

FINAL REPORT

# Element A

## *Spartina:* Distribution, Biology, and Ecology

Submitted to  
Washington State  
Department of Ecology

Submitted by  
EBASCO ENVIRONMENTAL  
*A Division of Ebasco Services Incorporated*

November 1992

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**Element A - *SPARTINA*:  
DISTRIBUTION, BIOLOGY, AND ECOLOGY**

**Submitted to:**

**Washington State Department of Ecology**

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**November 1992**

## ABSTRACT

Infestations of three species of introduced cordgrass, *Spartina alterniflora*, *S. patens*, and *S. anglica* are raising serious ecological and economic concerns in Washington. *Spartina* species are colonizing intertidal flats, and causing concern for displacement of native vegetation and accretion of sediments. In addition, there is concern for potential effects on habitat for fish, wildlife, and aquaculture species. Development of an effective management plan for *Spartina* species requires thorough knowledge of their biological characteristics and ecological requirements and interactions. This report provides information on historical and present-day distributions of *Spartina* species and on biological and ecological characteristics relevant to their control. Suggestions for further research are also provided. A discussion of the habitat value afforded to biota by *Spartina* will be provided in the report for Element C—No Action Alternative.

*Spartina* species present in Washington are rhizomatous, deep-rooted, perennial grasses that inhabit a wide range of tidal, salinity, and substrate conditions in intertidal areas. *Spartina* species can reproduce both vegetatively and sexually. However, not all populations in Washington currently reproduce by seed. Factors implicated in the onset and success of sexual reproduction in *Spartina* include seed source, photoperiod, soil temperature, salinity, tidal range, and herbivory.

Vegetative reproduction is important in the maintenance of existing stands, while seed dispersal and seedling recruitment are the primary modes of establishment of new colonies. Establishment of new colonies from dispersal of vegetative propagules is also possible, but its importance in the establishment of new colonies in Washington is not documented.

The onset of sexual reproduction increases the rate of *Spartina* spread. Dispersal of seeds or rhizome propagules occurs through transport by water, animals, or humans. Dieback and infestations by pathogens and herbivorous insects can impact the growth and vigor of stands and may consequently reduce populations and limit spread by causing death and suppression of vegetative and sexual reproduction in individual plants. Interspecific competition can also affect vegetative spread and seedling survival.

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## 1.0 INTRODUCTION

### 1.1 PURPOSE

The Washington State Departments of Agriculture, Ecology, Fisheries, Natural Resources, Wildlife, and the Washington State Noxious Weed Control Board, acting as co-lead agencies, have proposed to develop and implement a management plan for noxious emergent plant species occurring in the State of Washington. Species of concern include three species of cordgrass or *Spartina* (*S. patens*, *S. alterniflora*, and *S. anglica*), purple loosestrife (*Lythrum salicaria* and *Lythrum virgatum*), garden loosestrife (*Lysimachia vulgaris*), giant hogweed (*Heracleum mantegazzianum*), and indigo bush (*Amorpha fruticosa*). The lead agencies wish to determine which management alternative or combination of alternatives would provide the most effective management with the least environmental impacts. The ultimate goal of the proposal is to develop criteria and approaches for managing infestations of both existing noxious species and new invaders.

Through a public scoping process, the lead agencies have determined that management of these noxious emergent plant species could have a significant adverse impact on the environment. Thus, an environmental impact statement (EIS) is required under RCW 43.21C.030(2)(c). The lead agencies have identified topics to be discussed in the EIS, including biology and ecology of problem species, management alternatives, efficacy and impacts of alternatives, and mitigation strategies. Ebasco Environmental was contracted by the nominal lead agency, the Washington State Department of Ecology, to assemble and synthesize available information on the topics of interest for probable inclusion into the EIS. Infestations of three introduced species of *Spartina* are raising serious ecological and economic concerns in Washington. *Spartina* species are colonizing intertidal flats, and causing concern for displacement of native vegetation and accretion of sediments. In addition, there is concern for potential effects on habitat for fish, wildlife, and aquaculture species. The introduced *Spartina* species in Washington are included on the Washington State Noxious Weed List (Chapter 16-750 WAC).

Development of an effective management plan for a noxious emergent plant species requires thorough knowledge of the biological characteristics, ecological requirements, and interactions of the species. To assist in plan development, this report provides information on the biology, ecology, and distribution of the *Spartina* species in Washington. A separate report details the biology and ecology of purple loosestrife.

### 1.2 OBJECTIVES

The objectives of this report are to:

- (1) summarize information on the distribution of introduced *Spartina* species, including locations of infestations in Washington; and,

(2) characterize the plant biology and ecology of *Spartina* species introduced to Washington including:

- taxonomy
- physiology
- habitat requirements
- reproduction
- modes of dispersal
- factors affecting growth, spread, and dieback

Discussion of biological and ecological characteristics focuses on those attributes that contribute to the invasive nature of *Spartina* and have implications in its control. A discussion of the habitat value afforded to biota by *Spartina* will be provided in a later report. The appendix summarizes selected biological and ecological characteristics of *Spartina* species in their native habitat and in Washington.

The primary sources of information for this report were published journal articles and published and unpublished studies. Information was obtained from both national and international sources. A search for recent literature (1990-present) on *Spartina* augmented the extensive *Spartina* bibliography compiled by Aberle (1990).

## 2.0 DISTRIBUTION OF SPARTINA

### 2.1 HISTORICAL DISTRIBUTION

There are approximately 14 species of *Spartina* world-wide. The native distribution of the genus includes North America, South America, Europe, Africa, and several islands in the South Atlantic and South Indian Oceans. No native distribution has been observed in Asia (Chung 1983). The genus is thought to have originated in North America, from where it migrated eastward across the North Atlantic landbridge into Europe (Fernald 1929 cited in Pierce 1982). No *Spartina* species are native to the intertidal habitats of Washington. However, three *Spartina* species, *S. alterniflora*, *S. patens*, and *S. anglica* were introduced and have successfully established in the Pacific Northwest. Current distributions of these species in the Pacific Northwest are described in Section 2.3.

*Spartina alterniflora* is endemic to the Atlantic and Gulf Coasts of North America. It is the dominant salt marsh species in the lower intertidal zone along protected coastlines from Newfoundland to Texas (Smart 1982). *S. patens* is the dominant plant species present in the middle and higher reaches of salt marshes in its native range which extends along the Atlantic Coast from Canada to Central America and the Caribbean. The Carolinas mark the approximate center of its distribution (Silander 1984). Distinct zonal segregation of *S. patens* and *S. alterniflora* populations occurs within a salt marsh; *S. alterniflora* occupies the lower intertidal elevations while *S. patens* dominates the middle and upper intertidal areas.

Numerous environmental factors including nutrient availability, sediment composition, and tidal dynamics, and interspecific competition influence zonation (Bertness and Ellison 1987; McKee and Patrick 1988; Bertness 1991).

*Spartina maritima* is indigenous to the coast of Great Britain, the Atlantic seaboard of continental Europe, the Mediterranean Sea coast, and the shores of northwest Africa (Pierce 1982). *S. anglica* originated in salt marshes of the southern English coast in the late 1800s. This species is a fertile hybrid derived from the natural crossing of the native *S. maritima* and the exotic *S. alterniflora* (introduced around 1830). *S. x townsendii* is the male-sterile primary hybrid of the cross. Chromosome doubling of this primary hybrid led to the development of the fertile allopolyploid, *S. anglica* (Gray *et al.* 1990). *S. anglica* is often discussed collectively with *S. x townsendii* because the two species are difficult to distinguish morphologically. This report refers to the species separately when possible.

*Spartina foliosa* is native to California intertidal habitats. It occurs in coastal salt marshes from Baja to Bodega Bay, California (Spicher and Josselyn 1985). *S. foliosa* and *S. alterniflora* co-occur in San Francisco Bay. Calloway and Josselyn (1992) reported that *S. alterniflora* had a wider intertidal distribution and higher rates of above- and below-ground biomass production, seed production, lateral growth and seed germination than *S. foliosa* in San Francisco Bay.

## 2.2 PRESENT-DAY DISTRIBUTION

Introductions of *Spartina* into non-native habitats have occurred both accidentally and intentionally. *Spartina* has been introduced from ship ballast and through its use as packing material for oyster shipments. Cordgrass has also been intentionally planted for shoreline stabilization and erosion control, livestock forage, "land reclamation", and marsh creation. This section discusses introductions of *Spartina* species throughout the world, exclusive of the Pacific Northwest. The status of species introduced to the Pacific Northwest is described in Section 2.3.

