

The Status of Eelgrass, *Zostera marina*, as Bay Scallop Habitat: Consequences for the Fishery in the Western Atlantic

MARK S. FONSECA and AMY V. UHRIN

Description of the Plant

Zostera marina L. is one of a small genus of widely distributed seagrasses, all commonly called eelgrass (Fig. 1). This genus contains twelve species worldwide but only three species are found in North America (*Z. asiatica* and *Z. japonica* on the west coast) with *Z. marina* as the only confirmed native species. Eelgrass is found on sandy substrates or in estuaries, and rarely on the open ocean coastline and then, usually, in the shelter of boulders or other similarly immobile structures.

Mark S. Fonseca and Amy V. Uhrin are with the U.S. Department of Commerce, NOAA, National Ocean Service, Center for Coastal and Fisheries Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516 (email: Mark.Fonseca@noaa.gov).

The plant is almost always submerged or partially floating at low tide. In the western Atlantic it is only occasionally intertidal (Fig. 2).

However, eelgrass is actually not a grass—it is in the same Class grouping as other monocotyledonous plants, but it then branches into strictly aquatic plant groups at lower taxonomic levels:

Phylum: Anthophyta (flowering plants),
Class: Liliopsida (monocots),
Order: Potamogetonales,
Family: Zosteraceae (Greek ‘zoster,’ meaning ‘belt’),
Genus/species: *Zostera marina*.
Authority: Linnaeus, 1758.

A summary of the key identification features are as follows:

Relatively thin, flattened, blade-like leaves up to ~ 1 cm in width, dark green in color;

Leaves usually 20–50 cm but up to 2 m in length, 4–10 mm wide, with 5–11 veins and rounded leaf tips, sometimes with a very small, sharp point;

Leaf sheath forms an envelope around the aboveground stem;

Reproductive shoot, terminal, branched, and substantially longer than vegetative shoots;

Seeds ovoid or ellipsoid, ~2–3 mm long with 16–25 distinct ribs;

Rhizome color (when living) is dark brown and has a polished appearance;

At each rhizome node, there are typically two root bundles;

Branching is alternate along the rhizome and frequently irregular; each branch becomes an independent shoot.

To the casual observer there is little morphological difference between the two seagrass species that co-occur with eelgrass in the western Atlantic, shoal grass, *Halodule wrightii* Aschers, and widgeon grass, *Ruppia maritima* L. However, the three species can be distinguished particularly by their blade tips and rhizomes (Fig. 3). The leaf tip of eelgrass is round, sometimes with a very small apical point, whereas *H. wrightii* has a bicuspidate (crowned) appearance

ABSTRACT—*Zostera marina* is a member of a widely distributed genus of seagrasses, all commonly called eelgrass. The reported distribution of eelgrass along the east coast of the United States is from Maine to North Carolina. Eelgrass inhabits a variety of coastal habitats, due in part to its ability to tolerate a wide range of environmental parameters. Eelgrass meadows provide habitat, nurseries, and feeding grounds for a number of commercially and ecologically important species, including the bay scallop, *Argopecten irradians*. In the early 1930's, a marine event, termed the “wasting disease,” was responsible for catastrophic declines in eelgrass beds of the coastal waters of North America and Europe, with the virtual elimination of *Z. marina* meadows in the Atlantic basin. Following eelgrass declines, disastrous losses were documented for bay scallop populations, evidence of the importance of eelgrass in supporting healthy scallop stocks.

Today, increased turbidity arising from point and non-point source nutrient loading and sediment runoff are the primary threats to eelgrass along the Atlantic coast and, along with recruitment limitation, are likely reasons for the lack of recovery by eelgrass to pre-1930's levels. Eelgrass is at a historical low for most of the western Atlantic with uncertain prospects for systematic improvement. However, of all the North American seagrasses, eelgrass has a growth rate and strategy that makes it especially conducive to restoration and several states maintain ongoing mapping, monitoring, and restoration programs to enhance and improve this critical resource. The lack of eelgrass recovery in some areas, coupled with increasing anthropogenic impacts to seagrasses over the last century and heavy fishing pressure on scallops which naturally have erratic annual quantities, all point to a fishery with profound challenges for survival.

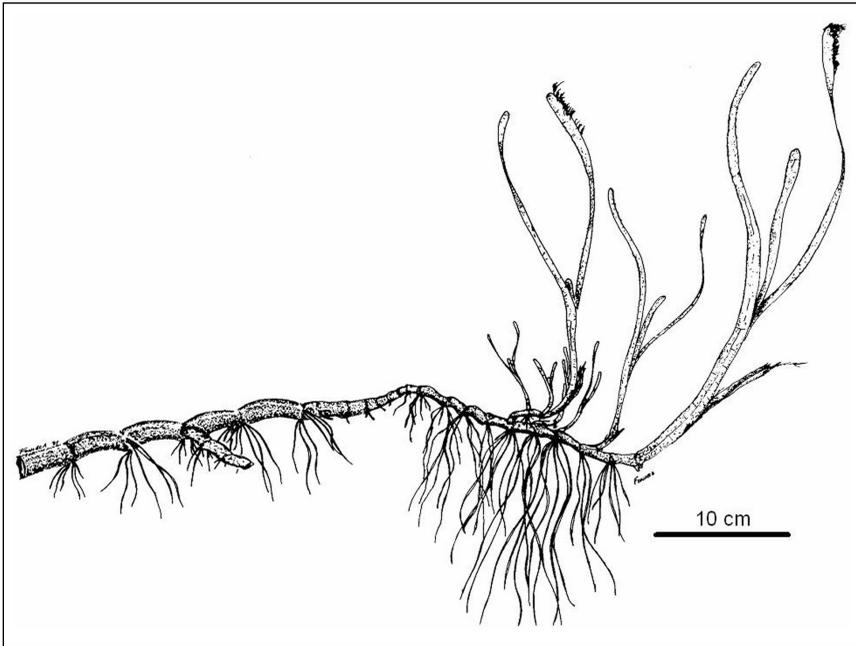


Figure 1.—*Zostera marina* (eelgrass) showing the whole plant structure.



Figure 2.—Eelgrass bed in Long Island Sound (Photograph by C. Pickerell).

and *R. maritima* is lanceolate (pointed). Also, the living rhizome of eelgrass is brown while the rhizomes of the other species are much lighter, almost white depending on sediment type.

Eelgrass is unlike all the other native North American seagrass species in that each seagrass shoot is a “terminal shoot”; that is, it is always located at the end of the rhizome. There are no shoots

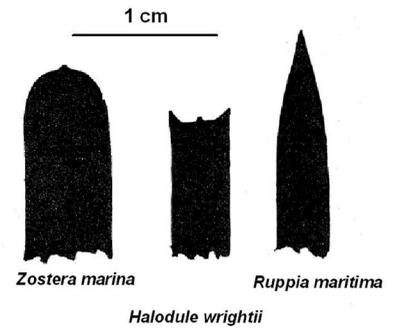
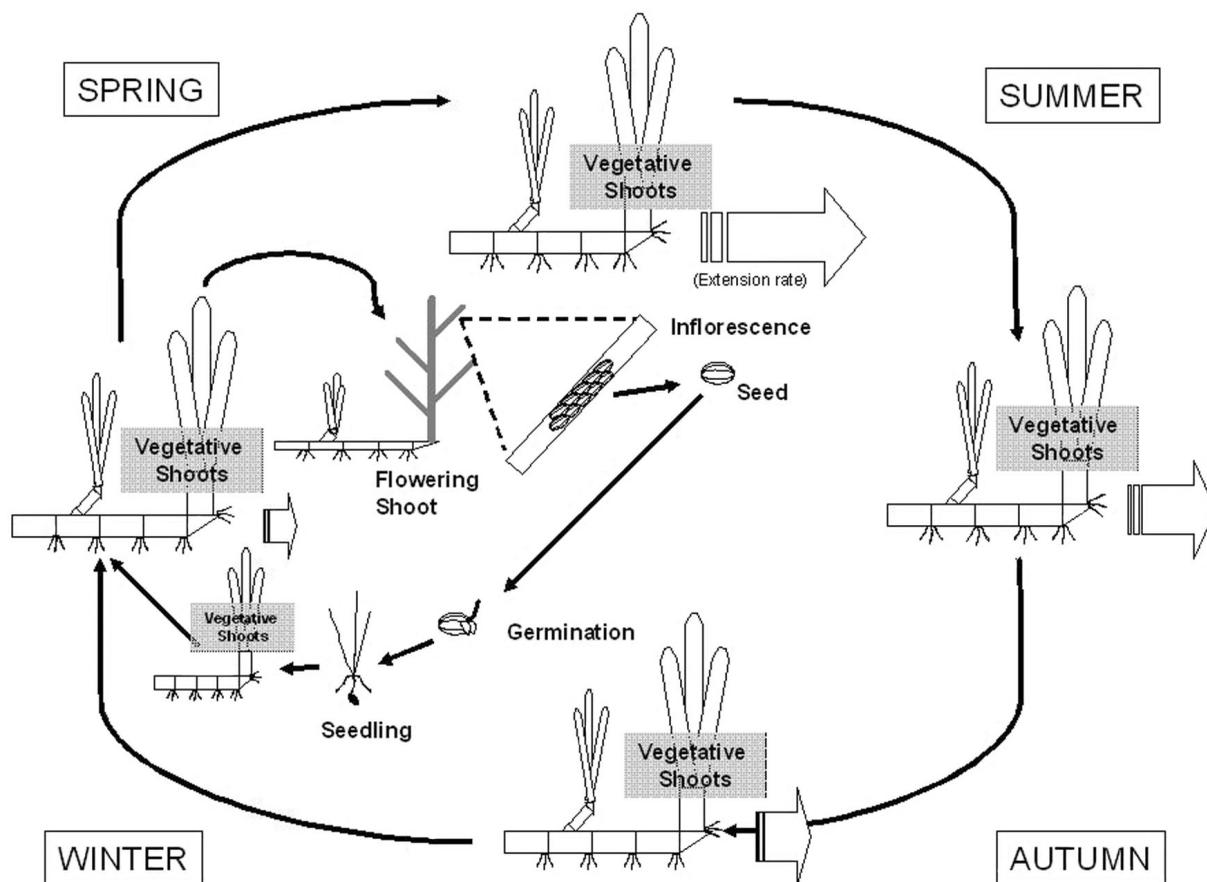


Figure 3.—Sketches of blade tips for the three congeners. Reproduced from Thayer et al., 1984.

left behind, rooted in place as with the other seagrass species—instead the terminal shoot actually migrates across the seafloor leaving a trail of rhizome rooted in place behind it which gives the plant unusual pattern development capabilities and high spatial recolonization rates.

