Transport of groundwater-borne nutrients from watersheds and their effects on coastal waters

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Abstract. Anthropogenic activities on coastal watersheds increase nutrient concentrations of groundwater. As groundwater travels downslope it transports these nutrients toward the adjoining coastal water. The resulting nutrient loading rates can be significant because nutrient concentrations in coastal groundwaters may be several orders of magnitude greater than those of receiving coastal waters. Groundwater-borne nutrients are most subject to active biogeochemical transformations as they course through the upper 1 m or so of bottom sediments. There conditions favor anaerobic processes such as denitrification, as well as other mechanisms that either sequester or release nutrients. The relative importance of advective vs. regenerative pathways of nutrient supply may result in widely different rates of release of nutrients from sediments. The relative activity of denitrifiers also may alter the ratio of N to P released to overlying waters, and hence affect which nutrient limits growth of producers. The consequences of nutrient (particularly nitrate) loading include somewhat elevated nutrient concentrations in the watercolumn, increased growth of macroalgae and phytoplankton, reduction of seagrass beds, and reductions of the associated fauna. The decline in animals occurs because of habitat changes and because of the increased frequency of anoxic events prompted by the characteristically high respiration rates found in enriched waters.

Introduction

In this paper we first argue that nutrient transport has been underestimated as a potential mechanism of eutrophication of coastal waters. We then examine how transport and transformations of nutrients may occur in the near shore. Lastly, we review more evidence of potential consequences of nutrient transport by groundwater for a shallow coastal ecosystem in the coast of New England.

Groundwater as a nutrient source

Ecosystems of the world's coastlines are receiving extraordinary amounts of nutrients as a consequence of human activities such as use of fertilizers, industrial emissions to the atmosphere, and disposal of waste water in watersheds adjoining coastal waters. The loadings of nitrogen and phosphorus to coastal aquatic environments even exceed those to fertilized agroecosystems (Nixon et

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al. 1986). Increased nutrient loading from anthropogenic sources is pervasive around the world, and is one of the major factors that will change the structure and function of shallow coastal ecosystems during coming decades.

Although increased nutrient loading by precipitation has been documented (Environmental Defense Fund 1988; Cowling & Linthurst 1981; Correll et al. 1984; Weller et al. 1986; Paerl 1985; Rapp 1983; Jordan et al. 1986; Likens et al. 1976; Heil et al. 1988), most research has focused on deeper estuaries (Jaworski 1981) in which flow from rivers and streams dominates water budgets and contributes the majority of nutrients. For example, rivers and streams contribute 74% of the nitrogen to the Baltic as a whole, while atmospheric deposition, sewers, and groundwater contribute only 13%, 10%, and 3%, respectively (Maksimova 1982). Rivers and direct precipitation, however, are not the sole source of freshwater-borne nutrients to coastal environments. Even in places without rivers, salinity is often depleted in coastal waters due to groundwater input (cf. for example, Bowman et al. 1981). Groundwater flow is especially important where underlying coastal sediments are coarse, unconsolidated sands of glacial or marine origin. In such situations flow of groundwater may be the major source of nutrients to coastal waters.

In unconsolidated sediments, groundwater moves through the watershed shoreward (Fig. 1, bottom diagram) in paths that have a downward vertical as well as horizontal vector. Downward flow is caused by additional water infiltrating along the path of the water. Freshwater eventually moves close enough to shore to meet the denser saltwater that saturates interstitial space in sediments beneath the sea. The presence of seawater in the porespace acts together with lower head pressures in the nearshore zone compared with offshore (Bear 1979) to deflect the path of fresh groundwater sharply upward. As a result, most of the groundwater flow occurs very near the shore (Du Commun 1828; Drabbe & Badon Ghyben 1888-1889; Herzberg 1901).

During the last decade, it has become apparent that groundwater flow and transport of nutrients into shallow coastal water are far more significant and widespread than had been realized (Valiela & Teal 1979; Johannes 1980; Bokuniewicz 1980; Capone & Bautista 1985; Lewis 1987). The importance of groundwater is not so much because of the magnitude of flow rates (Table 1), but rather because of the high nutrient concentrations in groundwater compared to those in receiving seawater. Although highly variable, the nitrate content of groundwater discharging onto coastal water may be up to five orders of magnitude larger than concentrations in receiving seawater (Table 2).

