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Biofiltration, water quality, and sediment processes

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Historical oyster populations in places such as Chesapeake Bay used to be able to filter algae and other particles from the water, thus regulating water quality (Fig. 220). Excess nutrient inputs and declines of oyster biofiltration have led to more turbid water, reducing the growth of benthic microalgae and affecting the exchange of nutrients between sediments and the overlying water. Oyster densities and bottom shear velocities were manipulated in mesocosm experiments to investigate their effects on benthic microalgae, nutrient regeneration from sediments, and overall water quality in the ecosystem. The mesocosm results demonstrate that biofiltration removes particles from the water

column, allowing light to reach the bottom, and stimulating benthic microalgal growth, which in turn stabilizes sediments and decreases nutrient release into the water column. Realistic shear velocities have the potential to erode these benthic microalgae; however, exerting an additional physical control on benthic biogeochemical exchanges. Even considering this physical limitation, the results indicate that management efforts to increase biofiltration (e.g., oyster restoration) will have multiple, synergistic positive ecosystem outcomes.

Problem description

Over the past half-century, water quality and transparency have declined in many eutrophic

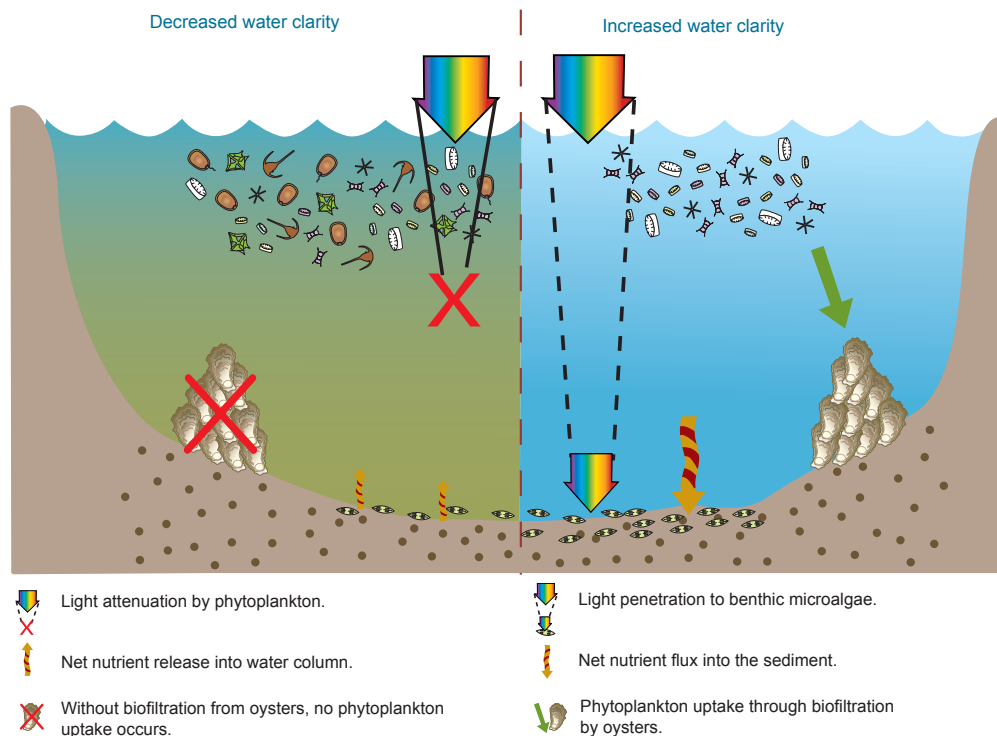


Figure 220: Healthy oyster populations can improve water quality and clarity.

estuaries. One such estuary, Chesapeake Bay, has also experienced a concurrent decline in abundance of the eastern oyster *Crassostrea virginica* which formerly supported a productive fishery. Management authorities in Chesapeake Bay and elsewhere have recommended that water quality conditions and fishery harvest could both be improved by restoring biomass of the eastern oyster to a modest fraction of historical levels.⁵⁷ In shallow-water environments, benthic and pelagic processes are closely coupled and water flow can regulate the supply of seston to bivalves. In addition, such flow may regulate water clarity and benthic-pelagic nutrient fluxes through mixing and resuspension of bottom sediments. Until recently, the complex interactions between oysters, nutrients, water clarity, and physical circulation were poorly understood.

