Removal of Sea Lettuce, *Ulva* spp., in Estuaries to Improve the Environments for Invertebrates, Fish, Wading Birds, and Eelgrass, *Zostera marina*

CLYDE L. MACKENZIE, Jr.

Introduction

In many estuaries of North America, Europe, China, Australia, and likely other parts of the world, abundances of macroalgae have increased sharply during the latter half of the 1900's and into the 2000's. The macroalgae have increased so much that they often form huge thick mats (biomasses) on wide shoreline flats. The principal mat-forming types are sea lettuce, *Ulva lactuca* (Fig. 1), *Enteromorpha* spp., *Gracilaria* spp., and *Cladophora* spp. Few macroin-

Clyde L. MacKenzie, Jr., is with the James J. Howard Marine Sciences Laboratory, Northeast Fisheries Science Center, 74 Magruder Road, Highlands, N.J. 07732 [e-mail: Clyde. MacKenzie@noaa.gov].

ABSTRACT—Mats (biomasses) of macroalgae, i.e. Ulva spp., Enteromorpha spp., Graciolaria spp., and Cladophora spp., have increased markedly over the past 50 years, and they cover much larger areas than they once did in many estuaries of the world. The increases are due to large inputs of pollutants, mainly nitrates. During the warm months, the mats lie loosely on shallow sand and mud flats mostly along shorelines. Ulva lactuca overwinters as buds attached to shells and stones, and in the spring it grows as thalli (leaf fronds). Mats eventually form that are several thalli thick. Few macroinvertebrates grow on the upper surfaces of their thalli due to toxins they produce, and few can survive beneath them. The fish, crabs, and wading birds that once used the flats to feed on the macroinvertebrates are denied these feeding grounds. The mats also grow over and kill mollusks and eelgrass, Zostera marina. An experiment was undertaken which showed that two removals of U. lactuca in a summer from a shallow flat in an estuarine cove maintained the bottom almost free of it.

vertebrates grow on the surfaces of Ulva spp. sheets (MacKenzie, 2000; Harder et al., 2004), and few can live beneath them (Soulsby et al., 1978; Nicholls et al., 1981; Olafsson, 1988; Bonsdorff, 1992; Norkko and Bonsdorff, 1996; MacKenzie, 2000; Rafaelli, 2000; Sfriso et al., 2001; Österling and Pihl, 2001; Jones and Pinn, 2006). The shoreline flats once provided good habitats for large numbers of macroinvertebrates that were the prey of small fishes, crabs, and shrimps, which were in turn, food for wading birds and other predators (Breber, 1985; Norkko and Bonsdorff, 1996; Thiel et al., 1998; MacKenzie and McLaughlin, 2000: Sfriso et al., 2001).

Where the algal or *Ulva* mats are present, they have covered and eliminated the areas as sources of food. In doing so, they have altered the estuaries' trophic food webs within the shallow zones and also within the entire estuaries, in part, because large commercial and sport fish in the deeper waters of estuaries had fed on some of the macroinvertebrate predators, especially the small fish (Valiela et al., 1992; Hartog, 1994; Isaksson et al., 1994; Peterson and Turner, 1994; Short et al., 1995; Norkko and Bornsdorff, 1996; Short and Burdick, 1996; Rafaelli et al., 1998; Hauxwell et al., 2001; Sfriso et al., 2001; Deegan et al., 2002; Cummins et al., 2004).

Large influxes of nitrates and also phosphates, carried by freshwater to the estuaries, have led to eutrophication of the waters and fueled the algal growth.





The influxes are the result of increased urbanization and industrialization of the estuaries' watersheds (Wilkinson, 1963; Sawyer, 1965; Buttermore, 1977; Soulsby et al., 1978, 1982; Montgomery and Soulsby, 1980; Nicholls et al., 1981; Rosenberg, 1985; Valiela et al., 1997; Deegan et al., 2002; DeJonge et al., 2002).

Sea lettuce, *Ulva lactuca*, has a bright green color and imparts an apparent healthy appearance (Fig. 2). Along the east coast of the United States, its presence has not been regarded by the public as pollution-related, and its overabundance has not been particularly noticed except by boaters and swimmers who regard it as a nuisance. Many people even consider that large amounts of a green plant, such as sea lettuce, in the water denotes a healthy environment. The name lettuce also connotes to some a positive impression (like lettuce as a human food). But in Europe, sea lettuce has become regarded as a "green tide," a term somewhat analogous with brown tides and red tides that cause harm to other marine life and are also caused by eutrophication (Vasserot, 1990).

Autecology of Sea Lettuce

Sea lettuce, Ulva spp., is present in the estuaries of eastern and western North America, South America, western and southern Europe from Norway southward into the Black Sea. Sea lettuce is also found in the western Pacific from Japan, Korea, and China to Australia and New Zealand, and also in India and Pakistan (Taylor, 1957; Tseng, 1983; Lavery et al., 1991; Tagliapietra et al., 1998; Sfriso et al., 2001; Harder et al., 2004). It grows in polyhaline areas (Pirou et al., 1991: Raffaelli et al., 1998: Brush and Nixon, 2003), and the mats occur on wide gently sloping sand and mud flats in low energy areas where tidal circulations and wind-driven waves are weak. Any flats that are exposed to moderate winds commonly have scattered sea lettuce thalli (leaf fronds). In exposed areas, winds may drive scattered thalli and small mats into piles against and onto shorelines.