Detailed local studies corroborate the conclusions evident from Table 2. We have studied flow of groundwater into Great Sippewissett Marsh, on the West coast of Cape Cod facing Buzzards Bay, and measured concentrations of nitrate, nitrite, ammonium, and phosphate (Table 3). Concentrations varied widely, but the upper ranges of dissolved inorganic nitrogen (DIN in Table 3) and phosphate are two to three orders of magnitude higher than those of the receiving seawater. These differences exist even where watersheds are still largely forested, rather than urbanized or agricultural. Studies such as ours in Buzzards Bay, and examination

Fig. 1. Vertical profiles of salinity (top panels) in sandy sediments and finer sediments of Waquoit Bay at different distances from shore. The average depth of the water column over the three stations is about 50, 1, 1.5 m, respectively (data obtained by N. Scholz and D. Bergles). The bottom diagram shows groundwater flowing through nearshore sands rather than through the finer sediments in the center of the bay (cf. Fig. 3). Seawater is shown by the dotted pattern.

of the values included in Tables 2 and 3 thus suggest that even though flow of freshwater may be modest, its nutrient content may be large enough to make significant contributions to the nutrient economy of receiving waters.

There are, unfortunately, too few studies that address the issue of relative magnitude of groundwater nutrient inputs into marine ecosystems, so that it is difficult to generalize. Some studies of larger, deeper coastal waters have con-

Table 1. Estimates of flow of groundwater compared to other water sources in various marine situations.

	% of water input	Reference
Great South Bay, NY, US	20	Bokuniewicz (1980)
Swan River Estuary, W. Australia	17	Johannes (1980)
Great Sippewissett Marsh, MA, USA		Valiela et al. (1978)
Buttermilk Bay, MA, US	83 ^a	Valiela & Costa (1988)
Ocean as a whole	10 ^b	Garrels & MacKenzie (1967)

^a Only freshwater inputs considered.

^h Compared to rivers and precipitation.

Table 2. Ranges of concentrations of nitrate in groundwater in coastal aquifers, in groundwater discharging into coastal waters, and in seawater.

cluded that groundwater nutrient transport is small (Bowman 1977). Clearly, in estuaries such as Chesapeake. Delaware or Narragansett Bays, rivers are the major nutrient source (Kremer & Nixon 1978; Neilson & Cronin 1981). In shallower nearshore systems with few streams, groundwater is likely to be more important: Maksimova et al. 1978, for example, concluded that 15% of the fixed nitrogen entering the Caspian Sea is supplied by groundwater. In shallow bays and lagoons common along many shorelines, groundwater can be of major importance: studies of nutrient budgets of coastal lagoons on Cape Cod and Rhode Island show that groundwater is the principal freshwater source of nitrogen and phosphorus to these ecosystems (Table 4).

Table 3. Range of nutrient concentrations (μM) measured in a comprehenisve survey of groundwater of Cape Cod (Frimpter & Gay 1979), in groundwater springs emptying into the shoreline of Great Sippewissett Marsh on Buzzards Bay (Valiela et al. 1978), and in seawater of Buzzards Bay (Roman & Tenore 1978).

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	Groundwater	Precipitation	Streams	Tidal exchange	Other
Buttermilk Bay, MA ^a	85.4	9.6	0.6		0.2 ^b
Siders Pond, MA°	97	1.5	0.2	Very small	1 ^b
Ninigret Pond, RI ^d	80	8.8	5.5	7	1e
Green Hill Pond, RI ^d	83	3.3	5.5	6.7	
Truston Pond, RI ^d	92.7	6.6		Very small	0.07 ^e
Cards Pond, RI ^d	93.8	1.2	3.9	Very small	1e
Potter Pond, RI ^d	94.0	5.5			0.05 ^e
Pt. Judith Pond, RI ^d	71.2	8.1	19		1.7 ^e

Table 4. Percent of nitrogen inputs into coastal bays and lagoons of New England by various mechanisms.

