappearing on both deltas due to urban encroachment and preferred crop types may not always be available because of changing market forces. I suspect that factors intrinsic to the interaction will ensure that bulrush is maintained at a low level on the deltas. In addition to monitoring bulrush stem density in permanent plots, the following studies would help improve our understanding of the interaction between Snow Geese and bulrush: assess grubbing rates and regeneration rates of rhizomes at different substrate depths through destructive sampling in fall and in spring; assess the benefits (nutrient and energy returns) and costs (energy expenditures) of grubbing in bulrush patches at different rhizome densities and the relative profitability of grazing crops versus grubbing rhizomes through foraging experiments with captive geese; and, finally, assess the response of the geese to a large-scale fertilization experiment of the marsh at Westham Island (see Chapter 3).

Chapter 5

Summary and Conclusions

5.1 Introduction

More than half of the Lesser Snow Geese that nest on Wrangel Island, Russia, overwinter on the Fraser River (B.C.) and Skagit River (Wash.) deltas. One of their principal foods is rhizomes of American three-square bulrush (Burton 1977). Snow Geese have reduced the primary production and biomass of salt marshes on the Atlantic coast (Smith and Odum 1981, Smith 1983) and on the St. Lawrence River estuary (Giroux and Bedard 1987a, Reed 1989). In 1974/75, a year when the Fraser/Skagit population was the smallest ever recorded, the geese consumed about one-third of the below-ground mass of bulrush on the Fraser delta (Burton 1977). Burton (1977) suggested that the marsh would be negatively affected if the number of geese doubled. The population increased by 3-4 fold in the late 1970s and has remained high throughout the 1980s and early 1990s (Anon. 1992, this study). The geese began to forage on agricultural crops on Alaksen NWA on the Fraser delta in the early 1980s (Hatfield 1991; *pers. comm.* with local farmers and hunters). This new foraging behaviour suggested that bulrush rhizomes may have been depleted to the point where Snow Geese were forced to use farm crops to meet their requirements for some essential nutrient (energy, protein). To address this concern, I studied the abundance and distribution patterns of Snow Geese on the deltas (Chapter 2), the seasonal and annual growth patterns of bulrush in patches at different densities (Chapter 3), and the interaction between rhizome growth and removal rates (Chapter 4).

5.2 Goose Abundance and Distribution

The number of Snow Geese on the deltas fluctuated considerably from year to year, coinciding with differences in recruitment. The size of the Fraser/Skagit population increased during the 1980s and this corresponded with an increase in the number of immature birds in the population each year. Differential harvest rates on largely distinct populations could account for recent increases in the proportion of Fraser/Skagit geese on the Fraser delta in fall and in the proportion of Wrangel Island geese on the Fraser and Skagit deltas in winter. Short-stopping during fall migration may also have contributed to the increases.

Telemetry observations showed that at least half of all Wrangel Island geese wintering in California staged on the Fraser and Skagit deltas in fall. The deltas supported a largely closed population from December to March, however, and this finding has important research and management implications. First, the dynamics of the Fraser/Skagit population can be modelled to improve our understanding of the relative importance of recruitment versus harvest. Second, the minimum size of the population can be predicted by applying a conservative return rate to photo counts conducted during the previous year. Hunting regulations could then be adjusted to help maintain the population within desired limits.

Snow Geese were consistent in their distribution and movement patterns across years and they showed high site-fidelity. Such tradition has resulted in the development of largely distinct populations and sub-populations on the deltas. Managers should be aware of these units and the long-term effects of different management regimes (e.g.

harvest, refuges) on goose abundance and distribution. I suspect that the traditional movement of geese from the Fraser delta to the Skagit delta in mid-winter developed from compromises made primarily with respect to food quality/quantity and hunting disturbance (discussed further below).

5.3 Bulrush Growth

Bulrush rhizomes on the Fraser delta grew only during July. Photosynthesis and translocation rates from shoots to rhizomes are probably at a maximum at this time because of the low tides at mid-day, high air temperatures, high number of sunlight hours, and peak shoot densities and lengths.

A bulrush patch at high stem density had considerably greater rhizome production in summer compared to a low density patch but both patches had the same net, annual increase in mass. This may reflect plasticity in how bulrush allocates resources to different plant components as patch density declines due to grubbing. Whatever the mechanism, the constant growth function is important to the stability of the interaction between Snow Geese and bulrush. In addition, rhizomes growing deep in the substrate (>20 cm depth) would ensure that some plant growth is maintained irrespective of grubbing intensity.

All bulrush components responded positively to the application of commercial fertilizers, suggesting that nitrogen is limiting to growth on the Fraser delta. Rhizome mass and quality in September increased significantly over controls at relatively low treatment levels. Fertilization of the bulrush zone at Westham Island would increase the carrying capacity of the delta for herbivorous birds and the input of organic matter to the detrital food chain of the estuary.

5.4 Interaction

Rhizome mass increased with distance down the bulrush gradient in Reifel MBS on the Fraser delta. Higher grubbing rates occurred in the upper half of the zone, resulting in a net decrease in substrate elevation each year and a reversal in marsh succession at Westham Island.

Mean rhizome masses on the Fraser and Skagit deltas were only at a small fraction of their potential, maximum levels and mass on the Skagit delta was almost half that on the Fraser delta. Most, if not all, grubbing in Reifel MBS occurred in the fall/early winter period. When the geese returned to the Fraser delta in spring, they grazed mostly on young sedge shoots which are abundant around the mouths of the main river channels.

Snow Geese maintained bulrush rhizome mass on the Fraser delta at a low level steady-state between 1988 and 1992. Similar equilibria have been measured on the Atlantic coast (Smith and Odum 1981, Smith 1983) and on the St. Lawrence River estuary (Giroux and Bedard 1987, Reed 1989, Belanger and Bedard 1994a). Both intrinsic and extrinsic factors (to the interaction) were responsible for the equilibrium. The net, annual increase in rhizome mass in the absence of grubbing was constant across all patch densities. Growth exceeded removal in patches with rhizome masses less than ca. 70 g m^{-2} but the opposite was true in patches with greater masses. A reserve of rhizomes beyond the probe depth of Snow Geese likely also helped maintain bulrush growth in areas where grubbing intensity was high.