The life history of eelgrass has been well-described for almost a century (Setchell, 1929). The plant typically follows a 2-year (perennial) life history (Fig. 4). For most of the range in the western Atlantic, eelgrass seeds germinate in the late winter and grow vegetatively through the summer, creating daughter shoots (ramets) almost continuously every 2–4 weeks. These clones then over-winter in a slow growth phase. In the second year of their existence, shoots of that age undergo a dramatic alternation of generation and transform into luxurious flowering structures that produce dozens of seeds. After setting seed, the shoot dies. Seeds tend to stay very near the parent plant yet the role of seeding in eelgrass bed maintenance remains somewhat of a mystery.

Like terrestrial plants, there appears to be “mast years” where extraordinary numbers of seedlings germinate which can result in significant new bed formation in locations otherwise long devoid of cover. Flowering stalks can break off and float for many miles (Phillips and Meñez, 1988; Harwell and Orth, 2002), providing a means for colonization at far distant locations.



Redrawn from Setchell 1929

Figure 4.—Stylized life history of perennial eelgrass. Redrawn from Setchell, 1929.

Limiting Factors

Eelgrass inhabits a wide range of coastal habitats, due in part to its ability to tolerate a wide range of environmental parameters. These parameters are discussed in more detail below.

Substrate

Eelgrass is limited to unconsolidated sediments, and thus, comparatively quiescent environments. However, luxurious eelgrass beds may be found clinging to cobble sediments behind highly exposed islands along the New England coast.

Light / Depth

Eelgrass is limited in its depth distribution by light at depth and emersion at

its upper limit. The emersion tolerance of eelgrass is not well quantified, but observations indicate that it has a low desiccation tolerance and thus cannot withstand prolonged exposure at low tide unless the environment is cool (typically below 20°C) and a film of water persists to keep the plant wetted. When exposed to truly dry conditions and a mild breeze, eelgrass blades can desiccate beyond recovery in minutes while the sheath bundle, which contains the meristems, may withstand much longer periods of true desiccation (Fonseca¹).

Eelgrass is generally limited to depths where light is at least 15–25% of surface

irradiance (Dennison, 1987; Gallegos, 1994) but these values are undergoing re-evaluation (Kenworthy²). Depth distribution of eelgrass varies with water quality on a local scale. For example, in both Chesapeake Bay and the North Carolina coastal zone, where waters can be turbid, eelgrass is usually limited to depths of 2 m or less (Dennison et al., 1993; Ferguson and Korfmacher, 1997; Fonseca et al., 2002; Kemp et al., 2004). In contrast, further north, estuaries become less turbid and light is able to penetrate to greater depths, with eelgrass growing in excess of 10 m in some areas (Maquoit Bay, ME:

¹Fonseca, M. Unpubl. data. NOAA, Center for Coastal Fisheries and Habitat Research, Beaufort, N.C.

²Kenworthy, J. NOAA, Center for Coastal Fisheries and Habitat Research, Beaufort, N.C. Personal commun., 2009.

Short and Short, 2003; Fort Weatherall, Jamestown, R.I.: Fonseca¹). Moreover, the periodicity of light-reducing events (acute versus chronic diminishment of light) may play a significant yet difficult-to-detect role in the distribution of eelgrass. Moore et al. (1997) found that a month-long elevated turbidity event at a site in Chesapeake Bay caused eelgrass to die off, an event that was otherwise very difficult to detect using data averaged over longer periods of time.

Temperature

Due to its widespread distribution, eelgrass can experience water temperature fluctuations from less than 0°C to greater than 30°C. Although eelgrass may grow at temperature extremes, physiological processes within the plant (i.e. photosynthesis, respiration) require a more limited range for optimum performance (Fig. 5; Penhale, 1977; Evans et al., 1986, Marsh et al., 1986). Although there are a number of factors to consider, it is widely considered that a sustained temperature approaching 25°C is the upper tolerance limit for eelgrass (Zimmerman et al., 1989; Bintz et al., 2003).

Water Motion

Eelgrass beds thrive in areas of moderate to high current speeds and can withstand current speeds of up to 1.5 m/s (Fonseca and Fisher, 1986; Koch, 2001). Water motion plays a role in structuring eelgrass meadows (Fonseca and Bell, 1998). Scouring by waves and currents at the leading edges of a meadow can erode sediments and plants and prevent sediment deposition. In some instances, large quantities of sediment may actually be carried off and deposited, burying significant portions of existing meadows which have limited burial tolerance (covering ~50% of the leaves kills the plants; Mills and Fonseca, 2003).

Eelgrass is effective in damping out waves and reducing current velocities within the canopy as water passes through the meadow, especially when the canopy extends to the water's surface (Fonseca et al., 1983; Fonseca and Cahalan, 1992). As a wave passes

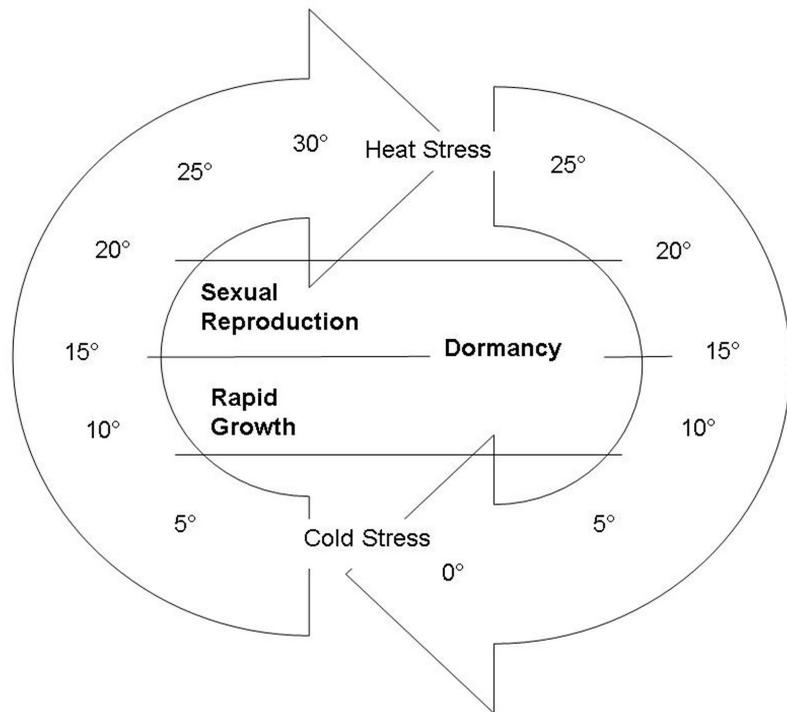


Figure 5.—Graphic illustration of Setchell's topology describing the relationship between temperature and eelgrass phenology. Redrawn from Setchell, 1929.

through the meadow, eelgrass shoots wave in synchrony with the passing crests (Grizzle et al., 1996) and troughs and create drag that diminishes waves rapidly especially if the plants occupy most of the water column. Under tidal currents, an eelgrass canopy will bend into a compact layer as current velocities increase. By deflecting water over it, the canopy shields the bottom from erosive forces.

Salinity

Eelgrass is euryhaline; it has been reported from areas experiencing periods of nearly fresh water to full-strength seawater or greater (Thayer et al., 1984). An optimum salinity for this species has, to our knowledge, never been determined, but photosynthesis virtually ceases below 10‰ and is probably optimal at oceanic salinity levels (approximately 32‰). Given the generally estuarine distribution of eelgrass, the importance of periodic freshwater events may play a significant role in periodically resetting its distribution.

Nutrients

Eelgrass growth, abundance, and morphology are clearly linked to available nutrient pools (Short 1983a, b, 1987). In the siliceous sedimentary environment typical of temperate eelgrass beds, plants appear to be nitrogen limited (Short, 1987 and references therein) but typically have ample supplies of phosphorous (McRoy and Barsdate, 1970; McRoy et al., 1972). Nutrients are absorbed from the sediment and associated interstitial water at the roots and are subsequently transferred to the rest of the plant. In addition, plant leaves are able to absorb nutrients from the water column.

The Wasting Disease

In the early 1930's, a marine event of near catastrophic proportions occurred in eelgrass beds of the coastal waters of North America and Europe. Within two years of its first observation, the "wasting disease," as it was termed, had eliminated over 90% of eelgrass

populations worldwide (Muehlstein, 1989). Total losses along the Atlantic coast of the United States cannot be quantified as systematic documentation of eelgrass distribution did not exist prior to the 1930's. Although often suspected, decades later the marine slime mold, *Labyrinthula zosterae*, was suggested as the responsible pathogen (Muehlstein et al., 1991). However, the actual conditions leading to the widespread outbreak have never been clearly determined. One long-held contention is that climatic shifts, particularly a sudden increase in water temperature and reduced incoming solar radiation in the 1930's led to increased susceptibility of eelgrass to infection through the influence of these abiotic factors on seagrass metabolism and photobiology (Tutin, 1938; Rasmussen, 1977). The controversy over the cause of the wasting disease, particularly in lieu of numerous studies regarding thermal tolerance and light requirements of *Z. marina*, and a paucity of good meteorological data for the early 20th century, is debated even today.

