Hybridization, speciation and polyploid genome evolution in *Spartina*

M. L. Ainouche

Univ. Rennes 1 France, UMR CNRS 6553. Genome Evolution and Speciation Lab. Bât. 14A Campus Scientifique de Beaulieu. 35 042 Rennes Cedex. France. Malika.Ainouche@univ-rennes1.fr

History and genome evolution of invasive *Spartina* species will be examined, with special interest in the role of reticulate evolution (hybridisation) and genome duplication (polyploidy) in the success of newly formed hybrid/allopolyploid lineages. *Spartina* species are tetraploid, hexaploid or dodecaploid perennials, most of them being native to the New World. The molecular phylogeny indicates an ancient split between the tetraploid and the hexaploid species. Recent hybridisation and polyploidisation events involved hexaploid species, resulting from introductions of the East-American *Spartina alterniflora*. In California, ongoing hybridisations with its sister species *Spartina foliosa* result in introgressant hybrid swarms. In Europe, independent hybridisation events with *Spartina maritima* resulted in *Spartina* x *neyrautii* (France) and *Spartina* x *townsendii* (England), with. *S. alterniflora* as the maternal parent in both cases. Chromosome doubling of *S.* x *townsendii* resulted in a particularly successful new allopolyploid species, *Spartina anglica* that has rapidly expanded in range and has now invaded several continents. Various molecular data indicate that *S. anglica* has undergone a severe genetic bottleneck at the time of its formation and that it contains two well divergent homoeologous genomes. The *Spartina* system is used to explore the genetic and epigenetics dynamics of the hybrid and allopolyploid populations in Western Europe.

Spartina in China:Introduction, history, current status and recent research

Shuqing An, Changfang Zhou, Zhongsheng Wang, Donghai Yu, Zhifa Deng and Lin Chen

School of Life Science, Nanjing University, Nanjing 210093, China; anshq@nju.edu.cn

In 1963, 400 seeds and 35 individuals were introduced from England into China, but most of the seeds and almost all individuals died during the trip. Forty-four individuals were obtained from all the seeds (400 seeds) and 21 of them were planted in the coast. The other was used to reproduce more offspring in Nanjing University and most of the offspring were planted in another 2 places. By 1966, a total of 110 ha plantation had developed! In 1979, about 0.5 kg seeds from North Carolina and hundreds of individuals from North Carolina, Georgia and Florida were introduced into China, but all the individuals died before the experiment. In the end of 1980, thousands of seedlings generated from the seeds were sent to field, and in the spring of 1981, all seedlings were planted in 1300 m^2, where 3 ecotypes. But, now most of the plants are the highest type. By 1985, there are 260 ha of *S. alterniflora* in 6 counties of coastal China. But by 2002, *S. alterniflora* area naturally grows more than 112,000 ha along Chinese coast. A rapid explosion and expand of the species. After the large area of *Spartina* was established, the plants have been used as green manure in cropland and forage to feed sheep and cows. They were also used to protect the coastal dykes. By 1985, there were more than 36000 ha of *S. anglica* in 18 counties along coastal China. But in 2002, only small area of *S. anglica* still existed in 3 counties along the coast. What caused the different area changes of the 2 species? Six possible causes were discussed here: (1) Switching of cultivation (2) Reclamation of tideland (3) different biological characters (4) Competition between species, (5) dieback of *S. anglica* and (6) different genetic diversity and differentiation. Management technique of the invasive species was also discussed in this paper.

Varying success of *Spartina* spp. invasions in China: Genetic diversity or differentiation?

Shuqing An,[1] Zhongsheng Wang,[1] Changfang Zhou[1] Bo Li,[2] Suhua Shi,[3] Donghai Yu,[1] Zhifa Deng,[1] Lin Chen[1]

[1] School of Life Science, Nanjing University, Nanjing 210093, China, anshq@nju.edu.cn;
[2]Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, 220 Handan Road, Shanghai 200433, China;
School of Life Science, Zhongshan University, Guangzhou 510275, China)

Biological invasions are widely envisaged as a component of global change, which not only threaten native biodiversity but also cause a considerable economic loss to the invaded areas. However, it is little known about the reason why some of species are successful invading new areas. At molecular level, most researchers have reported that high genetic diversity contributes to the success of plant invasions whereas a few other studies have shown that reduced genetic variation could make invasive species more successful. Obviously, they are contradictory. Our studies of *Spartina* in China shows that *S. alterniflora* with higher differentiation (*Fst*) were more successful in invading coastal ecosystems in China than *S. anglica* with low *Fst*, although the latter had much higher genetic diversity than the former. It is highly likely that greater number of chromosomes or higher genetic diversity (P and H) does not necessarily mean higher adaptability and more successful invasion for exotic species, but higher *Fst* confers higher invading ability on exotic species. Therefore, it is a rewarding work to further examine the genetic basis of successful invasions across taxa.

Potential for sediment-applied acetic acid for control of *Spartina alterniflora*

L.W.J. Anderson, B. Chae, A. Klug

U.S. Department of Agriculture, ARS Exotic and Invasive Weed Research, Davis, CA. lwanderson@ucdavis.edu

Acetic acid has been shown to kill sediment-borne propagules (e.g. hydrilla tubers and *Potamogeton nodosus* winter buds) and, most recently, attached algae on commercially produced mussels, at concentrations typically found in household vinegar (e.g. 1 to 5% vol/vol). We examined the effect of soil-applied acetic acid in replicated treatments of sediment-free rhizomes as well as drenches on sediments of transplanted, intact plants. Results showed that drenching transplanted, potted plants at 2.5 or 5 % acetic acid was sufficient to kill rhizomes and prevent regrowth in some replicates, though effects were variable. Exposure of cleaned rhizomes to these and lower concentrations (0.1, 1.0, 1.5% vol/vol) of acetic acid for a few hours to several hours resulted in increased conductivity in distilled water compared to unexposed controls, indicating loss of cellular integrity and leakage of electrolytes. Regrowth from exposed rhizomes was significantly inhibited at higher concentrations applied for 2 or 4h. When rhizomes that had been directly exposed to 1.5% acetic acid were transferred to outdoor conditions in Albany, CA, both shoot number and average plant height was reduced by over 90% nine months posttreatment. These results suggest that judicious drenching of sediments with acetic acid (e.g. at low tide) may be have utility as an alternative or adjunct to foliar applied herbicides. Most importantly, this approach may provide a winter-window of opportunity for treatments to prevent spring re-growth since Clapper rail nesting would not be impacted. Field assessment of efficacy and potential effects on non-target species will be conducted in 2005-2006.

Evolution of Invasive *Spartina* Hybrids in San Francisco Bay

D. R. Ayres[1] and D. R. Strong[2].

Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616
1drayres@ucdavis.edu
[2]drstrong@ucdavis.edu

Rapid evolution in contemporary time occurs where genetically variable individuals face strong selection pressures. Just such a conjunction is taking place in the intertidal marshes of the San Francisco estuary. Three decades ago, exotic smooth cordgrass, *Spartina alterniflora*, was planted in the Bay for erosion control and marsh restoration. The natural structure of the intertidal leaves broad expanses of open mud flats, critical foraging grounds for millions of birds. Fringing the upper mud flat margin is the native cordgrass, *S. foliosa* which, due to small stature and sparse growth, is unable to colonize the mud flats or modify their geomorphology, unlike the alien congener. Shortly after the introduction, the 2 species hybridized; in the last 20-odd years a broad array of genotypes has arisen through reciprocal hybridization and introgression.

Our research has found that some hybrids are taller, have more rapid rates of lateral expansion, have higher tolerance to salinity, have higher rates of self pollinated seed set, and are better sires on the native species than either parental species. We predict that these traits will result in 1, rampant colonization of open mud - both in the intertidal and in restoration sites, 2, invasion of the middle elevation *Salicornia*-dominated saline marsh plains, 3, isolated self-compatible plants founding new populations; and 4, hybrid pollen siring the lion's share of seed in surrounding *S. foliosa* plants in native marshes. Natural selection will favor these traits in a positive feedback that will result in an accelerating population growth rate of the fittest, most invasive hybrid genotypes. Indirect evidence that evolution has occurred is our finding of super-exponential growth of hybrid cordgrass cover in the Bay. Effective management and prediction of hybrid cordgrass invasion must incorporate a dynamic viewpoint of *Spartina* population parameters.

Spartina densiflora x *foliosa* Hybrids Found in San Francisco Bay

D. R. Ayres and A. K. F Lee

Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616,
drayres@ucdavis.edu, gerbil@mailbox.ucdavis.edu

Evolution in contemporary time can result when related species, brought together through human-aided introduction, hybridize. The outcomes can range from origination of new species through allopolyploidization to extinction of species through genetic amalgamation; both processes occur in the cordgrass genus, *Spartina*. Here we report the existence of a third *Spartina* hybridization, dis-covered in 2001, between introduced *S. densiflora* and native *S. foliosa* in San Francisco Bay, California. Coupling classical cytological methods with contemp-orary methods of flow cytometry, and nuclear and chloroplast DNA analysis, we were able to rapidly ident-ify hybrids and assess the entire known hybrid population for ploidy and genome size and most of the population for seed parentage. We found 30 F1 hybrids most of which had *S. densiflora* as the seed parent, and two triploid plants for which *S. foliosa* was the seed parent. No plants of higher ploidy have yet been found. The presence of triploid plants is important as it indicates that several avenues exist which may give rise to a new alloployploid species. Thus, this new hybridization offers us a chance to observe the origin of a new species. However, introductions of *Spartina* have resulted in major biological invasions in salt marshes around the world. Two of these invasions are driven by hybrids between native and introduced species. Given the history of *Spartina* invasions and hybridizations, we investigated whether *S. densiflora* x *foliosa* hybrids have the potential to spread and invade surrounding marshes in the Bay. This requires that hybrids tolerate marsh salinity and tidal inundation, and produce viable seed. A greenhouse experiment was performed with ten hybrid genotypes to assess their salinity tolerance against the parental species (*S. foliosa* - low elevation, low salinity; and *S. densiflora* -higher elevation, higher salinity). Salinity was increased by 10 ppt/week, and we measured several fitness indicators (tillars, height, inflorescences) for 10 weeks. In the field, we combined mapping data with elevational measurements (using a Total Station) to determine the tidal elevations and plant associations of hybrids. We also collected inflorescences from the field to measure their reproduction (seedset). We found that the salinity tolerance of some of hybrid genotypes exceeded that of both parental species.

Hybrid cordgrass (Spartina) and tidal marsh restoration in San Francisco Bay: If you build it, they will come

D. R. Ayres[1] and D. R. Strong[2]

Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616
[1]drayres@ucdavis.edu
[2]drstrong@ucdavis.edu

Restoration sites built on former salt ponds present an ideal combination of biotic and abiotic conditions for *Spartina* regeneration by seed. First, they are unvegetated so seedlings grow unhindered by competition with established plants. Second, they are graded to present a range of intertidal elevations enhancing the opportunity for colonization at elevations that are neither too saline, nor receive too much tidal innundation for cordgrass seedling germination and growth. Third, tidal waters enter through levee breaches, muting the force of the waves and reducing seedling loss due to physical removal by tidal action. And finally, many of the restored marshes in the southern and eastern regions of the Bay are near marshes invaded by hybrids, or are actually fed by tidal water which travels though hybrid *Spartina*-choked channels, thus ensuring a tidally-borne seed bank rich in hybrid *Spartina* seed. The result is that recent restoration sites in the area have been quickly colonized by large numbers of hybrid *Spartina*. This pattern can be expected to continue as more new marshes are opened until hybrid cordgrass is controlled.

Genetic divergence of native and invasive populations of *Spartina alterniflora*

K. J. Bando

Department of Environmental Science and Policy, Univeristy of California, Davis, CA 95616.
kjbando@ucdavis.edu

Exotic invasions of *Spartina* are associated with major alterations to mudflat habitat structure and function, nutrient dynamics, sedimentation, and hydrology. *Spartina alterniflora* was introduced to the Pacific Northwest, U.S. a century ago and has since invaded pristine open mudflats and undergone a large range expansion. Microsatellite markers were analyzed to characterize the genetic structure of native and invasive *S. alterniflora* populations. Native and invasive populations were genetically distinct, and populations within both ranges exhibited moderate to strong subdivision. These results indicate that *S. alterniflora* has undergone rapid evolution on the Pacific coast, and suggest the potential for local adaptation of invasive populations.