^a Valiela & Costa 1988. Tidal flow not calculated; values as % of freshwater-borne N.

b Inputs by waterflow.

^c Caraco (1986). Tidal influx very small.
^d Lee & Olsen (1985). ^e Inputs by ste

 $^{\circ}$ Inputs by storm runoff.

Flows and transformations at the sediment-water interface

Vertical profiles of salinity in nearshore sediments (Fig. 1, top row of graphs) suggest that there is flux of freshwater into the overlying water column. The data in Fig. 1 come from Waquoit Bay on the South shore of Cape Cod, an area underlain by fairly coarse sands of glacial origin (Fig. 1, bottom diagrams). Very near the shore of Waquoit Bay there is freshwater below 0.75 m or so (Fig. 1, top left panel). The salinities in interstitial water above that depth suggest that there is some degree of mixing with the overlying seawater, and the steeply changing slope of the curve in the upper layer of sediment implies an upward advective flux of freshwater. Thirty-five to 200m farther offshore (Fig. 1, top middle and right panels) interstitial salinity is the same as seawater salinity, so that no advection of groundwater seems to occur at the offshore stations. In this particular case the near-offshore gradient in flux is further emphasized by differences in sediment type: the nearshore is coarse sand, while the finer sediments offshore have low permeability. The sediments along the bottom of Waquoit Bay are therefore fairly neatly partitioned into coarse sands where advective flow of groundwater may transport 'new' nutrients to the water column, and fine sediments where diffusion of 'old' mineralized nutrients out of the sediments contributes regenerated nutrients to the overlying water.

Gradients of decreasing groundwater flux extending from nearshore to offshore appear to be a common feature of coastal embayments. This can be roughly seen to be true in one of our study sites on the Buzzards Bay shore (Fig. 2). Porewater chlorinity profiles at 120 m from shore show some salinity dilution with depth within the profile. This dilution increases, as we would expect, nearer to shore, at least up to 40 m. At 0.20m from shore the pattern is disrupted, perhaps due to small-scale heterogeneity in sediments.

Measurements of actual flow of freshwater through intertidal or shallow

Fig. 2. Chlorinity measurements of pore water at different depths in the sediment at the Pocasset site, in relation to distance seaward from mean tide level on the beach.

subtidal sediments have been done, primarily using hydraulically-vented seepage meters **and chambers set into** the sediments **(Capone & Bautista 1985;** Lewis 1987; **Bokuniewicz** 1980). We **have** used seepage meters to **measure flows out of** sediments at **two sites in** the Western shores **of Cape Cod on Buzzards Bay (Fig. 3). The** seepage meters **are 30cm diameter plastic cylinders whose head space is about 61., and can be sampled through ports** so that we **can measure salinity of the enclosed water at intervals. We attach a very thin-walled, wetted plastic bag to another port** to vent the **chamber, and also** so we **can**

Fig. 3. Frequency of different flow rates measured by chambers in the nearshore of two sites in Buzzards Bay. Data from several runs with two chambers.

Fig. 4. Calculated flow of fresh and seawater into chambers overa tidal cycle. Flow calculated from volumes and salinity data.

measure the volume of water that entered the seepage meter during set time intervals.

Flow rates measured using seepage meters are spatially quite heterogeneous (Fig. 3). There are differences between sites and within sites, as shown by the use of 10 replicate seepage meters set at 3 different distances from shore at each of the two different sites. The faster flows reached $301 \text{ m}^{-2} \text{h}^{-1}$. Our interpretation of Fig. 3 is that fast flows occur in scattered underwater springs augmenting a more widespread but much slower bulk flow through the interstices of the sediment. These springs are sporadically sampled, extending the tail of the distribution shown in Fig. 3 toward the right.

There is also temporal heterogeneity in flow through nearshore sediments. First, at least in our region, flows may vary seasonally because the height of the water table can fluctuate over a meter from spring to autumn (Teal 1983). This difference in pressure head may have an effect on flow rate. Further, there are interannual differences in groundwater recharge due to precipitation, which alter the height of water table. These intra- and interannual differences in water table elevation suggest that flows of groundwater to coastal waters are going to vary over time scales of months and years.