The thallus of sea lettuce begins as a thin, undifferentiated vegetal frond that



Figure 2.—Surface of a sea lettuce mat, *Ulva lactuca*, Navesink River, N.J., July 1994. Macroscopic animals and plants are nearly absent.

grows quickly and takes up nutrients rapidly (Littler and Littler, 1980). Its growth is nutrient limited rather than light limited (Valiela et al., 1997). Ulva spp. and Enteromorpha spp. can take up nutrients 4-6 times faster than slower growing perennial plants (Pederse and Borum, 1997). The thalli that grow in sewage-polluted waters contain more nitrogen than those in unpolluted waters (Fritsch, 1956; Wilkinson, 1963). The thallus is two cells thick and is laminate to rounded, often somewhat lobed and undulate (Taylor, 1957), and is usually about 30 cm long and nearly as wide, but may be twice this size (Lee, 1977). The cells are uninucleate and have a single cup-shaped chloroplast. Cell division may occur anywhere in thalli, but all divisions are in a plane perpendicular to the thalli surfaces (Smith, 1955). The stalk is thin and inconspicuous or absent (Taylor, 1957).

Toxin production in marine macroalgae may be common. Harder et al. (2004) observed that the thallus surfaces of *Ulva reticula* in China are free of macroinvertebrates. Upon investigation, they discovered that the surface boundary layer of the thalli produces antifouling agents, waterborne toxic macromolecular substances of at least two types, one of which originates from the thalli and the other from an epibiotic bacterium. Magré (1974) and Johnson and Welsh (1985) showed that, in finger bowls, fragments of sea lettuce are toxic to estuarine invertebrates. Also, Anéer (1987) found that in a natural situation in Europe, the eggs of the Atlantic herring, *Clupea harengus*, were killed in large numbers by exudates released by filamentous brown algae, predominantly *Pilayella littoralis*.

The published literature reports on the sizes of sea lettuce mats in two areas. In New Jersey estuaries, the *U. lactuca* mats are from 1.5 to 75 m across (MacKenzie and McLaughlin, 2000), and in the Venice lagoon, Italy, the mats of *Ulva rigida* are as wide as 650 m (Tagliaprietra et al., 1998). But in the Three Bays Area that encompasses 1,251 acres of surface water on the south side of Cape Cod, Mass., the distribution of *U. lactuca* was more extensive than in those areas in July 2003, and it filled every one of its coves with continuous broad mats, and the mats covered wide shallows between the coves. In various estuaries, the mats are not present in the same size mats among years (personal observations).

In the northern hemisphere, sea lettuce usually begins to cover estuarine bottoms in late April and May, and it persists into November but is scarce during the colder months (Sawyer, 1965; Nicholls et al., 1981; Soulsby et al., 1982; Kamermans et al., 1998; Tagliapietra et al., 1998). In winter, sea lettuce is present as buds attached to pebbles and empty shells, such as mud snails, *Ilyanassa obsoleta*, or as thallus fragments partly buried in surficial sediments (Kamermans et al., 1998). In the spring, new thalli grow from both buds and fragments and within a few weeks grow to full size. The earliest stage of a mat is a single layer of thalli, but eventually several free-floating thalli aggregate into layers forming a mat. Layering can be substantial, and the mats are often about 30 cm thick resting loosely on the bottom (Welsh, 1980; Hernández et al., 1997; MacKenzie and McLaughlin, 2000; Brush and Nixon, 2003). The layers are closely packed, and water flows slowly or not at all through the interstices between them. The thalli of mats near the bottom eventually die, become anoxic, black, and produce hydrogen sulfide gas. The rotting material penetrates into the sediment and creates anoxic conditions therein (Nicholls et al., 1981: Krause-Jensen et al., 1999: Brush and Nixon, 2003).

In some small protected coves, large mats of sea lettuce decay in such large volume in the autumn that the sediments remain permanently covered with a mass of black organic material. In the same areas, the decaying sea lettuce produces gasses that have an unpleasant odor and can blacken the oil paint of nearby houses due to the formation of lead sulfide (Wilkinson, 1963; Sawyer, 1965).

