Padilla Bay
National Estuarine Research Reserve

Technical Report No. 11

ESTIMATED NET AERIAL PRIMARY PRODUCTIVITY AND MONITORING OF SELECTED CHARACTERISTICS OF *SPARTINA ALTERNIFLORA* IN PADILLA BAY, WASHINGTON, APRIL 1992 - MAY 1993

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October 1994

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WASHINGTON STATE DEPARTMENT OF ECOLOGY

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ABSTRACT

The salt marsh plant, *Spartina alterniflora*, has been introduced to Washington state during the last century and is growing at latitudes north of the probable sites of origin. It has spread rapidly in some bays and has been designated a noxious weed by the Washington State Noxious Weed Board in some counties. The purpose of this study was to estimate the net aerial primary productivity (NAPP) of *S. alterniflora* in Padilla Bay, Washington (the most northerly known population of *S. alterniflora* on the west coast of North America), and to monitor selected characteristics of this plant for one year (April '92 - May '93). Data on growth form, stem density, mortality and the characteristics: culm elongation, leaf emergence, leaf senescence, and leaf abscission were obtained. Individual culms in twelve random 0.0625 m^2 quadrats were tagged in a section of marsh approximately 45 m x 80 m and measured monthly except for Dec '92 and Jan '93. New plants >10 cm tall were tagged each month and heights of plants <10 cm tall were recorded each month. NAPP was estimated using the nondestructive "summed biomass loss" method of Hardisky (1980). This method sums biomass losses resulting from leaf abscission from live culms and culm mortality within a population of tagged culms. Culms in a section of marsh adjacent to permanent quadrats were destructively harvested on a seasonal basis and regression equations of culm height vs. biomass were used to estimate biomass in the permanent quadrats. Dead leaves were harvested seasonally to estimate the biomass of abscissed leaves.

During the period of this study, culm elongation rates peaked in May '93 (0.59 cm/culm/day). Maximum culm heights ranged between 0.65 - 1.30 m and could be considered the tall growth form. Leaf emergence rates peaked from June '92 - Aug '92 (0.047, 0.045, 0.046 leaves/culm/day). Leaf senescence rates peaked in Jun - July '92 (0.037, 0.036 leaves/culm/day) and Nov '92 (0.040

leaves/culm/day) while leaf abscission rates were highest in Nov '92 (0.035 leaves/culm/day) and Mar '93 (0.038 leaves/culm/day). Culm densities (culms m^{-2}) for the live component during this study ranged from 223 (±19 s.e.) to 519 (±55 s.e.). Percent mortality was highest in Mar '93 (46.9%). Basal diameters of live and dead culms were measured in Oct '92 and Nov '92. They ranged between 2 - 11 mm both months with respective overall means of x = 6.72 mm (± 0.095 s.e.) and 6.06 mm (± 0.094 s.e.). NAPP was 1520 g/m^2/year in this salt marsh. A total production of 73,112 kg/yr was estimated for *S. alterniflora* in Padilla Bay in 1991 (4.81 ha). The turnover rate was 1.14 crops/yr, that is, the peak standing crop turned over in 0.88 years.

ACKNOWLEDGEMENTS

We would first like to thank the Dike Island Gun Club for allowing us to conduct this study on their property. We would also like to extend our heartfelt thanks to all the people who helped in the field and braved the weather and tedium: Deron Holzschu, Lori Hansen, Brandon Woods, John Martin, Forrest Pederson (all Washington Conservation Corps), Yvonne Bonser (volunteer), Brady Scott (summer intern), Glen Alexander, and Robin Cottrell (PBNERR staff). We would also like to thank Brady Scott for assisting with the revision of Hardisky and Reimold's allometric equations. A special thanks goes to Yvonne for helping gather data late into the night and spending a stormy October night in a tent on the beach.

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INTRODUCTION

Padilla Bay is a shallow estuary located in western Skagit County, Washington. It is approximately 5,700 hectares in size and contains the second largest contiguous seagrass beds (approximately 3,035 hectares) reported for the west coast of North America (Bulthuis, 1991). There are two species of seagrass in Padilla Bay including native *Zostera marina* and the introduced *Zostera japonica*. The bay is fringed by non-contiguous narrow bands of salt marsh that, in 1989, totalled about 62 hectares (Bulthuis, 1991). Native salt marsh plants include saltbush (*Atriplex patula*), pickleweed (*Salicornia virginica*), salt grass (*Distichlis spicata*), and seaside arrowgrass (*Triglochin maritimum*) (Granger and Burg, 1986; Bulthuis and Scott, 1993).

Spartina alterniflora (smooth cordgrass) is native to the east coast of North America from Newfoundland to Florida and the Gulf Coast from Florida to east Texas (Landin, 1991). Only one species of *Spartina*, *Spartina foliosa*, is native on the west coast ranging from San Francisco Bay to southern California (Callaway and Josselyn, 1989).

In bays in the Pacific Northwest that have shallow intertidal areas with mudflat, seagrass meadows, and/or macroalgal mats, *S. alterniflora* may alter the habitat by accreting sediment, raising the elevation of the mudflat, and channelizing the habitat. *S. alterniflora* also has the potential to compete with seagrasses and to displace native mudflat fauna (Landin, 1991). On the other hand, native *S. alterniflora* marshes on the Atlantic and Gulf coasts of North America are highly productive and play an important role in the energy flow of marshes and adjacent estuaries (Linthurst and Reimold, 1978; Gordon *et al.*, 1985). The role of *S. alterniflora* as an introduced, non-native primary producer in Pacific Northwest estuaries is not known, nor have there been any measurements of the productivity of this plant in the Pacific Northwest.

Spartina alterniflora was apparently first introduced to Washington State in 1894, probably as packing material in barrels containing a shipment of eastern oyster spat (Townsend, 1895). Scheffer (1945) noted reports of *S. alterniflora* growing in Willapa Bay as early as 1911 and flowering as early as 1941. Sayce (1988) estimated that about 405 hectares of *S. alterniflora* were growing in intertidal areas in Willapa Bay in 1988, but by using a growth model, Sayce predicted that it will cover 12,545 hectares of Willapa Bay by the year 2025. In Willapa Bay, the growth of *S. alterniflora* threatens habitat for oyster cultivation and has grown extensively in the Willapa Bay National Wildlife Refuge. In addition to Willapa Bay, *S. alterniflora* has also been documented at the following sites in Washington State: Damon Point in Grays Harbor, the Copalis River estuary, Thorndyke Bay, Kala Point, Gibson Spit (Sequim Bay), and Padilla Bay (Ebasco Environmental, 1992).

Spartina alterniflora was introduced to Padilla Bay sometime between 1940 and 1946 by members of the Dike Island Gun Club. It was planted on tideflats adjacent to Dike Island as an erosion control effort. The plantings were obtained from Winnebago Nurseries in Wisconsin (Parker and Aberle, 1979). Parker and Aberle (1979) recorded approximately 1.4 hectares of *S. alterniflora* in Padilla Bay in 1979. Wiggins and Binney (1987) conducted a baseline survey of *S. alterniflora* in Padilla Bay in 1987 and noted the plant was spreading vegetatively. A follow-up survey of the distribution of *S. alterniflora* in Padilla Bay in 1991 showed that it covered nearly 4.85 hectares and was spreading laterally at a rate of approximately 1.5 m/yr (Riggs, 1992). Flowering stems were first noted in October 1992 and were observed again in October 1993 (Riggs, unpublished data). Because the plants are flowering so late in the season, Sayce (personal communication, 1993) suggests the *S. alterniflora* present here may be a strain originally obtained from a more southerly location. It is not yet known whether the seed is viable.

Sayce (1988) reported the peak monthly shoot biomass of *S. alterniflora* in Willapa Bay as 302.3 g/0.1 m^2 (Leadbetter Point, August) and 180.3 g/0.1 m^2 (Jensen

Spit, October: still increasing). There are no published reports on the productivity of *S. alterniflora* in the Pacific Northwest. Estimates of aboveground productivity of *S. alterniflora* in its native habitats range from 200-3700 g dry wt/m^2/yr (Wiegert and Evans, 1964; Milner and Hughes, 1970, Hopkinson *et al.*, 1978; Hardisky, 1980; Reidenbaugh, 1983; Gordon *et al.*, 1985; Cranford *et al.*, 1989; and Morris and Haskin, 1990).

Hardisky and Reimold (1977) looked at the seasonal community change of several salt marsh plants, including *S. alterniflora*, along the Atlantic coast of the United States using a non-destructive method of tagging plants and found differences in leaf production, culm elongation and leaf senescence rates for the three species of *Spartina* they studied. Their data showed three ecotypes of *Spartina patens*, with increasing leaf production in the southern latitudes. Culm elongation and leaf production for *S. alterniflora* declined concurrently with a late-season increase in senescence and abscission rates. The mortality rate for *S. alterniflora* was 58 percent by August and 100 percent by October. Cranford *et al.* (1989) conducted a one-year field study of the growth, mortality, and loss dynamics of a *S. alterniflora* marsh in the Minas Basin at the head of the Bay of Fundy. In that study, shoots started to grow in April and reached maximum height and weight in October and shoot density reached a maximum in June. They found an average shoot produced about seven leaves and two to three were lost during the growing season. All the remaining vegetation died before November. No similar studies have been conducted for *S. alterniflora* on the west coast of North America.

Many different methods have been used to determine productivity, aboveground and belowground. Some methods involve the harvest of plants and are usually called "destructive". These methods include: peak or maximum standing crop, Smalley (1959), Wiegert and Evans (1964), Milner and Hughes (1968), modified Wiegert and Evans (Lomnicki *et al.*, 1968), Valiela *et al.* (1975), modified Smalley (Gordon *et al.*, 1985), and growth increment summation. Other methods, referred to as "non-destructive" utilize tagging of individual plants so the same plants can be measured at intervals. These methods include: the Allen Curve method (Mathews and Westlake, 1969), summed biomass losses (Hardisky, 1980), and the summed shoot maximum method (Dickerman *et al.*, 1986).