### 2.2.1 British Isles and Europe

*Spartina alterniflora* was initially introduced to southern England and southwestern France in the early 1800s through ship's ballast (Marchant 1967). *S. anglica*, the fertile polyploid hybrid of the cross between *S. alterniflora* and the native *S. maritima*, aggressively colonized bare mudflats throughout the southern, western, and eastern coasts of Britain. In addition, *S. anglica* was also extensively planted in the 1920s and 1930s in most of the major estuaries of England and Wales, and in seven estuaries in Scotland and 16 in Ireland. Several species of *Spartina* were also intentionally planted in France, Germany, the Netherlands, and Denmark (Ranwell 1967).

Competition from *S. anglica*, loss of habitat from navigational and industrial development, physical erosion of marsh habitat by rising sea levels, and natural successional changes are

thought to have significantly decreased the distribution of *S. alterniflora*, *S. maritima*, and *S. x townsendii* in Britain (Marchant 1967; Raybould *et al.* 1991a). *S. alterniflora* is now virtually extinct in England, but is thriving in a few locations on the north coast of France (Gross *et al.* 1986).

The distribution of *S. anglica* in Britain has also significantly changed in the last 30 years. Populations of *S. anglica* in southern England have experienced natural dieback, while the distributions on the west coast of Britain (which chronologically was invaded later) has substantially increased since the 1960s. The areal extent of *S. anglica* in Britain has decreased from an estimated 12,000 ha (29,600 acres) in the mid-1960s to an estimated 9,800 ha (24,200 acres) in 1990 (Charman 1990). Estimates from the mid-1980s range between 6,700 ha (16,550 acres) (or 15% of the total salt marsh area in Britain) (Doody, Estuaries Review) and 6,950 ha (17,200 acres) (or 16% of the total salt marsh area) (Way 1990).

### 2.2.2 China

*Spartina alterniflora* and *S. anglica* were introduced to coastal China from England in the early 1960s for the purposes of reclaiming arable land. *S. alterniflora* now covers about 1300 ha (3,200 acres) (Chung 1990). Four separate consignments of *S. anglica* were also planted along the north central coast of China in 1963. The total area of *S. anglica* was estimated at 110 ha (270 acres) in 1966. By 1980, approximately 36,000 ha (89,000 acres) had been planted (Chung 1990). One of the initial plantings was in the Yangtze Estuary, which now has the largest single area of *S. anglica* in the world (Aberle 1990).

### 2.2.3 New Zealand and Australia

*Spartina x townsendii* was introduced to New Zealand from England in 1913 to reclaim tidal flats for pasture and later to provide shoreline and bank protection. Successive plantings from the original stands and further imports of *S. anglica* from England and *S. alterniflora* from North America accelerated during the 1940-50s throughout New Zealand. *S. anglica* is now the most abundant species in New Zealand. *S. alterniflora* is successfully established only in the northern regions (Asher 1990). Only *S. anglica* produces seed. *S. gracilis*, an inland, freshwater species native to western North America, was also introduced to North Island, New Zealand, but did not persist (Partridge 1987 cited in Aberle 1990).

*Spartina x townsendii/anglica* was introduced to Australia from England beginning in the late 1920s. Although plantings occurred until the mid-1970s, the period of most intensive planting was in the late 1920s and early 1930s. Cordgrass was introduced for land reclamation, shoreline and seawall stabilization, and pasture. The area colonized by *Spartina* was estimated at 620 ha (1500 acres) in 1980. Major infestations are confined to estuaries and lagoons in northern Tasmania and Gippsland, Victoria (Boston 1992).

#### 2.2.4 Africa

*Spartina patens* was introduced from North America into the Mediterranean (Silander 1984) and *S. maritima* was introduced from the Mediterranean and western European coast to South Africa (Pierce 1982). As of 1982, *S. maritima* occurred in nine estuaries along the Cape of South Africa.

#### 2.2.5 California

*Spartina alterniflora*, *S. densiflora*, *S. patens*, and *S. anglica* are now established in San Francisco Bay, while *S. alterniflora* and *S. densiflora* are present in Humboldt Bay, California. *S. densiflora* is thought to have been introduced into Humboldt Bay from lumber ships returning from Chile (Spicher and Josselyn 1985).

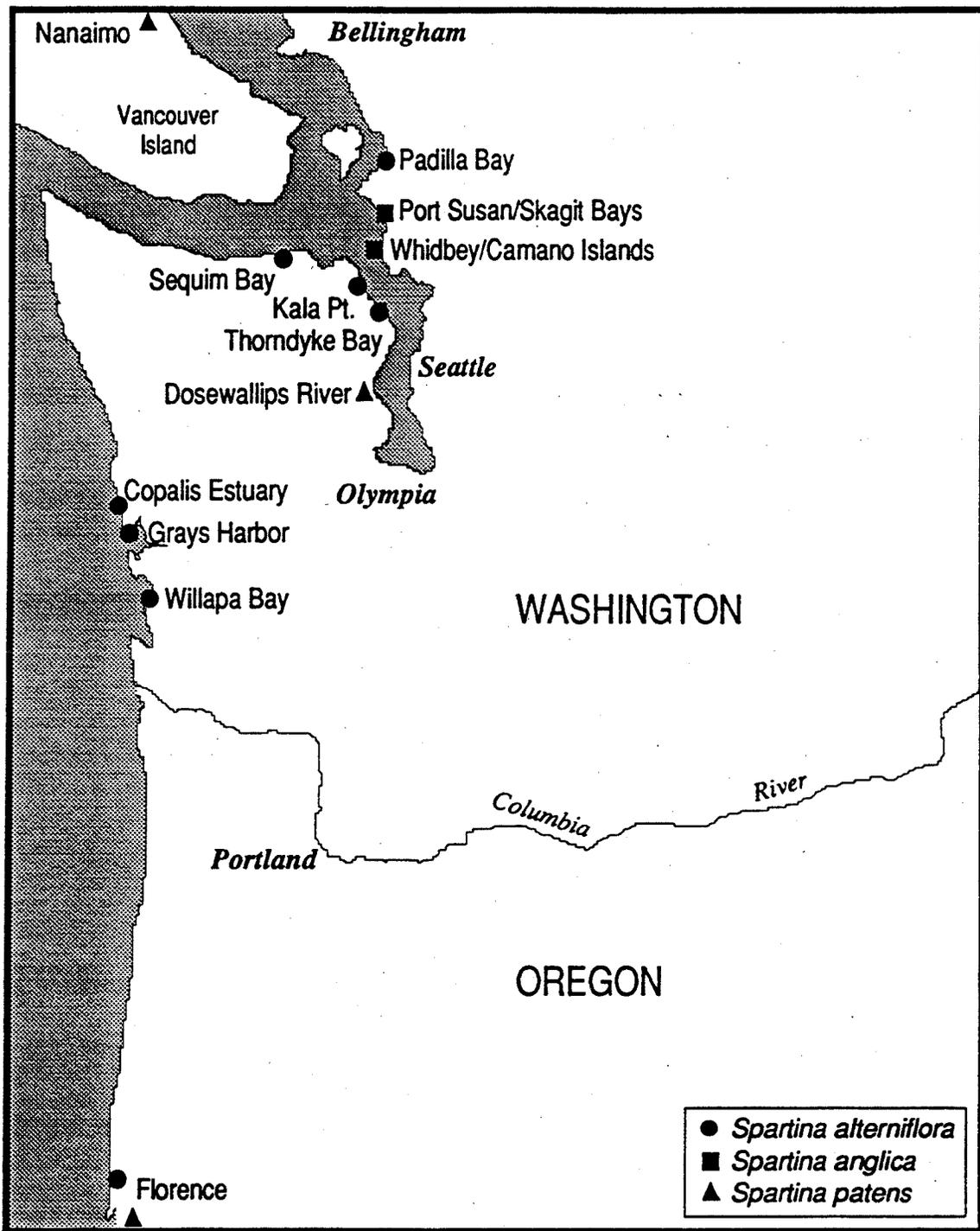
### 2.3 PACIFIC NORTHWEST DISTRIBUTION AND STATUS

Coastal salt marshes provide a demanding habitat to which relatively few species are adapted. Because of the unique physical and chemical characteristics of salt marsh environments, a floristic similarity exists among coastal salt marshes throughout the world. Furthermore, dominant salt marsh genera often occupy comparable ecological positions world-wide (Frenkel and Boss 1988). However, despite the generic similarity among salt marsh flora, biogeographic provinces may be recognized (Chapman 1977 cited in Frenkel and Boss 1988).