Eelgrass recovery was not apparent before the mid 1950's. By the 1960's, eelgrass populations had generally re-established and 30–40 years later had largely recovered, although many locations which once supported thriving eelgrass habitat have never recolonized (Short et al., 1988, 1993; Short and Short, 2003). It is believed that those populations inhabiting lower salinity environments (upper reaches of estuaries) were able to avoid infection and thus provide a stock of plants for recovery as salinity clearly plays a role in regulating *L. zosterae* activity, with reduced activity below 20–25‰ (Muehlstein et al., 1988, Burdick et al., 1993). Although a large-scale event akin to that of the 1930's has not occurred in recent history, symptoms and epidemiology of this alleged disease have manifested themselves in local eelgrass populations in the mid 1980's and may be associated with some small-scale die-offs (Short et al., 1986, 1987, 1988).

Following the virtual elimination of *Z. marina* meadows along the eastern

seaboard, catastrophic population declines were documented for bay scallop, *Argopecten irradians*, populations (see review in MacKenzie, 2008). Following the wasting disease event, eelgrass and bay scallops were absent from Nantucket Harbor for nearly 20 years (Andrews, 1990) and scallop landings reached an all-time low for the Long Island, New York fishery (MacKenzie, 2008). In Rhode Island, a tremendous harvest of scallops was described from "The Cove" at the north end of Aquidneck Island both in 1956 and again ~ 1959; intense dredging apparently destroyed the eelgrass beds in this water body and scallops were no longer found after that time (Cavanaugh³). Commercial harvest of the bay scallop fell precipitously in North Carolina and Chesapeake Bay (Thayer and Stuart, 1974; Orth and Moore⁴). In North Carolina, populations returned to near pre-event levels in the 1960's, but have fluctuated dramatically since that time. Moreover, North Carolina populations have exhibited a steady decline since 1995 to such a degree that the main harvest season was not opened in January 2006 and remained closed through 2009 (Burgess and Bianchi⁵; NCDMF^{6,7}), although this does not appear to be the result of concomitant changes in eelgrass abundance. Bay scallop populations in Chesapeake Bay have never been restored to commercially harvestable levels since the decline of the 1930's (MacKenzie, 2008; Orth and Moore⁴).

³Cavanaugh, D. (deceased) Fisherman, Portsmouth, Rhode Island. Personal commun., 1972.

⁴Orth, R., and K. Moore. 1982. The biology and propagation of *Zostera marina*, in the Chesapeake Bay, Virginia. Final Rep. to U.S. Environ. Protect. Agency, Chesapeake Bay Program pursuant to Grant No. R805953, 195 p.

⁵Burgess, C., and A. Bianchi. 2004. An economic profile analysis of the commercial fishing industry in North Carolina including profiles for state-managed species. N. C. Dep. Environ. Nat. Resour., Div. Mar. Fish. Morehead City, Unpubl. rep., 228 p.

⁶N.C. Dep. Environ. Nat. Resour., Div. Mar. Fish. 2008. Stock status of important coastal fisheries in North Carolina. <http://00de17f.netsolhost.com/stocks/index.html>

⁷N.C. Dep. Environ. Nat. Resour., Div. Mar. Fish. 2009. Proclamation SC-1-2009. <http://00de17f.netsolhost.com/procs/procs2k9/SC-1-2009.html>

Distribution

Throughout its range along the North American east coast, eelgrass is the dominant species of rooted submerged aquatic vegetation (SAV). The reported distribution of eelgrass along the east coast of the United States is from Maine to North Carolina (Fig. 6 and 7). Current estimates of eelgrass cover range from 6.75 km² in Connecticut to nearly 160 km² in Massachusetts (Table 1). When other SAV species are included, cover increases to ~500 km² (Table 1). Eelgrass populations are characterized by spatially and temporally fluctuating levels of abundance which is to be expected for a plant that is a prolific seed-setter and has a life history of only two years. Dynamic coverage has been well documented for many years (den Hartog, 1971) and is strongly associated with disturbance regime; for example, prior to the wasting disease, there is evidence that eelgrass had previously disappeared from many portions of the U.S. Atlantic coast in 1893–94, largely due to an extremely cold period, with additional losses along New England coasts in 1908 (Cottam, 1934, 1935). However, losses at that time were apparently nowhere comparable to the loss of eelgrass in the 1930's.

As coastal development accelerated in the post WWII economic boom of the United States, the depleted eelgrass populations beginning to recover from the 1930's event were faced with deteriorating water quality, increased physical disturbance from vessels and fishing, and even potential impacts from invasive species (e.g. European green crab, *Carcinus maenas*; and mute swan, *Cygnus olor*). As a result, eelgrass is at a historical low for most of the region with uncertain prospects for systematic improvement. As suggested by MacKenzie (2008) the lowered abundance of eelgrass has direct and negative implications for the scallop fisheries in the western Atlantic given this plant is historically a critical substrate for scallop.

Maine

Information regarding the historical distribution of eelgrass in Maine prior



Figure 6.—Eelgrass distribution along the north Atlantic coast of the United States: Maine to New Jersey. Reprinted with permission from Green and Short (2003). Copyright (2003) by the UNEP World Conservation Monitoring Center. Published by the University of California Press.

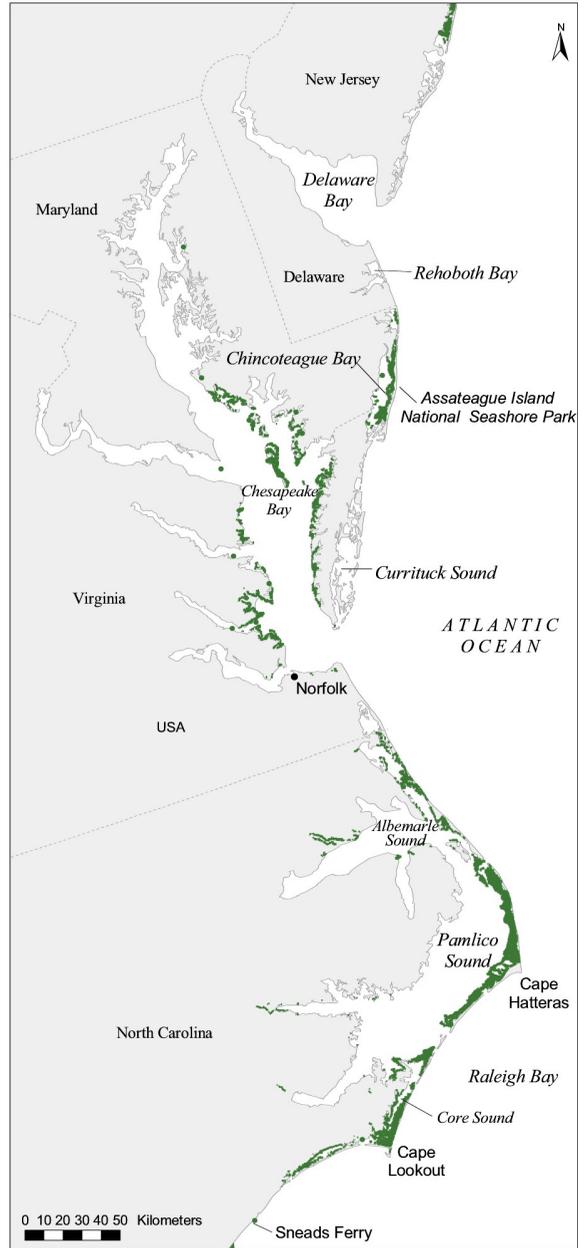


Figure 7.—Eelgrass distribution along the mid Atlantic coast of the United States: Delaware to North Carolina. Reprinted with permission from Green and Short (2003). Copyright (2003) by the UNEP World Conservation Monitoring Center. Published by the University of California Press.

to the wasting disease is scarce. Cottam (1934) documented a fisherman’s account that most of the eelgrass in Penobscot Bay had disappeared during 1893–94 and that many years passed before it returned. It would appear that Maine eelgrass populations suffered as elsewhere in 1908 and following the 1930’s wasting disease event (Cottam, 1934). In reference to post-1930’s recovery, Cottam and Munro (1954) reported

that, “Though marked improvement has occurred in many places in this state during the past two or three years, eelgrass is still far below former prevalence, varying from absent or scarce to moderately abundant.” Documentation of eelgrass distribution is generally lacking after the 1950’s, up until the early 1990’s when the Maine Department of Marine Resources (MEDMR) began mapping efforts (Barker⁸). Current

eelgrass maps for Maine (utilizing data from 1992–2005) are available through the MEDMR website (MEDMR⁹). The greatest area of eelgrass is found in Casco Bay, particularly the northern region, where it appears to be at or near

⁸Barker, S. State of Maine, Department of Marine Resources, Boothbay Harbor. Personal commun., 2009

⁹MEDMR <http://www.maine.gov/dmr/index.htm>

Table 1.—Reported eelgrass coverage along the eastern seaboard of the United States. *dominated by *Z. marina* and *R. maritima* but also includes additional species of SAV; **includes shoal grass, *Halodule wrightii*, and *R. maritima*.

| State | Year | Area (km ²) | Source |
|---|------------|-------------------------|---|
| Maine | 1992–2005 | 126.08 | Barker ¹ |
| New Hampshire | 2006 | 8.0 | NHEP ² |
| Massachusetts | 1995–2001 | 137.86 | Costello ³ |
| Rhode Island | 2006 | 1.88 | Bradley et al. ⁴ |
| Connecticut | 2006 | 6.75 | Tiner et al., 2007 |
| New York (Peconic Estuary, Long Island Sound) | 2001, 2006 | 7.20 | Tiner et al., 2007; PEP ⁵ |
| New Jersey (Barnegat Bay, Little Egg Harbor) | 1999 | 60.83 | Lathrop et al., 2001 |
| Delaware | 2008 | 0.01 | Anderson ⁶ |
| Maryland Coastal Bays | 2007 | 27.60* | Orth et al. ⁷ |
| Chesapeake Bay + tributaries | 2007 | 262.71* | Orth et al. ⁷ |
| Virginia Coastal Bays | 2007 | 16.03* | Orth et al. ⁷ |
| North Carolina | 1985–1992 | 500** | Ferguson et al., 1991, 1993; Ferguson and Wood ⁸ ; NOAA ^{9, 10, 11} |

¹ Barker, S. State of Maine, Department of Marine Resources, Boothbay Harbor. Personal commun., 2009

² New Hampshire Estuaries Project (NHEP). 2006. 2006 State of the Estuaries. Durham, 32 p.