The flow of freshwater is not constant over short time scales either. Flows may vary over tidal cycles (Fig. 4). We calculated the volume of fresh and seawater that fluxed into our seepage meters based on changes in volume and chlorinity over two-hour intervals during a complete tidal cycle. These calculations show that there was a net flow of freshwater from the sediments during ebb and low tide. In contrast, during high tide there was a net flow of seawater out of the sediments. This tidally-related shift did not occur in all sites where we measured seepage, but seems to imply that in at least some places seawater mixes into porespaces of shallow layers of sediment during a tidal cycle. This mixing suggests a remarkable degree of replacement of fluid within the near-surface

Fig. 5. Top: Surface of water table near shore in the Pocassett site. Data obtained from wells (noted as 4, 5, 6, 7, 8, 9). The bay is toward back and left in the Figure. Measurement of distance is from a line of markers established above the average high tide mark on land. Bottom: Changes in height of water table (crosses), in relation to simultaneous measurements of seawater level (squares), Pocassett site.

layers of sandy sediments, a feature with potential biogeochemical significance. This was pointed out some time ago by Riedl et al. (1972) in a paper that discussed the potential importance of tidal pumping for exchanges, filtering, and transformations of compounds and particulates in water in the nearshore, although they did not deal with freshwater contributions.

Changes in head pressure due to tidal fluctuation of sea surface probably cause the pattern of fresh and seawater flow in and out of sediments. These changes also influence the watertable in the upland above the high tide mark. We defined the surface of the nearshore watertable (Fig. 5, top) within wells placed in the upland. The water level within these wells was not at all static; in

addition to interannual and seasonal fluctuations in watertable elevations already mentioned, the well data indicated tidally related oscillations in the watertable on shore (Fig. 5, bottom). These oscillations were of significant magnitude (9cm or so in Fig. 5, bottom) and lagged about two hours behind the tidal elevation in Buzzards Bay. Such patterns seem to be common to other sites on Cape Cod (Teal 1983).

Flows of groundwater in the near shore therefore change over widely differing time scales, and also vary over 3-dimensions. Attention needs to be focused on inter- and intra-annual changes in groundwater flow as well as on tidal effects occurring over time scales of hours. Models designed to predict groundwater flow and nutrient transport to coastal water need to incorporate this variability and dimensionality (Wang & Anderson 1982; Huyakorn & Pinder 1983; Bear & Verruijt 1987).

N:P input from watersheds and water column

In addition to the rate of nutrient loading to a water body from its watershed, the ratio of inorganic N to P supplied by external sources may have important implications for eutrophication (Jaworski 1981). It has been suggested that nutrient inputs whose N:P exceeds the Redfield ratio leads to phosphorus limitation of primarily producers (Howarth 1988) while lower values of N:P result in nitrogen-limited growth. Recent work in Chesapeake Bay suggests that there are significant seasonal changes in N:P of inputs which may shift the identity of the limiting nutrient in estuaries from N during summer to P during winter and early spring (D'Elia et al. 1986; Sanders et al. 1987; Webb & Eldridge 1987).

In the shallow coastal bays and lagoons that we have been concerned with, the N:P ratio in the water column may be influenced by the N:P of groundwater inputs. We lack a complete data set, but we can use information from our work in Great Sippewissett Marsh and Buttermilk Bay plus two sites within Buzzards Bay to assess this supposition. The $N.P$ of groundwater percolating from springs into Great Sippewissett Marsh varied seasonally, peaking in winter (dashed line in Fig. 6, top). We can compare the seasonal change in N:P of this groundwater input to shifts in the N:P of the water column at 'nearshore' stations and at 'offshore' stations within Buttermilk Bay. The nearshore waters in Buttermilk Bay showed changes in N:P similar to those found in the groundwater entering Great Sippewissett Marsh. Nutrient concentrations at offshore sites were about an order of magnitude lower than those nearshore (Fig. 6, top). Though the change in N :P was somewhat attenuated at the offshore stations, where mixing with lower nutrient seawater presumably occurred, even offshore the seasonal pattern of N :P was similar to that of groundwater inputs. Thus, at least in our two sites, there is a remarkable resemblance between the seasonal pattern in N:P of groundwater and of coastal seawater.