MEERC researchers designed a series of studies using experimental mesocosms (Fig. 221) to quantify how the combined effect of oysters and increased bottom shear velocity directly or indirectly affect ecosystem processes and shift ecosystem function between the water column and sediments.^{58,59} Oysters and bottom shear velocity were used to examine effects on the following factors:

- Phytoplankton abundance in mesocosm experiments;
- Nutrient transformations and nutrient regeneration from the sediments;
- Overall water quality in whole-ecosystem experiments.

To address these questions, the interacting effects of juvenile oysters and bottom shear velocity on phytoplankton biomass and on nutrient regeneration in a series of three (spring, summer, fall) 4-week long mesocosm experiments were studied under different levels of bottom shear.^{58,59} The mesocosms were 1-m deep, had a 1 m² sediment surface area, contained 1000 L of water, and received the same water-column mixing designed to simulate conditions in nature (turbulence intensity 1 cm s⁻¹).^{58,59} A parallel set of smaller (0.1 m³) experimental systems was used for comparative studies.⁵⁸ Experimental systems included a

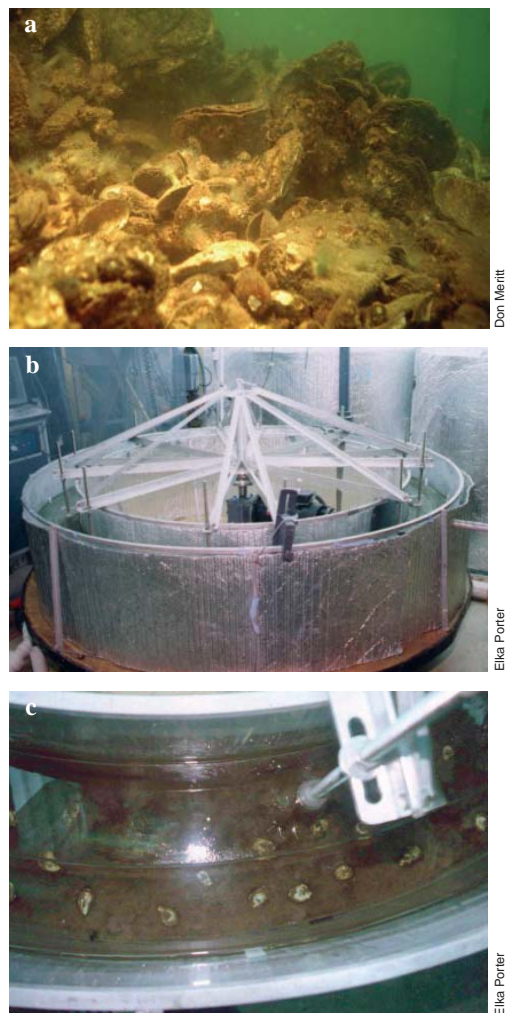


Figure 221: Experiments were performed to investigate how oyster populations in interaction with low and moderate bottom shear affect water quality. a) Healthy oysters can improve water clarity through biofiltration. b) A large linked mesocosm with an annular flume was designed and an experiment conducted to study the interaction of water flow and oysters on water quality. c) Oysters were placed in the annular flume and water column mixing and bottom shear scaled in comparative systems.

multi-component mesocosm with moderate bottom shear velocity (0.6 cm s⁻¹) and two standard cylindrical tanks with an unrealistically low bottom shear velocity (0.1 cm s⁻¹, Fig. 221