Extrinsic factors probably also contributed to the steady-state. Largely distinct sub-populations of Snow Geese were present on the Fraser and Skagit deltas. Further, Fraser geese consistently moved to the Skagit delta in mid-winter, the number of goose-days in the study area varied little across years, and goose-use of Alaksen NWA increased with increasing abundance. These extrinsic factors may have resulted in similar grubbing intensities each year.

5.5 Cover Crops

Snow Geese have been grazing on Skagit farms for decades (Jeffrey and Kaiser 1979) and at Alaksen NWA on the Fraser delta since the early 1980s (Hatfield 1991, *pers. obs.*). As previously noted, one explanation for this foraging behaviour is that bulrush rhizomes were grubbed down to a level where the geese were unable to meet their requirements for energy or some essential nutrient. An alternative explanation is that the geese were simply following a food-profitability gradient; that is, grazing on farms resulted in greater foraging returns compared to grubbing bulrush (Stephens and Krebs 1986, Krebs and Davies 1987).

Grazing is a familiar foraging strategy to Snow Geese. Adults spend almost half of their lives (fall and spring migrations and throughout most of the summer) grazing on grasses and sedges. Goslings graze from hatch to the end of fall migration and their grubbing efficiencies are probably relatively low when they arrive on the deltas. Cover crops have significantly higher concentrations of nitrogen and carbohydrates and lower levels of fibre compared to rhizomes (unpubl. data). Furthermore, grazing is probably less energy-expensive than grubbing because the geese do not have to excavate for their food. The above suggests that cover crops are likely a more profitable food than rhizomes and Snow Geese should graze them whenever and wherever it is safe to do so (i.e. no hunters). This appears to be the general pattern on the deltas. Geese usually begin to use farms on the Skagit delta in large numbers in January after the hunting season has closed; fields used prior to this date have hunting restrictions. On the Fraser delta, farms are used in fall on Alaksen NWA where hunting is prohibited. The geese often move onto other farmland on Westham Island but only during non-hunting periods. Further, all Fraser geese move to the Skagit delta in mid-winter. At this time, cover crops are available and hunting is prohibited on the Skagit delta but hunting has historically occurred on the Fraser delta. This traditional movement of Fraser geese to the Skagit delta and their recent use of Alaksen NWA in fall occur despite the fact that rhizomes are still relatively abundant (with many patches at medium-high rhizome density) in the lower half of the bulrush zone on Westham Island and at other areas such as the Outer Island (Chapter 4). Also, mean rhizome mass on the Fraser delta is almost double that on the Skagit delta (hence, the geese move from an area with a relatively high abundance of rhizomes to an area with low abundance) and rhizome quality (nitrogen and carbohydrate levels) improves from September to January (Chapter 3). Finally, when the geese return to the Fraser delta in spring, they mostly graze on young sedge shoots and on farm crops both of which are higher quality foods compared to rhizomes (unpubl.

data). These observations suggest that, as is the case for Arctic geese in Europe (Drent *et al.* 1978/79, Charman 1979, Boudewijn 1984, Madsen 1985), Snow Geese on the Fraser and Skagit deltas track a food-quality gradient from fall to spring. Hunting disturbance acts as a constraint with respect to where the geese can feed along this gradient. Proximate analysis and foraging experiments with captive geese should be conducted to help test this hypothesis.

I used a modified version of Noy-Meir's (1975) model to investigate the interaction between Snow Geese and bulrush on the Fraser and Skagit deltas. Noy-Meir's model assumes a simple, artificial grazing system in which herbivore density is constant and consumption and plant growth are continuous and simultaneous. The model also assumes that the target plant is limiting to the herbivore; that is, that the system is essentially closed. Few, if any, natural systems meet these criteria and the Snow Goose-bulrush system is no exception. Not only do the geese have access to alternate foods (cover crops), they may prefer them over bulrush rhizomes. This relaxes the dependence of Snow Geese on rhizomes and, thus, reduces the importance of the intrinsic factors (constant rhizome growth function and deep rhizomes) to the interaction within the current ecological context. The observed low level equilibrium rhizome mass may be more a "spill-over" result of the intense use of cover crops by geese rather than the cause of it.

The steady-state rhizome mass measured in my study should continue as long as there are no substantial changes to the abundance and distribution patterns of Snow Geese on the deltas. These patterns are bound to change, however, because they are influenced by factors such as the number and spatial/temporal distribution of hunters and the types and distribution of cover crops. The number of hunters and (thus) the number of geese harvested each year are expected to decline over time and goose abundance should increase as a result. Farmland is gradually being lost because of residential and commercial development and preferred crop types may not always be available because of changing market forces. If either of these predictions are realized, Snow Geese may have to depend increasingly on the marsh for survival. The intrinsic factors noted above, however, should maintain the bulrush zone at some low level biomass. A food-related, density-dependent effect should eventually emerge to reduce goose survival and/or reproductive rates, thereby imposing an upper limit to the number of geese that can be supported. Competition for food by a growing population of swans may accelerate this process (Boyd 1994).

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Appendix 1. Harvest Estimates

Harvest was estimated annually since 1948/49 on the Skagit delta by the Washington Dept. of Wildlife (Anon. 1992). Harvest estimates for the Fraser delta were collected on a far less consistent basis; 3 unpublished sources were available (Pacific Flyway Waterfowl reports, B.C. Wildlife Branch hunter surveys, and CWS regional hunter surveys) along with one published source (CWS National Harvest Surveys [NHS]). For years in which 2 different types of harvest data were available, the mean value was used. The ratio of the NHS to the average of the NHS and the B.C. Wildlife Branch survey was used to adjust the NHS when it was the only estimate. The ratio of the Fraser harvest to the Skagit harvest was used to predict the Fraser harvest for years when data were missing. Finally, although the hunting season on the Skagit delta generally preceded the mid-winter survey, this was not true for the Fraser delta. Since 1963, 2 hunting seasons have been in effect on the Fraser delta with the first season preceding the mid-winter census. About 75% of the total harvest occurs during the first season (unpubl. data) so this percent was used for all years after 1963. The percent of the hunting season that fell before mid-January was used for all other years.

Appendix 2. Airphoto Technique

Almost all surveys were conducted during mid-morning (ca. 10:00 h), weather and air traffic permitting. On the Fraser delta, the geese were within the control zone of the Vancouver International Airport so each survey had to be coordinated with airport control staff.