The decreased N :P in the water column during the summer months (Fig. 6,

Fig. 6. Top: N/P in groundwater near Great Sippewissett Marsh, and in nearshore and offshore water of Buttermilk Bay (both on Buzzards Bay), over a year. Bottom: N/P from Patuxent River estuary over a year, from D'Elia et al. (1986).

top) could be due to enhanced rates of denitrification during this season. Temperature, redox and organic matter supply can influence denitrification rates. It seems unlikely, however, that subsurface soil conditions could change sufficiently to alter the N:P ratio of the groundwater throughout the aquifer. Since seasonal changes in the composition of groundwater are slight at best, the biogeochemical processes underlying the alteration in N:P have to occur in very shallow sediments near the sediment/water interface. Seasonal increases in denitrification within the surface layer of sediments through which groundwaters move could account for the annual shift in the N:P ratio of effusing groundwater (Slater & Capone 1987). Changes in phosphate inputs may also be responsible for shifts in the N:P. Phosphate solubility increases under anoxic conditions which may develop within sediments during warm summer months, accelerating P release. These are likely to be among the mechanisms involved in altering the N:P.

Changes in N:P of groundwater may also take place during transit through a watershed. In our work in Buttermilk Bay we found that inputs of nutrients *into the watershed* had relatively low N:P (septic systems N: $P = 6$, precipitation $N:P = 8$, and fertilizer $N:P = 14$) (Valiela & Costa 1988). In contrast, the N to P ratios of the streams and groundwater that flowed from the watershed *to the Bay* were 20 and 26, respectively. Thus, there seems to be a 3- to 4-fold increase in N:P during transit. This suggests that if unaltered watershed inputs dominate the nitrogen economy of the bay, producers in the receiving waters may tend to *not* be nitrogen-limited. We should note, however, that the changes in N: P in transit through terrestrial systems greatly depends on the nature of the vegetation or land use mosaic in the watersheds (Jordan et al. 1986; Peterjohn & Correll 1986). Our data refer to sites where nutrient inputs are dominated by subsoil injection of wastewater. In watersheds dominated by swamps, farms, or forests, the effect of transit by nutrients may not increase N:P (Jordan et al. 1986). The relative effects of different land-use mosaics on nutrient transport still needs much study.

If we use the overly simple criterion of the 16:1 Redfield ratio of nitrogen to phosphorus to say what nutrient may limit producer growth, the seasonal fluctuations imply that producers are nitrogen-limited during the warm months, and perhaps phosphorus-limited in winter (Fig. 6, top). D'Elia et al. (1986), Sanders et al. (1987), and Webb & Eldridge (1987) also suggest seasonal variations in N and P limitation in producer growth in coastal waters. In fact, the N:P fluctuations, and the timing of the seasonal pattern D'Elia et al. (1986) found in the Patuxent River estuary (Fig. 6, bottom) resembled the pattern we found in Buttermilk Bay.

The relative magnitude of the regeneration ('old' nitrogen) pathway of the nitrogen cycle compared to the magnitude of the addition of 'new' externally provided nitrogen may affect the N:P in the water column. Nixon (1981) found markedly *lowered* N:P in regenerated nutrients diffusing out of sediments. The 'missing' N was thought to be lost by denitrification. If regeneration dominates the nutrient economy during late summer, decreases in the N:P of the water column such as those observed in Buttermilk Bay during June-August (Fig. 6) might be expected. To examine the relative rates of supply of nitrogen and phosphorus, and to understand how nitrogen and phosphorus supply may alter coastal production, we therefore need to conduct seasonal studies of nitrogen dynamics, including partition of advective vs. regenerative sources, producer uptake, microbial transformations, and physical transport.

