Chapter 3

Dominant Plant Communities

Once considered prime waterfowl habitat by local guides, some plant communities in the upper Kennebec Estuary, such as this wedge-shaped marsh known as the "Foot," are known to have experienced dramatic shifts in species composition since the middle of the last century. Photo: Slade Moore and John Sowles.

As natural communities of high complexity and ecological influence in the Kennebec Estuary, fresh tidal marshes and submerged aquatic vegetation (SAV) represent a cohesive source of stability and resilience supporting a disproportionately large share of ecosystem functions and services. Subject to environmental changes driven by land use, industry and urbanization, these communities have experienced wide distributional fluctuations since they were first monitored during the mid-20th century. Apart from gross trends, do we sufficiently understand the nature of these changes, including how our own management actions may influence them? What are, and have been, the implications of large-scale plant community shifts to ecosystem function and to the provision of ecosystem goods and services? What does the present condition of these communities indicate about how far restoration has progressed toward full ecosystem recovery?

Introduction

Several types of plant communities can be said to dominate the Kennebec Estuary, including those populated by phytoplankton, seaweed, submerged aquatic vegetation, and marsh plants. Among these, communities composed of submerged aquatic vegetation and marsh plants have captured the interest of natural resource managers, in part because they so obviously offer direct benefit to fish and wildlife populations. The term "submerged aquatic vegetation" (SAV) refers to a diverse group of rooted aquatic plant species that share, among other traits, a habit of growing beneath the water's surface. Except at lower tidal stages, they are often unseen by the casual observer. Freshwater tidal marsh plants, on the other hand, are species that emerge above the water's surface during much of the tidal cycle. These include the well-known rushes and grasses that dominate freshwater tidal marshes. SAV and tidal marsh communities can provide functions and services that influence ecosystems; these include nutrient sequestration and nutrient cycling, offering a habitat for a variety of organisms, providing food for invertebrates and vertebrates, sediment retention and stabilization, and wave attenuation (Catling et al. 1994, Sand-Jensen 1998; Fluharty 2000; Burton 2007) (Table 1-1). Although the long-term trend of freshwater tidal marsh plants and SAV has probably been one of spatial dominance in the estuary, dramatic shifts in distribution of these community types have profound implications for ecosystem integrity and resilience. As a result, distributional patterns of SAV and tidal marsh plants can be used as proxies or indicators that signal the status of environmental processes which are key to ecosystem function and to the delivery of the services and goods people want and need.

Submerged Aquatic Vegetation

Trends

The upper Kennebec Estuary supports SAV growth, although less than the amount Merrymeeting Bay is thought capable of supporting given the bay's expansive shallow subtidal acreage (Lichter et al. 2006; Köster et al. 2007). Submerged aquatic vegetation in the bay currently inhabits less than ~5% of substrates that are less than 3 m (~10 ft) deep at low tide (Köster et al. 2007). Köster and colleagues (2007) hypothesized that accelerated sedimentation and cultural eutrophication associated with historical land use led to increased turbidity levels in Merrymeeting Bay. Increased turbidity may be responsible for limiting distributions of SAV in Merrymeeting Bay much as it has in other estuaries such as the Hudson River (Nieder et al. 2004), the Potomac River (Carter and Rybicki 1990), and Chesapeake Bay (Stevenson et al. 1993).

In the 1950s and 1960s Howard Spencer, a waterfowl biologist for the state of Maine, conducted the first assessments of emergent and submerged aquatic plants in Merrymeeting Bay using aerial photography and field surveys. He found that between 1956 and 1961, SAV coverage in the lower intertidal and shallow subtidal areas declined by about 30% in Merrymeeting Bay (Table 3-1) (Spencer 1966). In some regions of the bay declines were more pronounced than in others. For example, the area around Swan Island lost almost 75% of its SAV coverage between 1956 and 1961. Notable declines of SAV also occurred in the Eastern River, in the mid-bay above Abagadasset Point, in the Androscoggin River, and around the Chops. However, these declines were not ubiquitous across the bay, as evidenced by increases in SAV acreage in the Muddy, Cathance, and Abagadasset Rivers during the same time period (Spencer 1966). Spencer (1959) listed bushy pondweed (*Najas flexilis*), flat-stemmed pondweed (*Potamogeton zosteriformis*), clasping-leaved pondweed (*Potamogeton perfoliatus*), water milfoil (*Myriophyllum humile*), greater bladderwort (*Utricularia* *vulgaris*), purple bladderwort (*Utricularia purpurea*), coontail (*Ceratophyllum demersum*), and musk grass (*Chara vulgaris*) as the principal SAV species in Merrymeeting Bay during the late 1950s, although he also listed tape grass (*Vallisneria americana*) as an important waterfowl food in Merrymeeting Bay (Spencer 1957).

In 1998 the Friends of Merrymeeting Bay initiated a project that analyzed vegetation trends in the upper estuary and a surrounding one-half mile upland buffer (James W. Sewall Company 2000). They

	1956	1961	Change 1956–1961	
	Hectares (Acres)	Hectares (Acres)	Area	Percentage
Swan Island	100 (247)	25 (62)	75 (185)	–75%
Eastern River	25 (61)	10 (26)	14 (35)	–58%
Mid-Bay	91 (225)	49 (122)	42 (103)	–46%
Abagadasset River	51 (125)	85 (210)	–35 (–85)	68%
Muddy-Cathance	12 (30)	24 (60)	–12 (–30)	100%
Androscoggin River	17 (43)	6 (14)	12 (29)	–67%
Chops	11 (28)	8 (19)	4 (9)	–32%
Merrymeeting Bay (total)	307 (758)	214 (529)	93 (229)	–30%

Table 3-1. Submerged aquatic vegetation (SAV) coverage in the upper subtidal and lower intertidal regions of Merrymeeting Bay estimated from aerial photograph data, 1956–1961. Adapted from Spencer (1966).

found that SAV coverage in the lower intertidal and upper subtidal (water depth <0.38 m or 15 in.) regions of Merrymeeting Bay decreased from 136 ha (336 acres) in 1956 to 72 ha (178 acres) in 1981 (–53%) and then increased 146% to 177 ha (438 acres) in 1998, for a net increase of 30% between 1956 and 1998. Using the same aerial photographs as those in the Friends of Merrymeeting Bay study, but a different methodology, Burton (2007) estimated that subtidal SAV coverage increased from 1.8% of the total area of Merrymeeting Bay in 1981 to 3.1% in 1998, representing a 72% increase (Figs. 3-1 and 3-2). Although the magnitude of change may be unclear, these results suggest a trend of increasing SAV acreage during the study period.