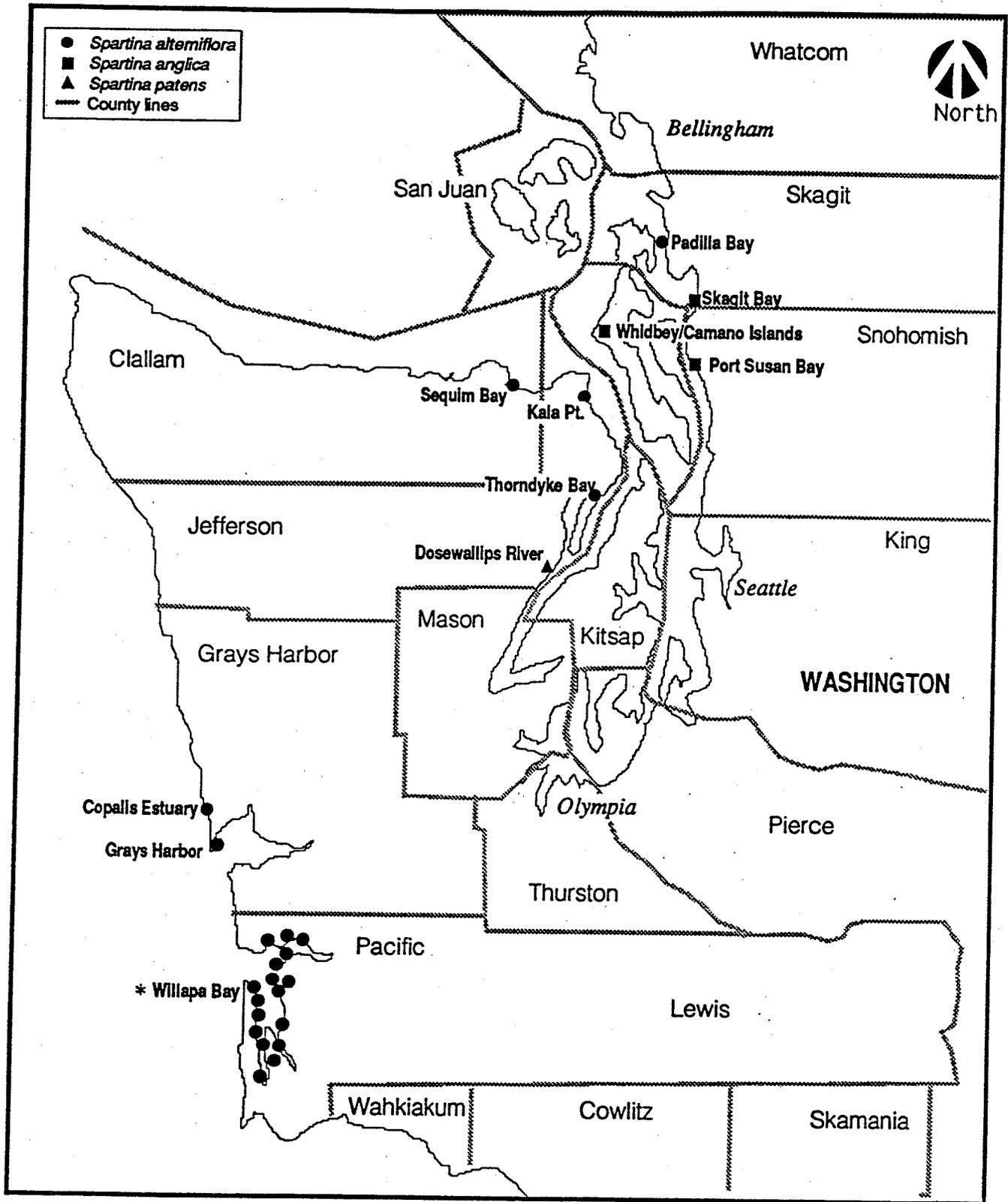
Geographically and historically isolated coastal marsh regions, such as the Pacific maritime marshes, exhibit distinctive flora at the species level and are particularly vulnerable to introduction of exotic species. Introductions into estuaries and salt marshes of the Pacific Northwest include: *Cotula coronopifolia*, *Spergularia marina*, *Zostera japonica*, *Spartina alterniflora*, *Spartina patens*, and *Spartina anglica* (Frenkel and Boss 1988).

#### 2.3.1 Washington

*Spartina alterniflora*, *S. patens*, and *S. x townsendii/anglica* have been introduced accidentally and intentionally into intertidal areas of Washington (Figures 1 and 2). *S. alterniflora* was introduced into Willapa Bay in the late 1800s, presumably from its use as packing material in the transport of eastern oyster shipments. *Spartina* covered approximately 430 acres (170 ha) in Willapa Bay in 1984. Current areal estimates range between 1,100 acres (450 ha) and 2,000-2,500 acres (810-1000 ha) (Sayce 1990). *Spartina* extent in Willapa represents the largest infestation of cordgrass in Washington. If *Spartina* continues to spread unchecked, it could potentially cover 30,000 acres in Willapa Bay by the year 2030 (Sayce 1988). *S. alterniflora* has also recently established at Damon Point in nearby Grays Harbor (ACOE 1992) and in the Copalis River estuary (pers. comm. J. Civile 1992).



**Figure 1.** General locations of *Spartina* infestations in the Pacific Northwest. Areal estimates of infestations, if available, are given in text. Redrawn from Mumford *et al.* (1990).



**Figure 2.** General locations of *Spartina* infestations in Washington. Areal estimates of infestations, if available, are given in text. Redrawn from Aberle (1990).

\**Spartina alterniflora* is present throughout Willapa Bay.

*Spartina alterniflora* was also introduced to Padilla Bay in Skagit County, Washington, between 1940 and 1946 by the Dike Island Gun Club to stabilize a long, narrow island in the south Bay (Parker and Aberle 1979). The areal extent of *S. alterniflora* was estimated at 26,700 m<sup>2</sup> (6.6 acres) in 1987 (Wiggins and Binney 1987). Riggs (1992) estimates a current figure of 48,100 m<sup>2</sup> (11.9 acres). The cordgrass appears to be spreading vegetatively since no evidence of flowers or seeds has been found.

*Spartina alterniflora* has also been introduced to increase vegetative cover at three other known localities in Washington: Thorndyke Bay, Kala Point, and Gibson Spit (Sequim Bay) (Figures 1 and 2). These areas are spit-enclosed lagoons with little tidal interchange and high salinities. As of 1984, these infestations were small (individual patches covered 350-1300 m<sup>2</sup> or 0.1-0.3 acres) and did not appear to be spreading rapidly (Frenkel and Kunze 1984). Frenkel and Kunze (1984) suggested the greatest potential for *S. alterniflora* spread in Washington and Oregon is in coastal marshes subject to regular tidal inundation.

The only occurrence of *S. patens* in Washington is a small infestation at Dosewallips State Park at the mouth of the Dosewallips River where it enters Hood Canal (Figures 1 and 2). The patch was established prior to 1968 (mode of introduction is unknown) and covered about 150 m<sup>2</sup> (0.04 acre) in 1984. The plants produce flowers, but seed viability is thought to be low (Frenkel and Kunze 1984).

*Spartina anglica* or a mixture of *S. anglica* and *S. x townsendii* occurs in Port Susan Bay, Skagit Bay, and Deer Lagoon on Whidbey Island, Washington (Figures 1 and 2). Informal observations suggest *S. anglica* is spreading quickly; rapid clonal expansion and seedling reproduction have been documented (Aberle 1990). In Skagit Bay, *S. anglica*/ *x townsendii* is present at West Pass near the entry of the Stillaguamish River and at the mouth of the north fork of the Skagit River. In 1989, *S. anglica* was discovered at Deer Lagoon on Whidbey Island (Aberle 1990). The mode of introduction is unknown.

The Washington State Departments of Natural Resources and Fisheries are conducting inventories for *Spartina* during summer 1992. Updated inventory information will be available in late winter 1992.

