Potential Ocean Dispersal of Cordgrass (Spartina spp.) from Core Infestations

Authors: Morgan, Vanessa H., and Sytsma, Mark D.

Source: Invasive Plant Science and Management, 6(2) : 250-259

Published By: Weed Science Society of America

URL: https://doi.org/10.1614/IPSM-D-12-00042.1

Invasive Plant Science and Management 2013 6:250–259

WSSA WEED SCIENCE SOCIETY OF AMERICA

Potential Ocean Dispersal of Cordgrass (*Spartina* spp.) from Core Infestations

Vanessa H. Morgan and Mark D. Sytsma*

Nonnative *Spartina* species (cordgrasses) are widely distributed along the West Coast of North America, but have not invaded all bays with susceptible habitat. We used drift cards to assess the patterns and rates of potential *Spartina* propagule dispersal by ocean currents from estuaries with significant populations of one or more *Spartina* species. Cards were released monthly for 1 yr from Willapa Bay, Washington; Humboldt Bay, California; and San Francisco Bay, California; with recovery information reported by volunteers. Recovery rates averaged 37% for all release sites. Cards were commonly recovered close to their bay of release but were repeatedly found hundreds of kilometers both north and south of their release location. Cards most generally traveled northward from the release sites. Cards from Humboldt and Willapa bays were commonly recovered along the British Columbia coast, particularly in the winter. Cards released from Humboldt Bay were found farthest from their release sites. One card from Humboldt Bay traveled 2,800 km to Kodiak Island, Alaska. The timing of seed production, combined with prevailing currents, puts bays currently uninfested by *Spartina* at risk of repeated propagule loading by ocean currents. A coordinated coast-wide strategy for eradication of all nonnative *Spartina* will be critical to the success of individual bay-wide eradication efforts.

Nomenclature: Common cordgrass, *Spartina anglica* C. E. Hubbard; dense-flowered cordgrass, *Spartina densiflora* Brongn.; saltmeadow cordgrass, *Spartina patens* (Ait.) Muhl.; smooth cordgrass, *Spartina alterniflora* Loisel.

Key words: Drift card, estuarine, invasive, long-distance dispersal.

Humans often play a role in long-distance dispersal of nonnative species (Mack and Lonsdale 2001; Suarez et al. 2001; Wonham and Carlton 2005), but after a population becomes established in a new range, natural dispersal mechanisms such as wind, water, or animals can facilitate further spread or secondary infestations (Moody and Mack 1988; Ridley 1930). Rare dispersal events via natural pathways might explain Reid's paradox, the disparity between real-world rates of spread and models' predictions based on average dispersal rates (Mack and Lonsdale 2001). Even small proportions of seeds traveling long distances could have significant implications for predicted dispersal rates. Understanding potential dispersal patterns can highlight areas at risk for invasion, improve early detection efforts, and facilitate management or eradication efforts (Higgins and Richardson 1999).

Dispersal of invasive cordgrasses (*Spartina* spp.) along the west coast of North America can occur through long-distance transport of propagules on ocean currents. Often considered ecological engineers, estuarine *Spartina* spp. successfully colonize low-gradient mudflats and existing salt marsh (Bouma et al. 2005; Crooks 2002; Odum and Odum 2003) in areas subject to tidal action and sheltered from wave action (Daehler and Strong 1996). High stem densities and thick rhizome mats increase sediment accumulation (Ranwell 1964; Sayce 1988; Thompson 1991), reduce shorebird foraging habitat (Goss-Custard and Moser 1988; Patten and O'Casey 2007; Stralberg et al. 2004), alter benthic communities (Chen et al. 2007; Levin et al. 2006; Neira et al. 2006), and might facilitate the establishment of other nonnative species (Carr and Dumbauld 2000).

Four nonnative species of *Spartina* are established in North America, Europe, Asia, South Africa, New Zealand, and Australia due to intentional plantings for marsh reclamation and forage, and through accidental transport of seed as a contaminant in shipments of other species (Crawford 2008; Mobberly 1956; Strong and Ayres 2009). Initial introductions of nonnative *Spartina* on the west coast of North America occurred 100 to 150 yr ago (Civille et al. 2005; Strong and Ayres 2009). A three-fold increase in novel infestations documented over the last 12 yr suggests the rate of spread to new habitats is increasing. By 1996, five infestation sites were documented, including: *Spartina anglica* C. E. Hubbard in Puget Sound,

DOI: 10.1614/IPSM-D-12-00042.1

* Research Assistant and Director, Center for Lakes and Reservoirs, Portland State University, P.O. Box 751-ESM, Portland OR 97207. Corresponding author's E-mail: sytsmam@pdx.edu

Management Implications

Nonnative estuarine cordgrasses (*Spartina* spp.) are invasive weeds of saltmarshes and open mudflats in many bays and estuaries of North America, Australia, China, India, New Zealand, and numerous European countries. In North America the largest core infestations established along the Pacific Coast during the last 150 yr at Willapa Bay, Washington; Humboldt Bay, California; and San Francisco Bay, California. Estuarine plants such as *Spartina* can disperse to new bays when propagule-laden wrack mats consisting of senescent stems are washed out to the ocean and then drift with the currents. Understanding this natural dispersal mechanism is critical to the success of a coast-wide *Spartina* eradication strategy because there is a high likelihood of secondary spread from existing infestations—especially those with large historic propagule production. Indeed, a marked increase in novel satellite populations in the last 12 yr suggests spread to new habitats is increasing. This study provides the first examination of the dispersal potential for weedy plant species within the near-shore ocean environment from these three estuaries. The recovery patterns of drift cards, released monthly over the course of 1 yr underscore increased propagule loading at areas proximal to existing infestations, but also highlight the ability of ocean currents to carry seeds great distances, well within known propagule viability ranges. Drift card recoveries spanned 2,044 km north and south of Willapa Bay, 3,304 km north and south of Humboldt Bay, and 661 km north and south of San Francisco Bay. The scope of potential ocean dispersal presented here reinforces the need for effective eradication programs in propagule source areas of not only *Spartina* spp., but also other weeds that can disperse along this same pathway such as dwarf eelgrass (*Zostera japonica*), perennial pepperweed (*Lepidium latifolium*), and Algerian sea lavender (*Limonium ramosissimum*).

