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Seagrass recovery in the Delmarva Coastal Bays, USA☆

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Abstract

Zostera marina (eelgrass) in the coastal bays of the Delmarva Peninsula, USA, declined precipitously in the 1930s due to the pandemic wasting disease and a destructive hurricane in 1933. This resulted in major changes in many of the ecosystem services provided by this seagrass, such as loss of bay scallops (*Argopecten irradians*) and disappearance of brant (*Branta bernicla*). Natural recovery of *Z. marina*, possibly deriving from either small remnant stands or undocumented transplant projects after the demise of *Z. marina*, has been significant in four northern bays, with over 7319 ha reported through 2003 compared to 2129 ha in 1986, an average expansion rate of 305 ha year^{-1}. This rapid spread was likely due to seeds and seed dispersal from recovering beds. However, no recovery had occurred in the southern coastal bays prior to restoration efforts, possibly due to both their distance from potential donor beds, restricted entrances to the bays, and the narrow time period when seeds are available for colonization via rafting reproductive shoots carrying viable seeds. Survival and expansion of small test plots (4 m^2) in these southern coastal bays between 1997 and 2000 demonstrated that propagule supply, rather than water quality, was limiting seagrass recovery in these bays. In 2001, we initiated a large-scale *Z. marina* restoration effort in the southern coastal bays utilizing seeds, while simultaneously monitoring water quality using spatially and temporally intensive water quality mapping techniques. Between 2001 and 2004, approximately 24 million seeds harvested from natural, dense beds in Chesapeake Bay were broadcast into experimental plots ranging in size from 0.2 to 2 ha in four coastal bays having no seagrass, totaling approximately 46 ha through 2004. Successful germination (estimated at 5–10% of seeds broadcast), growth and expansion of *Z. marina* in and around these plots over this 3-year test period, as well as water quality data, suggest conditions are appropriate for plant growth. Low-level aerial photographs in 2004 showed 38% of the bottom in 52–0.4 ha plots was covered by vegetation. Increasing *Z. marina* coverage will have important implications for fisheries and waterfowl but may potentially conflict with aquaculture, which is rapidly expanding in this region. Continued recovery will depend on maintaining good water quality to avoid the macro-algal accumulations and phytoplankton blooms that have characterized other coastal lagoons. The patterns of natural seagrass recovery and the results of restoration efforts we describe here, as well as seagrass recoveries from wasting disease outbreaks, anoxic events, hurricanes, and propeller scarring reported elsewhere, suggest that seeds and seed dispersal play an important role in the recovery and expansion of these beds.

Keywords: Seagrass; *Zostera marina*; Eelgrass; Recovery; Restoration; Delmarva Coastal Bays, USA

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1. Introduction

One of the most dramatic but least understood events in seagrass population biology was the pandemic decline of *Zostera marina* L., eelgrass, in the 1930s (Cottam, 1934; Milne and Milne, 1951; Hemminga and Duarte, 2000). Populations of *Z. marina* in the western Atlantic were almost completely eliminated in the span of just a few years. Speculation on the cause of this decline centered on climatic changes and a disease organism, the marine slime mold, *Labyrinthula zosterae* (Renn, 1936; Rasmussen, 1977; Short et al., 1988), but the exact cause was never conclusively proven. Recent work has shown that *L. zosterae* is capable of causing death to *Z. marina* on a local scale (Muehlstein et al., 1991; Muehlstein, 1992; Short et al., 1986, 1987, 1988; Ralph and Short, 2002) but its role in the pandemic decline remains unclear.

This pandemic decline had significant consequences for the many ecosystem services (Costanza et al., 1997) associated with seagrasses. Most notable were reductions in animal populations (Rasmussen, 1973), including commercially and recreationally important organisms, e.g. brant (*Branta bernicla*) and bay scallops (*Argopecten irradians*) (Milne and Milne, 1951), but the decline also completely eliminated one

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mollusc (*Lottia alveus*) (Carlton et al., 1991). In addition, shorelines that were once protected by the wave-baffling and sediment-stabilizing effects of leaves, roots, and rhizomes, sustained significant erosion of sediments after the loss of seagrasses (Wilson, 1949; Rasmussen, 1973; Christiansen et al., 1981).

Recovery of *Z. marina* occurred in many areas at varying time scales after the demise (Frederiksen et al., 2004), but other areas remained unvegetated (Cottam and Munro, 1954). However, full recovery in some areas has been compromised by anthropogenic inputs of sediments and nutrients from increasing human development (Short and Wyllie-Echeverria, 1996), and some subsequent losses have been attributed to re-occurring episodes of *L. zosterae* (Short et al., 1986, 1987).

In this paper, we highlight the natural recovery of *Z. marina* to several coastal bays in the mid-Atlantic region of the United States. We review the available evidence as to the reason for lack of recovery in several adjacent bays, and illustrate a case example of propagule limitation, demonstrating that targeted restoration efforts can be highly successful. We discuss implications of this recovery for fisheries and the potential for conflict with fisheries practices that have rapidly expanded in the region.

