Couplings of Watersheds and Coastal Waters: Sources and Consequences of Nutrient Enrichment in Waquoit Bay, Massachusetts¹,²

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ABSTRACT: Human activities on coastal watersheds provide the major sources of nutrients entering shallow coastal ecosystems. Nutrient loadings from watersheds are the most widespread factor that alters structure and function of receiving aquatic ecosystems. To investigate this coupling of land to marine systems, we are studying a series of subwatersheds of Waquoit Bay that differ in degree of urbanization and hence are exposed to widely different nutrient loading rates. The subwatersheds differ in the number of septic tanks and the relative acreage of forests. In the area of our study, groundwater is the major mechanism that transports nutrients to coastal waters. Although there is some attenuation of nutrient concentrations within the aquifer or at the sediment-water interface, in urbanized areas there are significant increases in the nutrient content of groundwater arriving at the shore’s edge. The groundwater seeps or flows through the sediment-water boundary, and sufficient groundwater-borne nutrients (nitrogen in particular) traverse the sediment-water boundary to cause significant changes in the aquatic ecosystem. These loading-dependent alterations include increased nutrients in water, greater primary production by phytoplankton, and increased macroalgal biomass and growth (mediated by a suite of physiological responses to abundance of nutrients). The increased macroalgal biomass dominates the bay ecosystem through second- or third-order effects such as alterations of nutrient status of water columns and increasing frequency of anoxic events. The increases in seaweeds have decreased the areas covered by eelgrass habitats. The change in habitat type, plus the increased frequency of anoxic events, change the composition of the benthic fauna. The data make evident the importance of bottom-up control in shallow coastal food webs. The coupling of land to sea by groundwater-borne nutrient transport is mediated by a complex series of steps; the cascade of processes makes it unlikely to find a one-to-one relation between land use and conditions in the aquatic ecosystem. Study of the process and synthesis by appropriate models may provide a way to deal with the complexities of the coupling.

We dedicate this paper to our friend and colleague, the late William E. Odum of the University of Virginia.

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Introduction

Coastal and estuarine waters are the most nutrient-enriched ecosystems on earth (Nixon et al. 1986; Kelly and Levin 1986). Nutrient loading has led to increased abundance of nuisance algae, reduced oxygen content of water, decimated shell
Fig. 1. Growth in housing units in Massachusetts counties, 1980-1990 in relation to distance from the sea. Housing data from U.S. Census. “Distance” is calculated as the average km from the center of the county to the shoreline.

and finfish, and many other changes in structure and function of aquatic communities. The increasing delivery of nutrients to coastal waters is caused largely by the many kinds of human activities on coastal watersheds. Urbanization increases release of wastewater, which in turn increases delivery of nutrients to groundwater, streams, and coastal waters. Deforestation attendant to urbanization reduces interception and storage of precipitation-borne nutrients, and may favor nitrification; both these effects increase loading rates to coastal waters. Agricultural land uses involve fertilizer and presence of livestock. Significant amounts of nutrients from fertilizer and manure leach into waterways, groundwater, and coastal bays.

Some nutrient inputs to coastal waters may originate from human activities far from shore. Nitric acid in acid rain, for instance, may contribute substantially to nitrogen budgets of estuaries in the Northeast United States (Culliton et al. 1989). In most cases, however, nutrient sources within watersheds are larger than contributions from remote sources (Valiela and Costa 1988).

Nutrient enrichment is the most pervasive agent for change in coastal waters, yet we lack knowledge of basic relationships between nutrient supply rates and many key ecological processes involved in function of ecosystems (Nixon et al. 1986). We cannot, for example, reliably quantify how a given rate of nitrogen loading will affect coastal macroalgae, phytoplankton, or fish.

We need experiments to quantify the effects of nutrient loading and identify causal mechanisms. The experiments should be done at sufficiently-large space and time scales to accommodate the regional nature of the land-sea coupling and the long-term features of the processes involved. Further, because waterflow, sediment characteristics, and bathymetry modify the effects of nutrient loading, design and execution of the experiments requires collaboration among diverse disciplines such as geology, hydrology, and hydrography, as well as the more usual suite of biological and chemical measurements.

The density of human populations within the coastal zones of the world is increasing. Nixon (1988) compiled data that showed that populations near 14 coastal bays in the United States had increased between 1860 and 1980. The increases ranged from 3-fold to 25-fold. Moreover, population densities in coastal areas have been increasing at rates faster than those of the general population. One recent survey, for instance, showed that the population of coastal counties in the United States was growing at a rate 3 times that of the total United States population (Culliton et al. 1989).