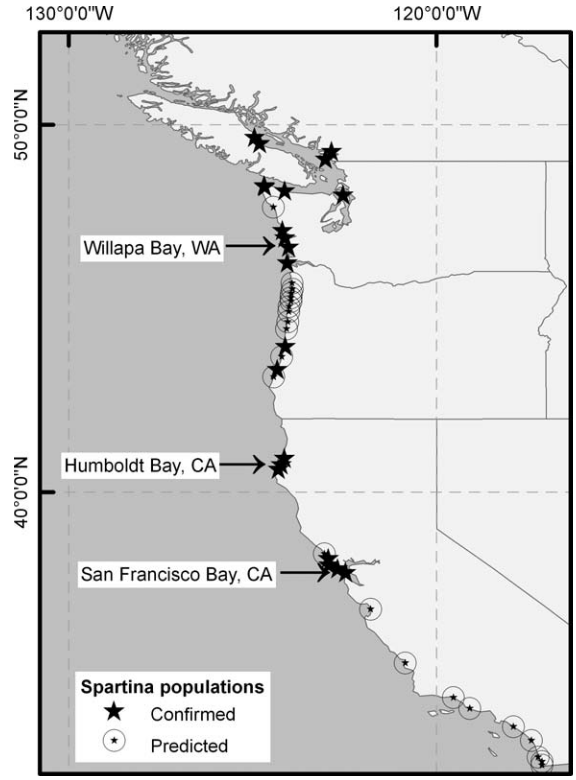

Figure 1. Confirmed infestations of one or more invasive *Spartina* species and bays/estuaries predicted to have susceptible habitat on the West Coast of North America (Daehler and Strong 1996; Howard et al. 2007; WSDA 2009).

Washington; *Spartina alterniflora* Loisel. in Willapa Bay, Washington; *S. alterniflora* and *Spartina patens* (Ait.) Muhl. in the Siuslaw River estuary, Oregon; *Spartina densiflora* Brongn. in Humboldt Bay, California; and all four species in San Francisco Bay, California (Frenkel and Boss 1988; Daehler and Strong 1996). Hybrids formed between the introduced *S. alterniflora* and the native *Spartina foliosa* Trin. now dominate San Francisco Bay, where clones of either parent species are increasingly difficult to find (Ayres et al. 2008). Sixteen new infestations were documented between 1996 and 2008 in British Columbia (4), Washington (5), Oregon (2) and California (5) by November 2008 (Howard et al. 2007; WSDA 2009) (Figure 1).

Because *Spartina* seeds float (Huiskies et al. 1995) and require periods of wet, cool conditions in order to germinate successfully (Kittelson and Boyd 1997; Plyler and Carrick 1993; Plyler and Proseus 1996), natural dispersal via ocean currents can lead to secondary invasions (Ayres et al. 2004; Sayce et al. 1997). *Spartina* sets seed in the late summer/fall and then senescing stems and inflorescences form floating rafts of wrack in mid- to late fall. These materials float within an estuary and can be carried on outgoing tides into the near-shore ocean zone (Minchinton 2006; Sayce et al. 1997). Waterlogging can cause loss of buoyancy; however, large wrack mats were reported by commercial fishermen in the open ocean off the Washington coastline (M. Pfauth, personal communication). During the winter months, the poleward Davidson Current, driven by south winds, typically occurs near shore in the eastern Pacific, whereas in the summer and during periods of fair weather, the equatorward California Current, driven by north winds, is more common (Banas et al. 2004; Hickey 1989). Biber and Caldwell (2008) showed germination of *S. alterniflora* seed peaked after 4 mo of cold, wet stratification, but also that even after 9 to 10 mo of stratification, over 10% of developed seeds remain viable. Similarly, when placed in comparable storage conditions, 5% of *S. anglica* seed remained viable for 300 d and some as long as 4 yr (Hubbard 1970) and large proportions of *S. densiflora* seed remain viable for 4 to 7 mo (Bortolus 2006; Kittelson and Boyd 1997).

Buoyant drift bottles and cards have been used previously to investigate near-shore surface currents (Chew et al. 1962; Dewees and Strange 1984; Schwartzlose 1962), shoreline accumulation of floating materials and pollutants (Ebbesmeyer and Coomes 1993; Schwartzlose and Reid 1972), and the fate of sewage effluent (Crone et al. 1998).

They have also been used to investigate the dispersal of abalone (Chambers et al. 2003; Tegner and Butler 1985) and nonnative mangroves in Hawaii (Allen and Krauss 2006), the effect of wind regimes on sea turtle strandings (Hart et al. 2006), and the connectivity of marine animal populations through larval dispersal to inform siting of Marine Protected Areas (Klinger and Ebbesmeyer 2001; Sauers et al. 2003).

We used drift cards to mimic wrack or floating seed of *Spartina* to study natural, ocean dispersal. Our goal was to assess the distance and velocity of propagule dispersal by ocean currents from core infestations of *S. alterniflora*, *S. densiflora*, and the hybrid *Spartina foliosa* × *alterniflora* on the west coast of North America. We examined spatial patterns of drift card recoveries and direction and distance from selected release sites to better understand ocean transport of materials, including *Spartina* wrack and seed from infested estuaries. We also compared our drift card results to previous reports of near-shore ocean dynamics off the west coast of North America.

Materials and Methods

Drift cards measured 15 by 10 by 0.3 cm (5.9 by 3.9 by 0.1 in) and were constructed from low-density (approximately 0.61 g cm^{-3} (0.35 oz in^{-3}) plywood painted bright yellow with nontoxic paint to facilitate detection (City Signs, Inc., Poulsbo, WA). Biodegradable materials were used with the expectation that they would degrade within a few months in the marine environment. The cards were similar to cards used for a study of ocean currents near Oahu, HI (NOAA 2010). We assigned each batch of cards a unique number denoting release date and site. Text printed on the cards instructed people to report the date and location they found the card along with the card number. Reporting options included telephone (local and toll free), email and postal service. Phone and electronic reports of card recoveries were collected for 5 mo after the last release was conducted.

Drift card deployments, conducted between September 2004 and August 2005, entailed pitching 200 cards from a boat or shoreline once per month within the first 2 h of an ebb tide. Deployments spanned the weak 2004 to 2005 El Niño (Lee and McPhaden 2010). We selected release bays based on the presence of large scale *Spartina* infestations (hundreds to thousands of acres). Release sites were close to each bay mouth; in Willapa Bay (WB), they took place southeast of Tokeland (46.6958°N, 123.9599°W), in Humboldt Bay (HB) from the bay-ward side of a narrow jetty channel (40.7543°N, 124.2305°W); and in San Francisco Bay (SF) from the shoreline at Fort Point (37.8110°N, 122.4772°W) (Figure 2).

