Improving Management Practices for Invasive Cordgrass in the Pacific Northwest:

A Case Study of *Spartina anglica*

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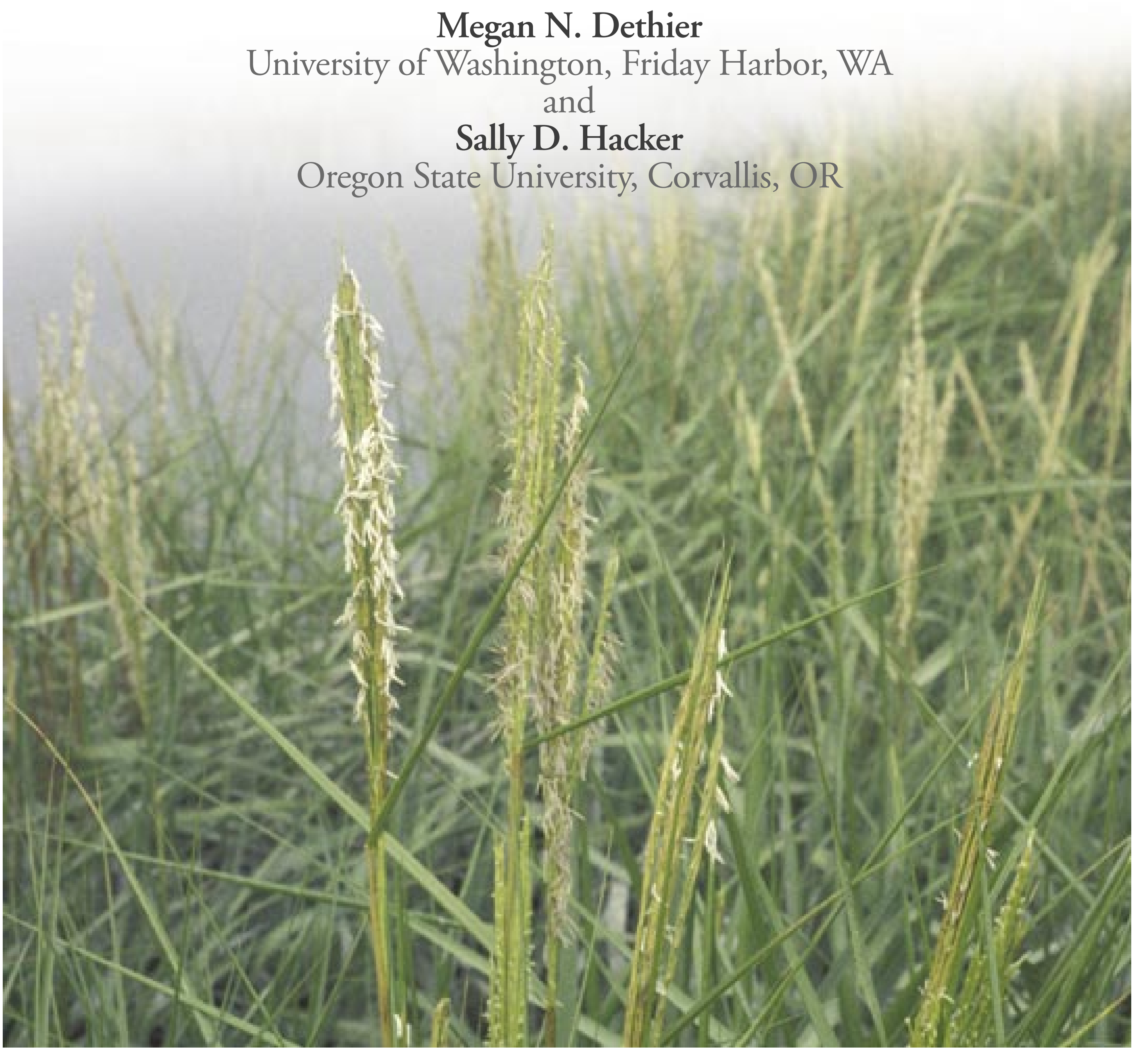

Executive Summary

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Invasive species can radically alter the landscape and crowd out native plants and animals — a problem that costs the United States more than $100 billion each year. Washington state wrestles with dozens of aquatic invasive species including several cordgrasses in the genus *Spartina*. *S. alterniflora* was introduced into Willapa Bay about 100 years ago and has colonized over 6000 hectares of previously unvegetated mudflats (Davis et al. 2004). *S. anglica* was introduced to the Puget Sound area from England in 1961 and, since then, it has spread over 3300 hectares of estuarine habitat in at least 73 sites in the region. Both species cause major changes in the ecosystem by transforming the physical habitats they invade, often making them less suitable for native organisms. *S. anglica* presents an unusual challenge for land managers because it is remarkably versatile and resilient. It is capable of establishing in different habitat types, an uncommon feature among marsh plants; it is also very effective at producing and dispersing seeds and resisting mechanical removal by storing a reserve of nutrients in large underground root masses.

This booklet describes *S. anglica*'s ecology and it is aimed at uncovering the most important factors in developing a control strategy. It describes the results of manipulative experiments that tease apart the timing of seed production and germination as well as physical factors that most contribute to *S. anglica*'s success. This booklet also links data from previous control efforts by the Washington State Department of Agriculture (WSDA) with the basic physiology of the plant and makes recommendations for developing future management plans. Lessons learned from work with *S. anglica* often may apply to control of invasive *S. alterniflora* because of similarities in the biology of these two species.

The methods used in this survey of *S. anglica* include a comprehensive literature review of the plant's reproductive physiology, distribution patterns, and reported responses to treatment efforts in the United States and elsewhere, as well as results of field experiments. We studied the invasion of *S. anglica* in the diverse habitats it occupies: low-salinity marshes, high-salinity marshes, mudflats, and cobble beaches. We measured to what extent it invades each of these different types of shorelines and the various tide levels within them. We quantified the modifications that cordgrass causes in each, i.e., how it "engineers" its physical habitat through sediment accretion and changes in sediment oxygen and salinity. We studied the degree of difficulty of cordgrass removal in each habitat type, including how readily it recovers from human attempts to manage it. We also studied how readily *S. anglica* colonizes each habitat type via seeds, and how rapidly seedlings grow and spread under these different physical conditions.

Several key findings pertain to the ecology of the plant:

- *S. anglica* germinates new seedlings and sprouts new shoots from established plants in early spring. It undergoes rapid photosynthesis and growth from May to August. It flowers mostly in July and sets its seed mostly in September. Most of its above-ground biomass dies off in the early fall.
- Physical conditions in low-salinity marshes and mudflats are best suited to seed production, germination, survival, and spread of *S. anglica*. High-salinity marshes and cobble beaches are less favorable for spread and establishment.
- *S. anglica* dramatically alters the structure of its physical habitat:
    1. Its roots stabilize loose sediments and its tall and dense shoots slow the movement of water through them.
    2. Sediment carried by the water builds up beneath the blades, raising the surface of the marsh.
    3. Specialized tissue in its blades transports oxygen from the surface down into the roots, making previously anoxic sediment more oxygenated.
    4. Rapid growth reduces competition from native plants and increased shade slows evaporation from the marsh surface, making the sediment in a *S. anglica* bed less saline than nearby unvegetated areas.
- The large biomass and extensive underground root system of an established *S. anglica* meadow has a high storage capacity, which enables the meadow to survive through the winter and makes it resistant to above-ground mechanical control such as mowing.

These ecological characteristics have clear implications for management strategies:

- A combination of mechanical efforts and herbicide sprays applied consistently every year for at least 3 to 4 years is the most successful and cost-effective approach to killing the plant.
- Low-salinity marshes have optimal conditions for the survival and spread of cordgrass; this means that they are the most challenging habitat type for management because the meadows are so resilient, but also that control of cordgrass there is critical for reducing the overall invasion.
- Control efforts should be timed to match *S. anglica*'s reproductive patterns. Spraying and mowing early in the growing season (July) is more effective in reducing plant growth and seed production than doing so late in the season (after mid-August).
- Long-term control efforts require vigilance about removing seedlings, since seeds disperse well and can start new clones readily.
- Long-term restoration efforts may involve "undoing" physical habitat changes, especially in mudflats, where the limited wave action may allow modified physical habitat to persist.