Shoreline development triggers massive ecosystem change in New England Salt Marshes

M. D. Bertness and B. R. Silliman

Recent work in New England salt marshes has revealed that local shoreline development is dramatically and likely irreversibly changing these ecologically valuable ecosystems. New England salt marshes have historically been nitrogen limited systems and the organization of these ecosystems has been largely structured by competition for nutrient resources. Local shoreline development that removes the woody vegetation terrestrial border that buffers marshes from runoff increases nitrogen supply and decreases salinity to marshes at very localized special scales. This results in a radical shift in the competitive dominance of marsh plants and increased herbivore pressure. The cordgrass, *Spartina alterniflora*, and the invasive reed, *Phragmites australis*, the best competitors in the community for light become the competitively dominant plants and drive the entire native salt marsh community to local extinction. Increased nitrogen supply also leads to increased herbivore pressure and potential consumer control of salt marsh primary production. Since *Phragmites* is a formidable ecosystem engineer that lowers the water table and increases the deposition of peat, the entire low marsh habitat of *Phragmites* dominated marshes can be lost along with many of the ecological services provided by tidal marshes. Ecosystem engineering by *Phragmites* makes the community shift initially triggered by shoreline development irreversible with marsh restoration requiring the physical removal of *Phragmites* peat.

Estimating the time for ecosystem recovery following *Spartina* eradication.

R.Blake, C. Tyler and E. Grosholz

UCDavis, One Shields Ave, Davis, CA 95616
reblake@ucdavis.edu

Invasive *Spartina* in Pacific Coast estuaries has had a dramatic impact on benthic habitats. As a result, both Washington and California have committed to broad scale programs aimed at eradicating *Spartina* as the first step in restoring native communities in estuarine habitats. One question regarding eradication is how long it will take the system to recover once *Spartina* has been eradicated. Typically when eradication is conducted using herbicides, the below ground portion of the plant consisting of roots and rhizomes remains in place, and this decaying plant matter produces high levels of porewater sulfide which could negatively affect recovery of native plants and animals. To determine how quickly recovery occurs following *Spartina* eradication, we measured the abundance and diversity of benthic invertebrates while simultaneously measuring porewater sulfide and ammonia at sites in Willapa Bay, WA that had experienced *Spartina* eradication either two years earlier or six years earlier. Results from the site with eradication two years earlier showed invertebrate abundance and diversity was still low at this site relative to control (noneradication) areas. Porewater profiles for sulfide and ammonia at this site showed high values indicating that the sediments were still affected by decaying below ground plant material. By contrast, results from the site with eradication six years earlier showed levels of invertebrate abundance and diversity that did not differ significantly from control (noneradication) areas. Here porewater profiles showed much lower levels of sulfide and ammonia similar to profiles from mudflat control areas that were never colonized by *Spartina*. We conclude that although rates of recovery may be site specific and can be strongly influenced by tidal height, sediment grain size, local flow conditions and other factors, full recovery following *Spartina* eradication may be expected for most sites between two and six years post-treatment.

Contrasting Effects of Native California Cordgrass and Invasive Hybrid Cordgrass on Benthic Invertebrates

E. D. Brusati and E. D. Grosholz

Environmental Science and Policy, University of California-Davis, 1 Shields Ave., Davis, CA 95616 USA
edbrusati@ucdavis.edu

In San Francisco Bay, California, mudflats and native California cordgrass (*Spartina foliosa*) marshes are being invaded by a hybrid cordgrass formed by hybridization between *S. foliosa* and introduced *S. alterniflora*. We investigated differences in vegetation and sediment structure, benthic infauna, and food webs within native and invaded *Spartina* marshes between San Francisco Bay and Bodega Bay, California.

The greatest impact of hybrid *Spartina* in San Francisco Bay appears to be its alteration of habitat structure rather than food webs. Habitat structure differed significantly between native and hybrid *Spartina*. Hybrid *Spartina* produced greater biomass both aboveground and belowground, and taller stem heights. *S. foliosa* contained significantly higher densities and biomass of infaunal organisms in benthic cores than did mudflats, while densities and biomass of infauna in hybrid *Spartina* were lower than, or did not differ from, mudflats. Stable isotopes of carbon and nitrogen were used to examine whether macrofaunal food webs differ between native or hybrid *Spartina* and mudflats. Some consumers collected within *Spartina* showed evidence of a shift in carbon isotope ratios indicating a possible increase in *Spartina* consumption within vegetation; however, the pattern was not consistent across species and sites. Due to the differences in their effects on infauna, hybrid *Spartina* and *S. foliosa* should not be considered equivalent for marsh restoration projects.

Wetland sediment dynamics in San Francisco Bay

J. C. Callaway

Department of Environmental Science, University of San Francisco, 2130 Fulton St., San Francisco, CA 94117;
callaway@usfca.edu

Spartina invasions are likely to cause increased rates of sediment accumulation due to greater plant stem densities and increased organic matter inputs. Despite these predictions, little research has evaluated sedimentation rates in native and introduced cordgrass patches in San Francisco Bay. Furthermore, very little baseline data are available to estimate sedimentation rates in native salt marsh habitats within the Bay. Anecdotal evidence supports the hypothesis that *Spartina alterniflora* colonization will lead to increased sediment accumulation. In addition, stations have been established to measure sedimentation rates in two natural marshes (Greco Island and the mouth of the Coyote Creek) and one restored marsh (Crissy Field) in the Bay. Rates are being measured using feldspar marker horizons and sedimentation-erosion tables (SETs). At each location, three replicate transects were established in summer and fall 2000, with stations in low-, mid-, and high-marsh areas; monitoring continues on an annual basis. Rates of sediment accretion at most sampling stations ranged from 2-5 mm/yr at both natural marshes, except at low-marsh sites along Coyote Creek, where accretion was up to 20 mm/yr. At Crissy Field, both accretion rates and changes in relative elevation were highly variable, with no consistent trends across the marsh. Although sedimentation in subtidal areas within Crissy Field have been reported to be high, accretion rates on the marsh surface were relatively low, averaging less than 1 cm per year.

Quantifying the potential impact of the *Spartina* invasion on invertebrate food resources for foraging shorebirds in San Francisco Bay

N. Christiansen and E. Grosholz

Department of Environmental Science and Policy, University of California, Davis, nicsen@ucdavis.edu, tedgrosholz@ucdavis.edu

San Francisco Bay holds extensive mud flat estuaries that are critical habitat for more than 1,000,000 migratory shorebirds making it the most important site in the western U.S. However, the mudflats productivity of invertebrate food sources is threatened by the encroaching invasive marsh grass *Spartina alterniflora* and hybrids with the native *foliosa*. Mudflats at higher tidal elevations are more valuable for foraging shorebirds because they are exposed for longer periods of time during the low tides. However, the upper mudflats are more likely to be colonized by the invading *Spartina*. To assess the potential effects of the advancing grass on the shorebird foraging habitat, the quality of foraging grounds relative to the extent of *Spartina* invasion are compared. We determined invertebrate abundance and biomass along transects extending from the edge of the *Spartina* meadow to the lowest tide line at two locations in the bay, San Lorenzo and Alameda. Along each of three transects, infauna cores were taken at intervals of 1, 10, 50, 100, 200 and 500 m or more from the *Spartina* edge. In each sample, we counted invertebrates and grouped them into annelid, mollusc, and crustacean, and calculated the biomass for each. We then analyzed these data to determine how abundance and biomass of invertebrate food resources changes with tidal heights that are predicted to be colonized by *Spartina*. We discuss the implications of these results with regard to future impacts of the *Spartina* for foraging shorebirds.

Remote Sensing, LiDAR and GIS Inform Landscape and Population Ecology, Willapa Bay, WA

J.C. Civille, S.D. Smith, D.R. Strong

Evolution and Ecology, University of California at Davis, Davis CA 95616 jcciville@ucdavis.edu

Spartina alterniflora (smooth cordgrass) is the mainstay of Atlantic and Gulf coastal salt marshes, but its introduction to Pacific estuaries has displaced native species, removed migratory shorebird habitat from use, and is rapidly filling in the shallow basin of Willapa Bay, WA. A fifty-five year time series of aerial photography has been developed into a high resolution dataset to study growth dynamics of the invasion, lateral spread of individual plants, elevation changes in the bay and to populate mathematic growth models. The final year of the series, comprised of color infrared images acquired in 2000, was orthorectified to remove radial and scale distortions, then classified through hierarchical supervised and unsuperived non-parametric methods into 330 thematic raster files, with <1m positional error and a 0.3m minimum mapping unit. These images became the spatial baseline for the remaining temporal *Spartina* datasets. These were either spatially adjusted (GIS layers), or georeferenced (aerial photography) to the Year-2000 data. LiDAR bathymetry data, acquired through a 2002 joint effort between UCDavis and NOAA's Coastal Services Center, has been incorporated into the demographic and population research, allowing detailed elevational change descriptions at levels previously unknown at this landscape scale. This has resulted in a high resolution temporal and elevational portrait of *Spartina*'s progress across Willapa's 190 km^2 of soft mud and sand tide flats. We have detected significant differences in *Spartina*'s growth rates across the bay, with increased lateral growth, meadow formation, and seedling establishment in soft mud substrates at mid-tidal elevations.

Controlling *Spartina* spp. with AquaMaster® and Habitat® herbicides: Why it works

R. P. Crockett

Monsanto Co. Vancouver, WA

AquaMaster® Herbicide containing the herbicide glyphosate, and Habitat® Herbicide containing imazapyr are effective when mixed together to control *Spartina* spp. AquaMaster provides post-emergence control of *Spartina* by interfering with the biosynthesis of three plant-specific amino acids, while Habitat interferes with the synthesis of three different plant-specific amino acids. Non-target, non-plant organisms are not affected by the mechanisms of action of these two products making them ideal choices for use in these sensitive habitats. The combination of mechanism of actions of these two herbicides has maximized *Spartina* control efforts in Washington State. Specific rate recommendations and methods of applications issues will be discussed in order to maximize control efforts.

Environmental factors, herbicide application timing issues, and using tide tables to your advantage when controlling *Spartina* spp.

R. P. Crockett

Monsanto Co. , Vancouver, WA

Successful control strategies used to remove *Spartina* spp. from tidal waters requires special attention be made to understand the relationships among all the interactive environmental conditions in addition to tide tables, and other mitigating issues. Herbicide performance in this otherwise 'hostile' environment depends upon the application methods, techniques used, methods employed, and careful understanding of maximum plant exposure issues. Debris on target plants poses special challenges for post-emergent herbicide effectiveness. A summary of research results and observations from work completed in San Francisco Bay, CA, and Washington State will be discussed.

Pollen limitation in a wind-pollinated invasive grass, *Spartina alterniflora*

H.G. Davis[1], C.M. Taylor[2], J.G. Lambrinos[3] and D.R. Strong[1,2]

[1]Center for Population Biology, University of California, Davis, California 95616, USA hgdavis@ucdavis.edu
[2]Section of Evolution & Ecology, University of California, Davis, California 95616, USA
[3]Department of Environmental Science & Policy, University of California, Davis, California 95616, USA

Limits to, and the consequences of, pollen availability in wind-pollinated plants have been little studied. Reproductive failure or depression because of a lack of available mates could lead to population demographic consequences for many species. Of particular interest is how pollen limitation affects the rate of spatial spread of invasive plants. We performed a manipulative pollen addition and exclusion study to investigate the role of pollen limitation in an invasive perennial estuarine grass, *Spartina alterniflora*. We found pollen impoverishment at the low density leading edge of a large invasion, causing an eight fold reduction in seed set among low density plants, though not among the high density plants. We found pollen loads on stigmas to be determined by pollen availability in the air. Furthermore, the amount of airborne pollen is dictated by the spatial pattern of plants, with much more pollen available over continuous meadows than in areas of low plant density. The delay of appreciable numbers of seed persists for decades until vegetative growth coalesces plants into continuous meadows, and this has slowed the rate of spread of the invasion.