We plotted coordinates of all recoveries using ArcMap™ 9.1 (ESRI, Redlands, CA) and classified each as either

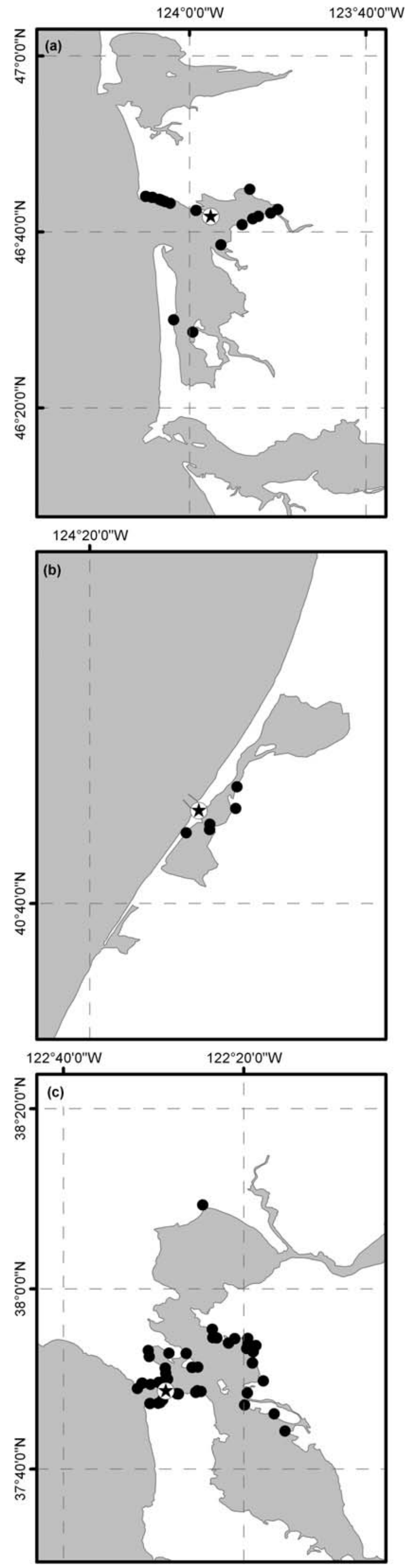

Figure 2. Locations of all in-bay drift card recoveries from releases sites at (a) Willapa, (b) Humboldt and (c) San Francisco bays. Stars indicates release site.

Table 1. The number of drift cards recovered inside and outside the bay of release by bay, month of release, and location. A total of 200 cards were released each month from each bay.[a]

	Willapa			Humboldt			San Francisco		
	Total	Bay	Coast	Total	Bay	Coast	Total	Bay	Coast
September	120	3	117	73	1	72	85	51	34
October	92	5	87	4	0	4	80	14	66
November	127	95	32	85	1	84	97	35	62
December	99	69	30	45	0	45	80	19	61
January	51	0	51	50	0	50	67	20	47
February	31	1	30	29	0	29	103	35	68
March	81	78	3	69	0	69	108	64	44
April	113	12	101	23	0	23	108	18	90
May	65	45	20	52	0	52	80	60	20
June	109	41	68	63	0	63	95	27	68
July	18	6	12	100	0	100	72	39	33
August	97	44	53	36	5	31	76	29	47
Total	1,003	407	596	629	7	622	1,051	411	640

[a] January and February 2005 releases from Willapa Bay had only 199 cards each.

"in-bay" or "coastal." "In-bay" recoveries occurred within the bay of release. "Coastal" recoveries include those reported from beaches and rocky shorelines, and those from embayments other than the card's original release location.

Because our primary interest was to assess risk of spread to distant locations, in-bay recoveries were used to measure total recovery rate, but were excluded from further analysis. For all coastal recoveries, we used Jenness Enterprises' Distance and Azimuth Matrix 2.0 (Jenness Enterprises, Flagstaff, AZ) to calculate the direction of travel and straight-line distance to each recovery location (Jenness 2005). These calculations were performed on unprojected data and based on the "Great Arc" method for calculating distance across a curved surface. We estimated velocity by assuming a straight-line of travel and no lag-time between actual stranding and recovery; both assumptions contribute to conservative estimates of velocity.

Results and Discussion

Of the 7,198 cards released in the three bays, 37.3% (2,683) were recovered by February 2006. Of these, 825 (30.7%) were found at in-bay locations and 1,858 (69.3%) were found in coastal areas (Table 1). Mean monthly retrieval rates were 41.8%, 43.8%, and 26.2% for WB, SF, and HB, respectively. In-bay recoveries regularly comprised over one-third of the total monthly SF recoveries (Figure 3). In WB, greater than 69% of the total recoveries in 4 different mo occurred within the bay. In HB just 1.1% of the 629 total recovered cards were found in the confines of the bay.

In-bay cards were repeatedly stranded in the same locations over multiple months of releases (Figure 2). The majority of SF in-bay recoveries were from the Berkeley/Alameda shoreline, due east of the deployment location at Fort Point, or along Chrissie Field Beach. WB in-bay recoveries often occurred at North Cove, Tokeland, and Bruceport Park. In both bays, repeated stranding sites typically already had established *Spartina* stands or were areas where *Spartina* wrack accumulated, but was habitat unsuitable for *Spartina* establishment and/or survival. After eliminating in-bay recoveries, the number of coastal cards recovered by bay of release was not significantly different (ANOVA, $P = 0.951$, $\alpha = 0.05$, $df = 2$) and ranged from 596 to 640. All results discussed hereafter refer to coastal cards only.

Cards were frequently recovered less than 25 km away from release sites, often within 1 to 6 d after release (DAR). Cumulative return rates for all 12 releases were similar between bays immediately following releases and after approximately 6 mo, but showed some disparities in the intermediate time range (Figure 4). Nearly half of the total cards recovered were found within 10 DAR and 96 to 99% within 180 DAR. Around 45 DAR the patterns from WB and SF remain similar, with 82% and 84% of total cards recovered, compared to only 72% from HB releases. After 100 DAR, recoveries from SF releases slowed considerably (one card found every 2 wk) whereas reports of cards from both WB and HB continued to be reported every 4 to 5 d.

WB-released cards were predominantly transported to the north; 88% of total coastal recoveries occurred to the north of the release site. Beaches from Grayland north to Moclips, and the south-facing coast of Vancouver Island were frequent collection zones for drift cards (Figure 5).