51. EPA 2000, 52. Porter et al. 2004a, 53. Porter et al. 2004b

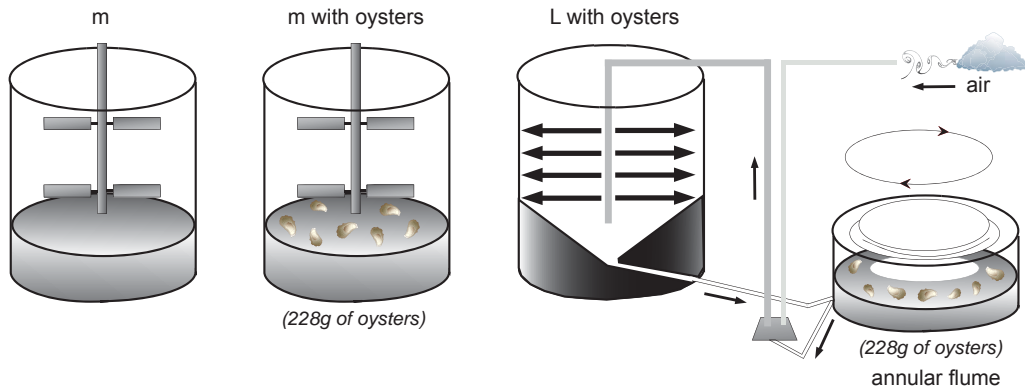


Figure 222: Experimental ecosystems with and without oysters and low and moderate bottom shear. All mesocosms were 1 m deep and contained 1000 L of water (the linked mesocosms together contained 1000 L). Two mesocosms and the annular flume had 1 m² of sediment surface area. m: mesocosm with low bottom shear and without oysters; m and oysters: mesocosm with low bottom shear and with oysters; L with oysters: linked mesocosm and annular flume with moderate bottom shear and with oysters.⁶⁰ Additional experiments were conducted using a similar system of mesocosms with and without realistic benthic boundary layer shear, but with water column volumes of 100 L.^{60,61}

and Fig. 222). Experiments were run with and without juvenile oysters, using oyster densities similar to oyster abundances in historic times (19th century) in Chesapeake Bay.⁶⁰

Research findings

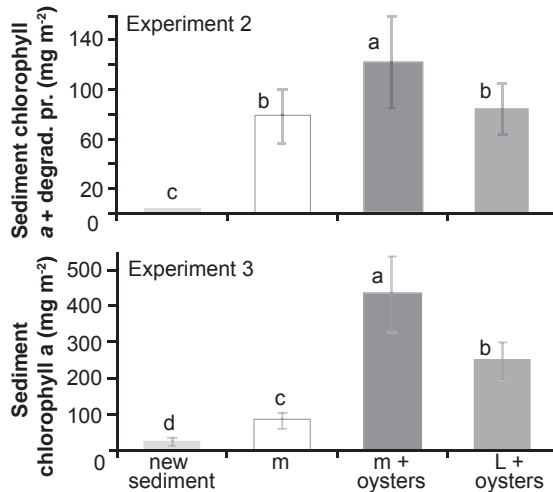
It was found that direct and indirect interactions between oysters and moderate bottom shear velocity affected phytoplankton biomass, light availability in the water column and at the

sediment bottom, microphytobenthos biomass, and nutrient regeneration from the sediments to the water column. Oyster feeding significantly decreased phytoplankton biomass. The isolated tank without oysters repeatedly developed a phytoplankton bloom while the mesocosms with oysters did not. The oyster-mediated decrease in phytoplankton biomass also consistently led to enhanced light penetration through the water column to the sediments.⁶¹



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Figure 223: Dense layers of oxygen bubbles formed from a benthic algal mat (top panel). In mesocosm experiments with moderate bottom shear these bubbles increase erosion of the microphytobenthos mat. Sediment chlorophyll a concentrations as indicator of microphytobenthos biomass at the end of experiments 2 and 3 (right panel). Different letters indicate statistically significant differences between treatments. Treatments m+oysters and L+ oysters had the same biofiltration (i.e. increased light levels at the sediment water interface); however, a shear velocity of 0.6 cm s⁻¹ eroded microphytobenthos.⁶¹



60. Newell 1988, 61. Porter et al. 2004a and Porter et al. 2004b

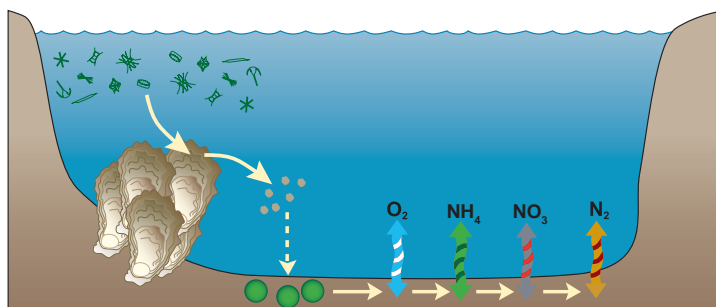


Figure 224: After consuming phytoplankton, oysters release biodeposits. These biodeposits begin the process of nutrient cycling in sediments. Benthic microalgae consume the biodeposits and coupled nitrification-denitrification takes place. This cycling was mimicked in mesocosm experiments (see Fig. 225).