Non-native cordgrass and the California Clapper Rail: biogeographical overlap between an invasive plant and an endangered bird

J. Evens[1], K. Zaremba[2] and J. Albertson[3]

[1]Avocet Research Associates, P.O. Box 839, Point Reyes Station, CA 94956 jevens@svn.net
[2]Invasive Spartina Project, 605 Addison, Suite Berkeley, CA 94710 kzaremba@spartina.org
[3]Don Edwards San Francisco Bay National Wildlife Refuge, P.O. Box 524, Newark, CA 94560 Joy_Albertson@r1.fws.gov

The federally-endangered California Clapper Rail (*Rallus longirostris obsoletus*) is a tidal-marsh dependent bird whose distribution is restricted almost entirely to San Francisco Bay. The native cordgrass, *Spartina foliosa*, has long been recognized as a critical component of clapper rail habitat. The distribution and abundance of the clapper rail has been monitored in the bay since the mid-1970s, and that effort has increased since the early 1990s. The concurrent invasion of the bay's tidal marshes by non-native *Spartina* has apparently impacted clapper rail abundance and distribution in some areas of the bay. In this poster we: (1) present the 2001 distribution of non-native *Spartina* relative to that of the clapper rails over the last 15 years; (2) discuss potential impacts of changing marsh ecology on rail distribution and abundance in both the near-term and the long-term, and (3) review "best management practices" for avoidance and minimization of impacts from *Spartina* control program activities on this endangered marsh bird.

Is ergot a natural component of *Spartina* marshes? Distribution and diversity of the fungal pathogen, Claviceps purpurea, from salt marsh habitats

A. J. Fisher

Department of Plant Pathology, One Shields Ave. Davis CA 95616. afisher@ucdavis.edu

Claviceps purpurea (Fr.) Tul, the cause of ergot disease, is a known component of Atlantic Coast *Spartina* marshes. A recent synthesis of previous research on *C. purpurea* morphology, alkaloid chemistry, and genetics identified three distinct groups within *C. purpurea* and one of these, Group 3 (G3), was found in two *Spartina* populations: on *S. alterniflora* in New Jersey, USA and on *S. anglica* in Southern England. This study was undertaken to better characterize the genetic diversity and geographic distribution of *Claviceps purpurea* in salt marsh habitats. Forty-three G3 isolates, representing 11 distinct populations were characterized based on the presence of an *Eco*RI restriction site in the 5.8S ribosomal DNA, and genetic similarity to isolates representing the other two *C. purpurea* sub-groups in (G1 and G2). According to random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) analysis, G3 *C. purpurea* is present on *S. alterniflora* along the Atlantic Coast of the United States, on *S. foliosa* in the San Francisco Bay, California, on *S. densiflora* in Argentina, and on *S. anglica* in Ireland. It is also found in Willapa Bay, WA on *Distichlis spicata* and on the invasive *S. alterniflora*. G3 isolates showed 35% within group similarity, Pacific Coast isolates showed 83% within group similarity and San Francisco Bay isolates were 90% similar. Three years of sampling show that rates of infection in *S. foliosa* marshes can be as high as 84%. This disease epidemic is likely to play a larger role in the survival of *S. foliosa* as invasive *Spartina* spp. continue to spread in the San Francisco Bay Area.

Will *Spartia anglica* invade northwards with changing climate?

A. Gray

ajg@ceh.ac.uk

Although other factors were involved (such as vigorous vegetative growth, hybridity, and extensive planting), the major reason for *Spartina anglica'*s success as an invasive species has been its ability to occupy mudflats to seaward of, and at lower elevations than, the previous lower limits of perennial saltmarsh vegetation. Slow early spread of the sterile hybrid, followed within 20 years by genetic isolation from its progenitor species due to polyploidisation, has meant that hybridisation with the native parent (unlike, for example, the invasion of *Spartina alterniflora* in San Francisco Bay), has not been a feature of the spread of the plant. Nor has it replaced the native *Spartina maritima* which largely occupies a different part of the saltmarsh.

The elevational niche of *S. anglica* was investigated in a range of UK saltmarshes and shown to extend below that of its main competitor, *Puccinellia maritima*, by an average of 68cm, a difference in elevation which can embrace a very extensive area of marsh. The niche of the two species overlapped by 20cm. The distribution of *Spartina* and *Puccinellia* within this zone of elevational overlap is likely to be determined by the outcome of their competitive interaction.

This paper considers the factors which affect the competitive interaction between the two species in relation to the projected changing climatic conditions under which this interaction will take place. A model, which describes the changes in the elevational niche of *Spartina* with increasing latitude, is linked to the observed differences in its fate in southern marshes, where it has formed extensive swards before suffering widespread dieback, and that in marshes at latitudes north of around 54 degrees N where it is replaced successionally by communities dominated by *Puccinellia.*

Biological control of *Spartina*

F. S. Grevstad[1], M.S. Wecker[2] and D.R. Strong[3]

[1,2]Olympic Natural Resources Center, University of Washington, Forks, WA 98331
grevstad@u.washington.edu
[3]Section of Ecology and Evolution, University of California, Davis, CA 95616

Biological control using introduced natural enemies can be an effective approach to the long term control of widespread weeds. A biological control program against *Spartina* spp. is underway in Washington State, where more than 10,000 ha of intertidal mudflat are affected by *S. alterniflora* and *S. anglica*. Releases of the planthopper *Prokelisia marginata* have been made into Willapa Bay each year since 2000 and into Puget Sound since 2003. Prior to introducing this insect, rigorous host specificity testing and a review by the Technical Advisory Group on Biological Control of Weeds confirmed that the risk to non-target plants was minute. Populations of the biocontrol agent were initially slow to establish and grow. However, early problems with high winter mortality have been remedied through a combination of improved release site selection and the use of cold-hardy east coast biotypes. At least two populations in Willapa Bay are well established and expanding. At a localized scale, we have measured 50% reductions of *Spartina* biomass and 90% reduction in viable seed set due to *P. marginata*. The full extent of the impact will only be known with time.

While the use of biological control in California may pose a risk to the closely related native *S. foliosa*, it would be an excellent option in other other parts of the world where *Spartina* has invaded and where there no closely related native *Spartina* species. In addition to *P. marginata*, other candidate biocontrol agents from the Atlantic Coast are currently being investigated.

Taking advantage of *Spartina*'s spatial pattern for efficient control

F. S. Grevstad

Olympic Natural Resources Center, University of Washington, Forks, WA 98331
grevstad@u.washington.edu

The invasion of open mudflats by *Spartina alterniflora* takes on a distinctive spatial pattern. This pattern of spread offers opportunity for strategic placement of control efforts. *Spartina* seedlings establish in open mud and then spread vegetatively to form expanding circular patches, which dot the mudflats and eventually coalesce into a contiguous monospecific meadow. The invasion typically begins in the upper tide zone and then moves down the tidal gradient. Using a spatially explicit model, I simulated the spread of *S. alterniflora* and compared various strategies for control in a situation where only a fraction of the total infestation could be controlled each year. A strategy of killing outlying patches first and then attacking the dense meadows (moving up the tidal gradient) led to eradication in up to 44% less time and effort than a strategy of targeting the dense meadows first and outlying patches second (moving down the tidal gradient). In the control of contiguous meadows located adjacent to the shoreline, the best strategy was to approach one end of the infestation, moving across the meadow to the other end. Suppression of seeds was not an effective control strategy by itself. In general, effective control strategies were those that first eliminate the plant in areas where current or future vegetative growth is greatest. Field application of these results for *S. alterniflora* and similar invasive plants could greatly reduce the costs of control work and improve the likelihood of local or complete eradication.

Spartina Control Approach and Experience in the San Francisco Estuary

E. K. Grijalva

San Francisco Estuary Invasive Spartina Project, 605 Addison St., Ste. B, Berkeley, CA 94710
ekgrijalva@spartina.org

In 2004, the San Francisco Estuary Invasive Spartina Project (ISP) initiated its first year of a region-wide, coordinated *Spartina* control program. The strategies for selection of the treatment locations and coordination of the projects was developed jointly by the ISP and its partners, which include a number of local, regional, state, and federal agencies and organizations. Funding for the work was contributed by many of the partners, by the ISP's hosting state agency, by grants from a State/Federal consortium, and other sources. The control plans were developed by the ISP, and implemented by the partners. Approximately 450 acres of non-native *Spartina* (*Spartina alterniflora* & hybrids, *S. densiflora*, and *S. patens*) were treated in 2004 using a variety of methods, including smothering or covering, digging, excavation with an amphibious excavator, and treatment with aquatic herbicide. The ISP facilitates acquisition of permits, grants, and contracts to implement the control work. Successful control of *Spartina* in the San Francisco Estuary is complicated by several factors, including an extremely short treatement season (September 1st to mid-October), and the greater-than-exponential spread of the S. *alterniflora* hybrid swarm. At the end of the 2004 control season, approximatly 1,550 acres if non-native *Spartina* remained untreated in the San Francisco Estuary. Assuming a treatment efficacy rate of 70% and an estimated expansion rate of over 100% per year, there will be greater than 3,000 acres of non-native *Spartina* in 2005. In order to address this, the ISP seeks to have plans in place for all non-native Spartina in the Estuary by the end of 2005, even though treatment may not be implemented on all sites until the following years due to the need to minimize impact on endangered species. One of the tools that the ISP hopes will help assure a successful control program the aquatic herbicide, Imazapyr, which will be registered for use in California by summer of 2005. The high efficacy and suitability of this herbicide for estuarine use bodes well for control efforts around the Estuary. Building upon the structure and partnerships developed during the 2004 Control Season, the ISP believes it is possible to set in place coordinated, sustainable, Estuary-wide management and control of non-native Spartina.

Consequences of *Spartina* invasion for migratory shorebirds and Canada geese

E. Grosholz[1], J. Black[2], P. Rosso[1], N. Christiansen[1] and R. Blake[1]

[1]*Department of Environmental Science and Policy, University of California, Davis, Davis, CA, tedgrosholz@ucdavis.edu, phrosso@ucdavis.edu, nicsen@ucdavis.edu, reblake@vims.edu*
[2]*Department of Wildlife, Humboldt State University, Arcata, CA, jmb7002@humboldt.edu*

Predicting the consequences of *Spartina* invasion on higher trophic levels may be complicated by indirect effects at lower trophic levels. Here we report two studies documenting interactions of *Spartina* with bird consumers. In the first study, we used high-resolution LIDAR data for two sites in San Francisco Bay to generate tidal elevation profiles in order to calculate the loss of foraging habitat under various scenarios of *Spartina* invasion. We also used benthic invertebrate data collected along extensive tidal elevation gradients to quantify invertebrate biomass that would accompany habitat loss. We found the magnitude of the impact *Spartina* depends significantly on the tidal elevation ultimately colonized. The second study examined the influence of herbivory by Canada geese on the spread of hybrid *Spartina*. Using manipulative field enclosures, behavioral studies with captive geese, and distributional data from San Francisco Bay, we found that Canada geese severely graze the native *Spartina foliosa* during winter and early spring, but avoid grazing on hybrid *Spartina* entirely. Additional experiments showed the rate of lateral spread of the hybrid *Spartina* into native *Spartina* areas was greater when geese were excluded suggesting their herbivory may accelerate the spread of hybrid Spartina. These studies emphasize the reciprocal impacts and complex interactions between invasive *Spartina* and foraging birds and the difficulty of predicting the consequences of *Spartina* invasion at higher trophic levels based on direct effects at lower trophic levels.

Toxicity of Rodeo® and Arsenal® Tank Mixes to Juvenile Trout

K. King, C. Curran, B. Smith, D. Boehm, K. Grange, S. McAvinchey, D. Sowle, K. Genther K, R. Higley, A. Schaaf, C. Sykes, J. Grassley, and C. Grue

School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195
cgrue@u.washington.edu

Efforts to utilize herbicides for the control of *Spartina* spp. have been hampered by concerns over potential non-target effects. As an initial step in comparing the non-target toxicity of tank mixes of Rodeo® (ai=glyphosate) and ARSENAL (ai=imazypyr), we determin-ed 96-h static LC50s for three formulat-ed products: Rodeo 53.8% ai (782 ppm); ARSENAL Herbicide, 28.7% ai, (77,716 ppm); and ARSENAL AC, 53.1% ai, (22,305 ppm) using juvenile rainbow trout (*Oncorhynchus mykiss*, ca. 0.65 g). We then determined LC50s for tank mixes expressed as ppm surfactant for Rodeo with the surfactants R-11® (5.4 ppm) and LI 700® (23 ppm) and ARSENAL Herbicide with the surfactants HASTEN® (113 ppm) and AGRI-DEX® (479 ppm), and compared these values with LC50s for the surfactants alone (R-11: 6.0; LI 700: 17; HASTEN: 74, AGRI-DEX: 271 ppm). Results suggest (1) all three herbicide formulations have relatively low toxicity to juvenile rainbow trout, but their LC50s differ by 2 orders of magnitude, (2) toxicity of the tank mixes is driven by the surfactants and also varies by 2 orders of magnitude, and (3) depending on the surfactant selected and its percentage of the tank mix, surfactants may pose a greater hazard to non-target species than the formulations tested.