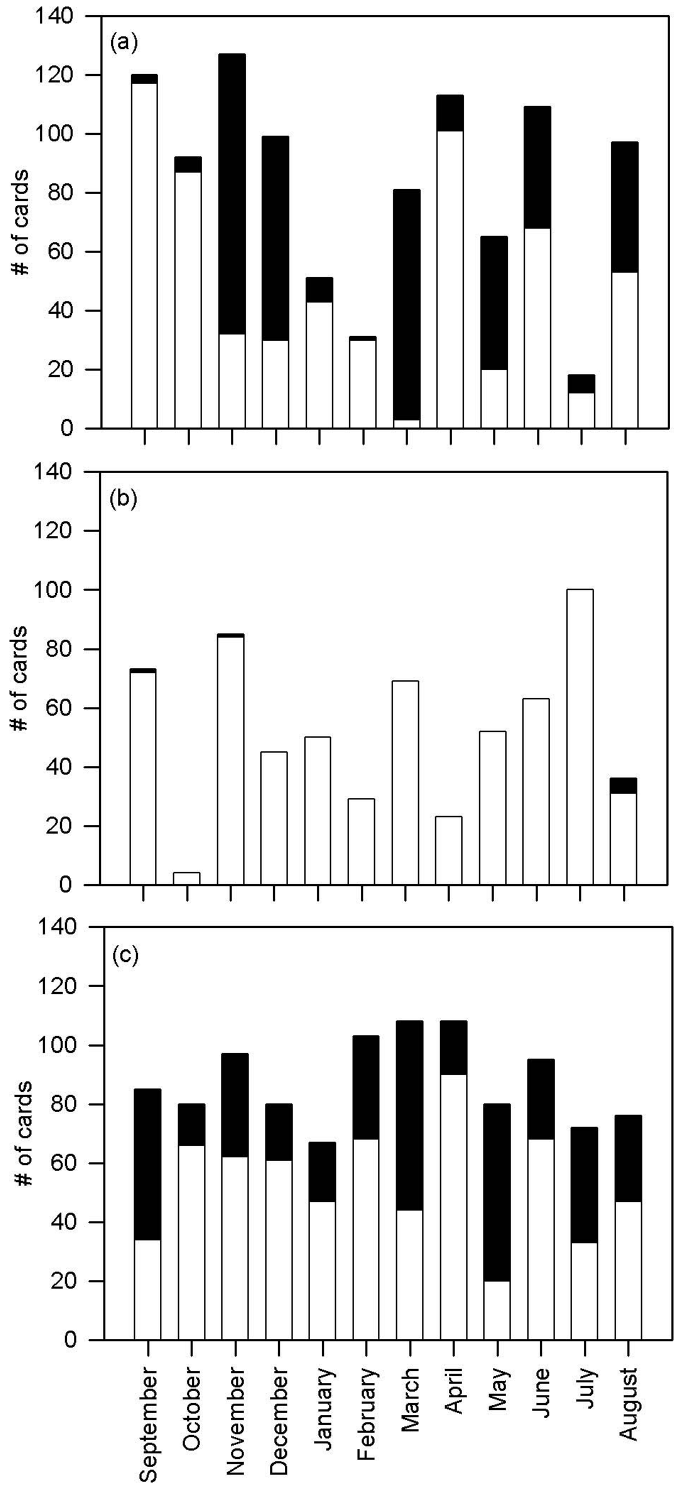

Figure 3. Coastal (white) and in-bay (black) recoveries of drift cards released between September 2004 and August 2005 at the mouth of (a) Willapa, (b) Humboldt, and (c) San Francisco bays.

Eleven cards were found inside of Grays Harbor just north of WB; the majority of these were deployed in October 2004. Northward transport was greatest during winter months (December to February) when the one card was reported over 2,000 km from WB at Middleton Island (129 DAR). The highest velocity of the study was estimated at over 36 km d^{-1} (found at Carmanah Beach, Vancouver Island, British Columbia, Canada, 221 km, 6 DAR). Many winter-released cards were also rapidly transported to SE Alaska, and the Queen Charlotte Islands and northern tip of Vancouver Island. For all other seasons, distances and estimated velocities were considerably less (Table 2). The furthest southward transport occurred during spring months (March to May), with cards recovered in Oregon as far as Newport (185 DAR) and Florence (227 DAR), but just 10% of recovered cards were carried south of WB during this period. Summer-released (June to August) cards were not carried far from WB with a total range of less than 200 km.

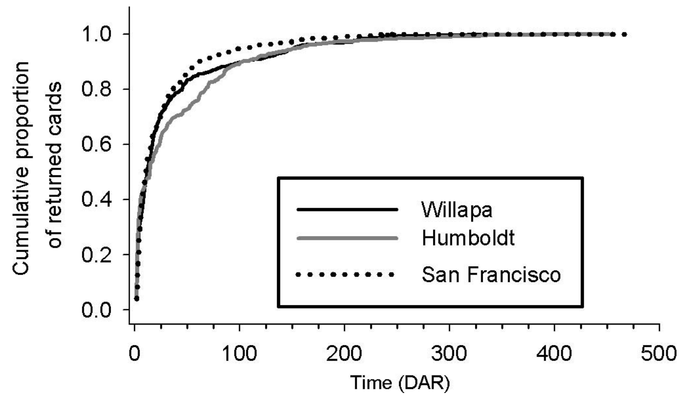

Figure 4. Cumulative recovery of drift cards as a function of the number of days after release (DAR) from 12 monthly releases in three bays.

HB-released cards traveled both north and south in relatively even proportions over the course all 12 deployments (59% vs. 41% respectively), with card recoveries widely scattered south as far as Asilomar State Beach, Pacific Grove, CA (36.63°N, 45 DAR) and north to the Ruby Beach Trail in Washington (47.71°N, 140 DAR) (Figure 5). Winter releases were heavily skewed to the north, with 27 cards transported up to 24.5 km d^{-1} reported at Fort Canby State Park Beach, Washington (613 km, 25 to 26 DAR), and recoveries from the Queen Charlotte Islands (1,360 to 1,607 km, 67 to 256 DAR) and Vancouver Island in British Columbia (937 to 1,159 km, 52 to 62 DAR). The maximum distance reported from this study was one card from the December HB release that was transported over 2,800 km in 214 DAR to the Uganik Island lagoon on Kodiak Island, Alaska (57.82°N, 153.51°W). Seasonal mean velocities to the north were approximately three to four times those to the south during fall, winter, and spring releases for HB. Velocities were lower for summer releases when a greatly reduced range (< 55 km), similar to that observed for WB releases,

