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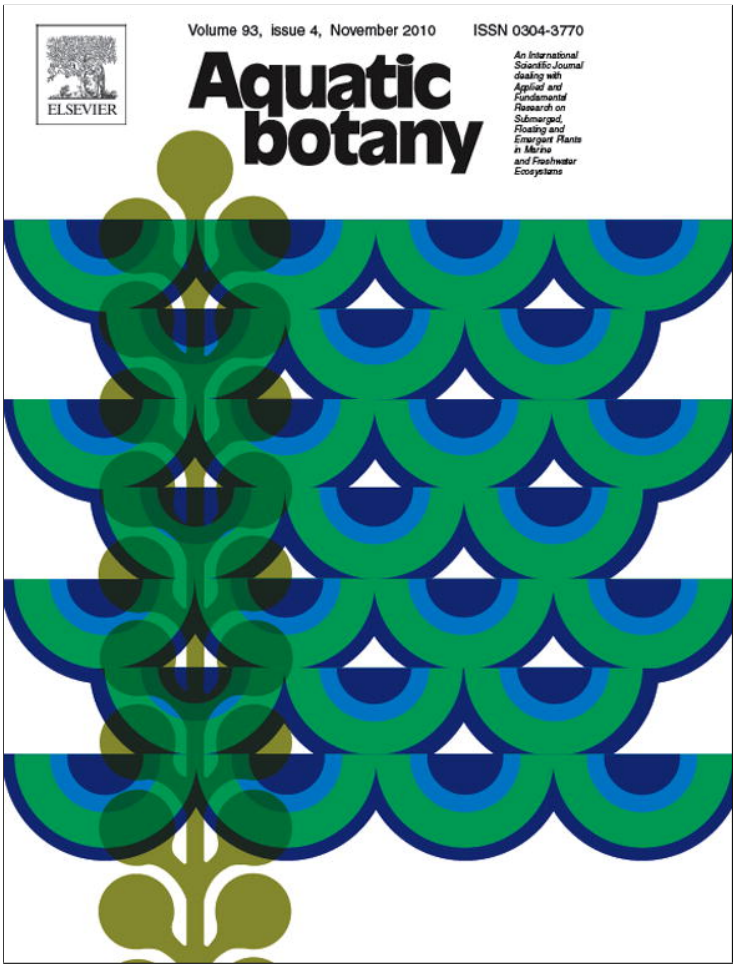

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Eelgrass recovery after nutrient enrichment reversal

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ABSTRACT

Mumford Cove, a 48 ha Connecticut embayment on Long Island Sound, has a history of excessive nutrient inputs and corresponding eutrophic conditions with concomitant eelgrass (*Zostera marina* L.) loss. From 1945 to 1987, a municipal wastewater treatment facility discharged into the cove. In 1987, when the wastewater outfall was diverted to another location, the cove supported a near monoculture of the green algae *Ulva lactuca* L., covering 74% of the bottom. By 1988, macroalgal areal cover in Mumford Cove had declined to 9%. When we first sampled the cove in 1992, *Z. marina* and *Ruppia maritima* L. were present. By 1999, areal distribution of *Z. marina* and *R. maritima* had expanded to cover a third of the bottom. Periodic summertime surveys from 2002 through 2004 indicated that *Z. marina* was present in approximately half of the cove; *R. maritima* was sparse. Fifteen years after termination of nutrient enrichment, this cove had recovered from 40 years of point source anthropogenic nutrient input, returning from an *Ulva*-dominated to a *Zostera*-dominated state.

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1. Introduction

Decline of seagrass populations has been observed in many estuarine embayments, and the declines are often associated with anthropogenic nutrient loading (Short and Burdick, 1996; Duarte, 2002; Hauxwell et al., 2003; Lotze et al., 2006; Orth et al., 2006a; Waycott et al., 2009). Increased availability of nutrients in eutrophic embayments may lead to blooms of macroalgae, phytoplankton, and epiphytes, all of which shade seagrass, reducing the light available for photosynthesis and decreasing seagrass productivity (Harlin and Thorne-Miller, 1981; Short et al., 1995; Hauxwell et al., 2001; Ralph et al., 2007).