During the summer of 2006, researchers from Bowdoin College conducted quantitative surveys of submerged aquatic vegetation in the subtidal region of Merrymeeting Bay between the Cathance and Abagadasset Rivers. They found five species of SAV at this site, including common waterweed (*Elodea canadensis*), musk grass, tape grass, bur-reed (*Sparganium* sp.), and clasping-leaved pondweed. Additional SAV species observed in other areas of the bay were bushy pondweed, coontail, and long-leaf pondweed (*Potamogeton nodosus*) (J. Reblin, unpublished data). Of the five species, tape grass (Fig. 3-3) was the most abundant by weight (67%) and was also the most widely distributed (being found in 76% of survey plots). Tape grass was mentioned as an important waterfowl food in earlier Maine state reports, but comparisons between contemporary SAV patterns of species dominance and those of the mid-20th century are hampered because earlier surveys apparently did not differentiate between SAV species but instead grouped them together under the aggregative “submerged aquatics” (Spencer 1959, 1966).

As water depth increases, the intensity of sunlight penetrating through the water column decreases exponentially due to absorption (Lampert and Sommer 1997). These losses influence the depth distribution of SAV when plant tolerances for low light conditions are exceeded. Of the five species identified in SAV surveys during the summer of 2006, tape grass grew in areas no deeper than 1.4 m (4.6 ft) at low tide, while the other species grew no deeper than 0.4 m (16 in.) (Fig. 3-4; Burton 2007). Maximum tape grass productivity also occurred at depths (0.2–0.5 m or 8–19 in.) that often exceeded the maximum depths attained by the other species (Burton 2007), probably an expression of tape grass's tolerance of low light conditions. Under ideal conditions, tape grass can grow at depths of up to 7 m (23 ft) (Korschgen and Green 1988) or where at least 5% of surface light can penetrate. However, the species typically experiences best growth when exposed to at least 10% of the amount of sunlight present at the surface (Carter and Rybicki 1985). During the growing season in Merrymeeting Bay, Burton (2007) found that the depth at which 10% of the surface light penetrated was ~1.25 m (4.1 ft) and the depth to which 5% of the light penetrated was ~1.75 m (5.7 ft). Thus the 0.2–0.5 m (8–19 in.) depth of maximum observed tape grass productivity in the bay was considerably less than what published accounts for other sites suggest would be typical for this locality (i.e., 1.25 m [4.1 ft]). Also, tape grass in the bay should conceivably grow at 1.75 m (5.7 ft), a depth that has surface light penetration of 5%, but in fact only obtains a maximum depth of 1.4

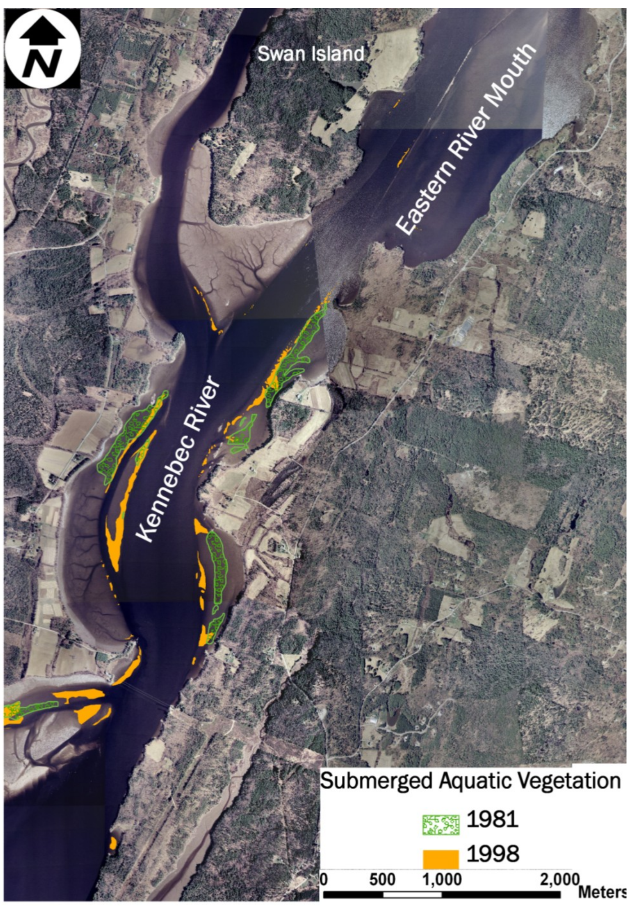


Figure 3-1. Submerged aquatic vegetation coverage in the sub-tidal region of the upper Kennebec Estuary near the mouth of the Eastern River. Data estimated from aerial photographs taken in 1981 and 1998 and digitized by James W. Sewall Company 2000. Raw data provided by the Friends of Merrymeeting Bay and adapted from Burton (2007).

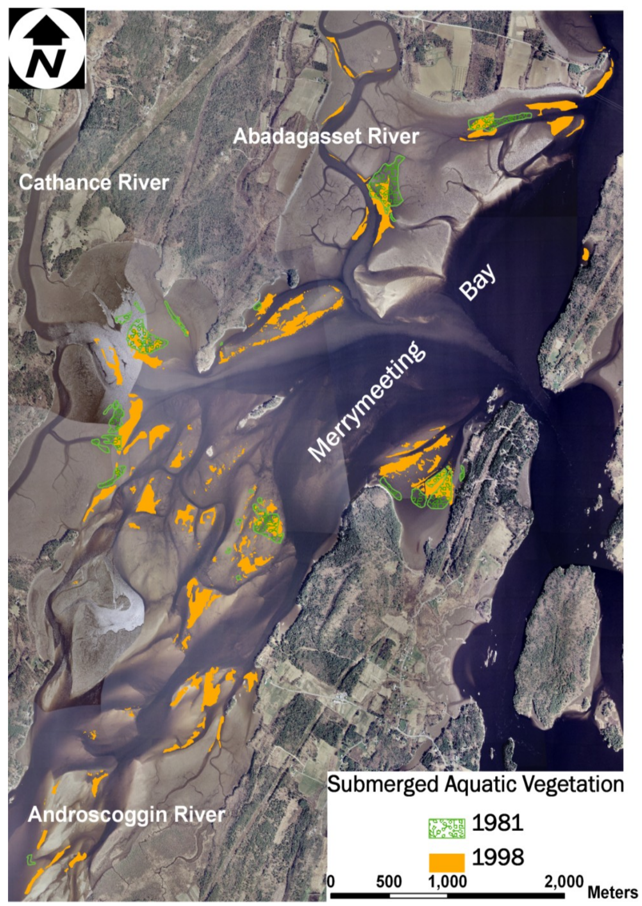


Figure 3-2. Submerged aquatic vegetation coverage in the sub-tidal region of Merrymeeting Bay south of Swan Island. Data estimated from aerial photographs taken in 1981 and 1998 and digitized by James W. Sewall Company 2000. Raw data provided by the Friends of Merrymeeting Bay and adapted from Burton (2007).

m (4.6 ft). The apparent discrepancy between predicted and observed maximum depths for tape grass productivity and survival in the bay may be within the range of natural variance or it may indicate that local conditions are less than ideal for SAV.