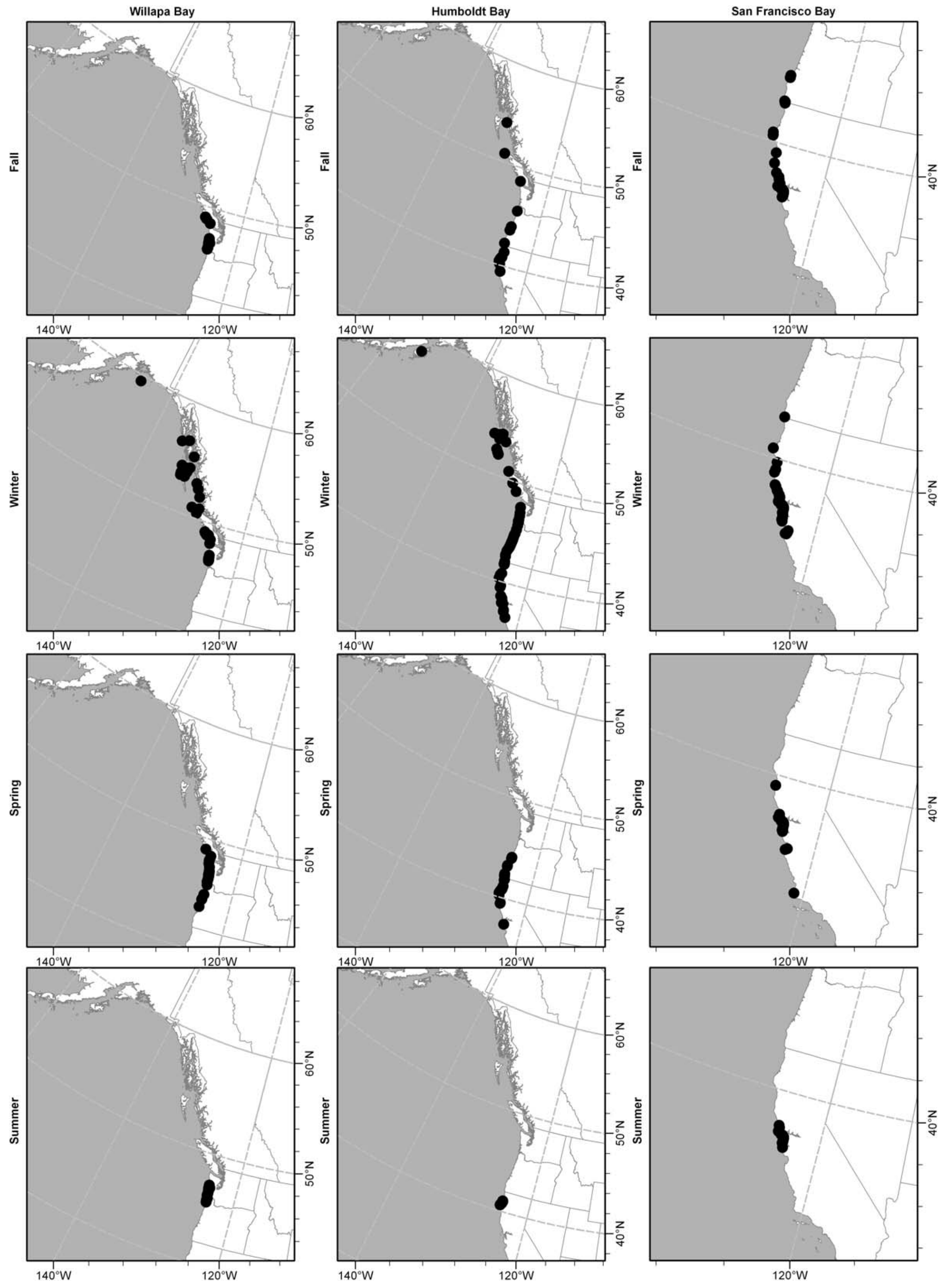

Figure 5. Recovery locations for drift cards grouped into fall (September to November), winter (December to February), spring (March to May), and summer (June to August) deployments and released from Willapa Bay, Washington; Humboldt Bay, California; and San Francisco Bay, California. Recovery locations were recorded for 5 mo past the last deployment in August 2005. Individual dots can represent more than one recovered drift card.

Table 2. Recoveries of drift cards found north and south of three release sites grouped by season of release (F, fall; W, winter; Sp, spring; Su, summer) with the mean, maximum (max), and minimum (min) distances (dist) to recovery location in km, and estimated velocity (vel) in km d^{-1}.

	Willapa Bay				Humboldt Bay				San Francisco Bay			
North	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su
No. of cards	197	103	111	113	85	110	67	104	88	136	104	127
Dist (mean)	33	330	40	20	66	534	60	14	80	51	22	13
Dist (min)	11	11	11	11	1	1	7	4	6	6	6	6
Dist (max)	297	2,044	293	63	1,535	2,802	381	33	632	495	219	75
Vel (mean)	3.8	7	2.4	5.3	1.8	10.7	2.9	2.9	2.1	3.1	3.4	1.8
Vel (min)	<0.1	0.2	0.1	0.1	< 0.1	< 0.1	0.1	< 0.1	0.2	0.1	0.1	0.1
Vel (max)	12.4	36.9	12.8	12.5	13.5	24.5	12.5	10.5	14.5	16.1	11.4	16.1
South												
No. of cards	39	0	13	20	75	14	77	90	74	40	50	21
Dist (mean)	38	—	121	61	12	247	16	9	11	33	24	12
Dist (min)	22	—	18	24	4	4	4	4	5	5	5	5
Dist (max)	41	—	305	111	153	502	395	21	30	144	385	55
Vel (mean)	5.4	—	2.6	2.9	0.5	3.4	1	2.1	1.6	1.4	1.9	1.6
Vel (min)	0.2	—	0.1	0.2	< 0.1	< 0.1	< 0.1	< 0.1	0.1	0.2	0.1	0.1
Vel (max)	13	—	6.8	7.8	5.3	11.1	6.2	4.9	6.7	5.4	14	3
All cards												
Total no. of cards	236	103	124	133	160	124	144	194	162	176	154	148
Dist (range)	338	2,044	598	175	1,688	3,304	776	55	661	638	605	130

occurred. Three cards from September 2004 and August 2005 HB deployments were recovered inside the Eel River estuary, 15 km to the south.

A majority (71%) of recovered SF-released cards were carried north of the bay mouth for all 12 deployments. Over 90% of the northbound cards were reported within 50 km of the release site, along the Marin Headlands and the Point Reyes National Seashore, whereas the remaining 10% were found at scattered locations up to Cape Arago, Oregon (632 km, 93 DAR) (Figure 5). Many of the southward recoveries were similarly concentrated close to the bay mouth with a few isolated reports from Moss Landing (140 km, 24 DAR) and Asilomar State Beach, Pacific Grove, CA (129 km, 10 to 27 DAR) within Monterey Bay. The maximum northward velocity (16 km d^{-1}) of SF-released cards occurred in winter and summer deployments. The maximum southward rate of 14 km d^{-1} occurred following spring releases.