Most flights were in a Cessna 172 at speeds of 140-170 km h^{-1} with the remainder in a Dehavailand Beaver at 130-140 km h^{-1}. The surveys were done at 400 m, an altitude that resulted in little disturbance to the geese, good coverage of large flocks, good photo resolution with the lens used, and little interference from clouds.

Upon locating a flock of geese, the airplane was manoeuvred to within 200 m and then banked for the photo set. Only a few photos were required for small flocks (<500 birds) but >30 photos were sometimes needed for large ones (>20,000 birds) at 25-50% overlap. The geese were not photographed if they were in the air because photo-delineation became difficult and the chance of missed or double counts increased. If a flock moved prior to or during a photo set, we flew some distance away (>2 km), waited for the geese to settle, and then gradually spiralled inwards.

I used a 35 mm SLR auto-wind camera equipped with a 30-110 mm zoom lens. The 110 mm focal length was used for the counts, resulting in photo scales of between 1:4,000 and 1:6,000. The 30 mm lens was used to take overview photos to help locate and delineate each flock.

A 300 mm lens was used for age ratios. Photos were taken randomly throughout each flock. Overcast days were best for discriminating between adult (white) and young (grey) birds.

High speed (1600 ASA) colour print film was used for most surveys, especially when the weather was overcast. On sunny days, 400 ASA film was preferred. Airplane vibration and the long lens used meant that it was important to have shutter speeds faster than 1/250 s.

All photos were automatically inscribed with a number using the camera data back. Flock numbers and their corresponding photo numbers were recorded onto maps of the study area along with the exact route flown. The film was printed on 10.2 cm x 15.2 cm paper at 3 times normal contrast to help discriminate between immature birds and background features.

For flocks with overlapping photos, common points on adjacent prints were identified and lines drawn around the geese to be counted. A dissecting microscope (12x power) and a modified pen (with a pin attached to a microswitch/digital tallier) were used for the counts. Pin-holes were punched through each goose image to avoid duplicate counts.

The same counting procedure was used for age ratios. Only high quality photo sets were used to make it easier to distinguish between adults and immature birds. Entire photographs or portions of photos were used as the sample units.

Appendix 3. Number of Snow Geese on the Fraser River and Skagit River deltas from 1987/88 to 1991/92.

Year	Date (y/m/d)	Fraser Delta	Skagit Delta	Total
87/88	871119	34197	21159	55356
	871210	26003	21654	47657
	880112	9590	41716	51306
	880216	0	47551	47551
88/89	881115	24143	19577	43720
	881215	24611	19188	43799
	890111	2891	36860	39751
	890317	5177	40864	46041
	890418	7371	13015	20386
89/90	891121	20404	14520	34924
	891207	18443	13729	32172
	891212	19947	13822	33769
	891221	20133	13785	33918
	900102	18290	15058	33348
	900111	0	33452	33452
	900312	1835	32540	34375
90/91	901114	18536	14970	33506
	901119	19305	14349	33654
	901126	18716	15034	33750
	901205	18548	13934	32482
	901227	11119	18296	29415
	910102	0	32054	32054
	910124	0	32434	32434
	910129	0	32524	32524
91/92	911015	17247	8818	26065
	911029	24291	17569	41860
	911113	26793	16944	43737
	911204	21270	16899	38169
	911217	12662	26738	39400
	911230	17244	21855	39099
	920120	1741	37371	39112
	920213	1556	37270	38826
	920225	4245	35617	39862
	920316	11222	29127	40349
	920323	12769	27608	40377
	920330	15100	25030	40130
	920406	13244	20215	33459
	920413	5485	16044	21529

Appendix 4. Number of Snow Geese on the Fraser River delta from 1987/88 to 1991/92, by date and location.

Date (y/m/d)	Sea Island Marsh	Lulu(N) Island Marsh	Lulu(S) Island Marsh	Outer Island Marsh	Reifel Refuge Marsh	Westham Island Marsh	Brunswick Point Marsh	Woodward Island Marsh	Alaksen NWA Fields	Other Areas	Total Fraser Delta
870912	0	0	0	0	0	0	0	0	0	0	0
870919	0	0	0	0	0	0	200	0	0	0	200
870921	0	0	0	0	0	0	50	0	0	0	50
871007	0	0	0	0	0	0	292	0	0	0	292
871014	0	0	0	0	103	0	385	0	0	0	488
871020	4298	592	0	293	3895	0	0	0	0	0	9078
871027	3730	0	0	0	9898	0	0	0	0	0	13628
871104	6758	2711	1303	472	0	12900	10010	0	2993	25	37173
871112	5581	3665	3665	0	0	0	4435	0	17401	0	34747
871119	3104	5523	7673	0	0	16840	286	0	771	0	34197
871125	1976	3549	3550	0	19023	0	0	0	6330	0	34428
871202	0	5014	5015	0	0	0	0	0	21787	0	31816
871207	0	7393	7231	0	441	0	0	0	18298	0	33363
871210	0	7490	7491	0	0	0	0	0	11022	0	26003
871215	502	3234	6358	720	2443	4156	6094	0	0	0	23507
871221	646	6255	863	0	0	3699	0	0	14498	0	25961
871229	1552	3648	3755	0	0	7545	0	0	6496	0	22996
880104	0	3527	0	0	6907	3037	0	0	0	0	13471
880112	2181	0	0	0	0	0	0	0	7409	0	9590
880118	0	0	0	0	0	0	0	0	0	0	0
880201	0	0	0	0	0	0	0	0	0	0	0
880216	0	0	0	0	0	0	0	0	0	0	0
880224	0	2245	0	0	0	0	0	0	0	0	2245
880302	5614	156	2158	0	0	2487	0	2549	0	0	12964
880308	4844	0	2797	0	7511	0	0	1520	0	0	16672
880314	0	4167	5551	0	0	5456	2161	0	0	0	17335
880321	0	6133	6235	208	0	100	6290	2984	0	0	21950
880328	444	6593	5252	330	0	91	408	8862	0	200	22180
880406	706	3288	5280	180	0	0	0	925	0	10214	20593
880411	370	433	292	462	993	1078	4006	1435	0	4830	13899
880418	66	0	0	2720	10	0	0	2067	0	0	4863
880425	0	0	0	904	0	1947	0	0	0	150	3001
880502	0	0	0	0	0	0	0	0	0	0	0

Appendix 4 continued....