Monitoring that began in the mid-20th century indicates that SAV spatial distributions in the upper Kennebec Estuary have experienced periods of expansion and decline, possibly with an overall net trend of increase. Ecologists regularly observe transient distributional shifts in some types of SAV communities (e.g. eelgrass), but the factors driving those changes are often poorly understood. Among causes of long-term SAV declines, research in ecosystems outside of Maine often implicates poor water quality (Cooper 1995). Unfortunately, data gaps during the years between SAV assessments in the Kennebec Estuary allow no insight into whether SAV populations experienced even more frequent or higher-amplitude oscillations in acreage between sampling events. Nor have analyses been conducted that would characterize shifts in the distributions of different density classes within mapped SAV communities in the estuary. This is an important management consideration because the number of stems per unit of area has implications for habitat quality, among other functions.

Even less is known about the abundance of SAV in Merrymeeting Bay before monitoring began. However, there is reason to suggest (Köster et al. 2007) that pre-colonial conditions in and around the upper estuary would have favored more extensive SAV growth than conditions in the period that followed extensive land clearance, which was marked by impaired water quality, or contemporary conditions, which indicate a lingering legacy of that impairment. Although many uncertainties remain, the reversal of the decline in SAV distribution may be related to improving water clarity resulting from implementation of the Clean Water Act.

Many of the anthropogenic factors implicated in initiating SAV declines elsewhere (e.g., cultural eutrophication, industrial and municipal waste disposal, land clearance, increased sedimentation, and non-native species introductions) were also present in the watersheds of the Kennebec and Androscoggin

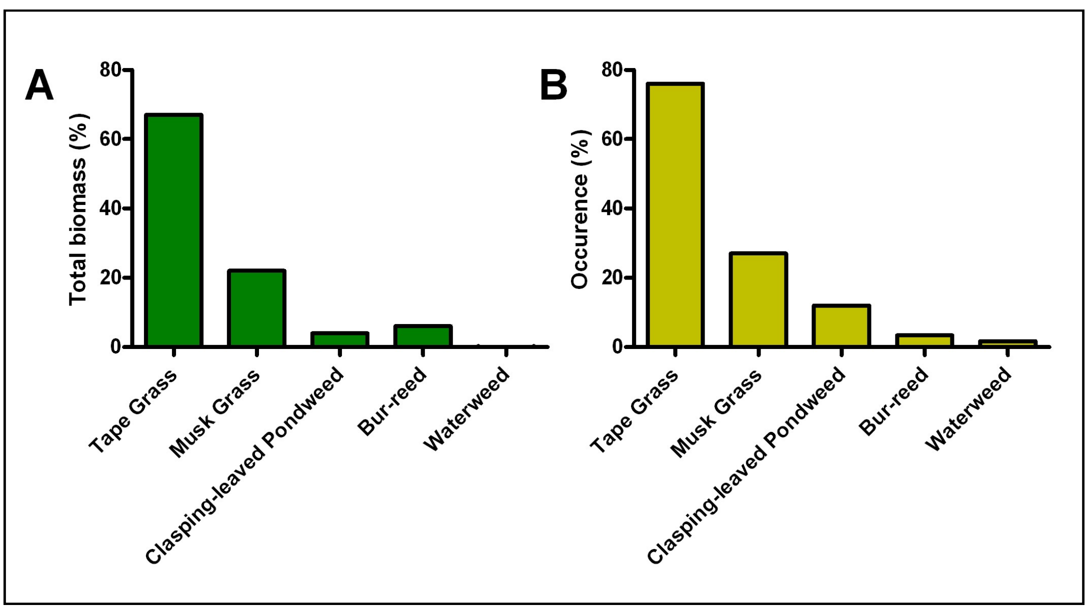


Figure 3-3. The (A) abundance (percentage of the total biomass) and (B) occurrence (percentage of plots containing a species) of submerged aquatic plant species in Merrymeeting Bay near Centers Point during summer 2006. Adapted from Burton (2007).