Light availability at the bottom enhanced benthic microalgal biomass (Fig. 223), thereby reinforcing feedback effects to retard sediment-water fluxes of nutrients. There was a significant increase in the daily sediment uptake of dissolved inorganic nitrogen with increasing sediment chlorophyll *a* abundance. Thus benthic microalgae significantly reduced the overall amount of regenerated nitrogen that was returned to the water column. The daily nitrogen release to the water column was lowest in the system with oysters and low bottom shear (m with oysters, Fig. 222) which generated the highest microphytobenthos biomass.

In these experiments⁶²⁻⁶⁴, well-developed benthic microalgal communities often formed cohesive microphytobenthos mats (Fig. 223), and microphytobenthos has been known to stabilize sediments.⁶⁴

However, toward the end of these 4-week long experiments, bubble formation within these mature benthic algal mats tended to increase their buoyancy and benthic friction (roughness), thereby making them more susceptible to erosion by bottom shear. Consequently, experiments in systems with moderate bottom shear velocity (0.6 cm s^{-1}) exhibited substantial erosion of benthic microalgae (Fig. 223), which resulted in higher benthic nutrient recycling, despite increased light availability due to oyster feeding.⁶⁴ The sediments in the experiments described above were fine-grain (mud). These studies emphasize the importance of considering both benthic feeding and bottom shear on water quality.

Subsequent independent benthic chamber

experiments demonstrated that the addition of particulate organic matter to simulate oyster biodeposits (Fig. 224) also significantly altered sediment nutrient cycling processes.⁶⁵ Experimental bio-deposition of organic matter simulating oyster processes led to small increases in ammonium recycling from sediments to overlying water (Fig. 225). However, rates of denitrification were greatly stimulated by bio-deposition, resulting in a large net removal of available nitrogen from the water column (Fig. 225). In estuaries such as Chesapeake Bay, this effect might ultimately lead to further reductions in phytoplankton biomass because of nitrogen limitation of cell growth.

Management implications

Results of these studies indicate that filter-feeding bivalves, in conjunction with water flow and bottom shear, can affect pelagic-benthic processes through a range of complex interactions. Bivalve filtration causes decreased phytoplankton biomass and increased water clarity. Clearer water promotes growth of benthic microalgae that tend to cap nutrient recycling fluxes from sediments to overlying water. Reduced benthic nutrient recycling further retards growth of phytoplankton. Bio-deposition of organic matter from oyster filtration increases nutrient delivery to the sediments but also enhances bacterial removal of fixed nitrogen through denitrification. These processes further reduce nutrient availability for sustaining phytoplankton growth. Benthic microalgal communities excrete mucus that tends to bind

62. Porter et al. 2004b, 63. Porter 1999, 64. Madsen et al. 1993, 65. Newell et al. 2002

sediment particles together, making them less susceptible to resuspension and therefore helping to maintain clearer water.

Under some conditions benthic microalgae form mats that become buoyant when bubbles of photosynthetically produced oxygen become trapped in the algal matrix. The erodability of bottom sediments will thus depend both on bottom shear velocities and on the nature of the benthic microalgal community. Bottom shear in Chesapeake Bay is higher (1.0-1.4 m s⁻¹) than the moderate bottom shear (0.6 m s⁻¹) used in this mesocosm experiment, which likely causes additional erosion of benthic microalgae.

Experiments and models designed to aid in prediction of the effects of bivalve suspensions-feeders and water flow on ecosystems must include realistic physical conditions. Data used in models must come from experiments

that consider direct and indirect effects of interactions between biological and physical components of the ecosystem. Controlled mesocosm experiments that vary physical variables like bottom shear and sediment type and biological variables like bivalve species and density are needed to further resolve the complex interactive effects of bivalves and water flow on benthic-pelagic coupling and on overall water quality. Specifically, MEERC researchers suggest the need for (1) designing a new generation of mesocosms with realistic water-column turbulence levels and high bottom shear stress, (2) conducting comparative ecosystem studies with tidal or episodic sediment resuspension and additional benthic species, and (3) considering effects of sediment type and age of benthic microalgal community on overall benthic-pelagic dynamics.