Date (y/m/d)	Sea Island Marsh	Lulu(N) Island Marsh	Lulu(S) Island Marsh	Outer Island Marsh	Reifel Refuge Marsh	Westham Island Marsh	Brunswick Point Marsh	Woodward Island Marsh	Alaksen NWA Fields	Other Areas	Total Fraser Delta
880919	0	0	0	0	0	0	0	0	0	0	0
880926	0	0	0	0	0	0	50	0	0	0	50
881004	0	0	0	0	0	0	0	0	0	50	50
881011	5768	0	0	0	5457	0	1565	0	0	0	12790
881017	2402	1117	1117	0	3793	6968	2943	0	3944	494	22778
881024	2196	0	7328	2499	0	3624	0	0	10655	0	26302
881031	5799	1832	1833	0	0	0	0	0	17456	0	26920
881106	2825	8095	0	3930	0	0	4100	0	6721	0	25671
881115	2199	415	415	0	9254	0	0	0	5042	6818	24143
881121	0	712	712	0	4526	6240	0	0	668	8835	21693
881128	1005	0	850	0	18238	0	0	0	5000	0	25093
881206	1768	1309	1309	0	12104	8151	0	0	0	0	24641
881215	0	5488	0	0	19123	0	0	0	0	0	24611
881219	0	3373	3374	0	13673	1376	0	0	0	0	21796
881228	0	4318	4319	0	0	0	0	0	259	0	8896
890103	0	3056	3984	0	0	0	0	0	687	0	7727
890111	0	0	0	0	0	0	0	0	2891	0	2891
890117	0	0	0	0	0	0	1438	0	0	0	1438
890123	0	0	0	0	0	0	0	0	0	0	0
890208	0	0	0	0	0	0	0	0	0	0	0
890222	0	0	0	0	0	0	0	0	0	0	0
890227	0	3027	0	0	0	0	0	0	0	0	3027
890306	0	344	344	0	94	0	0	0	38	0	820
890313	0	914	0	0	0	0	0	0	0	0	914
890317	0	3062	554	0	0	0	1561	0	0	0	5177
890322	57	6431	4600	186	0	2762	954	3804	0	10	18804
890328	0	4297	8296	0	0	2280	2654	5329	0	0	22856
890403	66	5332	6353	1790	0	1202	0	11394	0	0	26137
890410	426	3998	4509	0	0	11722	2282	1286	0	0	24223
890418	0	0	0	0	2556	368	0	1008	0	3439	7371
890424	0	0	0	0	0	0	0	1322	0	0	1322
890502	0	0	0	0	0	0	0	0	0	5	5
890509	0	0	0	0	0	0	0	0	0	0	0

Appendix 4 continued....

Date (y/m/d)	Sea Island Marsh	Lulu(N) Island Marsh	Lulu(S) Island Marsh	Outer Island Marsh	Reifel Refuge Marsh	Westham Island Marsh	Brunswick Point Marsh	Woodward Island Marsh	Alaksen NWA Fields	Other Areas	Total Fraser Delta
891003	0	0	0	0	0	0	0	0	0	0	0
891010	0	0	0	0	0	49	0	0	0	0	49
891016	1141	416	0	0	6210	0	0	0	55	0	7822
891023	2054	1287	440	416	1744	1371	8829	0	442	0	16583
891031	4828	904	980	0	2273	0	0	0	13955	0	22940
891107	3412	56	2490	50	0	0	0	0	16485	0	22493
891114	0	3014	3015	0	13605	0	0	0	0	0	19634
891121	0	3826	3826	3855	8236	0	661	0	0	0	20404
891127	0	4017	4017	0	12129	0	0	0	0	0	20163
891207	0	5097	2536	3860	6950	0	0	0	0	0	18443
891212	0	1243	7193	0	11511	0	0	0	0	0	19947
891221	0	0	7939	1346	2175	3659	5014	0	0	0	20133
900102	0	0	4865	423	0	13002	0	0	0	0	18290
900108	0	937	937	0	0	0	0	0	0	0	1874
900111	0	0	0	0	0	0	0	0	0	0	0
900125	0	0	0	0	0	0	0	0	0	0	0
900219	0	0	0	0	0	0	0	0	0	0	0
900227	0	933	0	1046	0	55	0	0	0	0	2034
900306	669	0	258	0	0	0	0	3071	0	0	3998
900312	158	1637	0	0	0	40	0	0	0	0	1835
900320	0	1808	3532	44	0	2509	1328	0	0	0	9221
900326	394	2323	2300	880	0	0	0	5203	0	0	11100
900402	0	1912	1769	1045	0	104	212	4625	0	0	9668
900410	99	0	0	1109	110	412	2166	1474	0	0	5370
900417	0	0	0	3307	0	464	470	969	0	0	5210
900424	0	0	0	2013	0	0	0	0	0	0	2013
900501	0	0	0	0	0	3	0	0	0	0	3
900508	0	0	0	0	0	0	0	0	0	0	0

Appendix 4 continued....

Date (y/m/d)	Sea Island Marsh	Lulu(N) Island Marsh	Lulu(S) Island Marsh	Outer Island Marsh	Reifel Refuge Marsh	Westham Island Marsh	Brunswick Point Marsh	Woodward Island Marsh	Alaksen NWA Fields	Other Areas	Total Fraser Delta
900928	0	0	0	0	0	0	0	0	0	0	0
901005	0	15	0	0	0	1280	2481	0	0	0	3776
901010	0	0	0	16	0	9841	2540	0	0	0	12397
901015	0	3643	0	221	0	6832	14346	0	0	0	25042
901022	0	5921	1828	0	2166	0	0	0	13335	0	23250
901029	689	1523	2294	2411	0	2962	11600	0	0	0	21479
901106	1083	2721	2722	0	13050	0	0	0	0	0	19576
901114	1155	1166	2796	1318	963	9940	1198	0	0	0	18536
901119	1258	938	1038	0	13910	0	0	0	2161	0	19305
901126	1943	0	547	511	15715	0	0	0	0	0	18716
901205	2157	961	961	0	14248	0	0	0	0	0	18327
901211	1700	2079	1662	0	10430	0	0	0	0	0	15871
901218	1435	717	3212	0	12185	0	0	0	0	0	17549
901227	0	2992	1823	0	3259	3045	0	0	0	0	11119
910102	0	0	0	0	0	0	0	0	0	0	0
910124	0	0	0	0	0	0	0	0	0	0	0
910129	0	0	0	0	0	0	0	0	0	0	0
910213	0	911	0	0	0	0	0	0	0	0	911
910219	4183	0	0	0	0	0	0	0	0	0	4183
910226	358	3600	2178	0	0	5064	0	0	0	0	11200
910305	0	2911	5969	80	0	0	0	0	0	0	8960
910312	2011	2905	3624	0	0	2526	319	607	0	0	11992
910318	0	5641	2219	141	0	191	1860	3629	0	858	14539
910327	42	4610	2202	751	0	0	0	8109	0	0	15714
910402	650	3386	1636	1827	181	1770	739	4026	940	834	15989
910409	0	54	0	126	0	0	0	4859	1408	2416	8863
910416	0	0	0	0	0	469	1621	0	0	5142	7232
910423	0	0	0	0	0	0	0	0	0	0	0