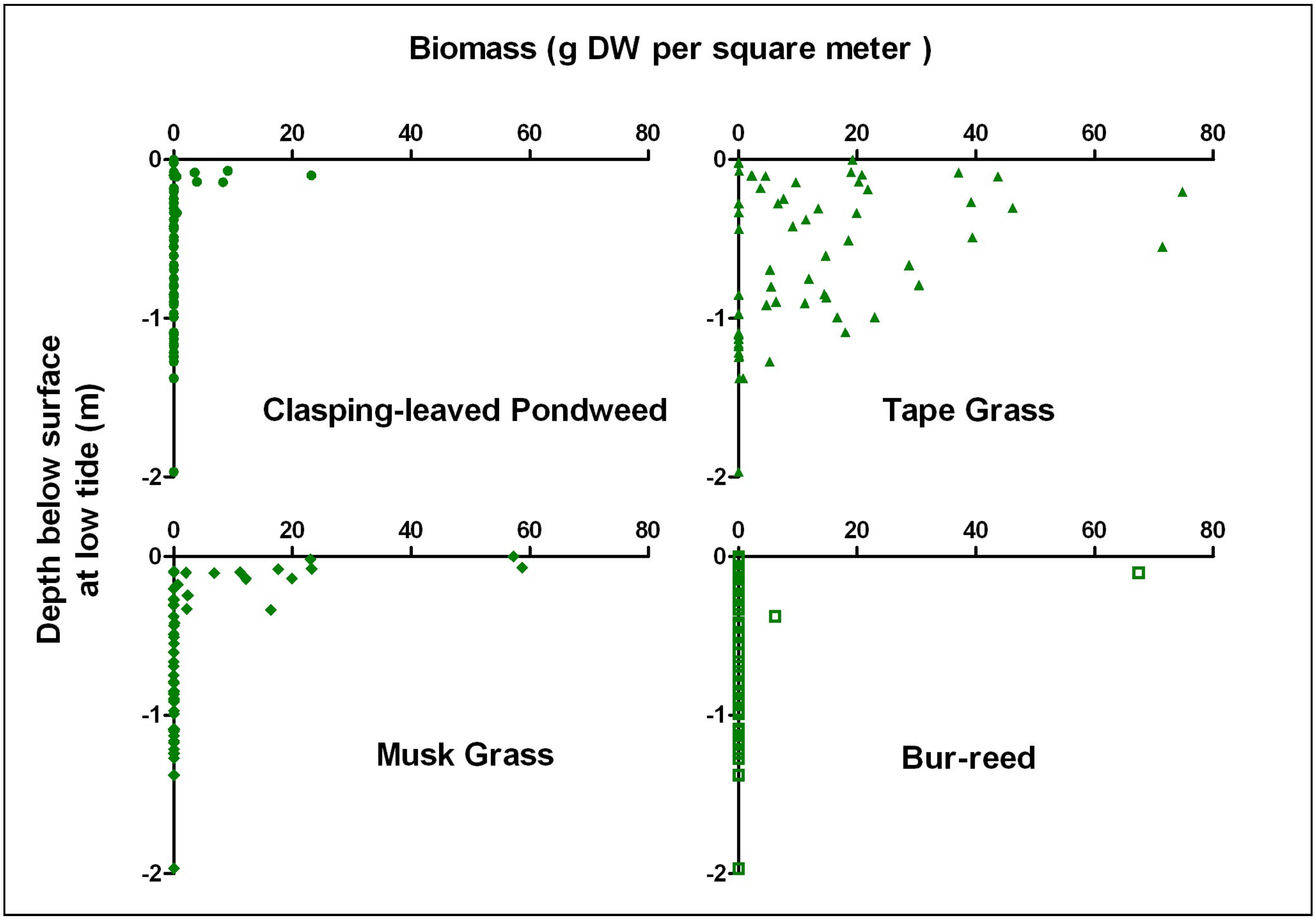


Figure 3-4. Depth and biomass (grams of dried plant material per m^2) distributions of dominant SAV species encountered during surveys in Merrymeeting Bay during summer 2006. Adapted from Burton (2007).

Rivers over the last 300 years and could plausibly have a local role in SAV distributional dynamics (Lichter et al. 2006; Köster et al. 2007). In a reconstruction of historical water quality conditions in Merrymeeting Bay, Köster and colleagues (2007) suggested that sedimentation rates, diatom productivity, planktonic to benthic diatom ratios, as well as levels of organic carbon, total phosphorus, and biogenic silica all indicate a history of post-European settlement eutrophication. This evidence from the sedimentary record corresponds well with known impacts to the upper estuary over the past several hundred years, which may have limited SAV distributions short of their pre-colonial era potential and have possibly led to a protracted or inhibited recovery.

Ecosystem responses to anthropogenic inputs are often difficult to predict, even in qualitative terms, given the number of interacting factors that influence natural systems. However, experience and observation have identified some of the more obvious human-induced responses, suggesting how historical and present-day resource uses integrate with ecosystem processes to influence water quality and SAV distributions (Fig. 3-5). For instance, the timing and magnitude of benthic diatom productivity decreases observed by Köster and colleagues (2007) tends to support the hypothesis that water clarity in Merrymeeting Bay during the last 300 years has declined, most likely as a result of interacting factors.

Early-stage cultural eutrophication that reduced the abundance of benthic diatoms due to light limitation could also have negatively impacted SAV distributions in the bay (Köster et al. 2007). Köster and colleagues (2007) also reported an overall increase in planktonic diatom productivity in Merrymeeting Bay, probably originating from land clearance-induced increases in nutrient availability and later being facilitated by agricultural, industrial, and municipal nutrient sources. At levels sufficient to drive diatom community change, productivity increases can cause turbidity-induced shading of benthic communities, resulting in less light available to support the growth of SAV. Reduced water clarity can instigate a self-limiting feedback interaction starting with SAV loss, benthic sediment destabilization (Sand-Jensen 1998), and as a consequence further water clarity degradation, light limitation, and more SAV declines (Fig. 3-5) (Korschgen and Green 1988).

Another potentially limiting factor in historical SAV distributions was sawdust, created in large quantities by sawmills. Foster and Atkins (1869) reported that fishing weirs in Merrymeeting Bay often filled with sawdust that drifted about the bay, smothering the bottom (Taylor 1951). While suspended in the water column, sawdust would have added to the suspended material pool that limits light transmission to benthic plants. Additionally, the log drives that moved pulpwood down the Kennebec until 1976 added woody debris and organic compounds to the water, reducing water clarity (NRC 2004). Logs would also scour the river bottom, resuspending sediments (and likely disturbing SAV) in ways that reduced water quality (NRC 2004).

The introduction of common carp near Richmond in the 1880s (Halliwell 2005) may also have contributed to water quality impairment. Carp are benthic foragers whose feeding activities disturb and resuspend sediments (Parkos et al. 2003), uproot aquatic vegetation (Becker 1983), and increase suspended