Many of these methods have been criticized because they were developed in terrestrial systems and they do not account for losses to grazing or for the effects of tidal activity. Shew, *et al.* (1981) compared five methods and found the methods used by Wiegert and Evans (1964) and Lomnicki *et al.* (1968) minimized tidal influences. Linthurst and Reimold (1978) used five harvest methods to estimate the net aerial primary production of salt marsh species and found differences as great as ten-fold between the five methods. They found that species morphology, location and general environmental conditions all affected the results of any method used. Dickerman *et al.* (1986) also found that sampling frequency can influence estimations as the longer the periods between sampling, the more production is lost through mortality, leaf turnover, weather damage and herbivory. Cranford *et al.* (1989) compared four methods and recommended methods based on population dynamics of individual shoots because they include the production of vegetation exported during the growing season.

The objectives of this study were to monitor *S. alterniflora* in Padilla Bay for a year and obtain data on growth form, stem density, mortality, culm elongation, leaf production, leaf senescence, and leaf abscission and to estimate the net aerial primary productivity of *S. alterniflora* using the non-destructive "summed biomass loss" method of Hardisky (1980) which is based on the population dynamics of individual shoots.

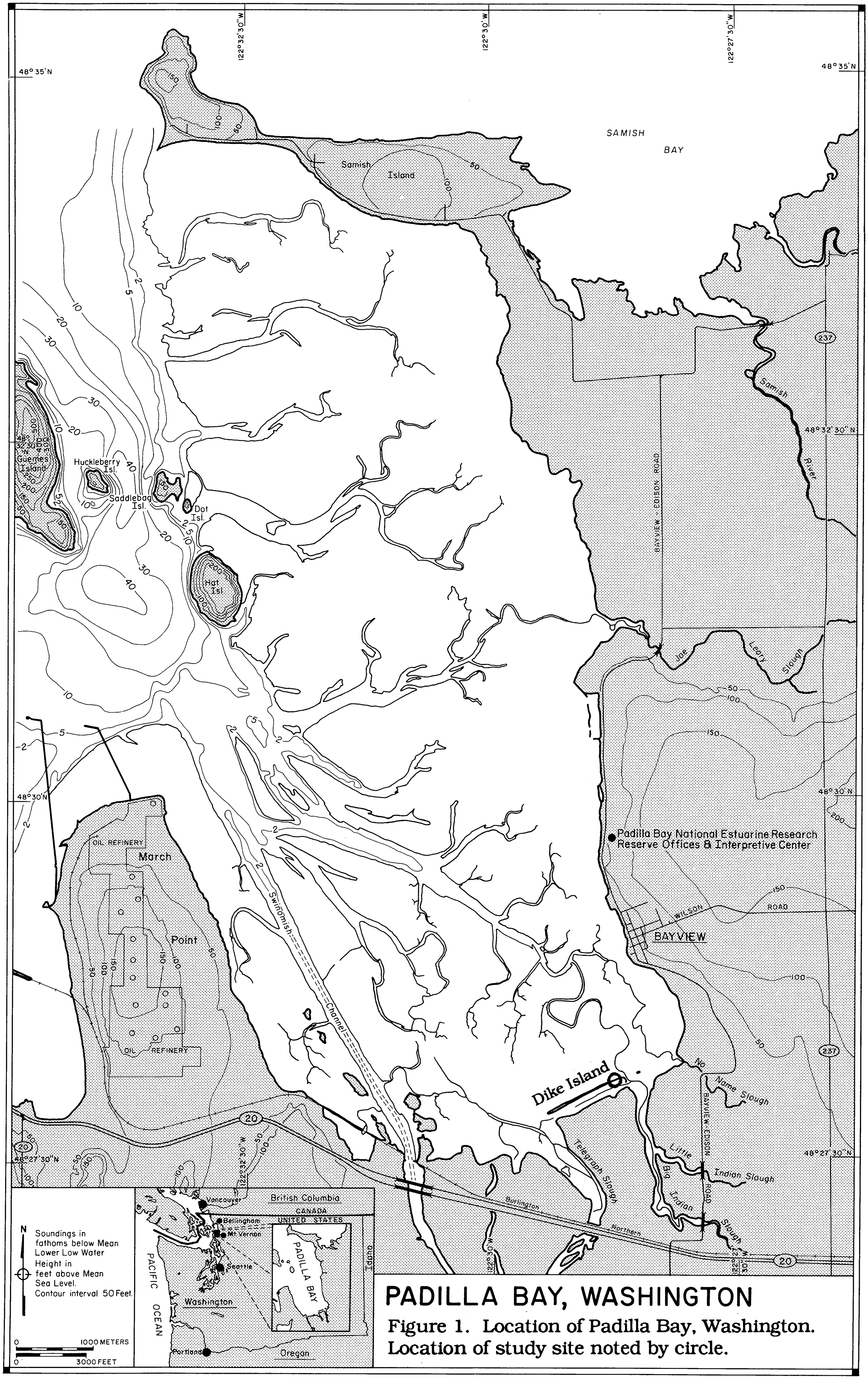
METHODS AND MATERIALS

Study site

Padilla Bay, located in western Skagit County, Washington, was designated a National Estuarine Research Reserve (Coastal Zone Management Act of 1970, Section 315) in 1980. The study site was located in southern Padilla Bay on private property on the southeastern side of Dike Island in a relatively homogeneous *Spartina alterniflora* stand (Figs. 1 & 2). Riggs (1992) reported the total area of this stand as 44,200 m^2 in 1991. Water flows into and away from the stand through a broad, shallow channel area south of the stand that connects Telegraph Slough to Indian Slough (Fig. 1). Indian Slough provides freshwater drainage from agricultural fields with tidegates at Bayview-Edison Road. The tidal elevation of the study quadrats ranged from +1.05 m to +1.45 m above Mean Sea Level (Table 1). The stand is somewhat protected from the southwesterly winds and wave action by an agricultural dike, and is protected from northerly winds and wave action by Dike Island itself.

Quadrats and Tagging

Twelve 0.0625 m^2 permanent quadrats were randomly placed in a section of the *S. alterniflora* marsh (approximately 45 m x 80 m) on April 18, 1992 (Fig. 3). All plants, alive and dead, were tagged using electrical ties and acetate labels marked with permanent pen. About halfway through the study the tags were replaced with heavier vinyl tags marked both with permanent pen and a heat marker. These tags were much easier to read and more durable. The ties were left loose enough so as not to interfere with plant growth.



PADILLA BAY, WASHINGTON

Figure 1. Location of Padilla Bay, Washington. Location of study site noted by circle.

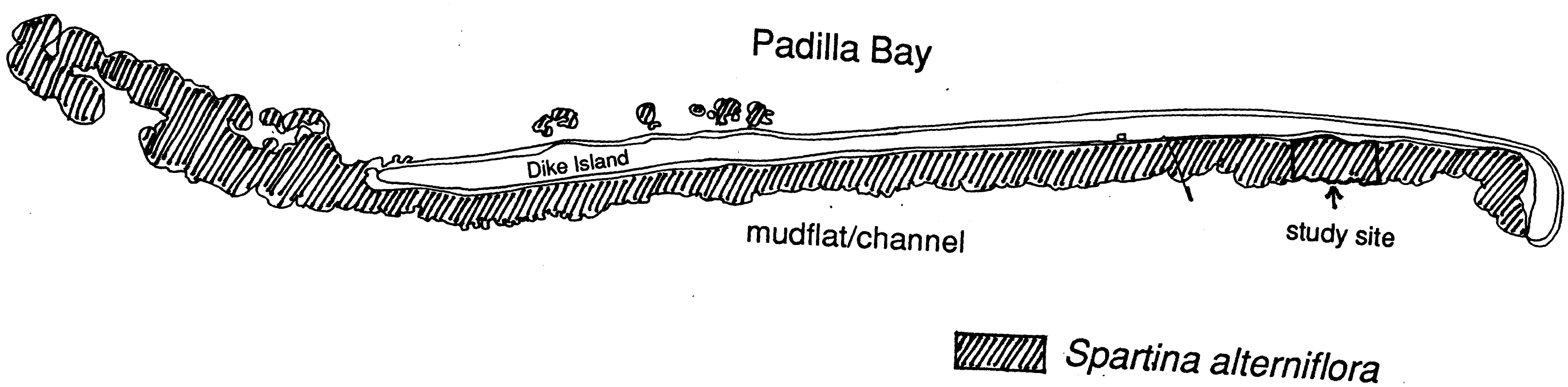


Figure 2. Location of study site in *Spartina alterniflora* marsh on the south side of Dike Island (Padilla Bay, Washington).

Table 1: Maximum culm heights and elevations of quadrats in study site relative to Mean Sea Level. Quadrat locations are shown in Fig. 3.

Quadrat	Elevation meters (feet)	Maximum culm height (cm)
E	+1.45 (+ 4.72)	65
B	+1.43 (+ 4.64)	80
K	+1.42 (+ 4.60)	95
J	+1.37 (+ 4.44)	92
D	+1.32 (+ 4.30)	107
H	+1.32 (+ 4.30)	100
G	+1.31 (+ 4.26)	95
L	+1.27 (+ 4.14)	95
I	+1.21 (+ 3.92)	103
A	+1.16 (+ 3.78)	116
C	+1.08 (+ 3.52)	130
F	+1.05 (+ 3.42)	120