Appendix 4 continued....

Date (y/m/d)	Sea Island Marsh	Lulu(N) Island Marsh	Lulu(S) Island Marsh	Outer Island Marsh	Reifel Refuge Marsh	Westham Island Marsh	Brunswick Point Marsh	Woodward Island Marsh	Alaksen NWA Fields	Other Areas	Total Fraser Delta
911002	0	0	0	0	0	0	0	0	0	0	0
911009	377	0	0	0	0	0	3588	0	0	0	3965
911015	3560	0	0	0	0	12318	0	0	1369	0	17247
911022	4405	0	7509	1131	13187	0	0	0	1375	0	27607
911029	3803	588	861	0	146	0	0	0	18893	0	24291
911108	3129	480	4985	0	18423	0	0	0	0	0	27017
911113	2989	1378	2361	0	0	0	0	0	20065	0	26793
911118	2544	1257	1803	0	208	0	1686	0	18401	0	25899
911125	4293	85	86	0	21906	116	0	0	0	0	26486
911204	2261	626	1249	0	10428	5900	806	0	0	0	21270
911209	2489	1380	1380	0	31	0	0	0	18508	0	23788
911217	1032	1635	3148	0	2554	2056	120	0	2117	0	12662
911223	1233	1917	3077	0	6359	0	0	0	0	0	12586
911230	2528	2639	1477	0	3694	2084	0	0	4822	0	17244
920106	3187	0	0	0	1986	3472	0	0	0	0	8645
920113	1439	0	0	0	0	0	0	0	0	2123	3562
920120	0	0	0	0	0	1741	0	0	0	0	1741
920127	0	0	0	0	0	0	0	0	0	0	0
920207	0	0	0	0	0	0	0	0	0	0	0
920213	0	1556	0	0	0	0	0	0	0	0	1556
920225	321	2162	1260	0	0	502	0	0	0	0	4245
920303	2913	108	991	34	0	3227	0	2371	0	0	9644
920312	1105	3575	973	0	0	0	0	2932	2424	0	11009
920316	382	3981	1153	0	0	0	0	5706	0	0	11222
920323	0	3275	1520	0	0	0	0	0	7974	0	12769
920330	0	2426	1381	939	273	2027	0	4200	0	3854	15100
920406	290	0	137	3096	2393	0	0	4762	2566	0	13244
920413	0	0	0	4131	0	1032	0	322	0	0	5485
920421	0	0	0	0	0	0	300	0	0	0	300
920428	0	0	0	0	0	0	100	0	0	0	100
920505	0	0	0	0	0	0	0	0	0	0	0

Appendix 5. Percent of immature birds (mean ± 1SE) in the Snow Goose population on the Fraser River delta from 1987/88 to 1991/92, by date and location. Sample sizes are given in brackets. Overall percents for the delta were calculated by weighting flock means by flock sizes.

Date (d/m/y)	Sea Island marsh	Lulu Island marsh	Westham Island marsh	Brunswick Point marsh	Westham Island fields	Fraser Delta
201087	31.6±10.5 (377)					31.6±10.5 (377)
041187		27.0±5.4 (2697)	26.0±6.2 (750)			26.5±4.2 (3447)
191187		32.8±7.8 (695)	27.7±9.5 (519)			29.9±6.3 (1214)
251187	30.9±10.8 (644)	28.1±6.2 (1379)	27.3±5.3 (1320)			27.8±4.0 (3343)
021287		39.2±10.3 (638)			28.5±6.9 (813)	31.9±5.7 (1451)
071287		29.1±6.7 (1140)			31.2±6.0 (1678)	30.3±4.5 (2818)
151287	42.2±30.4 (90)	28.4±5.8 (853)	38.4±8.5 (1115)			32.8±4.8 (2058)
211287	40.9±29.2 (105)	30.9±9.9 (372)	25.9±8.1 (424)			29.8±6.9 (901)
291287		30.1±10.6 (286)			24.8±14.3 (105)	27.6±8.8 (391)
Mean	32.8±7.4 (1216)	29.4±2.7 (8060)	29.9±3.4 (4128)		30.1±4.5 (2596)	
171088		6.9±3.6 (2182)	5.1±1.4 (12063)		8.3±9.9 (2214)	6.1±2.5 (16459)
311088		1.9±0.5 (4958)	0.4±0.1 (2006)		18.5±9.3 (1364)	9.7±4.5 (8328)
211188		1.4±0.8 (1836)	3.8±1.9 (4902)		8.4±3.7 (3828)	6.3±2.6 (10566)
281188		0.0±0.0 (473)	1.7 ± 0.6 (2824)		15.2±5.9 (3175)	4.5 ±1.3 (6472)
191288		8.8±2.6 (3917)	4.6 ± 1.1 (6372)			6.0 ±1.1 (10289)
281288		6.1±1.6 (4770)				6.1±1.6 (4770)
Mean		5.0±0.8 (18136)	4.1 ± 0.7 (28167)		11.7±3.3 (10581)	

Appendix 5 continued....