The characteristic increases in human populations can also be seen on Cape Cod, Massachusetts. The rate of growth in housing units in Barnstable County, for example, was 35.3% between 1980 and 1990 (United States Census data). Barnstable, which covers all of Cape Cod, is the fastest growing of all the mainland Massachusetts counties. The rate of increase in housing units during 1980–1990 in Massachusetts was about 10% for inland rural counties (lower right of Fig. 1) and for coastal counties in and around Boston (lower left Fig. 1). The latter are either fully developed or economically incapable of supporting further urbanization. In contrast, relatively rural coastal areas (Nantucket, Martha’s Vineyard, and Cape Cod) show increases of 30 to 45% in housing units (top left of Fig. 1). The high rate of urbanization on Cape Cod (and similar coastal areas elsewhere) must result in more nutrient delivery to groundwater, streams, and coastal waters.

Information on mechanisms involved in the coupling of watersheds and receiving waters is of basic and applied interest. In terms of basic principles, we need to know how processes within forests, aquifers, and the sediment-water interfaces, as well as hydrodynamic flow and mixing, affect cycling, sources, and fates of biogeochemically important substances. We also need to know more about basic controls of primary and secondary producers on coastal bays. From an applied perspective, we need
to evaluate the consequences of a given house density—or other land use—on water quality in the receiving bay, and determine how far back from shore do we need to extend management practices if we intend to protect coastal environmental quality.

We have addressed these kinds of basic and applied questions in case studies of shallow coastal bays and their watersheds by evaluating contributions of different sources of nutrients, and assessing the consequences of increased nutrient loading to shallow bays along the coast of Massachusetts. We chose to study small, shallow water bodies because these are the coastal ecosystems that are affected first. Shallow nearshore waters can be thought of as bellwethers of future trends in eutrophication, and moreover, are easier to study because of their smaller size. Results from studies in shallow ecosystems could then be used to develop and test hypotheses relevant to larger, harder-to-study systems.

In this paper we first review some of our earlier work on how human activities on coastal watersheds lead to increased nutrients in groundwater and how this in turn increases nutrient loading to adorning receiving waters. Then we describe an interdisciplinary study on Waquoit Bay, where we have been conducting a regional-scale experiment in nutrient loading that permits examination of how loading rates from watersheds take place, and quantifies the effects of loading on components of the coastal aquatic ecosystem.

**Watersheds as Nutrient Sources**

The major sources of nitrogen to coastal watersheds in our area are precipitation, fertilizers, and domestic wastewater. In earlier studies in Buttermilk Bay, a small, shallow bay on Cape Cod, Massachusetts, we found that precipitation brought almost \(1.2 \times 10^8\) moles of nitrogen per year to the surface of the watershed (Fig. 2). This value was obtained by multiplying the annually-averaged volume of precipitation by the average concentration of dissolved inorganic nitrogen (\(\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-\)) (Valiela et al. 1978; Valiela and Costa 1988; Valiela et al. 1990). Fertilizer added \(8.1 \times 10^5\) moles of \(N\) yr\(^{-1}\) to the watershed surface, an estimate obtained using information on agricultural use of fertilizers and area of cropland around the bay.

![Fig. 2. Inputs and fates of nitrogen (mol N x 10^8 yr\(^{-1}\)) entering the watershed and traveling toward Buttermilk Bay (from Valiela and Costa 1988).](image-url)
Nitrogen delivered to the watershed surface can be taken up by vegetation, be denitrified in the soil, or percolate through soil. Some of the N added in fertilizer was harvested as crops, so our calculation of fertilizer input is somewhat of an over-estimate. Incorporation of N into aggrading forests is quantitatively important in our study area (Fig. 2), because forests of Cape Cod have been growing since the mid-1800s, when most of Cape Cod was pastureland. The rates of accumulation of nitrogen in the pine-oak forest that cover Cape Cod are about 5–10 kg N ha\(^{-1}\) yr\(^{-1}\) (unpublished data, J. Melillo and colleagues). This range of nitrogen accretion could account for more than half to all of the nitrogen delivered to the watershed surface (Fig. 2).

Losses of nitrogen from the watershed surface caused by denitrification in soils are likely to be relatively low. Rates of denitrification (Groffman and Tiedje 1989) in sandy soils similar to those of our study area would remove only 10 to 20% of the nitrogen reaching the watershed surface (Valiela and Costa 1988). The 10% estimate seems most likely for soils in our study area (Peter Groffman, personal communication).