2. The Delmarva Coastal Bays

The coastal bays along the Atlantic margin of the Delmarva Peninsula, which extend approximately 200 km from Delaware Bay to Chesapeake Bay (Fig. 1), are comprised of shallow, back barrier island lagoons and salt marshes. The lagoons are characterized by extensive shallow (intertidal to 1 m MLW) shoals drained by deeper channels. The tidal range varies across the system from ~0.5 to 1.5 m. Reported flushing times for these lagoons vary considerably from as long as 100 days for Indian River Bay (Cerco et al., 1994) to as short as 2 days for Hog Island Bay (Fugate, unpublished data; median flushing time for Hog Island Bay ≈ 15 days). There are no major urban centers within the watershed, but a general south to north pattern of increasing population density and residence time for water in the lagoons contribute to a general pattern of

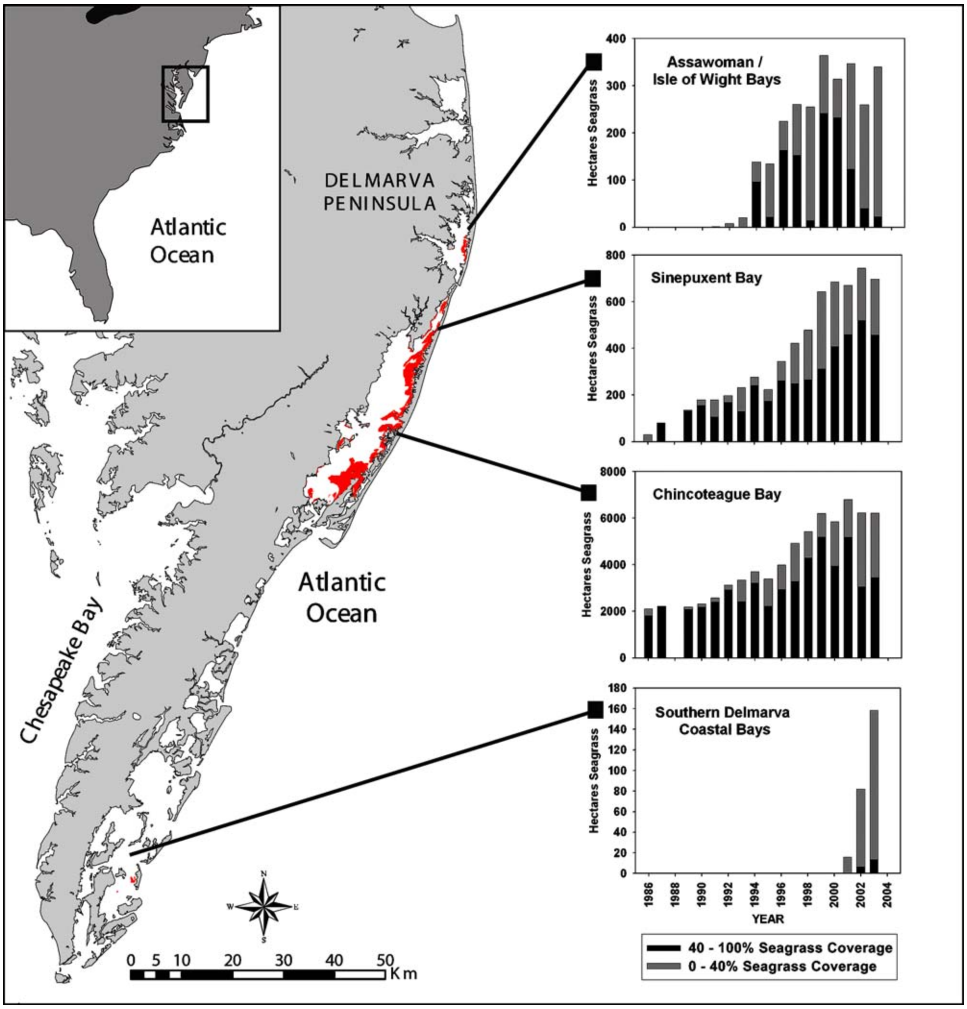

Fig. 1. Map of the Delmarva Peninsula in the mid-Atlantic region of the United States showing the 2004 distribution of seagrass (in red), and annual changes in seagrass coverage in two cover categories (sparse with 1–40% coverage, and dense with 40–100% cover) for each of the bays that had seagrass between 1986 and 2003. The Southern Delmarva Coastal Bays includes five bays where *Z. marina* restoration (see Table 3) is now underway: Magothy, South, Cobb, Spider Crab, and Hog Island bays.

increasing nutrient loading and eutrophication in the same direction (U.S. EPA, 2002). The primary land use within the watershed is agriculture, with an increasing shift towards industrial-scale poultry production. Southern watershed areas are better drained than northern areas and have a larger proportion of forested areas (Stanhope, 2003). Lacking major tributaries, most of the freshwater and nutrient inputs to the coastal bays are via small tributary creeks, groundwater discharge and atmospheric inputs (Stanhope, 2003).