We demonstrated that rapid and long-distance coastal movement of *Spartina* on ocean currents is possible. We found average poleward velocities between 2 to 7 km d^{-1} (2.3 to 8 cm sec^{-1}) and peak velocities of 24.5 to 36.9 km d^{-1} (28.4 to 42.7 cm sec^{-1}). Velocities for the California Current have been reported between 4 to 50 cm sec^{-1} with typical mean speeds around 10 cm sec^{-1} (Hickey and Banas 2003; Jennings and Schwartzlose 1960; Lynn and Simpson 1987; Poulain and Niiler 1989; Reid and Schwartzlose 1962; Schwartzlose 1962, Schwartzlose and Reid 1972;). Our estimated mean velocities were within the known current velocities of the California Current, which suggests that our simple drift cards provided a realistic estimate of potential dispersal of *Spartina*. Drift cards were buoyant due to their construction from low-density (approximately 0.61 g cm^{-3}) materials. Fall-gathered wrack of *Spartina densiflora* and *S. foliosa* × *alterniflora* were approximately one third less dense (0.38 and 0.41 g cm^{-3} respectively) than the cards; thus, wrack would therefore be comparatively more buoyant than the cards, encountering more wind-forcing and potentially travel farther than the drift cards suggest. Sayce et al. (1997) demonstrated that for *S. alterniflora*, large proportions of vegetative shoots were capable of floating for more than 2 mo, but seeds and inflorescences with ripe seed attached floated for less than 1 mo. Prior to control program successes, large wrack mats were regularly stranded on shorelines just outside Willapa Bay and San Francisco Bay (F. Grevstad and J. Graves, personal communication). During storm conditions, these mats would presumably break apart, reducing their rafting capability and causing seed to sink more rapidly (K. Sayce, personal communication). Thus, turbulent surface water might lessen the chances of propagules traveling long distance via ocean currents.

We observed evidence of transport from three bays sufficient to consistently convey floating material to nearby locations and often to distant sites via ocean currents. Releases at HB resulted in the greatest transport range, a span of 3,300 km of the coastline. Movement was predominantly northward from September through February when *S. densiflora* seed and wrack would be expected to be present in the bay. Seed production by this species is highly variable, but up to 79% of seeds from the Humboldt population are viable (Kittelson and Boyd 1997). *S. densiflora* was introduced in the 1800s to HB where it currently occupies 385 ha (951 ac); (Grazul and Rowland 2011). Thus, natural dispersal from HB on ocean currents could account for the subsequent appearance of *S. densiflora* in proximal water bodies such as the Mad River and Eel River delta, where a total of 269 ha are currently infested (Grazul and Rowland 2011), as well as in estuaries as far north as British Columbia. Our results suggest that HB could be a source of propagules for susceptible habitats as far north as southern Alaska. Other vectors, such as solid ballast in dredges, waterfowl, and recreational and fishing vessels, could also be important in *S. densiflora* dispersal.

Temperature, wave exposure, inundation periods, and salinity tolerances for *S. densiflora* might limit the northern spread of this species (Bortolus 2006; Castillo et al. 2000, 2005). In its native range, *S. densiflora* survives in wave-exposed areas of rocky shores and cobble beaches (Bortolus 2006), which suggests that undiscovered populations on the open coast, outside of embayments, could also serve as seed sources. Infestations on the open coast could allow the species to move along the coastline in a series of short-distance dispersal events.

Transport of drift cards from WB was also far-ranging ($\sim$ 2,350 km) and similarly favored deposition to the north in the fall and winter months, a pattern especially pronounced December through February. We observed transport of multiple WB drift cards into neighboring Gray's Harbor, which reinforces the likelihood of inter-bay transport suggested by Strong and Ayres (2009). No cards were recovered within the Strait of Juan de Fuca, nor within Puget Sound; this might reflect that card releases did not coincide with the occasional surface current reversals known to occur in the western Strait of Juan de Fuca (Cannon 1983; Holbrook and Halpern 1982) or possible retention within the cyclonic Juan de Fuca Eddy, which forms just outside the entrance to the Strait (Hickey and Banas 2003). Since the height of the *Spartina alterniflora* infestation in WB in 2003 when it occupied 3440 ha (net), the population has been reduced to just 1 ha in 2011 (C. Phillips, personal communication). Thus, WB no longer serves as a large annual source of propagules for potential ocean transport or other pathways.

Releases from San Francisco showed the least coast-wise transport across most seasons, but similar directional patterns as the other two bays: predominant northward transport resulting from September through February releases, and balanced north and south movement during spring and summer. SF is one of the most invaded ecosystems in the world (Cohen and Carlton 1998; Ruiz et al. 2000), and secondary spread from this point of introduction is considered likely for multiple species on the west coast (Grosholz and Ruiz 1995; Petersen 2006; Wasson et al. 2001). Hybrid cordgrass (*S. foliosa* $\times$ *alterniflora*) comprises the majority of cordgrass cover in this estuary system (Ayres et al. 2004) and its spread from San Francisco threatens native West Coast populations of cordgrass with extinction through pollen swamping (Anttila et al. 1998; Ayres et al. 2008). Control efforts in SF have mirrored the success achieved in WB; the SF infestation has been reduced by 90% from its peak of 327 ha (net) in 2006 (Olofson Environmental Inc. 2012). Since surveys were begun in 2001, small populations of *S. alterniflora, S. foliosa* $\times$ *alterniflora*, and *S. densiflora* have repeatedly been documented in lagoons and bays as far north as Tomales Bay (P. Olofson, personal communication)

Estuaries are often viewed as isolated from one another, but ocean currents effectively link the entire near-shore environment, including salt marshes and intertidal flats. Effective eradication programs targeting *Spartina* spp. or other invasive estuarine organisms such as green crab [*Carcinus maenas* (Linnaeus, 1758)], dwarf eelgrass (*Zostera japonica* Aschers. and Graebn.), perennial pepperweed (*Lepidium latifolium* L.), and Algerian sea lavender [*Limonium ramosissimum* (Poir.) Maire.] in propagule source areas would inhibit their potential dispersal on ocean currents. Furthermore, our results suggest that individual bay-focused *Spartina* eradication efforts will be ineffectual in the long-term without integration into a coast-wide strategy, such as that proposed within the West Coast Governors' Agreement on Ocean Health (2008).

Acknowledgments

Funding for this project came from the San Francisco Estuary Institute, the Oregon Department of Agriculture, and the Washington Department Natural Resources. Collaborators essential to the success of the project included Dave Heimer, Les Holcomb, Russell Nunez, and Travis Haring from the Washington Department of Fish & Wildlife; Kristen Ward from the National Park Service Golden Gate National Recreation Area; and William Pinnix from the U.S. Fish & Wildlife Service—Arcata Fish and Wildlife Office. We also recognize the invaluable participation of hundreds of curious beachcombers, students, visitors, and residents who took the time to report their cards as well as the various organizations which encouraged awareness of the project, including: Stop Oregon Litter and Vandalism (SOLV); the Grass Roots Garbage Gang; the Coastal Observation and Seabird Survey Team (COASST); and Sightline Daily (Tidepool.org).

Thanks to Catherine de Rivera (Portland State University) for her review and feedback of this manuscript.

Literature Cited

Allen, J. A. and K. W. Krauss. 2006. Influence of propagule flotation longevity and light availability on establishment of introduced mangrove species in Hawai'i. Pac. Sci. 60:367–376.