### 2.3.2 Oregon and British Columbia

The only Oregon locality of *Spartina* is the Siuslaw Estuary near Florence, Oregon (Figure 1). *S. patens* was introduced to Cox Island in the Siuslaw Estuary prior to 1939, perhaps from attempts to establish oyster culture in the estuary (Frenkel and Boss 1988). It now occupies more than 3,000 m<sup>2</sup> (0.7 acre) (Frenkel 1990). The plants flower, but neither pollen nor seed production has been observed (Frenkel and Boss 1988). In addition, *S. alterniflora* was established on Port of Florence land in the estuary as an experimental planting in 1978 or 1979 for possible use in salt marsh restoration projects (Frenkel and Boss 1988; Aberle 1990). One patch occupied about 200 m<sup>2</sup> (0.05 acre) in 1991. A second smaller patch is also present. The plants appear to have spread vegetatively since flowering

has not been observed. *S. alterniflora* and *S. patens* were placed on the Oregon Noxious Weed "A" List in 1990 (Aberle 1990).

A small population of *S. patens* is present just north of Nanaimo on Vancouver Island, British Columbia. The mode of introduction is not known. This infestation does not appear to be spreading. *S. patens* is not considered a noxious species in British Columbia (Aberle 1990).

### 3.0 BIOLOGY AND ECOLOGY

#### 3.1 TAXONOMY AND PHYSIOLOGY

##### 3.1.1 Taxonomic Status of Species Present in Washington

*Spartina alterniflora* Loisel., *Spartina patens* (Aiton) Muhl., and *Spartina anglica* C.E. Hubbard are present in Washington. *S. anglica* is often discussed collectively with *S. x townsendii* as *S. x townsendii* agg. or *S. x townsendii (sensu lato)*, because the two species are difficult to distinguish morphologically (Hubbard 1978).

*Spartina anglica* originated in salt marshes of the southern English coast in the late 1800s. After the accidental introduction of *S. alterniflora* through shipping ballast in the early 1800s, this native North American species hybridized with its European cogenor, *Spartina maritima* (Curtis) Fernald. The result was the sterile F<sub>1</sub> hybrid, *Spartina x townsendii* H. & J. Groves. Subsequent chromosome doubling in *S. x townsendii* produced a new fertile species, *S. anglica* (Thompson 1991). The hybrid origin of *S. anglica* and its origin from chromosome doubling in *S. x townsendii* is substantiated by recent isozyme studies of the hybrid and parent populations (Raybould *et al.* 1991b; Gray *et al.* 1990; Guenegou *et al.* 1988).

It is uncertain which species, *S. anglica* or *S. x townsendii*, was originally planted in Washington. The original planting, which was intended to provide forage for cattle, occurred in 1961 on the east shore of Port Susan Bay (three miles south of Stanwood) (Frenkel and Kunze 1984). Although the original planting died back, the grass has since spread to other areas of Port Susan Bay and north into Skagit Bay. Plants in Port Susan Bay are producing viable seed and morphological descriptions match that of *S. anglica* (Aberle 1990). Therefore, either *S. x townsendii* was originally planted and a natural doubling of the chromosomes subsequently occurred to produce *S. anglica*, or the original planting was *S. anglica*. Since *S. anglica* and *S. x townsendii* are very difficult to distinguish morphologically, it is also possible that a mixture of the two species occurs in some areas.

### 3.1.2 Physiological Processes

*Spartina* grasses photosynthesize through the C<sub>4</sub> pathway, that is, their first product of carbon dioxide (CO<sub>2</sub>) incorporation is a 4-carbon acid. The first compound resulting from CO<sub>2</sub> incorporation in C<sub>3</sub> plants is 3-carbon phosphoglyceric acid. Most C<sub>4</sub> species are monocots, especially grasses and sedges, while all gymnosperms, ferns, mosses, liverworts, hornworts, and algae that have been studied, and nearly all trees and shrubs are C<sub>3</sub> plants (Raven *et al.* 1981).

The utilization of the C<sub>4</sub> pathway of photosynthesis is one adaptation to surviving in a drought-stressed environment. Plants in saline wetland environments have the similar problem of water availability as do plants in arid areas. C<sub>4</sub> plants utilize lower concentrations of CO<sub>2</sub>, exhibit lower photorespiration rates and loss of CO<sub>2</sub> during respiration, and experience less water loss from evapotranspiration than C<sub>3</sub> plants (Mitsch and Gosselink 1986). C<sub>4</sub> plants also exhibit higher photosynthetic rates than C<sub>3</sub> plants at temperatures at or above about 30°C (86°F) (Thompson 1991). C<sub>4</sub> plants then have a distinct competitive advantage over C<sub>3</sub> plants when photosynthesis is limited by CO<sub>2</sub> concentration, which occurs under high light intensities and high temperatures, and when water availability is low. However, C<sub>4</sub> species generally show lower photosynthetic rates than C<sub>3</sub> species at cooler temperatures. For example, *Spartina anglica* shows a rate of photosynthesis much lower than many C<sub>3</sub> species at temperatures at or below 10°C (50°F). Importantly though, *S. anglica* has also been shown to maintain rates of photosynthesis, at 5-10°C (41-50°F), equivalent to those of a C<sub>3</sub> grass, *Lolium perenne*, with which it directly competes in British marshes (Dunn *et al.* 1987). Other C<sub>4</sub> salt marsh species found in northwest Europe do not have this ability (Thompson 1991). This metabolic capability of *S. anglica*, which may extend to other *Spartina* species as well, has no doubt significantly contributed to the success of *Spartina* in the cooler temperate regions of Great Britain and the Pacific Northwest.

Species of *Spartina* also possess other physiological adaptations to tolerate drought-stress and high concentrations of salt and other toxins. Both *S. anglica* and *S. alterniflora* have specialized organs on their leaves that secrete excess salts while accumulations of organic compounds in the cell cytoplasm help maintain the osmotic potential to ensure adequate water absorption (Mitsch and Gosselink 1986; Thompson 1991). *S. anglica* has also been shown to restrict the entry of excess quantities of toxic ions into the roots (Rozema *et al.* 1985a); to internally oxidize potential toxins such as iron, manganese, and sulfur (Larher *et al.* 1977; Stewart *et al.* 1979); and to externally oxidize such toxins through the outward diffusion of oxygen from the roots into the interstitial solution (Rozema *et al.* 1985b). Finally, water conservation mechanisms present in cordgrass may also function to reduce the rate at which soil toxins are drawn towards the roots thereby increasing the likelihood of detoxification (Armstrong 1975).

### 3.2 HABITAT REQUIREMENTS OF SPARTINA

Exotic species that are successful in colonizing habitats where they have never previously occurred usually have certain features that increase their fitness, including the abilities to colonize over a wide geographic range, exist over a range of localized environmental conditions, and form a dominant component of their newly colonized habitat (Thompson 1991). Species of *Spartina* that have been introduced in the Pacific Northwest possess these abilities.

Both *S. alterniflora* and *S. patens* have roughly the same native distribution, the Atlantic coast between Canada and Central America. The coastal waters of the Atlantic are considerably warmer than those of the northwest coast of the United States. Thus, in their native range, *S. alterniflora* and *S. patens* are essentially warm water species and the cooler waters of the Pacific Northwest may have prevented initial rapid expansion (ACOE 1992). However, *Spartina* has persisted and, in the case of *S. alterniflora*, is now rapidly spreading in some areas. *S. anglica* evolved in the maritime, temperate climate of the British Isles and thus appears well-adapted to the Pacific Northwest maritime environment.

*Spartina* grasses are dominant members of the intertidal salt marsh community and usually form dense, monospecific stands. Within its native range on the east coast of the United States, *S. alterniflora* dominates the lower intertidal zone and ranges from a maximum of +0.7 m (2.3 ft) above mean high water (MHW) to a minimum of -0.24 m (0.8 ft) below mean low water (MLW) (McKee and Patrick 1988). *S. alterniflora* may also inhabit the upper intertidal zone along with *S. patens*, *Distichlis spicata*, and *Juncus* spp. Variation in distribution of *Spartina* within the intertidal zone may generally be attributed to differences in tidal range or wave energy among locations, and localized biotic or abiotic influences, including interspecific competition, and soil aeration, nutrient, and salinity levels.

*Spartina patens* dominates the middle and upper reaches of salt marshes along the Atlantic coast of North and Central America and may also colonize beaches and sand dunes in the southern one-third of its native range (Silander 1984). A distinct zonation exists where *S. patens* and *S. alterniflora* co-occur and the MHW line typically delineates the boundary between zones (Bertness 1991). *S. patens* is generally restricted to the upper marsh by its limited ability to transport oxygen to its roots through its internal network of aerenchyma. In contrast, *S. alterniflora* appears restricted to lower marsh habitats by competitive displacement from *S. patens*. Removal and transplant experiments in a New England marsh indicated that *S. alterniflora* rapidly invaded higher marsh areas in the absence of *S. patens* (Bertness 1991; Bertness and Ellison 1987).