The Biological Environment of Estuarine Shallow Zones

The estuaries in the eastern United States that contain little sea lettuce (and this was the status of most before they



Figure 3.—Adult striped killifish, *Fundulus majalis* (female, top; male, bottom), about 10 cm long (TL). From Bigelow and Schroeder, 1953.

became eutrophic) commonly are bordered by marshes shoreward with deeper water offshore. Their broad shallow zones provide habitats for large numbers of macroinvertebrates (arthropods, polychaetes, mollusks, and others) and decapods, including blue crabs, Calli*nectes sapidus*, and shrimp; juvenile and adult killifish and mummichogs, Fundulus spp.; and commercially-important mollusks. The fish may also include Atlantic silversides, Menidia menidia; bay anchovies, Anchoa mitchilli; spot croaker, Leiostomus xanthurus; fourspine sticklebacks, Apeltes quadracus; American eels, Anguilla rostrata; and northern pipefish, Syngnathus fuscus (Subrahmanyam and Drake, 1975; Daiber, 1982; Able and Fahay, 1998; Deegan et al., 2002), and their eggs and larvae (Daiber, 1982). Some shallow zones support meadows of eelgrass, Zostera marina, that comprise their own habitat, and they have a role in stabilizing sediments and shorelines (Belding, 1909; Thayer and Stuart, 1974; Orth, 1977; Fonseca et al., 1982, 1998; Weinstein and Brooks, 1983; Reise, 1985; Sogard and Able, 1991).

In the eastern United States, the killifish and mummichogs (Fig. 3, 4) are the primary transients that move back and forth between the shallows and deeper water with each rise and fall of the tide to feed on the macroinvertebrates (Hettler, 1989; Kneib and Wagner, 1994; MacKenzie and McLaughlin, 2000). The extent that crabs and shrimp may move back and forth similarly is unknown.

Many of the macroinvertebrates feed on filamentous algae, diatoms, and detritus (Daiber, 1982). Striped killifish and mummichogs feed on amphipods and isopods and also the juveniles of several mollusks, including softclams, *Mya arenaria* (Fig. 5); eastern melampus, *Melampus bidentatus*; mud snails; Atlantic slipper snails, *Crepidula fornicata*; and juvenile polychaetes and horseshoe crabs, *Limulus polyphemus* (3 mm). Some sea lettuce, insects, and detritus are also eaten (Vince et al., 1976; Kneib and Stiven, 1978; Daiber 1982; MacKenzie and McLaughlin, 2000). MacKenzie and McLaughlin (2000) observed that killifish guts were about 3/5 full of food items when collected, but the food passes through them quickly: 80% of that passes through in 3 h, and 100% in 24 h. This suggests a high consumption rate. Blue crabs feed mainly on mollusks and also consume some polychaetes (Meise and Stehlik, 2003). The shrimp feed mainly on diatoms, dinoflagellates, and tiny crustaceans, such as copepods (Bello-Olusoji et al., 2005).

In the deeper waters, some adult killifish and mummichogs and the other transient fishes are eaten by such larger fish as striped bass, *Morone saxatilis*; bluefish, *Pomatomus saltatrix*; weakfish, *Cynoscion* spp.; and others (Hildebrand and Schroeder, 1928; Kneib and Stiven, 1978; Collette and Klein-MacPhee, 2002). While the killifish and mummichogs have no commercial importance, except for sale as bait, their tidal movements into the shallow flats and back to the deeper estuarine



Figure 4.—Adult mummichog, *Fundulus heteroclitus*, about 11 cm long (TL). From Bigelow and Schroeder, 1953.



Figure 5.—Softshell clams, *Mya arenaria*, in the gut of a striped killifish, *Fundulus majalis*, from the Navesink River, N.J., July 1994. The softshells when whole were about 10 mm long.

environments comprise a trophic link between the macroinvertebrates and the larger sport and commercial fish in the estuaries (Butner and Brattstrom, 1960; Subrahmanyam and Drake, 1975; Kneib and Stiven, 1978; Weisberg and Lotrich, 1982; Ryer, 1987; McIvor and Odum, 1988; Kneib and Wagner, 1994).

In the eastern United States, the inner edges of the estuarine shallows are also feeding areas for wading birds, particularly great blue herons, Ardea herodias; green herons, Butorides virescens; great egrets, Casmerodius albus; and snowy egrets, Egretta thula. They stalk fishes including killifish and gobies in the shallows (Weise and Smith-Kenneally, 1977). The foods of willets, Catoptrophorus semipalmatus, and clapper rails, Rallus longirostis, consist of aquatic insects, polychaetes, small crabs, mollusks, fish larvae and small fish (Bent, 1929, 1963). Over 80% of the diet of seaside sparrows. Ammodramus maritimus, consists of marine insects, small crabs, and snails. Saltmarsh sharp-tailed sparrows, Ammodramus caudacutus, eat insects, amphipods, and small snails. The birds that feed in the shallows also include grebes (Podicipediformes), various ducks and swans (Anatidae), gulls (Laridae), terns (Sternidae), and belted kingfishers, Ceryle alcyon (Bent et al., 1968).

How Macroalgal Mats Have Degraded Estuaries

The development and spread of the mats of sea lettuce and the other macroalgae have degraded estuarine environments. They have altered water chemistry, nearly eliminated large sections of their shallows as feeding zones of fish, arthropods, and birds (Baird and Milne, 1981; Hull, 1987; Raffaelli and Milne, 1987), and they have overgrown and killed mollusks and eelgrass.