³ Costello, C. 2007. MassDEP Eelgrass Mapping Program, 1994–2007. Unpubl. rep., State of Mass., Dep. Environ. Protect., Boston.

⁴ Bradley, M., K. Raposa, and S. Tuxbury. 2007. Report on the analysis of true color aerial photography to map and inventory *Zostera marina* L. in Narragansett Bay and Block Island, Rhode Island. Environ. Data Ctr., Univ. Rhode Island, unpubl. rep., 17 p. + Eelgrass Atlas.

⁵ Peconic Estuary Program (PEP), Yaphank, NY. Unpubl. data

⁶ Anderson, B. State of Delaware, Department of Natural Resources and Environmental Control, Dover. Personal commun., 2009.

⁷ Orth, R. J., D. J. Wilcox, L. S. Nagey, A. L. Owens, J. R. Whiting, and A. K. Kenne. 2008. 2007 Distribution of submerged aquatic vegetation in Chesapeake Bay and Coastal Bays. Virginia Inst. Mar. Sci., College of William and Mary, Gloucester Point, VIMS Special Scientific Report No. 151 pursuant to U.S. Environ. Prot. Agency Award #CB973013-01-0.

⁸ Ferguson, R., and L. Wood. 1994. Rooted vascular beds in the Albemarle–Pamlico estuarine system. Albemarle–Pamlico Estuarine Study Report No. 94-02, 108 p.

⁹ National Oceanic and Atmospheric Administration. 1994. SAV habitat from Ocracoke Inlet to Pea Island, North Carolina. NOAA, Center for Coastal Fisheries and Habitat Research, Beaufort, N.C. Unpubl. GIS data

¹⁰ National Oceanic and Atmospheric Administration. 1992. Submerged aquatic vegetation of Bogue Sound, North Carolina 1992. NOAA, Coastal Services Center, Charleston, N.C., Unpubl. GIS data

¹¹ National Oceanic and Atmospheric Administration. 1990. Core Sound, North Carolina Composite SAV Data Set 1985–1990. NOAA, Coastal Services Center, Charleston, N.C., Unpubl. GIS data.

its maximum areal distribution covering much of the lower intertidal and shallow subtidal areas (Neckles et al., 2005; CBEP¹⁰). Commercial fishing activities contribute to localized impacts in smaller coves and embayments, particularly Maquoit Bay (Neckles et al., 2005; CBEP¹⁰). Additional eelgrass habitat is found in the Great Bay Estuary system, on the border of Maine and New Hampshire (see New Hampshire section below).

New Hampshire

Eelgrass was prevalent throughout the Great Bay Estuary system (GBE) prior to a reported re-occurrence of the wasting disease in the mid 1980's which virtually eliminated the population by 1989 (Nelson, 1981; Short et al., 1986, 1993). Recovery was slow, and after reaching peak extent in 1996, eelgrass distribution in the GBE has steadily re-

ceded, accompanied by a decline in total eelgrass biomass (NHEP¹¹), ostensibly due to rapidly declining water quality (nutrient loading and sedimentation; NHEP¹¹; Short¹²; Beem and Short, 2009). The largest expanse of eelgrass in New Hampshire remains in Great Bay, despite a 49% decline in coverage since the 1996 peak (Short¹²). Smaller patches once scattered throughout Little Bay and deeper portions of the Piscataqua River have all but disappeared, with a combined 99% loss reported in a one-year period (2006–2007; Short¹²). Losses include an established bed of transplanted eelgrass (0.8 hectares) in the Piscataqua River from the New Hampshire Port Authority Mitigation Project (Beem and Short, 2009). The New Hampshire Estuaries Project (NHEP), administered by the University

¹¹New Hampshire Estuaries Project (NHEP). 2006. 2006 State of the Estuaries. Durham, 32 p.

¹²Short, F. 2008. Eelgrass distribution in the Great Bay Estuary 2007. Final rep. of the Univ. N. H. to the N. H. Estuaries Project, Durham, 6 p.

of New Hampshire, continues to survey eelgrass cover in the GBE on an annual basis. Additional information can be found at the NHEP website.¹³

Massachusetts

Nautical charts and herbarium records from the mid 1800's through the 1920's document the prevalence of eelgrass in rivers, embayments, and nearshore coastal environments north of Boston as well as extensive eelgrass meadows throughout Boston Harbor and further south in Duxbury, Plymouth, eastern Cape Cod Bay, Waquoit Bay, and Buzzards Bay (Colarusso¹⁴). Eelgrass loss was documented in Massachusetts during the 1893–94 cold snap and again in 1908 (Cottam, 1934, 1935). Following the near elimination of eelgrass during the 1930's, Addy and Aylward (1944) recounted, "Eelgrass is returning in substantial amounts at many points along the Massachusetts coast and has steadily increased during the past four years, but is not as abundant anywhere as before 1930." Observations by Cottam and Munro (1954) highlight the spatial and temporal variability of the recovery process, "In some of these areas the plant is so plentiful as to impede boat travel and hinder commercial fishing. Least improvement is reported in the Gloucester–Plum Island–Newburyport section, parts of which are devoid of eelgrass."

The Massachusetts Department of Environmental Protection (MassDEP) began a comprehensive state-wide eelgrass mapping program in 1993 and interactive maps are currently available from data collected in 2001 (MassDEP¹⁵). Prior to this effort, quantitative mapping of the extent of eelgrass in Massachusetts is lacking, limiting efforts for longer trend analysis. However, Costa (1988) examined historic trends for Buzzards Bay although current changes (after 1980's) are not documented.

¹³<http://www.nhep.unh.edu/about/index.htm>

¹⁴Colarusso, P. U.S. Environmental Protection Agency, Boston. Personal commun., 2009.

¹⁵MassDEP <http://www.mass.gov/dep/>

By the 1980's it appeared as if eelgrass "had saturated most available substrate" in Buzzards Bay (Costa, 1988). However, mapping efforts in the early 1990's and in 2001 indicated a renewed steady decline; over 60% of eelgrass in Buzzards Bay had been lost primarily from nutrient enrichment (Hauptert and Rasmussen¹⁶). Similarly, nitrogen loading from coastal development has led to extensive eelgrass loss in Waquoit Bay, with 60% loss reported in a 5-year period (Short and Burdick, 1996; Hauxwell et al., 2003). Moreover, the once abundant eelgrass beds in Boston Harbor are now limited to a few locations, a result of urbanization. Despite localized losses, the coastal waters of Massachusetts support the largest quantity of eelgrass in New England.

Rhode Island

For a detailed reconstruction of historical eelgrass locations in Narragansett Bay, consult Doherty¹⁷ and references therein. Eelgrass is reported from 1848 herbarium records and from U.S. Coast and Geodetic Survey 1865 survey sheets (Doherty¹⁷). In the early 1900's, eelgrass was "harvested for fertilizer and insulation," perhaps an indication of its widespread prevalence in Narragansett Bay (Doherty¹⁷). Setchell (1929) observed that "*Zostera marina* occurs abundantly in the inner waters of Narragansett Bay as well as in the large protected salt ponds of southern Rhode Island." Although the wasting disease did impact a number of eelgrass populations in Narragansett Bay, significant declines are often attributed to a 1938 hurricane (Doherty¹⁷). In the 1950's, Rhode Island eelgrass exhibited substantial recovery following the natural disturbances of the 1930's, "In some places it is regarded as plentiful as before 1931" (Cottam and Munro, 1954).

Trend analysis conducted by the Narragansett Bay Estuary Program in-

dicates that upper-Bay eelgrass populations have been entirely lost in the past 50–100 years due to nutrient enrichment (Bradley et al.¹⁸). Present-day distributions are limited to coastal ponds and isolated pockets in the lower-Bay from Prudence Island south and along the rocky eastern coast at Sakonnet Point (Bradley et al.¹⁸). The Rhode Island Coastal Resources Management Council (CRMC) and the University of Rhode Island's Environmental Data Center (EDC) have created a comprehensive repository for eelgrass distribution data. Interactive maps of eelgrass distribution are available through the CRMC website.¹⁹

Connecticut

Historically, the distribution and abundance of eelgrass in Long Island Sound (LIS) has experienced dramatic fluctuations. A detailed description of historical distributions of eelgrass in LIS can be found in a report by the Connecticut Department of Environmental Protection and Department of Agriculture and references therein (CTDEP and CTDA²⁰). In Connecticut, at the beginning of the 20th century, eelgrass was "common along the coast in bays, salt rivers, and creeks ... extensively used by farmers as a fertilizer" (Graves et al., 1910). The wasting disease event virtually eliminated eelgrass from the region (Marshall, 1947) but eelgrass had shown "encouraging improvement" following the event (Cottam and Munro, 1954). By the 1970's, populations in eastern LIS had rebounded so remarkably that eelgrass was considered a nuisance. In the Niantic River Estuary, explosives

were used to selectively remove eelgrass in an attempt to improve water circulation (Ludwig, 1977). However, despite a number of restoration attempts, eelgrass populations in western LIS never recovered following the wasting disease.

Throughout the 1980's and 1990's, eelgrass populations experienced a number of localized declines, most notably in the Niantic River where eelgrass became virtually non-existent (Short et al., 1988). More recently, 2006 aerial surveys conducted by the Connecticut Department of Environmental Protection and U.S. Fish and Wildlife Service inventoried 6.75 km² of eelgrass throughout eastern Long Island Sound (Connecticut waters), an increase of 1.13 km² from 2002 mapping efforts (Tiner et al., 2007). However, coverage continues to vary spatially and temporally within and among coves and small embayments. Declines are typically attributed to nutrient enrichment (Keser et al., 2003) with recovery often a result of removal of nutrient inputs (Vaudrey²¹). Following the diversion of a sewage-treatment facility wastewater outflow in 1987, portions of Mumford Cove were transformed from algal dominated communities to *Zostera marina* dominated communities within 10 years (Vaudrey²¹).