Although there are no precise *Z. marina* abundance data, anecdotal reports, fishery practices, and local historical knowledge indicate that *Z. marina* was very abundant in these bays in the early 1900s. These lagoonal seagrass beds were completely eliminated by the end of 1933, with the effects of the wasting disease compounded in August, 1933, by one of the most significant hurricanes to impact the region in the 20th century. An immediate effect of the loss of *Z. marina* was the elimination of the commercial bay scallop (*A. irradians*) fishery in 1933 (Table 1) and disappearance of brant (*B. bernicla*) that fed exclusively on *Z. marina*.

Some recovery of *Z. marina* has occurred in a few bays that once supported dense *Z. marina* beds. The recovery mechanisms are unknown, but may have involved small remnant populations, no longer present today because of poor water quality, that may have survived the pandemic in lower salinity regions of the small rivers entering the bays. Alternatively, undocumented transplanting activity may have played a role. Cottam and Munro (1954) comment on transplanting efforts in several bays (Indian River and Chincoteague Bay) but report that transplants were unsuccessful in one (Chincoteague Bay). Recovering *Z. marina* in two of the northern bays (Indian River Inlet and Rehoboth Bay) died out completely in the 1950s (Orth and Moore, 1987), while those beds documented in Chincoteague Bay in the late 1960s and early 1970s continued to recover (Anderson, 1970; Orth, 1973). An annual seagrass monitoring program in these coastal bays that was initiated in 1986 using aerial photography (Orth et al., 1987) documented continued changes in seagrass coverage (Orth et al., 2004) as well as impacts to seagrass beds from mechanical harvesting of hard clams (*Mercenaria mercenaria*) in four coastal bays (Chincoteague, Sinepuxent, Isle of Wight and Assawoman Bays) (Orth et al., 2002). The discovery of several small ($<$1–2 m^2), natural patches of *Z. marina* in two Southern Delmarva Coastal Bays, which had shown no recovery since 1933, resulted in a targeted restoration program aimed at reintroducing *Z. marina* primarily using seeds (Orth et al., 2003; unpublished data).

Table 1
Harvest of bay scallops (kg) from the seaside Delmarva Peninsula prior to the *Z. marina* decline of 1933

Year	Harvest (kg)
1920	51,709
1925	163,969
1929	520,726
1930	829,522
1931	557,490
1932	299,356
1933	0

3. Methods

3.1. Distribution and abundance

3.1.1. Aerial photography and seagrass mapping

Vertical aerial photography and standard mapping procedures were used to assess distribution and abundance of seagrass in the Delmarva Peninsula coastal bays beginning in 1986 and continuing annually through 2003, except for 1988. Black and white photography (scale 1:24,000; 60% flightline overlap and 20% sidelap) was acquired with a standard mapping camera with acquisition timing guidelines that optimized tidal stage, plant growth, sun angle, atmospheric transparency, water turbidity, and wind conditions to insure visibility of seagrass beds (Dobson et al., 1995). Mapping of seagrass beds was initially accomplished by manually tracing seagrass bed outlines onto translucent United States Geological Survey 7.5′ quadrangle maps directly from the photographs, and then digitizing bed boundaries into a Geographic Information System (GIS) dataset for analysis. More recently, the aerial photography was scanned from negatives and orthorectified using Erdas image processing software. Seagrass beds boundaries were then directly photointerpreted on-screen while maintaining a fixed scale using ESRI GIS software (Orth et al., 2004). Seagrass beds were categorized as very sparse, sparse, moderate, or dense based on a visual comparison with a scale based on percent cover estimates (Paine, 1981; Orth et al., 2004). In this paper, we collapse the four categories into sparse (0–40%) and moderate to dense (40–100%).

3.1.2. Ground surveys for species information

Two species have been reported from this region, *Z. marina* and *Ruppia maritima* (widgeongrass). Because it was impossible to delineate species from the aerial photography, field surveys from a diversity of private and public agencies, including private citizens, university researchers, and state and federal managers provided the necessary species information. Significant contribution to total area by monospecific *R. maritima* is limited to the two northern bays (Isle of Wight and Assawoman Bays), where *R. maritima* coverage is greater than 95% of the total seagrass coverage. In Chincoteague Bay and further south, the distribution patterns discussed are almost exclusively derived from *Z. marina*.

3.2. Water quality studies

Water quality surveys measuring nutrients, turbidity and phytoplankton within the coastal bays largely began during the 1970s (Boynton et al., 1996). At that time they were undertaken for specific research or monitoring purposes and it was not until the late 1990s that long-term, consistent monitoring programs began (Maryland Department of Natural Resources (MDNR), 2004). Routine monitoring has been undertaken from Chincoteague Bay northward under programs conducted by the National Park Service at Assateague Island National Seashore (Lea, 2000), the Maryland Department of Natural Resources, the Maryland Coastal Bays Program (MCBP) Volunteer Water Quality Monitoring Program and the Delaware Department of Natural Resources and Environmental Control. In the southern bays of Virginia water, quality measurements have been conducted by both the Virginia Institute of Marine Science from 1997 to 1999 (Wesson et al., 2000) and the Virginia Coast Reserve Long-term Ecological Research Project from 1992 to present (http://www.vcrlter.virginia.edu).