Date (d/m/y)	Sea Island marsh	Lulu Island marsh	Westham Island marsh	Brunswick Point marsh	Westham Island fields	Fraser Delta
051090			1.8±0.6 (2194)	1.3±0.7 (683)		1.5±0.5 (2877)
101090			6.3±3.8 (2260)	9.0±6.6 (1986)		6.8±3.3 (4246)
151090		9.3±4.1 (2535)	11.9±5.9 (2222)	9.0±3.1 (2375)		9.8±2.5 (7132)
221090		6.4±1.1 (5688)	7.6±2.4 (2843)		12.4±3.1 (5796)	9.9±1.8 (14327)
291090		9.5±2.1 (3026)	19.4±9.6 (4001)	10.2±1.9 (8629)		12.3±2.6 (15656)
061190	18.7±18.9 (1463)	12.1±3.6 (2086)	11.2±2.8 (6937)			11.9±2.4 (10486)
141190	21.4±8.3 (2274)	8.5±3.8 (1478)	9.9±2.4 (8405)	12.8±4.5 (1099)		10.6±1.9 (13256)
261190		22.1±16.2 (651)	10.1±2.2 (5299)			10.5±2.2 (5950)
111290	13.3±7.4 (1439)	12.7±4.4 (2243)	5.4±1.6 (7140)			7.8±1.7 (10822)
181290		8.8±4.3 (2248)	6.0±3.3 (1464)			6.7±2.7 (3712)
Mean	18.4±6.8 (5176)	10.0±1.2 (19955)	9.5±1.3 (42765)	9.6±1.5 (14772)	12.4±3.1 (5796)	
091091				7.6±4.4 (1856)		7.6±4.4 (1856)
151091	26.6±9.7 (2511)		14.2±5.6 (4388)		33.2±23.5 (1839)	18.3±4.8 (8738)
221091	33.6±23.5 (715)	28.9±9.9 (1748)	28.0±10.1 (2054)		53.9±33.8 (629)	30.4±7.0 (5146)
081191	22.0±11.7 (1480)	24.1±6.7 (5009)	29.3±7.6 (8954)			27.5±5.6 (15443)
181191		15.7±6.8 (1858)		13.9±6.6 (2793)	29.4±7.6 (9479)	26.8±6.3 (14130)
231291	42.6±19.3 (1301)	24.4±8.9 (2663)	24.6±7.7 (2313)			26.3±5.6 (6277)
Mean	29.8±7.1 (6007)	23.5±4.1 (11278)	24.8±4.4 (17709)	11.4±4.3 (4649)	31.3±7.3 (11947)	

Appendix 6. Number and percent of Snow Goose-days in areas of the Fraser River delta during fall and spring periods, 1987/88 to 1991/92.

	1987/88		1988/89		1989/90		1990/91		1991/92	
Location	Days	%	Days	%	Days	%	Days	%	Days	%
Fall:										
Sea Is. marsh	218268	9.8	162104	8.4	82916	5.2	83588	5.3	274094	14.2
Lulu Is. north marsh	313432	14.0	205168	10.6	148795	9.3	158720	10.1	79441	4.1
Lulu Is. south marsh	267115	12.0	176998	9.2	306904	19.2	137885	8.8	190669	9.9
Outer Is. marsh	9641	0.4	45003	2.3	75418	4.7	32144	2.1	7917	0.4
Reifel Refuge marsh	287421	12.9	611792	31.7	471833	29.5	631748	40.3	580388	30.0
Westham Is. marsh	335485	15.0	189448	9.8	166039	10.4	208180	13.3	187766	9.7
Brunswick Pt. marsh	155929	7.0	67005	3.5	123161	7.7	209690	13.4	39920	2.1
Woodward Is. marsh	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Alaksen NWA fields	647431	29.0	358650	18.6	223730	14.0	105231	6.7	558720	28.9
Other	200	0.0	112149	5.8	0	0.0	0	0.0	14861	0.8
Fraser delta	2234921	100.0	1928316	100.0	1598794	100.0	1567183	100.0	1933774	100.0
Spring:										
Sea Is. marsh	76731	8.3	3938	0.6	8758	2.5	46961	6.9	37667	6.3
Lulu Is. north marsh	166230	17.9	166692	23.6	60559	17.1	165653	24.4	122781	20.5
Lulu Is. south marsh	191260	20.6	155082	21.9	54619	15.4	122458	18.0	53830	9.0
Outer Is. marsh	33496	3.6	12658	1.8	67268	19.0	18719	2.8	59500	9.9
Reifel Refuge marsh	51094	5.5	18550	2.6	825	0.2	1086	0.2	18662	3.1
Westham Is. marsh	73155	7.9	127175	18.0	25395	7.2	67203	9.9	52514	8.8
Brunswick Pt. marsh	85377	9.2	45311	6.4	30421	8.6	31805	4.7	2950	0.5
Woodward Is. marsh	147027	15.9	152912	21.6	106307	30.0	146095	21.5	134558	22.5
Alaksen NWA fields	0	0.0	266	0.0	0	0.0	15496	2.3	89536	14.9
Other	103128	11.1	24166	3.4	0	0.0	64345	9.5	26978	4.5
Fraser delta	927496	100.0	706749	100.0	354151	100.0	679819	100.0	598976	100.0

Appendix 6 continued....

Location	1987/88 Days	%	1988/89 Days	%	1989/90 Days	%	1990/91 Days	%	1991/92 Days	%
Total:										
Sea Is. marsh	294999	9.3	166042	6.3	91674	4.7	130549	5.8	311761	12.3
Lulu Is. north marsh	479661	15.2	371860	14.1	209354	10.7	324361	14.4	202222	8.0
Lulu Is. south marsh	458375	14.5	332080	12.6	361523	18.5	260353	11.6	244499	9.7
Outer Is. marsh	43137	1.4	57661	2.2	142686	7.3	50862	2.3	67417	2.7
Reifel Refuge marsh	338515	10.7	630342	23.9	472658	24.2	632834	28.2	599050	23.7
Westham Is. marsh	408640	12.9	316623	12.0	191433	9.8	275382	12.3	240280	9.5
Brunswick Pt. marsh	241306	7.6	112316	4.3	153582	7.9	241494	10.7	42870	1.7
Woodward Is. marsh	147027	4.6	152912	5.8	106307	5.4	146095	6.5	134558	5.3
Alaksen NWA fields	647431	20.5	358916	13.6	223730	11.5	120727	5.4	648256	25.6
Other	103328	3.3	136314	5.2	0	0.0	64345	2.9	41839	1.7
Fraser delta	3162417	100.0	2635064	100.0	1952945	100.0	2247002	100.0	2532750	100.0

Appendix 7. Bulrush (*Scirpus americanus*) components in Grids 1 and 2 during 1989 and 1990 (mean ± 1SE). N = sample size. Means with the same superscript do not differ at $P=0.05$ (Tukey multiple comparison test).