Like *S. alterniflora* and *S. patens*, *S. anglica* has a wide ecological amplitude and is capable of growing in several marsh zones. However, *S. anglica* appears to tolerate a wider range of environmental conditions than native North American *Spartina* species. In Britain, *S. anglica* inhabits a wider range of intertidal elevations than either of its parent species (*S. alterniflora*, *S. maritima*) (Hill 1990).

Optimal salinity for *S. alterniflora* is 10-20 parts per thousand (ppt). However, it has been shown to tolerate salinities as high as 50-60 ppt during summer droughts (Landin 1990). *S. anglica* tolerates salinities of 5-40 ppt (Aberle 1990). The tolerance of *S. x townsendii* is thought to be similar to that of *S. anglica* (Marchant 1967).

*Spartina alterniflora* in Willapa Bay does not appear to be limited by the same ecological parameters as native populations on the east coast. *Spartina* in Willapa Bay appears able to inhabit a wider tidal range and tolerate higher salinities than in its native habitat. Speculation exists that Willapa Bay populations may have experienced genetic changes that resulted in greater ecological tolerances (ACOE 1992). This phenomenon is not unknown for the genus. The wide ecological amplitude and plasticity exhibited by *S. anglica* is likely associated with increased genetic diversity brought upon by allopolyploidy (Thompson 1991). In addition, studies from North Carolina indicate that extensive genetic divergence has occurred in adjacent subpopulations of *S. patens* across marsh zones resulting in differing morphologic and physiologic traits among zones (Silander 1984; Silander and Antonovics 1979). It is possible that genetic changes in populations of *S. alterniflora* in the Pacific Northwest may have resulted in increased ecological tolerances. However, studies on *S. alterniflora* in the eastern United States found a general absence of genetic differentiation between phenotypically variable populations (Silander 1984). It has also been shown that *S. alterniflora* on the east coast has the ability to colonize both high and low marsh zones and is restricted to low marsh zones by competition from *S. patens* and other high marsh perennials (Bertness and Ellison 1987; Bertness 1991). Therefore, it is also possible that *Spartina* in Willapa Bay, in the absence of interspecific competition, is inherently able to establish and persist over a wide range of salinities and tidal elevations.

In Willapa Bay, *S. alterniflora* has been observed naturally growing between approximately 1.75 m (5.7 ft) and 2.75 m (9.0 ft) above mean lower low water (MLLW) (Sayce 1988). Transplants also survived to within about 1 m above MLLW. *S. alterniflora* in Willapa Bay has established monospecific stands on tidal flats. Some mixing with stands of native species, including *Salicornia virginica*, *Triglochin maritimum*, *Deschampsia cespitosa*, and *Distichlis spicata*, has also occurred at the edges of cordgrass stands, although there appears to be little direct competition between *S. alterniflora* and native salt marsh species (ACOE 1992). *S. alterniflora* in Grays Harbor is currently established within a stand of *Scirpus americanus* and within a second stand of *S. virginica* (ACOE 1992). The Oregon population of *S. patens* in the Siuslaw Estuary is confined to the intertidal marsh ranging in elevation from 1.8 (5.9 ft) to 2.1 m (6.9 ft) above MLLW, comparable to its indigenous east coast tidal position (Frenkel and Boss 1988). It became established in bare areas in the relatively "open" middle marsh community dominated by *D. cespitosa* and *Scirpus maritimus*. *S. anglica* in Port Susan Bay has colonized low intertidal silt or sand tideflats to an elevation 50 cm (1.6 ft) above MLLW and has also established in native brackish marsh dominated by *Scirpus americanus* on sands, and *Scirpus maritimus* and *T. maritimum* on silts. In addition, *S. anglica* has moved into the lower marsh community characterized by *D. spicata* and *S. virginica* (Frenkel and Kunze 1984).

As evidenced by *S. anglica* in Port Susan Bay, *Spartina* species colonize a variety of substrates. *S. alterniflora* can also grow in a broad range of substrates including silt, clay, sand, gravel, and cobble (Landin 1990). *S. alterniflora* colonization, however, may be limited by peat accumulation (Bertness 1988). In Willapa Bay, *S. alterniflora* occurs on both sand and silt substrates. *S. anglica* was also recently observed colonizing gravel beaches on Camano Island (ACOE 1992).

The ability of *Spartina* stems and rhizomes to trap sediments is well-recognized. Sediment accretion increases the elevation of a growing *Spartina* marsh above the surrounding tidal flats, although occasionally compaction may keep pace with accretion. In contrast to the formerly bare, gently sloping flats with shallow tidal channels, fully-developed *Spartina* marshes have steeply sloping seaward edges and deep, steep-sided tidal channels. Once the sediment in a *Spartina* marsh accretes to the level of the higher marsh areas, *Spartina* stands may be invaded and displaced by native species such as *Salicornia* spp. and *D. spicata*. Apparent displacement of *S. alterniflora* by native species has been observed in Willapa Bay (ACOE 1992).

### 3.3 REPRODUCTION

*Spartina* species present in the Pacific Northwest are rhizomatous perennials that exhibit vigorous vegetative reproduction to form dense, monospecific stands. All species in Washington have the ability to reproduce sexually, however, successful reproduction by seed is occurring in only some Washington populations. Sections 3.3.1 and 3.3.2 further describe relevant reproductive characteristics of *S. alterniflora*, *S. patens*, and *S. anglica*, and their Washington populations. Environmental factors that influence success of sexual reproduction are also discussed.

#### 3.3.1 Sexual Reproduction

All species of *Spartina* present in Washington are capable of reproducing sexually. However, seedling reproduction has only been documented for populations of *S. alterniflora* in Willapa Bay and populations of *S. anglica* in Port Susan Bay (Aberle 1990). Inflorescence production has been observed for the population of *S. patens* on Hood Canal, although seed viability is thought to be low (Frenkel and Kunze 1984). Riggs (1992) found no evidence of flowering or seed production in populations of *S. alterniflora* in Padilla Bay in 1991. Flowering in the recently confirmed infestation of *S. alterniflora* in Grays Harbor was observed this past summer. However, pollen viability and success of seed set were not investigated (ACOE 1992). Factors implicated in the onset and success of sexual reproduction in *Spartina* include seed source, photoperiod, soil temperature, salinity, tidal range, and herbivory (Seneca 1974a, 1974b; Somers and Grant 1981; Marks and Mullins 1990; Bertness *et al.* 1987).

Onset of sexual reproduction may also require accumulation of sufficient underground biomass. Examinations of below-ground plant productivity in newly created or colonized

systems indicates plants are less likely to produce viable seed until some critical level of below-ground production is achieved (ACOE 1992). Thus, recently established colonies of *Spartina* may devote the majority of resources to underground biomass to ensure colony persistence. Once some critical biomass level is attained, levels of sexual reproduction may increase to direct resources toward establishment of new colonies.

### 3.3.1.1 Phenology and Seed Production

*Spartina alterniflora* in Willapa Bay flowers from early August through October and sets seed in late October (Sayce 1988). Timing of stigma and anther emergence in the bisexual flowers indicate that *Spartina* in Willapa Bay is primarily cross-pollinated. Populations of *S. alterniflora* in the eastern United States are largely cross-pollinated (Somers and Grant 1981). The phenology of *S. patens* and *S. anglica* populations in Washington is not known. However, *S. patens* in New England marshes begins flowering in early July and most flowers emerge before August (Bertness *et al.* 1987). The main period of flowering for *S. anglica* in Britain is July to November, a period longer than most British salt marsh species, but flowering may continue until February (Mullins and Marks 1987).

Sayce (1988) noted that flowering of *S. alterniflora* in Willapa Bay was sporadic among clumps and occurred primarily in clumps of medium to tall shoot height and medium to low shoot density, and that the variation in shoot height and density appeared to be independent of elevation in the marsh. She further observed that onset and extent of flowering can vary considerably from year to year. In cool summers, flowering, production of viable pollen, and successful seed set were greatly restricted.

Temperature likely affects successful sexual reproduction of *Spartina* in the Pacific Northwest. Both temperature and photoperiod have been shown experimentally to influence occurrence and time of flowering in *S. alterniflora* and *S. patens* in the eastern United States (Seneca 1974a; 1974b). Marks and Mullins (1990) also suggested that low soil temperature (3-13°C or 37-55°F) and hypersaline soil conditions (due to lack of tidal exchange) during spring and early summer delayed flowering and prevented seed production in British *S. anglica*.