Where do we go from here? Alternative control and restoration trajectories for a marine grass (*Spartina anglica*) invader in different habitat types

S.D. Hacker[1] and M.N. Dethier[2]

[1] *Department of Zoology, Oregon State University, Corvallis, OR 97331; hackers@science.oregonstate.edu*.
[2] *Department of Biology and Friday Harbor Labs, University of Washington, Friday Harbor, WA 98250; mdethier@u.washington.edu.*

It is well known that some invasive species can cause ecosystem-level effects by modifying important structural and functional attributes of communities. These species have extraordinary influence because they alter ecological processes in multiple ways, are hard to control, and their removal may result in unexpected changes that lead the system away from restoration and towards an alternative state. The English cordgrass, *Spartina anglica*, has invaded large areas of protected shoreline in Washington state and is the target of intensive removal efforts. English cordgrass invades and modifies a variety of habitat types, from unvegetated mudflats and cobble beaches to establish low and high salinity native marshes. We show, using observational and experimental data, that cordgrass invasion, modification, removal, and restoration vary dramatically among these habitats. Cordgrass has the largest effects in mudflats and low salinity marshes, where its spread is rapid, modifications are the most dramatic, and removal is problematic without consistent efforts. In contrast, cordgrass has a more meagre existence in cobble beach and high salinity marshes, where its spread is slow, modifications are modest, and removal is more successful. Early evidence suggests that cobble beaches show a post-removal restorative response while the other habitats will continue to retain the legacy effects of the invasion and follow an alternative trajectory.

Modeling the spread of invasive *Spartina* hybrids in San Francisco Bay

R. J. Hall, A. M. Hastings and D. R. Ayres

University of California, 1 Shields Avenue, Davis, CA 95616, rjhall@ucdavis.edu

The emergence of highly fit hybrids between native and introduced species is an increasingly widespread problem which can impact on entire ecosystems. In San Francisco Bay, a swarm of hybrid cordgrass (*Spartina foliosa* x *alterniflora*) is covering vast areas of intertidal mudflat vital for feeding shorebirds, and threatens the native cordgrass *S. foliosa* with extinction. Here we present a simple integro-difference equation model to assess the importance of enhanced hybrid fitness traits in explaining this invasion. We find that incorporating elevated hybrid growth rate, seedling survival and pollen production into the model predicts the observed faster than exponential spread of hybrid cordgrass in the Bay. The model provides a novel approach to evaluating the contributions of population dynamic and genetic processes in the study of hybrid invasions.

A survey of spatial spread with applications to the *Spartina* question

A. Hastings

amhastings@ucdavis.edu

There have been recent advances in understanding the dynamics of spatial spread, emphasizing issues that are of importance to understanding invasive *Spartina*. I will give an overview of the current state of the art in the modeling of spread, with an emphasis on recent developments that focus on discrete time dynamics and the role of different dispersal patterns and temporal and spatial heterogeneity. I will discuss how these more abstract developments influence the development of models specifically designed to understand spread of *Spartina*, indicating what kinds of data are needed.

Implementing the Strategy for the Management of Rice Grass, *Spartina anglica*, in Tasmania, Australia.

P. Hedge[1], C. Shepherd[2] and C. Dyke[3]

[1]*National Oceans Office, GPO Box 2139 Hobart Tasmania 7001 Australia*
[2]*Department of Primary Industries, Water and Environment, GPO Box 44 Hobart Tasmania 7001 Australia*
[3]*Rice Grass Advisory Group, PO Box 83 Triabunna Tasmania 7190 Australia*

The development of an integrated management strategy marked an important turning point in the management of *Spartina anglica* in the waterways and estuaries of Tasmania. This paper focuses on the implementation of the management strategy in the period from 1998 to 2004. Risks to the success of the management program are identified and linked to specific management tasks, including the development of environmental monitoring programs and environmentally responsible, safe, practicable and cost effective control techniques. The tools and approaches used to develop and maintain stakeholder support for rice grass management, assemble and manage an expert management team and assess the success of the management program are identified and discussed. Current challenges and lessons learnt from the Tasmanian approach are summarised.

Assessing the role of *Spartina anglica* productivity in bivalve diets using stable isotope mixing models

C. E. Hellquist and R. A. Black

School of Biological Sciences Washington State University Pullman WA 99164-4236, ehellqui@mail.wsu.edu

Spartina anglica has converted native coastal mudflat communities that had little or no emergent vascular vegetation into expansive cordgrass meadows in northern Puget Sound, WA, USA. A consequence of *Spartina* productivity on invaded mudflats may be altered trophic patterns. Three bivalves (*Macoma balthica, Mya arenaria*, and *Mytilus* sp.) are common at the edges of *Spartina* meadows. To understand whether *Spartina* is contributing to these bivalves' diets, we compared the stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) of the bivalves to potential food sources including *Spartina*, suspended particulate organic matter, macroalgae, and other vascular plants. Using a multiple source linear mixing model (IsoSource), we estimated the feasible contributions of potential food sources to the diets of *Macoma, Mya*, and *Mytilus*. In duel isotope scatterplots ($\delta^{13}C$ and $\delta^{34}S$; $\delta^{13}C$ and $\delta^{15}N$), the isotopic ratios of *Macoma* were similar to values for *Spartina*, macroalgae, and *Zostera marina*. Our estimates suggest that *Spartina* biomass may be 55-65% of the diet of *Macoma*, while dead *Spartina* biomass may contribute an additional 5-15%. For *Mya* and *Mytilus*, the mixing model did not provide strong resolution of potential dietary contributions. The lack of resolution for *Mya* and *Mytilus* indicates that the sampled potential food sources contribute little ($\leq$ 15%) to the diets of these bivalves or that our sampling was inadequate. Unlike *Macoma*, it appears that the contributions of *Spartina* to *Mya* and *Mytilus* diets are small, despite the extensive *Spartina* meadows in close proximity to these common bivalves.

The influence of intertidal zone and native vegetation on the growth of *Spartina anglica* in northern Puget Sound, WA, USA

C. E. Hellquist and R. A. Black

School of Biological Sciences Washington State University Pullman WA 99163 ehellqui@mail.wsu.edu

Spartina anglica is an invasive species of mudflats, tidal channels, salt marshes, and gravel beaches in northern Puget Sound, WA, USA. This non-native cordgrass is especially adept at spreading in soft-sediment habitats (e.g. mudflats and tidal channels) where native vegetation is sparse or absent. *Spartina* cover decreases as both intertidal elevation and native plant cover increases. This pattern is especially apparent where mudflats with *S. anglica* abut high salinity pocket salt marshes. We measured *S. anglica* seedling growth and physical conditions (salinity and redox potential) along an intertidal gradient from mudflat to high salt marsh. Along the intertidal gradient, we measured the growth of transplanted *Spartina* seedlings in plots with native vegetation intact and removed. In the mudflat, unmanipulated (*in situ)* seedlings had 0% mortality and produced 425 (SE±112) tillers whereas seedlings transplanted within the mudflat had 40% mortality and produced 171 (SE±33) tillers on average. In the *Salicornia virginica*-dominated low marsh zone, *Spartina* mortality was 6% and tiller production averaged 157 (SE ±14) without competition from *Salicornia*. Grown among *Salicornia*, *Spartina* seedling mortality was 10% and mean tiller production was 81 (SE±10). At the highest intertidal zone dominated by *Distichlis spicata*, *Spartina* mortality was 43% and on average 32 (SE±7) tillers were produced without competiton from *Distichlis*. Among *Distichlis, Spartina* seedling mortality was 100%. Total *Spartina* biomass was also lower at higher intertidal elevations and within native vegetation. The spread of *S. anglica* into upper intertidal levels is attenuated by both physical conditions and competition with native salt marsh plants.

Fragment Propagules of *Spartina alternaflora* & Potential Eastern Pacific Dispersal

V. Howard and M. Sytsma

PSU, Center for Lakes & Reservoirs – ESR, PO Box 751 Portland, OR 07207-0751, vhoward@pdx.edu

Commonly used mechanical control methods on *Spartina alternaflora* involve varying levels of disturbance to rhizomes and roots. We examined the viability of rhizome fragments and their potential role in dispersal.

Production of rhizome fragments by rototilling was studied in Willapa Bay, Washington. The top 10 cm of the sediment contained an average of 310 fragments/meter^2. Median rhizome length was 3.7 cm (95% CI = 3.2 to 4.5 cm, n=233). At least one vegetative shoots was attached to 87% of rhizomes.

Survivorship of *S. alternaflora* rhizome fragments from Willapa Bay and San Francisco populations was investigated using a three-way factorial design. Two fragment sizes, approximating the those found in the Willapa Bay, were immersed in freshwater, 15 ppt or 35 ppt saltwater for 3, 8 or 15 days. Fragments were then individually planted and grown in greenhouse ponds for four months. Rhizome survivorship was low (8.6% or less) in all 35 ppt treatments. Survivorship ranged from 37.3 to 87.5% in freshwater and 15 ppt treatments.

Large rhizomes appeared to have higher survivorship than small rhizomes at all salinities. The length of time the rhizome fragments were immersed prior to planting appeared to have little or no effect on survivorship.

Low survival in high salinity water, even for short periods, suggests that rhizome fragments have a low probability of surviving ocean dispersal between estuaries. Higher survival at lower salinities suggests that dispersal within an estuary may be more likely for large and small rhizome fragments. Rototilling for control of *Spartina* may spread the infestation within an estuary but is unlikely to result in spread to other estuaries. Tilling should be used with caution in estuaries with small, isolated populations of *Spartina*.

While ocean transport of rhizome fragments appears to be a small risk, ocean transport of viable *S. alterniflora* seed is likely. A drift card study was begun in late September 2004 with the goal of better understanding potential dispersal patterns from invaded west coast estuaries. Monthly releases of cards from Humboldt and San Francisco bays in California, as well as Willapa Bay, Washington will aid identification of wrack deposition sites. Data from the first two months of this year-long study will be presented.

Coevolutionary ecology of *Spartina alterniflora* and the common phloem-feeding insect *Prokelisia marginata*: Lessons from the native and invasive ranges

M. L. Katz

Section of Evolution and Ecology, One Shields Avenue, Davis, CA 95616 USA, mlkatz@ucdavis.edu

Theory predicts that when species invade new regions and escape from their coevolved natural enemies, natural selection should result in the evolution of reduced levels of defense against those enemies, provided there is a cost to such defenses. In Willapa Bay, Washington, *Spartina alterniflora* appears to have evolved reduced defense to the phloem-feeding planthopper *Prokelisia marginata*, a common herbivore on *S. alterniflora* throughout the plant's native range. However, analysis of plant genets from areas that differ in the age of invasion in Willapa Bay indicates that this evolution of reduced defense may be largely due to a founder effect rather than natural selection. Analysis of a cpDNA gene indicates that Willapa Bay *S. alterniflora* lacks the genetic variation that is found in the native range, corroborating the role of a founder effect as the primary cause of evolutionary change in this invasive population. To determine how important a selective agent *P. marginata* is on *S. alterniflora*, a greenhouse study was performed using genets from throughout the native range of *S. alterniflora*, and *P. marginata* from three representative locations: Georgia, Virginia and Rhode Island. This study demonstrates that this plant-herbivore interaction impacts the evolution of both plant and insect traits across the native range of *S. alterniflora*. These results may aid in the successful implementation of biocontrol of Willapa Bay *S. alterniflora* using *P. marginata*.