New York

By the 1950's, although a number of Long Island locales showed "noticeable improvement" following the wasting disease, eelgrass had attained less than a quarter of its 1931 status (Cottam and Munro, 1954). In the 1960's, a number of small embayments along the southern shore of Long Island reportedly harbored extensive eelgrass beds to the point of impeding small boat traffic (Dennison et al., 1989). Brown tide events in the mid 1980's caused additional large-scale die offs of eelgrass in Long Island coastal waters (Cosper et al., 1987; Dennison et al., 1989). Only about 12% of the

¹⁶Hauptert, C., and M. Rasmussen. 2003. 2003 State of the Bay. Coalition for Buzzards Bay, New Bedford, MA, 11 p.

¹⁷Doherty, A. 1995. Historical distributions of eelgrass (*Zostera marina*) in Narragansett Bay, Rhode Island. Narragansett Bay Estuary Prog. Rep. NBEP-95-121, 25 p. + app.

¹⁸Bradley, M., K. Raposa, and S. Tuxbury. 2007. Report on the analysis of true color aerial photography to map and inventory *Zostera marina* L. in Narragansett Bay and Block Island, Rhode Island. Environ. Data Ctr., Univ. Rhode Island, Unpubl. rep., 17 p. + Eelgrass Atlas.

¹⁹<http://www.edc.uri.edu/Eelgrass/default.html>

²⁰CTDEP, and CTDA. 2007. An assessment of the impacts of commercial and recreational fishing and other activities to eelgrass in Connecticut's waters and recommendations for management. A report to the Environmental Committee of the Connecticut General Assembly pursuant to Public Act 01-115.

²¹Vaudrey, J. 2008. Establishing restoration objectives for eelgrass in Long Island Sound Part I: Review of the seagrass literature relevant to Long Island Sound. Univ. Conn. final rep. pursuant to Conn. Dep. Environ. Protect. cooperative agreement LI-97107201/CDFA#66-437. 58 p.

7.69 km² of eelgrass mapped in LIS in 2006 are in New York waters (Tiner et al., 2007). Cornell University's Cooperative Extension Eelgrass Program (CCE) monitors a number of existing eelgrass beds around Long Island and has established a number of restoration sites in Long Island Sound, Peconic Estuary, South Shore Estuary, and the Hudson–Raritan Estuary.

Prior to the wasting disease, eelgrass was prevalent in the Peconic Estuary, with an estimated coverage of 35.29 km² (CCE²²). Eelgrass acreage from 2000 aerial surveys reported by Tiner et al. (2003) indicate an approximate 85% loss in a 70 year period. Data from the Peconic Estuary Program's Long-Term Eelgrass Monitoring Program, initiated in 1997, indicates a continual steady decline in eelgrass since the late 1990's (Pickerell and Schott^{23,24}).

New Jersey

Roughly 75% of New Jersey's SAV is found in Barnegat Bay (Lathrop et al., 2001). Following the wasting disease event, Cottam and Munro (1954) reported "excellent recovery" of eelgrass in northern Barnegat Bay but less so in the southern part of the bay. Further south, beyond the bay, "the plant is absent, or nearly so, in areas where it was once abundant" (Cottam and Munro, 1954). Continued escalation in coastal development since the mid 1970's has led to the progressive eutrophication of the Barnegat Bay–Little Egg Harbor Estuary (Kennish et al.²⁵). Eelgrass acreage in the estuary peaked

in the 1970's and 1980's, followed by significant declines in the 1990's and present day (Lathrop et al., 2001; Bologna et al.²⁶). Recurring brown tide, phytoplankton, and macroalgae blooms have plagued the region since the mid 1990's, worsening the situation (Bologna et al., 2001; Olsen and Mahoney, 2001; Gastrich et al., 2004). In 2006, a reported 50–88% of seagrass biomass in the Barnegat Bay–Little Egg Harbor Estuary was lost, a result of accelerated macroalgal growth (Kennish et al.²⁵). The Center for Remote Sensing and Spatial Analysis (CRSSA) at Rutgers University has digitized existing SAV maps dating from 1968 through 2003 to create a regional SAV time series. The interactive maps may be viewed at CRSSA's website.²⁷

Delaware

The Inland Bays of Delaware never recovered from the wasting disease of the 1930's. Cottam and Munro (1954) reported "no known stands" although restoration attempts were being made. By the late 1960's, declining water quality led to the local extinction of eelgrass in the region (Orth and Moore²⁸; Sellner²⁹). New environmental regulations in the 1980's, in addition to natural erosion events that led to increased flushing of the bays, greatly improved water quality in the region. Although a restoration program initiated by the Delaware Department of Natural Resources and Environmental Control (DNREC) in 1997 has resulted in approximately 0.02 km² of viable eelgrass habitat in a

small region of Indian River Bay (Anderson³⁰), excessive nutrient loading elsewhere prevents successful re-introduction of eelgrass (Price, 1998).

Maryland

Eelgrass can be found from the Choptank River south to the mouth of the Chesapeake Bay and throughout the coastal bays. The extent of eelgrass habitat in Maryland's coastal bays is nowhere near its reported coverage of the 1900's. However, eelgrass coverage in the bays has increased steadily since annual monitoring began in 1986 (Wazniak et al., 2004). In contrast, many of Maryland's river estuaries, which are tributaries of Chesapeake Bay, have experienced significant declines in eelgrass primarily due to water quality issues (Stankelis et al., 2003). Large-scale restoration efforts (via seed broadcasting) initiated by the Maryland Department of Natural Resources in 2003 for the Potomac and Patuxent Rivers have met with mixed success (Busch and Golden³¹).

Chesapeake Bay and Tributaries

Information regarding the abundance and distribution of eelgrass prior to the 1950's is lacking (Stevenson and Confer, 1978) although it appears as if eelgrass populations in the Chesapeake Bay succumbed to the cold snap experienced by New England in 1893–94 (Cottam, 1934). In 1889, eelgrass was also reported to have "almost died out in the Chesapeake area and that it were upwards of 25 years before the maximum growth had returned" (Cottam, 1934).

In the early 1900's, evidence suggests that eelgrass and other species of SAV were prevalent throughout the bay and its tributaries (Orth and Moore, 1984). Following the wasting disease event, SAV beds experienced increasing re-

²²CCE http://counties.cce.cornell.edu/suffolk/habitat_restoration/seagrassli/index.html

²³Pickerell, C., and S. Schott. 2004. Eelgrass trend analysis report: 1997–2002. Rep. to the Peconic Estuary Program, Yaphank, NY, 100 p.

²⁴Pickerell, C., and S. Schott. 2008. Peconic Estuary Program 2006 eelgrass (*Zostera marina*) long-term monitoring program. Progress rep. to the Peconic Estuary Program, Yaphank, NY, 27 p.

²⁵Kennish, M. J., S. M. Haag, and G. P. Sakowicz. 2007. Demographic investigation of submerged aquatic vegetation (SAV) in the Barnegat Bay–Little Egg Harbor Estuary with assessment of potential impacts of benthic macroalgae and brown tides. Inst. Mar. Coast. Sci., Rutgers Univ. New Brunswick, Tech. Rep. 107-15, 366 p.

²⁶Bologna, P. A. X., R. Lathrop, P. D. Bowers, and K. W. Able. 2000. Assessment of the health and distribution of submerged aquatic vegetation from Little Egg Harbor, New Jersey. Inst. Mar. Coast. Sci., Rutgers Univ., Tech. Rep. #2000-11, 30 p.

²⁷<http://www.crssa.rutgers.edu/>

²⁸Orth, R. and K. Moore. 1988. Submerged aquatic vegetation in Delaware's inland bays. In K. Sellner (Editor), Phytoplankton, nutrients, macroalgae, and submerged aquatic vegetation in Delaware inland bays, 1985–1986, p. 86–109. Acad. Nat. Sci. final rep. to D. E. Dep. Nat. Res.

²⁹Sellner, K. 1988. Phytoplankton, nutrients, macroalgae, and submerged aquatic vegetation in Delaware inland bays, 1985–1986. Acad. Nat. Sci. final rep. to D. E. Dep. Nat. Res., 140 p.

³⁰Anderson, B. State of Delaware, Dep. Nat. Resour. Environ. Control, Dover. Personal commun., 2009.

³¹Busch, K., and R. Golden. 2009. Large-scale restoration of eelgrass (*Zostera marina*) in the Patuxent and Potomac Rivers, Maryland. Final rep. of the Maryland Dep. Nat. Resour. pursuant to NOAA Award #NA03NMF4570470.

covery through the 1960's (Cottam and Munro, 1954; Orth and Moore, 1984) but experienced a major setback from the effects of runoff following Tropical Storm Agnes in 1972. Again, increasing nutrient and sediment loads from development led to a precipitous bay-wide decline of all submerged aquatic vegetation in the 1970's (Kemp et al., 1983; Orth and Moore, 1983). Annual surveys initiated in 1984 and conducted by the Virginia Institute of Marine Science (VIMS) indicate that there continues to be considerable annual variation in all SAV coverage across the bay, with declines in some areas and recovery in others. Interactive maps can be viewed at the VIMS website.³² Water quality issues continue to be the primary factors affecting SAV growth in Chesapeake Bay.

Virginia Southern Coastal Bays

Following the wasting disease event and a catastrophic hurricane in 1933, eelgrass beds in this region were decimated. In the mid 1990's, the discovery of small, natural patches of eelgrass prompted an eelgrass restoration effort in the Delmarva Southern Coastal Bays of Virginia. Between 2001 and 2004, 24.2 million eelgrass seeds were broadcast by hand, resulting in the re-introduction of eelgrass to areas devoid since 1933 (Orth et al., 2006). The final, sustained acreage arising from this work remains undetermined.