Consequences of groundwater nutrient transport

There is an enormous freshwater literature that deals with the consequences of eutrophication. In a very real sense we in marine work are on the threshold of finding out what has been known to limnologists for a long time. The response of primary producers to nutrient loading within an estuary must be dependent on the balance between increased growth due to elevated inputs of the limiting nutrient and losses related to the flushing rate, as per the Vollenweider (1976) model. This is the point of the well-documented relation between phosphorus loading and phytoplankton chlorophyll (Vollenweider 1976). Additional evidence, based on correlations and inference from N:P values, on enrichments within small containers, and on whole-system enrichments in fresh waters, is

	Mean concentrations (μM)						
	NH,	NO,	DIN	PO.	N:P		
Groundwater	16.2	70	86	3.3	26		
Streams	8.6	5.5	14	0.7	20		
Surface runoff	n	21	27	1.2	23		
Precipitation	8.7	13.7	22.4	2.9	7.9		

Table 5. Concentrations of inorganic nutrients in fresh source waters entering Buttermilk Bay. Data from Valiela & Costa (1988).

consistent with the phosphorus loading results, and shows that in fresh water phosphorus limits potential primary production (Hecky & Kilham 1988).

In coastal systems the evidence for the role of nitrogen in limiting phytoplankton growth is based on inferences from loading calculations (Nixon & Pilson 1983; Boynton et al. 1982), on ambient nutrient concentrations, and more importantly, on nutrient enrichment experiments. Fertilization experiments in Scottish Sea lochs (summarized by Nixon et al. 1986), in salt marshes (Valiela et al. 1982, Teal 1986), and from the MERL mesocosm studies at the University of Rhode Island (Nixon et al. 1986) indicate that externally added nutrients increase primary production, change species composition, alter elemental cycles, rates of decay, energy flow, and affect upper trophic levels of food webs.

Although most of the data points to nitrogen as the primary limiting factor for potential net primary production in coastal waters, some of the evidence is not entirely consistent with a conclusion that nitrogen limits production (Kilham $\&$ Hecky 1988). There is also the matter of seasonality of N and P limitation (Howarth 1988). We still need to know much more about the specifics of eutrophication in shallow coastal waters, especially about the balance between loading and flushing rates, about nutrient transformations, and about sources of nutrients.

We have been examining the ecological consequences of nutrient loading in Waquoit Bay as a case study of nutrient loading to a representative shallow water system in a temperate region. Loading of nutrients, particularly of nitrate, from watersheds into Waquoit Bay has increased in recent decades and has, we believe, caused marked changes in the receiving waters, and in the ecosystem.

Groundwater entering Waquoit Bay flows from watersheds where urbanization has taken place. Human activities such as disposal of wastewater via septic tanks, and use of fertilizers increase nutrient concentrations in groundwater (Valiela & Costa 1988, and many other sources). We presently lack data for groundwater around Waquoit Bay, but can make preliminary comparisons using data from nearby Buttermilk Bay, where watersheds include some urbanized areas (Valiela & Costa 1988). Although degradation of wastewater yields $NH₄⁺$, nitrification converts most of the ammonium to nitrate in short order (Table 5). Because phosphate is readily adsorbed by sediment surfaces, groundwater concentrations of phosphate are relatively low (Table 5). The nutrient loading of coastal waters is therefore primarily an exercise in nitrate loading, at least in the sandy sediments of southern New England.

Table 6. Range of concentrations of ammonium, nitrate, and chlorophyll in water of different areas of Waquoit Bay (1987-1988) and in nearby groundwater. Vineyard Sound chlorophyll data form Goldman & Dennett (1983).

We have recorded four major potentially important types of changes in the ecology of Waquoit Bay, and interpret the changes as primarily a response to nitrogen enrichment. These include:

1. Somewhat elevated dissolved nutrient content

Nutrient content of water varies over Waquoit Bay, but tends to be somewhat higher in areas adjoining highly developed subwatersheds (Table 6). In view of the large differences in groundwater nutrient content (Table 6), the differences actually seen in the receiving water columns seem small.

2. Macroalgal growth is greatly increased

Fast growing opportunist taxa of macroalgae *(Cladophora* and *Gracilaria)* thought to be favored by high nutrient loadings (Rosenberg $\&$ Ramus 1982; Sewell 1982; Hanisak 1983) have taken over much of the bay floor (Fig. 7, top panels). These areas were previously dominated by eelgrass meadows (Curley et al. 1971). Lee & Olsen (1985) emphasized that in shallow embayments macrophytes can grow profusely at shoal depths where light is not limiting, and may carry out in excess of 60% of the primary production in these ecosystems (Nowicki & Nixon 1986; Costa 1988). We have measured layers of *Cladophora* of up to 75 cm thick in certain areas of Waquoit Bay. Such layers contain a large pool of nutrients.