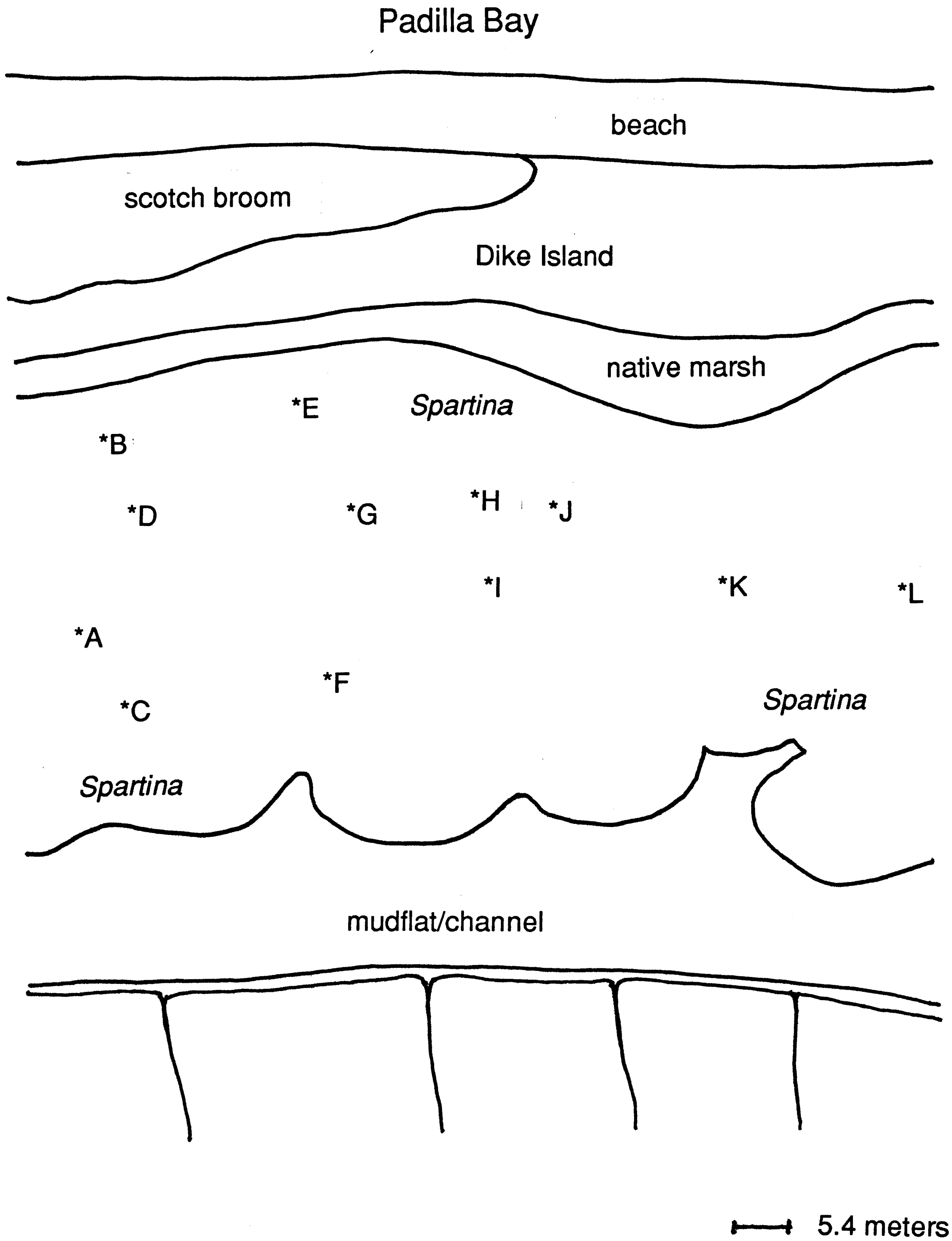


Figure 3. Location of study quadrats in *Spartina alterniflora* marsh study site on Dike Island (Padilla Bay, Washington).

Selected characteristics

Culm height and number of live and dead leaves were measured approximately monthly on all tagged plants using the methods of Hardisky and Reimold (1977). Stem density was calculated from monthly data. Culm height was measured by gathering all the leaves together loosely and recording the height of the tallest leaf. Live and dead leaves were counted and recorded for each culm. Live leaves were considered to be any leaf with green tissue present. Measurements for all quadrats were recorded monthly from April 1992 to May 1993 with the exception of December 1992, and January 1993, because of poor accessibility to the island due to weather. Each month new plants greater than 10 cm tall were tagged. Height was also recorded for new plants less than 10 cm tall, but these plants were not tagged.

Culm elongation, leaf emergence, leaf senescence and leaf abscission were determined using allometric equations (Table 2) based on Hardisky and Reimold (1977). Means were calculated for each characteristic by quadrat in each sampling period and a grand mean for each sampling period was calculated for all quadrats. Rates of culm elongation, leaf emergence, leaf senescence, and leaf abscission were obtained by dividing the mean for each quadrat each sampling period by the number of days in that sampling period (Tables 3 and 4).

Culm height, basal diameters, and mortality

Mean culm height was calculated for each quadrat and a grand mean obtained from those means. Maximum culm height is an indicator of the growth form of *S. alterniflora* (Reidenbaugh, 1983). Basal diameters of live and dead culms were measured with calipers in Oct '92 and Nov '92. Percent mortality was calculated as follows:

$$\% \text{ mortality} = \frac{\text{\# of plants alive the previous month that died}}{\text{\# plants alive the previous month}} \times 100$$

Table 2: Allometric equations for selected *Spartina alterniflora* characteristics (modified from Hardisky and Reimold, 1977).

<u>Culm elongation</u>		
$C = \Delta H$	if	$\Delta H > 0$
$C = 0$	if	$\Delta H \leq 0$
<u>Leaf emergence</u>		
$E = Net$	if	$Net > \Delta L$
$E = \Delta L$	if	$Net \leq \Delta L$
$E = 0$	if	$\Delta L \leq 0 \geq Net$
<u>Leaf senescence</u>		
$S = 0$	if	$\Delta L \geq 0$ and $\Delta D \leq 0$
$S = \Delta D$	if	$\Delta L \geq 0$ and $\Delta D > 0$ <u>or</u> $\Delta L < 0$ and $\lvert \Delta L \rvert < \Delta D$
$S = \lvert \Delta L \rvert$	if	$\Delta L < 0$ and $\lvert \Delta L \rvert > \Delta D$
<u>Leaf abscission</u>		
$A = \lvert Net \rvert$	if	$Net < 0$ and $\Delta L < 0$
$A = \lvert \Delta D \rvert$	if if if	$Net < 0$ and $\Delta L \geq 0$ <u>or</u> $Net = 0$ and $\Delta L > 0$ <u>or</u> $Net > 0$ and $\Delta L > 0$ and $\Delta D < 0$
$A = 0$	if	$Net \geq 0$ and $\Delta L \leq 0$ <u>or</u> $Net > 0$ and $\Delta L > 0$ and $\Delta D \geq 0$

Abbreviations:

C = culm elongation
ΔH = change in height (cm)
E = leaf emergence;
ΔL = change in number of live leaves for a culm over any interval
ΔD = change in number of dead leaves for a culm over any interval
Net = $\Delta L + \Delta D$ over any interval
S = leaf senescence
A = leaf abscission

Table 3. Culm elongation, leaf emergence, leaf senescence, and leaf abscission (mean ± s.e. of the mean) of *S. alterniflora* in Padilla Bay, Washington (n = 12 quadrats, about 14 to 32 plants per quadrat). The dates for each sampling period are listed in Table 4.

Period	Culm elongation (cm/culm/day)	Leaf emergence (leaves/culm/day)	Leaf senescence (leaves/culm/day)	Leaf abscission (leaves/culm/day)
May 1992	0.32 ±0.021	0.035 ±0.0035	0.025 ±0.0031	0.011 ±0.0022
June 1992	0.20 ±0.029	0.047 ±0.0044	0.037 ±0.0025	0.0059 ±0.0012
July 1992	0.19 ±0.033	0.045 ±0.0062	0.036 ±0.0023	0.014 ±0.0042
August 1992	0.19 ±0.025	0.046 ±0.0027	0.027 ±0.0033	0.012 ±0.0018
September 1992	0.12 ±0.016	0.030 ±0.0039	0.025 ±0.0017	0.019 ±0.0023
October 1992	0.083 ±0.0093	0.019 ±0.0022	0.030 ±0.0024	0.0082 ±0.00092
November 1992	0.065 ±0.0052	0.024 ±0.0039	0.040 ±0.0032	0.035 ±0.054
February 1993	0.040 ±0.025	0.0075 ±0.0037	0.027 ±0.0031	0.013 ±0.0021
March 1993	0.048 ±0.0082	0.014 ±0.0037	0.033 ±0.0048	0.038 ±0.0041
April 1993	0.27 ±0.028	0.035 ±0.0046	0.017 ±0.0042	0.011 ±0.0020
May 1993	0.59 ±0.031	0.033 ±0.0024	0.017 ±0.0020	0.011 ±0.0017
Overall mean	0.192 cm/culm/day	0.0305 leaves/culm/day	0.0285 leaves/culm/day	0.0162 leaves/culm/day
Annual rate	70.21 cm/culm/year	11.13 leaves/culm/year	10.42 leaves/culm/year	5.91 leaves/culm/year

Table 4: Sampling intervals for *Spartina alterniflora* data collection in Padilla Bay, Washington, April 1992 - May 1993.

Interval	Dates	Days per period
May '92	4/18/92 - 5/16/92	28
June '92	5/17/92 - 6/18/92	33
July '92	6/19/92 - 7/17/92	29
August '92	7/18/92 - 8/15/92	29
September '92	8/16/92 - 9/11/92	27
October '92	9/12/92 - 10/22/92	41
November '92	10/23/92 - 11/12/92	20
February '93	11/13/92 - 2/11/93	92
March '93	2/12/93 - 3/11/93	28
April '93	3/12/93 - 4/22/93	41
May '93	4/23/93 - 5/21/93	29

Elevation

Elevations of the quadrats were measured against a reference point using a transit and stadia on May 21, 1993. These elevations were adjusted to a bench mark (+1.65 m above Mean Sea Level) placed on Dike Island June 15, 1993.

Salinity wells

Simple salinity wells were made of 3/4-inch PVC pipe with a plastic disk glued on the bottom. A line was drawn about an inch from the top and a 1/4-inch hole was drilled through the pipe 10 cm below this line. A very fine mesh screen was glued over the holes inside the pipe to exclude most sediment. Wells were placed in the sediment to the depth of the line near two upper intertidal quadrats, two mid-intertidal quadrats and two lower intertidal quadrats. Samples were collected from the pipes with a suction device and carried back to the lab in glass collection bottles. Salinity was determined at room temperature with an Atago hand refractometer after any sediment settled.

Net aerial primary productivity

Net aerial primary productivity was measured by methods based on Hardisky and Reimold (1977) and Hardisky (1980) using measurements of culm height, leaf production and leaf abscission for individual culms. Production was estimated from living tissue that passes into the dead component. Because dead leaves were counted in the estimates of live standing biomass, a leaf was not considered to be in the dead component for the purposes of this method until it detached. Biomass was destructively harvested from an area of marsh adjacent to and east of the tagged quadrats (Fig. 2) on March 11, May 21, August 20, and October 30, 1993. All biomass was harvested from 0.0625 m^2 quadrats every 2 meters along the length of a transect placed randomly and perpendicular to the length of the marsh. Dead culms were discarded. Live culms were taken to the laboratory, rinsed free of sediment under running tap water, blotted dry and dried in a drying oven at 100-105^{o}C. Three weights were taken at hourly intervals after at least 24 hours of drying.