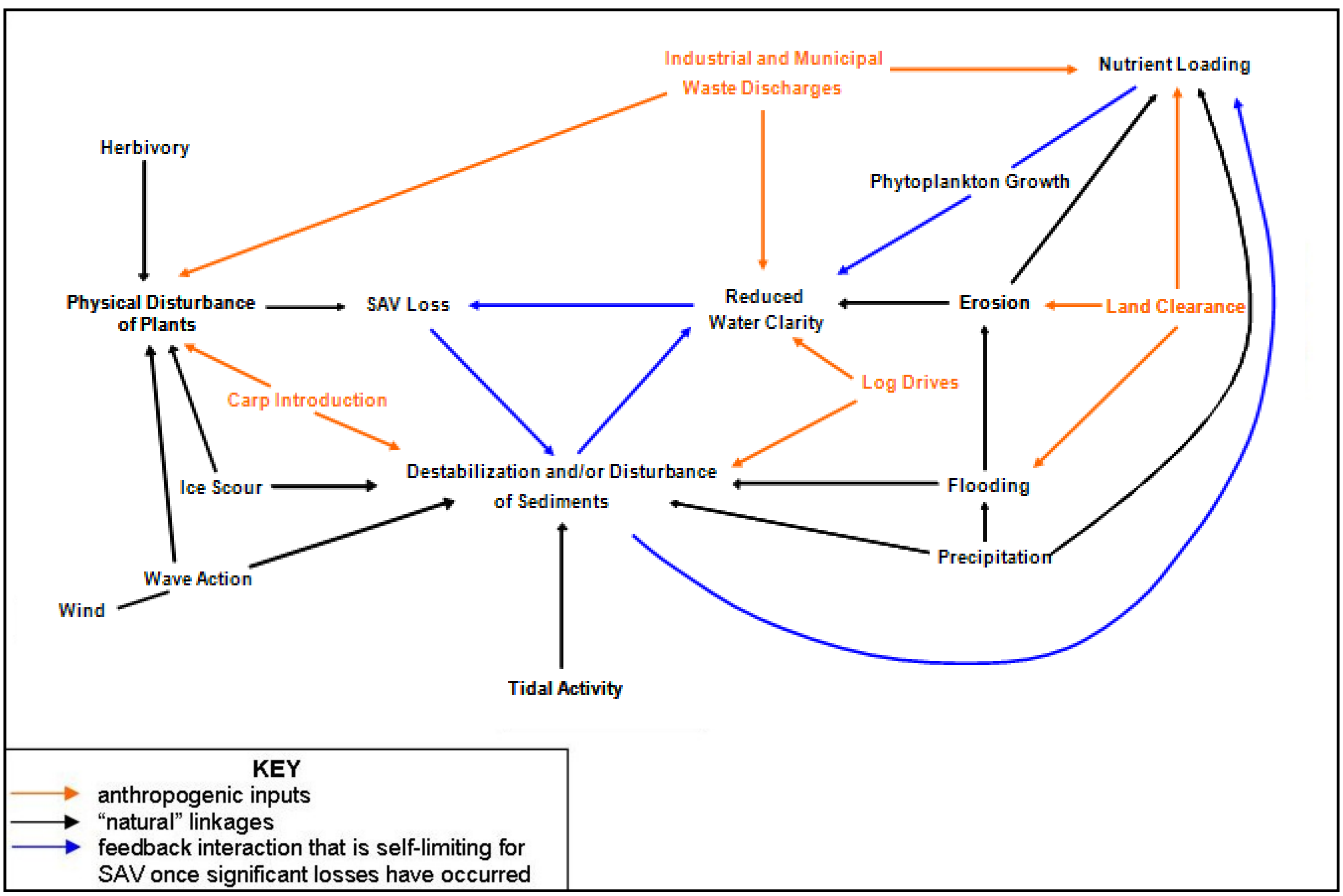


Figure 3-5. Conceptual model indicating historic and ongoing factors potentially limiting submerged aquatic vegetation distributions in the upper Kennebec Estuary.

phosphorus and nitrogen. Biological implications of carp may include increased phytoplankton growth (Lougheed et al. 1998; Parkos et al. 2003), declining macroinvertebrate abundance (Lougheed and Chow-Fraser 2001; Parkos et al. 2003) and reduced habitat cover, if the magnitude of water quality impacts and physical disturbance to vegetation is sufficiently large. Relative to other species, carp are particularly tolerant of low dissolved oxygen levels, higher temperatures, and high levels of turbidity (Becker 1983). Given their broad environmental tolerances, carp would have been uniquely suited to persisting and possibly expanding despite dramatically degraded water quality in the Kennebec Estuary. Connors and colleagues (1982) suggested that carp were at least partially responsible for reductions in water clarity that occurred during the mid to late 20th century in the Eastern River. Today, carp biomass may be the highest of any resident fish species in the Kennebec Estuary between Richmond and the Chops (Yoder et al. 2006). Their abundance suggests that carp may exert more than an incidental influence on water quality and the health of SAV beds, but directed research is required to determine this with any certainty.

Freshwater Tidal Marshes

Freshwater tidal wetlands form where downstream freshwater discharges dilute tidally driven saltwater inflows to an average annual salinity of less than 0.5 ppt (Simpson et al. 1983; Odum 1988). Thought to serve as long-term sinks and sources of nutrients, these wetlands play a vital role in nutrient cycling and transformation in coastal ecosystems (Mitsch and Gosselink 1993). Primary productivity (i.e., the growth of photosynthetic organisms) in freshwater tidal wetlands is typically very high, ranging between 1,000 and 3,000 g C/m^2/yr (Mitsch and Gosselink 1993) and often rivals the productivity of tropical or temperate forests (1,250–1,800 g C/m^2/yr; Whittaker and Likens 1973). The high productivity in freshwater tidal systems is thought to result from the large influx of organic matter from upstream watersheds, rapid rates of decomposition, and high rates of nutrient turnover (Simpson et al. 1983; Odum et al. 1984), all of which tend to support diverse communities of plants and animals (Odum 1988).

The Kennebec Estuary contains one of the largest freshwater tidal systems on the Atlantic coast north of Chesapeake Bay. Roughly half of Merrymeeting Bay's total area (4,340 ha or 16.8 mi^2) is composed of intertidal mudflats that support a diverse and productive plant community (James W. Sewall Company 2000). Wild rice and other freshwater emergent plants such as soft stem bulrush (S*choenoplectus tabernaemontanii*), river bulrush (*Bulboschoenus fluviatilis*), broadleaved arrowhead (*Sagittaria latifolia*), pickerelweed (*Pontedaria chordata*), common three square (*Schoenoplectus pungens*), and yellow water lily (*Nuphar advena*) dominate the intertidal plant communities in Merrymeeting Bay (James W. Sewall Company 2000; Grinvalski 2004). These tidal marshes also provide regional habitat of importance for rare wetland plant species (Fig. 1-4; Table 1-2; MNAP 2008*a*) and have not yet apparently been subject to significant colonization of invasive plant species (A. Cutko, MNAP, personal communication).

Trends

In 1998, 42% (492 of 1,161 hectares) of the vegetated intertidal area (excluding submerged aquatic vegetation) in Merrymeeting Bay was colonized by wild rice (James W. Sewall Company 2000) (Fig. 3-6). Mixed stands of emergent vegetation made up 40% of the total intertidal vegetated area with the remaining 18% being composed of stands of soft stem bulrush (8%), pickerel weed (4%), broad leaved cattail (*Typha latifolia*) (3%), river bulrush (1%), yellow water lily (1%), and sweet flag (*Acorus calamus*) (<1%) (James W. Sewall Company 2000). While some increases are detectable (30% for wild rice), the overall trend in

Merrymeeting Bay appeared to be one of declining total area occupied by tidal emergent marsh since 1956 (Fig. 3-6, Fig 3-7) (James W. Sewall Company 2000).

Researchers, wildlife managers, and local experts alike have long suspected that declines in Merrymeeting Bay's intertidal productivity may be related to water quality improvements that limit the estuary's capacity to support emergent plant growth, as compared to the years of peak eutrophication when reportedly lush growth was the norm. Local hunters with multi-decadal experience in the upper estuary note that the density and vigor of wild rice appears much reduced compared to late 20th-century conditions (H. Prout, Bowdoinham, personal communication). Indeed, recent fertilization experiments in Merrymeeting Bay seem to support this hypothesis, with nitrogen addition having a positive effect on both the density and biomass of wild rice (J. Lichter, unpublished data).