The rough estimates we calculated for Fig. 2 suggest that, at least in our study area, most of the nitrogen delivered by precipitation is intercepted at the watershed surface. Percolation of nutrients through to the subsoil and water table should be a small fraction of the inputs.

Domestic wastewater from septic tanks provides more nitrogen than precipitation or use of fertilizers (Fig. 2). Moreover, septic tanks release nitrogen deep in the subsoil, below the root systems of nearby trees. We calculated that about 1.5 \times 10^6 moles N yr\(^{-1}\) leave septic tanks in the watershed of Buttermilk Bay, move toward the water table, and then are entrained down-gradient in groundwater. This estimate was made using results from engineering studies on septic tank performance, and data on house occupancy patterns in our area (Valiela and Costa 1988).

The nitrogen (mainly ammonium) released by septic tanks is largely nitrified as it moves toward the water table. It is highly likely that the remaining ammonium is adsorbed to surfaces of particles along the way (Caeezan et al. 1987; Kipp 1987). It is also possible that some of the nitrate will be denitrified while passing through the aquifer (Smith and Duff 1988). Denitrification is indeed likely to take place near septic systems, where there may be both NO\(_3^-\) and sufficient amounts of low molecular dissolved organic matter (DOM). Such DOM is needed as an energy source by denitrifier organisms. The engineering estimates of loading from septic tanks do include losses by denitrification in the vicinity of septic tanks. Activity of denitrifying bacteria in aquifers may be limited at greater distances from septic tanks because of low concentrations of DOM. This is a supposition that needs confirmation by further studies.

We do not know the extent of nutrient attenuation by denitrification during transport of nitrogen in groundwater. However, a rough estimate of potential nitrogen reductions in the aquifer can be made by comparing the inputs from septic tanks with the amounts of groundwater-borne nitrogen near Buttermilk Bay (Fig. 2). Concentration of nitrogen in groundwater adjacent to Buttermilk Bay were measured by sampling and analyzing groundwater obtained from shallow well points (Valiela and Costa 1988). We also had estimates of groundwater flow into the bay. From these data we calculated that 1.1 \times 10^6 moles N yr\(^{-1}\) were carried into Buttermilk Bay by groundwater. This value is somewhat smaller than the 1.5 \times 10^6 moles N yr\(^{-1}\) delivered by septic tanks (Fig. 2). This 27% difference may be caused by adsorption and denitrification. On the other hand, because our calculations are based on rough approximations, we cannot be sure that the difference is significant. More accurate measurements need to be done, but to be conservative we assume for the moment that all of the nitrogen that enters the aquifer from septic tanks eventually makes its way to the shore of receiving waters.

We conclude, first, that in watersheds with accreting forests, nitrogen inputs to groundwater are largely uncoupled from precipitation-borne inputs to the watershed. Second, concentrations of nutrients in groundwater seem more closely related to the density of septic tanks in the watershed. Evidence for the second conclusion is provided by Persky (1986), who carried out a survey of solute concentrations in groundwater below areas of Cape Cod with different building densities. This study found that median nitrate concentrations increased as building density increased (Fig. 3), a result that implies that nutrient enrichment of groundwater—and hence of receiving coastal waters—will increase along with urbanization. Of course, urbanization results in felling of forests, so that, in addition to direct input of nutrients via septic tanks, urbanization may also increase loading to groundwater by removing forests that intercept precipitation-borne nutrients.

**A Regional Experiment in Nutrient Loading: The Waquoit Bay LMER Project**

The Waquoit Bay Land-Margin Ecosystems Research project (WBLMER) is a regional-scale experiment in nutrient loading in which we can examine how major components of coastal landscapes
Couplings of Watersheds and Coastal Waters

(watersheds, sediment-water interface, coastal bay) are coupled by nutrient transport and transformations. These studies involve understanding nutrient dynamics in the terrestrial components (watershed vegetation, soils, and aquifers), and transport and transformations of nutrients at and through the second component, the sediment-water interface. Lastly, we follow the dynamics of nutrients, and the first-, second-, and third-order effects of the different nutrient loading rates on the receiving aquatic ecosystem.

The basis of the nutrient-loading experiment is that the degree of urbanization in different subwatersheds differs markedly. We delineated subwatersheds of Waquoit Bay on the basis of water table elevations (Fig. 4). Thus we can show that the watershed of Childs River, for example, is more densely urbanized than other subwatersheds such as Quashnet River and Sage Lot Pond (Fig. 5). We intend to show that differences in the land-use mosaic among subwatersheds result in differences in the rate of nutrient loading to groundwater, and hence to receiving coastal waters. The choice of subwatersheds therefore provides a regional-scale experiment in nutrient loading.