Any long-term strategy for controlling *S. anglica* in Puget Sound must involve both a concerted attempt to reduce the impact of the plant in low-salinity marshes and to monitor satellite populations that can act as "stepping-stones" to other suitable habitats. Efforts should be consistent (every year), timed early in the growing season, and rely on a combination of mechanical methods and herbicide sprays. Understanding the biology of the plant and the ecology of its reproduction is crucial to the success of long-term management.

Introduction

Spartina anglica is an invasive, perennial marsh grass capable of transforming the habitats it invades. Commonly called English cordgrass, it was deliberately introduced to Puget Sound, Washington, from England in 1961. *S. anglica* arose through the hybridization of two species (*S. alterniflora* from eastern North America and *S. maritima* from England) and became fertile after a chromosome-doubling event (Raybould et al. 1991, Ferris et al. 1997, Ayres and Strong 2001). English cordgrass was also deliberately introduced into temperate estuaries of the US, UK, Netherlands, France, China, New Zealand, mainland Australia, and Tasmania, mainly for reclamation purposes, cattle fodder, and stabilization of dikes and sea walls (Ranwell 1967).

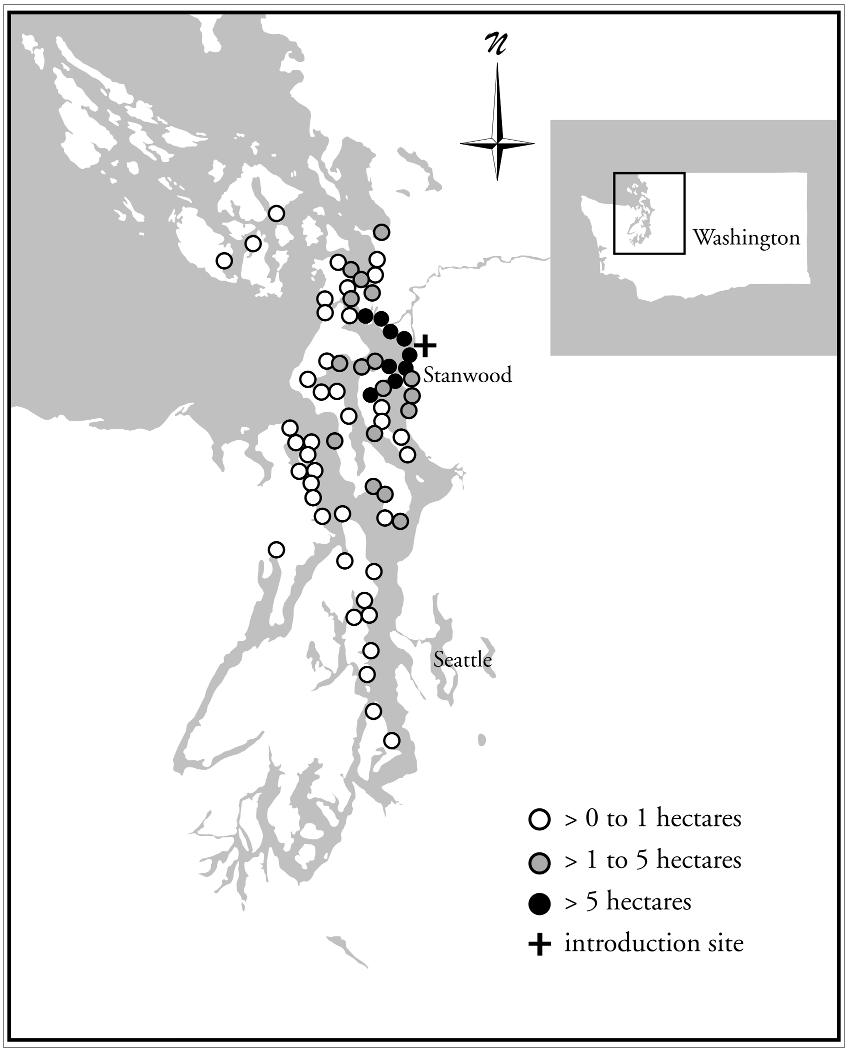

Figure 1. Map showing *S. anglica* invasion sites (circles) and introduction site (plus) within Puget Sound, WA (Source: Hacker et al. 2001).

Coverage of *S. anglica* in the Puget Sound region increased steadily from 1961 until formal removal efforts by the State of Washington began in the mid-1990s. By 1997, *S. anglica* had invaded at least 73 sites and affected approximately 3300 hectares (ha) with major ecosystem-level consequences (Fig. 1, Hacker et al. 2001). The greatest number and most severely impacted sites occur in the vicinity of the original transplant site (northern Port Susan Bay and the Skagit area), but some populations were reported in south-central Puget Sound and as far north as the Fraser Delta (Williams 2004). Because seed production and dispersal from established populations are difficult to control, new infestations are likely to be an ongoing management challenge.

S. anglica can invade a wide variety of habitats – an unusual feature for marsh plants, which tend to be specialists to one environment. The habitats include: low-salinity and high-salinity marshes, which are dominated at most intertidal elevations by native plants; mudflats, which are unvegetated at lower levels but contain many animals used as food by shorebirds and other organisms; and cobble beaches, which are higher-energy habitats, sometimes containing sparse marsh vegetation high on the shore but with unvegetated mud low on the shore. Much *S. anglic*a is found on low-salinity marshes; over 700 ha were covered in 1997 (Fig. 2), and these invaded areas are often solidly covered by the cordgrass. It is especially abundant at the mouths of the Stillaguamish and Skagit rivers, where it has outcompeted large flats of native marsh dominated by *Scirpus* spp. and *Carex* (See Table 1 for scientific species names).

In contrast, *S. anglica* is less successful at establishing in native marshes of higher salinity (Fig. 2). In these, it primarily colonizes tidal channels and the lower limits of the marsh and is less effective at outcompeting native vegetation (dominated by *Distichlis, Salicornia,* and *Triglochin*). Only 450 ha of high-salinity marsh habitat were occupied in the 1997 survey, and the plant did not usually spread beyond the "fringe" areas of tidal channels.

Mudflats are the habitat type with the most affected area, over 2000 ha (Fig. 2), although the populations on the flats may be relatively sparse. In these, *S. anglica* colonizes unvegetated areas on the mid- to upper shore and spreads rapidly. *S. anglica* occupies a relatively small area (about 10 ha) of higher energy beaches with a mix of cobble, gravel, and sand (Fig. 2), where it tends to outcompete seaweeds and the already small populations of native marsh plants (primarily *Salicornia* and *Triglochin*).

The purpose of this booklet is to describe a series of observations and manipulative experiments designed to increase our understanding of *S. anglica* ecology, and to present data and findings that have direct relevance for management practices.

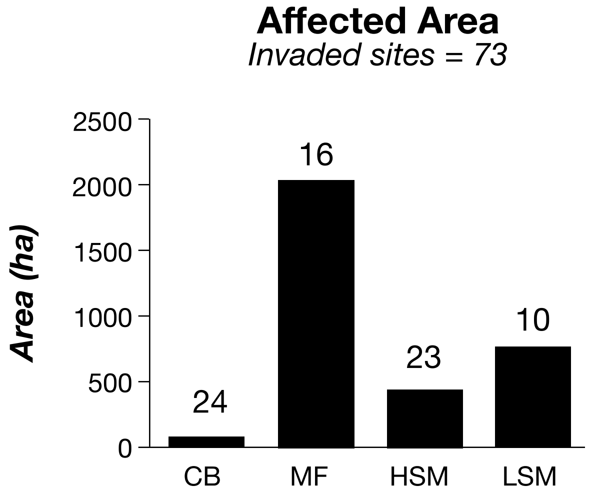

Figure 2. Mean (± 1 SE) affected (ha) of *S. anglica* at sites of different community type (LSM = low-salinity marsh, MF = mudflat, CB = cobble beach, and HSM = high-salinity marsh) in Puget Sound, WA. Numbers above histograms are numbers of sites (Source: Hacker et al. 2001).

Biology of the Invasion

The biology of *S. anglica* affects, in various ways, the spread, success, and community-level impacts of its invasion into different habitat types. Understanding where and why *S. anglica* can spread most quickly, as well as how its patterns of growth help it resist control efforts, should help to direct management efforts to maximize efficiency.