Recent management strategies for coastal waters have focused on the use of indicator species to identify systems in need of mitigation (Orth et al., 2002; Neckles et al., 2005; Greening and Janicki, 2006; Steward and Green, 2007; Wazniak et al., 2007). Seagrass ecosystems have been described as "coastal canaries": loss of seagrass indicates ecosystem degradation and loss of ecosystem services (Orth et al., 2006a). While seagrass populations show a significant decline on a worldwide basis (Waycott et al., 2009), instances of natural recolonization of beds have been documented following physical disturbances (Hastings et al., 1995; Dawes et al., 1997; Olesen et al., 2004; Whitfield et al., 2004; Hammerstrom et al., 2007; Di Carlo and Kenworthy, 2008; Martin et al., 2008; Boese et al., 2009); construction (Park et al., 2009); storm events (Preen et al., 1995; Campbell and McKenzie, 2004; Frederiksen et al., 2004; Kendall et al., 2004; Fernandez et al., 2006; Ridler et al., 2006); the 1930s wasting disease outbreak (Rasmussen, 1977; Frederiksen et al., 2004); anoxic events (Plus et al., 2003; Greve et al., 2005); and accumulation of organic matter (Morris and Virnstein, 2004). A number of studies document seagrass recovery following reduction of anthropogenic nutrient inputs (Table 1). Two of these cases involve recolonization by *Zostera marina* L. (eelgrass). In the first case, a large expansion of eelgrass from 1986 to 2001 corresponded with nutrient reduction and improving water quality in a number of bays on the Delmarva Peninsula, MD, U.S.A. (Wazniak et al., 2007; Orth et al., 2010). However, a subsequent decline occurred after 2001, associated with increasing nutrient inputs and a degradation of water quality (Orth et al., 2010). In the second case, Boston Harbor, nutrient inputs from wastewater treatment facilities were reduced by 90% between 1997 and 2000 (Taylor, 2010). In 2008, a *Z. marina* patch was found at 1 of the 60 sampling stations, though areal extent and long-term stability of the bed were not quantified (Maciolek et al., 2009).

Documenting cases of natural seagrass recovery provides information to the management community on potential recovery time and expansion rates for seagrass recolonization of disturbed areas. An understanding of the time frame for this process allows for the development of realistic goals for seagrass recolonization following

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Table 1
Documented cases of natural seagrass recovery following nutrient load reductions.

Species	Location	Remediation	Area studied (km^2)	Pre-existing bed size (ha)	Area recovered (ha)	Time period of recovery	Selected references
Halodule wrightii	Tampa Bay, Florida, USA	N reduction in domestic wastewater discharges (57% reduction, 1976–1992)	959	8800	2171	1982–2004	Johansson and Lewis (1992) Greening and Janicki (2006)
Mixed beds, dominant: *Halophila australis*	Gulf St., Vincent, Southern Australia	N reduction, sewer sludge outfall decommissioned (October, 1993)	0.02[a]	0	0.56[a]	1993–2001	Bryars and Neverauskas (2004)
Posidonia australis, *Posidonia sinuosa*	Oyster Harbor, Western Australia	N and suspended solids reduction, decrease in agricultural run-off	16	[b]	[b]	1988–1996	Cambridge et al. (2002)
Posidonia oceanic	Marseilles, France	N reduction, WWTF opened	0.005[c]	C	0.18[c]	1987–1999	Pergent-Martini et al. (2002)
Thalassia testudinum	Sarasota Bay, Florida, USA	N reduction in domestic wastewater discharges (46% reduction, 1988–2002)	135	3416	214	1988–2002	Tomasko et al. (2005)
Zostera noltii	Mondego Estuary, Portugal	N reduction , altered flow regime (40–50% N reduction, 1998)	3.4	0.02	3.98	1997–2004	Cardoso et al. (2010)
Zostera marina	Delmarva Peninsula, Maryland, USA	N and P reduction, better management of anthropogenic sources					
	Assawoman Bay		21[d]	0	265	1991–1999[e]	Orth et al. (2006b)
	Chincoteague Bay		377[d]	2100	4695	1986–2001[e]	Orth et al. (2006b)
	Isle of Wight Bay		21[d]	0	135	1992–2003[e]	Orth et al. (2006b)
	Newport Bay		16[d]	0	46	1990–2002[e]	Wazniak et al. (2004)
	St. Martin River		8.4[d]	0	0.8	1999–2002[e]	Wazniak et al. (2004)
	Sinepuxent Bay		24[d]	12	743	1986–2002[e]	Orth et al. (2006b)
Z. marina	Boston Harbor, Massachusetts, USA	N reduction, relocated 2 WWTF outfalls (90% reduction, primarily 1997–2000)	122	0	[f]	2000–2008	Maciolek et al. (2009), Taylor (2010)
Z. marina	Mumford Cove, Connecticut, USA	N reduction, relocated WWTF outfall (>66% reduction, October 1987)	0.5	0	25	1987–2002	This study