Two dead culms were collected on the west side of each biomass quadrat the entire length of the transect to estimate the dry weight of dead leaves. Twenty-five of these culms were chosen randomly in the laboratory. The lower six leaves of each culm were clipped off next to the stem. If there was a partial leaf it was skipped and the next leaf was collected. If there were fewer than six leaves, it was noted in the data. The leaves were rinsed free of sediment under running tap water, blotted dry and placed in pre-weighed aluminum foil packets for drying at 100-105^{o}C. All leaves from one culm were placed in one packet and an average leaf weight was calculated after drying. The first weight was taken at least 24 hours after drying, and successive weights (3 total) were taken at one hour intervals to ensure drying to a constant weight.

Sampling periods ranged from 20-92 days (Table 4). No data was collected in December 1992 or January 1993 due to inclement weather which made accessibility to Dike Island difficult.

<u>Data Analysis for NAPP</u>. Hardisky (1980), in comparing regression models for live culms and dead culms, found that the predictive ability of the dead culm model was inconsistent so he used the live culm model. Therefore, the following equations used to estimate biomass of dead culms in this study are based on destructively harvested live culms, not dead culms. Hardisky (1980) also indicated that seasonal regression models might better predict biomass, so we collected data for biomass each season.

Biomass (in grams) of live culms gathered in destructive harvests (Feb '93, May '93, Aug '93, Oct '93) was plotted against culm height (in cm) and regressions were run on the data. The best r^2 values (Feb = 0.92, May = 0.82, Aug = 0.84, Oct = 0.88) were obtained after using a square root transformation for both the x and y axes. The following equations were then used to estimate biomass for the tagged culms where "w" = weight (in grams) and "h" = height (in cm):

The February estimate was used for the months January, February, and March.

$$w = [(0.27)(\sqrt{h})-0.573]^2$$

The May estimate was used for the months of April, May, and June.

$$w = [0.16)(\sqrt{h})-0.260]^2$$

The August estimate was used for the months of July, August ,and September.

$$w = [0.29)(\sqrt{h})-0.645]^2$$

The October estimate was used for the months of October, November, and December.

$$w = [0.30)(\sqrt{h})-0.568]^2$$

The data from tagged plots were reviewed for: 1) the last date the culm was noted as "alive" and the culm height, and 2) the first date the culm was noted as "dead" and the culm height. The taller of these two heights was chosen in every case and used in one of the above equations. The taller height was used because between any two sampling dates a dead culm may have broken off and the height it attained during that particular growing season would be underestimated. Estimated biomass was summed for each quadrat and a mean biomass was calculated.

Leaves abscissed per culm per day were multiplied by the number of days per month and the number of live culms per month. This total was multiplied by the mean dead leaf biomass determined for each quarter. This biomass was summed over the study months and added to the summed dead culm biomass.

Turnover rate was calculated as follows:

$$\frac{\text{Maximum biomass } (gdw/m^2)}{\text{Estimated NAPP } (gdw/m^2/yr)} = \text{crops/year}$$

Turnover time was calculated as follows:

$$\frac{\text{Estimated NAPP}(gdw/m^2/yr)}{\text{Maximum biomass } (gdw/m^2)} = \text{years}$$

Maximum biomass was based on weights of live culms only. These weights were estimated using the regression equations described above.

RESULTS

Soil salinities

Mean soil salinity ranged from 26.3 - 29.5 $^{o}/oo$ during February to May 1993 with no evidence of a change over time or of difference between plots at different elevations (Table 5).

Culm density

The density of live stems remained similar throughout the study, ranging from 220 to 520 stems/m^2, without any strong seasonal pattern (Fig. 4). The density of dead stems generally increased during the study.

Culm height, basal diameters, and mortality

Maximum culm height ranged between 65 - 130 cm (Table 1). The grand mean for culm height was 52.9 ($\pm$ 3.6 s.e.). The mean basal diameter of live and dead plants measured was 6.72 mm ($\pm$ 0.095 s.e.) in Oct '92, and 6.06 mm ($\pm$ 0.094 s.e.) in Nov '92. The range in both months was 2-11 mm. Percent mortality of culms was greatest in Mar '93 (46.9%) and lowest in Nov '92 (1.8%) (Fig. 5).

Culm elongation

The lowest elongation rates (0.040 and 0.048 cm/culm/day) were observed during winter (Feb '93 and Mar '93; Table 3) and the highest elongation rates were

Table 5: Sediment salinity (10 cm depth) in a *Spartina alterniflora* marsh in Padilla Bay, Washington. Elevation is in meters (feet) above mean sea level.

Quadrat	Elevation meters (feet)	Salinity (°/oo) Feb '93	Mar '93	April '93	May '93
E	+1.45(+ 4.72)	ND	26	25	25
B	+1.43(+ 4.64)	31	27	27	27
K	+1.42(+ 4.60)	28	28	ND	26
H	+1.32(+ 4.30)	29	28	26	26
A	+1.16(+ 3.78)	30	27	27	27
C	+1.08(+ 3.52)	ND	27	27	27
Means		29.5	27.2	26.4	26.3

Feb '93: Samples collected 2/13/93, read samples at room temperature on 2/16/93.

Mar '93: Samples collected 3/11 & 13/93, read 3/14/93. Quadrat K sample contained some particles (diatoms?).

Apr '93: Samples collected 4/22/93. Quadrat E sample contained some particles (sediment?)

May '93: Samples collected 5/21/93. Quadrat E sample contained some particles (sediment?)

ND: no data collected that day at that site.

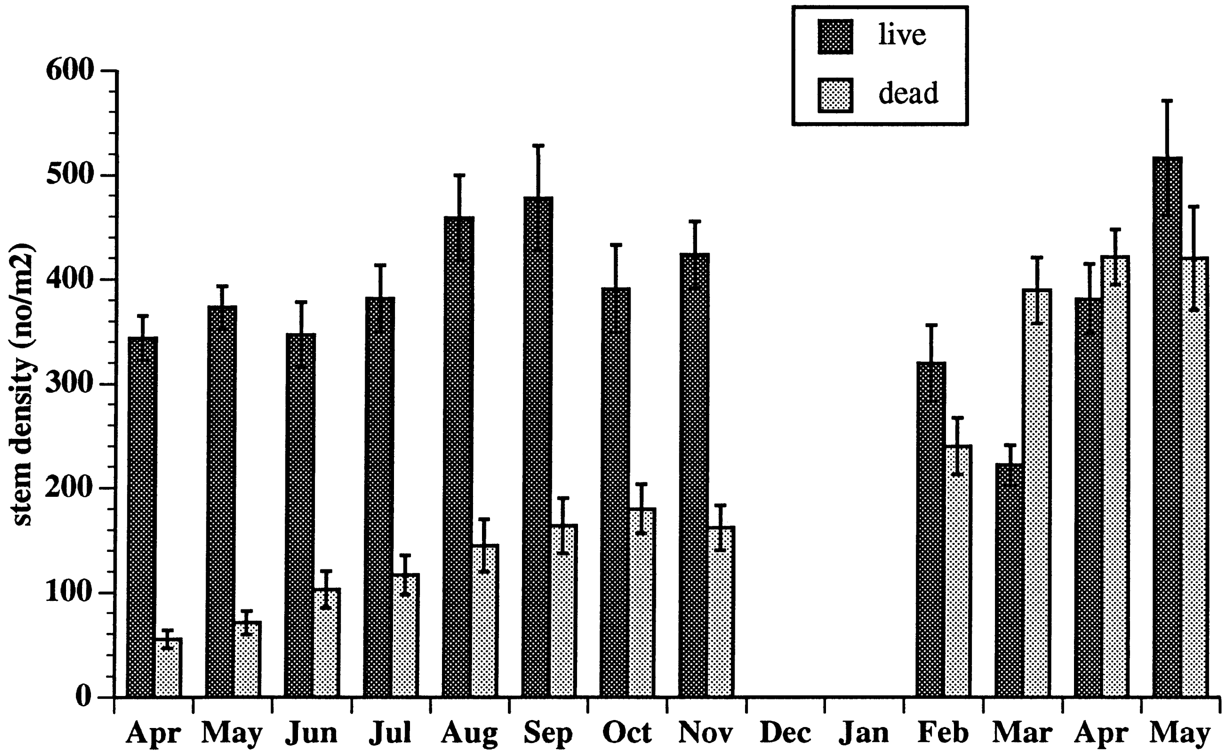


Figure 4. Culm densities (number/m^2) of live and dead *Spartina alterniflora* in Padilla Bay, Washington, from April 1992 - May 1993. Mean ± standard error, n = 12 quadrats (about 14 to 32 plants per quadrat).

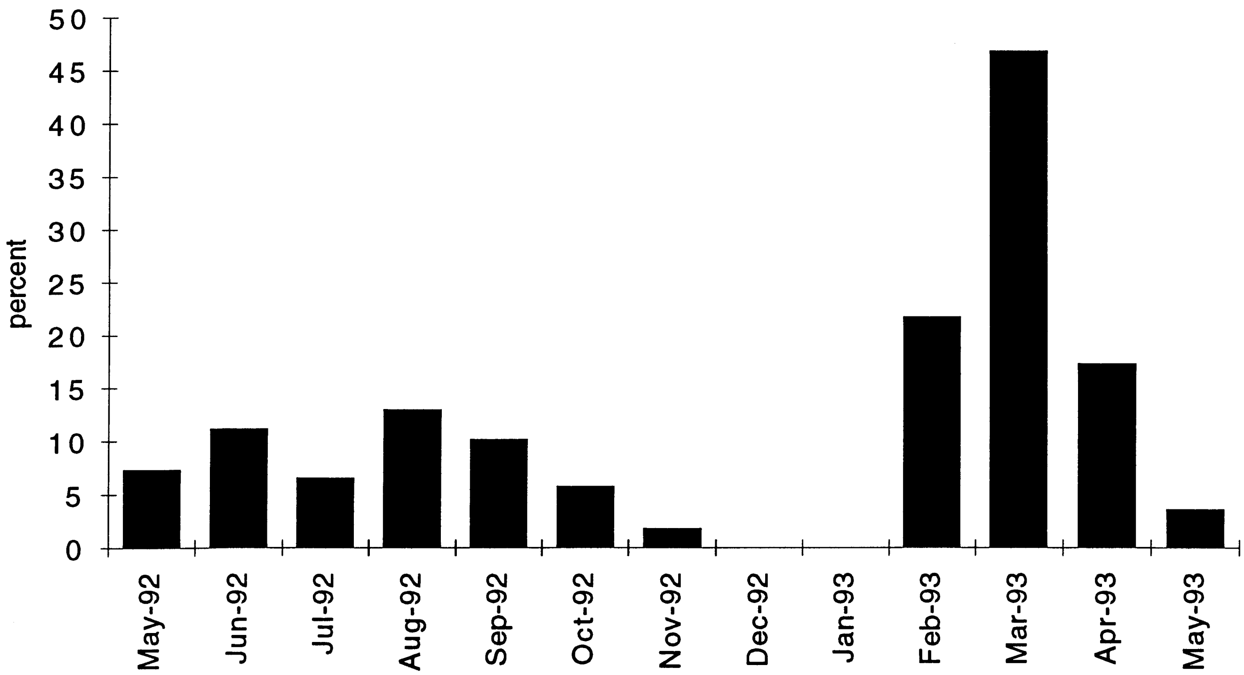


Figure 5. Percent mortality of *S. alterniflora* culms in Padilla Bay, Washington, from May 1992 - May 1993. No data was collected in Dec '92 and Jan '93. Feb '93 mortality includes 3 months of data. Sample intervals for each month are presented in Table 4.