Regulators of *Spartina alterniflora* recruitment in Willapa Bay, WA

J.G. Lambrinos[1], D.R. Strong[2], J.C. Civille[3] and J. Bando[4]

[1]Department of Environmental Science and Policy, University of California, Davis CA 95616. jglambrinos@ucdavis.edu [2]drstrong@ucdavis.edu [3]jcciville@ucdavis.edu [4]kjbando@ucdavis.edu

The spatial expansion of *Spartina alterniflora* populations in Willapa Bay, WA has been driven primarily by seedling recruitment. We measured this recruitment at the landscape scale using a series of precision GPS guided airboat censuses. Recruitment is highly variable across both space and time. Over the four years of observation, yearly average estuary wide recruitment varied from a low of 12/ha to a high of 500/ha. Variability across individual census plots was even greater, ranging from 0/ha to over 4000/ha. Several factors influence this variability. 1) Local recruitment tracks variation in local seed production. 2) Tidal elevation and hydrological conditions influence the spatial pattern of seed deposition and retention, and this is reflected in micro-spatial recruitment patterns. 3) Substrate characteristics independent of elevation and hydrology significantly influence seedling survivorship and growth. These results have broad implications for the management of invasive *Spartina* populations. Poor recruitment years afford windows of opportunity for effective control, but could equally lead to complacency and an inadequate response during recruitment pulses. The strong relationship between local seed production and local recruitment suggests that control strategies that do not explicitly account for inter-regional dispersal can still be successful over the short term, even if long term management requires an explicit understanding of regional dispersal pathways. Finally, the strong differences in recruitment and growth patterns caused by substrate differences may allow the categorization of sites by recruitment risk.

Influence of *Spartina* hybrid invasion of tidal flats on belowground communities and trophic processes in San Francisco Bay

L.A. Levin[1], C. Neira[1] and E. Grosholz[2]

[1] Scripps Inst. of Oceanography, La Jolla CA, 92093-0218
[2] Dept. of Environmental Science and Technology One Shields Ave, University of California Davis Davis, CA 95616

By vegetating previously open tidal flats, the invasion of *Spartina* has introduced a myriad of changes to benthic ecosystems of San Francisco Bay. Our recent research has examined mechanistic explanations for these changes in several arenas. We have conducted experiments to illucidate *Spartina* induced-plant structure effects, predation, sulfide stress and detritus availability. This talk will focus on use of stable isotopic methods (natural abundance and enrichment with tracers) to examine feeding preferences of soil invertebrates and how these might mediate effects of *Spartina* invasion on food web structure. We documented a shift away from algal-consuming infauna on the open tidal flat to detritus feeders in the *Spartina* marsh. Experiments using ^{15}N-labeled *Spartina* hybrid show that oligochaetes, nereid and capitellid polychaetes are primary *Spartina* detritus consumers. This observation was true independent of habitat (tidal flat vs marsh), detritus location (surface vs subsurface), and exposure time. These consumers are also the taxa most tolerant of *Spartina* invasion. In contrast bivalves and gammarid amphipods that consume surface (^{13}C-labeled) algae have much lower densities on *Spartina*-vegetated habitat than in open tidal flats. *Spartina*-induced changes in macrofaunal feeding modes and life habits have implications for a variety of ecosystem services including support of higher trophic levels and nutrient cycling. Our data also suggest that *Spartina* detritus may influence other benthic ecosystem functions (primary productivity, structural attributes) indirectly through N leaching or degradation and sulfide buildup.

Spartina alterniflora invasions in the Yangtze River estuary, China: Current status and consequences

Bo Li, Jihua Wu, QingWang, Zhongyi Chen, Bin Zhao, Zhijun Ma, Jiakuan Chen

Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, #220 Handan Road, Shanghai 200433, China, bool@fudan.edu.cn

The Yangtze River estuary is an important ecoregion as it is the home for many economically and ecologically important species, and provides important stopover sites for migratory birds on E. Asian-Australasian Flyway. However, *Spartina alterniflora*, native to North America, was introduced to the estuary in mid 1990s by both natural dispersal and humans and has become a dominant species in tidal flats and salt marshes in the estuary within less than 10 years, whose invasions led to multifold consequences to the estuary:

1) *S. alterniflora* had great competitive effects on native species, including *Scirpus mariqueter* and *Phragmites australis*. The decline of *Scirpus* abundance might eventually affect shorebird communities through different mechanisms.

2) *Spartina* invasions were found to significantly affect the nematode communities: the structure of trophic groups of nematodes was significantly altered, with more bacterial feeders and fewer algal and plant feeders and predacious nematodes in *Spartina* communities.

3) The total density of macrobenthonic invertebrates was not affected by *Spartina* invasions, but the abundance of dominant species was significantly altered, with detritivores decreasing and suspensivores and herbivores decreasing.

Measuring the impacts of benthic invertebrates on elemental cycling, nutrient chemistry and consequences for growth *Spartina* seedlings.

U. H. Mahl, A. C. Tyler and E. D. Grosholz

Department of Environmental Science and Policy, UC Davis, Davis CA, uhmahl@ucdavis.edu, actyler@ucdavis.edu, tedgrosholz@ucdavis.edu

The invasion of *Spartina* in Pacific Coast estuaries has had a profound effect on both the physical characteristics of the system and on benthic community structure. These changes in the benthos may have an important reciprocal effect on the growth of *Spartina* and the progression of its invasion. Invertebrate communities can influence elemental cycling and nitrogen availability, which can either limit or facilitate the growth of the *Spartina.* To determine how different functional groups of invertebrates may influence *Spartina* growth, we conducted mesocosm experiments with simulated tidal conditions in the laboratory using representative species from each of three groups (surface deposit feeders, subsurface deposit feeders, and grazers). In the first experiment, we measured the effects of these species on nutrient cycling without plants. In a second experiment, we used a single representative species from each group and measured its effects on the growth of *Spartina* seedlings. In a third experiment, we measured the impact that these species had on the growth of a native species of green macroalgae, *Ulva* sp. Large blooms of *Ulva* sp. create anoxic conditions during the late summer, which may have negative consequences for seedling establishment as well as strongly modifying nutrient cycling in this habitat. The magnitude of the effects on *Spartina* and *Ulva* growth gives some insight into how different functional groups of invertebrates may influence growth and spread of *Spartina* in the field by mediating elemental cycling and nutrient availability in sediments.

Oxygen transport and physiological mechanisms influencing zonation in salt marsh grasses

B. R. Maricle and R. W. Lee

School of Biological Sciences, Washington State University, Pullman, WA 99164-4236 bmaricle@mail.wsu.edu

Many wetland plants have been shown to transport atmospheric oxygen internally to support respiration in submerged tissues. This ability may allow plant survival in low intertidal marsh areas and is often implicated in estuarine zonation. Oxygen transport and metabolic characteristics related to anoxia tolerance and rhizosphere oxidation were studied in the emergent estuarine species *Spartina alterniflora*, *S. anglica*, *S. densiflora*, *S. patens*, and *Distichlis spicata* (Poaceae). Plants were grown in greenhouse experiments under simulated estuarine conditions. Experiments were conducted to monitor how oxygen transport is affected by hypoxic conditions typical of estuarine mudflats. All species showed a strong ability to respire anaerobically. The high intertidal marsh species *S. densiflora*, *S. patens*, and *D. spicata* were found to have high root aerobic respiration rates, low to moderate oxygen transport rates, and an apparent high sensitivity to sulfide. The low intertidal marsh species *S. alterniflora* and *S. anglica* had lower aerobic respiration rates, moderate to high oxygen transport rates, and a lower sensitivity to sulfide. *Spartina anglica* appeared to have the greatest ability to transport oxygen and was more resistant to mudflat-related stressors compared to the other plants in this study. While oxygen transport is usually regarded as the most important physiological determinant of saltmarsh zonation, it was found that both high and low marsh species are capable of substantial internal oxygen transport. Evidence is presented that other physiological differences, especially aerobic respiration rates and sulfide sensitivity, may account for differences in estuarine zonation between species.

Effects of salinity on photosynthesis in C_4 estuarine grasses

B.R. Maricle, O. Kiirats, G.E. Edwards and R.W. Lee

School of Biological Sciences, Washington State University, Pullman, WA 99164-4236
bmaricle@mail.wsu.edu

The effects of salinity on gross and net photosynthetic rates were measured in estuarine C_4 grasses. CO_2 fixation rates were most affected by increasing salinity in *Spartina densiflora* and *S. alterniflora*. Photosynthetic rates were moderately affected in *Distichlis spicata* and *S. patens*. In *S. anglica* photosynthetic rates were maintained with increasing salinity, although there was a decrease in the internal CO_2 concentration, suggesting some decrease in stomatal conductance. The results suggest *S. anglica* has a superior level of salt tolerance compared to other species in the study. The maximum quantum efficiency of CO_2 fixation measured under limiting light decreased with increasing salinity in *S. alterniflora* and *S. patens*, indicating an increase in leakage of CO_2 from the CO_2 pump. While carbon fixation was decreased under increasing salinity in most species, fluorescence yield data showed there was little affect on the use of solar energy in photochemistry. This indicates additional sinks are induced under salinity for use of photochemically generated energy (e.g., increase in the CO_2 pump, photorespiration, or Mehler reaction). Also, in *S. patens* and *D. spicata,* which had moderate decreases in photosynthesis, nonphotochemical quenching mechanisms increased with salinity indicating some of the excess light energy was lost as heat. Therefore, excess excitation energy was diverted away from the photosynthetic reaction centers to prevent photoinhibition. F_V/F_M ratios were not significantly decreased by increasing salinity, suggesting there was no damage to PSII reaction centers in any species.

Spatial Analysis of *Spartina* Invasion in San Bruno Marsh using Aerial Photos

Y. Matsumoto

Department of Geography, San Francisco State University, yukmatsu.aol.com

Invasive *Spartina* was introduced into San Francisco Bay over 30 years ago and has become widespread. I used remote sensing (RS) and geographic information systems (GIS) to study the dynamics of this invasion in San Bruno Marsh. I assessed the feasibility of using RS and GIS for monitoring invasive *Spartina*. *Spartina* invaded via the establishment of new patches mostly in an alongshore direction with little expansion into mudflats. The growth rates of *Spartina* patches declined as they aged. Estimates of the acreage of *Spartina* and expansion rates based on RS and GIS are comparable to estimates from field surveys. However, estimates from image analysis may be more accurate because of subjectivity in estimating *Spartina* cover in the field. These comparisons suggest that RS and GIS along with limited field surveys may be more reliable and cost effective in monitoring invasive *Spartina.*

The impact of *Spartina alterniflora* on song sparrow and marsh wren territories in San Francisco Bay salt marshes

J. McBroom[1], J. C. Nordby[1], A. N. Cohen[2] and S. R. Beissinger[1]

[1] U. of CA, Berkeley, Department of Environmental Science, Policy and Management
[2] San Francisco Estuary Institute, Oakland, CA
sparrow_wrangler@yahoo.com

The invasion of *Spartina alterniflora* alters the structure and composition of the tidal marsh ecosystem in San Franciscio Bay. These changes in habitat directly impact the Alameda song sparrow (*Melospiza melodia pusillula)*, a resident saltmarsh bird that is a California Species of Special Concern. These sparrows are also affected by the subsequent occupation of this invaded habitat by a potential competitor: the marsh wren (*Cistothorus palustris*). During the breeding season, we used focal observations to map the territorial boundaries for each male song sparrow and marsh wren at each of three field sites. We then assessed the vegetation composition of each territory as well as the amount of territory overlap between the two species. Although song sparrows did include some invasive *S. alterniflora* habitat in their territories, no male sparrow had a *Spartina*-only territory. In contrast, marsh wren territories were more highly correlated with invasive *S. alterniflora* and many territories were exclusively composed of the invasive cordgrass. We also found that there was little overlap between the territories of the two species, possibly due to differing habitat preferences. These findings suggest that the changes in salt marsh habitat associated with the invasion of *S. alterniflora* may favor marsh wrens over song sparrows and could eventually result in a decrease in saltmarsh song sparrow populations.

Controlling invasive *Spartina*: The New Zealand success story

G. Miller[1] and K.Crothers[2]

[1]Department of Conservation, PO Box 743 Invercargill, New Zealand. gmiller@doc.govt.nz
[2]Environment Southland,Private Bag 90116 Invercargill, New Zealand

Spartina is being successfully controlled in the estuaries of southern New Zealand. With an estimated 800ha (2000 acres) of the New River estuary near Invercargill being affected by *Spartina* in 1988, this has now been reduced to less than 1 ha (2.5 acres). Within the next two years *Spartina* will be at zero density in these estuaries.
Spartina was originally planted in the Invercargill district in the 1930's to reclaim land in the estuary for the increased industrial activities in the area. It wasn't until the 1970's that *Spartina* was first acknowledged as a serious problem causing significant impacts on the estuarine values, including wading birds and shellfish habitats, and thus declared an invasive weed to the area.
Various control techniques were trialled starting in the early 70's producing some good results but were discontinued in the mid 80's. In 1988 the newly formed Department of Conservation took over the responsibility for the control of *Spartina* and trials were started to find a method to control its spreads.
Trials with different chemicals show Haloxyfop (registered as Gallant[nf]) to be the most successful herbicide with up to 95% kill on first application. Trials on application techniques have seen the combination of helicopter boom spraying of meadows and an 8 wheeled Argo fitted with tracks and spray unit for follow-up as the most efficient methods of applying this chemical. These methods are now being used extensively around New Zealand.