[a] Sampled a 2 ha area near the decommissioned outfall. An area of 365 ha around the outfall had completely lost seagrass.
[b] *Posidonia australis* radial expansion rate from 20 naturally occurring patches averaged 20 cm y^{-1}, 1994–2000, no area provided.
[c] Determined by tracking the reclamation of a sand patch (0.5 ha) in the seagrass bed. Deep edge of bed also expanded, no area provided.
[d] Data are from the Coastal Bays Program, http://www.mdcoastalbays.org/bays.
[e] Year of first appearance or monitoring—year of maximum abundance. In subsequent years seagrass has declined (Orth et al., 2010).
[f] Present at one station (of 60) in 2008, area not quantified.

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mitigation efforts. Here we present a clear-cut case of natural recovery of *Z. marina* following the termination of a nutrient point source. We evaluated the evidence available with the goal of adding to the growing database on seagrass bed recovery rates and identified likely factors contributing to successful recolonization.

2. Materials and methods

2.1. Site description and history

Mumford Cove is a small embayment in eastern Long Island Sound located in Groton, Connecticut, U.S.A. (N41°19.472′, W72°01.117′). The 48 ha area of the cove is defined by a fluctuating sand bar along its southern boundary. The cove has an average depth of 1 m with deeper areas in the northern arm (Fig. 1), a flushing time of 3.5 d (French et al., 1989a,b), and tidally driven current flows in the range of 0.03 to 0.09 m s^{-1} (Vaudrey, 2007). Recently, salinity values from 25.5 to 32 psu were measured (Vaudrey, 2007). Much of the shoreline is typical New England salt marsh, except for 500 m of sandy beach along the eastern shore and rocky and wooded areas on the western shore of the upper arm. Mumford Cove's watershed area is 972 ha and comprises wooded uplands, marshes, residential areas, roads, a wastewater treatment facility, and a railroad line.

In 1945, a wastewater treatment facility (WWTF) for Groton, CT began discharging into Fort Hill Brook, which drains into Mumford Cove; the history of nutrient loading to Mumford Cove is reflected in nitrate + nitrite concentrations (Fig. 1). By 1971, ~1500 m^3 d^{-1} of treated wastewater were discharged from the WWTF into the cove (Buck, 1971). By 1974, the WWTF had expanded in size, output, and service area, resulting in an increase of discharge volume to 13,200 m^3 d^{-1} (Curtis and Dunbar, 1985). The 1981–1982 WWTF nitrogen load normalized to the area of the cove was estimated by Buck and Feng (1983) at 185 kg N ha^{-1} y^{-1}, based on outflow data and monthly nutrient samples from Fort Hill Brook. The wastewater outflow was relocated to a site in the Thames River in October 1987, eliminating the wastewater nutrient load to Mumford Cove. Of course some loading continued from the adjacent watershed. Hindcasting the loading rate is beyond the scope of this paper, but we can make a rough estimate to approximately quantify the decline. The 2002 nitrogen load to Mumford Cove has been modeled using a variation of the Estuarine Loading Model, which uses land use and housing data to calculate the N input (Valiela et al., 1997). A loading estimate for 2002 of 94 kg N ha^{-1} y^{-1} was calculated using the CLEAR land-cover dataset and housing density data received from the town of Groton (Hurd et al., 2003; A. Branco, pers. comm.). This estimate differentiated the houses on septic (with N going to Mumford Cove) and sewer (with N exported from the watershed) based on the housing data from the town. If the septic–sewer split is ignored and all houses are assumed to deliver N to Mumford Cove, the estimate is increased to 176 kg N ha^{-1} y^{-1}. This value closely matches an independent estimate of the N load for the 1990s which also ignores the septic–sewer split: 183 kg N ha^{-1} y^{-1} (calculated from the total load of 8761 kg N y^{-1} applied to the 48 ha cove area, Latimer and Charpentier, 2010). Using the 2002 estimate for the nitrogen load, the removal of the WWTF outfall from the cove resulted in a 66% reduction of total N input. This percentage is a minimum estimate as the 1980s input of N from non-WWTF sources should be lower than the 2002 estimate, given the increasing human population in the watershed through time.

