AN ABSTRACT OF THE THESIS OF

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Title: The Influence of Intertidal Macroalgae on Exchanges of

Nutrients and Oxygen in a Pacific Northwest Estuary

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Jonathan H. Garber

My working hypothesis was that macroalgae on intertidal

mudflats in the Yaquina Estuary represented a significant sink for

dissolved inorganic nitrate. To test this hypothesis, I studied

exchanges of dissolved inorganic nutrients and dissolved oxygen between

sediment and overlying water at two intertidal sites using an in situ

stirred bell-jar technique. By using transparent and opaque

plexiglass chambers and control bottles, both with and without

macroalgae, I partitioned changes in analyte concentrations into

changes caused by macroalgal metabolism and by sediment processes.

Initial and final measurements of dissolved oxygen and

nutrients (nitrate, nitrite, phosphate, ammonium, and dissolved organic

nitrogen) from both chambers and bottles allowed calculations that

partitioned the flux into sediment regeneration and macroalgal uptake

and production.

Macroalgal productivity ranged from 0.58 to 14 mg C m^{-2} h^{-1}

resulting in a demand for nitrate and phosphate that exceeded river

loading in the summer and fall. Far more phosphate was supplied to the

estuary by sediment regeneration and probably by exchange with ocean

water than by river flow. Macroalgal demand for phosphate exceeded supply only in July. Macroalgae may be responsible for at least part of the nitrate sink observed in mixing curves during summer and fall. However, macroalgal uptake is out of phase with most of the river supply of nitrate.

Sediment uptake and regeneration of nitrate and uptake of ammonium in Yaquina Estuary are among the highest reported for coastal sediment, and suggest that denitrification and nitrification may be active processes in this estuary.

Macroalgal uptake showed evidence of a seasonal shift from fall uptake of ammonium to winter-spring uptake of nitrate.

Predictions of nutrient demand based on oxygen production and stoichiometric ratios indicate that macroalgal metabolism follows ratios more similar to those listed by Atkinson and Smith (1983) than the traditionally employed Redfield ratios (1963).

Macroalgal productivity correlated with ambient inorganic nitrogen at the lower-estuary site, and with ambient phosphate at the upper-estuary site. This result, and element ratios from sediment regeneration, macroalgal tissue, and macroalgal uptake indicated that 1) nitrogen is more likely to be be limiting in summer and fall, and may be limiting in the lower estuary before upper regions; 2) phosphorus is more likely to be limiting in spring and summer, and may be limiting in the upper estuary before the lower. This is evidence of a gradient of potentially limiting nutrient from nitrogen in seawater to phosphorus in freshwater. The gradient varies with location in the estuary and with seasonal variations in the direction and magnitude of nutrient supply.

The Influence of Intertidal Macroalgae
On Exchanges of Nutrients and Oxygen
In a Pacific Northwest Estuary

by

John L. Collins, Jr.

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APPROVED:

Redacted for privacy

‾‾‾
Assistant Professor of Oceanography in charge of major

Redacted for privacy

‾‾‾
Dean of College of Oceanography

Redacted for privacy

‾‾‾
Dean of Graduate School

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Typed by researcher for_____ John L. Collins, Jr. _____

DEDICATION

To Sally and Casey;

their love, sacrifice, encouragement, and patience

were essential.

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TABLE OF CONTENTS

APPENDICES

LIST OF FIGURES

LIST OF TABLES

THE INFLUENCE OF INTERTIDAL MACROALGAE
ON EXCHANGES OF NUTRIENTS AND OXYGEN
IN A PACIFIC NORTHWEST ESTUARY

INTRODUCTION

This thesis focused on how much influence intertidal macroalgae (Ulva and Enteromorpha spp.) have on the exchanges of dissolved inorganic nutrients and oxygen between sediments and water in the Yaquina River Estuary, Oregon. In particular, it assessed macroalgal potential as a nitrate sink. An in situ bell-jar technique was used to measure fluxes of dissolved nutrients and oxygen across the sediment-water boundary. By comparing fluxes in chambers containing macroalgae with those covering macroalgae-free sediment, the contribution of macroalgae to the observed fluxes was estimated. Macroalgal production and nutrient uptake were also measured in light and dark bottle experiments. The monthly supply of nitrate to the estuary was calculated and compared to estuary-wide macroalgal removal capacity.