Chemical Alterations

The sea lettuce mats remove some nitrates and phosphates and other nutrients from the water as they grow and metabolize, but when they die and disintegrate each October and November they release them back to the water. This release sustains the highly eutrophic condition of the ecosystem (Naldi and Viaroli, 2002). A series of biochemical effects that are likely to affect entire food webs follows (Perkins and Abbott, 1972; Valiela et al., 1997; Deegan et al., 2002).

Seasonal Effects on Macroinvertebrates

Sea lettuce has reduced the number of macroinvertebrates on the sediment surfaces of estuarine shallows at least threefold in the Venice lagoon, Italy (Tagliapietra et al., 1998; Sfriso et al., 2001), and nearly 100% in Jamaica Bay, New York (Franz and Freidman, 2002). To estimate the effects of U. lactuca mats in the Navesink River, New Jersey, MacKenzie (2000) counted the combined numbers of nematodes, harpacticoid copepods, amethyst gem-clams, Gemma gemma, polychaetes, and eastern mudsnails, Ilyanassa obsoleta, per unit area, in unvegetated sediments next to sea lettuce mats and in sediments under the mats. The unvegetated sediments had an average number of 2.117/area while the matted sediments had 57/area, a 37-fold difference. The negative effects of the mats are further pronounced because their maximum bottom coverage, June through August, coincides with the main time when the larvae of the fauna would settle onto the sediments (Bonsdorff, 1992: Bonsdorff et al., 1995: Norkko and Bonsdorff, 1996).

Tagliapetra et al. (1998) described how the seasonal occurrences of U. *rigida*, affect the infauna in the Venice lagoon, Italy. In May and June, the sea lettuce grows over and kills nearly all the invertebrates and their numbers remain low for 9-10 months from June into February and March. The sea lettuce dies in the fall, decomposes, and enriches the bottom sediments with organic matter. During the following spring, juvenile invertebrates settle and then survive and grow well. The subsequent mats of sea lettuce grow over them and the annual cycle is repeated. A patchy distribution of sea lettuce mats produces discrete patterns of infaunal distribution in the Venice lagoon and elsewhere (Everett, 1991; Sfriso et al., 2001).

Overgrowth of Clams

The macroalgal mats have overgrown and killed clams. Breber (1985) found that mats of Ulva rigida and Gracilaria spp. kill carpet-shell clams, Tapes decussatus, in Italy. Thiel et al. (1998) observed that overgrowths of Enteromorpha prolifera kill softshell clams in Maine. MacKenzie and McLaughlin (2000) reported that overgrowths of U. lactuca killed softshell clams in New Jersey; initially, the clams emerged from the sediment, then laid on the bottom, and ultimately died (Fig. 6). In addition, Everett (1994) observed that bent-nose macomas. Macoma nasuta. were more abundant in areas devoid

of *Ulva expansa* than in areas where it formed mats in California.

Degraded Feeding Habitats of Wading Birds

Wading birds normally feed at the edges of marshes at low tide but not where sea lettuce is abundant. Nicholls et al. (1981) and Jones and Pinn (2006) observed that wading birds avoid algal mats, probably because their prey is not available.

Overgrowth of Eelgrass

In some estuaries, the algal mats have also overgrown and killed eelgrass and other seagrasses (Valiela et al., 1992). The extent of this is not precisely known, but Hauxwell et al. (2001) conclude that eelgrass losses from this overgrowth may be quite large worldwide.



Figure 6.—Mass of dead softshell clams, *Mya arenaria*, in the Navesink River, N.J., August 1994. The clams were smothered by an overgrowth of sea lettuce, *Ulva lactuca*, emerged from the bottom sediments, and died. Most softshells are 40–45 mm long.

Faunal Species That Sea Lettuce Mats Benefit

Relatively small mats of sea lettuce may be beneficial in estuaries, because their edges can be focal points for fishes and crustaceans, and they provide refuges from predators (Heck and Thoman, 1984; Wilson et al., 1990; Ferrell and Bell, 1991; Kneib and Wagner, 1994; Timmons, 1995). In the Navesink River, New Jersey, large age-0 winter flounder are strongly associated with small habitats vegetated with U. lactuca, and young-of-the-year oyster toadfish, Opsanus tau, can use sea lettuce as a habitat (Stoner et al., 2001). Fish in small sea lettuce mats had lower mortality than they did when over bare sand and lower mortality in eelgrass meadows than in sea lettuce meadows. Prey vulnerability appeared to be related to the role of vision in the predators' attack strategy and prey activity levels (Manderson et al., 2000).

In the Little Egg Harbor–Great Bay estuary in southern New Jersey, Sogard and Able (1991) found that small mats of sea lettuce harbored more fish and decapods than the adjacent unvegetated habitats. Sea lettuce was an important habitat in areas that lacked eelgrass, but for the decapods the eelgrass and sea lettuce provided habitats of equal quality.

The primary foods of brant, *Branta bernicla*, a type of North American goose, have been known to be eelgrass, widgeon grass, *Ruppia maritima*, and sea lettuce. But since the eelgrass meadows have become scarce, first noted during the 1930's, the brant have eaten mainly sea lettuce (Trippensee, 1953; Burger, 1996).