Preliminary calculations (based on unpublished data and Fujita 1985) show that the layer of *Cladophora* on the bottom of Waquoit Bay contains (very conservatively) 0.2 to 11.2 \times 10⁴ kg N. This estimate does not include the N contained in other species. The range of the pool of N in *Cladophora* biomass brackets our preliminary estimate of annual N loading to the entire Bay, 2.7×10^4 kg N yr⁻¹, obtained by counting the number of dwellings in the watershed of Waquoit Bay and estimating nutrient loading using mass-balance methods, and estimates of per-capita production of nitrogen and phosphorus for people in the watershed (Frimpter et al. 1988; Valiela & Costa 1988). The explanation for the relatively low nutrient concentrations found in some nu-

Fig. 7. Distribution of 4 major species of benthic macrophytes in 1987 in Waquoit Bay. Contours are at intervals of 25% cover for *Cladophora, Gracilaria,* and *Zostera* and 10% for *Polysiphonia.* Data collected by S. Mulsow.

trient-loaded estuaries such as Waquoit Bay (Table 6) may thus be that nutrients are stored in increased macroalgal biomass.

The lack of high nutrient concentrations in waters of shallow coastal enbayments cannot, therefore, be taken to mean that nutrient loading rates are low: nutrients may simply be stored in macrophyte biomass (Lee & Olsen 1985; Thorne-Miller et al. 1983). These nutrients may be released at times of year during which macroalgae senesce and decay (Thorne-Miller et al. 1983; Birch et al. 1983). Enrichment has so fostered macroalgal growth in Waquoit Bay that macroalgae, in turn, may have become the dominant governors of nutrient dynamics in the bay.

Phytoplankton and macroalgae in the bay may compete seasonally for nutrients. If macroalgae indeed control nutrient availability, phytoplankton abundance and productivity may be depressed during times of the year when macroalgae grow, and phytoplankton ought to bloom when macroalgae senesce. These hypotheses need confirmation. As yet we lack data with which to evaluate directly the N or P limitation question; current experiments with

Fig. 8. Distribution of eelgrass beds within Waquoit Bay from 1938 to 1982, mapped from aerial photographs. Mapping was done only in the area to the east of the dotted line. Further decreases have occurred, so that eelgrass cover is much reduced since 1982. We intend to complete our study of the history of eelgrass over the remainder of the Bay, and will also keep records of distribution during each season we work in the Bay. Data of Costa 1988.

small-scale containers, and study of subestuaries exposed to different rates of nitrogen loading may help us address this matter.

3. Eelgrass growth is reduced

The eelgrass *Zostera marina* and other macrophytes such as *Polysiphonia* were formerly widely distributed in Waquoit Bay (Curley et al. 1971; Costa 1988) and still dominate bays with non-urbanized watersheds, such as nearby Popponessett Bay. These species have retreated to the southern area of Waquoit Bay (Fig. 7, lower panels). Aerial photographs over the past several decades show that there has been a sharp decrease in eelgrass bed distribution in recent years (Fig. 8). This decline is even more notable in that it is contrary to the regional trends, since eelgrass beds have been expanding on the eastern seaboard since the early 1930s, when wasting disease virtually eliminated eelgrass from our shores (Costa 1988).

Indirect effects of nutrient loading are likely involved in the decrease in

eelgrass. Nutrient loading increases growth of light-intercepting epiphytes on leaves of eelgrass (Sand-Jensen 1977; Sand-Jensen & Borum 1983; Sand-Jensen & Sondergaard 1981; Borum 1985; Twilley et al. 1985; Orth & Moore 1983; Costa 1988). Eelgrass production is not nutrient-limited (Harlin & Thorne-Miller 1981; Dennison & Alberte 1985), but light-limited (Dennison et al. 1987), so a decrease of light has serious consequences.