3.3. *Seagrass restoration*

A seagrass restoration program was initiated in 1997 in the Delmarva Southern Coastal Bays (Fig. 1) where no seagrass recovery had occurred. The discovery of several small, natural patches of *Z. marina* in the mid 1990s suggested that water quality conditions were adequate for plant growth. Initially, small (4 m^2) test plots were planted with approximately 100 adult plants obtained from naturally occurring beds in Chesapeake Bay, following protocols developed earlier including appropriate time of year (Orth et al., 1999, in press-a), to determine habitat suitability for possible larger scale experiments. Subsequently, seed addition experiments were conducted in 1999 and 2000 (Orth et al., 2003). With successful growth of each year's plantings over a 4-year period (1997–2000) from both adult plants and seeds, larger scale efforts were initiated in 2001, and have continued through 2004, using primarily seeds. Between 2001 and 2004, approximately 24.2 million seeds were broadcast by hand (Orth et al., in press-a, in press-b) or from floating bags of reproductive shoots with viable seeds (after Pickerell et al., in press) into plots ranging in size from 1.0 m^2 to 2.0 ha. Seed densities in small plots ranged from 1 to 1250 seeds m^{-2}, while in larger plots (>0.4 ha) seed densities ranged from 1.2 to 7.4×10^5 seeds ha^{-1}. Seeds were collected from natural beds in Chesapeake Bay by harvesting reproductive shoots with mature seeds (Orth et al., 1994, 2003, in press-a, in press-b). Seed harvesting has not influenced the donor beds, as less than 1% of shoots (and thus seeds) are removed. Seed production estimates for our donor beds range from 60 to 250 million seeds ha^{-1} $year^{-1}$ (unpublished data), and thus our annual harvests generally represent a very small percentage (<1%) of total seed production. Donor beds have remained relatively stable during the period of seed harvesting, as observed in our annual monitoring of all beds in Chesapeake Bay (Orth et al., 2004).

4. Results

4.1. *Distribution and abundance*

The first aerial survey of the coastal bays in 1986 revealed the presence of seagrass in only two coastal bays: 2100 ha were mapped in Chincoteague Bay and 29 ha in Sinepuxent Bay (Fig. 1). Eighty six percent of the beds were classified as moderate to dense and 14% as sparse. Seagrass beds were not detected or reported from any other coastal bays. By 2003, 7319 ha of seagrass were present in seven coastal bays, an average increase of 305 ha $year^{-1}$, with 50% of the beds classified as moderate to dense and 50% as sparse.

In Chincoteague Bay, where the majority of seagrass, dominated by *Z. marina*, is now found, by 2003 seagrasses had increased in abundance to 6220 ha, although the peak came in 2001 when 6794 ha were delineated. Ninety percent of this seagrass is found along the bay's eastern shore behind the barrier islands. Since 1986, seagrasses have expanded an average of 242 ha $year^{-1}$. Seagrass beds in this bay have been mostly moderate to dense in cover (Fig. 1).

In Sinepuxent Bay, by 2003 seagrasses, dominated by *Z. marina*, had increased in abundance to 696 ha, an expansion of 41 ha $year^{-1}$ since 1986, although 743 ha were mapped in 2002. Seagrass beds in this bay have been mostly moderate to dense in cover (Fig. 1).

Seagrasses appeared in Isle of Wight Bay in 1992 and reached a maximum of 135 ha in 2003. In Assawoman Bay, seagrasses appeared in 1991 and reached a maximum of 265 ha in 1999 (Fig. 1) with cover declining slightly to 136 ha in 2003. Cover has been highly variable, likely due to the dominance of *R. martima* in these bays.

In the Southern Delmarva Coastal Bays, no seagrass was observed until the mid-1990s when small patches of *Z. marina* were found. By 2003, 158 ha of seagrass were mapped, 92% being sparse, in both the transplanted areas, as well as in a natural bed discovered in one coastal bay in 2002.

4.2. *Water quality*

Summaries of data from some of the water quality monitoring programs conducted in the coastal bays region over the past 30 years are presented in Table 2. Specific data include those parameters (Chl a, DIN, DIP, total suspended solid (TSS), secchi depth, Kd) whose levels have been related to successful seagrass survival as habitat requirements (Dennison et al., 1993) or diagnostic tools for evaluating factors affecting light available for seagrass growth (Kemp et al., 2004). Lack of temporal or spatial continuity in sampling over the long term has hindered trend analysis (Boynton et al., 1996), but there is little indication that levels of seagrass-relevant variables have changed significantly over the past 30 years. For example, water quality monitoring in Newport and Sinepuxent Bays by Fang et al. (1977) from 1975 to 1977 and the Maryland Department of Natural Resources (2004) from 2001 to 2003 revealed that most stations would meet growing season DIN habitat criteria of 0.15 mg l^{-1} (Table 2). There is evidence that stations near seagrass beds tend to have lower levels of nutrients and phytoplankton than those stations located closest to loadings from the western watersheds (Lea, 2000; VCR/LTER, unpublished data). Most stations located within the coastal bays meet seagrass habitat requirements for nutrients and chlorophyll (Table 2) but stations in Newport Bay, St. Martin River, and the Indian River, which are tributaries located along the western reaches of the systems, typically did not meet the requirements (Table 2). Although, total suspended solid