Date	N	Live Stem Mass[1] (g m^{-2})	Dead Stem Mass (g m^{-2})	Root Mass (g m^{-2})	Rhizome Mass (g m^{-2})	Below-ground[2] Mass (g m^{-2})	Total[3] (g m^{-2})	Percent Below-ground (%)	Stem Density (Current)[4] (stems m^{-2})	Mean Stem Mass (g stem^{-1})	Stem Density (Adjusted)[5] (stems m^{-2})
Grid 1: 1989											
6 June	3	106 ± 19^{a}	0 ± 0^{a}	771 ± 54^{a}	163 ± 28^{a}	934 ± 72^{a}	1040 ± 87^{a}	90	1348 ± 203^{a}	0.08 ± 0.01^{a}	1402 ± 187^{a}
4 July	12	322 ± 37^{b}	16 ± 3^{b}	932 ± 228^{a}	170 ± 24^{ab}	1102 ± 243^{a}	1424 ± 261^{a}	77	1621 ± 217^{a}	0.21 ± 0.02^{b}	1621 ± 217^{a}
31 July	13	280 ± 36^{b}	95 ± 10^{c}	822 ± 138^{a}	315 ± 38^{b}	1137 ± 165^{a}	1417 ± 187^{a}	80	1364 ± 146^{a}	0.21 ± 0.02^{b}	1622 ± 173^{a}
31 August	12	35 ± 8^{c}	123 ± 20^{c}	1091 ± 136^{a}	303 ± 42^{ab}	1395 ± 175^{a}	1430 ± 174^{a}	98	325 ± 42^{b}	0.11 ± 0.02^{a}	1608 ± 291^{a}
2 October	13	1 ± 1^{d}	23 ± 4^{b}	938 ± 114^{a}	310 ± 49^{b}	1248 ± 162^{a}	1249 ± 161^{a}	100	0 ± 0^{c}	NA	1651 ± 223^{a}
Grid 1: 1990											
29 May	12	105 ± 14^{a}	0 ± 0^{a}	1238 ± 152^{a}	185 ± 25^{a}	1423 ± 170^{a}	1528 ± 179^{a}	93	1753 ± 217^{a}	0.06 ± 0.01^{a}	1416 ± 176^{a}
3 July	13	336 ± 36^{b}	0 ± 0^{a}	1004 ± 77^{a}	205 ± 28^{a}	1209 ± 102^{a}	1545 ± 133^{a}	78	1804 ± 181^{a}	0.19 ± 0.01^{b}	1554 ± 183^{a}
9 August	12	237 ± 16^{c}	106 ± 11^{b}	1060 ± 101^{a}	369 ± 37^{b}	1429 ± 132^{a}	1666 ± 144^{a}	86	1284 ± 113^{a}	0.19 ± 0.01^{b}	1689 ± 203^{a}
Grid 2: 1989											
6 June	13	43 ± 6^{ac}	0 ± 0^{a}	295 ± 30^{a}	77 ± 11^{a}	372 ± 37^{a}	415 ± 41^{a}	90	471 ± 56^{ab}	0.09 ± 0.01^{a}	594 ± 50^{a}
4 July	12	176 ± 23^{b}	7 ± 1^{b}	277 ± 24^{a}	85 ± 16^{a}	361 ± 37^{a}	538 ± 56^{ab}	67	617 ± 91^{a}	0.30 ± 0.02^{b}	617 ± 91^{a}
31 July	13	229 ± 21^{b}	57 ± 5^{c}	276 ± 30^{a}	163 ± 11^{b}	439 ± 34^{a}	667 ± 42^{bd}	66	638 ± 40^{a}	0.35 ± 0.02^{c}	570 ± 37^{a}
31 August	12	95 ± 8^{a}	101 ± 9^{d}	582 ± 23^{b}	165 ± 15^{b}	748 ± 34^{b}	842 ± 40^{c}	89	382 ± 38^{b}	0.26 ± 0.02^{b}	538 ± 49^{a}
12 October	13	10 ± 2^{c}	82 ± 11^{cd}	575 ± 24^{b}	154 ± 13^{b}	729 ± 29^{b}	739 ± 30^{cd}	99	0 ± 0^{c}	NA	522 ± 63^{a}
Grid 2: 1990											
29 May	12	45 ± 5^{a}	0 ± 0^{a}	588 ± 20^{ab}	109 ± 10^{a}	697 ± 28^{a}	742 ± 32^{a}	94	505 ± 43^{a}	0.09 ± 0.01^{a}	477 ± 60^{a}
3 July	13	148 ± 17^{b}	0 ± 0^{a}	577 ± 16^{a}	111 ± 9^{a}	689 ± 24^{a}	837 ± 33^{a}	82	625 ± 55^{a}	0.23 ± 0.01^{b}	585 ± 58^{a}
9 August	12	166 ± 20^{b}	46 ± 4^{b}	653 ± 21^{b}	174 ± 15^{b}	828 ± 35^{b}	994 ± 52^{b}	83	566 ± 44^{a}	0.29 ± 0.02^{c}	568 ± 44^{a}

[1] Live stems included below-ground stem mass.
[2] Below-ground = rhizome mass plus root mass.
[3] Total = below-ground mass plus live stem mass.
[4] Stem density on day of sampling.
[5] Stem density on 4 July 1989.

Appendix 8. Below-ground components of bulrush (*Scirpus americanus*) in top and bottom substrate layers in Grids 1 and 2 during 1990 (mean ± 1SE). Top = 0-15 cm substrate depth. Bottom = 16-30 cm substrate depth. N = sample size. Means with the same superscript do not differ at $P=0.05$ (Tukey multiple comparison test).