4. Effects of vegetation changes on benthic fauna

The changes in vegetation brought about by nutrient loading have thoroughly altered the rest of the trophic web of Waquoit Bay. Nutrient loading has increased production and consumption of oxygen sufficiently that macroalgal metabolism determines the $O₂$ content in the water column. We have evidence that the release of $O₂$ by macroalgal photosynthesis is large enough to affect water column oxygen concentrations (Peckol et al. in prep., and unpublished data of C. D'Avanzo). The large macroalgal biomass itself respires, and also produces large amounts of dissolved and particulate organic matter. Both lead to high rates of $O₂$ consumption. Increased nutrient (specifically, we think, nitrogen) loading has therefore poised the system in a very productive but unstable state. A few days of cloudy weather are sufficient for respiration of organisms to exceed production and consume enough O_2 to create anoxic conditions to the bottom waters killing invertebrates and fish. This has occurred in Waquoit Bay during the summers of 1987, 1988, and 1989.

The vegetation change also alters the habitat available to benthic animals: the bottom of the Bay is increasingly covered by thick layers of loose fronds, in which settled animals such as suspension or deposit feeders, or even active invertebrates such as seed scallops, sink. Suspension feeding is difficult within this canopy, and the lower levels of the macroalgal layer near the Bay floor are anoxic. These habitat changes thus result at least in reduction of growth, and probably in an increase in mortality for most benthic species.

We hypothesize that increases in macroalgae in Waquoit Bay have led to decreases in animal abundance. We have unpublished data on extensive mortality of flounder, shrimp, and crabs after anoxic events. We have also recorded recent decreases of scallops and a variety of other benthic invertebrates in Waquoit Bay. Harvests of scallops and area of scallop beds in Waquoit Bay have sharply decreased compared to earlier reports from several thousand bushels per season in the mid-60s (data of Merryl Alber, unpubl., and Curley et al. 1971) to less than 100 in 1988-89.

The changes in benthic vegetation and oxygen conditions prompted by added nutrients transported primarily by groundwater have reduced benthic fauna to a suite of species (including surface-feeding polychaetes, a few amphipods, shrimp, some sea cucumbers, an ophiuroid, and a few tunicates) that can survive on top of the macroalgal canopy or are tolerant of low O_2 conditions. Similar effects of nutrient loading and habitat alteration have been reported elsewhere (Williams Couper 1978; Gage & Coghill 1977; Rasmussen 1973; Pearson & Rosenberg 1978; Thrush 1986).

Conclusions

There is experimental evidence that nutrient loading, particularly of nitrogen, alters components of some coastal ecosystems. Yet we still cannot say what the effects of different rates of nutrient loading may be, nor what the specific response of many components will be. There is a broad variability to the relation of nitrogen loading and producer standing crop, for example (Nixon & Pilson 1983, Boynton et al. 1982) found a clear but variable correlation of chlorophyll and dissolved inorganic nitrogen loading. We also cannot predict the effect of nitrogen loading on upper trophic levels. We cannot, for example, say how given increases in nutrient loading will affect fish stocks in receiving waters (Nixon et al. 1986).

We know that nutrient loading from watersheds to coastal waters leads to many effects in nature, some of which are drastic enough to attract public attention, such as fin- and shellfish kills in situations with lowered oxygen concentration, phytoplankton blooms, shellfish bed contamination and closures, turbid waters, reduction of seagrasses, growth of opportunistic macroalgae, blooms of red and brown tide organisms, among others. Widespread and strong coupling between watersheds and receiving waters through nutrient loading therefore seems evident, but comprehensive and compelling data detailing the mechanisms involved are too sparse to explain how loading takes place, or to allow prediction of specific consequences of given levels of such loading (Nixon et al. 1986).

Increased nutrient inputs from anthropogenic sources are so pervasive that they will no doubt impose major changes on the structure and function of shallow coastal ecosystems for decades to come. To understand processes driving nutrient fluxes in land/sea margin ecosystems, we have to determine how rates of nutrient loading from watersheds are linked to responses of receiving coastal ecosystems. This understanding will only evolve after long-term interdisciplinary studies of eutrophication. Such studies should contrast watersheds that experience different rates of loading. The experimental design should combine the need to work at the whole-landscape level with the power of manipulative approaches to provide insight into processes and controls.

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