Marked differences have been observed in inflorescence and seed production, and seed viability of *S. anglica* in different zones in British marshes: pioneer (low), transitional (middle), mature (high), and invaded (most landward) (Marks and Truscott 1985). An interesting finding was the poor production of viable seeds in the mature marsh zone, which had prolific vegetative growth, large inflorescences, and many floral spikelets. Only 4.8% of the mature marsh spikelets contained seed while 88% of the spikelets on the smaller plants of the transition zone set seed. Flowers from all zones produced similar levels of viable pollen. Successful seed production was closely related to the date of inflorescence emergence. The majority of inflorescences in the pioneer and transitional zones emerged by mid-August. Most inflorescences in the mature marsh, however, did not emerge until September and failed to set seed. Subsequent findings suggest that high marsh zones present in estuaries

with large tidal ranges and without lengthy periods of tidal submergence are subject to depressed soil temperature and hypersaline conditions which delay inflorescence production and limit sexual reproductive capability. Studies on *S. alterniflora* in the United States also found that hypersaline conditions induce nitrogen deficiency and may consequently reduce growth and lead to suppression of sexual reproduction (Cavalieri and Huang 1981; Jefferies *et al.* 1979).

Herbivory has also been shown to directly impact seed production in eastern populations of *S. patens* and *S. alterniflora*. The grasshopper, *Conocephalus spartinae*, feeds on flowers and seeds of both *Spartina* species. The planthopper, *Prokelisia marginata*, consumes flowers of *S. alterniflora*. In addition to destroying seeds directly, these consumers also markedly affect the timing and reduce the frequency of flowering. In particular, such predation drastically reduces the number of male flowers, which could result in pollen limitation of seed set (Bertness *et al.* 1987). In addition, several species of insect stem-borers and sap-sucking leaf feeders have been shown to reduce seed set and, at high insect densities, kill *S. alterniflora* plants along the Gulf Coast (Strong 1990). However, none of these insect species are present in Washington, and it is unknown if any insect species that could potentially control *Spartina* populations are associated with local populations.

Thus, total seed production within a population of *Spartina* is the result of numerous factors, including number of inflorescences, number of spikelets per inflorescence, pollen viability, and date of inflorescence emergence. These are, in turn, influenced by both genetics and environmental elements, including tidal elevation, temperature, photoperiod, salinity, and nutrient levels, and herbivory.

### 3.3.1.2 Seed Germination and Seedling Establishment and Survival

Viability of *S. alterniflora* seeds from Willapa Bay is variable, but generally low. Sayce (1988) measured a germination rate of 0.04% for *S. alterniflora* seeds gathered from several sites in Willapa Bay. Viability of seeds determined by the indication of living tissue upon staining has also been measured at two other sites in the Bay. Seeds from the first site (near Willapa National Wildlife Refuge Headquarters) had an average viability of 4.3%; seeds from the second (in the Riekkloa Unit of the Willapa National Refuge) had an average viability of 1.9%. The lower viability of seeds from the second site may have resulted from an extensive infestation of ergot (*Claviceps purpurea*) (pers. comm., J. Friebaum 1992). This fungus has effectively prevented viable seed set in infested populations of *S. anglica* in Britain by infecting all the embryos in an inflorescence (Thompson 1991). No data are available on germination rates of seeds from other *Spartina* populations in Washington.

Germination rates for *S. anglica* in Britain range from 0.6-5.2% and variation exists in germination success and onset of seed germination among different marsh zones (Marks and Mullins 1990; Marks and Truscott 1985).

Temperature, soil moisture, and salinity have been shown to affect germination in *Spartina*. Seeds of *S. alterniflora* in San Francisco Bay do not germinate until late winter or early spring when soil salinities drop and water temperatures increase (Calloway and Josselyn 1992). Germination in eastern populations also occurs during spring and early summer. Salinities decrease during this period due to seasonal flooding (Landin 1990). Laboratory studies have also shown that seeds of *S. alterniflora* cannot withstand long periods ( $\geq 40$  days) of dry, warm ( $\geq 21^{\circ}\text{C}$  or  $\geq 70^{\circ}\text{F}$ ) conditions (Mooring *et al.* 1971). Similarly, experiments on *S. anglica* indicated that long-term storage ( $\geq 60$  days) at warm temperatures ( $\geq 15^{\circ}\text{C}$  or  $\geq 59^{\circ}\text{F}$ ) delayed germination, and low temperature storage ( $5^{\circ}\text{C}$  or  $41^{\circ}\text{F}$ ) for the same period promoted germination (Marks and Truscott 1985). In addition, under conditions of adequate moisture and salinity, germination of *S. anglica* seeds was shown to occur more rapidly at  $20^{\circ}$  than  $10^{\circ}\text{C}$  (or more rapidly at  $68^{\circ}$  than  $50^{\circ}\text{F}$ ).

*Spartina* seeds are apparently adapted to germinate in freshwater to brackish conditions. High salinities have been shown to inhibit germination. Germination in *S. anglica* seeds was reduced by initial moistening with salt water (Marks and Truscott 1985). *S. alterniflora* germination was also inhibited by high salinities ( $\geq 4\%$  NaCl by weight) (Mooring *et al.* 1971). Saline conditions were also shown to impact germination of *S. alterniflora* seeds from San Francisco Bay (Calloway and Josselyn 1992).

Neither *S. alterniflora* or *S. anglica* appear to develop long-term seed banks. Laboratory studies found that viability of *S. alterniflora* seeds from the eastern United States was approximately eight months (Mooring *et al.* 1971). Hill (1984) determined seeds of *S. anglica* in Britain are viable for only a single growing season.

Seedling establishment is variable in both natural and introduced populations of *Spartina*. Sayce (1988) and Calloway and Josselyn (1992) noted variations among years in seed output and seedling establishment in *S. alterniflora* populations. Bursts of seedling establishment followed by periods of coalescence have been observed in British populations of *S. anglica* (Hill 1984; Gray *et al.* 1990). High rates of seedling establishment in *S. alterniflora* have been linked to high seed production and germination rates (Calloway and Josselyn 1992), which are themselves influenced by a complex of environmental factors. Gray *et al.* (1990) suggested several factors that may be responsible for spatial and temporal variations in the seedling establishment in British *S. anglica* populations including: genetic controls, the accretion of sediments within the colony to some threshold elevation, and natural variations in tidal cycles.

Once seedlings are established, their survival appears to be primarily affected by competition with other plants. Survival of *S. alterniflora* seedlings in a New England salt marsh was found to be limited in *Spartina* monocultures due to shading from adult plants, but was high in natural and created openings (Metcalf *et al.* 1986). Thus, seedling establishment appears to be of little importance in the maintenance of existing stands, but seedling recruitment does appear to play a role in the recolonization of disturbed areas, initial colonization of bare

areas in stands dominated by other species, and in the formation of new marshes on tidal flats.

### 3.3.2 Vegetative Reproduction

*Spartina* species reproduce vigorously by lateral spread of underground rhizomes and above-ground tillers and subsequent development of individual shoots with deep, adventitious roots. Laterally growing rhizomes intermingle, which results in the formation of characteristic circular patches or clones. Clones ultimately coalesce to form dense, monospecific stands, often displacing native salt marsh species in the process. Plants may also establish from fragments of rhizomes dispersed to new colonization sites.

## 4.0 BIOLOGY OF INFESTATION

Establishment and persistence of vigorous colonies of *Spartina* in areas previously not inhabited by the species depend on: 1) dispersal of seeds or vegetative propagules to the site; 2) establishment of rooted plants; and 3) successful competition with other species at the site.

### 4.1 DISPERSAL AND ESTABLISHMENT

Unexploited potential habitat for *Spartina*, such as unvegetated mudflats and areas vegetated with less vigorous competitors, is widespread in temperate areas, as shown by its distribution around the world. Dispersal of seeds or living rhizomes to remote sites and their establishment is often the primary factor controlling the regional spread of *Spartina* infestations. For example, Calloway and Joselyn (1992) indicate that lack of dispersal is the main factor preventing *S. alterniflora* from becoming established in new areas in San Francisco Bay. Rapid bursts of colonization of *S. anglica* in southern England may reflect occurrence of favorable years for seed production and seedling establishment, or opening of habitat by change in elevation of mudflats (Gray *et al.* 1990).

The most prevalent form of *Spartina* dispersal is by humans, who have intentionally planted various species throughout the world. In nature, seeds and dislodged rhizome fragments are most often dispersed to new sites through water-borne transport. Dispersal distances via water-borne transport are related to patterns of currents and to magnitude of tidal fluctuations. Transport may also be accomplished by animals, especially waterfowl or other birds that ingest seeds or rhizomes. Ranwell (1967) noted that swans and other waterfowl consume large quantities of *S. anglica* seeds in British marshes.