Some have suggested that wild rice was not native to Merrymeeting Bay (Federal Writers Project 1937). Both *Zizania aquatica* and *Zizania palustris* are native to Maine and grass (family *Poaceae*) pollen consistent in size and shape with that of Zizania was identified throughout a sediment core from the bay dated to 230 A.D. (Köster et al. 2007). *Z. aquatica* is more indicative of freshwater tidal marshes and is probably native to the bay. Seeds of the shorter *Z. palustris*, which more typically occurs on inland pondshores, were apparently scattered extensively around Swan Island in the 1950s and 1960s, the result being that the large marsh at the southern tip of Swan Island ("the Foot") is currently dominated by *Z. palustris*

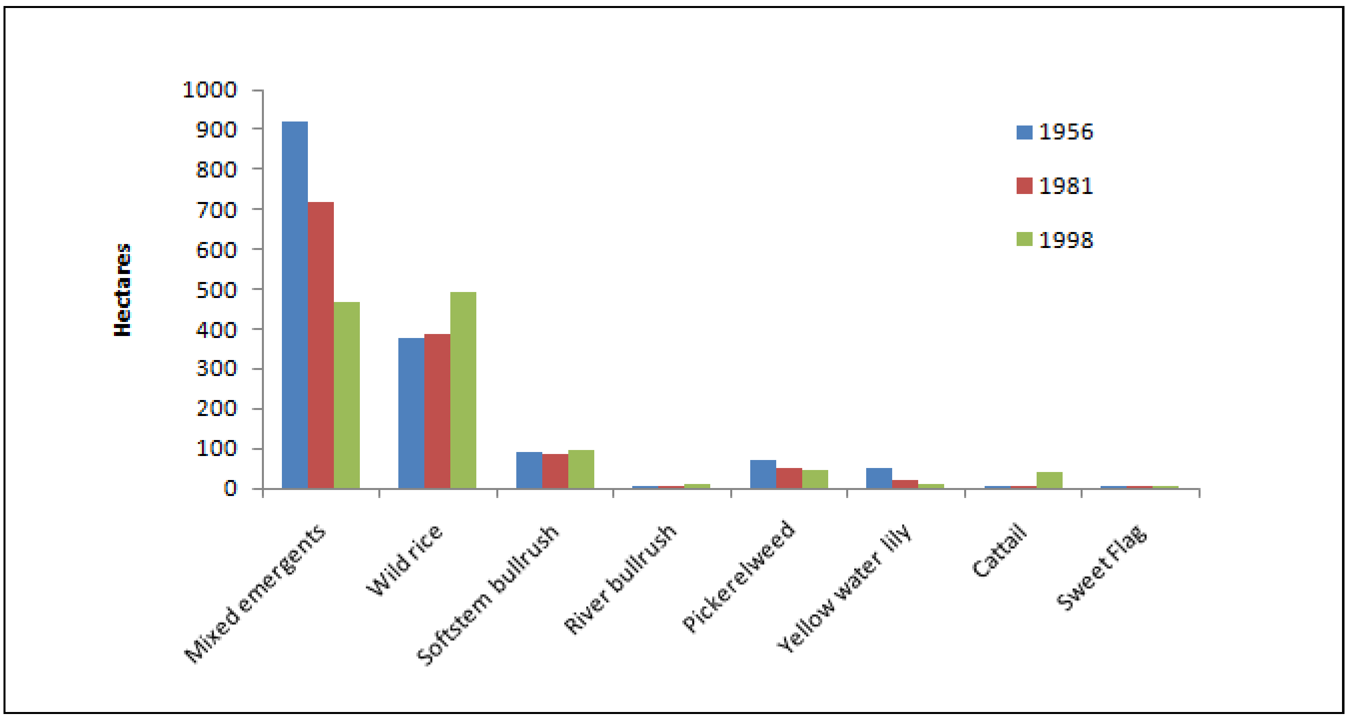
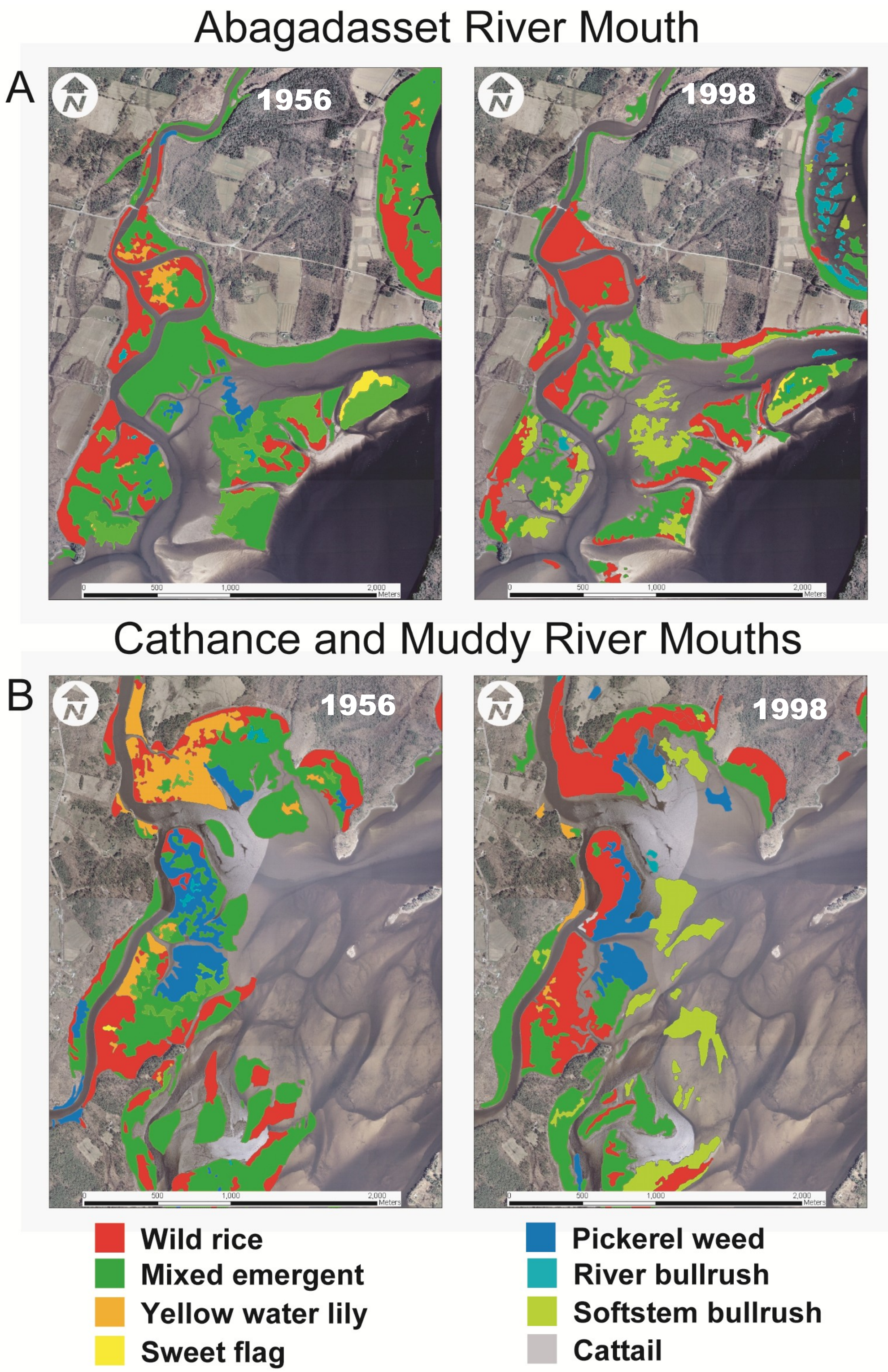