Seed Production and Dispersal

To control the invasion of *S. anglica*, it is ultimately necessary to prevent seed production and dispersal. *S. anglica* colonizes new areas primarily via floating seeds, although pieces of the underground stems, called rhizomes, can also establish new plants (Ranwell 1964). Seed production varies hugely among sites and habitat types. As early as their second season of growth (Thompson et al. 1993, C.E. Hellquist pers. comm.), mature plants send up tall "spikes", which bear flowers that are wind-pollinated. Both self- and cross-pollination lead to viable seeds, although some data suggest that more seeds are produced by cross-pollination (van Schreven 1952; our data). Dense populations probably have a greater chance of fertilization than sparser ones because of high local pollen availability (Davis et al. 2004). Flowering mostly occurs between June and September, but can occur as late as November (Mullins and Marks 1987, our data). It appears that late-flowering (November) spikes do not produce seeds that mature. Thus, management efforts would be better spent controlling early-flowering spikes than late-flowering ones.

In high-salinity marshes, low-salinity marshes, and mudflats, the number of spikes averages 20-30 per 0.25 m^2, but only 15-20 per 0.25 m^2 in cobble beach habitats (unpublished data). This figure varies with tidal elevation; it is often highest in the middle to low end of the tidal range of the plant, where physical conditions such as salinity and soil water content may be optimal. The average number of seeds produced per 0.25 m^2 ranges from 175 in the cobble beach sites to 200 in high-salinity marshes, 320 in low-salinity marshes, and 350 in mudflats. A hectare of *S. anglica* monoculture, which is a more useful unit for management, would thus produce an extraordinary number of seeds. The number and timing of spike and seed production

Table 1. Scientific names of principal plant species used in this document.

GENUS AND SPECIES	COMMON NAME	NAME USED HERE
Spartina anglica	English cordgrass	*S. anglica*
Spartina alterniflora	Smooth cordgrass	*S. alterniflora*
Triglochin maritimum	Sea arrow grass	*Triglochin*
Carex lyngbyei	Lyngby's sedge	*Carex*
Scirpus maritimus	Seacoast bulrush	*Sc. maritimus*
Scirpus americanus	American bulrush	*Sc. americanus*
Jaumea carnosa	Fleshy jaumea	*Jaumea*
Salicornia virginica	Saltwort or Pickleweed	*Salicornia*
Distichlis spicata	Seashore saltgrass	*Distichlis*
Fucus spp.	Rockweed	*Fucus*

for *S. anglica* also varies highly in British populations (Marks and Truscott 1985, Mullins and Marks 1987, Scott et al. 1990). Mature *S. anglica* monocultures higher in the intertidal produce the greatest density of "spikelets" (single flowers on spike), but only five percent of the spikelets were filled with seed. This contrasts with 88% of the spikelets filled with seeds in younger, lower-elevation plants. Seeds from younger plants were also more viable.

Little is known about factors affecting successful dispersal of *S. anglica*, but it is undoubtedly influenced by wind and currents. A critical, unanswered question for managers pertains to how distant populations get established: is it by rare transport of seeds over large distances or via "stepping stones" from satellite populations? In the Pacific Northwest, seeds are likely to drop to the marsh floor or be blown into the water in the late summer or early fall and be kept damp and cool by their surroundings and the weather. Most seeds in water sink in less than 10 days (David Heimer, pers. comm.). Seeds that have not washed ashore by this time probably will not survive. Seeds can also float in rafts of dead plant material (wrack), where they can probably remain viable until the following spring if they remain in cool and damp conditions. *Spartina* seeds become inviable if left in dry or warm conditions for more than a few weeks (Goodman et al. 1969, Probert and Longley 1989). We found that none of the seeds washed up in wrack that had been in the field for a second season was still viable.

S. anglica appears to germinate most successfully in damp and cool conditions in brackish water. Seeds from Puget Sound sites stored in damp and cool conditions in the laboratory had greenhouse germination rates of up to 25%, depending on soil conditions (Dethier and Hacker in review). The highest rates occurred when seeds were planted in continuously flooded sediment, where the salinity was brackish (15 parts per thousand [ppt]) although some germination was seen at all salinities. Sediment type is less important to germination, but seeds planted in sand germinated better than those in mud or cobble. The poorest germination (<1%) occurred in cobble and mud that had been watered (then drained) with full-strength seawater. Other researchers have found corresponding evidence that *S. anglica* germinates best when continuously flooded at low salinity and that high-salinity water inhibits germination (Taylor and Burrows 1968, Goodman et al. 1969, Marks and Truscott 1985, Huckle et al. 2000).

We examined seed germination in the field by planting seeds in packets (to prevent accidental dispersal) in a wide range of habitat types and tidal elevations in the early fall (Dethier and Hacker in review). Germination took place in early spring (March-April) as the weather warmed and light levels increased. Overall, seeds planted in low zones germinated the most predictably, presumably because they remained damp and the salinity remained closer to bay values. Out of 50 seeds per packet, an average of 10-15 germinated in the low zones. The exception was at cobble beaches, where germination was very low (usually <2 seedlings) across zones. Low germination rates were attributed to the seeds drying out as the result of the coarse sediment draining effectively, and seed damage from crushing or scouring in the higher wave energy environment. Germination in high marshes was consistently poor, probably owing to a combination of high salinity, dry soil, and competition from native plants. Germination in the high zone of low-salinity marshes was much more successful than in high-salinity marshes, again illustrating the positive benefits of lower salinity for *S. anglica*. Extensive germination in high zones occurred only in mudflats; this was especially true at the one muddy site where the high zone was damp, with soft mud.

Habitat type has profound implications for survival and spread of *S. anglica* seedlings (Fig. 3) and, therefore, helps to determine which areas would best benefit from focused control efforts. Overall, germination, survival, and growth were generally greater in lower zones. In cobble beaches, seedling growth from April to September was almost non-existent; no seedling produced more than one shoot, and few grew more than 10 cm tall. In contrast, seedlings grew prolifically in the mudflats; at one site, 25 seedlings produced 252 tillers and some were almost 1 m tall. Growth at low-salinity marsh sites was less dramatic but still rapid, with 10-15 seedlings producing 20-30 tillers roughly 0.5 m tall.

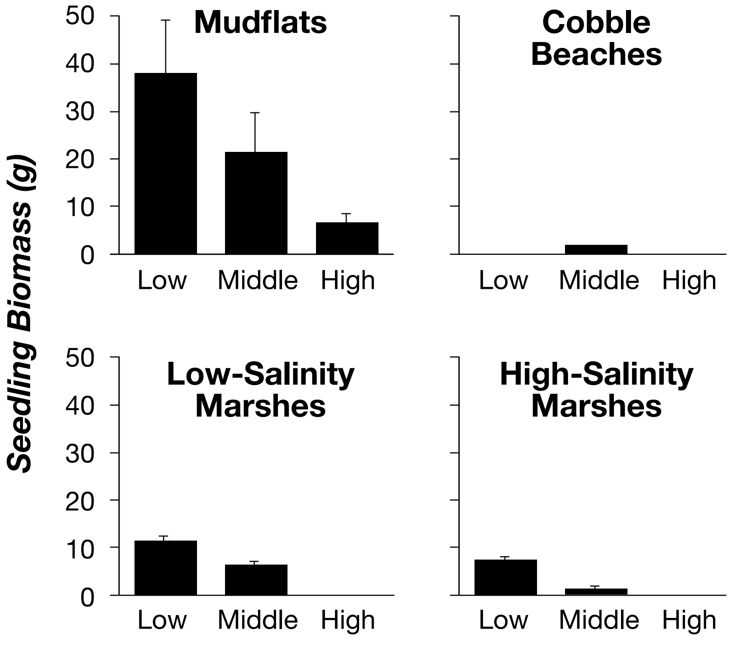

Figure 3. Biomass (mean ± SE) of *S. anglica* seedlings that germinated in plots in different habitat types at different intertidal heights (low, middle, high) in Puget Sound, WA. Fifty seeds were placed in each plot. (Source: Dethier and Hacker, in review).