observed in spring, May '92 (0.32 cm/culm/day) and May '93 (0.59 cm/culm/day; Table 3). Elongation declined from May '92 to Feb '93 then increased rapidly during the next three months (Fig. 6). Annual mean culm elongation was 0.19 cm/culm/day or culm elongation was 70.2 cm/culm/year.

Leaf emergence

New leaves are produced all year with maximum rates of leaf emergence during summer (0.048, 0.045, and 0.046 leaves/culm/day for June, July and August; Table 3) and minimum rates during Feb '93 and Mar '93 (0.0075 and 0.014 leaves/culm/day; Table 3). Mean leaf emergence for all dates was 0.030 leaves/culm/day or 11.3 leaves/culm/year.

Leaf senescence

Rates of leaf senescence were lowest in April '93 and May '93 (0.017 and 0.017 leaves/culm/day) and highest during June '92, July '92, and Nov '92 (0.037, 0.036, 0.040 leaves/culm/day; Table 3). Rates of leaf emergence were greater than or equal to leaf senescence from May '92 until late Sept '92. Leaf senescence rates were then greater than leaf emergence rates from late Sept '92 until March '93 (Fig. 7). Mean leaf senescence over all dates was 0.029 leaves/culm/day or 10.6 leaves/culm/year.

Leaf abscission

The leaf abscission rate was between 0.0082 - 0.019 leaves/culm/day (mean) during all months measured except in Nov '92 and Mar '93 when the highest rates were observed (0.035 and 0.038 leaves/culm/day, respectively; Table 3). Leaf abscission rates were consistently lower than leaf senescence rates except in Mar '93 when abscission was higher (0.038 leaves lost/culm/day vs. 0.033 leaves senesced/culm/day) (Fig. 7). Therefore, during the course of this 13 month study, there was a net increase in

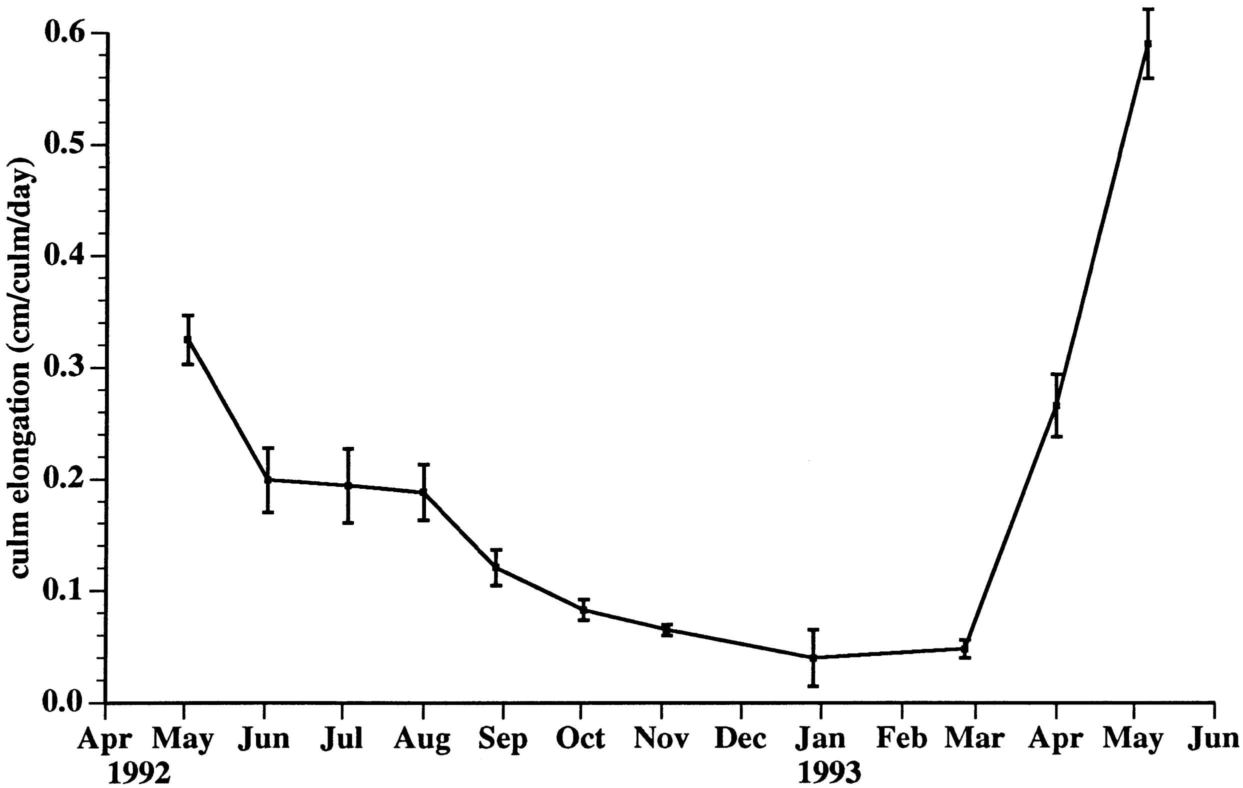


Figure 6. Rates of culm elongation (cm/culm/day) of *Spartina alterniflora* in Padilla Bay, Washington. Means ± standard error, n = 12 quadrats (about 14 to 32 plants per quadrat). Data points represent the midpoints of the sampling periods.

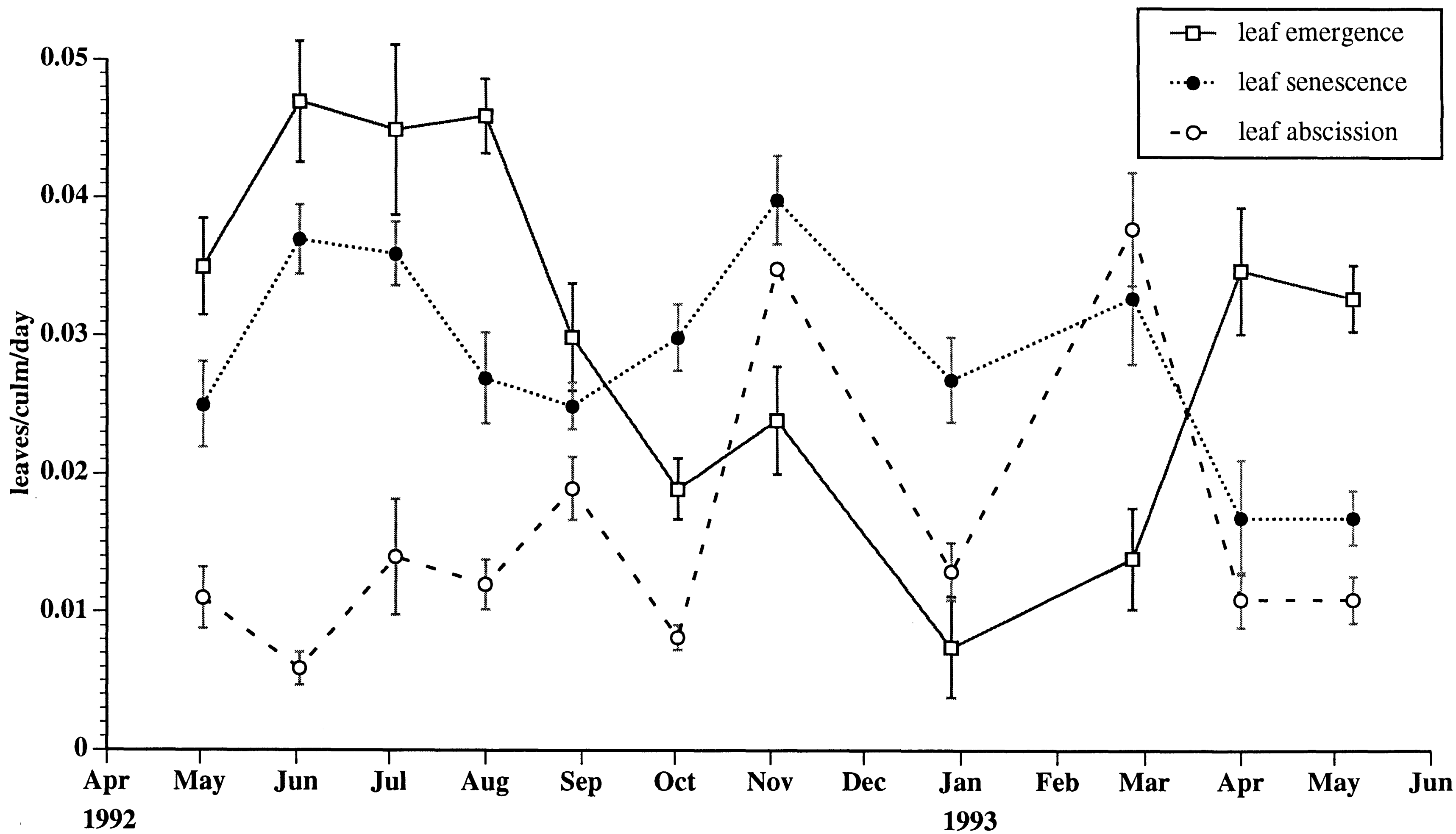


Figure 7. Rates of leaf emergence, leaf senscence, and leaf abscission (leaves/culm/day) of *Spartina alterniflora* in Padilla Bay, Washington. Means ± standard error (not shown for leaf abscission in November where s.e. exceeded mean), n=12 quadrats (about 14 to 32 plants per quadrat). Data points on graph represent the midpoints of sampling periods.

the number of standing dead leaves. Mean leaf abscission over all dates was 0.016 leaves/culm/day during this study or 5.9 leaves lost/culm/year.