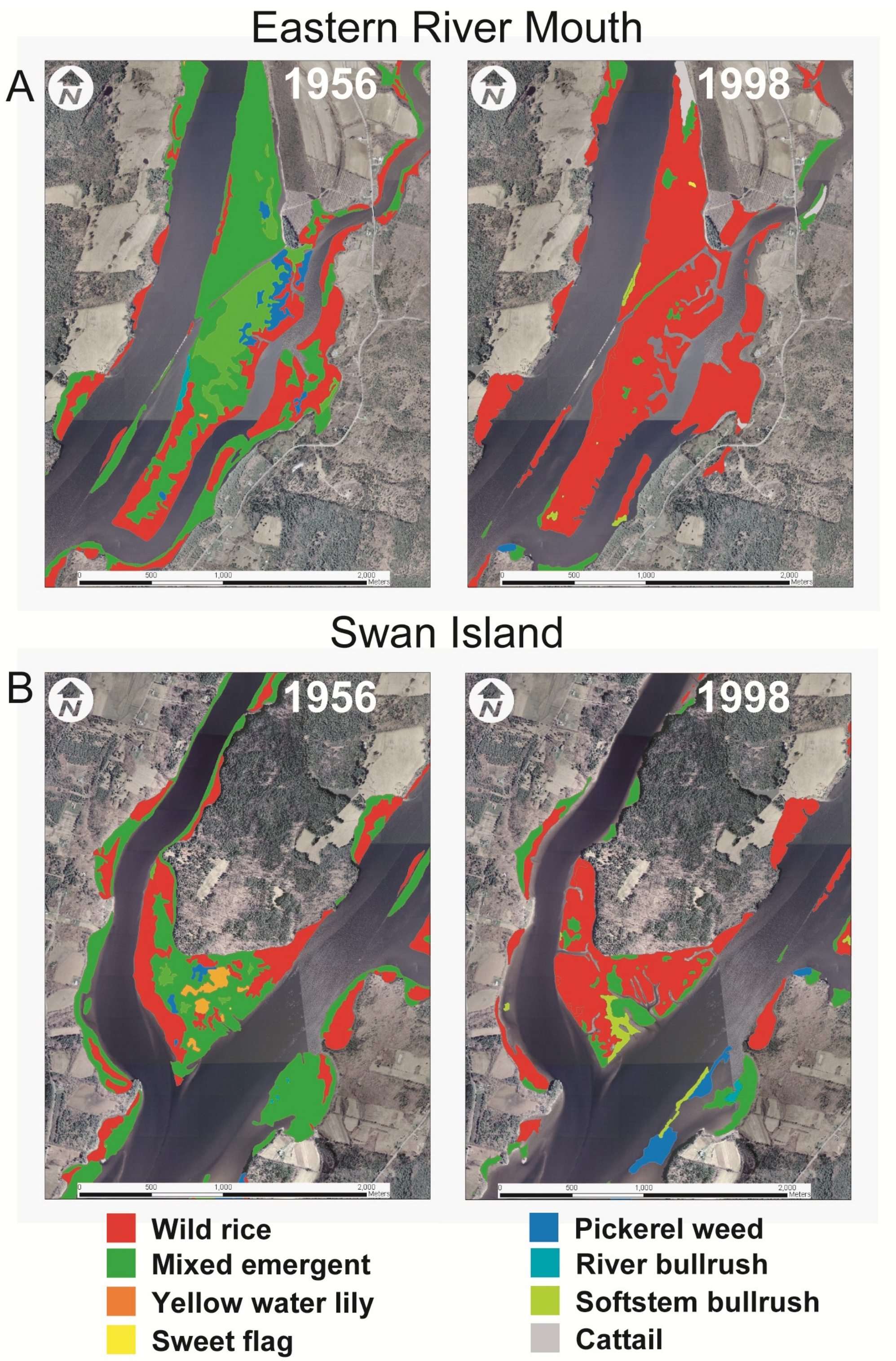
Figure 3-6. Dominant emergent plant species in tidal marshes of the upper Kennebec Estuary. Adapted from James W. Sewall Company (2000).

(A. Cutko, personal communication). In vegetation surveys conducted in Merrymeeting Bay during the summer of 2003, wild rice stem densities ranged from 25–225 plants/m² at maturity (Grinvalski 2004) and biomass of wild rice ranged from 248–557 g/m² of intertidal area (J. Lichter, unpublished data). Using the latest (1998) aerial photography data, if 42% of the 1,161 ha (4.5 mi²) of vegetated intertidal area in Merrymeeting Bay is composed solely of wild rice, the bay can be expected to produce 1,220–2,739 metric tons



Vegetation data from Aquatic & Upland Habitat Assessment of Merrymeeting Bay, 2000. James Sewell Co.
Courtesy: Friends of Merrymeeting Bay. www.friendsofmerrymeetingbay.org

Figure 3-7. Emergent intertidal plant species at the mouths of the Abagadasset River (A) and Cathance-Muddy Rivers (B), 1956 and 1998. Vegetation cover was interpreted and digitized by the James W. Sewall Company (2000).



Vegetation data from Aquatic & Upland Habitat Assessment of Merrymeeting Bay, 2000. James Sewell Co.
Courtesy: Friends of Merrymeeting Bay. www.friendsofmerrymeetingbay.org

Figure 3-8. Emergent intertidal plant species at the mouth of the Eastern River (A) and at southern Swan Island (B), 1956 and 1998. Vegetation cover was interpreted and digitized by the James W. Sewall Company (2000).

(mt) of wild rice plant biomass annually, not accounting for wild rice biomass produced in mixed stands of emergent plant species. Much of that biomass is annually released into the estuary where it contributes to the detrital food web.