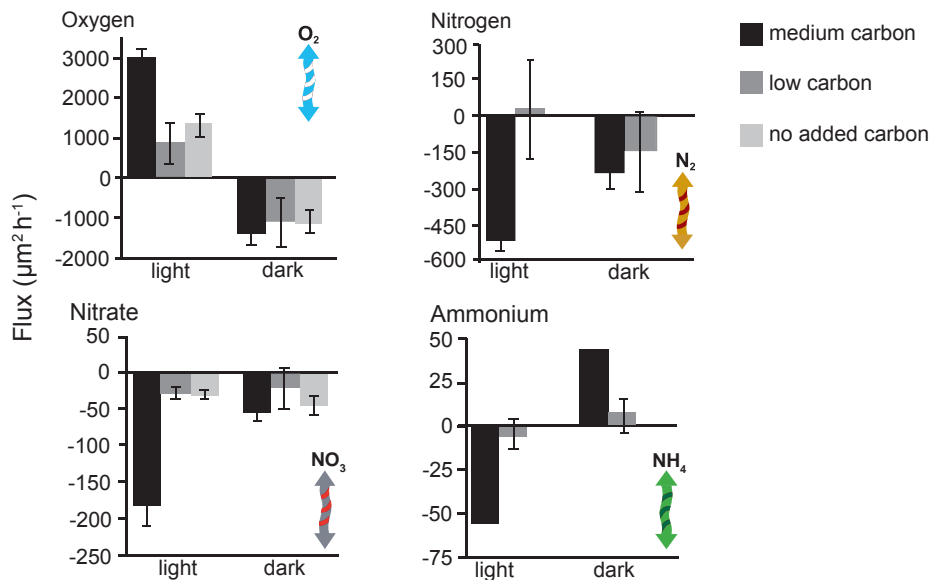


Figure 225: Light:dark experiment. Fluxes of oxygen, nitrogen gas, nitrate, and ammonium 17 days after addition of medium, low, and zero amounts of particulate organic matter. “Carbon” were added to benthic chambers. The bars indicate the means ± standard deviations). As indicated on the x-axis, sediment fluxes on the cores were determined in the light and in the dark. Positive values indicate a flux out of the sediment to the overlying water; negative values indicate flux into the sediment. Control cores only containing water to check for water column processes exhibited minor nitrogen and ammonium fluxes that do not show at the scale of these figures.