North Carolina

North Carolina represents the southern geographic boundary for eelgrass along the U.S. eastern seaboard. Although affected by the wasting disease, eelgrass populations in North Carolina were able to substantially recover and have remained relatively stable since the 1970's (Fonseca³³). Eelgrass is found south of Oregon Inlet down through Bogue Sound. As is typical in most regions, estuaries and sounds with higher turbidity do not support

eelgrass (i.e. Albemarle Sound, western Pamlico Sound). There has been no sustained effort to monitor or map seagrass state-wide until very recently, although portions of the coast were mapped in the mid 1980's and early 1990's (Ferguson et al., 1991, 1993; Ferguson and Wood³⁴; NOAA^{35,36,37}). The Submerged Aquatic Vegetation Mapping Partnership, facilitated by the Albemarle-Pamlico National Estuary Program (APNEP), acquired digital aerial photography from along the entire coast of North Carolina in 2007–2008. A state-wide GIS eelgrass database resulting from this imagery is in progress. For more information, consult the APNEP website.³⁸

Faunal Communities

Faunal use of eelgrass habitat is widely divergent; eelgrass fauna may include seasonal or year-round residents, may use eelgrass meadows for all or a portion of their life cycle, or may only visit the meadow for grazing purposes. The structural organization of individual eelgrass plants and eelgrass meadows as a whole allows for exploitation of a number of habitat types. Eelgrass fauna may attach directly to the leaves of the plant, bury into the sediments within a meadow, live on top of the sediment, associate with blades but remain unattached, or actively swim amongst the canopy. With the exception of some fishes, sea turtles, Brant and Canada geese, and some mollusks, few animals actually feed directly on live

eelgrass plants, primarily due to the high cellulose content of the leaves, which is difficult to digest. The dominant food pathway for eelgrass itself is through the detrital food chain; its contribution to estuarine productivity is more complex and is intertwined with habitat-associated microalgae. The detritivores (crabs, shrimps, mollusks) in turn, are prey items for larger species (fish, birds).

Eelgrass meadows provide habitat, nurseries, and feeding grounds for a number of commercially, recreationally, and ecologically important species (Table 2), including the bay scallop, *Argopecten irradians*. As juveniles, bay scallops attach directly to the blades of eelgrass plants, but later drop to the sediment surface (Thayer and Stuart, 1974; Eckman, 1987; Garcia-Esquivel and Bricej, 1993). In North Carolina, eelgrass is often the only available "hard" substrate for scallops to settle on, keeping the scallops away from predators, indicating its local importance as essential fish habitat for this species (Kirby-Smith, 1970). In addition to individual plants serving as habitat, the structure of the eelgrass meadow influences the population dynamics of the bay scallop. It has been shown that the spatial patterning of eelgrass beds can alter rates of predation on bay scallops (Irlandi et al., 1995); higher rates of predation were observed as the level of fragmentation of the bed increased (Irlandi et al., 1995). Due to the tight linkages between eelgrass and bay scallops, any change in eelgrass populations should directly affect that of the bay scallop.

Human Threats to Eelgrass

Point and non-point source nutrient loading and sediment runoff are the primary threats to eelgrass along the Atlantic coast and are believed to be the number one cause of eelgrass decline locally. Orth and Moore (1983) reported significant declines of eelgrass in Chesapeake Bay in the late 1970's and early 1980's apparently the result of increased runoff and watershed development. Similar trends were documented by Costa (1988) for Buzzards Bay, Mass..

³²<http://www.vims.edu/bio/sav/>

³³Fonseca, M. NOAA, Center for Coastal Fisheries and Habitat Research, Beaufort, N.C. Personal observ.

³⁴Ferguson, R., and L. Wood. 1994. Rooted vascular beds in the Albemarle-Pamlico estuarine system. Albemarle-Pamlico Estuarine Study Rep. No. 94-02, 108 p.

³⁵National Oceanic and Atmospheric Administration. 1994. SAV habitat from Ocracoke Inlet to Pea Island, North Carolina. NOAA, Center for Coastal Fisheries and Habitat Research, Beaufort, N.C. Unpubl. GIS data.

³⁶National Oceanic and Atmospheric Administration. 1992. Submerged aquatic vegetation of Bogue Sound, North Carolina 1992. NOAA, Coastal Services Center, Charleston, N.C., Unpubl. GIS data

³⁷National Oceanic and Atmospheric Administration. 1990. Core Sound, North Carolina Composite SAV Data Set 1985-1990. NOAA, Coastal Services Center, Charleston, N.C., Unpubl. GIS data

³⁸<http://www.apnep.org/>

Table 2.—Non-inclusive list of representative commercially, recreationally, and ecologically important species using eelgrass beds along the Atlantic coast of the United States. Life history stages are represented as A = adult, J = juvenile, L = larvae, E = eggs, M = migratory. Modified from Thayer et al., 1979, 1984.

| Common Name | Scientific Name | Life Stage |
|--------------------------|--------------------------------------|------------|
| Fish | | |
| Spotted seatrout | <i>Cynoscion nebulosus</i> | J |
| Mullet | <i>Mugil cephalus</i> | J |
| Spot | <i>Leiostomus xanthurus</i> | A, J |
| Pinfish | <i>Lagodon rhomboides</i> | A, J |
| Pigfish | <i>Orthopristis chrysoptera</i> | J |
| Gag grouper | <i>Mycteroperca microlepis</i> | J |
| Sheepshead | <i>Archosargus probatocephalus</i> | A, J |
| Thread herring | <i>Opisthonema oglinum</i> | J |
| Permit | <i>Trachinotus falcatus</i> | J |
| White grunt | <i>Haemulon plumieri</i> | J |
| Bluefish | <i>Pomatomus saltatrix</i> | A, J |
| Tautog | <i>Tautoga onitis</i> | J, E |
| Summer flounder | <i>Paralichthys dentatus</i> | A, J |
| Southern flounder | <i>Paralichthys lethostigma</i> | A, J |
| Winter flounder | <i>Pseudopleuronectes americanus</i> | J |
| Menhaden | <i>Brevoortia tyrannus</i> | A, J, L |
| Smelt | <i>Osmerus mordax</i> | M |
| Striped bass | <i>Morone saxatilis</i> | A |
| Elasmobranchs | | |
| Cownose ray | <i>Rhinoptera bonasus</i> | A, J |
| Southern stingray | <i>Dasyatis sabina</i> | A, J |
| Decapods | | |
| Brown shrimp | <i>Penaeus aztecus</i> | A, J |
| Pink shrimp | <i>Penaeus duorarum</i> | A, J |
| Blue crab | <i>Callinectes sapidus</i> | A |
| American lobster | <i>Homarus americanus</i> | J |
| Horseshoe crab | <i>Limulus polyphemus</i> | A, J |
| Mollusks | | |
| Bay scallop | <i>Argopecten irradians</i> | A, J |
| Hard clam | <i>Mercenaria mercenaria</i> | A, J |
| Soft-shell clam | <i>Mya arenaria</i> | A, J |
| Whelks | <i>Busycon</i> spp. | A, J |
| Blue mussels | <i>Mytilus edulis</i> | A, J |
| Variable Bittium | <i>Bittium varium</i> | A, J, E |
| Slipper limpet | <i>Crepidula convexa</i> | A, J, E |
| Birds | | |
| Brant goose | <i>Branta bernicla</i> | M |
| Canada goose | <i>Branta canadensis</i> | M |
| Greater scaup | <i>Aythya marila</i> | M |
| Redhead duck | <i>Aythya americana</i> | M |
| Great blue heron | <i>Ardea herodias</i> | A |
| Great egret | <i>Casmerodius albus</i> | A |
| Reptiles | | |
| Kemp's ridley sea turtle | <i>Lepidochelys kempi</i> | A, J |
| Loggerhead sea turtle | <i>Caretta caretta</i> | A, J |
| Green sea turtle | <i>Chelonia mydas</i> | A, J |

Nutrient inputs from land development, sewage treatment plants, agricultural activities, and impervious surfaces can lead to eutrophication (i.e. algal and phytoplankton blooms which reduce the amount of light penetrating to the grass bed leading to large-scale declines and/or dieoffs; Short et al., 1995; Short and Burdick, 1996). Deforestation and other disturbances to the coastal terrain (i.e. land development) deliver high amounts of sediment to inshore waters leading to increased turbidity and reduced light penetration at depth. As the coastal zone continues to be developed, these threats will not go away.

Eelgrass meadows are also vulnerable to disturbance from commercial fishing activities, especially those associated with scallop harvesting. The epibenthic dredges used to harvest bay scallops lead to dramatically decreased shoot densities and biomass of eelgrass (Fonseca et al., 1984). Bishop et al. (2005) reported a 9% loss of meadow biomass in just 10 minutes of dredge activity. Orth et al. (2002) reported on significant eelgrass impacts resulting from hard clam harvest and how careful monitoring was used to quickly modify fishing regulations to prevent further habitat loss.

Biological Disturbance

Distribution of eelgrass is also mediated by biological disturbance (animals). Orth (1975) described substantial removal of healthy eelgrass by large numbers of cownose rays. Townsend and Fonseca (1998) showed the role of animal disturbance in the maintenance of eelgrass bed margins. Biological disturbance is also one of the primary problems facing restoration projects (Fonseca et al., 1998; see Restoring Eelgrass below).

Restoring Eelgrass

Addy's (1947) basic logic was to match eelgrass planting and harvest site environments, and this remains a fundamental tenet in almost all seagrass planting today. Aside from early interest by Phillips (1960), almost 30 years elapsed before serious attention to planting seagrass developed. It was not until the 1970's that documents again began to emerge presenting seagrass planting in a guideline format, culminating in a national guidelines document (Fonseca et al., 1998). But even though suitable planting methods have long existed, the track record for successful mitigation of impacts to eelgrass beds remains variable (see review by Phillips, 1982).

Much emphasis was placed on technique development in the late 1970's and early 1980's, but relatively little attention was given to developing a management framework within which these techniques could be effectively implemented. As a result, most seagrass mitigation projects have failed to achieve even the goal of 1:1 habitat replacement (i.e. offset a net loss of seagrass habitat). Nonetheless, eelgrass beds have often been successfully planted and have come to perform much as naturally-propagated beds (see review by Fonseca et al., 1998).