Net aerial primary productivity

The estimated productivity from culms passing from the live to the dead component was 73.6 gdw/0.0625 m^2/year. The estimated productivity of leaves abscissed from live culms was 21.4 gdw/0.0625 m^2/year (Table 6). These were summed for an estimate of net aerial primary productivity of 95.0 gdw/0.0625 m^2/year. Approximately 22.5% of the total NAPP in this study was attributed to leaf loss. Mean aerial biomass per month ranged from 7.45 gdw/0.0625 m^2 to a maximum aerial biomass of 83.46 gdw/0.0625 m^2 (Table 7). Turnover time was 0.88 years. Turnover rate was 1.14 crops/year.

DISCUSSION

Stem density was 223-519 culms/m^2 in the present study compared to the U.S. Army Corps of Engineers average stem density of 25 culms/0.25 m^2 (100 culms/m^2) for *S. alterniflora* on Dike Island in the summer of 1992 (USACE, 1993). Bulthuis and Scott (1993) reported stem densities of 100-300 culms/m^2. The density reported in the USACE (1993) study is quite low compared to the current study and Bulthuis and Scott (1993) and might be due to a limited number of samples. The current study showed densities similar to those reported for the tall form in Delaware and the short form in Georgia, but much lower than reported for New Hampshire, Nova Scotia, and Bay of Fundy (Table 8).

This study followed part of the 1992 growing season and the first portion of the 1993 growing season, and the trends in mortality are conflicting. From May 1992 - November 1992, mortality was highest in June (11.2%), August (13.0%), and September (10.2%) and lowest in November (1.8%) (Fig. 5). No data was collected in December 1992 or January 1993. In the 1993 growing season, mortality was highest in March (46.9%)

Table 6. Mean live *Spartina alterniflora* culms/0.0625 m^2 in a Padilla Bay, Washington, salt marsh and estimated dry weight of leaves abscissed from those live culms. Not reported = nr. Numbers 1-5 in "quadrat" column represent equations which are explained directly below table.

Quadrat	May '92	Jun '92	Jul '92	Aug '92	Sep '92	Oct '92	Nov '92	Feb '93	Mar '93	Apr '93
A	19	20	23	25	27	23	20	19	18	29
B	19	28	27	26	25	24	22	26	31	22
C	15	15	14	13	18	16	17	nr	19	31
D	16	27	26	26	32	31	35	31	20	25
E	26	28	30	29	33	31	29	22	12	22
F	15	8	8	4	3	3	nr	3	5	6
G	15	22	24	26	26	22	21	16	12	18
H	16	17	28	34	37	32	30	30	16	30
I	15	18	21	31	34	31	35	nr	13	25
J	23	23	23	22	24	22	24	18	10	20
K	23	21	24	20	18	19	20	18	15	27
L	31	29	33	35	37	33	32	21	15	30
1)	19.42	212.33	23.42	24.25	26.17	23.92	25.91	20.40	15.50	23.75
2)	0.31	0.35	0.38	0.39	0.42	0.39	0.42	0.33	0.25	0.38
3)	9.75	10.37	11.76	12.18	12.72	12.01	12.59	9.25	7.78	11.54
4)	2.10	2.23	1.99	2.06	2.15	2.24	2.35	2.06	1.73	2.48
5)	21.40									

1) Mean live culms/0.0625 m^2

2) (#1) x leaves abscissed/culm/day. From Table 3, leaves abscissed/culm/day is 0.0162.

3) (#2) x number of days/month

4) (#3) x mean dry weight of a dead leaf (from Appendix 1)

5) (#4) summed = 21.4 grams dry weight/0.0625 m^2/year

Table 7. Mean *Spartina alterniflora* biomass (grams dry wt./0.0625 m^2) for live culms in Padilla Bay, Washington. Bold type indicates annual maximum monthly biomass.

Date	gdw/0.0625 m^2
4/18/92	17.25[1]
5/18/92	19.64[1]
6/18/92	19.71[1]
7/17/92	58.87[1]
8/15/92	61.47[1]
9/11/92	64.14[1]
10/22/92	78.20[1]
11/12/92	**83.46**[2]
2/11/93	38.41[3]
3/11/93	12.33[1]
4/22/93	7.45[1]

[1] mean of 12 quadrats

[2] mean of 11 quadrats

[3] mean of 10 quadrats

Table 8: Comparison of culm density of *Spartina alterniflora* at locations in the United States and Canada.

Location	Growth Form	Culms/m^2	References
Padilla Bay, Washington, USA (48°N)	T	223-519	This study
Padilla Bay, Washington, USA (48°N)	nr	100	USACE (1993)
Padilla Bay, Washington, USA (48°N)	nr	117-272	Bulthuis and Scott (1993)
Delaware, USA (~39°N)	S	1038	Gross *et al.* (1991)
Delaware, USA (~39°N)	T	314	Gross *et al.* (1991)
Georgia, USA ((~31-35°N)	S	331	Gross *et al.* (1991)
New Hampshire, USA (~42-45°N)	S	1139	Gross *et al.* (1991)
S. Carolina, USA (31-35°N)	S	565	Gross *et al.* (1991)
S. Carolina, USA (31-35°N)	nr	650-2200	Morris and Haskin (1990)
Virginia, USA (36-39°N)	S	647	Gross *et al.* (1991)
Nova Scotia, CANADA (45°N)	S	1029	Gross *et al.* (1991)
Bay of Fundy, CANADA (45°N)	nr	900-1600	Cranford *et al.* (1989)

S = short form. <90 cm tall at peak height
T = tall form. >90 cm tall at peak height
nr = not reported

and April (17.3%). Mortality was also high in February (21.7%), but that figure included three months of data so mortality may have actually been lower in February. Cranford, *et al.* (1989) studied *S. alterniflora* in the Bay of Fundy and found that mortality started as early as May and was greatest in October. However, it appears in Padilla Bay that the growth cycle is such that mortality may be most evident, not in the fall as on the east coast, but in the spring after the rigors of winter.

Dead culms are evident throughout the year in the marsh in Padilla Bay and may function in helping to keep *Spartina* alive through the winter. Wijte and Gallagher (1991) found that in a mid-Atlantic salt marsh, *S. alterniflora* overwinters with two types of aerial biomass: dead culms from the preceding growing season, and young live shoots that emerge in the fall. They found that when both live and dead shoots were removed in December, the plants did not survive the winter. The presence of either live or dead shoots enabled the plants to survive by providing oxygen to the underground plant parts.

Sayce (1988) reported that individual shoots generally live less than one year and this was true in the present study. Most of the plants tagged in April 1992 were dead in April 1993, but were still present in the quadrats. Reidenbaugh (1983) reported that many *Spartina* shoots may be biennial, emerging during one growing season and surviving over the winter to elongate into culms the following growing season. This was observed in the present study as well. It seems in Padilla Bay that shoots that appear early in the growing season are likely to be annual, dying before the next growing season, but that shoots appearing late in the growing season could be considered biennial as they appear in one growing season, overwinter, and finish their growth during the next growing season.

Three forms of *Spartina* (tall, medium, and short) generally increase in height in descending tidal zones and in proximity to marsh creeks. This appeared to be true in our study (Table 1). The forms are considered ecophenes and are recognized by maximum culm heights, though not all culms attain these heights (Reidenbaugh, 1983). The growth form of *Spartina alterniflora* in Padilla Bay appears to be "tall" with maximum heights in this study ranging between 65-130 cm, although the delineation of "tall" and "short" forms is not consistent among authors. Gallagher *et al.* (1988) reported the short form as ranging between 8-40 cm, while tall ranged from 15-80 cm. Nixon and Oviatt (1973) reported the tall form as ranging from 50-142 cm, while Shea *et al.* (1975) reported the tall form as 200+ cm, and Valiela *et al.* (1978) reported heights of up to 300 cm for the tall form. In Padilla Bay, plants were generally shorter in the higher marsh than toward the channel area. Factors influencing the growth form of *Spartina* include: nutrient supply (Valiela *et al.*, 1975; Valiela *et al.*, 1978), competition for light (Valiela *et al.*, 1978), salinity (Nixon and Oviatt, 1973), and soil salinities (Shea *et al.*, 1975). Nixon and Oviatt (1973) found a significant negative correlation between salinity and both *Spartina* biomass and height. However, they found a strong positive correlation between *Spartina* height and biomass and ammonia. Adams (1963), in a laboratory study, found *S. alterniflora* grew best in fresh water and that a high iron requirement restricted *S. alterniflora* to the low marsh. Average soil salinity on Dike Island in the summer of 1992 was 26.5 ppt at a depth of 10 cm (USACE, 1993). This was in the same range as this study (Table 5).

During the course of the study several factors were noted that could have affected the results. As permanent quadrats were used in the current study, areas leading to the quadrats were trampled and the area around the quadrats became trampled over time. This may have increased light to the plants. Infrequently, a tender young plant or leaf would break off during the tagging or data collecting process. These were noted in the data. With handling, dead plants sometimes broke off sooner than they would have. These also were noted in the data. Another factor that may have affected growth of the plants was that the opaque plastic tags used may have increased shading around the base of the plants and may have shaded new shoots until they overgrew the level of the tags. In October 1993 it was interesting to note that the areas leading to and from the quadrats which had been trampled prior to June 1993 had taller *Spartina* than did the surrounding marsh.

Some grazing occurred in this marsh. The tips of leaves were missing occasionally and voles were observed in the nearby native salt marsh areas. Grazing was not considered in this study and only would have affected leaf or culm counts if the entire leaf was grazed or the entire plant was grazed and gone the following month.