Feedbacks among mean sea level, productivity, and the equilibrium elevation of east coast salt marshes

James T. Morris

Department of Biological Sciences and Baruch Institute, University of South Carolina, Columbia, SC 20208

Long-term measurements in South Carolina have shown that *Spartina alterniflora* marshes remain in equilibrium with mean sea level (MSL) by virtue of feedbacks between MSL, primary productivity, and sediment accretion. Moreover, the equilibrium elevation of a marsh, and its productivity, are functions of the *rate* of increase of MSL. As sea level increases or decreases relative to the marsh surface, primary productivity increases or decreases, respectively, which alters the net accretion rate and raises or lowers the elevation of the marsh surface. These homeostatic adjustments in marsh elevation are slow in comparison to interannual anomalies and long-period (decadal) cycles of sea level, and this lag in the marsh response results in significant variation in annual primary productivity. Negative feedback and stability exist only at elevations that are super-optimal for primary production. In this range, sediment salinity is sensitive to flooding and evapotranspiration, and primary production is stimulated, and salinity decreased, by increases MSL. Adjustments in productivity and sedimentation rate help to maintain the marsh in a dynamic equilibrium with sea level, as long as the marsh elevation remains within the range that is super-optimal for the vegetation. The equilibrium elevation varies inversely with the rate of sea-level rise. A long-term trend of increasing productivity averaging 32 g m^{-2} yr^{-1} in South Carolina, accompanied by major changes in biogeochemistry, suggests that S.E. coast marshes have lost elevation in response to rising sea level.

Washington State *Spartina* Program – A comprehensive look at the management of *Spartina* eradication in Washington State

K. Murphy[1], D. Heimer[2] andW. Brown[3]

[1]Washington State Department of Agriculture; P.O. Box 42560, Olympia, WA 98504-2560, kmurphy@agr.wa.gov
[2]Washington State Department of Fish and Wildlife; 4516 N 28th, Tacoma, WA 98407, heimer@harbornet.com
[3]Washington State Department of Fish and Wildlife P.O. Box 47027 Olympia, WA 98504-7027 Wendy.Brown@wadnr.gov

Washington State has been fighting the spread of invasive *Spartina* since the early 1990's. Until recently the progress in Puget Sound was slow or in the case of Willapa Bay, being lost. However, with appropriate funding, increased support, improved tools, and better cooperation between the entities involved, the, eradication in Puget Sound is progressing at a rapid pace, and the tide is finally being turned in Willapa Bay.

This presentation will focus on the challenges that have led to where we are today in Washington State from an on-the-ground management prospective. We will focus on everything from choosing the correct control tools to the importance of community-wide support and cooperation necessary to have a successful program, no matter the size of the infestation that is being dealt with.

The goal of this presentation will be to give the managers in California more information to help in their fight against *Spartina* and to educate everyone on the progress of the *Spartina* Eradication Program in Washington State.

Mechanistic processes driving shifts in benthic infaunal communities following *Spartina* hybrid tidal flat invasion

C. Neira[1], L.A. Levin[1] and E.D. Grosholz[2]

[1] Integrative Oceanography Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0218, USA. cneira@coast.ucsd.edu
[2] Department of Environmental Science and Policy, One Shields Ave. University of California, Davis, CA 95616

Recent studies performed at Elsie Roemer (south San Francisco Bay) showed up to 75% reduction in macrofaunal abundances, as well as important shifts in species composition in the *Spartina* hybrid-invaded patches relative to tidal flats. Surface feeders such as *Gemma gemma* (Bivalvia), *Corophium* and *Grandidierella* (Amphipoda), and *Tharyx* and *Eteone* (Polychaeta) were the most affected by invasion, while subsurface feeders such as capitellid polychaetes and tubificid oligochaetes were less or unaffected. Such changes can have profound implications for food web function because surface feeders are the taxa most accessible to epibenthic consumers including fishes and birds. The causes and mechanisms of the changes observed, however, remained unknown. We tested several mechanisms that could underlie observed changes in macrofaunal community structure following tidal flat invasion by the *Spartina* hybrid. Specifically we performed a series of manipulative studies to examine *Spartina* influence on vegetation structure, larval supply (and animal migration), water flow, food availability, and predation, as mediators of change for sediments and macrobenthos.

The impact of invasive *Spartina alterniflora* on song sparrow populations in San Francisco Bay salt marshes

J. C. Nordby[1], A. N. Cohen[2] and S. R. Beissinger[1]

[1] U. of CA, Berkeley, Department of Environmental Science, Policy and Management
[2] San Francisco Estuary Institute, Oakland, CA
nordby@nature.berkeley.edu

The profound changes in habitat structure and composition that accompany the *S. alterniflora* invasion will likely have the greatest impact on species, such as birds, that are wholly dependent on the tidal salt marsh system. Alameda song sparrows (*Melospiza melodia pusillula*), a California Species of Special Concern, reside entirely within the salt marshes in San Francisco Bay. These sparrows are affected not only by the *S. alterniflora* invasion directly, but also indirectly by an increase in competitive interactions with marsh wrens (*Cistothorus palustris*) who are occupying the newly available habitat. To assess the impact of the *S. alterniflora* invasion on song sparrow populations we studied nesting habitat preferences and nesting success and also looked for evidence of the destruction of song sparrow eggs by marsh wrens. During the 2002 and 2003 breeding seasons we followed 363 nests in 45+ territories across three study sites. We found that song sparrows did use *S. alterniflora* as nesting habitat, but these nests were much more likely to fail due to tidal flooding than nests placed in native vegetation. As a result, overall nesting success was slightly lower in areas of *S. alterniflora*. We also found strong evidence of marsh wren destruction of sparrrow eggs, particularly in areas of high marsh wren density. These results suggest that the spread invasive *S. alterniflora* may be negatively impacting saltmarsh song sparrow populations in San Francisco Bay.

Community *Spartina* Education and Stewardship Project

K. O'Connell

People For Puget Sound, 407 Main Street, Suite 201, Mount Vernon, WA 98273, koconnell@pugetsound.org

State agencies and organizations involved in *Spartina* control agree that education of the public is an essential key to its eradication from Puget Sound. People For Puget Sound's new Community *Spartina* Education and Stewardship Project is designed to educate, organize, and mobilize citizens in an effort to remove the invasive weed from their shorelines. This approach will act as an investment in the future of Spartina-free beaches in Puget Sound, by focusing on community involvement and highlighting the importance of stewardship. The project enhances our own current programs, other local stewardship programs, and builds the key link between the agencies committed to *Spartina* removal and the citizens who depend of the health of the Sound.

Three to five priority shoreline communities are targeted for outreach each year of this project. People For Puget Sound staff assists stewards from the community in hosting an educational 'Spartina social' with neighbours and discussing control options specific to their infestation and needs. Community stewards are trained in baseline surveying and monitoring the site twice a year, and are equipped and supported to continue monitoring for 15+ years.

The project's success is maximized through partnerships with other agencies in Puget Sound. WSDA, County Noxious Weed Control Boards, the Northwest Straits Commission, Washington State University 'Beach Watchers' program, and tribal communities assist in building connections with the community and staging large public dig events to raise awareness of the Spartina problem.

Evolving Invasibility of Exotic *Spartina* Hybrids in Upper Salt Marsh Zones of San Francisco Bay

M.R. Pakenham-Walsh[1], D.R. Ayres[2], and D.R. Strong[2]

[1]*Environmental Science Associates, 8950 Cal Center Drive, Bldg. 3, Ste. 300, Sacramento, CA 95826*
[2]*Section of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616*

Invasion by a hybrid cordgrass (*Spartina alterniflora* X *Spartina foliosa*) is profoundly altering habitat structure within the intertidal zone of San Francisco Bay, California. *Spartina* hybrids exhibit wide ecological tolerance compared to native *S. foliosa* and are invading the naturally unvegetated lower intertidal zone. Heterogeneous hybrid genotypes exhibit traits of both salinity tolerance and competitive vigor, which may enable invasion of higher marsh zones historically dominated by the highly salt-tolerant native pickleweed species *Salicornia virginica*.

We conducted two experiments to address the threat of hybrid colonization of *Sa. virginica* habitat. A greenhouse experiment investigated salinity tolerance of hybrids. A field experiment examined competitive suppression of hybrids by *Sa. virginica*. Results indicate that hybrids exhibit great variability in morphological traits, response to salinity stress and competitive suppression by *Sa. virginica*. Certain hybrids show a combination of competitive vigor in the field and relatively stronger performance in higher salinity conditions. The native *Sp. foliosa* has weaker competitive abilities and tolerance for salinity. Informed by potential mechanisms of hybrid spread in *Sa. virginica* habitat, we posit that the proliferation of *Spartina* hybrids in San Francisco Bay should be viewed in a habitat-dependent framework, wherein natural selection drives niche differentiation among diverse hybrid genotypes.

Comparison of chemical and mechanical control efforts for invasive *Spartina* in Willapa Bay, WA

K. Patten

Washington State University Long Beach Research and Extension Center.2907 Pioneer Road, Long Beach WA 98631, pattenk@wsu.edu

Willapa Bay, Washington, hosts the largest invasive *Spartina* population in North America. State and federal agencies have been conducting large-scale mechanical and chemical control efforts on the affected lands during the past decade. These efforts have had variable degrees of success. Assessments of the long-term efficacy, cost effectiveness and ecological risk of the various control tools will be presented. No long-term control was achieved with multiple years of disking. Crushing *Spartina* was only successful when the plant was driven well below the surface sediment. This occurred on soft sediment and a thin root mat. Winter tilling provided good control, spring and summer tilling only marginal control. In sites where seed stalks were tilled into the sediment during the winter, there was a solid stand of seedlings the following spring. Spartina control with glyphosate at the high hand-sprayed rates (5 – 8% v/v) averaged approximately 50%, with permanent control taking several years of re-treatment. Control from late season (September/October) hand-sprayed glyphosate was poor. Control with broadcast application of glyphosate (8.4 kg ai/ha) was highly variable. Although brown-down was usually observed, there was no permanent control unless there were ideal conditions (clean leaves, clean spray water and several days of dry time). Under ideal conditions, up to 74% control was achieved with broadcast rates of glyphosate. Based on same season observations, large-scale control appears promising using broadcast (aerial and ground) and hand-sprayed imazapyr. Most variability with imazapyr occurred when hand spraying applications failed to achieve good canopy coverage. Best control, lowest long-term cost and least ecological risk occurred with broadcast imazapyr application in June.

Shorebird use of *Spartina*-affected tidelands – Can we achieve functional habitat post-control?

K. Patten

Washington State University Long Beach Research and Extension Unit., 2907 Pioneer Road, Long Beach WA 98631, pattenk@wsu.edu

One of the major threats of invasive *Spartina* impacts is the loss of shorebird foraging habitat. The Audubon Society lists the invasion of Willapa Bay (WB) by *Spartina* as the second most critical threat to shorebird habitat in the nation. Studies were conducted on how large-scale mechanical and chemical control efforts affect shorebird and waterfowl usage of *Spartina* meadows in WB. Food abundance and accessibility, shorebird, waterfowl and bird of prey density, and bird behaviour were evaluated on treated meadows and compared to untreated meadows and bare mudflats. Based on long-term point counts and remote video monitoring, there was no bird usage (of any species) in *Spartina* meadows. Highest food abundance and accessibility was found in mudflats. Waterfowl and birds of prey preferred herbicide-treated sites over the tilled and mudflat sites. Shorebirds preferred mudflats followed by tilling over that of herbicide-treated sites. Bird behaviour (feeding or resting) was variable and dependent on species, time of year and treatment. Although tilling appears to be initially effective in expediting restoration for shorebirds, it is too costly to implement on a large scale. The most significant long-term concern for shorebird usage is the *Spartina*-induced increase in tidal elevations on these meadows (> 35 cm). Less than 20% of the gain in elevation was attributable to sediment accretion; the rest was root biomass. Due to the change in bathymetry, once *Spartina* was controlled at these sites, native salt marsh plants (*Salicornia*, *Triglochin* and *Spergula)* immediately invaded more than 400 meters out into what were previous intertidal mudflats. This potentially permanent large scale conversion of mudflat to salt marsh will have profound implications for shorebird habitat. Some potential remedies will be suggested.