Both sediment conditions and competition from native plants deter the spread of *S. anglica* in high-salinity marshes. No seedlings survived in the dense, saline marsh in the high zone and very few survived in the middle zone (Fig. 3). Only the unvegetated channels proved suitable for growth, where 20-30 seedlings produced approximately one 10-15 cm tall tiller each. Starting from the same number of seeds, biomass differed by an order of magnitude among habitats after 6 months. Biomass generation was high for mudflats and low-salinity marshes, somewhat lower for high-salinity marshes, and very low for cobble beaches. Studies on British *S. anglica* growth have shown similar negative effects of competition with native plants (e.g., Huckle et al. 2000) and of high salinity.

Habitat-dependent germination and growth of *S. anglica* makes certain types of shoreline more vulnerable to rapid invasion, which has important implications for control efforts and monitoring (summarized in Table 2). Mudflats, the low to middle zones of low-salinity marshes, and channels in high-salinity marshes are ideal for seed germination and rapid vegetative spread of small plants because of damp sediment, moderate salinities, low wave energy, and scant competition from native plants. Invasions and spread are relatively unlikely on cobble beaches and in high zones of marshes. Vigilant removal of seedlings and rapid response to control infestations are, therefore, especially critical for mudflats and low-salinity marshes. Although unvegetated channels of high-salinity marshes can be readily invaded, *S. anglica* cannot spread rapidly from these invasion points into the marsh itself. Plants in high-salinity marsh sites, and even cobble beaches, can still produce seeds that can then be exported to other areas; remote populations in any habitat may be stepping stones to optimal habitats further afield (see *Landscape-Scale Considerations*, page 14).

Plant Morphology and Vegetative Spread

A germinated *S. anglica* seed becomes a large clone via rapid asexual spread. One seedling can send many rhizomes and roots through the substrate, binding the sand or mud with a dense set of rootlets. Each rhizome then sends up multiple shoots. Ultimately, a substantial proportion of the total biomass of an *S. anglica* clone is below-ground in this mass of roots and rhizomes.

In first-season plants, much energy goes into photosynthetic shoots, and root/shoot biomass ratios are generally about 1:2. In high-salinity marsh channels, these ratios may be higher, about 1:3 (i.e., more effort is put into shoots), and in cobble beaches the ratios are lower, about 1:1 (i.e., equal biomass goes into roots and shoots). Cobble beaches presumably require a greater investment in roots to help stabilize the sediment and anchor the plants against wave action and shifting substrate. Mature plants develop a higher ratio of root to shoot biomass. Samples taken in mature *S. anglica* marshes in the four habitat types had root/shoot ratios ranging from about 1:1 (low- and high-salinity marshes) to 2:1 (some mudflats and cobble beaches) (unpublished data).

The large below-ground biomass of *S. anglica* has several important management implications. One of the primary ways that roots "engineer" their physical habitat is by binding sediment, causing a large ecological impact. Additionally, during the productive season (May–September), *Spartina* puts much energy into growth but some energy is shunted into below-ground storage in the rhizomes. Stored nutrients allow the plants to survive the long, unproductive winter season. They also allow *Spartina* to withstand mowing and spraying of herbicide on surface material without being killed, because the rhizomes can regenerate new shoots. For this reason, mowing early in the growing season (August–September) is more damaging to the plant than mowing late in that season (See *Control Strategies and Recommendations* page 11).

Habitat Engineering

Habitat "engineers" are organisms such as reef building corals or trees in a forest that create or substantially alter their physical environment. (Jones et al. 1994) *S. anglica,* along with other species in this genus, engineers its habitat in various ways (Hacker and Dethier, in review). First, the roots and rhizomes bind together and stabilize loose sediments. Second, the tall and dense shoots slow the movement of water through them, which causes sediment carried by the water to be deposited beneath the blades. As a result, *Spartina* beds accrete sediment at a much faster rate than unvegetated areas and, probably, faster than in native marshes (Fig. 4). The effects of *S. anglica* on accretion rates vary highly with habitat type. Normal (no-*Spartina*) accretion in mudflats and cobble beaches is very slow, probably due to the relatively high wave activity and the absence of any native sediment-trapping vegetation. In marshes, wave action is lower and native vegetation also causes sediment accretion, especially in high-salinity marshes. In England, *S. anglica* has been shown to accrete ~1 m of mud over the course of a 50-year invasion

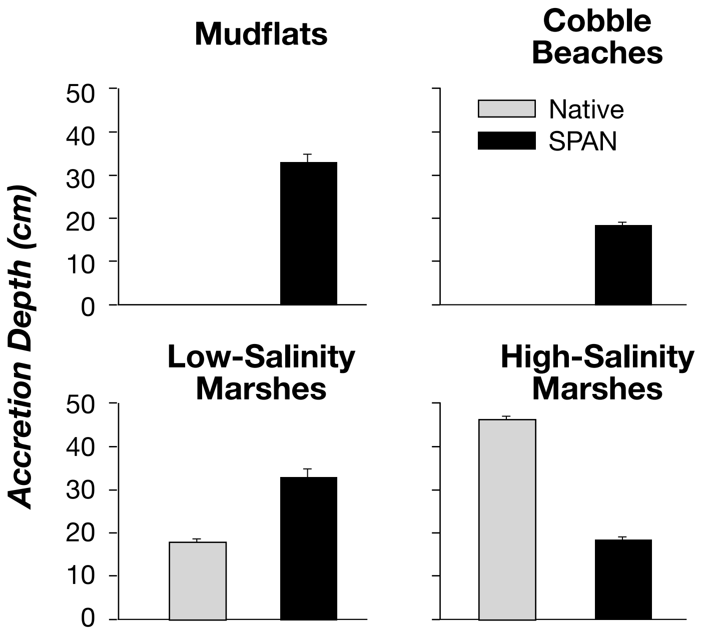

Figure 4. Comparisons (mean ± SE) of sediment accretion depth for *S. anglica*-invaded areas (SPAN) and uninvaded native areas (Native) at the same intertidal elevation within Puget Sound, WA in 2000. (Source: Hacker and Dethier, in review).

(Gray et al. 1991, Thompson 1991). This causes the marsh surface to gradually become elevated, converting a gently sloping mudflat to a raised marsh dissected by steep-sided channels (Fig. 5).

Third, *S. anglica* can alter sediment oxygen. It has specialized tissue (aerenchyma) in its blades that transports oxygen from the surface down into the rhizomes (Maricle and Lee 2002). Physiologically, this keeps the roots and rhizomes healthier and able to undergo aerobic metabolism and thus tolerate waterlogging (Holmer et al. 2002). Ecologically, *S. anglica* transports oxygen into the sediment, which would otherwise be anaerobic a few centimeters below the surface. Oxygenating marsh sediment improves the environment for other plants and animals.

Lastly, a dense patch of *S. anglica* provides significant shade to the surface of the marsh. Since *S. anglica* grows larger and faster than any native species, it can outcompete other plants. Shade also slows evaporation from the marsh surface, which makes the sediment in an *S. anglica* bed less saline than nearby unvegetated areas. It is likely that the combination of reduced salinity with enhanced oxygen improves conditions for colonization of *S. anglica* seedlings under a canopy of adult plants, although low light is clearly detrimental. Several British studies indicate that in poorly drained, soft-sediment soils in brackish conditions, the perennial life history and greater height of *S. anglica* give it a competitive advantage over the dominant native marsh species *Puccinellia maritimum* (Scholten and Rozema 1990).