References

- Anderson, D.A., P.M. Glibert, and J.M. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25:562-584.
- Ashley, J.F.A. 1998. Habitat use and trophic status as determinants of hydrophobic organic contaminant bioaccumulation within shallow systems. Ph.D. Dissertation, University of Maryland, College Park, 318 pp.
- Bartleson, R. D., W. M. Kemp, and J. C. Stevenson. 2005. Use of a simulation model to examine effects of nutrient loading and grazing on *Potamogeton perfoliatus* L. communities in microcosms. *Ecol. Model.* 185: 483-512.
- Berg, G.M., P.M. Glibert, and C.C. Chen. 1999. Dimension effects of enclosures on ecological processes in pelagic systems. *Limnol. Oceanogr.* 44: 1331-1340.
- Berg, G.M., P.M. Glibert, M.W. Lomas, and M. Burford. 1997. Organic nitrogen uptake and growth by the Chrysophyte *Aureococcus anophagefferens* during a brown tide event. *Mar. Biol.* 129: 377-387
- Bergeron, C.M. 2005. The impact of sediment resuspension on mercury cycling and the bioaccumulation of methylmercury into benthic and pelagic organisms. M.S. Thesis, University of Maryland, College Park, 108 pp.
- Berman, T. and D.A. Bronk. 2003. Dissolved organic nitrogen: a dynamic participant in aquatic ecosystems. *Aq. Microb. Ecol.* 31: 279-305.
- Bianchi, T.S. 2007. *Biogeochemistry of Estuaries*. Oxford University Press, New York, 706 pp.
- Borum, J. 1985. Development of epiphytic communities on eelgrass (*Zostera marina* L.) along a nutrient gradient in a Danish estuary. *Mar. Biol.* 87: 211-218.
- Bricker, S., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks, and J. Woerner. 2007. Effects of Nutrient Enrichment in the Nation's Estuaries: A decade of change. NOAA Coastal Ocean Program Decision Analysis Series No. 26. National Centers for Coastal Ocean Science, Silver Spring, MD. 322pp.
- Brooks, M. T. 2004. Trophic complexity, transfer efficiency and microbial interactions in pelagic ecosystems: A modeling study. MS Thesis, Univ. of Maryland, College Park.
- Bromilow, R.H., R.F. de Carvalho, A.A. Evans, and P.H. Nicholls. 2006. Behavior of Pesticides in Sediment/Water Systems in Outdoor Mesocosms. *Journal of Environmental Science and Health Part B*, 41:1-16.
- Caddy, J.F. 1993. Towards a comparative evaluation of human impact on fishery ecosystems of enclosed and semi-enclosed seas. *Rev Fish Sci* 1: 57-95
- Cerco, C. and K. Moore. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. *Estuaries*. 24: 522-534.
- Cosper, E.M., W.C. Dennison, E.J. Carpenter, V. M. Bricelj, J.G. Mitchell, S.H. Kuenstner, D. Colflesh, and M. Dewey. 1987. Recurrent and Persistent Brown Tide Blooms Perturb Coastal Marine Ecosystem. *Estuaries*.10(4): 284-290.
- de Leiva Moreno J.I., Agostini V.N., Caddy J.F., and Carocci F. 2000. Is the pelagic-demersal ratio from fishery landings a useful proxy for nutrient availability? A preliminary data exploration for the semi-enclosed seas around Europe. *ICES Journal of Marine Science*. 57: 1091-1102.
- Dennison W.C., R.J. Orth, K.A. Moore, J.C. Stevenson, V. Carter, S. Kollar, P.W. Bergstrom, R.A. Batiuk. 1993. Assessing Water-Quality with Submersed Aquatic Vegetation. *Bioscience* 43(2):86-94.
- Di Torro, D.M., J.A. McGrath, D.J. Hansen, W.J. Berry, P.R. Paquin, R. Mathew, K.B. Wu, and R.C. Santore. 2005. Predicting sediment metal toxicity using a sediment biotic ligand model: Methodology and initial application. *Environ. Toxicol. Chem.* 24: 2410-2427.
- Duarte, C. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87-112.
- Dugdale, R.C. and J.J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary production. *Limnology and Oceanography*. 12(2): 196-206.
- EPA. 2000. Chesapeake Bay Program. *Chesapeake 2000*.
- EPA. 2004. The incidence and severity of sediment contamination in surface waters of the United States. USEPA Office of Science and Technology, Washington DC, Report # EPA-823-R-04-007.
- Gacia, E. and C. Duarte. 2001. Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuar. Coast. Shelf Sci.* 52: 505-514.
- Glibert, P. M. and D. G. Capone. 1993. Mineralization and assimilation in aquatic, sediment, and wetland systems. Pages 243-272 in R. Knowles and T. H. Blackburn, editors. *Nitrogen Isotope Techniques*. Academic Press, San Diego.
- Glibert, P.M., J. Harrison, C. Heil, and S. Seitzinger. 2006. Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochemistry* 77:441-463.
- Glibert, P.M. and C. Heil. 2005. Use of urea fertilizers and the implications for increasing harmful algal blooms in the coastal zone. Contributed papers, the 3rd International Nitrogen Conference, Science Press USA Inc., 2005, 539-544.
- Glibert, P.M., C.A. Heil, D. Hollander, M. Revilla, A. Hoare, J. Alexander, and S. Murasko. 2004. Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. *Mar. Ecol. Prog. Ser.* 280: 73-83
- Glibert, P.M. and C. Legrand. 2006. The diverse nutrient strategies of HABs: Focus on osmotrophy. pp 163-176 in: E. Graneli and J. Turner (eds), *Ecology of Harmful Algae*. Springer.
- Glibert, P.M. S. Seitzinger, C.A. Heil, J.M. Burkholder, M.W. Parrow, L.A. Codispoti, and V. Kelly. 2005. The role of eutrophication in the global proliferation of harmful algal blooms: new perspectives and new approaches. *Oceanography* 18 (2): 198-209
- Hagy, J. D. 2002. Eutrophication, hypoxia and trophic transfer efficiency in Chesapeake Bay. PhD Thesis, Univ. Maryland, College Park.
- Hallagraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99.
- Hengst, A. M. 2007. Restoration ecology of *Potamogeton perfoliatus* in mesohaline Chesapeake Bay: The nursery bed effect. MS Thesis, University of Maryland, College Park.