A second purpose in choosing subwatersheds that are at different stages in the process of change from forest to urban is to use them as a space-for-time substitution (Pickett 1988), and thereby obtain a depiction of the effects that result as nutrient loading increases over time. Development of the present differences in land use can be reconstructed from analysis of aerial photographs taken at intervals from 1938 to the present. We will ultimately provide a detailed account of different types of land use in each subwatershed, but the history of urbanization is captured by a simple count of buildings within each subwatershed over the course of time (Fig. 5).

Quantification of nutrient loading to receiving waters begins with an assessment of freshwater flow. Fresh water flows into Waquoit Bay via groundwater seepage and spring-fed streams. The flow of groundwater via seepage into the three selected subestuaries of Waquoit Bay was estimated by means of hydrological stream-tube calculations (Freeze and Cherry 1979), and thereby obtain a depiction of the effects that result as nutrient loading increases over time. Development of the present differences in land use can be reconstructed from analysis of aerial photographs taken at intervals from 1938 to the present. We will ultimately provide a detailed account of different types of land use in each subwatershed, but the history of urbanization is captured by a simple count of buildings within each subwatershed over the course of time (Fig. 5).

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![Fig. 3. Nitrate concentrations in groundwater below areas of Cape Cod having different densities of buildings. Data from Persky (1986).](image)

almost completely account for entry and exit of fresh water, and can therefore carry out the calculations needed for nutrient loading estimates.

We estimated nutrient loadings to groundwater in the three selected subwatersheds, using land-use data and procedures by Frimpter et al. (1988) and other (Table 2). In these calculations only nitrogen provided by precipitation and septic tanks is considered. For each subwatershed, surface N inputs were divided into those intercepted by forests and those passing into the subsoil. These calculations were made based on estimates of forest area. Precipitation N entering the subsoil was added to septic system inputs to calculate loading to the water table.

The estimated nitrogen loading rates to the different subwatersheds span a range of up to 2 orders of magnitude. The range of nitrogen loading rates that affect subestuaries of Waquoit Bay span much of the range of loading rates seen in other estuaries (cf., the span across the x-axis in Fig. 7).

To see if differences in house density, and hence in presumed N loading, actually translated into differences in nutrients concentrations in groundwater near the shoreline, we used well points to obtain samples of groundwater at or above the high tide mark. Samples were obtained from well points placed at 1-m intervals on transects visited at different times of the year, and on one occasion at intervals of 20 m to 50 m around the periphery of the subestuaries receiving water from each subwatershed. Concentrations of dissolved inorganic nitrogen (DIN) in groundwater from Childs River were an order-of-magnitude greater than those
from Quashnet River or Sage Lot watersheds (Table 2). The differences were most marked for nitrate, so that the comparison of subwatersheds constitutes an experiment in nitrate loading.

The concentrations of nitrogen measured in the well-point samples can be used to check estimates derived from loading calculations. We calculated predicted concentrations of DIN expected to appear at the water’s edge assuming that outflow of fresh water over a year is roughly equivalent to annual recharge to the aquifer, and that no nutrient attenuation occurs during transport in the aquifer (Table 2). The expected concentrations of dissolved inorganic nitrogen match closely the values actually found in the well-point samples (Table 2). Even though these calculations are rough, they do suggest that we can have some confidence about the magnitude of transport of nitrogen from wa-
TABLE 2. Nitrogen contributions (kg N yr^-1) by precipitation and septic systems, and N loading to water table and hence to estuaries.

<table>
<thead>
<tr>
<th>Subwatersheds</th>
<th>Childs River</th>
<th>Quashnet River</th>
<th>Sage Lot Pond</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precipitation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercepted by forests</td>
<td>1,092</td>
<td>4,809</td>
<td>114</td>
</tr>
<tr>
<td>To soil in nonforest areas</td>
<td>1,209</td>
<td>2,634</td>
<td>11.5</td>
</tr>
<tr>
<td>Septic systems</td>
<td>13,000</td>
<td>11,900</td>
<td>320</td>
</tr>
<tr>
<td>Loading to water table</td>
<td>14,209</td>
<td>14,534</td>
<td>331.5</td>
</tr>
<tr>
<td>Calculated DIN conc (M)*</td>
<td>160</td>
<td>3.6</td>
<td>6.2</td>
</tr>
<tr>
<td>Measured DIN conc (M) in well point samples (geometric mean)</td>
<td>132.7</td>
<td>4.2</td>
<td>15.1</td>
</tr>
</tbody>
</table>

* Assuming that seepage plus stream flow equals recharge.