Impacts on Other Species

Once seedlings are successfully established in a marsh, the rapid spread and tall growth form of several species in the *Spartina* genus make these seedlings formidable competitors against most other plant species. Mature clones (meadows) thus tend to become virtual monocultures. In Australia, Hedge and Kriwoken (2000) found that "prostrate or stout species," including mangrove seedlings, appear to be particularly

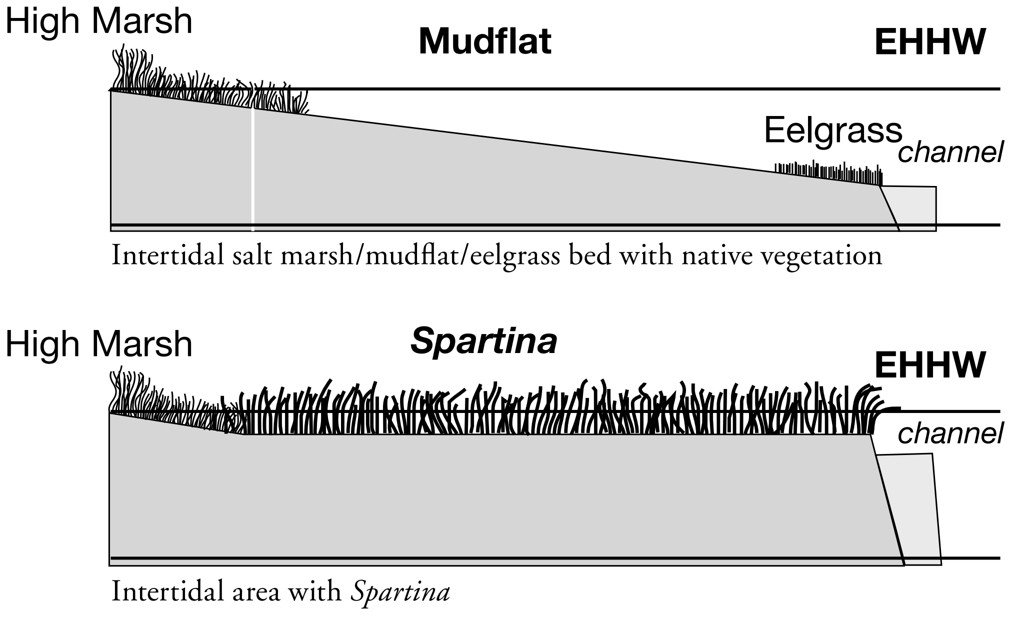

Figure 5. Profiles of intertidal areas with native vegetation and after invasion by *Spartina.* Note higher elevation relative to extreme higher high water (EHHW) in *Spartina* marsh, due to increased sedimentation.

prone to competitive exclusion by *S. anglica*. Below-ground competition also helps *S. anglica* to dominate.

Many of the critical impacts of *S. anglica* on other species are probably indirect. The plant's increased structure (both above- and below-ground) and primary productivity have potentially far-reaching impacts to the rest of the ecosystem. Relatively little literature exists on the secondary impacts of invading *S. anglica*, but more exists for *S. alterniflora* that has invaded estuaries on the West Coast. Some of these impacts are reviewed by Zipperer (1996), Feist and Simenstad (2000), O'Connell (2002), and Wonham (2003).

Former mudflats invaded by *S. alterniflora* become unusable by waterfowl and shorebirds and by some species of juvenile fishes, crustaceans, and mollusks. In England, *S. anglica* marshes have been shown to have fewer wading birds, such as dunlin (Goss-Custard and Moser 1990). There is concern that Dungeness crabs, cultured oysters, and eelgrass (*Zostera* spp.) beds may also be displaced. However, the overall effects on invertebrates appear to be variable (McCorry and Otte 2001). Cobble beaches with *S. anglica* appear to have less infauna (worms, small bivalves, and small crustaceans) because of the dense root mats formed. Invaded mudflats often have fewer clams and polychaete worms (C.E. Hellquist, pers. comm.) but may have more mobile surface fauna, such as amphipods, presumably attracted by the increased surface structure. In contrast, mudflats invaded by *S. anglica* in Tasmania had more abundant and diverse invertebrates than did unvegetated mudflats, perhaps because of the spatial complexity and increased oxygen provided by the root masses (Hedge and Kriwoken 2000). Areas invaded by *S. anglica* or *S. alterniflora* have more insects, such as grasshoppers, and spiders (Cordell et al. 1998, pers. obs.). The high primary productivity may also contribute in other positive ways to the nearshore ecosystem (Cordell et al. 1998). The lower edges of these marshes may actually become important nurseries for bass (Doody 1990) or for chinook salmon in Washington state (Simenstad and Thom 1995). However, this possible benefit might only accrue at the edges of marshes and in channels; the large acreage of elevated *S. anglica* meadow (Fig.5) cannot be used by fishes.

Control Strategies/ Recommendations

Control Methods

Data on the effects of *S. anglica* control methods and strategies come from the Washington State Department of Agriculture (WSDA) and our obsevations and experiments (Reeder and Hacker 2004, Hacker et al. in review). We obtained and analyzed management records from all known *S. anglica* sites within Puget Sound. We also examined removal work conducted by the Swinomish Tribe and performed small-scale experiments within sites being treated by WSDA.

Between 1997 and 2001, WSDA used predominately used push mowers, weed cutters, and herbicide sprays of 5% glyphosate combined with 1% of the surfactant R-11 to control *S. anglica.* The WSDA has recently modified its control practices, which are discussed in the *New Techniques of Control* section. Although our results are based on WSDA's earlier, smaller-scale mowing/glyphosate treatment method, which is still commonly used at many sites, they may also apply to other control techniques. The resilience of *S. anglica* plants means that any control technique will need to be applied repeatedly and consistently in order to eradicate the plant. Our results may also apply to *S. alterniflora* and other species because the various species within the genus are ecologically similar.

Consistency of Control

Our studies, examination of the WSDA work, and the experiences of *Spartina* managers all illustrate clearly that eradication of *S. anglica* from an area can only occur when control efforts are applied for multiple years. We found (Hacker et al. in review) that after 1 year of spraying and mowing, *S. anglica* declined by less than 10% in all habitat types. After 2 years, *S. anglica* declined by 20-60% (depending on habitat type), and after 3 years it declined by 20-80%. Only after 4 years of consistent removal did any area approach complete eradication (See next section for habitat effects).

If a site is not treated each year, removal gains are often compromised. In our study, *S. anglica* declined by 88% with a consistent, yearly effort between 1997 and 2001, but only by 49% with intermittent (≥ 1 year missed) effort (Fig. 6). Furthermore, successful removal was significantly more costly under intermittent control than under consistent control, regardless of the total number of years of effort (Fig. 6). Consistent removal effort is important for all habitat types, although yearly regrowth varies by habitat (Fig. 6).

Because of its unique biology, *S. anglica* has a remarkable ability to regrow full-sized shoots, even after years of repeated treatment. The large root biomass stores nutrients, so mowing must be repeated for 3-4 years to sufficiently deplete these stores and kill the plant. In addition, rapid regrowth means that root stores do not take long to be restocked each spring. Furthermore, because the plant is clonal, removing or even killing blades and roots in one portion will not necessarily kill the whole plant, because photosynthates or new rhizomes can be moved into the affected area by healthy parts of the clone.

Even consistent, multi-year mowing without the use of herbicides is unlikely to kill an *S. anglica* patch. This was the case at several sites located on Swinomish tribal lands. When herbicides were used after 3 years of mowing alone, there was a 50% decline in 1 year, as compared with simply mowing (unpublished data). Similar results have been found in England. Hubbard (1970) found that mowing patches of *S. anglica* to the ground level every month during the growing season actually had a positive effect on the mass of shoots seen the next summer. To find an optimal harvest time of *S. anglica* for biofuel, Scott et al. (1990) mowed areas of *S. anglica* over 3 successive years. In plots harvested in fall or winter, total biomass declined slowly to about half of the original yield, even when fertilizer was added. Plants remained alive, although with lower cover, throughout the harvested area; however, plots harvested in the summer showed a great decline in cover and gradual replacement by the native *Puccinellia*. Limited success of concerted mechanical efforts suggests, overall, that herbicide (which kills portions of the root system) is necessary for effective removal.

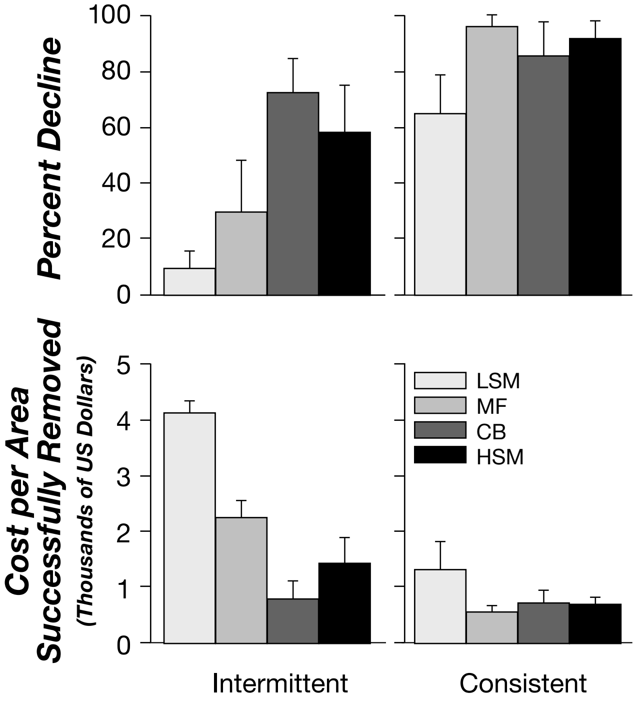

Figure 6. Mean (± SE) percent decline of *S. anglica* and cost per area (ha) successfully removed for sites adjusted for years of removal effort. Factors include two removal regimes (intermittent or consistent) and different habitat types (LSM = low salinity marsh, MF = mudflat, CB = cobble beach, and HSM = high salinity marsh) (Source: Hacker et al. in review).