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- Hillbricht-Ilkowska, A. 1977. Trophic relations and energy flow in pelagic plankton. Polish Ecological Studies. 3:3-98.
- Kemp, W. M. 2000. Seagrass ecology and management: An introduction, pp. 1-8. In: S. Bortone (ed.) Seagrasses: Monitoring, ecology, physiology, and management. CRC Publ., Boca Raton, FL
- Kemp, W.M., W.R. Boynton, J.C. Stevenson, R.R. Twilley and J.C. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. Mar. Techn. Soc. J. 17:78-89.
- Kemp, W. M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, G. Gallegos, W. Hunley, L. Karrh, E. Koch, J. Landwehr, K. Moore, L. Murray, M. Naylor, N. Rybicki, J. C. Stevenson, and D. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. Estuaries 27: 363-377.
- Kemp, W.M., W. Boynton, J. Adolf, D. Boesch, W. Boicourt, G. Brush, J. Cornwell, T. Fisher, P. Glibert, J. Hagy, L. Harding, E. Houde, D. Kimmel, W.D. Miller, R. I.E. Newell, M. Roman, E. Smith, and J.C. Stevenson. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. Mar. Ecol. Prog. Ser.303: 1-29.
- Kemp W.M., M.T. Brooks and R.R. Hood. 2001. Nutrient enrichment, habitat variability and trophic transfer efficiency in simple models of pelagic ecosystems. Mar Ecol Prog Ser 223:73-87
- Kim, E-H. 2004. The importance of physical mixing and sediment chemistry in mercury and methylmercury biogeochemical cycling and bioaccumulation within shallow estuaries. Ph.D. Dissertation, University of Maryland, College Park, 273 pp.
- Kim, E-H. R.P. Mason, and C.M. Bergeron. (In review). Modeling methylmercury bioaccumulation in an estuarine environment: An examination of the major controlling factors.
- Kim, E-H., R.P. Mason, E.T. Porter and H.L. Soulen. 2004. The effect of resuspension on the fate of total mercury and methylmercury in a shallow estuarine ecosystem. Mar. Chem. 86: 121-137.
- Kim, E-H., R.P. Mason, E.T. Porter, and H.L. Soulen. 2006. The impact of resuspension on sediment mercury dynamics, and methylmercury production and fate: A mesocosm study. Mar. Chem. 102: 300-315.
- Kirk, J. T. O. 1994. Light and Photosynthesis in Aquatic Ecosystems. Second Edition. Cambridge University Press, Cambridge, UK. 525 pages.
- Landry, M.R. 1977. A review of important concepts in the trophic organization of pelagic ecosystems. Helgolander wis Meeresunters 30: 8-17.
- Langston, W.J., G.R. Burt and N.D. Pope. 1999. Bioavailability of metals in sediments of the Dogger Bank (central North Sea): A mesocosm study. Est. Coast. Shelf. Sci. 48: 519-540.
- Luo, J. and S.B. Brandt. 1993. Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. Mar. Ecol. Prog. Ser. 98:223-236.
- Orihel, D.M., M.J. Paterson, C.C. Gilmour, R.A. Bodaly, P.J. Blanchfield, H. Hintelmann, R.C. Harris, and J.W.M. Rudd. 2006. Effect of Loading Rate on the Fate of Mercury in Littoral Mesocosms. Environ. Sci. Technol. 40: 5992-6000.
- Madsen, K.N., P. Nilsson, and K. Sundback. 1993. The influence of benthic microalgae on the stability of a subtidal sediment. Journal of Experimental Marine Biology Ecology. 170: 159-177.
- Madden, C. J. and W. M. Kemp. 1996. Ecosystem model of an estuarine submersed plant community: Calibration and simulation of eutrophication responses. Estuaries. 19 (2B): 457-474.
- Malone, T. C., H. W. Ducklow, E. R. Peele and S. Pike. 1991. Picoplankton carbon flux in Chesapeake Bay. Marine Ecology Progress Series 78:11-22.
- Malone, T.C., D.J. Conley, P.M. Glibert, L.W. Harding, Jr., and K. Sellner. 1996. Scales of nutrient limited phytoplankton productivity: The Chesapeake Bay example. Estuaries.19: 371-385.
- Mason, R.P. 2002. The bioaccumulation of mercury, methylmercury and other toxic elements into pelagic and benthic organisms. pp. 127-149. In: M.C. Newman, M.H. Roberts, and R.C. Hale [eds.], Coastal and Estuarine Risk Assessment, CRC/Lewis Publ.
- Melton, J. H. 2002. Environmental quality and restoration of mesohaline submerged aquatic vegetation. MS Thesis, University of Maryland, College Park.
- Naeem, S., J. Lindsey, P. Sharon, J.H. Lawton, and R.M. Woodfin. 1994. Declining biodiversity can alter performance of ecosystems. Nature. 368: 734-737.
- Naeem, S., K. Hakansson, J.H. Lawton, M.J. Crawley, and L.J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. Oikos. 76: 259-264.
- Nagel, J. 2007. Plant-sediment interactions and biogeochemical cycling for seagrass communities in Chesapeake and Florida Bays. PhD Thesis, University of Maryland, College Park.
- Newell R.I.E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? Pages 536-546 in M.P. Lynch and E.C. Krome (eds.). Understanding the estuary: Advances in Chesapeake Bay research. Chesapeake Research Consortium Publication 129 (CBP/TRS 24/88), Gloucester Point, VA.
- Newell, R.I.E., J.C. Cornwell and M.S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. Limnol. Oceanogr. 47: 1367-1379.
- Nixon S.W. and B.A. Buckley 2002. "A strikingly rich zone" – nutrient enrichment and secondary production in coastal marine ecosystems. Estuaries 25: 782-796
- Oviatt, C. A. 1994. Biological considerations in marine enclosure experiments: Challenges and revelations. Oceanography 7:45-51.
- Pauly D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres 1998. Fishing down the food chain. Science 279: 860-863
- Porter E.T., J.C. Cornwell, and L.P. Sanford. 2004a. Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic-pelagic coupling and estuarine water quality. Marine Ecology Progressive Series. 271: 61-75.
- Porter, E.T. L.P. Sanford, G. Gust, and F.S. Porter. 2004b. Combined water-column mixing and benthic boundary-layer flow in mesocosms: key for realistic benthic-pelagic coupling studies. Mar. Ecol. Prog. Ser. 271: 43-60.