Controlling Mats of Ulva spp.

The best way to reduce eutrophication and its negative effects is to control it at its source by reducing the quantities of nutrients, especially nitrates, that enter estuaries. In lieu of that, manual removal of algal mats can be an alternative means to help return the estuaries to their pre-eutrophic condition, although another harmful effect of eutrophication, the presence of dense phytoplankton blooms, would remain.

In 1994, my experience with removing sea lettuce from a shoreline flat in a sheltered area in the Navesink River, New Jersey, showed that two removals were sufficient to maintain the flat nearly free of it. Each time the sea lettuce was removed, the mat was only one thallus thick, and consequently the quantity handled was relatively small.

The test area was located along the edge of a cordgrass, Spartina alterniflora, marsh. The test area measured 20 m long and 20 m wide. The water depth at low tide was 0.1 m along its inner edge and 1 m deep along its outer edge. The thalli had begun to grow in late April and by early June they had nearly covered the bottom with a single floating layer. The sea lettuce was removed then with an 18 m minnow seine, which extended from the water surface to the bottom. Scattered pieces of thalli remained, but nearly the entire benthic habitat was free of this layer of sea lettuce. The thalli pieces began to grow, and by early September the test area again was covered with a single layer of thalli. The area was cleared of the sea lettuce again with the same minnow seine at that time. The remaining pieces of thalli began to grow again, but they did not cover the area in a single layer before they began to disintegrate and decompose in the autumn. Space was available consistently for fish, crabs, and birds to feed in the test area.

A floating machine, like those used in freshwater lakes to control aquatic weeds, might be effective in controlling algal mats in large areas. The machines collect grasses with whirling rakes around a spoke. They have a shallow draft, they are propelled by paddlewheels, and they deliver grasses to beaches. Trucks can haul them to composting facilities (Lockwood, 2002). In small areas, haul seines and even hand rakes can be used to remove sea lettuce (Town of Harwich, Mass.¹). Mazé et al. (1993) recommends that collections of sea lettuce should be composted with a small quantity of lingocellulose substrate to stabilize them. Otherwise, storage of non-composted sea lettuce results in objectionable odors and the release of some liquid. The composted product can be used as fertilizer. If sea lettuce is left piled on shores, some nitrogen will escape to the air and some will leach back into the water. Such piled sea lettuce attracts flies.

Conclusion

Many studies have demonstrated that the prolific growths of macroalgae, especially sea lettuce, have degraded the environments of estuaries. Removal of the macroalgae would help to restore the shallow habitats to their former condition. The macroinvertebrates would become abundant, the feeding grounds of fish, arthropods, and birds would be restored, more clams would survive, some eelgrass meadows might return, and likely more small fish and perhaps arthropods would become available as food for larger fish in the deeper waters. Moreover, some excess nitrate and phosphate would be removed from the estuaries. The actions to remove sea lettuce from the shallows would not remove all the thalli, and there likely would be some remaining for the various fauna to use as cover and food. Brant are not present in many locations where sea lettuce occurs, and, where they are present, they appear to consume only a moderate amount of the available sea lettuce. Brant might be only lightly affected if the sea lettuce was partly removed from the few areas where they congregate and feed. The overall benefits of removing most of the macroalgae would seem to far outweigh any of the potential small negative effects.

Acknowledgments

I thank D. Schwinn and Three Bays Preservation, Inc., Osterville, Mass., for helping me survey the sea lettuce coverage and describing how it degraded the Three Bays Area, Cape Cod, Mass., and R. N. Reid, A. Riportella, and L. L. Stehlik for constructive comments on earlier drafts of the manuscript.

¹Town of Harwich, Mass., Nat. Resourc. Dep. 2004. Harwich Sea Lettuce Control Project. Conservation Commission Approval (negative determination)Tuesday,12Jan.1998.Availableon-line at: http://www.vsa.cape.com/harharb/sealet tucecontrol.html. Site assessed and printed 1 June 2004.