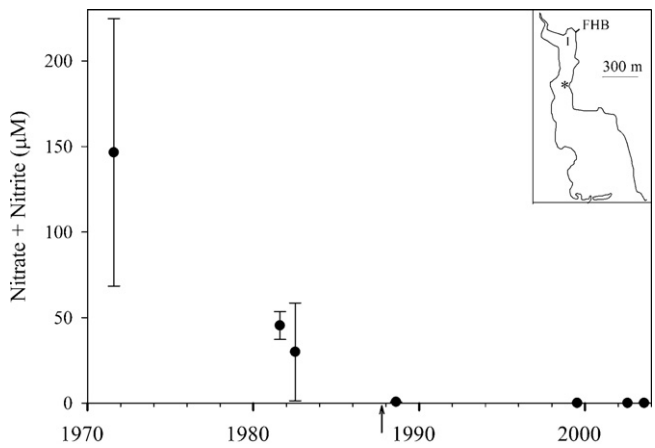

Fig. 1. Water column nitrate + nitrite concentrations. Data were averaged over the summer sampling dates (June 15 to July 30) for the northern portion of the cove, near Fort Hill Brook (FHB) and the previous WWTF outfall. Historical data for 1970–1988 were gathered from reports (Buck, 1971; Buck and Feng, 1983; French et al., 1989a). Other years were sampled in this study. An arrow on the *x*-axis indicates the date of the WWTF diversion. Data through 1990 were collected within 40 m of station 1. In 1999, data were collected from station 1 and a point 400 m south of station 1 (*). The 2002–2004 data are from the southern station (*).

During the last years of the WWTF discharge into Mumford Cove, the cove contained a near monoculture of *Ulva lactuca* L. and no seagrass was observed (Curtis and Dunbar, 1985). In the fall of 1987, just prior to the diversion of the wastewater outfall, the average biomass of *U. lactuca* was 400 g DW m^{-2} and covered 74% of the benthic area in the cove (French et al., 1989a). One year after the WWTF diversion, *U. lactuca* biomass dropped to an average of <1 g DW m^{-2} and areal cover decreased to 9% (French et al., 1989a,b). We reviewed the history of Mumford Cove, its nutrient status and the available information on macrophyte distribution, together with our own field observations made between 1992 and 2004, to assess the rate of eelgrass recovery following nutrient reduction.

2.2. Sampling year 1992

At the end of June 1992, the cove was sampled for *Z. marina* biomass at five stations (Fig. 2) corresponding to stations sampled by French et al. (1989a). At each station, four replicate *Z. marina* samples were taken using a 1/16 m^2 quadrat. The *Z. marina* samples were cleaned and dried at 60 °C to determine dry weight biomass. The presence of *Ruppia maritima* L. was noted. Benthic macrophytes were mapped with aerial photography conducted by the J.W. Sewall Company (Old Town, Maine) on July 7 using the C-CAP protocol (Klemas et al., 1993).

2.3. Sampling year 1999

In mid-August 1999, above-ground macrophyte biomass was harvested from four replicate 1/16 m^2 quadrats at each of the five stations sampled in 1992. The samples were processed as described in Section 2.2. Benthic macrophytes were mapped using data from a visual survey conducted by divers on August 10 and 11. The survey yielded >8000 geo-referenced data points. A towed diver signaled the presence or absence of each of the two seagrasses with electronic toggle switches. The information was logged to a computer which recorded the DGPS location every 4 s. The map of presence vs. absence for each seagrass species was developed by interpolating between data points with a kriging algorithm in the program Surfer (v.7.00). Mapping efforts were verified during the diver survey by an observer on the boat; the bottom was visible from the surface throughout the areas with seagrass.