Of all the North American seagrasses, eelgrass has a growth rate and strategy that makes it especially conducive to restoration. As mentioned earlier, eelgrass plants migrate across the seafloor and are morphologically plastic which provides an adaptive advantage in that

they have some capacity to locate more favorable conditions. They are also prolific in their seed production, giving them another advantage in that they can disperse broadly. Finally, as each shoot is terminal on a rhizome, each shoot is a viable contributor to both daughter ramets (new members of the population) and seeds (in their second year when in their perennial form). Unlike many other seagrasses that put down stationary shoots that do not subsequently add to population growth (with the exception of infrequent branching for some species) and are thus not useful in vegetative transplants, eelgrass shoots are all viable transplanting units and thus fewer shoots are needed for harvest and installation. For a full review of eelgrass and other seagrass restoration, see Fonseca et al. (1998).

While methodological innovations continue, the limitations to restoring this crucial national resource are rarely technical (there are many viable techniques), but instead lay in the utilization of extant knowledge. Recent advances in eelgrass seeding and whole plant restoration technologies (see review in Fonseca et al., 1998) demonstrate the ongoing decline of methodological limitations. Problems tend to emerge in the application of this knowledge; for example, the expectations of eelgrass restoration are grossly unrealistic being held as they are to standards often higher than agricultural crops despite the huge disparity in our knowledge base and economic subsidy among these practices. Aside from unrealistic expectations of success, chief among the problems facing resource managers today is the tendency for project applicants to select planting areas where there is no prior history of their existence (unless of course the site was created for the purposes of planting seagrass). The chronic absence of seagrass from a site, especially when there are propagule sources nearby, usually indicates that the site cannot consistently support seagrasses. Ensuring sufficient light, moderate nutrient loads, and protecting plantings from disturbance constitute the other major caveats for developing a persistent eelgrass bed.

Conclusions

Eelgrass has been shown to be a critical part of the bay scallop life cycle, providing substrate for settlement and subsequent shelter and feeding (Thayer and Stuart, 1974; Eckman, 1987; Garcia-Esquivel and Bricelj, 1993; Irlandi et al., 1995). Thus, bay scallop abundance and the success of the fishery appear to be inextricably linked to the health of eelgrass habitat. However, eelgrass in the western Atlantic is almost certainly at an historic low since the wasting disease event of the 1930's, a result of human development of the coastal zone. We conclude that the reduced distribution of eelgrass, together with periodic heavy fishing pressure on scallops (MacKenzie, 2008) combine to produce the current marginal health of that fishery. Moreover, natural fluctuations in both eelgrass distribution and the erratic nature of the bay scallop population cycle (MacKenzie, 2008) may further limit scallop population persistence through habitat fragmentation and scallop recruitment limitation which all point to a fishery with profound challenges for survival.

Acknowledgments

We would like to thank D. Field, W. Hobart, D. Johnson, P. Marraro, G. Matlock, J. Strader, J. VanderPluym, and two anonymous reviewers for constructive comments. Special thanks to B. Anderson, S. Barker, D. Cavanaugh, P. Colarusso, J. Costa, C. Costello, K. Hogeland, J. Kenworthy, C. MacKenzie, R. Orth, C. Pickerell, K. Raposa, and F. Short for providing unpublished data and copies of grey literature, and for permitting the use of photographs and previously published graphics.

Literature Cited

- Addy, C. E. 1947. Eel grass planting guide. Maryland Conserv. 24:16-17.
- _____ and D. A. Aylward. 1944. Status of eelgrass in Massachusetts during 1943. J. Wildl. Manage. 8(4):269-275.
- Andrews, J. C. 1990. Fishing around Nantucket. The Maria Mitchell Assoc. Nantucket, Mass., 76 p.
- Beem, N. T., and F. T. Short. 2009. Subtidal eelgrass declines in the Great Bay estuary, New Hampshire and Maine, USA. Estuaries Coasts 32:202-205.

- Bintz, J. C., S. W. Nixon, B. A. Buckley, and S. L. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. Estuaries 26(3):765-776.
- Bishop, M. J., C. H. Peterson, H. C. Summer-son, and D. Gaskill. 2005. Effects of harvesting methods on sustainability of a bay scallop fishery: dredging uproots seagrass and displaces recruits. Fish. Bull. 103:712-719.
- Bologna, P., A. Wilbur, and K. Able. 2001. Reproduction, population structure, and recruitment limitation in a bay scallop (*Argopecten irradians* Lamarck) population from New Jersey, USA. J. Shellfish Res. 20(1):89-96.
- Burdick, D. M., F. T. Short, and J. Wolf. 1993. An index to assess and monitor the progression of wasting disease in eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 94:83-90.
- Cosper, E. M., W. C. Dennison, E. J. Carpenter, V. M. Bricelj, J. G. Mitchell, S. H. Kuenster, D. Colflesh, and M. Dewey. 1987. Recurrent and persistent brown tide blooms perturb coastal marine ecosystem. Estuaries 10(4): 284-290.
- Costa, J. 1988. Eelgrass in Buzzards Bay: distribution, production, and historical changes in abundance. U.S. Environ. Protect. Agency Rep. EPA 503/4-88-002, Wash. D.C., 204 p.
- Cottam, C. 1934. Past periods of eelgrass scarcity. Rhodora 36(427):261-264.
- _____. 1935. Further notes on past periods of eelgrass scarcity. Rhodora 37(440):269-271.
- _____ and D. A. Munro. 1954. Eelgrass status and environmental relations. J. Wildl. Manage. 18(4):449-460.
- den Hartog, C. 1971. The dynamic aspect in the ecology of seagrass communities. Thalassia Jugosl. 7:101-112.
- Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. 27(1):15-26.
- _____, R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. Bioscience 43(2):86-94.
- _____, G. J. Marshall, and C. Wigand. 1989. Effect of "brown tide" shading on eelgrass (*Zostera marina* L.) distributions. In E. M. Cosper, V. M. Bricelj, and E. J. Carpenter (Editors), Novel phytoplankton blooms: Causes and impacts of recurrent brown tides and other unusual blooms, p. 675-692. Springer-Verlag, Berlin.
- Eckman, J. E. 1987. The roll of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomie simplex* (D'Orbigny) within eelgrass meadows. J. Exp. Mar. Biol. Ecol. 106(2):165-191.
- Evans, A. S., K. L. Webb, and P. A. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. Aquat. Bot. 24(2):185-197.
- Ferguson, R. L., and K. Korfmacher. 1997. Remote sensing and GIS analysis of seagrass meadows in North Carolina, USA. Aquat. Bot. 58(3-4):241-258.
- _____, L. L. Wood, and D. B. Graham. 1993. Monitoring spatial change in seagrass habitat with aerial photography. Photogram. Eng. Rem. Sens. 59(6):1033-1038.
- _____, _____, and B. T. Pawlak. 1991. SAV habitat from Drum Inlet to Ocracoke Inlet, North Carolina. NOAA Coastal Ocean Program Submerged Aquatic Vegetation Study. U.S. Dep. Commer., NOAA, NMFS