Consequences of Nutrient Loading in Waquoit Bay

Above we reviewed evidence on delivery of nutrients, particularly of nitrate additions, from watersheds to the water's edge of Waquoit Bay, and concluded that differences in urbanization led to different concentrations of nitrate in groundwater moving from the watershed to receiving waters. Below we focus on how the different rates of nitrate loading change some key ecological components of the aquatic components of the three selected subwatersheds of Waquoit Bay (Childs River, Quashnet River, and Sage Lot Pond).

Nutrients in Water Increase With Urbanization of Watersheds

Concentrations of nitrate in the water column of Childs River were larger than those of Quashnet River; concentrations of nitrate in Sage Lot Pond were the lowest (Fig. 6). The negative relationship to salinity suggests that the source of nitrate must be the freshwater end-member of the estuaries. Clearly, the nitrate must come from the watershed, either from seepage along the shores of the subestuary or from the spring-fed streams.

The translation between loading to a watershed and conditions in the water is articulated through a series of steps. The first step involves the entrainment and possible attenuation of nitrogen in flowing groundwater. The total quantity of nitrogen furnished by wastewater and precipitation to the aquifers of the Childs River and Quashnet River subwatersheds is about the same (Table 2). However, the Quashnet River watershed is larger than the Childs River watershed (Table 2). Consequently, there is more water involved in nutrient transport within the aquifer of the Quashnet River watershed. We calculate mean concentrations of nitrate in groundwater about to enter Quashnet River by dividing the loading rate by the recharge volume, and assuming that nitrogen mixes uniformly within the aquifer. The calculated concentrations of nitrogen in groundwater about to discharge into the Quashnet estuary are much lower than those calculated for Childs River (Table 2). Because the assumption of mixing within the aquifer is too simple, we are presently using ground-
The second step in the translation occurs in the shallow sediments where groundwater enters the estuaries. Groundwater about to enter Childs River holds about 133 μM NO₃⁻ (Table 2), but these concentrations were not found in the receiving water column (Fig. 6). At most, extrapolations of the nitrate vs. salinity curve for Childs River in Fig. 6 yields about 60 μM at salinity of 0%. This suggests a loss of about half the dissolved inorganic nitrogen during passage of groundwater through the thin sediment-water interface. Denitrification could be responsible for these losses (Seitziger 1988). Such losses are not seen in the Quashnet River data (Table 2 and Fig. 6). Perhaps, as argued by Seitzinger and Nixon (1985) and Seitzinger (1988), rates of nitrification and denitrification increase as nitrogen loading rates increase. If such were the case, we might expect that denitrification rates are higher in Childs River than in Quashnet River and Sage Lot Pond.

Differences in location of homes (and hence septic tanks) may be an alternative explanation for the discrepancy between measured concentrations in groundwater near the shore and in regional estimates. Perhaps the nearshore concentrations are higher because of the greater density of houses very close to the water's edge (Fig. 7). Further, a location away from shore also means longer travel time for nitrate in the groundwater. Average velocity of groundwater in our area is about 0.3 m d⁻¹, so a distance of only 300 m away from shore implies a year's travel time. If there is any attenuation along the travel path, the importance of septic tanks located farther away could be proportionally smaller. Thus, septic tanks near the water's edge are probably the most critical for nutrient loading. This idea needs testing with actual measurements of attenuation and with groundwater models.

**PHYTOPLANKTON PRODUCTION AND BIOMASS INCREASE WITH ENRICHMENT**

Production by phytoplankton varied seasonally, and reached 100–200 mg C m⁻³ h⁻¹ in Childs River during middle to late summer. These are consid-

<table>
<thead>
<tr>
<th>Subestuary</th>
<th>Chlorophyll concentrations (mg m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upstream Sites</td>
</tr>
<tr>
<td>Childs River</td>
<td>47.7 ± 21.1</td>
</tr>
<tr>
<td>Quashnet River</td>
<td>8.6 ± 2.6</td>
</tr>
<tr>
<td>Sage Lot Pond</td>
<td>--</td>
</tr>
</tbody>
</table>
erably higher rates than the 10–50 mg C m⁻³ h⁻¹ measured in Sage Lot Pond during the peak of the season. At other times of year, phytoplankton production was very low, generally less than 1 mg C m⁻³ h⁻¹ everywhere in Waquoit Bay.