Many eradicated *S. anglica* meadows in the northern Puget Sound region exhibit conditions ideal for re-invasion via seed dispersal. This impedes the restoration of native plant and animal communities. Cordgrass seedling densities were found to be highest in areas where *S. anglica* removal had occurred (Fig. 7). Since seeds disperse effectively through various pathways, reinvasion will be a chronic problem. Many seeds in dead plant material (~2,500 per 0.25m^2) that washed ashore in control areas were found to have germination rates of nearly 20%, potentially resulting in ~500 seedlings per 0.25 m^2.

Although wrack formed naturally or left behind by mowing can be a vector of seed dispersal, it also can limit *S. anglica* growth in the following year. Wrack can significantly decrease the number of tillers and the number of flowering spikes produced in the following season, most likely by limiting sunlight availability (Reeder and Hacker 2004). Crushing of meadows with heavy vehicles may have similar effects, as it leaves dead plant material behind (See *New Techniques of Control,* page 15). Also, van Hulzen et al. (2003) found that algal mats deposited on the surface of *S. anglica* marshes in the Netherlands significantly reduced the cover of cordgrass the following year.

Habitat Type

Habitat effects on germination and growth rates of *S. anglica* also have important implications for management (summarized in Table 2, page 17). Success of *S. anglica* removal efforts varies inversely with abundance (Fig. 6). Percent decline under multiple years of consistent removal has been relatively high in cobble beach and high-salinity marsh habitats, where regrowth is slower because the physical habitats are marginal. Control efforts in mudflats have also been fairly successful, presumably because salinity and waterlogging issues make the plant less productive and thus less resilient to disturbance. However, because of the large size of the invasion in mudflats, *S. anglica* has been hard to eradicate. Moreover, four years of consistent control efforts in low-salinity marshes resulted in less than 60% decline in abundance (Fig. 6). In this optimal habitat, the plant can regrow very quickly from rhizomes and untreated portions. Intermittent control (skipping a year) in low-salinity marshes results in virtually no overall decline because resilience is so high; thus, the cost of successful removal of *S. anglica* under these conditions is extremely high (Fig. 6). Because low-salinity marsh sites are so large, cordgrass removal may benefit from the large-scale mowing and spraying techniques underway (See *New Techniques for Control*).

Size of the Invasion

Size of the local invasion also affects the success of management efforts (Hacker et al. in review). Small areas (<10 ha) experienced greater proportional declines in *S. anglica* abundance post-treatment than large ones (>10 ha). This is probably true because small invasions are easier to treat completely. Additionally, larger invasions may have more stored reserves to shunt to treated areas. Even small invasions (<10 ha) in low-salinity marshes showed relatively low removal success, again illustrating the high regrowth potential of plants in these habitats.

In the last two seasons, WSDA has attempted to use crushing of *S. anglica* meadows with large invasions as an additional control strategy. This may be a significant help in dealing with large meadows, although, like any strategy, it will need to be multi-year, consistent, and used in combination with other methods to be effective. In addition, preliminary data suggest that one year of crushing may actually increase root biomass in the second season although we cannot yet assess the mechanism behind this response (See *New Techniques for Control*).

Herbicide Spray Time

Experiments suggest that timing of herbicide spraying (i.e., early vs. late in the growing season) has an important effect on subsequent growth and seed production of *S. anglica*. In 2002, in cooperation with WSDA personnel, we sprayed separate experimental swaths in a low-salinity marsh at 2-week intervals starting in mid-July onwards, and compared them to unsprayed swaths. Regrowth in the plots was measured the following year, and the experiment was repeated with a second series of herbicide spraying.

Early season spraying (July to mid-August) greatly reduced the mass of blades produced that season. This effect was fairly linear; areas sprayed in July, August, and September showed progressively less impact on blade production (Fig. 8). Spraying had only a small negative effect

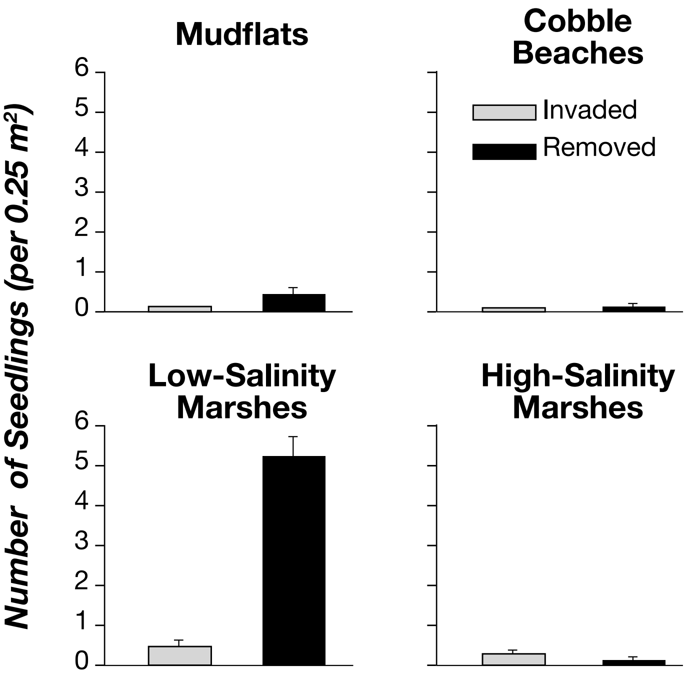

Figure 7. Comparisons (mean ± SE) of cordgrass seedling numbers in areas invaded by *S. anglica* and areas where it had been removed at the same intertidal elevation within Puget Sound, WA (Source: Reeder and Hacker 2004).

on root biomass relative to unsprayed areas. Spraying very early (July 11) reduced the number of flowering spikes, but later spray dates had no effect. Most dramatically, early spraying virtually eliminated seed production, whereas spraying later than mid-August had almost no effect on fertility (Fig. 8). Intermediate dates progressively reduced seed output.

The results differ during the second season after herbicide spraying. Spraying at any time during the previous summer has a negative effect on above-ground biomass and essentially ceases all cordgrass production relative to unsprayed plots (Fig. 9). Growth, flowering spike production, and seed production were virtually eliminated by two consecutive years of spraying, although late-sprayed plots did show less of a decline (Fig. 9). The effect was much less dramatic for the below-ground biomass. While above-ground production was virtually halted after the 2 spraying events, 60-70% of the root biomass was still present and alive (Fig. 9). In addition, early spraying (before July) resulted in roughly a 10% greater decline in below-ground biomass, suggesting that early spraying over multiple years is beneficial. Even more important, if control of these plots ceased after these two years, regrowth from the living roots would probably still occur.

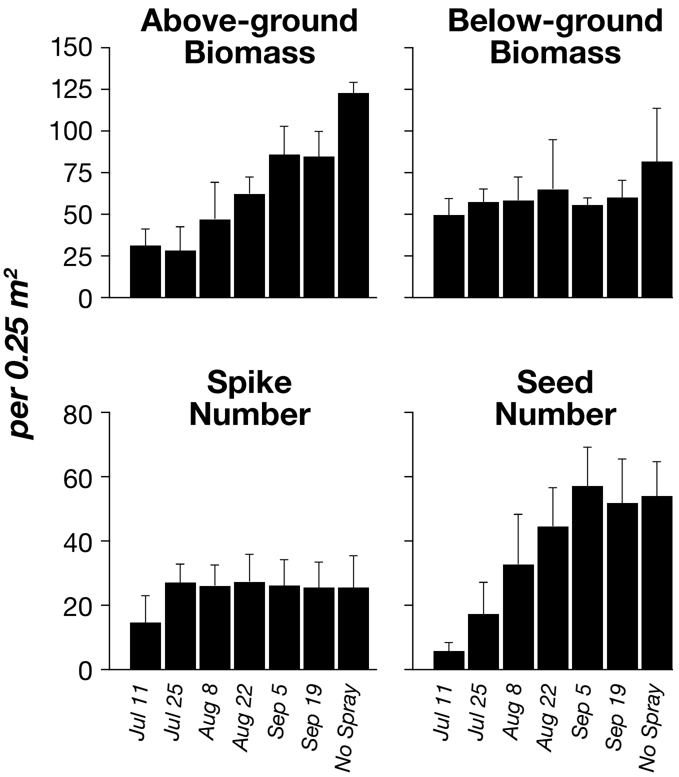

Figure 8. *S. anglica* (mean ± SE) above-ground biomass, below-ground biomass, spike number, and seed number for six different herbicide spray dates at one site on Skagit Bay, Puget Sound, WA (Source: Hacker and Dethier unpublished data).