Table 2
Summary of Coastal Bays water quality monitoring results relative to Chesapeake Bay submerged aquatic vegetation habitat requirements (Dennison et al., 1993; Kemp et al., 2004)

Location	Years of survey	Sampling frequency	Number of stations	Sampling period	Reference	Stations meeting habitat requirement[a]					Stations NOT meeting hab. req.				
						Chl a	DIN	DIP	TSS	Kd/Secchi	Chl a	DIN	DIP	TSS	Kd/Secchi
Delaware Inland Bays	1985–1986	Monthly	11	September-to-September	Sellner (1987)	Bay	Bay	Bay		Bay	River	River	River	All	River
Assawoman Bay	2001–2003	Monthly	6	March-to-November	MDNR (2004)	†	All	All	All	●	†				●
St. Martin River	2001–2003	Monthly	11	March-to-November	MDNR (2004)					●	Most	Most	Most	Most	●
Isle of Wight Bay	2001–2003	Monthly	9	March-to-November	MDNR (2004)	Most	Most	Most	Most	●					●
Isle of Wight Bay	1975–1976	Monthly	4	February-to-December	Fang et al. (1977)		All		●	●	Most		Most	●	●
Sinepuxent Bay	2001–2003	Monthly	5	March-to-November	MDNR (2004)					●	Most	Most	Most	Most	●
Newport Bay	1975–1976	Monthly	5	February-to-September	Fang et al. (1977)		All		●	●	Most		Most	●	●
Newport Bay	2001–2003	Monthly	9	March-to-November	MDNR (2004)					●	Most	Most	Most	Most	●
Chincoteague Bay	2001–2003	Monthly	17	March-to-November	MDNR (2004)	Most	Most			●			Most	Most	●
Chincoteague Bay	1970	Monthly	3	January-to-December	Boynton (1973)		All		●		Most		Most	●	Most
Chincoteague Bay	1975–1976	Monthly	7	February-to-September	Fang et al. (1977)		All		●	●	Most		Most	●	●
Magothy Bay	1997–1999	Biweekly	5	November (1997)-to-November (1999)	Wesson et al. (2000)	All	All	Most		All				All	
Hog Island Bay	1992–2001	Monthly	10	January-to-December	VCR/LTER (unpublished data)	●	Bay	Bay	●	●	●	Creek	Creek	●	●
Northern Bays[b]	1998, 1999	Monthly (1998), biweekly (1999)	12	March-to-October	Lea (2000)	All	All	All	All	Veg					Unveg

Station codes: Bay, stations located within Delaware Inland Bays; River, stations in tidal tributaries to Delaware Inland Bays; †, one station near SAV met Chl a requirement; All, all stations; Most, most stations; Veg, stations with SAV; Unveg, unvegetated stations; ●, parameter not measured; blank, no major trend.

[a] Threshold values for SAV habitat requirements—Chl a (15 ug/l); DIN (0.15 mg/l); DIP (0.02 mg/l); TSS (15 mg/l); Secchi (0.96 m); Kd (1.5 l/m).

[b] Northern Bays = Assawoman, Isle of Wight, Sinepuxent, Newport, and Chincoteague Bays.

concentrations were often found to be higher than levels associated with *Z. marina* vegetated areas in the Chesapeake Bay (Table 2), turbidity levels were equal to or lower than those same vegetated Chesapeake Bay areas (Moore et al., 1996).

Loading rates of nutrients have been found to be typically higher in the northern coastal lagoons compared to southern areas (Stanhope, 2003). The same study found a positive relationship between annual stream base flow exports of NO_3^- and watershed developed land cover, and a negative relationship with percent forest cover. Southern watersheds had higher forest cover than northern areas. Groundwater residence time in the watersheds is only 10–20 years. Surface water area in the coastal lagoon region is approximately equal to watershed area, therefore direct atmospheric deposition of nitrogen to the overall bay region bays is quantitatively more important (up to four-fold) than base flow input (Stanhope, 2003).

4.3. Restoration efforts

Table 3 lists restoration projects conducted in the Delmarva Southern Coastal Bays between 1998 and 2004 and their current status. Through 2004, approximately 46 ha have been seeded with *Z. marina* (Table 3). Of the 24.2 million broadcast seeds, we estimate that 5–10%, or 1.2–2.4 million seeds, developed into viable seedlings, based on previous seed germination and subsequent seedling success work in this region (Orth et al., 2003; unpublished data). In general, most of the small- and large-scale *Z. marina* restoration projects have survived and continue to do well, as evidenced in the aerial photographs taken in November and December, 2004, showing successful transplant plots in South Bay (Fig. 2). Preliminary analysis, based on a photographic resolution of 31 cm^2, of these aerial photographs of the 52–0.4 ha plots in the southern coastal bays revealed an average 38% canopy coverage by *Z. marina* within the plots after less than four years. In addition, *Z. marina* is visibly expanding by seedling spread into the area between the restoration plots. This additional sparsely vegetated area is incorporated into the 158 ha of seagrass mapped in 2003 from higher altitude photography by the annual survey.