Standing crops of phytoplankton, measured as chlorophyll, are higher in Childs River than that in Quashnet River, and both of these estuaries in turn have more phytoplankton chlorophyll than Sage Lot Pond (Table 3), the estuary that is exposed to the lowest potential nutrient loading (Table 2). The chlorophyll values are averages of mean, integrated water-column chlorophyll measurements taken over many sampling periods during 1988–1989. There are strong down-estuary gradients in chlorophyll concentrations in our subestuaries (Table 3), but the differences between Childs River, Quashnet River, and Sage Lot Pond are maintained down-estuary.

The responses of average chlorophyll in the water to potential nutrient loading rate in our estuaries fall within the ranges observed in other estuarine environments (Fig. 8). The values for Childs River, the most nutrient-loaded estuary, lie within the scatter around the line fitted to observations from Valiela (1991).

TABLE 4. Mean (+ SD) of biomass of macrophytes in three selected subestuaries of Waquoit Bay. Data averaged from multiple samples per site collected monthly over one year. Data of D. Hersh.

<table>
<thead>
<tr>
<th>Subestuary</th>
<th>Number of Samples</th>
<th>Biomass (g m⁻²)</th>
<th>Cladophora vagabunda</th>
<th>Gracilaria tikouahiae</th>
<th>Total Macroalgal Biomass</th>
<th>Zostera marina</th>
</tr>
</thead>
<tbody>
<tr>
<td>Childs River</td>
<td>150</td>
<td>220 ± 29.4</td>
<td>109 ± 10.5</td>
<td>335 ± 39.8</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Quashnet River</td>
<td>150</td>
<td>85 ± 11.1</td>
<td>48 ± 6</td>
<td>150 ± 14.3</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Sage Lot Pond</td>
<td>78</td>
<td>56 ± 6</td>
<td>56 ± 5.9</td>
<td>90 ± 12.1</td>
<td>117 ± 12.6</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 5. Mean (± SD) growth rates for *Cladophora vagabunda* from Childs River and Sage Lot Pond. Measurements were done in situ as increases in fresh weight in tethered fronds situated above the canopy and within the canopy.

<table>
<thead>
<tr>
<th>Location</th>
<th>Above Canopy (High Light Intensity)</th>
<th>Within Canopy (Low Light Intensity)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Childs River</td>
<td>0.09 ± 0.02</td>
<td>0.04 ± 0.02</td>
</tr>
<tr>
<td>Sage Lot Pond</td>
<td>0.04 ± 0.02</td>
<td>0.03 ± 0.02</td>
</tr>
</tbody>
</table>

comparison's sake, we can see that the potential uptake over a day, by only one of the algal taxa present in Childs River, is an order of magnitude higher than the stock of DIN. The nitrogen loading rate (Table 2), when converted to appropriate units, is $2-8 \times 10^{10}$ μmol N d$^{-1}$. Loading rate is therefore of the same magnitude as the potential uptake by *C. vagabunda*, which of course is only one of the macroalgal species present in Childs River. All these comparisons are rough and ignore features such as regeneration of DIN, but they do suggest the potential importance of macroalgae in nutrient dynamics in our estuaries. In fact, uptake by macroalgae, we believe, is responsible for low nutrients in the water of Waquoit Bay during warmer months (unpublished data).

A second example of the importance of macroalgae is their effect on oxygen content of the water. Photosynthesis and respiration by macroalgae determine the vertical profiles of oxygen in Waquoit Bay and its estuaries. This is unusual, since physical mixing by wind, currents, and tides commonly overwhelm biological processes and largely determine oxygen content in coastal waters. Evidence for the role of macroalgal control of oxygen content is presented in detail elsewhere (D'Avanzo et al. in preparation), but Fig. 10 is a clear example. At dawn, oxygen is depleted near the bottom (Fig. 10, black circles). As the sun comes up, photosynthesis by phytoplankton and macroalgae generates oxygen, and the profile of oxygen concentrations slides to the right (Fig. 10, open circles). The dominant effect of macroalgal photosynthesis is evident from the pattern of the daily swing; the largest change in oxygen occurs just above the macroalgal canopy. After dusk, respiration consumes oxygen, and the daily fluctuation is completed. Of course, there are many kinds of organisms in the bay, all of which respire, but unpublished data of P. Peckol suggest that respiration by the macroalgae may account for most of the oxygen depletion that takes place during the night.