Anttila, C. K., C. C. Daehler, N. E. Rank, and D. R. Strong. 1998. Greater male fitness of a rare invader (*Spartina alterniflora*, Poaceae) threatens a common native (*Spartina foliosa*) with hybridization. Am. J. Bot. 85:1597–1601.

Ayres, D., D. Smith, K. Zaremba, S. Kolhr, and D. R. Strong. 2004. Spread of exotic cordgrasses and hybrids (*Spartina* sp.) in the tidal marshes of San Francisco Bay, California, USA. Biol. Invasions 6: 221–231.

Ayres, D. R., K. Zaremba, C. M. Sloop, and D. R. Strong. 2008. Sexual reproduction of cordgrass hybrids (*Spartina foliosa* × *alterniflora*) invading tidal marshes in San Francisco Bay. Divers. Distrib. 14: 187–195.

Banas, N. S., B. M. Hickey, P. MacCready, and J. A. Newton. 2004. Dynamics of Willapa Bay, Washington: a highly unsteady, partially mixed estuary. J. Phys. Oceanogr. 34:2413–2427.

Biber, P. E. and J. D. Caldwell. 2008. Seed germination and seedling survival of *Spartina alterniflora* Loisel. Am. J. Agric. Biol. Sci. 3(3):633–638.

Bortolus, A. 2006. The austral cordgrass *Spartina densiflora* Brong.: its taxonomy, biogeography and natural history. J. Biogeogr. 33: 158–168.

Bouma, T. J., M. B. De Vries, E. Low, G. Peralta, I. C. Tanczos, J. van de Koppel, and P.M.J. Herman. 2005. Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. Ecology 86:2187–2199.

Cannon, G. A. 1983. An overview of circulation in the Puget Sound estuarine System. NOAA Technical Memorandum. ERL PMEL-48. Pacific Marine Environmental Laboratory, Seattle, WA. 34 p.

Carr, E. M. and B. R. Dumbauld. 2000. Status of the European green crab invasion in Washington coastal estuaries: can expansion be prevented? J. Shellfish Res. 19:629–630.

Castillo, J. M., L. Fernández-Baco, E. M. Castellanos, C. J. Luque, M. E. Figueroa, and A. J. Davy. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in Mediterranean salt marsh determined by different ecophysiological tolerances. J. Ecol. 88:801–812.

Castillo, J. M., A. E. Rubio-Casal, S. Redondo, A. A. Álvarez-López, T. Luque, C. Luque, F. J. Nieva, E. M. Castellanos, and M. F. Figueroa. 2005. Short-term responses to salinity of an invasive cordgrass. Biol. Invasions 7:29–35.

Chambers, M. D., H. Hurn, C. S. Friendman, and G. R. Van Blaricom. 2003. Drift card simulations of larval dispersal from San Nicolas Island, California, during black abalone spawning season. Pages 421–433 *in* Proceedings of the Sixth California Islands Symposium. Ventura, CA: Institute for Wildlife Studies and National Park Service.

Chen, H., B. Li, J. Hu, J. Chen, and J. Wu. 2007. Effects of *Spartina alterniflora* invasion on benthic nematode communities in the Yangtze Estuary. Mar. Ecol. Prog. Ser. 336:99–110.

Chew, F., K. L. Drennan, and W. J. Demoran. 1962. Some results of drift bottle studies off the Mississippi Delta. Limnol. Oceanogr. 7: 252–257.

Civille, J. C., K. Sayce, S. D. Smith, and D. R. Strong. 2005. Reconstructing a century of *Spartina alterniflora* invasion with historical records and contemporary remote sensing. Ecoscience 12:330–338.

Cohen, A. N. and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–558.

Crawford, R.M.M. 2008. Plants at the Margin: Ecological Limits and Climate Change. New York: Cambridge University Press. 478 p.

Crone, T. J., C. C. Ebbesmeyer, and W. J. Ingraham. 1998. Dispersion of 1,000 drift cards over Victoria's sewage outfalls. Pages 259–266 *in* Puget Sound Research '98 Proceedings. Olympia, WA: Puget Sound Water Quality Action Team.

Crooks, J. A. 2002. Characterizing Ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153–166.

Daehler, C. C. and D. R. Strong. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biol. Conserv. 78:51–58.

Dewees, C. M. and E. M. Strange. 1984. Drift bottle observations of the nearshore surface circulation off California, 1977–1983. Calif. Coop. Ocean Fish. 25:68–73.

Ebbesmeyer, C. C. and C. A. Coomes. 1993. Historical shoreline recoveries of drifting objects: an aid for future shoreline utilization. Pages III-159–III-164 *in* Proceedings of Oceans '93 Engineering in Harmony with Ocean. Seattle, WA: Evans-Hamilton, Inc. Frenkel, R. E. and T. R. Boss, 1988. Introduction, establishment and spread of *Spartina patens* on Cox Island, Siuslaw Estuary, Oregon. Wetlands 8:33–49.

Goss-Custard, J. D. and M. E. Moser. 1988. Rates of change in the numbers of dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. J. Appl. Ecol. 25:95–109.

Grazul, Z. I. and P. D. Rowland. 2011. The Distribution of *Spartina densiflora* in the Humboldt Bay Region: Baseline Mapping. Arcata, CA: U.S. Fish and Wildlife Service, Humboldt Bay National Wildlife Refuge. 13 p.

Grosholz, E. D. and G. M. Ruiz. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar. Biol. 122:239–247.

Hart, K. M., P. Mooreside, and L. B. Crowder. 2006. Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. Biol. Conserv. 129:283–290.

Hickey, B. M. 1989. Patterns and processes of circulation over the shelf and slope. Pages 41–115 *in* B. M. Hickey and M. R. Landry, eds. Coastal Oceanography of Washington and Oregon. Amsterdam, The Netherlands: Elsevier Science.

Hickey, B. M. and N. S. Banas. 2003. Oceanography of the U.S. Pacific Northwest coast and estuaries with application to coastal ecology. Estuaries 26:1010–1031.

Higgins, S. I. and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. Am. Nat. 153:464–475.

Holbrook, J. R. and D. Halpern. 1982. Winter-time near-surface currents in the Strait of Juan de Fuca. Atmos.-Ocean 20:327–339.

Howard, V., M. Pfauth, M. Sytsma, and D. Isaacson. 2007. Oregon Spartina Response Plan. Portland, OR: Center for Lakes and Reservoirs, Portland State University. 80 p.

Hubbard, J.C.E. 1970. Effects of cutting and seed production in *Spartina anglica*. J. Ecol. 58:329–334.

Huiskies, A.H.L., B. P. Koutstaal, P.M.J. Herman, W. G. Beeftink, M. M. Markusse, and W. de Munck. 1995. Seed dispersal of halophytes in tidal salt marshes. J. Ecol. 83:559–567.