The substantial positive benefits of early season spraying are consistent with the seasonal biology of this plant. Over the course of the winter, roots have been metabolizing the reserves they have stored. Sending up new blades in the spring must consume a significant portion of these reserves. Thus, when young shoots are sprayed early, the plants have relatively few reserves left for overcoming this stress and growing new shoots or flowering spikes. By late in the season, plants have already stored newly photosynthesized carbon in the roots, which gives the plant more scope for recovery after spraying. Spraying late in the growing season thus will not substantially reduce plant production in that year (Fig. 8). However if the plants are green and actively photosynthesizing, which is true until late September, then spraying will still allow herbicide to be carried throughout the plant, which leads to reduction in growth parameters the following year, albeit less than in those plants sprayed earlier (Fig. 9).

Landscape-Scale Considerations

A strategy for statewide management of *S. anglica* must consider the problem at a landscape scale. This is especially an issue for a species like *S. anglica*, which has a clear center of distribution, with the largest and densest populations, and many outlying or “satellite” populations. Should a control strategy involve killing the core populations first and then working on the smaller outlying ones, or should it take an inverse approach? The ecology of *S. anglica* should enter this decision, in terms of seed dispersal and ability of small clones to spread vegetatively.

While the core populations of *S. anglica* (near Stanwood, at the mouths of the Skagit and Stillaguamish rivers, Fig. 1) may produce most of the seeds within Washington state, these seed sources may not be the major threat in terms of overall spread of the species. If satellite populations are fertile (and this is likely, especially on mudflats), they constitute stepping stones that may allow the species to spread much farther from the center of distribution — especially because it takes only a few viable seeds to start a large, fast-spreading clone. The appearance of *S. anglica* in Boundary Bay, near the Canadian border, and in the Fraser Delta in Canada (Williams 2004) may be a good example of "stepping stone" spread. A few seeds from small populations in the San Juan Islands or near Fidalgo Island could readily travel north and generate populations that could spread very rapidly if not controlled. We recommend a policy of working to eradicate satellite populations and surveying vigilantly for new ones, even if it may be a less efficient, short-term use of human resources.

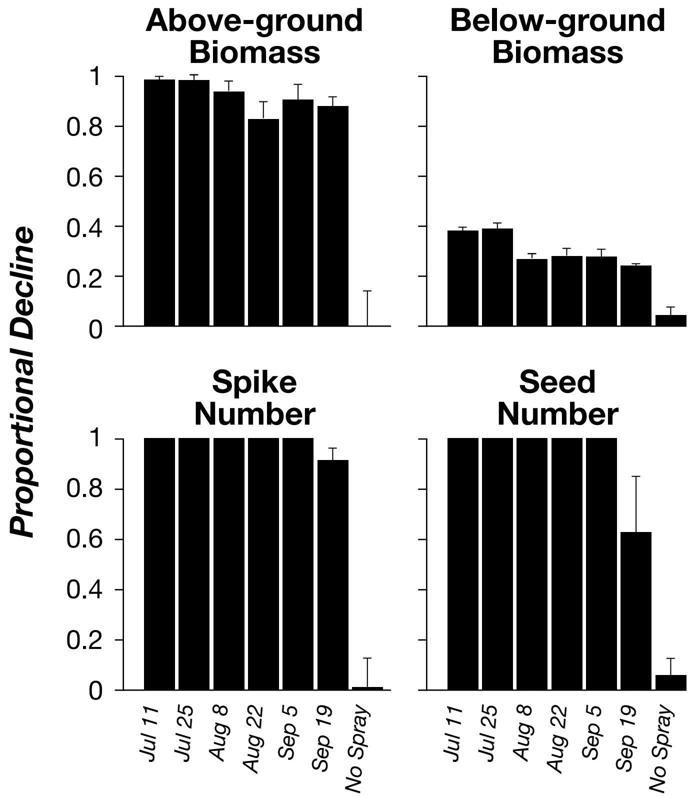

Figure 9. Proportional decline (relative loss of plant from one year to the next; mean ± SE) of *S. anglica* over 2 years in above-ground biomass, below-ground biomass, spike production, and seed production for six different herbicide spray dates (in 2002 and 2003) at one site in the Skagit Bay, Puget Sound, WA (Source: Hacker and Dethier unpublished data).

New Techniques of Control

Since 2001, control methods at sites with large infestations of *S. anglica* have shifted away from less efficient methods of small-scale mowing and spraying to larger-scale methods (David Heimer and Kyle Murphy, WSDA, pers. comm.). Larger-scale mechanical control efforts other than hand-mowing have increased to extend coverage and allow less overall herbicide use. In particular, large *S. anglica* meadows are often treated with mowing, crushing, or discing (i.e., plowing) with tracked, low ground-pressure amphibious vehicles. Often this work is done later in the growing season or very early in the spring to knock down the largest amount of biomass. This makes spraying during the subsequent growing season more efficient, because new growth is easier to access. These methods also leave plant material on-site, acting as a cover and reducing regrowth. Another approach is to crush different parts of a large meadow in different months and then spray the new growth during the month after crushing, thus extending the temporal window for spraying.

Long-term effects of crushing have not been monitored, although we have begun to examine its effects on root biomass. During the first spring after a single crushing event in the previous fall, below-ground biomass actually increased significantly, relative to that of adjacent uncrushed areas (crushed mean ± SE = 50 ± 4 g; uncrushed mean ± SE = 39 ± 3 for 3 separate sites that did not significantly differ in biomass values). The mechanism is unknown, but because blades may remain attached to roots even when crushed, carbon may still be translocated below-ground. However, this positive effect disappears with more crushing. After 2 or 3 full crushing events, there is a significant decrease in the above-ground and below-ground biomass of *S.*

anglica, compared with no crushing (Fig. 10). The decline in root biomass, however, is still quite slow (Fig. 10).

Various other mechanical methods, such as covering meadows with black geotextile fabric, have been attempted but are not broadly used. Digging is feasible and effective only where there is good access and plants are small. Workers in Tasmania (Natural Heritage Trust and Tasmania Dept. of Primary Industries, Water, and Environment 2002) found that once clones are more than 15 cm in diameter, removing rhizomes by digging is very difficult. Burning and steam-treating have been attempted in various parts of the world, but blades and root masses are generally too wet to transfer heat underground or to sustain burning without the use of accelerants. Research in Tasmania has similarly found that smothering, heat treatments, and many other techniques are too non-selective or cost-inefficient compared with herbicide use. The chemical used in Tasmania is Fusilade®, applied with a low-pressure sprayer fitted with a hand-held boom. There has also been experimental testing on *S. alterniflora* in Willapa Bay with a different herbicide, Imazapyr (Patten 2002), which is now (2004) registered for use in estuaries. Another herbicide, Gallant®, has been used in New Zealand with great success. The herbicide is sprayed from a helicopter a few meters from the ground. Using this method, *S. anglica* has been nearly eradicated in estuaries on the South Island (Keith Crothers, Environment Scotland, pers. comm.). Biocontrol is also being attempted on an experimental basis; the plant-hopper *Prokelisia marginata* was released into Turner's Cove on Swinomish land, with the cooperation of the Swinomish Tribe, University of Washington, Olympic Natural Resource Center, and Washington Department of Fish and Wildlife (F. Grevstad, pers. comm.). Biocontrol with *Prokelisia* on *S. alterniflora* in Willapa Bay has shown positive preliminary results (Grevstad et al. 2003).