- Beaufort Lab., Beaufort, N.C. (3- × 4-foot chart with text and illust.)
- Fonseca, M. S., and S. S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar. Ecol. Prog. Ser.* 171:109–121.
- _____, and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine Coastal Shelf Sci.* 35(6):565–576.
- _____, and J. S. Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Mar. Ecol. Prog. Ser.* 29:15–22.
- _____, W. J. Kenworthy, and G. W. Thayer. 1998. Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Prog. Decision Analysis Ser. No. 12. NOAA Coastal Ocean Off., Silver Spring, Md., 222 p.
- _____, G. W. Thayer, and A. J. Chester. 1984. Impact of scallop harvesting on eelgrass (*Zostera marina*) meadows: implications for management. *N. Am. J. Fish. Manage.* 4(3):286–293.
- _____, P. E. Whitfield, N. M. Kelly, and S. S. Bell. 2002. Modeling seagrass landscape pattern and associated ecological attributes. *Ecol. Appl.* 12(1):218–237.
- _____, J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine Coastal Shelf Sci.* 17(4):367–380.
- Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: role of optical models. *Estuaries* 17(1):198–209.
- Garcia-Esquivel, Z., and V. M. Bricej. 1993. Ontogenetic changes in microhabitat distribution of juvenile bay scallops, *Argopecten irradians irradians* (L.), in eelgrass beds, and their potential significance to early recruitment. *Biol. Bull.* 185(1):42–55.
- Gastrich, M. D., J. A. Leigh-Bell, C. J. Gobler, O. R. Anderson, S. W. Wilhelm, and M. Bryan. 2004. Viruses as potential regulators of regional brown-tide blooms caused by the alga, *Aureococcus anophagefferens*. *Estuaries* 27(1):112–119.
- Green, E. P., and F. T. Short. 2003. World Atlas of Seagrass. Prepared by the UNEP World Conservation Monitoring Centre. Univ. Calif. Press, Berkeley, 298 p.
- Graves, C. B., E. H. Eames, C. H. Bissel, L. Andrews, E. B. Harger, and C. A. Weatherby. 1910. Catalogue of the flowering plants and ferns of Connecticut. *Conn. Geol. Nat. Hist. Survey Bull.* No. 14, Hartford, Conn., 569 p.
- Grizzle, R. E., F. T. Short, C. R. Newell, H. Hoven, and L. Kindblom. 1996. Hydrodynamically induced synchronous waving of seagrasses, “monami” and its possible effects on larval mussel settlement. *J. Exp. Mar. Biol. Ecol.* 206(12):165–177.
- Harwell, M. C., and R. J. Orth. 2002. Long-distance dispersal potential in a marine macrophyte. *Ecology* 83(12):3319–3330.
- Hauxwell, J., J. Cebrian, and I. Valiela. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Mar. Ecol. Prog. Ser.* 247:59–73.
- Irlandi, E. A., W. G. Ambrose, Jr., and B. A. Orlando. 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* 72(3):307–313.
- Kemp, M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C. L. Gallegos, W. Hunley, L. Karrh, E. W. Koch, J. M. Landwehr, K. A. Moore, L. Murray, M. Naylor, N. B. Rybicki, J. C. Stevenson, and D. J. Wilcox. 2004. Habitat requirements for submersed aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. *Estuaries* 27(3):363–377.
- _____, W. R. Boynton, J. C. Stevenson, R. R. Twilley, and J. C. Means. 1983. The decline of submersed vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. *Mar. Technol. Soc. J.* 17:78–89.
- Keser, M., J. T. Swenarton, J. M. Vozarik, and J. F. Foertch. 2003. Decline in eelgrass (*Zostera marina* L.) in Long Island Sound near Millstone Point, Connecticut (USA) unrelated to thermal input. *J. Sea Res.* 49(1):11–26.
- Kirby-Smith, W. W. 1970. Growth of the scallops, *Argopecten irradians concentricus* (Say) and *Argopecten gibbus* (Linné), as influenced by food and temperature. Ph.D. Dissertation, Duke University, Durham, N.C., 126 p.
- Koch, E. W. 2001. Beyond light: physical geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24(1):1–17.
- Lathrop, R., R. Styles, S. Seitzinger, and J. Bognar. 2001. Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* 24(6):904–916.
- Ludwig, M. 1977. Environmental assessment of the use of explosives for selective removal of eelgrass (*Zostera marina*). In G. A. Young (Editor), *Proceedings of the Second Conference on the Environmental Effects of Explosives and Explosions*, p. 63–68. Naval Surface Weapons Center, Silver Spring, Md.
- MacKenzie, C. L., Jr. 2008. The bay scallop, *Argopecten irradians*, Massachusetts through North Carolina: its biology and the history of its habitats and fisheries. *Mar. Fish. Rev.* 70(3–4):6–79.
- Marsh, J. A., W. C. Dennison, and R. S. Alberte. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *J. Exp. Mar. Biol. Ecol.* 101(3):257–267.
- Marshall, N. 1947. An abundance of bay scallops in the absence of eelgrass. *Ecology* 28(3):321–322.
- McRoy, C. P., and R. J. Barsdate. 1970. Phosphate adsorption in eelgrass. *Limnol. Oceanogr.* 15(1):6–13.
- _____, R. J. Barsdate, and M. Nebert. 1972. Phosphorous cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnol. Oceanogr.* 17(1):58–67.
- Mills, K., and M. S. Fonseca. 2003. Mortality and productivity of eelgrass *Zostera marina* under conditions of experimental burial with two sediment types. *Mar. Ecol. Prog. Ser.* 255:127–134.
- Moore, K. A., R. L. Wetzel, and R. J. Orth. 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. *J. Exp. Mar. Biol. Ecol.* 215(1):115–134.
- Muehlstein, L. K. 1989. Perspectives on the wasting disease of eelgrass *Zostera marina*. *Dis. Aquat. Org.* 7:211–221.
- _____, D. Porter, and F. T. Short. 1988. *Labyrinthula zosterae* sp. nov., and _____. 1991. *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. *Mycologia* 83(2):180–191.
- Neckles, H. A., F. T. Short, S. Barker, and B. S. Kopp. 2005. Disturbance of eelgrass *Zostera marina* by commercial mussel *Mytilus edulis* harvesting in Maine: dragging impacts and habitat recovery. *Mar. Ecol. Prog. Ser.* 285:57–73.
- Nelson, J. I. 1981. Inventory of natural resources of Great Bay estuarine system. Vol. 1. N.H. Fish and Game Dep., Concord, 254 p.
- Olsen, P. S., and J. B. Mahoney. 2001. Phytoplankton in the Barnegat Bay–Little Egg Harbor estuarine system: species composition and picoplankton bloom development. *J. Coast. Res.* 32(SI):115–143.
- Orth, R. J. 1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. *Chesapeake Sci.* 16(3):205–208.
- _____, and K. A. Moore. 1983. Chesapeake Bay: An unprecedented decline in submersed aquatic vegetation. *Science* 222:51–53.
- _____, and _____. 1984. Distribution and abundance of submersed aquatic vegetation in Chesapeake Bay: historical perspective. *Estuaries* 7(4):531–540.
- _____, J. R. Fishman, D. J. Wilcox, and K. A. Moore. 2002. Identification and management of fishing gear impacts in a recovering seagrass system in the coastal bays of the Delmarva peninsula, USA. *J. Coast. Res.* 37(SI):111–129.
- _____, M. L. Luckenbach, S. R. Marion, K. A. Moore, and D. J. Wilcox. 2006. Seagrass recovery in the Delmarva coastal bays, USA. *Aquat. Bot.* 84(1):26–36.
- Penhale, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *J. Exp. Mar. Biol. Ecol.* 26(2):211–224.
- Phillips, R. C. 1960. Observations on the ecology and distribution of the Florida seagrasses. *Fla. State Board Conserv. Prof. Papers Ser.* No. 2, 72 p.
- _____. 1982. Seagrass meadows. In R. R. Lewis (Editor), *Creation and restoration of coastal plant communities*, p. 173–202. CRC Press, Boca Raton, Fla.
- _____, and E. G. Meñez. 1988. Seagrasses. *Smithsonian Contrib. Mar. Sci.* 34:1–104.
- Price, K. S. 1998. A framework for a Delaware Inland Bays environmental classification. *Environ. Monit. Assess.* 51(1–2):285–298.
- Rasmussen, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In C. P. McRoy and C. Helfferich (Editors), *Seagrass ecosystems: a scientific perspective*, p. 1–52. Marcel Dekker, N.Y.
- Setchell, W. A. 1929. Morphological and phenological notes on *Zostera marina* L. *Calif. Publ. Bot.* 14(19):389–452.
- Short, F. T. 1983a. The response of interstitial ammonium in eelgrass (*Zostera marina* L.) beds to environmental perturbations. *J. Exp. Mar. Biol. Ecol.* 68(2):195–208.
- _____. 1983b. The seagrass *Zostera marina* L.: plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquat. Bot.* 16(2):149–161.

- _____. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquat. Bot.* 27(1):41–57.
- _____, and D. M. Burdick. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19(3):730–739.
- _____, and C. A. Short. 2003. The seagrasses of the western North Atlantic. In E. P. Green and F. T. Short (Editors), *World Atlas of Seagrasses*, p. 207–215. Univ. Calif. Press, Berkeley.
- _____, D. M. Burdick, and J. E. Kaldy. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina* L. *Limnol. Oceanogr.* 40(4):740–749.
- _____, _____, J. S. Wolf, and G. E. Jones. 1993. Eelgrass in estuarine research reserves along the east coast, USA. Part I: Declines from pollution and disease. U.S. Dep. Commer, NOAA Coastal Ocean Prog. Publ., 83 p.
- _____, B. W. Ibelings, and C. den Hartog. 1988. Comparisons of a current eelgrass disease to the wasting disease in the 1930's. *Aquat. Bot.* 30(4):295–304.
- _____, A. C. Mathieson, and J. I. Nelson. 1986. Recurrence of the eelgrass wasting disease at the border of New Hampshire and Maine, USA. *Mar. Ecol. Prog. Ser.* 29:89–92.
- _____, L. K. Muehlstein, and D. Porter. 1987. Eelgrass wasting disease: cause and recurrence of a marine epidemic. *Biol. Bull.* 173(2):557–562.
- Stankelis, R. M., M. D. Naylor, and W. R. Boynton. 2003. Submerged aquatic vegetation in the mesohaline region of the Patuxent Estuary: past, present, and future status. *Estuaries* 26(2):186–195.
- Stevenson, J. C., and N. M. Confer. 1978. Summary of available information on Chesapeake Bay submerged aquatic vegetation. U.S. Fish and Wildl. Serv. FWS/OBS 78/66, Wash. D.C., 335 p.
- Thayer, G. W., and H. H. Stuart. 1974. The bay scallop makes its home of seagrass. *Mar. Fish. Rev.* 36(7):27–30.
- _____, W. J. Kenworthy, and M. S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/02, Wash. D.C., 147 p.
- _____, H. H. Stuart, W. J. Kenworthy, J. F. Ustach, and A. B. Hall. 1979. Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. In P. E. Greeson, J. R. Clark, and J. E. Clark (Editors), *Wetland functions and values: the state of our understanding*, p. 235–247. Am. Water Res. Assoc., Minneapolis, Minn.
- Tiner, R., H. Bergquist, T. Halavik, and A. MacLachlan. 2003. Eelgrass Survey for Eastern Long Island Sound, Connecticut and New York. Natl. Wetlands Inventory Prog. Rep. U.S. Fish Wildl. Serv., Hadley, Mass., 14 p. + app.
- _____, _____, _____, and _____. 2007. 2006 Eelgrass Survey for Eastern Long Island Sound, Connecticut and New York. Natl. Wetlands Inventory Prog. Rep., U.S. Fish Wildl. Serv., Hadley, Mass., 24 p. + app.
- Townsend, E., and M. S. Fonseca. 1998. The influence of bioturbation on seagrass landscape patterns. *Mar. Ecol. Prog. Ser.* 169:123–132.
- Tutin, T. G. 1938. The autecology of *Zostera marina* in relation to its wasting disease. *New Phytol.* 37(1):50–71.
- Wazniak, C., L. Karrh, T. Parham, M. Naylor, M. Hall, T. Carruthers, and R. Orth. 2004. Seagrass abundance and habitat criteria in the Maryland coastal bays. In C. E. Wazniak and M. R. Hall (Editors), *Maryland's coastal bays: Ecosystem health assessment 2004*, p. 6.1–6.17. Maryland Dep. Nat. Resour., Annapolis.
- Zimmerman, R. C., R. D. Smith, and R. A. Alberte. 1989. Thermal acclimation and whole-plant carbon balance in *Zostera marina* (eelgrass). *J. Exp. Mar. Biol. Ecol.* 130(2):93–109.