		Root Mass ($g\ m^{-2}$)		Rhizome Mass ($g\ m^{-2}$)		Rhizome Length ($m\ m^{-2}$)		Rhizome Density ($g\ m^{-1}$)		Below-ground Stem Mass ($g\ m^{-2}$)	
Date	N	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
Grid 1:											
29 May	12	724 ± 116^{a}	514 ± 53^{a}	88 ± 11^{a}	96 ± 16^{a}	11.4 ± 1.5^{a}	10.9 ± 2.2^{a}	8.9 ± 1.3^{a}	10.5 ± 1.4^{a}	12.7 ± 2.3^{a}	0 ± 0^{a}
3 July	13	543 ± 50^{a}	461 ± 32^{a}	99 ± 14^{a}	106 ± 16^{a}	11.9 ± 1.8^{a}	12.7 ± 2.1^{a}	8.6 ± 0.4^{a}	11.8 ± 3.0^{a}	12.3 ± 1.4^{a}	0.4 ± 0.4^{b}
9 August	12	567 ± 56^{a}	493 ± 49^{a}	168 ± 15^{b}	202 ± 29^{b}	13.2 ± 1.3^{a}	16.4 ± 2.9^{a}	12.9 ± 0.5^{b}	14.8 ± 1.6^{a}	12.1 ± 1.2^{a}	0.8 ± 0.8^{b}
Grid 2:											
29 May	12	287 ± 13^{ab}	301 ± 10^{a}	36 ± 4^{a}	73 ± 8^{a}	3.4 ± 0.5^{a}	5.9 ± 0.8^{a}	11.6 ± 1.1^{a}	13.7 ± 1.1^{a}	6.7 ± 1.4^{a}	0 ± 0^{a}
3 July	13	277 ± 8^{a}	299 ± 11^{a}	41 ± 4^{a}	70 ± 8^{a}	3.8 ± 0.5^{a}	6.1 ± 0.9^{a}	11.2 ± 0.4^{a}	12.7 ± 0.9^{a}	10.2 ± 1.2^{a}	0.2 ± 0.2^{b}
9 August	12	319 ± 9^{b}	334 ± 15^{a}	58 ± 5^{b}	117 ± 12^{b}	3.8 ± 0.4^{a}	7.0 ± 1.0^{a}	15.6 ± 0.7^{b}	17.9 ± 1.0^{b}	13.0 ± 2.6^{a}	0.3 ± 0.3^{b}

Appendix 9. Non-destructive Sampling

Summarized briefly below is the methodology I used for the non-destructive technique to estimate rhizome mass. More details are given in Boyd (in prep.).

I established a relationship between bulrush stem density and rhizome mass via destructive sampling on 5 July, 1988. At several locations on the Fraser delta, small quadrats (25 cm by 25 cm) were subjectively positioned in uniform patches at low, medium, and high stem densities (n=64 total). Live stems were counted and 2 cores (12.5 cm diameter by 30 cm long) were excavated from diagonal positions in each quadrat. The resulting rhizome mass was regressed against stem density (Fig. 45).

Stem growth was assumed to be a good integrator of abiotic conditions during the growing season and equivalent stem lengths across years were assumed to represent the same point on bulrush's allocation-reallocation cycle. Every summer, stem lengths and stem densities were measured in permanent plots at biweekly intervals. The resulting data were used to adjust stem densities measured in open and closed plots to those that would have been present on 5 July 1988. Adjusted densities were then used in the allometric equation (Fig. 45) to predict rhizome mass in each plot.

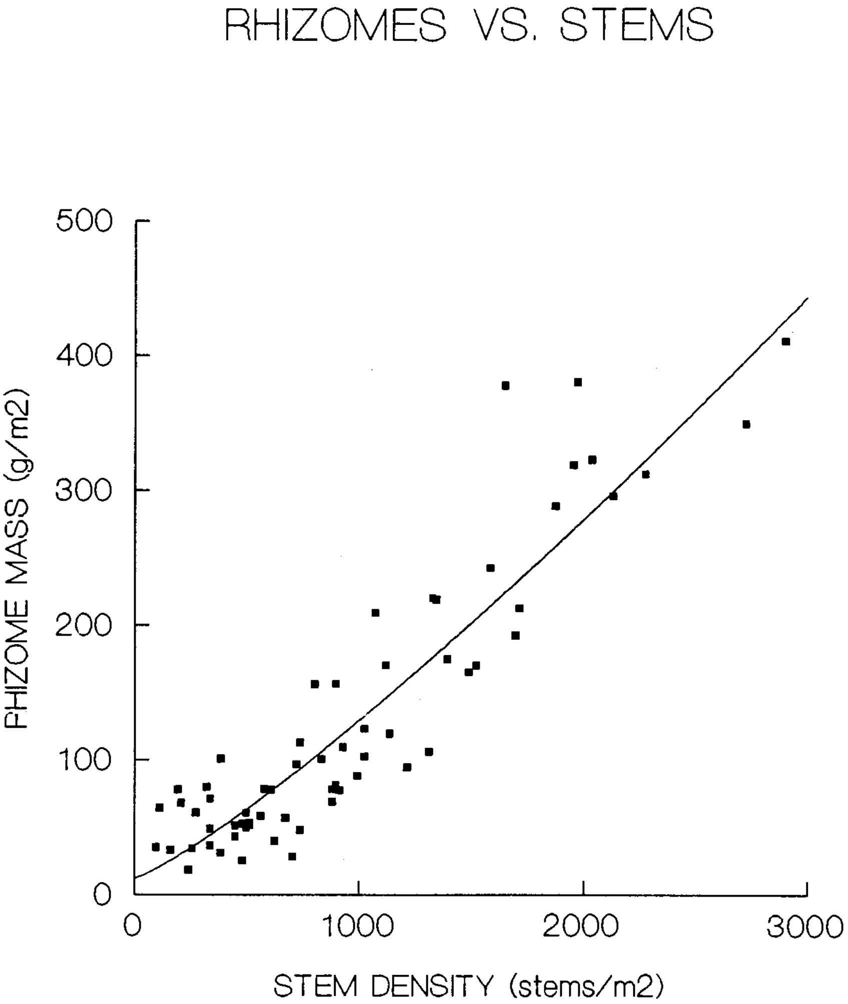

Figure 45. Relationship between bulrush (*Scirpus americanus*) rhizome mass and patch stem density on 5 July 1988. The equation describing the regression is: $Y=12+0.031X^{1.192}$ ($r^2=0.85$, $P<0.001$, $n=64$).