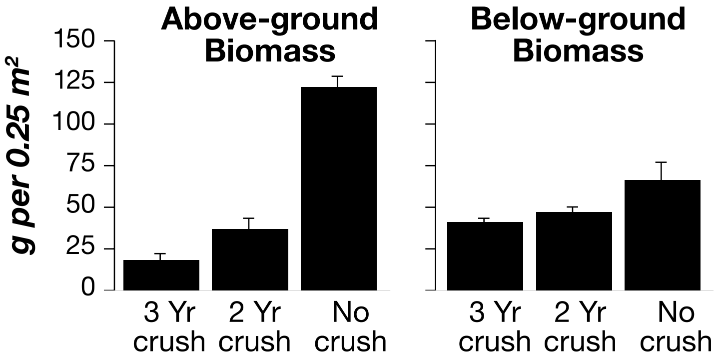

Figure 10. Mean (± 1 SE) above-ground and below-ground biomass for *S. anglica* after 2, 3, and no crushing events at one site on Skagit Bay, Puget Sound, WA. (Source: Hacker and Dethier unpublished data).

Restoration Potential

Very little research has been focused to date on how readily native communities can reestablish following successful removal of *S. anglica.* It is likely that restoration potential will be habitat-dependent (Table 2).

When *S. anglica* is killed (except by digging), it leaves behind residual roots and accumulated sediment that are bound together firmly, usually forming a surface that is elevated over the original shore configuration, especially in mudflats and cobble beaches (Fig. 4 and Fig. 5). This elevated root mat becomes colonized by native marsh plants (Fig. 11), as well as by *Spartina* seedlings (Fig. 7), and will require continued control efforts . Colonists include: *Triglochin, Carex* and *Scirpus* spp. in low-salinity marshes; *Jaumea* and *Salicornia* in high-salinity marshes; and *Triglochin*, *Salicornia*, and *Distichlis* in mudflat and cobble beach habitats. Colonization of the

HABITAT TYPE	SPEED OF SPREAD	INVASION SIZE/IMPACT	REMOVAL SUCCESS		RESTORATION POTENTIAL	INVASION RISK/ SEVERITY
			Consistent	Intermittent		
Mudflat	Fast	Large	High	Low	Low	High
Cobble Beach	Slow	Small	High	Medium	High	Low
Low-Sal. Marsh	Fast	Large	Low	Very Low	High	High
High-Sal. Marsh	Slow	Small	High	Medium	High	Low

Table 2. Assessment of the relative risk and severity of the cordgrass invasion to 4 habitat types in Puget Sound, Washington, considering speed of spread, invasion size/impact, removal success, and restoration potential.

elevated root mat by appropriate native species means that communities similar to those present prior to an invasion should be able to establish and resist re-invasion better than the sparse assemblages present immediately after *S. anglica* is killed. Selective plantings of native species, as well as other forms of active intervention, may also improve restoration; however this is an area requiring additional research.

Pre-invasion cobble beach and mudflat habitats do not naturally have the sort of consolidated and elevated root mat found there once *S. anglica* has been killed. Cobble beaches in the region are normally sparsely vegetated with seaweed (*Fucus* and green algae) in the mid-shore and patchy *Salicornia* and *Triglochin* in the high shore. Mudflats tend to be unvegetated at all levels. The presence of *S. anglica* root mats provide stable physical habitat not normally present on these shores. This new habitat is colonized by native marsh plants but not ones that are part of the "natural" assemblage (Fig. 11). To return to a pre-invasion state, not only must the *S. anglica* be killed but the accumulated root mat and its colonists must disappear. This may happen fairly readily on cobble beaches, where wave action should erode the mat. In mudflats, however, restoration to a pre-invasion state may be a very slow process because wave energy is low. Mudflats provide key foraging habitat for shorebirds, and some areas may require a more aggressive restoration strategy. We recommend monitoring of restoration processes and vigilant removal of new *S. anglica* seedlings in all habitat types.

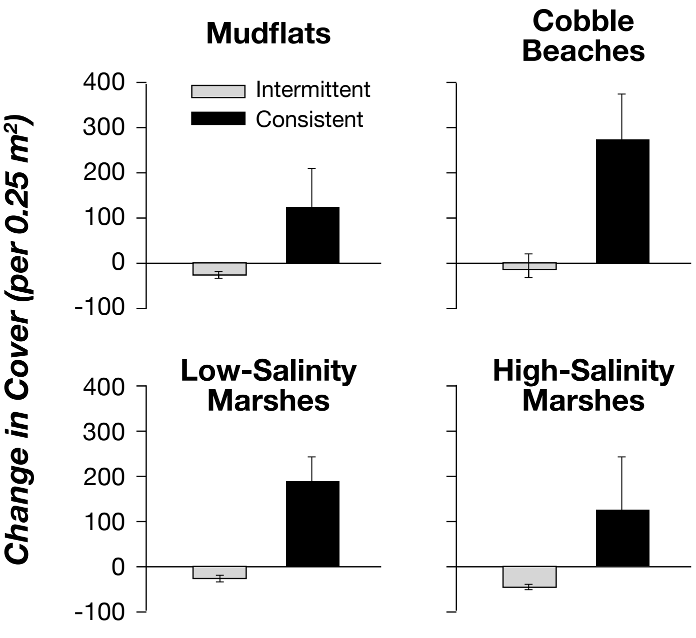

Figure 11. Comparisons (mean ± SE) of change in native plant cover in areas intermittently or consistently treated for *S anglica* at the same intertidal elevation within Puget Sound, WA (Source: Reeder and Hacker 2004).

Key Conclusions

- *Spartina anglica* germinates new seedlings and generates new shoots from established plants in early spring; undergoes rapid photosynthesis and growth of new and old plants from May to August; flowers primarily in July; and sets its seed primarily in September. In the early fall, most of its above-ground biomass becomes senescent.
- Seed production per area of *Spartina* monoculture is generally highest in low-salinity marshes and mudflats.
- Seed germination is highest in reduced salinities and wet conditions. Lower intertidal zones and damp channels have the greatest germination rates; few seeds germinate in high-salinity marshes or cobble beaches.
- Mudflats and low-salinity marshes have more favorable conditions for survival and spread of *S. anglica* than cobble beaches or high-salinity marshes; even a few seedlings in bare mud or among sparse native marsh plants near the mouths of rivers can rapidly spread into huge clones. Survival is high in the channels of high-salinity marshes, but physical conditions, along with competition from native plants, seem to slow *S. anglica*'s spread upwards from channels.
- The large biomass and high storage capacity of the root systems of *Spartina* mean that mowing *S. anglica* meadows will only kill the plants if repeated over many years and that even repeated mowings are minimally effective when herbicides are not used. Similarly, crushing plants is only likely to kill *S. anglica* meadows if used in combination with other methods and over multiple years.
- Mowing or crushing plants late in the growing season (August-September) has less effect than early in the season because, by late season, the root systems have been "recharged" with the storage products that will enable them to survive the winter. If mowed or crushed material (wrack) remains on site, the cover may reduce above-ground growth the following season because of shading. However, crushed material may also serve as a carbon reserve to recharge roots and rhizomes for the next season.
- Mowing late in the growing season probably *aids* dispersal of seeds, because the seeds survive well in the damp wrack that washes around among beaches.
- Skipping control efforts for even one year allows *S. anglica* to rebound quickly, negating previous years' successes. Thus, only *consistent* removal for at least 3-4 years is genuinely cost-effective.
- Because the physical habitat for *S. anglica* is optimal in low-salinity marshes, control efforts at these sites will always be the most difficult, with the slowest gains. These habitats are also the most important to control in terms of reducing overall invasion.
- Spraying early in the growing season (July) has the greatest effects in terms of reducing subsequent plant growth and seed production over the rest of that season. Spraying late in the season has almost no effect on fertility or growth during that year. Spraying at any time of the year, however, had significant negative effects on growth and seed production the following year. However, even 2 years of intensive spraying leaves behind below-ground biomass capable of regrowth.
- Long-term control efforts must include vigilant removal of seedlings, because seeds disperse well and can start new clones readily.
- Long-term restoration efforts may need to involve undoing the physical habitat modifications (e.g., root mat production) at some beaches, especially in mudflats, where the limited wave action may allow modified physical habitat to persist.

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