Jennings, F. D. and R. A. Schwartzlose. 1960. Measurements of the California Current in March 1958. Deep-Sea Res. 7:42–47.

Kittelson, P. M. and M. J. Boyd. 1997. Mechanisms of expansion for an introduced species of cordgrass, *Spartina densiflora*, in Humboldt Bay, California. Estuaries 20:770–778.

Klinger, T. and C. Ebbesmeyer. 2001. Using oceanographic linkages to guide marine protected area network design. Pages 1–24 *in* Proceedings of the 2001 Puget Sound Research Conference. Olympia, WA: Puget Sound Action Team.

Lee, T. and M. J. McPhaden. 2010. Increasing intensity of El Niño in the central–equatorial Pacific. Geophys. Res. Lett. 37:L14603.

Levin, L. A., C. Neira, and E. D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432.

Lynn, R. J. and J. J. Simpson. 1987. The California Current system: the seasonal variability of its physical characteristics. J. Geophys. Res. 92: 12,947–12,966.

Mack, R. N. and W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. BioScience 51: 95–102.

Minchinton, T. E. 2006. Rafting on wrack as a mode of dispersal for plants in coastal marshes. Aquat. Bot. 84:372–376.

Mobberley, D. G. 1956. Taxonomy and distribution of the genus *Spartina*. Iowa State Coll. J. Sci. 30:471–574.

Moody, M. E. and N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. J. Appl. Ecol. 25: 1009–1021.

Neira, C., E. D. Grosholz, L. A. Levin, and R. Blake. 2006. Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. Ecol. Appl. 16:1391–1404.

[NOAA] National Oceanic and Atmospheric Administration. 2010. National Ocean Survey, Office of Response and Restoration, Hazardous Materials Division. Barber's Point, Oahu, Hawaii Drift Card Study 2002–2004. http://coris.noaa.gov/metadata/records/faq/barbers_pt_oahu_drift_card_survey_2002-2005.html#what.1. Accessed February 11, 2012.

Odum, H. T. and B. Odum. 2003. Concepts and methods of ecological engineering. Ecol. Eng. 20:339–361.

Olofson Environmental, Inc. 2012. San Francisco Estuary Invasive *Spartina* Project—California Clapper Rail Habitat Enhancement Program Progress Report. Berkeley, CA: prepared by Olofson Environmental, Inc. for the State Coastal Conservancy. 84 p.

Patten, K. and C. O'Casey. 2007. Use of Willapa Bay, Washington, by shorebirds and waterfowl after *Spartina* control efforts. J. Field Ornithol. 78:395–400.

Petersen, C. 2006. Range expansion in the northeast Pacific by an estuary mud crab—a molecular study. Biol. Invasions 8:565–576.

Plyler, D. B. and K. M. Carrick. 1993. Site-specific seed dormancy in *Spartina alterniflora* (Poaceae). Am. J. Bot. 80:752–756.

Plyler, D. B. and T. E. Proseus. 1996. A comparison of the seed dormancy characteristics of *Spartina patens* and *Spartina alterniflora* (Poaceae). Am. J. Bot. 83:11–14.

Poulain, P. and P. P. Niiler. 1989. Statistical analysis of the surface circulation in the California Current system using satellite-tracked drifters. J. Phys. Oceanogr. 19:1588–1603.

Ranwell, D. S. 1964. *Spartina* salt marshes in southern England. II. Rate and seasonal patterns of accretion. J. Ecol. 52:79–94.

Reid, J. L. and R. A. Schwartzlose. 1962. Direct measurements of the Davidson Current off central California. J. Geophys. Res. 67: 2491–2497.

Ridley, H. N. 1930. The Dispersal of Plants throughout the World. Ashford, Kent: L. Reeve & Co. 744 p.

Ruiz, G. M., P. W. Fofonoff, J. T. Carlton, M. J. Wonham, and A. H. Hines. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annu. Rev. Ecol. Syst. 31:481–531.

Sauers, K. A., T. Klinger, C. Coomes, and C. C. Ebbesmeyer. 2003. Synthesis of 41,300 drift cards released in Juan de Fuca Strait (1975–2002). Pages 1–12 *in* Proceedings of the 2003 Georgia Basin/Puget Sound Research Conference. Olympia, WA: Puget Sound Action Team.

Sayce, K. 1988. Introduced Cordgrass, *Spartina alterniflora* Loisel, in Salt Marshes and Tidelands of Willapa Bay. Ilwaco, WA: Willapa National Wildlife Refuge. USFWS–87058 (TS). 70 p.

Sayce, K., B. Dumbauld, and J. Hidy. 1997. Seed dispersal in drift of *Spartina alterniflora*. Pages 27–31 *in* Proceedings of the Second International *Spartina* Conference. Olympia, WA: Washington State University-Cooperative Extension.

Schwartzlose, R. A. 1962. Nearshore currents of the western United States and Baja California as measured by drift bottles. Cal. Coop. Ocean. Fish. 9:15–21.

Schwartzlose, R. A. and J. L. Reid. 1972. Near-shore circulation in the California current. Cal. Coop. Ocean. Fish. 16:57–65.

Stralberg, D., V. Toniolo, G. W. Page, and L. E. Stenzel. 2004. Potential Impacts of Non-Native *Spartina* Spread on Shorebird Populations in South San Francisco Bay. Stinson Beach, CA: PBRO Conservation Science. 61 p.

Strong, D. R. and D. A. Ayres. 2009. *Spartina* introductions and consequences in salt marshes: arrive, survive, thrive, and sometimes hybridize. Pages 3–22 *in* B. R. Silliman, T. Grosholz, and M. D. Berness, eds. Human Impacts on Salt Marshes—A Global Perspective. Berkeley, CA: University of California Press.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc. Natl. Acad. Sci. U. S. A. 98:1095–1100.

Tegner, M. J. and R. A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for the recovery of depleted populations. Mar. Ecol. Prog. Ser. 26:73–84.

Thompson, J. D. 1991. The biology of an invasive plant. BioScience 41: 393–401.

Wasson, K., C. J. Zabin, L. Bediger, C. M. Diaz, and J. S. Pearse. 2001. Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol. Conserv. 102:143–153.

West Coast Governors' Alliance on Ocean Health. 2008. West Coast Governors' Agreement on Ocean Health Action Plan.116 p. http://www.westcoastoceans.org. Accessed February 11, 2012.

Wonham, M. J. and J. T. Carlton. 2005. Trends in marine biological invasions at local and regional scales: the northeast Pacific Ocean as a model system. Biol. Invasions. 7:369–392.

[WSDA] Washington State Department of Agriculture. 2009. Progress of the 2008 *Spartina* eradication program. Olympia, Washington: Washington State Department of Agriculture. 39 p.

Received May 8, 2012, and approved December 29, 2012.