Local and geographic variation in *Spartina*-herbivore interactions

S. C. Pennings

Department of Biology and Biochemistry, University of Houston, Houston, TX 77204, spennings@uh.edu

Spartina alterniflora is consumed by a variety of herbivores, and the nature of these plant-herbivore interactions varies on both local and geographic scales. The palatability of *S. alterniflora* to herbivores varies within single marshes as a function of elevation. Tall-form plants, which occur close to creek banks, are more palatable and less resistant to herbivores than are short-form plants, which occur on the marsh platform. The proximate causes of this local variation in palatability include variation in leaf nitrogen content and chemical defenses. Differences in these leaf traits are driven by variation in sediment biogeochemistry across the elevational gradient. The extent to which the distribution and abundance of herbivores is dictated by local variation in plant palatability is determined by herbivore mobility and vulnerability to predators in the different habitats.

The palatability of *S. alterniflora* to herbivores also varies geographically. High-latitude plants (New England) are more palatable to herbivores than are low-latitude (South Atlantic Bight) plants. This difference persists over 5 clonal generations in a common greenhouse, and thus is probably genetically determined. The proximate causes of this geographic variation in palatability include variation in leaf nitrogen content, toughness, and chemical defenses. A number of processes may contribute to driving this variation in leaf traits: interactions between plant biochemistry and temperature, the length of the growing season, herbivore pressure, eutrophication and variation in soil type all could play a role.

Covering the *Spartina* threat: An alternative control method for non-native *S. patens* in a west coast salt marsh

D. L. Pickering

The Nature Conservancy 2499 North Bank Road, Otis, Oregon 97368; dpickering@tnc.org

The only Oregon occurrence of the introduced salt-marsh grass *Spartina patens* occurs on The Nature Conservancy's Cox Island Preserve. *S. patens* is native to the Atlantic and Gulf coasts of the United States but it was introduced to the western United States in the early 1900s. *S. patens* invades middle marsh communities and forms monotypic stands that exclude native plants and seriously degrade wildlife habitat. *Spartina* patches trap more sediment than native marsh vegetation thus altering the succession of the site. To restore Cox Island and prevent *S. patens* from spreading to other estuaries in the State, we field-tested methods that have shown promise at controlling *S. patens* elsewhere. Covering with heavy-duty landscaping fabric anchored by spikes pushed into the soil was the most effective control method of those we tried. Leaving the fabric on for two years kills the *Spartina*. After removal, native salt-marsh vegetation re-colonizes on its own. To date, 0.81 ha (2 ac) have been restored and another 1.62 ha (4 ac) are now covered. This methodology may not be feasible for large-scale control efforts on well-established infestations, but it is a very viable option for control efforts at the most effective time to eliminate invasive non-native species, at early stages of an infestation.

Fungal symbiosis: A potential mechanism of plant invasiveness

R. Rodriguez[1,2,3], R. Redman[1,3], M. Hoy[1,2] and N. Elder[1]

[1]*U.S. Geological Survey, Seattle, WA*
[2]*University of Washington, Biology, Seattle, WA*
[3]*Montana State University, Microbiology, Bozeman, MT*
Rusty_Rodriguez@usgs.gov

All plants in natural ecosystems are thought to be symbiotic with endophytic fungi that reside entirely within plant tissues. These fungi are known to be important to the structure, function, and health of plant communities. In fact, without fungal symbioses, plant communities do not survive many environmental stresses. Fungal symbionts express a variety of symbiotic lifestyles including mutualism, commensalism, and parasitism. Mutualistic fungi have been shown to increase plant growth and productivity, and confer stress tolerance against drought, salt, temperature, disease, herbivory.

We propose that fungal endophytes provide a mechanism for the habitat expansion of invasive plants species including *Spartina* spp. We have determined that *Spatina* spp. are symbiotic with endophytic fungi and the host changes it's symbiotic partner in response to mircohabitat stresses (a phenomenon we describe a Symbiotic Modulation). We are determining the biogeographic distribution of *Spartina* endophytes and thier significance in the invasiveness of this plant species in the Pacific Northwest. We have found that one of the fungal endophytes confers salt tolerance to plants and may be required for the inavsion of *Spartina* spp. in salt marshes. The role of symbiosis in the invasion of invasive species and the evolution of plants in high stress habitats will be discussed.

Assessment of the potential consequences of large-scale eradication of *Spartina anglica* from the Tamar Estuary, Tasmania

M. Sheehan[1] and J. Ellison[2]

[1]*School of Geography and Environmental Studies, University Of Tasmania, Locked Bag 1-376, Launceston Tasmania Australia 7250 Matthew.Sheehan@utas.edu.au*
[2]*School of Geography and Environmental Studies, University Of Tasmania, Locked Bag 1-376, Launceston Tasmania Australia 7250 Joanna.Ellison@utas.edu.au*

Patterns of sediment deposition and erosion within the Tamar Estuary, Tasmania have been significantly altered following the introduction of *Spartina anglica* in the 1940's. Now Australia's largest *Spartina* infestation, this study assesses the potential impacts of large-scale eradication. Using transect based topographic surveys and coring, the volume of sediment trapped under *Spartina* has been calculated and sediment characteristics examined. Topographic surveys of mud banks conducted during this study will be compared with surveys undertaken between 1970 and 1989. An integral part of the study is the determination of contaminant levels within the fine grain sediments that could become mobilised following removal of *Spartina*. Behaviour of sediment with respect to erosion rates, sediment redeposition and causative hydrodynamics are being monitored within a test area from which *Spartina* cover has been removed. Analysis of these interdisciplinary lines of inquiry will allow for a greater understanding of the biogeomorpholoigcal responses to restoration attempts within intertidal zones and provide a sound basis on which to formulate and implement future management of *Spartina*.

Invasive hybrid cordgrass (*Spartina alterniflora* x *S. foliosa*) recruitment dynamics in open mudflats of San Francisco Bay

C. M. Sloop, D. R. Ayres and D. R. Strong

Section of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA. cmsloop@ucdavis.edu

Hybrid *Spartina* are currently expanding their range in the San Francisco Bay (SFB) at a rate exceeding exponential growth. A subset of transgressive hybrid *Spartina* plants that positively exceed the fitness trait values of their parent species are competitively and reproductively superior to both parents and other hybrids, and likely drive the invasion. In order to colonize the vast open SFB mudflats and found new populations hybrid cordgrass plants have to evolve self-compatibility and exhibit fast vegetative and rapid lateral growth. The mudflat tidal cycle covers or exposes plants for up to six hours, so new seedlings have to be robust and fast growing to survive and establish. A small number of hybrid and native *Spartina* have colonized the open mudflats along the eastern shore of SFB. To discern mudflat seedling recruitment dynamics we investigated (1) the numbers and locations of recruiting seedlings at three SFB sites in 2003 and 2004 via GPS/GIS, and (2) the relationship of all established adult plants and parentage of seedlings using microsatellite markers. Our results identify all sampled seedlings as hybrids, and show a dramatic increase in seedling recruitment numbers in 2004. Molecular investigations reveal distinct family groups with inter-related adult clones as sires for most seedlings. Seedling recruitment is spatially heterogeneous, and is in some cases in direct proximity to adult clones. Isolated plants on the outer edge of the mudflat produced more self-fertilized seedlings than more aggregated plants. These results give support to transgressive hybrid plants as the drivers of the invasion.

Modeling potential impacts of non-native *Spartina* spread on shorebirds in south San Francisco Bay

D. Stralberg, V. Toniolo, G. W. Page and L. E. Stenzel

PRBO Conservation Science, 4990 Shoreline Highway, Stinson Beach, CA 94970, dstralberg@prbo.org

San Francisco Bay holds 70% of California's mudflats and provides habitat to more wintering and migratory shorebirds than any other wetland along the Pacific coast of the contiguous U.S. The Bay's mudflats are currently threatened by *Spartina alterniflora*, and associated hybrids, which grow at lower elevations than the native *S. foliosa* and can render large mudflat areas effectively unavailable to shorebirds for foraging. Using shorebird survey data, tidal benchmark data, and GIS-based habitat data, we analyzed the potential effect of *S. alterniflora* on shorebird habitat in the South Bay, creating grid-based spatial models of shorebird habitat value and potential *S. alterniflora* spread. We developed six potential scenarios of habitat value loss for shorebirds, based on assumptions about the inundation tolerance of *S. alterniflora*, and temporal availability of mudflat resources. *Spartina* spread models predicted that between 14% and 54% of the total South Bay mudflat area could be encroached upon by *S. alterniflora* and associated hybrids. Predictions of habitat value loss for shorebirds ranged from 14% to 80%. We identified the upper mudflats, due to their greater exposure time, and the east and south shore mudflats, due to the high numbers of birds detected there, as the areas of highest value to shorebirds in the South Bay. These areas also coincide with the areas of greatest *Spartina* invasion potential.

Invasive *Spartina* in Pacific Estuaries

D. Strong

drstrong@ucdavis.edu

Spartina spp., cordgrass, are tall dense emergent intertidal grasses of estuaries. *S. alterniflora* and *S. anglica* have spread aggressively after human introductions, most in the Pacific, over the past 100 years. Invasive cordgrasses can substantially affect hydrology, sediment levels, native organisms and the commercial uses of estuaries. Detailed studies show that invasion history and consequences varies greatly among estuaries. In Willapa Bay, WA, *S. alterniflora* has spread exponentially throughout the 43 km long Bay since its introduction 100 years ago and now occupies about 8% of intertidal lands suitable for its growth. Rate of spread is slowed by a weak Allee effect caused by pollen limitation in colonies at the leading edges of the invasion, which set little viable seed. Without the Allee effect much more than 8% of suitable intertidal area would have been colonized by now. In San Francisco Bay, introduced *S. alterniflora* has hybridized during the 25 years since its introduction with the native California cordgrass, *S. foliosa*. Hybridization is reciprocal, and both parental species have been seed parents to hybrids. Hybrids are spreading at a rate greater than exponential. A subset of transgressive hybrid genotypes, with greater vegetative and reproductive fitness than either parent is probably driving the invasion. Hybrid pollen swamps natives, which then produce hybrid seed. This produces positive feedback with no limit to the displacement of native *S. foliosa* by hybrids; this could threaten the very existence of California cordgrass. In both estuaries, open intertidal lands are being converted to dense cordgrass meadows. Fishing, mariculture, recreation, navigation, and drainage are threatened by these *Spartina* invasions, as is habitat for native species. Understanding of the biology of *Spartina* invasions is contributing greatly to its management.

Modeling the spread and control of *Spartina alterniflora* in a Pacific Estuary

C. M. Taylor[1], H.G. Davis[2], J. C. Civille[2], F.S. Grevstad[3] and A. Hastings[1]

[1]Department of Environmental Science and Policy, University of California at Davis, One Shields Avenue, Davis, California, 95616-8755, USA
[2]Section of Evolution of Ecology, University of California at Davis, One Shields Avenue, Davis, California, 95616-8755, USA
[3]Olympic Natural Resources Center, University of Washington, 2907 Pioneer Road, Long Beach, WA, 98331, USA

Results from both a spatially-explicit simulation model and a spatially-implicit deterministic model show that an Allee effect can slow the spread of an invasive plant, *Spartina alterniflora* at sites within a Pacific coast estuary. The average rate of spread with the Allee effect is about 20%. Removing the Allee effect results in an average rate of spread of about 30%. The deterministic model partitions the population according to density classes, instead of the more usual age or stage classes. This demonstrates a novel way of representing density-dependence and an Allee effect in population biology.
We used the deterministic model in conjunction with a genetic algorithm to investigate density-based eradication strategies. We ask whether it is more efficient to first remove low-density plants at the edge of an invasion site that produce fewer propagules but spread rapidly by rhizomes or to remove high-density plants that spread slowly but produce most of the new recruits. We explored the consequences of the Allee effect, different annual budget levels and the addition of seedling control on the optimal strategy. We found that the optimal strategy was dependent on annual budget levels. At low and medium budgets, it was necessary to remove the low-density areas first to achieve eradication but if a high budget is available then the optimal strategy is to prioritise high-density areas. Without an Allee effect the optimal strategy would always prioritise the removal of the fast-growing low-density areas. Seedling control did not change the optimal strategy but did reduce the cost of eradication. Given uncertainty in future budgets, we recommend a strategy that prioritises the removal of low density plants over the high density plants. The reproductive Allee effect in this system is not sufficiently strong to outweigh the importance of the rapid vegetative spread.