During bi-weekly trips in June and July of 1999, nine stations were sampled throughout the cove. Only data from the five stations sampled in 1992 are presented here. A Birge–Ekman benthic grab (15 cm per side) mounted on a solid pole was used to collect three

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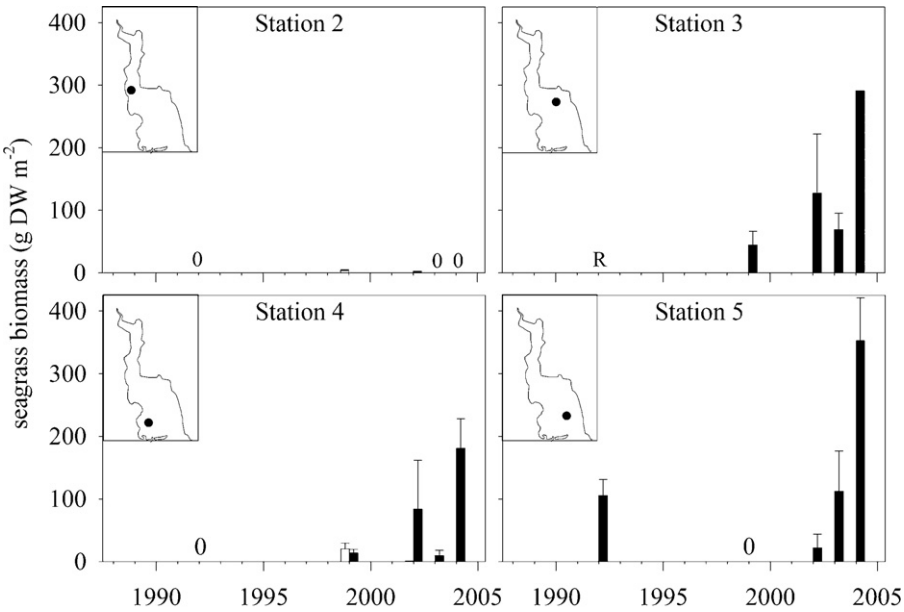

Fig. 2. Seagrass biomass at stations 2–5. No seagrass was present at station 1 during any year (location shown in Fig. 1). Sampling occurred in 1992, 1999, and 2002–2004. Black bars = *Zostera marina*; white bars = *Ruppia maritima*. 0 = sampled but absent; R = *R. maritima* present, not quantified. Error bars indicate the standard error.

bottom samples from each of the stations. Approximately 20 mL of surface sediment (<1 cm deep) was collected from each of the grabs with the criterion that the sediment surface must be undisturbed by the action of the grab. Each sediment sample was homogenized and larger organic matter fragments (*Z. marina*, macrophytes, shells) and rocks with a diameter larger than 5 mm were removed. The sediment organic matter (% of DW) was analyzed following standard method 2540G for total volatile solids (Greenberg, 1992). Triplicate water samples were collected from both 0.25 m depth and 0.25 m above the bottom for nutrient analysis. Samples were pumped from depth through a Whatman GF/F filter into acid washed bottles and held on ice for a few hours, then stored at −20 °C. Samples were later analyzed on a Lachat QuikChem AE continuous flow analyzer following EPA standard methods (Clesceri et al., 1998).

2.4. Sampling years 2002–2004

In the summers of 2002 through 2004, multiple geo-referenced benthic grabs were taken throughout the cove to map macrophytes and assess biomass. Mid-summer sampling occurred on: July 1, 2002 (66 grabs), August 8, 2003 (62 grabs), and July 15, 2004 (43 grabs). A composite map of *Z. marina* presence vs. absence for the 2002 through 2004 data was created, as in 1999. The accuracy of the cover map developed for the 2002 sampling date was verified using the aerial photos and cover estimates from that same time period obtained by the U.S. Fish and Wildlife Service (Tiner et al., 2003). In addition to the macrophyte sampling, water samples for nutrient analysis and sediment samples for organic matter analysis were collected monthly during the summers. Again, only data from stations corresponding to earlier field efforts are presented (Fig. 1). Samples were collected and handled as described in Section 2.3.

During the summers of 2002 and 2004, YSI 6600 multiparameter sondes were occasionally deployed at stations 3, 4, and 5 as part of a separate project (Vaudrey, 2007). These recorded temperature, salinity, and oxygen every 15 min for periods of up to 2 weeks. Sondes were typically deployed once per month, June through August, with occasional deployments during the spring, fall and winter. A pair of sondes were standardized and deployed, one fixed at 0.3 m above the bottom and another floating 0.4 m below the surface.