5. Discussion

5.1. Seagrass recovery, propagule supply, and the role of restoration

The pattern of seagrass recovery in the Delmarva Coastal bays, both natural and from recent restoration efforts in bays not having any seagrass since 1933, provides interesting insights in seagrass population dynamics, propagule supply, seed dispersal ecology, and the role restoration can play in restoring seagrass. Interestingly, while worldwide concerns center on loss of seagrass due to anthropogenic inputs of sediments and nutrients from human induced perturbations (Short and Wyllie-Echeverria, 1996; Duarte, 2003), the emerging story from these coastal bays is increasing coverage of seagrass from natural spread, and since 2001, from large-scale restoration efforts using seeds.

We still do not fully understand the factors influencing the rates and time course of *Z. marina* recovery highlighted above following the wasting disease. Habitat and water quality alterations due to the loss of sediment stabilizing beds (e.g. Rasmussen, 1973) may have been particularly important. Recovery in Chincoteague Bay may have been fueled by survival and subsequent spread of propagules from remnant stands in lower salinity regions of small tributaries that are part of the northern, but not southern, bays, although it is unknown whether undocumented transplant efforts following the 1933 demise were successful in re-establishing small pockets of *Z. marina*. Today, these lower salinity regions no longer support *Z. marina*, as water quality has been compromised by human growth. The rapid rate of spread of *Z. marina* within Chincoteague Bay, especially since 1986 (average of 305 ha $year^{-1}$), and in the three bays north of Chincoteague would not be achievable by clonal growth alone. *Z. marina's* reproductive characteristics, including dense annual flowering producing up to 8000 seeds m^{-2} or greater (Silberhorn et al., 1983; unpublished data), seed dispersal over short distances with air bubbles (Churchill et al., 1985), and long distances via floating reproductive fragments with seeds (Harwell and Orth, 2002) were likely essential for the distribution to expand so rapidly under adequate water quality conditions.

Deteriorating water quality conditions may have played a role in terminating recovery in two northern bays (Rehoboth Bay and Indian River Inlet) in the1950s and 1960s, as these bays were being measurably altered by rapid human population growth (Sellner, 1987). The Southern Delmarva Coastal Bays have not experienced similar population growth. Forests here still comprise a large proportion of stream buffers, and the water quality data available for these bays still demonstrate water quality consistent with *Z. marina* growth (Table 2). However, many of these bays, especially in the north, are characterized by extensive mats of opportunistic macro-algae blooms in many localized, shallow areas during the summer (McGlathery et al., 2001; Tyler et al., 2001). These studies and those of Stanhope (2003) suggest that additional base flow inputs of nitrogen are contributing to these bloom events. In areas where the blooms are significant, seagrass re-colonization would be limited.

A combination of short dispersal period for rafting *Z. marina* reproductive shoots (mid May to early June), large distances from any possible source beds, and narrow entrance tidal channels to the southern bays could contribute to a very low probability of a flowering shoot entering one of these bays and depositing a seed that germinates and develops into a viable seedling. The appearance of a few natural patches in these bays does demonstrate that these events are possible (Harwell and Orth, 2002), but we believe they may be rare. Even once small patches become established, they may not survive (Olesen and Sand-Jensen, 1994).

We have achieved a significant degree of success in efforts to restore *Z. marina* to several coastal bays that have not had seagrass since 1933. Approximately 46 ha of *Z. marina* have been planted with seeds, and plants derived from these seedlings remain thriving through 2005 (personal observation). The longest successful small-scale transplant is now 8 years old

Table 3
Summary of *Z. marina* restoration efforts in Magothy, South, Cobb, Spider Crab, and Hog Island bays from 1997 to the present

Bay	Year	Test plots		Large-scale restoration attempts					2004 Status	Comment
		Number of sites	Adult plants (AP) or seeds	Method	Plot size	Seeds per plot	Number of plots	Total seeds		
Magothy	1997	6	AP						Survival in only one plot	Massive macro-algal bloom in 1997 smothered most plots
	1998	5	AP						Survival at two sites	Plant loss attributed to water quality and shifting sand habitats
	2000	2	AP	Seed broadcast	100 m^2	2 × 50 k, 1 × 100 k	3	200,000	Survival in all seed plots, and at one test plot site	Test plot loss at shallowest site
	2001				0.4 ha	100,000	6	600,000	Survival in 4 of 6 plots	Cause of plot losses unknown
South	1998	4	AP						Survival at 1 of 4 sites	1 site too shallow, cause of death unkown at other 2
	1999	2	AP	Seed broadcast	Linear strips covering ∼1 ha		2	150,000	Robust growth and expansion by seedlings	Plants first flowered in 2001; see Fig. 2
	1999			Adult transplants	300 m^2				No plants remaining	Buried by sand spit
	2000	4	Both		100 m^2	6 × 50 k, 3 × 100 k	9	600,000	Robust growth in all 9 plots	See Fig. 2; seed density expt. Reported in Orth et al. (2003)
	2001			Seed broadcast	0.4 ha	12 × 100 k, 12 × 200 k	24	3,600,000	Survival in all plots	Plants first flowered in 2003; Fig. 2
	2002			Seed broadcast	0.4 ha	12 × 50 k, 12 × 100 k	24	2,400,000	Survival in most plots	
	2004			Seed buoys	2 ha		1	150,000		Spring deployment
Cobb	2001			Seed broadcast	0.4 ha	2 × 100 k, 2 × 200 k	4		Robust growth	Flowering in 2003 and 2004
	2002	4	Both						Survival at 3 of 4 sites	Flowering in 2004
	2003			Seed broadcast	0.2 ha	12.5–100 k	24	1,125,000	Seedlings observed	
Spider Crab	2002	4	Both						Plants still present	Flowering in 2004
	2003	3	AP	Seed broadcast	0.2 ha	12.5–100 k	11	575,000	Plants robust in 2 of 3 plots, seedlings observed	
	2004			Seed buoys	0.8, 2 ha	150–300 k	2, 5	6,695,000		
	2004			Seed broadcast	0.2 ha	150 k	8	600,000		
Hog Island	2004	9	Both							