Literature Cited

- Able K. W., and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers Univ. Press, New Brunswick, N.J., 342 p.
- Anéer G. 1987. High natural mortality of Baltic herring (*Clupea harengus*) eggs caused by algal exudates? Mar. Biol. 94:163–169.
- Baird, D., and H. Milne. 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. Estuarine Coastal Shelf Sci. 13(4):455–474.
- Belding, D. L. 1909. A report upon the mollusk fisheries of Massachusetts. Wright and Potter Printing Co., State Printers, 18 Post Office Square, Boston, 243 p.
- Bello-Olusoji, O. A., M. O. Afunmiso, and Y. M. Bankole. 2005. Some aspects of the feeding habits of commercially important Penaeids from part of FAO fishing zone 34. J. Anim. Vet. Adv. 4(10) 818–824.
- Bent, A. C. 1929. Life histories of North American shore birds. U.S. Natl. Mus. Bull. 146, 412 p.
- . 1963. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 235, 392 p.
- ______ and collaborators. Compiled and edited by O. L. Austin, Jr. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237, 1,889 p.
- U.S. Natl. Mus. Bull. 237, 1,889 p. Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish. Wildl. Serv., Vol. 53, 577 p.
- Bonsdorff, E. 1992. Drifting algae and zoobenthos-effects on settling and community structure. Neth. J. Sea Res. 30:57–62.
- , E., A. Norkko, and A. Bostrom C. 1995. Recruitment and population maintenance of the bivalve *Macoma balthica* (L.)-factors affecting settling success and early survival on shallow sandy bottoms. *In* Proceedings 28th European Marine Biology Symposium, p. 253–260. Olsen and Olsen, Fredensborg.
- Breber, P. 1985. On growing of the carpet-shell clam (*Tapes decussates* (L.)): two years of experience in Venice Lagoon. Aquaculture 44:51–56.
- Brush, M. J., and S. W. Nixon. 2003. Biomass layering and metabolism in mats of the macroalga *Ulva lactuca* L. Estuaries 26(4A):916– 926.
- Burger, J. 1996. A naturalist along the Jersey shore. Rutgers Univ. Press. New Brunswick, N.J., 304 p.
- Butner, A., and B. H. Brattstrom. 1960. Local movements in Menidia and Fundulus. Copeia. p. 139–141
- Buttermore, R. E. 1977. Eutrophication of an impounded estuarine lagoon. Mar. Poll. Bull. 8:13–15.
- Collette, B. B., and G. Klein-MacPhee (Editors). 2002. Bigelow and Schroeder's Fishes of the Gulf of Maine. 3rd Edition. Smithson. Inst. Press, Wash., D.C., 748 p. Cummins, S. P., D. E. Roberts, and K. D. Zim-
- Cummins, S. P., D. E. Roberts, and K. D. Zimmerman. 2004. Effects of the green *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Mar. Ecol. Prog. Ser. 266:77–87.
- Daiber, F. C. 1982. Animals of the tidal marsh. Van Nostrand Reinhold Co. N.Y., 422 p.
- Deegan, L. A., A. Wright, S. G. Ayvazian, J. T. Finn, H. Golden, R. R. Merson, and J. Harrison. 2002. Nitrogen loading alters seagrass

ecosystem structure and support of higher trophic levels. Aquat. Conserv. Mar. Freshw. Ecosystems 12(2):193–212.

- De Jonge, V. N., M. Elliot, and E. Orive. 2002. Causes, historical development, effects and future challenges of a common environmental problem: eutrophication. Hydrobiologia 475–476:1–19.
- Everett, R. A. 1991. Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. J. Exp. Mar. Biol. Ecol. 150:223–247.

. 1994. Macroalgae in soft-sediment communities: effects on benthic faunal assemblages. J. Exp. Mar. Biol. Ecol. 175:253–274.

- Ferrell, D. J., and J. D. Bell. 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bar sand over a large spacial scale. Mar. Ecol. Prog. Ser. 72:15–24.
- Fonseca, M. S., W. J. Kentworthy, and G. W. Thayer. 1982. A low cost transplanting procedure for sediment stabilization and habitat development using eelgrass (*Zostera marina*). Wetlands 2:138–151.
- , ____, and _____. 1998. Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. U.S. Dep. Commer., NOAA Coast. Ocean Off., Silver Spring, Md., 222 p.
- Franz, D. R., and I. Friedman. 2002. Effects of a macroalgal mat (*Ulva lactuca*) on estuarine sand flat copepods: an experimental study. J. Exp. Mar. Biol. Ecol. 271(2):209–226.
- Fritsch, F. E. 1956. The structure and reproduction of the algae. Camb. Univ. Press., N.Y., 791 p.
- Harder, T., S. Dobretsov, and P.-Y. Qian. 2004.
 Waterbourne polar macromolecules act as algal antifoulants in the seaweed *Ulva reticulate*. Mar. Ecol. Prog. Ser. 274:133–141.
 Hartog, C. den. 1994. Suffocation of a littoral
- Hartog, C. den. 1994. Suffocation of a littoral Zostera bed by Enteromorpha radiata. Aquat. Bot. 47:21–28.
- Hauxwell J., J. Cebrian, C. Furlong, and I. Valelia. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuaries. Ecology 82:1007–1022.
- Heck, K. L., Jr., and T. A. Thoman. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7:70–92.
- Hernández, I., G. Peralta, J. L. Pérez-Lloréns, J. J. Vergara, and F. X. Niell. 1997. Biomass and dynamics of growth of *Ulva* species in Palmones River estuary. J. Phycol. 33:764–772.
- Hettler, W. F., Jr. 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. Mar. Ecol. Prog. Ser. 56:111–118.
- Hildebrand, S. H., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay (repr. 1972). Smithson. Instit. Press, Wash., D.C., 388 p.
- Hull, S. C. 1987. Macroalgal mats and species abundance: a field experiment. Estuarine Coastal Shelf Sci. 25:519–532.
- Isaksson, I., L. Pihl, and J. van Montfrans. 1994. Eutrophication-related changes in macrovegetation and foraging of young cod (*Gadus morhua* L.): a mesocosm experiment. J. Exp. Biol. Ecol. 177:203–217.
- Johnson D. A., and B. L. Welsh. 1985. Detrimental effects of *Ulva lactuca* (L.) exudates and low oxygen on estuarine crab larvae. J. Exp. Mar. Biol. Ecol. 86:73–83.
- Jones, M. and E. Pinn. 2006. The impact of a macroalgal mat on benthic diversity in Poole Harbor. Mar. Pollut. Bull. 53:63–71.