2.5. Statistical analyses

Data are presented as the mean ± 1 SE. A one-way ANOVA and Tukey–Kramer HSD were used to evaluate the spatial differences in sediment organic matter by year and the temporal change in organic matter by station. The expansion of *Z. marina* cover in Mumford Cove was evaluated with a non-linear regression using a two parameter exponential growth equation. Significant differences were determined at $\alpha = 0.05$. All statistical analyses were performed in JMP 6.0.0 (SAS Institute, Cary, NC, USA). Nutrient data were limited and statistical comparisons were not applied to these data.

3. Results

By 1992, sparse plants of *Z. marina* were present at station 5, interspersed with an *U. lactuca* bed, and *R. maritima* was present near station 3 (Figs. 2 and 3). In 1999, both *R. maritima* and *Z. marina* were found in the cove in greater abundance than in 1992, but distribution just south of the sand bar had declined (Fig. 3). South of the sand bar is a depositional area and the sand bar itself shifts position. The dynamic nature of this area likely accounts for the reduced

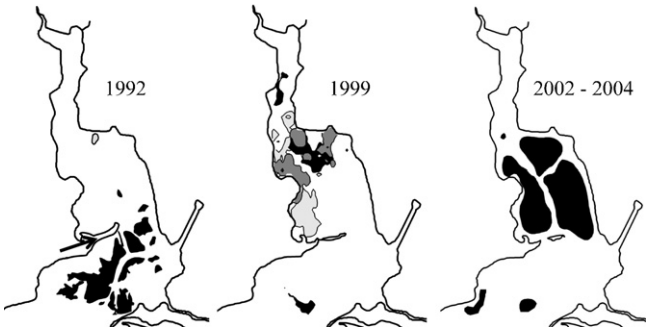

Fig. 3. Presence of macrophytes in Mumford Cove determined by aerial photography in 1992, diver based visual survey in 1999, and geo-referenced benthic grabs for 2002 through 2004. An arrow on the 1992 map designates the sand bar defining the southern end of the cove. Black = *Z. marina*, light grey = *R. maritima*, dark grey = mixed beds of the two seagrasses.

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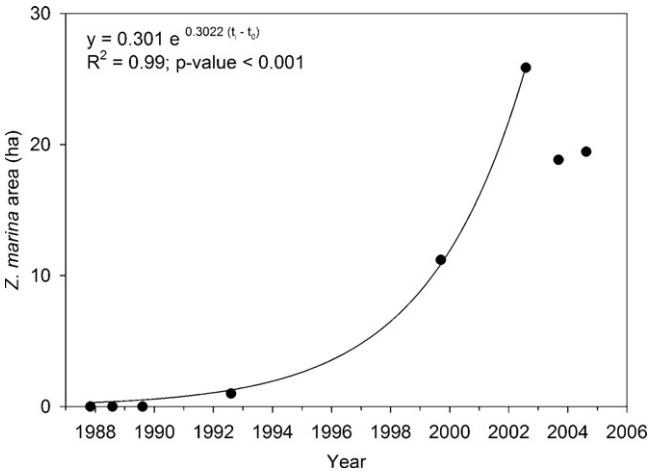

Fig. 4. Area of *Z. marina* calculated from coverage maps in Fig. 3. For the regression equation, t_0 is set as the date of the WWTF diversion and t_i is a date on the *x*-axis. The regression was fit through the year of maximum extent (2002).

cover of *Z. marina*. By 2002, *Z. marina* was the dominant macrophyte in the cove in terms of areal cover and biomass (Figs. 2 and 3). *R. maritima* was found in trace amounts at stations 2 and 4 in 2002, but in 2003, no *R. maritima* was found. By the summer of 2004, average biomass of *Z. marina* in the cove had reached 44 g DW m^{-2}. *Z. marina* was abundant at stations 3 and 4, patchy around station 2, and absent from areas north of station 2 (Fig. 3). A quantitative comparison of the biomass from benthic grab stations showed a 99% decrease in *U. lactuca* biomass compared to before the WWTF diversion in 1987.

The data from the mapping efforts were used to estimate the area of *Z. marina* north of the sand bar (Fig. 3). An exponential regression was applied to the data from 1987 through 2002, which was the sample year of maximum coverage, yielding an expansion rate of 0.3 y^{-1} (R^2 = 0.99, *p*-value < 0.001, Fig. 4). The *Z. marina* in Mumford Cove exhibited reduced distribution of unknown cause in 2003 and 2004 compared to 2002.