I. Generation of the Hypothesis

The impetus for this study came from a survey of seasonal variations in dissolved inorganic nutrient concentrations in the Yaquina Estuary during 1983-1984 (Garber et al. 1984, Butler 1986). Analysis of these data suggested that significant amounts of nitrate were removed from bay water in regions near broad mudflats in the bay.

Mudflats make up approximately 35% of the total estuarine surface area in Yaquina Bay (Cox 1973). The mudflats are covered by

dense mats of macroalgae from late spring to early fall. Mid-summer

biomass of the two most common macroalgal species in the Pacific

Northwest, <u>Ulva expansa</u> and <u>Enteromorpha prolifera</u>, is often greater

than 400 gdw m^{-2} (Davis 1981, Thom 1984). Of the sediment-associated

plants present in the bay, macroalgae have the highest gross production

per unit chlorophyll (Davis 1981). As for other marine primary

producers, macroalgal growth depends on a supply of dissolved inorganic

nitrogen and phosphorus, and several species generally increase their

growth rate and uptake of inorganic nitrogen when additional nitrogen

is available (Hanisak 1983). Preliminary calculations suggested that

the uptake of nitrogen by sediment-associated macroalgae could

represent a significant nitrate sink (Table 1).

These two lines of circumstantial evidence suggested that

macroalgal uptake of nitrate may contribute to the non-conservative

behavior of nitrate in the Yaquina Estuary. The sediment-chamber

experiments described in this thesis were designed to test the

hypothesis that macroalgal growth represents a significant sink of

dissolved nitrate in the Yaquina Estuary.

II.   Estuarine Loading, Eutrophication, and Macroalgal
       Growth

The preliminary survey of nutrient concentrations in Yaquina

Estuary (Garber <u>et al</u>. 1984) revealed a large seasonal flush of nitrate

that was apparently associated with fall and winter rainfall. The

introduction of large amounts of inorganic nitrogen to the headwaters

of estuaries in the Pacific Northwest is a point of concern for both

Table 1: Unit area production and components of total daily system net primary production of carbon, nitrogen and phosphorus during August in the Yaquina Estuary. Modified from Garber et al. (1984). Numbers in parentheses are normalized to phosphorus.

	Net Daily Production mmol m^{-2} d^{-1}			Partitioning of Daily Estuarine Production, % of Total (g,h)		
	C	N	P	C	N	P
Macroalgae (a,b)	560	30	1	49	39	31
Benthic Microalgae (c,d)	23 (115)	3 (13)	0.2	3	6	6
Phytoplankton (d,e)	83 (104)	13 (16)	0.8	11	26	38
Seagrasses & Epiphytes (b,d,f)	420 (525)	23 (29)	0.8	37	30	26
Epiphytes (b,f)	8 (800)	0.4 (40)	0.01	1	1	1

a) For Enteromorpha (Kautsky 1982, Owens and Stewart 1983)
b) C:N:P ratios equal 550:30:1 for macroalgae, seagrasses and epiphytes (Atkinson and Smith 1983)
c) Davis and McIntire (1983)
d) C:N:P ratios equal 106:16:1 for benthic microalgae and phytoplankton (Redfield et al. 1963)
e) Karentz and McIntire (1977)
f) Kentula (1983)
g) Area of the estuary calculated by planimetric methods in Cox (1975)
h) Areas available for plant growth, m^2 x 10^6 (% of total)

Total	15.7
Macroalgae	5.23(33)
Benthic Microalgae	7.69(49)
Phytoplankton	7.99(51)
Seagrasses and Epiphytes	5.23(33)

Total daily estuarine production for Yaquina Estuary (moles d^{-1} x 10^6) = Daily production (mol d^{-1} m^{-2}) x Area (m^2)

C	5.965
N	0.405
P	0.016

those involved with estuarine water quality and river watershed management. The latter group includes foresters, whose management practices may be responsible for a significant portion of the nitrate pulse (Brown et al. 1973, Miller 1974).

Implications of increased nutrient loading on estuarine eutrophication have been studied for many years. In spite of considerable research on such diverse topics as sediment regeneration of nutrients (Nixon et al. 1976), benthic oxygen demand (Hargrave 1969, Pamatmat 1975, Kemp and Boynton 1981, Nowicki and Nixon 1985b, Officer et al. 1985), nutrient absorption reactions (Carritt and Goodgal 1954, Pomeroy et al. 1965, Stirling and Wormald 1977), limits on and regulation of estuarine primary productivity (Cardon 1982, Owens and Stewart 1983, Graneli and Sundback 1985, Pregnall and Rudy 1985), infaunal metabolism (Henriksen et al. 1980, Kristensen et al. 1985, Kelly 1983), and input of organic matter (Pocklington and Leonard 1979, Garber 1982, Naiman and Siebert 1978, Andersen 1986), our understanding of the controls and balances that regulate nutrient cycling remain incomplete (Schindler 1981, Nixon 1981).