Phytoplankton of course are partially responsible for the excursion of oxygen concentrations seen in Fig. 10. The increased oxygen within the upper
portion of the water column is probably due in some measure to phytoplankton production. K. Foreman's measurements of phytoplankton production suggest that during most of the year phytoplankton are not as productive as macroalgae, and account for about 20% of total primary production. During a few weeks in mid to late summer phytoplankton peak, and contribute perhaps 70% of the oxygen.

If there is a sequence of a few cloudy days, photosynthesis by the macroalgae may be low enough that the daytime recovery of oxygen content seen in Fig. 10 does not take place. In as little as three cloudy days, the consumption of oxygen by respiration uncompensated by photosynthesis can produce hypoxic or anoxic conditions (Fig. 10, triangles) near the bottom, or even over the entire water column.

Anoxic events have far-reaching second- and third-order effects throughout the food web of Waquoit Bay. During the summer of 1988, for example, we recorded a prolonged overcast period July 19–23 (Fig. 11, top graph). This occurred

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Fig. 11. Time course of light, temperature, oxygen, ammonium, phosphate, and chlorophyll in water of Waquoit Bay, summer 1988. Modified from Costa et al. (in press).
during a time when the water was warm (Fig. 11, second graph) and the water column was strongly stratified. During this period, net production by macroalgae was nil, while macroalgal respiration exceeded $80 \leq \text{mol O}_2 \text{d}^{-1} \text{h}^{-1}$ (Peckol et al. in preparation). The oxygen content of surface water decreased sharply after that cloudy period (Fig. 11, second graph). The lower oxygen was accompanied by increases in ammonium and phosphate concentrations (Fig. 11, third graph), presumably caused by increased regeneration. The increase in nutrients was followed almost immediately by a bloom of phytoplankton growth, as shown by the chlorophyll data (Fig. 11, bottom graph). We have unpublished data that show that phytoplankton are nitrogen-limited in the more saline areas of Waquoit Bay. Anoxic events thus have repercussions throughout key components of aquatic ecosystems. Anoxic events may occur on occasion in unenriched shallow coastal water bodies, even if macroalgae are scarce, and these events have effects on their ecosystems also. The point here, however, is that abundant macroalgae may increase the frequency of such events and hence increase the consequent changes in nutrient availability and phytoplankton as well as throughout the food webs.

Enrichment leads to dominance of macroalgae, and the effect of macroalgae on the vertical distribution of oxygen therefore poises the bay ecosystem in a rather unstable state, one in which there is an increase in the frequency of anoxic events that can severely alter the trophic web and geochemistry of the bay. Consumers, as well as nutrients and producers, are affected by increased frequencies of anoxia. Anoxic events can result in extensive kills of fish and invertebrates. In Waquoit Bay we have recorded kills following anoxic events in each of the summers during our study (1988 to present). Nutrient loading thus leads to a cascade of fairly complicated second- and third-order effects.

Loading rates are also likely to prompt third-order effects on bacteria. One of the always puzzling features of denitrification is the paradox of how anaerobic bacteria manage to find sufficient nitrate, a compound that is obviously in short supply in anaerobic environments. Perhaps one reason for the increases in denitrification we have already mentioned is that in enriched waters there are wide daily fluctuations in oxygen conditions, as implied in Fig. 10. These fluctuations could allow nitrate to reach the vicinity of anoxic microzones where denitrifiers can survive and somehow have access to the new nitrate.
Eelgrass Abundance is Reduced by Loading

Eelgrass is absent from nutrient-loaded subestuaries of Waquoit Bay (Table 4). This is a second-order phenomenon rather than a direct consequence of nutrient additions (Costa 1988). Growth of eelgrass is light-limited rather than nutrient-limited in Cape Cod (Dennison and Alberte 1985). Nutrient enrichment encourages growth of epiphytes on eelgrass leaves, and epiphytes intercept light (Costa 1988). The potential result is a decrease in vigor of eelgrass, with eventual reduced cover, and loss of the eelgrass habitat.

There is a historical parallel to the differences in eelgrass cover we found in comparing the subwatersheds exposed to different loading rates. Eelgrass habitat in Waquoit Bay has decreased (Fig. 12), while the number of dwellings and the resulting potential nutrient loading have increased during recent decades. The data of Fig. 12 were obtained from aerial photographs using interpretive methods developed by Costa (1988). We cannot be sure that the decrease in eelgrass was the direct result of nutrient loadings, but there is a negative correlation between nutrient loading calculated from the number of houses in the watershed and the loss of eelgrass cover in the bay (unpublished data). The disappearance of eelgrass over recent decades is documented by long-time residents, who recall that Childs River was an eelgrass-dominated estuary before the 1960s. Moreover, in the space-for-time substitution afforded by comparisons of the subestuaries (Table 4), it is clear that macroalgae replace eelgrass in the bottom of enriched estuaries.