Nitrate + nitrite data were used for a temporal comparison as these were available for all years, suggesting a drastic decrease through time (Fig. 1). All post-diversion nitrate + nitrite concentrations were less than 0.2 μM. Average water column nutrient concentrations for both total inorganic nitrogen and total inorganic phosphorus (data not shown) were less than 1 μM in 1999, 2002, and 2003.

The sonde deployments indicated that late July and early August bottom water temperatures at station 3, near the northern limit of the seagrass bed, typically exhibited the highest temperature of the three stations sampled (stations 3–5). Values were consistently above 22 °C and frequently above 24 °C (10 out of 14 days). Mid-afternoon temperatures often reached 26 °C, with a maximum recorded value of 28.8 °C on July 23, 2002. The occurrence of low oxygen in the bottom water was evident at station 3 during the 3 years, and at station 5 during 2003. Low oxygen was observed solely in July and in all cases persisted for less than an hour, just before dawn. Specifically, oxygen values below 4 mg L^{-1} occurred on 13 sample days in 2002, 3 days in 2003, and 3 days in 2004. Oxygen values below 3 mg L^{-1} occurred on 4 days in 2002 and 1 day in 2004, 2003 did not experience values below 3 mg L^{-1}.

Temporally, a significant decrease in station 1 sediment organic matter occurred following the diversion of the WWTF outfall (Table 2, *p*-value = 0.02). All other stations were similar through time (*p*-value > 0.05). Pooling the 1999 through 2004 data, there is a significant difference among stations (one-way ANOVA, *p*-value < 0.001) with the Tukey–Kramer HSD indicating station 1 is similar to station 2, but higher than stations 3 and 4 (Table 2).

Table 2
Mean (standard error) for sediment organic matter (% of DW) at the stations indicated in Figs. 1 and 2. The 1982 data are from one sample date (Buck and Feng, 1983). Pooled data for station 1 are from 1999 only (*n* = 3), all other stations from years shown (*n* = 12).

Station	1982	1999, 2002–2004	Tukey–Kramer HSD
1	24	10.9 (1.0)	A
2	13	12.0 (0.5)	A, B
3		7.9 (0.7)	B
4		8.6 (0.8)	B

Letters A and B indicate statistical similarity among stations for the 1999, 2002–2004 data (Tukey–Kramer HSD).

4. Discussion

Z. marina was absent from Mumford Cove during the years of excess nutrient loading from the Groton WWTF. Within 5 years of the diversion of the WWTF's outfall and a concomitant reduction in nutrient inputs, *U. lactuca* was drastically reduced in biomass and areal cover, followed by *Z. marina* and *R. maritima* recolonization of the southern half of the cove (Fig. 3). By 1992, Mumford Cove was no longer a macroalgae-dominated community. By 1999, *R. maritima* had expanded its cover along the western edge of Mumford Cove but was essentially absent by 2002. Within 15 years of the WWTF diversion, *Z. marina* was again the dominant macrophyte in Mumford Cove and could be found as patches or moderately dense beds over an area of approximately 24 ha.

The pattern of seagrass recolonization following N load reduction in Mumford Cove supports the relationship identified by Steward and Green (2007), which relates N load per estuarine area to seagrass loss; their study predicts complete loss of seagrass at loading values above 175 kg N ha^{-1} y^{-1}. In Mumford Cove, the nutrient load associated only with the WWTF was 177 kg N ha^{-1} y^{-1}. The actual N load was higher, as this estimate did not include the N entering via groundwater, atmospheric deposition, or from other natural and anthropogenic inputs to Fort Hill Brook and the cove. By 2002, the estimated N load per area of the estuary from all sources was 90 kg N ha^{-1} y^{-1}. Steward and Green's (2007) relationship indicates that at this lower load, seagrass should be present in all otherwise suitable areas, as is supported by the 2002–2004 distribution in Mumford Cove.