REFERENCES

- Porter, E.T. 1999. Physical and Biological Scaling of Benthic-Pelagic Coupling in Experimental Ecosystem Studies. Ph.D. Thesis. Marine Estuarine Environmental Sciences program, University of Maryland, College Park, Maryland.
- Romdhane, M. S., H. C. Eilertsen, O. K. D. Yahia and M. N. D. Yahia. 1998. Toxic dinoflagellate blooms in Tunisian lagoons: Causes and consequences for aquaculture. Pages 80–83 in B. Reguera, J. Blance, M. L. Fernandez, and T. Wyatt. (eds). Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of United Nations Educational, Scientific and Cultural Organization, Paris, France.
- Schneider, A.R. 2005. PCB desorption from resuspended Hudson River sediment. Ph.D. Dissertation, University of Maryland, College Park, 211 pp.
- Schneider, Porter E.T., Baker J.E. 2007. PCB release from resuspended Hudson River sediment. Environmental Science and Technology 41(4) 1097-1103.
- Schulte, K. 2003. Spatial structure and heterogeneity in beds of the seagrass *Ruppia maritima* and comparison to ecological variables. MS Thesis, University of Maryland, College Park.
- Short, F. T., D. Burdick, and J. E. Kaldy. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnology and Oceanography. 40: 740-749.
- Short, F. T. and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation. 23: 17-27.
- Smayda, T. J. 1997. Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. Limnology and Oceanography 42:1137–1153.
- Stankelis, R. M., M. Naylor, and W. R. Boynton. 2003. Submerged aquatic vegetation in the mesohaline region of the Patuxent estuary: Past, present and future status. Estuaries. 26 (2A): 186-195.
- Sturgis, R.B. and L. Murray. 1997. Scaling of nutrient inputs to submersed plant communities: Temporal and spatial variations. Marine Ecology-Progress Series 152:89-102.
- Tilman, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. Ecology 58:338–348.
- Tomasko, D. C. Dawes, and M. O. Hall. 1996. The effects of anthropogenic nutrient enrichment on Turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. Estuaries. 19 (2B): 448-456.
- Twilley, R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson and W.R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities: I. Algal growth and effects on production of plants and associated communities. Mar. Ecol. Progr. Ser. 23:179-191.
- Yamamoto, T. 2003. The Seto Inland Sea—eutrophic or oligotrophic? Marine Pollution Bulletin 47: 37-42.
- Zedler, J. B., and J. C. Callaway. 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? Restoration Ecology 7:69-73.