The onset of flowering and production of viable seed can dramatically increase spread of *Spartina* to new sites. Thus, rate of *S. alterniflora* spread in Willapa Bay increased once seedling reproduction occurred (Aberle 1990). Spread of the infertile hybrid *S. x townsendii* was slow in Britain because its reproduction was limited to vegetative propagation. However, the fertile *S. anglica*, which arose from chromosome doubling in *S. x townsendii*, spread rapidly, presumably through seed dispersal (Thompson 1991). The dissemination of

rhizome fragments or other vegetative propagules enhances the ability of *Spartina* clones to establish at new sites. Although not certain of the role of seed and vegetative propagule dispersal in establishment of new colonies, Frenkel and Boss (1988) surmised that new clones of *S. patens* in Siuslaw Estuary, Oregon, could be established from dispersal of rhizome fragments capable of developing new plants after fragmentation. The role of vegetative propagules in establishing new *Spartina* colonies in Washington is unknown.

## 4.2 PERSISTENCE AND SPREAD

### 4.2.1 Growth and Rate of Spread

*Spartina* species are strongly rhizomatous, forming solid and sometimes extensive mats of vegetation. *Spartina* species produce deep roots that are effective in stabilizing soils. *S. alterniflora* roots have been found to a depth of 0.7 m in Willapa Bay (Aberle 1990) and *S. anglica* roots extend to a depth of 1.2 m (Way 1987). An expanding stand is most vigorous and dense just inside its periphery. In the center, buildup of organic debris often leads to anaerobic conditions and decreased vigor (Frenkel and Boss 1988). Cordgrasses are deciduous; stems die back at the end of each growing season. Vegetative reproduction is by underground rhizomes or by side shoots (tillers) arising at ground level. Rhizomes of *S. anglica* develop during winter while the above-ground stems are not growing (Goodman 1960). This strategy enables massive shoot production to begin with the advent of warm temperatures. Roots and rhizomes can persist for many years after death of above-ground culms.

In suitable habitats, species of *Spartina* are capable of phenomenal rates of growth. Lee and Partridge (1983) measured maximum rates of lateral spread of *S. anglica* in New Zealand at 5.3 m/yr (17.4 ft/yr). Single offsets of *S. alterniflora* in New Zealand planted at 10-meter (33-foot) intervals in an area of 2428 m<sup>2</sup> (0.6 acre) coalesced to form a solid mat in only six years (Bascand 1970). In the Siuslaw Estuary in Oregon, Frenkel and Boss (1988) found that *S. patens* expanded at an exponential rate from a total area of less than 90 m<sup>2</sup> (0.02 acre) in 1929 to an area of approximately 3000 m<sup>2</sup> (0.74 acre) in 1980. In recent decades they found rates of about 200 m<sup>2</sup>/yr (0.05 acre/yr). They surmised that initial rates of expansion were limited by lack of inoculum and that ultimately spread of colonies will be limited by availability of suitable habitat. Populations of *S. anglica* in Britain exhibit lateral growth rates between 0.3 m/yr (1 ft/yr) (Chater and Jones 1957 cited in Thompson 1991) and 0.64 m/yr (2.1 ft/yr) (Hubbard 1965). In Willapa Bay, lateral growth of rhizomes in individual *S. alterniflora* clones has been measured at 0.5 m/yr (1.6 ft/yr) (Sayce 1988) and, in Padilla Bay, 1.1-1.7 m/yr (3.6-5.6 ft/yr) (Riggs 1992).

Among Washington populations of *Spartina*, rates of spread have increased in Willapa and Port Susan Bays in recent years, probably due to the occurrence of sexual reproduction in these populations (Aberle 1990). Cooler temperatures in the Pacific Northwest may have kept the populations in check until relatively recently. Low soil temperature has been shown to delay or suppress flowering and reduce seed production in *Spartina* (Marks and Mullins

1990; Seneca 1974a, 1974b; Cavalier and Huang 1981; Jefferies *et al.* 1979). Sayce (1988) also noted increased plant vigor and inflorescence production of *S. alterniflora* in Willapa Bay during warmer years. However, large amounts of sediment have been introduced into embayments in Willapa which decreased water depths and may have resulted in corresponding increases in water and soil temperatures. A study comparing distributional changes and changes in water temperature data would test this hypothesis (ACOE 1992).

Within individual marshes, *Spartina* typically exhibits distinct zones of varying morphology (Marchant 1967; Ranwell 1972; Marks and Truscott 1985; Hill 1984; Silander 1984; Thompson 1990). Variation in vegetative growth has also been observed among populations of *S. anglica* (Hill 1984) and *S. alterniflora* (Reindenbaugh 1983) across marsh zones. Marks and Mullins (1984, 1990) identified four zones within a British *S. anglica* marsh with varying shoot density, height, vigor, seed/spikelet production, seed viability, and germination. Tall, high-vigor forms of *S. alterniflora* are found along tidal creeks and shorter, low-vigor forms occur inland in more waterlogged conditions (Kirby and Gosselink 1976 cited in Mendelssohn and McKee 1988). A number of environmental factors have been shown to affect growth and productivity of *Spartina*, including soil drainage and associated changes in sediment redox potential, nitrogen concentrations, soil temperature, salinity, and sulfide concentrations. Genetic controls have also been implicated from observations of plants grown in common gardens (Anderson and Treshow 1980; Hill 1990; Silander and Antonovics 1979) and isozyme studies (Silander 1984).

Soil drainage conditions and nitrogen and salinity levels are thought to influence occurrence of tall, short, and medium forms of *S. alterniflora* (Mendelssohn and Seneca 1980; Mendelssohn *et al.* 1981; Howes *et al.* 1986), although Mendelssohn and McKee (1988) found that soil salinity was not a significant factor in limiting growth. ACOE (1992) found differences in plant morphology (stem density, stem height, plant vigor) within populations established on silt and sand in Willapa Bay, but these differences did not appear to be directly correlated with any easily observable environmental parameter, including soil salinity and elevation. Growth rates and productivity typically change over time at different points within a colony, as sediments are trapped and soil drainage conditions change.

#### 4.2.2 Competition

*Spartina* species are aggressive colonizers that, within their limits of environmental tolerances, often outcompete other salt marsh species. In the Pacific Northwest, *Spartina* stands are encroaching into stands of native low and high marsh vegetation through vegetative spread. However, spread of *Spartina* has been shown to be limited by interspecific competition. *S. anglica* in Dutch marshes is outcompeted by *Puccinellia maritima* on silty and sandy soils of the upper and middle marsh zones. The earlier and more rapid seasonal development of *Puccinellia* shoots results in shading of developing *Spartina* shoots and reduces the competitive ability of *Spartina* (Scholten and Rozema 1990). In addition, *S. alterniflora* in New England marshes was shown to be restricted to low marsh zones by direct competition with high marsh species (Bertness 1991; Bertness and Ellison

1987). Thus, once sediment accretes in a *Spartina* marsh to a level critical for growth of higher marsh species, *Spartina* may be outcompeted. The apparent displacement of *S. alterniflora* in Willapa Bay by the native high marsh species *Salicornia virginica*, *Deschampsia cespitosa*, and *Distichlis spicata* has been observed (ACOE 1992).

### 4.2.3 Dieback

"Dieback" refers to recession or senescence of patches of *Spartina*. Symptoms include death of rhizomes, soft-rotting of rhizome apexes, production of fewer and weaker tillers, general yellowing, and death of plants (Goodman 1960, Goodman and Williams 1961). It typically occurs in shallow depressions or "pans" within stands of the grass, or along the edges of the stands. Diebacks can be small, localized phenomena or may be extensive. Localized dieback has been observed in *S. alterniflora* populations in Willapa and Padilla bays (ACOE 1992; Riggs 1992). More rapid and extensive decline due to diebacks has been found in *S. townsendii/anglica* marshes along the southern coast of England since about 1960 (Tubbs 1984). For example, the area covered by *Spartina*-dominated marshland in Holes Bay was reduced from 63% of the total intertidal area of the bay in 1924 to 29% of the intertidal area in 1980 (Gray and Pearson 1984). In inland locations in Louisiana, *S. alterniflora* dieback has resulted in formation of shallow, unvegetated ponds and significant land loss (Mendelssohn and McKee 1988). Dieback is a "natural" phenomenon, in which *Spartina* initiates its own destruction by altering drainage and sedimentation patterns, leading to formation of anaerobic, reducing soils (Gray *et al.* 1990). Raybould *et al.* (1991b) suggested the rapid, extensive decline of *S. anglica* in Britain may be a function of the species' low frequency of allelic recombination. Low rates of genetic recombination and mutation contribute to genetic uniformity within stands and make populations more susceptible to environmental changes or attack from pests and pathogens.