While the recolonization of the cove by *Z. marina* followed a large reduction in water column nutrients, other conditions had to be suitable for the return of eelgrass, including a nearby source of seeds (Short et al., 2002; Morris and Virnstein, 2004; Erftemeijer et al., 2008). The *Z. marina* beds at the mouth of the cove (<100 m south) and *R. maritima* in a reconstructed salt marsh directly north of station 3 likely provided a source of seeds for the proliferation of both seagrass species in the cove.

In 1992 and 1999, the beds of eelgrass were small and patchy. The density and distribution of the beds continued to be variable, as reported elsewhere for recovering eelgrass populations (e.g. Frederiksen et al., 2004; Evans and Short, 2005). While a number of factors influence eelgrass success, three were monitored as part of other research efforts in Mumford Cove: temperature, sediment organic content, and dissolved oxygen concentration. Optimal temperatures are between 15 and 20 °C for *Z. marina* (Lee et al., 2007). The mid- to late-summer temperatures in the cove reach values well above 22 °C, with bottom water often as high as 27 °C. While there is some plasticity in the upper limit due to the ability of local populations to acclimate to higher temperatures (McRoy and McMillan, 1977; Zimmerman et al., 1989; Enríquez et al., 2004), values above 25 °C have been cited as detrimental to the growth of *Z. marina* (Bintz et al., 2003; Enríquez et al., 2004; Lee et al., 2005; Plus et al., 2005). The sediment organic matter content in the beds are within a range identified as suitable for *Z. marina* (0.4–10%:

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Batiuk et al., 2000; Vaudrey, 2008); however the levels found at stations 1 and 2 were marginal (Table 2). The 2002 through 2004 data indicated that Mumford Cove experiences oxygen levels below 4 mg L^{-1} infrequently during July, persisting for an hour or less, and occurring just before dawn. During all other months, oxygen levels are typically near or greater than 100% saturation, in contrast to the persistent daytime hypoxia and anoxia observed in July and August of 1983, prior to the WWTF diversion (Curtis and Dunbar, 1985). Oxygen levels improved within months of the WWTF diversion and based on a limited number of sampling dates, were similar to the 2002–2004 oxygen conditions in the cove (French et al., 1989b). Plus et al. (2003) observed that extended periods of anoxia (>1 week) resulted in wholesale mortality of *Z. marina*, followed by reestablishment from the seed bank the following year. Considering both the sediment organics and high summer temperatures, the areas at station 2 and further north are currently unlikely to support stable beds of eelgrass, though seedlings were found just north of station 2 in 1999 and again in 2002.

Mumford Cove exhibited a 3–5 year time lag between the nutrient load reduction and the initiation of seagrass recolonization and a 12–15 year time lag to a relatively stable distribution. These values are within the range expected based on other cases of recovery (Table 2). For example, time to initial establishment for sites with no pre-existing seagrass beds range from 3 to 8 y (St. Martin River, Boston Harbor). Expansion of seagrass into stable beds for cases with no pre-existing beds or small beds range from 7 to 16 y. In areas where extant beds expanded, maximum cover was achieved in 14 to 22 y (Chincoteague, Sarasota, and Tampa Bays). Not all sites presented have reached a stable or maximum cover, so direct comparisons between sites must be conducted with caution (Table 2).

An exponential growth curve fit to the cover data yields an annual expansion rate of 0.3 y^{-1} (Fig. 4), higher than the median rate of 0.054 y^{-1} (mean: $0.12 \pm 0.036\,y^{-1}$) for multiple seagrass species from all climate zones (Waycott et al., 2009), and within the range of *Z. marina* expansion rates observed by Olesen and Sand-Jensen (1994; 0.19 y^{-1} for 10 m^2 patches, 0.65 y^{-1} for 1 m^2 patches). Calculation of the expansion rate in this and other sites provides a tool for estimating the response time following nutrient reductions for eelgrass beds. Similar techniques have been used to describe the trajectory of recovery for various *Z. marina* metrics in restored beds (Evans and Short, 2005) and to describe the rate of loss for multiple species of seagrass (Short and Burdick, 1996; Waycott et al., 2009).

Z. marina was present in the cove within 5 years and firmly established within 15 years of the WWTF diversion. However, growing anthropogenic nutrient input associated with rising coastal populations could reverse the trend for Mumford Cove, as was seen in bays of the Delamarva Peninsula (Orth et al., 2010). The Mumford Cove eelgrass recovery clearly demonstrates natural seagrass recolonization capacity in response to decreased nutrient conditions.

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