Because wild rice is an important waterfowl food, wildlife biologists actively promoted its growth and expansion in Merrymeeting Bay (Spencer 1960, 1961), in some cases to the disadvantage of other species. Between 1956 and 1998, the acreage of yellow water lily in Merrymeeting Bay decreased by 84% (James W. Sewall Company 2000) although the species was apparently abundant in Merrymeeting Bay during the early 20th century (Fassett 1928). Yellow water lily is currently considered a Species of Concern by the MNAP (MNAP 2008*b*). Much of the decline in this species' distribution in the bay occurred near the mouths of the Cathance and Muddy Rivers where its coverage (Fig. 3-6) was 72% greater in 1956 than in 1998 (James W. Sewall Company 2000). Some of this decline may be directly attributable to vegetation management that occurred in Merrymeeting Bay during the late 1950s and 1960s. Considered a low value plant for waterfowl production, yellow water lily was also noted as being especially abundant and problematic near the mouths of the Muddy and Cathance Rivers (Spencer 1959). Beginning in 1959 the state of Maine began an experimental program using a variety of chemical herbicides (e.g., 2-4D, 2-4-5T, and Kuron) in Merrymeeting Bay to "control" yellow water lily and promote the production of vegetation thought to be more beneficial to waterfowl (Spencer 1960, 1961). Treated stands of yellow water lily were all recolonized by "dense, luxuriant" stands of wild rice within one or two years of treatments (Spencer 1961). Between 1956 and 1961 yellow water lily areal coverage at the mouth of the Muddy and Cathance Rivers decreased by 30.4% from 85 ha (211 acres) to 60 ha (147 acres) (Spencer 1966). Interestingly, the relative abundance of *Nuphar* sp. pollen in an intertidal sediment core collected near the Abagadasset River was greater between 1940 and approximately 1960 than it was at any time during the previous ~1700 years (Köster et al. 2007). *Nuphar advena*, the species known to occur in Merrymeeting Bay, responds positively to eutrophication (e.g., Egertson et al. 2004), possibly suggesting that 20th-century water quality degradation in Merrymeeting Bay (Lichter et al. 2006) benefited this species.

Ecological Implications of Plant Community Shifts

Declines in freshwater tidal marsh acreage and limitations on SAV expansion reaching its likely historical potential have wide-ranging and profound implications for ecosystem function and services. Merrymeeting Bay's reputation as an exemplary waterfowl staging area has long been secure among local historians, hunters, naturalists, and the cultures that preceded European settlement (Wheeler and Wheeler 1878; Noble 1905; Coffin 1937; Palmer 1949). As late as the mid-20th century, ducks numbering in the tens of thousands were observed on a single day during the fall migration, and Canada geese (*Branta canadensis*) in similar quantities were important spring migrants (Noble 1905; L. Carr, Richmond, personal communication; H. Prout, Bowdoinham, personal communication). At its peak, the magnitude of waterfowl use of Merrymeeting Bay was unparalleled in the state and had considerable influence on shoreside communities. Waterfowl in such numbers provisioned people of the estuary with a reliable source of wild protein and were also the basis of a unique tradition of gunning that had economic, cultural, and social importance.

For decades it has been rare to see more than a few thousand ducks at once on the bay, and spring geese often number in the hundreds rather than tens of thousands. Conventional wisdom suggests that the egregious nutrient pollution of the last century boosted Merrymeeting Bay's productivity in ways that benefited waterfowl during that period. By extension, then, it is implied that recent improvements in water

A group of hen mallards (*Anas platyrhynchos*) flashes violet speculum feathers as they skim over the Abagadasset River channel. Photo: Slade Moore.

quality may have the effect of suppressing waterfowl populations. However, Merrymeeting Bay's reputation as prime waterfowl habitat probably predated European settlement (Wheeler and Wheeler 1878); at the very least, that reputation preceded cultural eutrophication of the system. Long before the sewage-associated nutrient enrichment of the mid to late 20th century, huge aggregations of waterfowl used the bay (Noble 1905). If pollution boosted these already sizeable waterfowl numbers to superabundance, why have water quality improvements not been accompanied by a return to the pre-eutrophication abundance?

Not often recognized is the nutrient enrichment potential that historically immense numbers of birds in Merrymeeting Bay would have represented. Elsewhere, waste excretion and carrion decomposition associated with large aggregations of waterfowl were demonstrated as significant to energy flow and the process of nutrient enrichment, sometimes to the point of eutrophication (Parmenter and Lamarra 1991; Manny et al. 1994; Kitchell et al. 1999). Historical anadromous fish runs could have had a similar effect, if research elsewhere (Garman and Macko 1998) is any indication. The magnitude of vertebrate biomass that migrated in seasonal pulses through the estuary can be likened to vast, mobile nutrient and carbon reserves that nourished the ecosystems through which they passed, possibly increasing productivity along the way.

The apparent causal relationship between water quality, plant community distributions, and use of the system by fish and wildlife populations remains largely untested in the Kennebec Estuary. This warrants investigation so that ecosystem responses to management actions can be more fully understood. Many unanswered questions remain. Were mid- to late-20th century declines in SAV related to decreases in water transparency? Were these declines initially responsible for declines in waterfowl populations? Did pollution abatement measures restrict nutrient inputs in ways that limited the distribution and vigor of tidal marsh communities? Did this further suppress waterfowl numbers? Now, without the intense pulses of migrating waterfowl and fish, have we lost a seasonal nutrient input that benefited system productivity? Or do nutrient inputs play a smaller role in waterfowl use than water transparency, which is influenced by suspended sediments, or factors that influence waterfowl populations outside the estuary? Restoration and management efforts might well be assisted by current waterfowl data specific to Merrymeeting Bay, a thorough assessment of other ecosystem indices, and an analysis of exogenous contributions to waterfowl declines. These uncertainties show that understanding all the major ecosystem-level responses to management actions requires more current monitoring of relevant parameters and experimental research.

Conclusions

SAV distributions in the Kennebec Estuary have apparently experienced wide swings in distribution and community structure since the 1950s. Overall, a net increase of 30–72% of SAV areal coverage between 1981 and 1998 suggests that this community type might be recovering, but a lack of more recent, frequent, and reliable data hinders confident assessments. Identification and tracking of density classes within SAV stands, like those performed for eelgrass in coastal areas, is necessary to inform managers about the condition of SAV, not merely its distribution. If SAV recolonization is indeed inhibited, the lingering influence of several interacting factors causing reduced water transparency, which limits the maximum depth at which SAV can persist, should be investigated. Freshwater tidal marshes in the upper estuary have also been subject to some distributional expansion, contraction, and species turnover, but differ significantly from SAV by demonstrating an overall trend of decline in coverage from amounts recorded in the previous century. Also in contrast with SAV, tidal marsh declines may actually be related to water quality improvements that limit nutrient availability to marsh plants.

Major declines in either marsh or SAV acreage can be attended by profound ecosystem-level consequences including reduction and suppression of highly valued fish and wildlife populations. Mid-20th century data describing plant community distributions in the estuary provide a benchmark against which to compare present conditions, but those data represent only a snapshot within a longer continuum that transcends the memory of the last few human generations. Moving forward, one of the greatest necessities will be to determine at which point in the continuum of ecosystem recovery (or degradation) we are now positioned. This will require increasing use of historical reconstructions relying on anecdotes, environmental proxies (e.g., seed banks, diatoms, and sediment profiles), and other indirect data sources that can characterize the ecological potential of the estuary prior to the sweeping changes that caused its degradation. If, as other ecosystems have demonstrated, centuries of environmental abuses have predisposed this estuary to an ecological regime shift that is resistant to restorative management inputs, successful restoration may depend on novel approaches that are not currently part of the management repertoire.