Abundance of Animals Decreases With Loading

The abundance and species richness of invertebrates found on the bottom and macroalgal canopy are lower in parts of Waquoit Bay in which more macroalgae are present (Fig. 13). These results are from replicated samples obtained using an Ekman dredge at several sites over Waquoit Bay.

We can show a historical parallel to the spatial comparison of Fig. 12, using data from shellfish catch reports. The catch of bay scallops (*Argopecten irradians*) from Waquoit Bay have decreased since the 1960s (Fig. 14). The decrease has been even more marked in Eel Pond, which is on the western section of the bay and receives loadings from the Eel Pond and Childs River subwatersheds (Fig. 4), the two most urbanized estuaries of Waquoit Bay. The scallop yield from the more urbanized waterbody decreased more than that in the relatively less urbanized Waquoit Bay proper (Fig. 14).

On the other hand, the catch of quahogs (*Mercenaria mercenaria*) in Waquoit Bay and Eel Pond has remained about the same over the last several decades (Fig. 14), so not all benthic invertebrate species are affected similarly. There may be some differential tolerance for low oxygen between these two shellfish species. Perhaps more likely to account for the difference between the responses of scallops and clams may be differential effects of eutrophication on the specific habitats used by these species.
two stocks of shellfish: clams use the very shallow sandy littoral strips, and scallops depend on eelgrass beds in deeper areas. Eutrophication has, for some reason, not greatly altered the vegetation cover of littoral sands in Waquoit Bay. The strip of littoral sands is still largely devoid of vegetation. In contrast, the favored habitat of scallops has been much reduced by nutrient enrichment (Fig. 12).

Macrolgal canopies are rather inhospitable habitats for scallops—scallops that move into macroalgal beds sink into the thick canopy of loose fronds. Suspension feeding within the canopy must be impaired, and water within the canopy often becomes anoxic on a daily basis. Scallops that wander into the macroalgal beds certainly are unlikely to thrive there.

It may be argued that the decrease in scallop catch reported in Fig. 14 is a regional recruitment phenomenon, perhaps unrelated to local eutrophication. This may be so, but even if there were a sudden increase in larval recruitment of scallops into Waquoit Bay, we suspect that the great reduction in eelgrass habitat brought about by eutrophication would make it difficult for the current population or for new recruits to find sufficiently large areas of suitable habitat. In addition, the increased frequency of anoxia must deplete scallop populations.

**General Conclusions**

Nutrient loading has had pervasive repercussions throughout the food web of the Waquoit Bay ecosystem. The first-, second-, and third-order effects associated with different degrees of nutrient loading result in very different configurations of the food web, differences in nutrient and carbon cycling, elemental budgets, and input-output budgets. Although we have enough knowledge to show that the differences exist, we need further study to establish cause and effect mechanisms and to quantify actual trends created by increased nutrient loading.

The suite of effects that seem related to nutrient enrichment in Waquoit Bay strongly imply the im-
portance of "bottom-up" controls in this aquatic ecosystem. We have as yet not explored the importance of "top-down" controls.

Our data so far suggest that land-use mosaics on coastal watersheds, even though separated by considerable distances from receiving waters, are strongly coupled to adjoining aquatic ecosystems, and this coupling has fundamental consequences for the structure and function of the receiving water ecosystem. Human activities on the watersheds work to increase "natural" nutrient sources and transport, and are ultimately responsible for increases in nutrient delivery to coastal waters.

Ideally, we would like to have a suitable index of land use, for example, "number of houses" or "area of accreting forests," or some combination of these variables. We could then search for a correspondence of the index to water quality in the receiving water body. As is obvious from the discussion above, one-to-one translations of land use to nutrient loading, and to consequences for water quality and resources are unlikely. The many linked mechanisms, and their first-, second-, and third-order effects, make the finding of such correspondences a challenging task. Many ostensibly "obvious" relationships fail to materialize. There is no doubt that the translation exists. Comprehensive, interdisciplinary study and modelling of the interactions, and of the responses of processes involved, promise timely answers to the central question of how land use on watersheds is coupled to consequences in the receiving aquatic ecosystem.

LITERATURE CITED


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