Hardisky and Reimold (1977) compared culm and leaf characteristics for a number of salt marsh plants on the east coast, including *Spartina alterniflora* in Maine. Their study ran from May - October, 1975. They tagged 50 plants while the present study tagged about 300 live plants and 200 dead plants over the course of a year. These characteristics are compared in Table 9. Hardisky and Reimold's sampling periods were 8-week intervals (56 days), while the sampling periods in the present study ranged from 20 - 92 days (Table 4). The maximum rates in the Maine study were more than double the rates in the present study for culm elongation, leaf senescence, and leaf abscission. The maximum rates for leaf emergence were similar. The times of year these maximums occurred were similar for Maine and the current study with the exception of leaf abscission and leaf senescence which peaked in October in Maine (1.9 leaves/culm) and in February in the current study (0.8 leaves/culm). Leaf senescence in June was at a minimum in Maine and at a maximum in Padilla Bay (Table 9). The differences in leaf abscission may be due to differences in weather patterns in the two study areas or to locations of the study sites. Most of the winds are from the southwest or northwest in this area. The Dike Island site is fairly protected from the wave action of winter storm events by a dike to the south and the island itself to the north. Also, in the current study culm elongation had slowed by October, but had not reached a minimum until February, while in Maine culm elongation was at a minimum in October.

Table 9. Comparison of data collected on *Spartina alterniflora* growth characteristics by Hardisky and Reimold (1977)[1] in Maine and the present study in Padilla Bay, Washington.

	Hardisky and Reimold (1977)	Present Study (1992-1993)
<u>Culm elongation (cm/culm)</u>		
Maximum	28	10
Month	June	May[2]
Minimum	1	1.2
Month	October	February
<u>Leaf production (leaves/culm)</u>		
Maximum	1.8	1.5
Month	June	July
Minimum	0.2	0.3
Month	August	February
<u>Leaf senescence (leaves/culm)</u>		
Maximum	3	1.2
Month	August	June
Minimum	0.8	0.6
Month	June	April
<u>Leaf abscission (leaves/culm)</u>		
Maximum	1.9	0.8
Month	October	February
Minimum	0.1	0.3
Month	June	April

1 Data from Hardisky and Reimold (1977) obtained from graphs so data is approximate. Based on midpoints of 8-week sampling periods.

2 Average of culm elongation for May 1992 and May 1993.

Another study on *S. alterniflora* conducted by Hardisky (1980) in Georgia showed lower maximums for leaf production (0.040 leaves/culm/day), senescence (0.046 leaves/culm/day) and abscission (0.022 leaves/culm/day) than in the current study. The maximums in Georgia also occurred at different times of the year (leaf production peaked in December, April, and October; leaf senescence peaked in December and August; and leaf abscission peaked in August) than in either Maine or the current study.

Cranford *et al.* (1989) indicated the growing season in the Bay of Fundy started in April. Although our location is even farther north (48°28' N) than their location (45°06'N), the growing season for *Spartina alterniflora* in Padilla Bay is from February - November. In fact, some shoots that appear in November overwinter and resume growth in February or March the following year. Wijte and Gallagher (1991) report this same event in a Delaware *Spartina* marsh. Therefore, this study covered most of the 1992 growing season and the first few months of the1993 growing season. El Nino conditions prevailed during the period of this study and are indicated by higher than normal sea surface temperatures (NOAA, 1992; NOAA, 1993). However, local air temperatures were particularly cold for an extended period (late December 1992 - January 20, 1993) in the winter of 1992-1993 (WSU Research Station, 1993), and this may account for more dead culms being present in spring 1993 than in spring 1992 (Fig. 8).

This study presents the first estimate of net aerial primary productivity (NAPP) for *Spartina alterniflora* in the Pacific Northwest. A non-destructive method was chosen for this study because of the relatively small size of the salt marsh, the fact the study was on private property and also that the plant has been used to control erosion on the study site. The methods of Hardisky and Reimold (1977) and Hardisky (1980) were used because of the disadvantages of other methods (Table 10) and the advantages listed by Hardisky (1980):

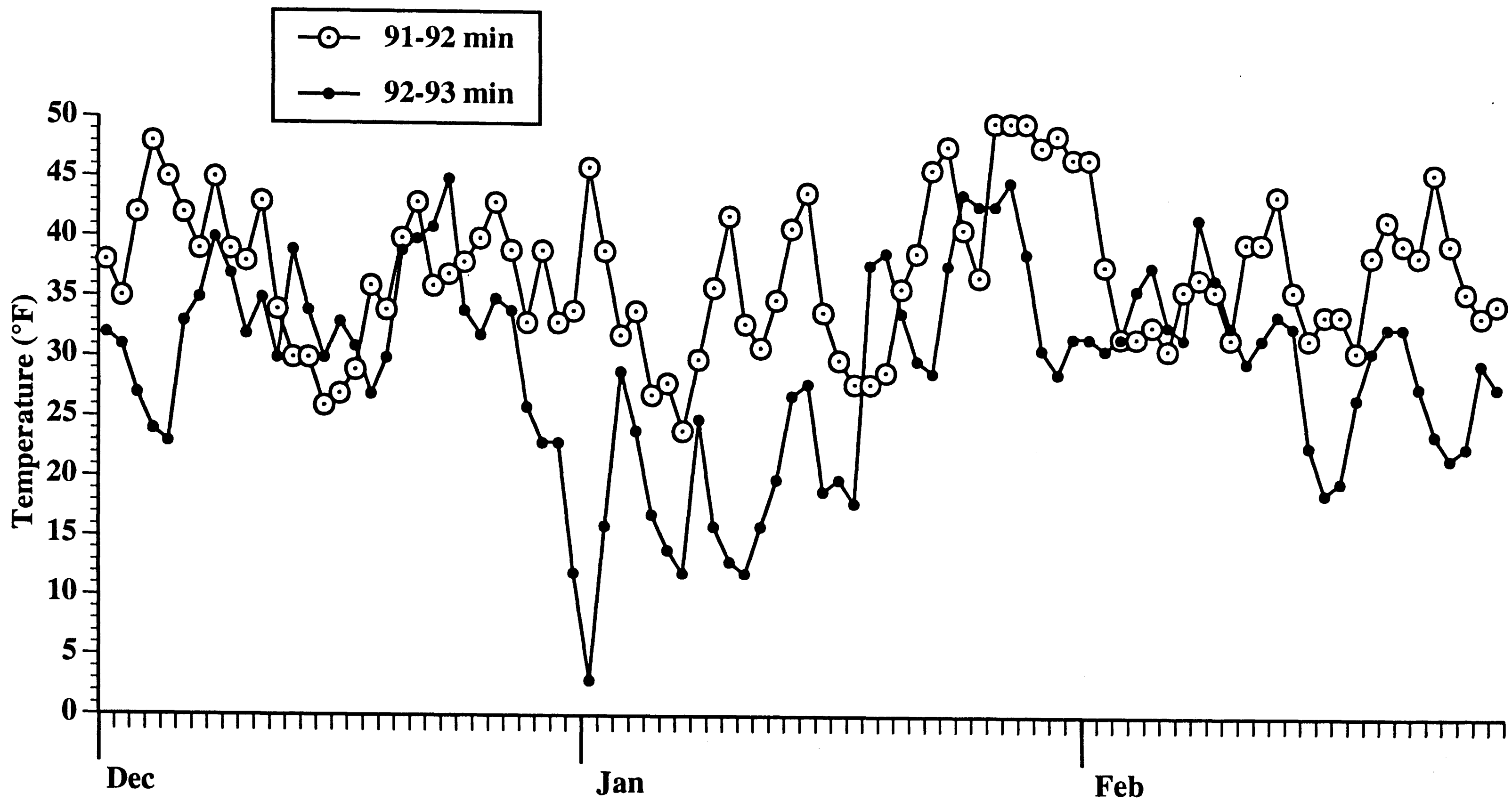


Figure 8. Minimum air temperatures measured near Padilla Bay (Mount Vernon, WA) during the winters of 1991-1992 and 1992-1993 (WSU Research Station, 1993).

Table 10. Comparison of some harvest methods for computing net aerial primary productivity (NAPP) from Linthurst and Reimold (1978) and Shew *et al.* (1981).

Method	Linthurst and Reimold (1978)	Shew *et al.* (1981)
Peak standing crop	underestimates NAPP	Severely underestimates NAPP. Does not account for mortality, decom-position, or growth after the "peak".
Milner and Hughes (1968)	underestimates NAPP	Does not account for dead material or decomposition
Smalley (1959)	underestimates NAPP	Does not account for decomposition.
Lomnicki *et al.* (1968)		Does not account for decomposition.
Valiela *et al.* (1975)	underestimates NAPP	
Wiegert and Evans (1964)	may overestimate NAPP	Does consider live vegetation, dead vegetation produced and present at the time of harvest and decomposition.

1) The same population of plants is continually monitored, eliminating sampling errors which large numbers of replicates attempt to diminish in destructive harvest,

2) Recruitment can effectively be monitored within stationary quadrats with tagged plants, and

3) Size of a homogeneous stand of plants necessary for a nondestructive assessment is much less than would be required by a destructive procedure.

Cranford *et al.* (1989) compared four methods of determining NAPP for *Spartina alterniflora*, one of which was the Hardisky (1980) method. They felt the advantages of this method were that it directly measured leaf loss during the growing season and also accounted for shoot export. They found this method gave the highest values of NAPP at all the stations in their study. They also felt the disadvantages of this method were that:

1) it is based on following the growth dynamics of a relatively small population of tagged plants, and

2) it assumes the vegetation is homogeneous.

In regards to #1 above, Hardisky and Reimold (1977) tagged only 50 live culms at the start of that study. In the current study 13.9-32.4 live stems were present per 0.0625 m^2 which means approximately 278 live plants were tagged (range: 167-389) during any one month of the study which is considerably more than in Hardisky & Reimold (1977). Hardisky (1980) tagged ten replicate 0.1 m^2 circular quadrats but did not indicate average culm density in each quadrat, however, it was probably similar to the number tagged in the current study.

Hardisky (1980) indicated that, in theory, the nondestructive method he designed is similar to the Lomnicki *et al.* (1968) method and the modified Lomnicki *et al.* method described by Shew *et al.* (1981). While the Lomnicki method uses live plots to estimate mortality from living plants and adds any change in live biomass during an interval of time, Hardisky's method estimates live culm production in the form of culm mortality as it passes to the dead component and adds leaf mortality.