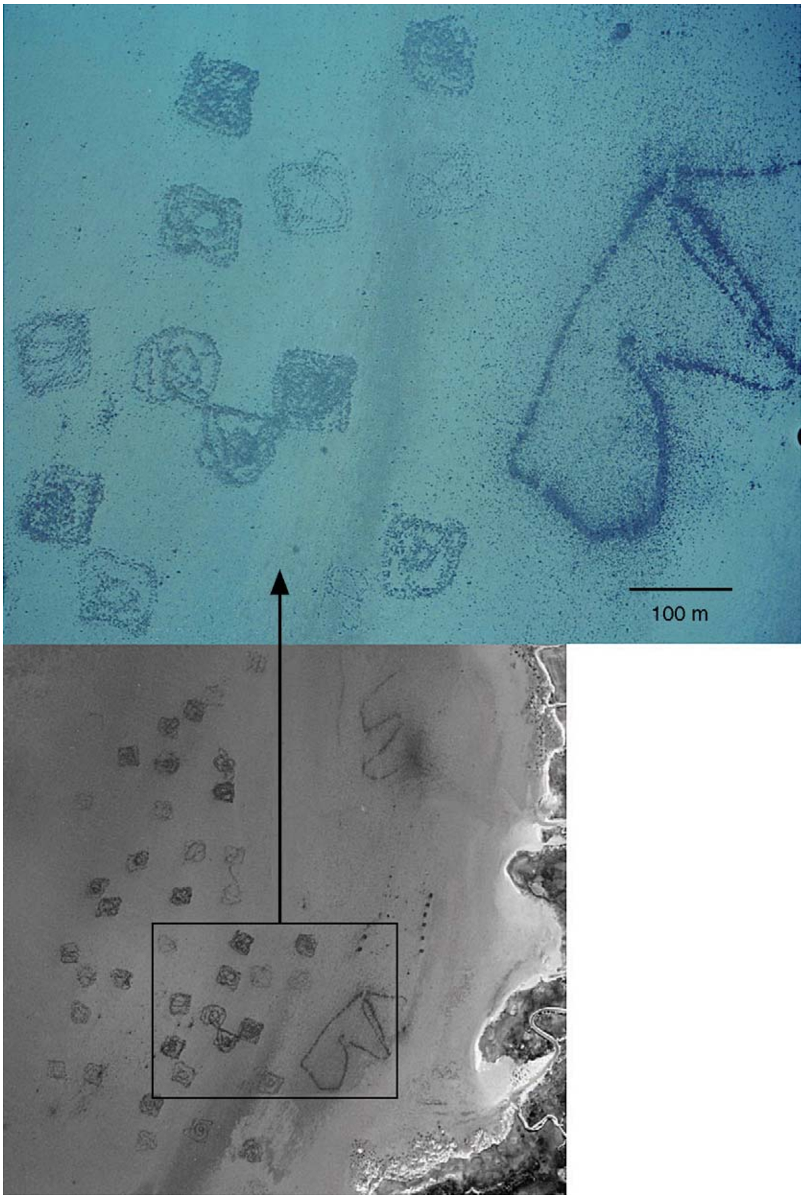

Fig. 2. Vertical aerial photographs (scale 1:24,000) of the South Bay restoration site taken in December 2004, showing the 0.4 ha plots of *Z. marina* resulting from seeds broadcast into unvegetated areas in 2001 and 2002. The color inset is from a vertical aerial photograph (scale 1:4000) taken in November 2004, showing plant patterns in 12 of these plots. Also notable are two areas of dense plants that are in the shape of a "B" and "W". This configuration resulted from a haphazard broadcast of 150,000 seeds into each area in 1999. The pattern noted here reflects the actual path of the boat broadcasting seeds, consistent with our earlier research showing that seeds do not move far from where they settle on the sediment surface (Orth et al., 1994).

and larger areas of 0.4 ha in size are 4 years old. Field observations immediately adjacent to many of the older plots have shown the presence of numerous *Z. marina* patches offering evidence of spread of seeds from these restored plots. Our preliminary estimates in December, 2004, of 52 of the large (0.4 ha) plots planted with seeds between 2001 and 2002 now cover approximately 38% of the bottom with plants. Water quality studies currently underway (Moore, unpublished data) show water quality capable of supporting this growth (Dennison et al., 1993), which has important consequences for continued growth and expansion of restored *Z. marina*. Interestingly, recent attempts to transplant *Z. marina* in one of the northern bays, Indian River Inlet, where *Z. marina* died out in the 1950s, have achieved modest success with smaller scale plantings, suggesting water quality conditions there are now adequate for *Z. marina* survival (B. Anderson, personal communication).