Genetic Structure of Native and Restored Populations of *Spartina alterniflora* and its Implications for Controlling Invasions

S. E. Travis[1,2], C. E. Proffitt[1], and M. W. Hester[3]

[1]*USGS National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, LA 70506*
[2] *steven_travis@usgs.gov*
[3]*Coastal Plant Sciences Laboratory, Department of Biological Sciences &Pontchartrain Institute for Environmental Sciences, University of New Orleans, New Orleans, LA 70148*

In its native range, *Spartina alterniflora* occurs throughout the northern Gulf of Mexico and western North Atlantic coasts (as far north as Nova Scotia), where it is used extensively for salt marsh restoration. By comparing natural and restored populations in this region, we may begin to deduce critical aspects of the ecology and population genetics of this species which may prove useful to its control or eradication from those regions where it has become invasive. We have used a combination of experimental and comparative approaches, including both created marshes aged < 60 years and natural marshes of up to 1,500 years, to characterize population genetic structure and its effects on population viability at the population, clonal, and individual levels in *S. alterniflora*. Beginning at the invidudual level, we performed a common-garden experiment on 5 genotypes that had been differentiated on the basis of neutral genetic markers to ascertain whether they exhibited quatifiable differences in adaptive traits related to growth. We found statistically relevant differences in the rate of mortality and rate of incrase in clone diameter, as well as average stem height and density. At the clonal level, we used space-for-time substitutions to compare 3 created and 8 natural marshes to test the hypothesis that *S. alterniflora* is characterized by initial seedling recruitment, which leads to a continuous decline in genotypic diversity with increasing population age and concomitant decreases in rates of outcrossing. We found that genotypic diversity increases on young marshes, with a hypothetical maximum achieved at approximately 30 years based on regression analysis. Beyond 30 years there is a continuous decline in genotypic diversity at a rate of approximately 1% per 100 years.

Spartina alterniflora invasion of San Francisco Bay changes intertidal ecosystem metabolism

A.C. Tyler and E.D. Grosholz

[1]*Dept of Environmental Science & Policy, University of California – Davis, Davis, CA 95616.*
tyler@alumni.virginia.edu

In San Francisco Bay, Atlantic smooth cordgrass, *Spartina alterniflora,* and its hybrids have invaded unvegetated mudflats and native marshes formerly dominated by *Salicornia virginica* and *Spartina foliosa*. This recent, rapid invasion has dramatically changed ecosystem processes and food web structure. Above ground plant production increased 2-5 x relative to native species upon invasion. In contrast, benthic chlorophyll *a*, a proxy for microalgal biomass, shows no clear pattern with vegetation type. However, sediment microalgal primary productivity (GPP) showed substantially higher rates on mudflats than in any vegetated area. At the same time, sediment respiration rates were generally higher (3-5 x) in hybrid and *S. virginica* dominated areas relative to mudflats and *S. foliosa* marshes. Net sediment metabolism flipped from autotrophy to heterotrophy following invasion of mudflats. However, the higher respiration rate in native vegetation, especially *S. virginica*, relative to hybrid areas, suggests slower decomposition of hybrid detritus. This result is corroborated by litterbag decomposition rates and indicates a build-up and/or export of refractory organic matter following hybrid invasion. The switch from a microalgal-dominated system to a refractory detritus-dominated system has clear implications for support of higher trophic levels within the intertidal zone of San Francisco Bay.

Spartina foliosa (Poaceae: Chloridoideae), an endemic to salt marsh habitats along the Pacific coast of western North America

M.C. Vasey

Department of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132
mvasey@sfsu.edu

Pacific cordgrass (*Spartina foliosa*) is threatened by the introduction of a closely related, non-native relative, smooth cordgrass (*S. alterniflora*). So as to evaluate the significance of this threat, I review the contribution that *S. foliosa* makes to its native community.

Spartina foliosa is a keystone resource in the low intertidal zone of salt marsh habitats. It historically ranged along the west coast of North America from Sonoma County, California, USA to northern Baja California, Mexico. Spartina foliosa can spread by floating rhizome fragments or seed. It is extraordinarily tolerant to highly saline and frequently inundated mud flat habitats. Although seed viability is low in this hexaploid lineage, once established, clonal spread of *S. foliosa* results in dense growth and increased sediment accumulation. Consequently, *S. foliosa* is an important element in the initiation of salt marsh plains and it provides important habitat for cover and foraging of numerous species, including clapper rails (*Rallus longirostrus* sensu lato).

Ecological investigations of natural enemies for an interstate biological control program against *Spartina* grasses

D. Viola, L. Tewksbury, and R.A. Casagrande

University of Rhode Island, Kingston, RI 02881
dviola@myrealbox.com

Spartina alterniflora (smooth cordgrass) is a dominant member of salt marsh communities in its native east coast range as well as an introduced invasive in west coast intertidal regions. In 2000, a biological control agent, *Prokelisia marginata* (Homoptera: Delphacidae), was released in Willapa Bay, Washington where *S. alterniflora* is rapidly spreading. Despite establishment of this agent, the invasive population has not been brought under control. Although the natural enemies of *S. alterniflora* have been previously catalogued, little is to be found regarding their ecology, with the exception of *P. marginata*. The purpose of this study was to provide ecological investigations of insect herbivores of *S. alterniflora* in Rhode Island in support of a larger effort to develop biological control agents. An intensive survey of insect species on *S. alterniflora* in Rhode Island was conducted in order to describe thoroughly the composition of the insect herbivore community. Vacuum samples taken at both high and low marsh facilitated the characterization of species assemblages. Our results suggest that there is little variation in insect herbivore species richness among Rhode Island salt marshes. In addition, two flies with stem boring larvae*, Chaetopsis aenea* (Diptera: Otitidae) and *C. apicalis,* were successfully reared in the lab from field collected adults. Damage due to *Chaetopsis* spp. is easily observed in the field, but the frequency of damaged stems varied greatly between sites. Additional research is needed to determine the factors responsible for this variation.

Why did it take so long to turn things around in Willapa Bay? The Human side of the *Spartina* invasion

M. Wecker

PO Box 160, Naselle, WA 98638

Oystergrowers first noticed clones of exotic cordgrass growing in Willapa Bay in the 1950s and brought their concerns about the alien grass to the attention of the staff of the Willapa Refuge. At that time, the infestation involved no more than a handful of clones. *Spartina* now infests over 15,000 acres of mudflats in Willapa Bay, seriously degrading one of the most ecologically productive and otherwise undegraded estuarine areas along the entire Pacific Coast. The human story that parallels the expansion of *Spartina* reveals more than just the inevitable physical, logistical, and biological challenges of responding to an aggressive invasive species. Many of our environmental organizations were unprepared for this problem and reacted in ways that made the problem far worse. Our government structures were also not well designed to meet the challenges of a highly damaging but very natural process. This paper will present the views of one person who has been both an observer from the sidelines and an involved participant in the Willapa Bay *Spartina* program for the past 13 years. I will discuss how the *Spartina* problem was grossly aggravated by confused priorities, biases influencing key decisionmakers, and a general lack of accountability towards the expenditure of public funds. It is important to acknowledge errors made and draw lessons from them in order to assure that the same mistakes are not repeated when we face the next invasion.

Discovery and Management of *Spartina anglica* in the Fraser River estuary, British Columbia, Canada

G. Williams

GL Williams & Associates Ltd., 2907 Silver Lake Place Coquitlam, BC V3C 6A2 Canadam glwill@telus.net

Spartina anglica (English cordgrass) was discovered on August 21, 2003 during marsh surveys of the intercauseway area on Roberts Bank for a proposed Vancouver Port Authority (VPA) container terminal expansion. This was a new species discovery for the estuary and province of British Columbia, and a control program was immediately initiated by VPA. Components of the control program included collecting preliminary data on the *Spartina anglica* infestation in September, stalk density, height, GPS surveys, GIS mapping, manual removal in October, and deep in situ burial, using a specially equipped excavator, and post-removal monitoring and followup. *Spartina* clones, measuring 3-4.5 m diameter, had average stalk density of approximately 800 stalks/m^2 and average height of 1 m, but most of the growth was in the form of tussocks <0.3 m diameter. Manual removal included digging up plants, washing to remove excess sediment, bagging, and disposal by incineration at the Greater Vancouver Regional District incinerator. Subsequent surveys of the outer Fraser estuary conducted in December using the Canadian Coast Guard hovercraft located a 4 km patchy infestation in Boundary Bay. In 2004, a multi-agency was setup including Department of Fisheries and Oceans, Canadian Wildlife Service, VPA, Ministry of Water, Land and Air Protection, City of Delta, and several NGO's to conduct a removal effort. The work to-date has removed all existing *Spartina* from Roberts Bank and substantially reduced it in Boundary Bay.

Integrating Volunteers into *Spartina* Eradication Efforts in Washington State

L.Younger, H. Rogers, R. Fuller

The Nature Conservancy, 217 Pine Street, Suite 1100, Seattle, WA 98101 Lyounger@tnc.org

Incorporation of volunteers into an integrated regional approach to *Spartina* represents an innovative program that has increased the scope of *Spartina* control. The strategic targeting of volunteer involvement to both geographic and programmatic 'holes' in the regional eradication program is a compelling example of an effective linkage of restoration, regional conservation strategy, and environmental education.

Spartina anglica is an invasive plant that has invaded thousands of acres of estuarine marsh and tidal flat habitats in Washington state. The scale of the problem requires an integrated approach to eradication. State and local agency crews are aggressively treating the large, central meadows where efficiency of scale can take advantage of large machinery. However, due to financial and institutional constraints, there are several areas where volunteers supply critical help in eradicating *Spartina* from the region. Examples include monitoring and controlling small peripheral infestations; assisting agency crews by providing extra 'eyes' to find the scattered seedlings and clones hidden in native marsh vegetation; using mechanical control to remove *Spartina* from key places of ecological importance; and field testing new strategies for *Spartina* control that can then be integrated into the regional program. Through these and other activities, volunteers provide a strategic, cost-effective component of a well integrated approach to regional invasive species eradication.

Spread of Invasive *Spartina* in the San Francisco Estuary

K. Zaremba[1], M. McGowan[2] and D.R. Ayres[3]

[1]*San Francisco Estuary Invasive Spartina Project, 605 Addison St., Suite B, Berkeley, CA 94710, kzaremba@spartina.org*
[2]*Maristics, 1442A Walnut St., Suite 188, Berkeley, CA 94709, maristics@comcast.net*
[3]*U.C. Davis, Evolution and Ecology, Davis, CA 95616, drayres@ucdavis.edu*

We mapped the location and extent of all non-native *Spartina* in the San Francisco estuary in 2000 and 2001. We incorporated aerial photographs, ground surveys, and genetic analyses into a GIS. Radiating from sites of deliberate introduction, *Spartina alterniflora* and *S. alterniflora* x *foliosa* hybrids covered ca 190 ha, mainly in the South and Central Bay. Estimates of rate of aerial cover suggested that hybrids were spreading at an accelerating rate of increase. The total coverage of 190 ha by hybrids in 2001 was slightly less than 1% of the Bay's tidal mudflats and marshes. In 2003, we evaluated change in area of non-native *Spartina* by mapping a subset of 28 sites stratified across the SF Estuary by subregion (latitude) and marsh type. We also determined control efficacy at sites treated by various means in 2002-3. The average increase in area between 2001 and 2003 for all species of non-native *Spartina* in the Estuary was 244%. The net acreage of non-native *Spartina spp.* bay-wide may now be as high as 793 hectares (1,960 acres). Spread of *S. alterniflora* x *foliosa* hybrids continued to grow at an accelerating rate and had increased 317%. Greatest spread was in tidal marshes or former diked baylands and mudflats and less in creeks or sloughs and urbanized marsh (rip-rap, boat ramps). Genetic testing found no new invasion sites. Treatment site monitoring indicated that manual methods of *Spartina* control – digging or covering with geo-textile fabric – were effective at removing or killing small populations or single plants of *Spartina* species.