Cranford *et al.* (1989) also indicates that if larger shoots are tagged at the start of the growing season NAPP can be overestimated using this method. To address that problem, the study quadrats for the present study were placed randomly within a section of the marsh and all plants in the quadrats were tagged. The quadrats ranged from +1.05 to +1.45 meters above mean sea level, and maximum culm heights ranged from 65 - 130 cm (Table 1).

The estimate of net aerial primary productivity for *Spartina alterniflora* in this study is higher than those obtained for studies at similar latitudes on the Atlantic coast of North America (Table 11). However, because east and west coast climates are different it is possible that the growing season in the Pacific Northwest is longer due to the milder winters. Hatcher and Mann (1975) compared the productivity of *S. alterniflora* at various sites along the Atlantic Coast and found that the productivity of *S. alterniflora* tended to decrease with increasing latitude. However, they also noted that other factors such as nutrient availability also can influence productivity.

The generally higher rates of net aerial primary productivity in this study also may be due to the non-destructive method used, whereas most studies listed in Table 11 used destructive methods. The Wiegert & Evans (1964) method, although destructive, does take into account the rate of litter disappearance and those estimates appear to be closer to this study. Shew, *et al.* (1981) found the Wiegert & Evans method minimizes tidal influences. However, Dickerman, *et al.* (1986) noted that the Wiegert & Evans (1964) method was developed for old-field vegetation and felt it was not suitable for use in salt marshes where litter is moved by the tides.

The 22.5% of NAPP attributed to leaf loss in this study is comparable to that reported by Hatcher and Mann (1975) at the end of a growing season for tall form

Table 11. Comparison of net aerial primary productivity (g dry wt./m^2/year) of *Spartina alterniflora.*

Location	Method	N/D*	Productivity	Reference
Washington	Hardisky (1980)	N	1520	This study
Nova Scotia	Smalley (1959)	D	710	Hatcher and Mann (1975)
Maine	Peak standing crop	D	431(creekbank)	Linthurst and Reimold (1978)
	Milner and Hughes (1968)	D	431 (creekbank)	(compared 5 methods)
	Smalley (1959)	D	758 (creekbank)	
	Valiela *et al.* (1975)	D	758 (creekbank)	
	Wiegert and Evans (1964)	D	1602 (creekbank)	
	Peak standing crop	D	246 (high marsh)	
	Milner and Hughes (1968)	D	246 (high marsh)	
	Smalley (1959)	D	763 (high marsh)	
	Valiela *et al.* (1975)	D	662 (high marsh)	
	Wiegert and Evans (1964)	D	1611 (high marsh)	
Bay of Fundy	Smalley (1959) modified	D	272 (low marsh)	Gordon *et al.* (1985)
Bay of Fundy	Peak standing crop	D	398	Cranford *et al.* (1989)
	Smalley (1959) modified	D	371	(compared 4 methods)
	Growth incremt. summation	D	507	
	Hardisky (1980)	N	616	
Virginia	Reidenbaugh (1983)	N	1169 (tall form)	Reidenbaugh (1983)
North Carolina	Peak standing crop	D	242.2	Shew *et al.* (1981)
	Milner and Hughes (1968)	D	214.1	(compared 5 methods)
	Smalley (1959)	D	224.6	
	Wiegert and Evans (1964)	D	1028.6	
	Lomnicki *et al.* (1968)	D	1027.8	
South Carolina	Dickerman *et al.* (1986) modified	N	408-1042 (5-yr study)	Morris and Haskin (1990)
Georgia	Wiegert and Evans (1964)	D	3700 (creekbank)	Gallagher *et al.* (1988)
Georgia	Schubauer and Hopkinson	D	2840 (med. form)	Schubauer and Hopkinson (1984)
Georgia	Smalley (1959)	D	931	Hardisky (1980)
	Hardisky (1980)	N	635	
Louisiana	Wiegert and Evans (1964)	D	750-2600	Kirby and Gosselink (1976)
Louisiana	Wiegert and Evans (1964)	D	2658 (2523-2794)	Hopkinson *et al.* (1978)

* N: Non-destructive method; D: Destructive or "harvest" method.

Spartina in a Nova Scotia marsh (23.3%) and somewhat lower than that reported by Hardisky (1980) in a Georgia marsh (31%).

Riggs (1992) reported a total area of 48,100 m^2 of *S. alterniflora* in Padilla Bay in 1991. This included 19 stands that ranged from 6.3 m^2 to 44,200 m^2. If the estimate obtained in this study is applied to the *S. alterniflora* that existed in the bay in 1991 an estimate for total annual aboveground productivity of *S. alterniflora* in Padilla Bay is 73,112 kg dry weight.

Table 12 compares turnover rates and turnover times for *S. alterniflora*. However, because the equation for turnover includes net aerial primary productivity (NAPP), turnovers may vary because of the methods used for estimating NAPP rather than solely because of other factors such as study location or latitude. The method that appears to address more of the necessary variables also apparently overestimates NAPP (Wiegert and Evans, 1964; Table 11). The Smalley (1959) method was used in studies in Georgia, North Carolina and the Bay of Fundy and the respective turnover rates were: 3.22 crops/year, 0.9 crops/year, and 1.0 crop/year. From this data, it appears that turnover rates generally decrease with an increase in latitude. In comparing data analyzed using the Wiegert and Evans method in North Carolina and Maine, the turnover rates of 4.2 crops/year and 4.0 crops/year, respectively, are similar. However, the Maine study distinguished between two growth forms of *S. alterniflora*: creekbank and high marsh. Turnover rate for the creekbank plants was lower (4.0 crops/year) than the high marsh plants (7.0 crops/year). Turnover rate in this current non-destructive study (1.14 crops/year) was similar to the 1.0 crops/year found by da Cunha Lana *et al.* (1991) in Brazil, by Gordon *et al.* (1985) in the Bay of Fundy, and by Shew *et al.* (1981) in North Carolina; all of which used harvest methods.

Table 12. Comparison of selected literature for turnover time and percent turnover of aboveground *Spartina alterniflora*. Bold type indicates how data was reported in the original study. CB = creekbank. HM = high marsh.

Location	Turnover rate (crops/year)	Turnover time (years)	NAPP Method	Percent turnover per year	Literature Cited
Washington	1.14	0.88	Hardisky (1980)	114	This study
Bay of Fundy	1.0	**1.0**	Smalley (1959)	100	Gordon *et al.* (1985)
Maine	**4.0** (CB)	0.25	Wiegert and Evans (1964)	400	Linthurst and Reimold (1978)
	7.0 (HM)	0.14	Wiegert and Evans (1964)	700	
North Carolina	**1.0**	1.0	peak standing crop	100	Shew *et al.* (1981)
	0.9	1.11	Milner and Hughes (1968)	90	
	0.9	1.11	Smalley (1959)	90	
	4.2	0.24	Wiegert and Evans (1964)	417	
	4.2	0.24	Lomnicki *et al.* (1968)	417	
Georgia	**3.22**	0.31	Smalley (1959)	323	Schubauer and Hopkinson (1984)
Brazil	0.99	**1.01***	Milner and Hughes (1968) Smalley (1959) Valiela *et al.* (1975) Wiegert and Evans (1964) Linthurst and Reimold (1978)	**90-150**	da Cunha Lana *et al.* (1991)

* This is the average of the five methods listed for this study.

SUMMARY

This study provides the first measurements of leaf emergence, leaf senescence, leaf abscission, and culm elongation and mortality of the introduced *Spartina alterniflora* in Washington state, and reports the first estimates of net aerial primary productivity of this introduced cordgrass in the Pacific Northwest. This study has shown that *S. alterniflora* in Padilla Bay, Washington, grows throughout the year. Culm elongation peaks in spring and leaf emergence is maximum in summer. On an average, culms in this study grew 70.2 cm/yr, produced a 11.3 leaves per year, had 10.6 leaves die and 5.9 leaves were carried off the culm. The density of live stems does not show a strong seasonal fluctuation. The density of dead stems increased during the course of this study, probably because of a harsh winter. Leaf abscission (and potential export from the marsh) is maximum in autumn, but continues throughout the year providing a continuous supply of detrital material.

The estimated annual production (1520 g dry wt./m^2/year) is high compared to most estimates for indigenous populations on the east coast of North America. The fate of this high productivity is not known for the Pacific Northwest, but it is likely that most of the net aerial production enters the detrital food chain and is a positive contribution to estuarine productivity. The population at Padilla Bay is the northernmost reported population of *S. alterniflora* on the west coast of North America, but the high productivity indicates a healthy, productive population. This study indicates that low productivity is not the reason that this is the most northerly population. If *S. alterniflora* is deemed an undesirable species for various reasons (e.g. habitat alteration), this study emphasizes the importance of acting early to control or eradicate the population in Padilla Bay. There is no indication that this population is only marginally productive and may die back if there is no intervention.

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Appendix 1. Grand mean dead leaf biomass (in grams) of *Spartina alterniflora* in a Padilla Bay, Washington, salt marsh. Weights in table are means of 3-6 leaves from each culm.

Culm	3/11/93	5/21/93	8/20/93	10/30/93
1	0.24	0.25	0.13	0.16
2	0.20	0.18	0.15	0.19
3	0.16	0.23	0.11	0.16
4	0.17	0.27	0.11	0.21
5	0.26	0.20	0.17	0.19
6	0.24	0.23	0.14	0.23
7	0.22	0.15	0.19	0.14
8	0.24	0.28	0.17	0.21
9	0.26	0.16	0.14	0.15
10	0.24	0.24	0.16	0.16
11	0.18	0.24	0.20	0.13
12	0.27	0.19	0.11	0.26
13	0.16	0.23	0.21	0.18
14	0.19	0.17	0.18	0.24
15	0.15	0.12	0.16	0.15
16	0.26	0.24	0.21	0.19
17	0.22	0.26	0.19	0.18
18	0.30	0.21	0.22	0.19
19	0.15	0.12	0.18	0.20
20	0.30	0.23	0.20	0.21
21	0.18	0.28	0.25	0.12
22	0.23	0.22	0.22	0.33
23	0.28	0.19	0.19	0.20
24	0.27	0.23	0.08	0.15
25	0.19	0.26	0.16	0.14
Grand mean	0.22	0.21	0.17	0.19