- Kamermans, P., E.-J. Malta, J. M. Versschuure, L. F. Lentz, and L. Schrijvers. 1998. Role of cold resistance and burial for winter survival and spring initiation of an *Ulva* spp. (Chlorophyta) bloom in a eutrophic lagoon (Veerse Meer lagoon, The Netherlands). Mar. Biol. 131:45–51
- Kneib, R. T., and A. E. Stiven. 1978. Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31:121–140.
- and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats of different stages of tidal inundation. Mar. Ecol. Prog. Ser. 106:227–38.
- Krause-Jensen, D., P. B. Christensen, and S. Rysgaard. 1999. Oxygen and nutrient dynamics within mats of the filamentous macroalga Chaetomorpha linum. Estuaries 22:31–38.
- Lavery, P. S., R. J. Lukatelich, and A. J. McComb. 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuarine Coast. Gulf Sci. 33:1–22.
- Lee, T. F. 1977. The seaweed handbook. Mariners Press, Boston, 217 p.
- Littler, M. M., and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Nat. 116:25–44.
- Lockwood, J. 2002. Boats will slash excessive seaweeds. The Star-Ledger (Newark, New Jersey, newspaper). May 22, p. 23 and 27.
- MacKenzie, C. L., Jr. 2000. The abundances of small invertebrates in relation to sea lettuce, *Ulva lactuca*, mats. Bull. N.J. Acad. Sci. 45(1):13–17.
- and S. McLaughlin. 2000. Life history and habitat observations of softshell clams *Mya arenaria* in northeastern New Jersey. J. Shellfish Res. 19(1):35–41.
- Magré, E. J. 1974. Ulva lactuca L. negatively affects Balanus balanoides (L.)(Cirripedia Thoracica) in tidepools. Crustaceana 27:231– 234.
- Manderson, J. P., B. A. Phelan, A. W. Stoner, and J. Hilbert. 2000. Predator-prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251:17–39.
- Mazé, J., P. Morand, and P. Potoky. 1993. Stabilization of 'green tides' by a method of composting with a view to pollution limitation. J. Appl. Phycol. 5:183–190.
- McIvor, C. C., and W. E. Odum. 1988. Food, predation risk and microhabitat selection in a marsh fish assemblage. Ecology 69:1341– 1351.
- Meise, C. J., and L. L. Stehlik. 2003. Habitat use, temporal abundance variability, and diet of blue crabs from a New Jersey estuary. Estuaries 26(3):731–745.
- Montgomery, H. A. C., and P. G. Soulsby. 1980. Effects of eutrophication in the intertidal ecology of Lanfstone Harbour, UK, and proposed control measures. Prog. Water Technol. 13:287–294.
- Naldi, M., and P. Viaroli. 2002. Nitrate uptake and storage in the seaweed Ulva rigida C. Agardh in relation to nitrate availability and thallus nitrate content in a eutrophic coastal lagoon (Sacca di Goro, Po River Delta, Italy). J. Exp. Mar. Biol. Ecol. 269:65–83.

- Nicholls, D. J., C. R. Tubbs, and F. N. Haynes. 1981. The effect of green algal mats on intertidal macrobenthic communities and their predators. Kiel. Meeresforsch. 5:511–520.
- Norkko, A., and E. Bonsdorff. 1996. Rapid zoobenthic community responses to accumulations of drifting algae. Mar. Ecol. Prog. Ser. 131:143–157.
- Olafsson, E. B. 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. Mar. Biol. 97:571–574.
- Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. Mar. Biol. 44:187–194.
- Österling, M., and L. Pihl. 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. J. Exp. Mar. Biol. Ecol. 263:159–183.
- Pederse, M. F., and J. Borum. 1997. Nutrient control of estuarine macroalgae: growth strategy and future challenges of a common environmental problem: eutrophication. Hydrobiologia 475–476:1–19.
- Perkins, E. J., and O. J. Abbott. 1972. Nutrient enrichment and sand flat fauna. Mar. Pollut. Bull. 3:70–72.
- Peterson, G. W., and R. E. Turner. 1994. The value of salt marsh edge vs. interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17(1B):235–262.
- Pirou, J. Y., A. Menesguen, and J. C. Salomon. 1991. Green tides (green algae) due to Ulva sp.: necessary conditions of appearance, evolution and site comparisons. In M. Elliott and J. P. Ducrotoy (Editors), Estuaries and coasts: spatial and temporal intercomparisons, 19. ECSA Symposium, Estuarine and Coastal Sciences Association, Caen, France, 4–8 September 1989.
- Raffaelli, D. G. 2000. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. Helgol. Mar. Res. 54:71–79.
- and H. Milne. 1987. An experimental investigation of the effect of shorebird and flatfish predation on estuarine invertebrates. Estuarine Coast. Shelf Sci. 27:1–13.
- _____, J. A. Raven, and L. J. Poole. 1998. Ecological impact of green macroalgal blooms. Oceanogr. Mar. Bot.: Annual Rev. 36:97–125.
- Reise, K. 1985. Tidal flat ecology an experimental approach to species interactions. Springer-Verlag, N.Y., 191 p.
- Verlag, N.Y., 191 p. Rosenberg, R. 1985. Eutrophication-the future marine coastal nuisance? Mar. Pollut. Bull. 16:227–231.