The most frequently cited causes of dieback are soil waterlogging and wave action. Numerous other possible causes of *Spartina* dieback have been suggested, including excessive salinity, coverage by vegetative debris, lack of available iron, hydrogen sulfide toxicity, oxygen deficiency in roots, change in tidal regime, and pollution (Smith 1970 cited in Linthurst and Seneca 1980; Doody 1984). Some studies have shown that soil salinity and pH (Mendelssohn and McKee 1988) or oxygen starvation in rhizomes (Goodman and Williams 1961) are not significant factors leading to diebacks.

Dieback in "pans" is most frequently induced by extremely reducing conditions caused by extended periods of soil waterlogging and lack of tidal flushing, particularly at warm temperatures. This leads to anaerobic conditions in the soil and accumulation of significant amounts of free sulphide, beyond the range that normal growth of *Spartina* can be supported, resulting in stunting or death of plants (Goodman and Williams 1961, Mendelssohn and McKee 1988, King *et al.* 1982, Delaune *et al.* 1983). Sulphide may have a direct toxic affect on plants and may also interfere with ammonia uptake (Mendelssohn and McKee 1988).

Substrate type may influence the occurrence of dieback. ACOE (1992) noted that dieback areas were more common on silt than on sand substrates in Willapa Bay. Goodman *et al.* (1959) found that dieback in populations of *S. townsendii* in Britain occurred on particularly soft, wet substrates with fine particles. Lower incidence of dieback in sandy substrates may be related to their greater porosity and oxygen exchange ability. Indirect evidence suggests that dieback may sometimes be associated with cessation of accretion in stands of cordgrass (Goodman 1960).

#### 4.2.4 Herbivores and Pathogens

Herbivory and pathogen infestations have also been shown to affect growth and spread of *Spartina* by impacting seed production and causing death of individual plants (Bertness and Ellison 1987; Strong 1990; Thompson 1991). However, none of the insect herbivores which are associated with *Spartina* populations in the eastern United States are present in Washington, and it is unknown if any insect species that could potentially control *Spartina* in Washington are associated with local populations. In addition, the fungus, *Claviceps purpurea*, has been observed growing on *S. alterniflora* in Willapa Bay and infestations may have resulted in lower seed viability (pers. comm., J. Friebaum 1992).

## 5.0 INFORMATION AND RESEARCH NEEDS

Several studies have been completed on the distribution, biology/ecology, and control of *Spartina* in Washington. Riggs (1992), Aberle (1990), Sayce (1988), and Frenkel and Kunze (1984) provide information on the distribution, biology, and ecology of Washington *Spartina* populations. In addition, the Army Corps of Engineers has recently completed a study characterizing several *Spartina* communities in western Washington (ACOE 1992). Relevant information from these studies was incorporated into this report.

Updated information on the extent of *Spartina* populations in Washington is required to accurately assess current distribution and potential for spread. Additional studies are also necessary to more fully understand the impacts of infestations and determine feasibility of control measures. Suggestions for further information and research include:

- **Surveys of intertidal elevations and substrate types inhabited and salinity levels tolerated by *Spartina* in Washington.** This information is useful to determine potential for spread and feasibility of various control measures for a given area.
- **Expanded reproductive studies** in the various infestation areas (Willapa Bay, Padilla Bay, Port Susan Bay, Skagit Bay, Hood Canal, Grays Harbor, etc.), including observations on importance of vegetative propagules in development of new colonies, continued monitoring of occurrence and timing of flowering, measurements of seed viability and seedling reproduction, and determination if differences exist in flowering phenology and seed production across marsh zones. This information will be useful to assess potential for spread and to determine method(s), timing, and intensity of control efforts for a given area.

- **Monitoring the occurrence of dieback and determining the environmental conditions under which it occurs.** Control measures could be designed to approximate conditions in which diebacks occur.
- **Long-term monitoring of dieback areas** to determine whether the areas are recolonized by *Spartina* or native species, or whether a return to pre-invasion conditions occurs.
- **Comparisons of growth and response to control methods among populations of *Spartina* species in Washington.** This information would enable populations that are especially vigorous or particularly susceptible to a given control method to be targeted for priority control efforts.
- **Studies on the interactions of *Spartina* species** with existing intertidal vegetation, including native and introduced eelgrasses.
- **Studies on the algal, and insect, benthic invertebrate, fish, and wildlife fauna associated with *Spartina* in Washington** to determine the habitat value of *Spartina* in Washington, the impacts to aquaculture species and resident and migratory fish and wildlife from infestations, and any existing opportunities for potential biological control of infestations.
- **Long-term productivity studies** to determine the potential contribution of *Spartina* to food chains in Pacific Northwest estuaries.
- **Studies of host specificity of ergot fungus and possible use to control seed production.**

## 6.0 REFERENCES

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## APPENDIX

Appendix. Summary of distribution and selected biological and ecological characteristics for *Spartina* species present in Washington. Characteristics of *Spartina* in its native habitat and Washington are described. Question marks indicate the response is speculative because limited data are available on the characteristic.

NATIVE HABITAT

Characteristic	<i>S. alterniflora</i>	<i>S. patens</i>	<i>S. anglica</i>
Native distribution	Atlantic and Gulf coasts of North and Central America	Atlantic and Gulf coasts of North America	Originated as a hybrid in southern England
Ecological tolerance (tidal range, salinity levels, substrate type)	Wide	Wide	Wider than <i>S. alterniflora</i> or <i>S. patens</i>
Intertidal zone(s) typically inhabited	Low	Middle to high	Low to high
Salinity tolerance	10-60 parts per thousand (ppt)	10-60 ppt	5-40 ppt, possibly higher
Substrate types colonized	Silt, sand, clay, gravel, cobble	Silt, sand, clay, gravel, cobble	Silt, sand, clay, gravel, cobble

WASHINGTON

Characteristic	<i>S. alterniflora</i>	<i>S. patens</i>	<i>S. anglica</i>
Locations of infestations	Willapa, Padilla, Thomdyke, and Sequim Bays; Grays Harbor; Kala Point; Copalis River Estuary	Dosewallips River delta	Port Susan and Skagit Bays; Whidbey and Camano Islands
Ecological tolerance of Washington populations compared to native populations	Possibly wider than native	Unknown	Unknown
Intertidal zone(s) inhabited	Low to high	Middle to high?	Low to high?
Salinity tolerance	Willapa Bay <i>Spartina</i> thought to tolerate higher salinities than native populations	Unknown	Unknown

Appendix table cont.

Characteristic	<i>S. alterniflora</i>	<i>S. patens</i>	<i>S. anglica</i>
Substrate types colonized	Silt, sand, mud (clay, silt)	Unknown	Gravel, silt and sand probable, but not specified
Occurrence of flowering	Observed in Willapa Bay and Gray Harbor. Not occurring in Padilla Bay. Not investigated at other locations.	Documented in Dosewallips River delta	Observed in Port Susan Bay. Not investigated at other locations.
Phenology	Investigated only in Willapa Bay. Flowering: August-October; seed set: late October	Unknown	Unknown
Occurrence of successful seedling reproduction	Documented in Willapa Bay. Not occurring in Padilla Bay. Not investigated at other locations.	Unknown	Documented only in Port Susan Bay. Not investigated at other locations
Seed viability	Investigated only in Willapa Bay. Ranged from 0.04% - 4.3%	Exact values unknown, but appears low	Unknown
Growth rates within colonies	Willapa Bay: 0.5 m/yr; Padilla Bay: 1.1-1.7 m/yr. Not investigated at other locations.	Unknown	Unknown
Occurrence of dieback	Localized dieback observed in Willapa and Padilla Bays. Not investigated at other locations.	Unknown	Localized dieback documented in Port Susan Bay. Not investigated at other locations.
Current relative rate of spread	Rapid in Willapa Bay. Slow in Padilla Bay. Unknown for other locations.	Appears slow	Rapid in Port Susan Bay. Unknown for other locations.
Potential for dispersal and establishment at new locations	High from Willapa Bay. Low from Padilla Bay. Unknown for other locations.	Appears low	High from Port Susan Bay. Unknown for other locations.