We believe the patterns emerging in these coastal lagoons from both natural seagrass recovery and restoration efforts, when coupled with recent studies from other areas that also document seagrass recovery from the wasting disease (Frederiksen et al., 2004), anoxic events (Plus et al., 2003; Greve et al., 2005), hurricanes (Kendall et al., 2004), or propeller scarring (Whitfield et al., 2004), suggest that seeds and seed dispersal play an important role play in the recovery and expansion of these beds. While seagrass research has emphasized clonal growth, the above work suggests seeds should be a focus of seagrass population dynamic studies (Orth et al., in press-b).

5.2. Water quality, land use changes, and macro-algal problems

Water quality within the middle and eastern regions of most of the coastal bay systems has been characterized by low water column inorganic nutrients, relatively low phytoplankton and relatively high light levels (Table 2). The more northern bays in Maryland and Delaware, which are closer to anthropogenic nutrient inputs, tend to have higher nutrient levels that are poorer for seagrass growth than the more southern bays in Virginia. Total suspended sediment concentrations throughout the coastal bay systems were often found to be higher than levels associated with successful *Z. marina* growth in the lower Chesapeake Bay (Moore et al., 1996). However, turbidity levels (which are usually directly related to suspended sediment concentrations) in the coastal bays were equal to or lower than many seagrass areas in the Chesapeake Bay. This difference may be related to the type of suspended sediments among the systems with a higher proportion of resuspended sandy sediments in the coastal bays that have lower absorptive coefficients (Kirk, 1994) compared to the Chesapeake Bay. Overall, water quality conditions in the middle and eastern regions of the coastal bays appear suitable for SAV growth, and the noted expansion of coverage in Chincoteague Bay and the success of restoration attempts in the southern bays are consistent with this assessment.

Nutrient loadings into the coastal bays are especially high in the western tributaries, and these watershed loadings have been related to the high concentrations of nitrogen and of phytoplankton found in the water in these tributaries (Boynton et al., 1996). For some of these tributaries it has been estimated that nutrient loadings would have to be reduced an order of magnitude or more before conditions suitable for seagrass would occur (Boynton et al., 1996). The coastal bay systems are effective recycling systems for nutrients (Tyler et al., 2001; McGlathery et al., 2001; Anderson et al., 2003) with nitrogen rapidly recycled through benthic micro- and macro-algae as well as bacteria. This compounds the impacts of any new nitrogen that is added to the system. Dissolved organic nitrogen (DON) makes up a large fraction of the total nitrogen in the coastal bays and there is evidence that this DON helps support the large macro-algal biomass that occurs throughout many areas within this region (Tyler et al., 2001). This macro-algae can be an important competitor with the seagrass, *Z. marina*, for light and space here (Hauxwell et al., 2001; Valiela et al., 1997). Macro-alga abundance is highly variable throughout these coastal bays. McGlathery et al. (2001) found biomass ranging from 0 to 650 g dw m^{-2} with an early summer peak followed by a decline by late summer and subsequent accumulation through the fall and winter. Temporary, localized water column anoxia and rapid release of dissolved nitrogen was observed following the mid-summer collapse of the macro-algae (McGlathery et al., 2001; Tyler et al., 2001).

5.3. Fisheries and aquaculture conflicts—management implications

Hard clams, *M. mercenaria*, are abundant in these shallow coastal lagoons and have been harvested both commercially and recreationally. In 1997, the seagrass aerial monitoring program identified the rapid increase in damage to seagrass beds in the coastal bays where seagrass was recovering, caused by commercial clam harvesting using either hydraulic dredges or a modified oyster dredge. The recognition of the value of seagrass beds in this region led management agencies in the states of Maryland and Virginia to enact regulations protecting seagrass beds from commercial clamming (Orth et al., 2002). The state of Virginia prohibited commercial clamming using mechanical methods in most seagrass beds in Chincoteague Bay by marking a zone that did not allow any dredging, while the state of Maryland set marked protection zones based on the mapped seagrass coverages for 3 consecutive years (Orth et al., 2002). The regulations have been generally successful in protecting seagrass beds (Orth et al., 2002) although continued monitoring has been necessary. The resurging *Z. marina* in the bays south of Chincoteague is currently not protected by regulation.

The Southern Delmarva Coastal Bays have had a rapid growth in aquaculture of *M. mercenaria* over the past 15 years. This aquaculture involves planting hatchery-produced juvenile clams on intertidal and subtidal mudflats under plastic predator exclusion nets. Some of these aquaculture operations are very extensive and overlap with potential *Z. marina* habitat. The complete suite of potential interactions between clam aquaculture and *Z. marina* (e.g., water quality effects and seed entrapment) has not been fully investigated. Clarifying and minimizing the extent of resource conflicts between these two uses of the shallow water habitats of the coastal bays will be an important issue for resource managers as *Z. marina* restoration proceeds.

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