- Ryer, C. H. 1987. Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in a tidalmarsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. Estuaries 10(2):136–140.
- Sawyer, C. H. 1965. The sea lettuce problem in Boston Harbor. J. Water Pollut. Control Fed. Aug., p. 1,122–1,133.
- Short, T. S., and D. M. Burdick. 1996. Quantifying edgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. Estuaries 19:730–739.
- _____, ____, and J. E. Klady, III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnol. Oceanogr. 40:740–749.
- Sfriso, A. T., T. Birkmeyer, and P. F. Ghetti. 2001. Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds. Mar. Environ. Res. 52:323–349.
- Smith, G. M. 1955. Cryptogamic botany. Volume I: algae and fungi, 2nd ed. McGraw-Hill Book Co., N.Y., 546 p.
- Sogard, S., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuarine Coast. Shelf Sci. 33:501–519.
- Soulsby, P. G., D. Lowthion, and M. Houston. 1978. Observations on the effects of sewage discharged into a tidal Harbour. Mar. Pollut. Bull. 9:242–245.
- _____, ____, and _____. 1982. Effects of macroalgal mats on the ecology of intertidal mudflats. Mar. Pollut. Bull. 13(5):162–166.
- Stoner, A. W., J. P. Manderson, and J. P. Pessutti. 2001. Spatially-explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. Mar. Biol. Prog. Ser. 213:252–271.
- Subrahmanyam, C. B, and S. H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes. Bull. Mar. Sci. 25(4):445–465.
- Tagliapietra, D., M. Pavan, and C. Wagner. 1998. Macrobenthic community changes related to eutrophication in *Palude della Rosa* (Venetian Lagoon, Italy). Estuarine Coast. Shelf Sci. 47:217–226.
- Taylor, W. R. 1957. Marine algae of the northeastern coast of North America. Univ. Mich. Press, Ann Arbor, 509 p.
- Thayer, G. W., and H. H. Stuart. 1974. The bay scallop makes its bed of seagrass. Mar. Fish. Rev. 36(7):27–30.
- Thiel, M. L., L. M. Stearns, and L. Watling. 1998. Effects of green algal mats on bivalves

in a New England mud flat. Helgol. Meeresunters 52:15–28.

- Timmons, M. 1995. Relationships between macroalgae and juvenile fishes in the inland bays of Delaware. Ph.D. thesis, Univ. Del., Newark
- Trippensee, R. E. 1953. Wildlife management. Fur bearers, waterfowl, and fish, Vol. 2. McGraw-Hill Book Co., Inc., N.Y., 572 p.
- Tseng, C. K. 1983. Common seaweeds of China. Science Press, Beijing, China, 216 p.
- Valiela I., K. Foreman, M. LaMontagne, D. Hersh, J. Costa, P. Pekol, B. DeMeo-Andreson, C. D'Avanzo, M. Babione, C.-H. Sham, J. Brawley, and K. Lajtha. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15(4):443–457.
- , J. McClelland, P. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42(5), Part 2:1,105–1,118.
- Vasserot, J. 1990. Perspectives of biological control of harmful proliferations of multicellular seaweeds: 1. Possibilities for control and use by grazing animals of "green tides" formed by Ulva. J. Rech. Oceanogr. 15(1–2):34–37.
- Vince, S., I. E. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the salt mash killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23:255–266.
- Weinstein, M. P., and H. A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12:15–27.
- Weisberg, S. B., and V. A. Lotrich. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: an experimental approach. Mar. Biol. 66:307–310.
- Weise, J. H., and T. Smith-Kenneally. 1977. A heron colony called Pea Patch. Del. Conserv. 21(2):8–15.
- Welsh, B. L. 1980. Comparative nutrient dynamics of a marsh-mudflat ecosystem. Estuarine Coast. Mar. Sci. 10:143–164.
- Wilkinson, L. 1963. Nitrogen transformations in a polluted estuary. Air Water Pollut. 7:737– 752.
- Wilson, K. A., K. W. Able, and K. L. Heck, Jr. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Mar. Ecol. Prog. Ser. 58:243–251.