A lively discussion surrounds the question of which inorganic nutrient is most likely to be limiting to primary productivity in estuaries. Finding the answer to this question is critical to a better understanding of eutrophication in estuaries. In most instances, the choices include: nitrogen, the element considered limiting in most marine systems (Ryther and Dunstan 1971), and phosphorus, the element known to be limiting in freshwater systems (Schindler 1981), or both of these (Smayda 1974).

Both nitrogen (Nixon and Pilsen 1983) and phosphorus (Smith 1984, Nowicki and Nixon 1985b) have been interpreted as limiting in estuaries. Because the estuary is the "ecotone"[1] between freshwater and marine communities, it seems logical that a gradient of nutrient limitation may exist from freshwater phosphorus limitation to marine nitrogen limitation.

Anthropogenic supplies of nutrients, unquestionably a source for much nutrient loading on estuaries (Jaworski 1981, Maybeck 1982), may obscure the gradient between phosphorus and nitrogen limitation. Sewage now accounts for 50% or more of the inorganic nitrogen and phosphorus loading on the Hudson River Basin, Lake Superior, the Potomac River Estuary, and Chesapeake Bay (Jaworski 1981).

Problems associated with eutrophication in estuaries can be exacerbated by estuarine filtering processes that retain material delivered by inflow. The concept of estuaries as filters has received considerable attention. Recently, an entire symposium was devoted to this topic alone (Kennedy 1983). Sharp et al. (1983) divide estuarine filtering processes into a two-stage model. The upstream stage operates at the turbidity maximum zone, and is a geochemical filter in which flocculation is the main process. This filter is most efficient when river flow is low. High river flow can overcome the flocculation kinetics of the first stage, pushing more material through to a second stage: a biochemical filter. In this second stage, the main processes are biological uptake and recycling of materials: processes that have much faster kinetics than flocculation. With this two-stage filter, an

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[1] An "ecotone" is the zone of intergradation between ecological communities.

estuary is equipped to trap some river input (e.g. dissolved nutrients) regardless of the amount of river discharge. Thus, estuaries concentrate nutrient resources, a characteristic that can accelerate estuarine eutrophication as river loading increases.

If nutrient loadings on estuaries were not excessive, the concentration of resources in these systems may actually enhance production. And, if production exceeded degradation, the net surplus might be exported to coastal water. This concept, called "outwelling", has spawned much controversy since first elaborated by Odum (1980). The outwelling hypothesis is still under debate with evidence for and against its importance (Nixon 1981).

Unfortunately, estuaries can be so overloaded with nutrients that internal cycling processes break down, precluding outwelling of useful materials. When nutrient loading causes eutrophication, several results are possible: increased health hazards to humans and blocked migratory corridors for anadromous and catadromous fish (Casapieri 1983), lost recreational fishing opportunities and damaged nursery capacity for fish that spawn and develop in the estuary (Stoevener et al. 1972), and large-scale disturbances such as the die-back of seagrass in Chesapeake Bay (Tippie 1984).

Using data from Garber et al. (1984), I have calculated that the current nitrogen loading of the Yaquina Estuary is about 19 g N m^{-2} y^{-1} of nitrate alone, compared to total nitrogen loading of 4.9 g N m^{-2} y^{-1} on Narragansett Bay, 9.5 g N m^{-2} y^{-1} on Chesapeake Bay, 1.2 g N m^{-2} y^{-1} on the North Sea, and 9.3 g N m^{-2} y^{-1} on Lake Erie (Jaworski 1981). It is clear from the nitrate loading on Yaquina Estuary, that nitrogen dynamics in this Pacific Northwest estuary may differ significantly

from other estuarine and freshwater systems. The impacts of such a substantial load on what appears to be a relatively unpolluted, undeveloped estuary are unknown.

Phosphate, on the other hand, comes to the estuary from the ocean more than from the river (Garber et al. 1984, Butler, 1986). This bidirectional nutrient supply system provides an opportunity to examine nutrient dynamics at the interface between freshwater and saltwater systems.

III. Macroalgal Response to Nutrient Availability

Estuarine macroalgae are usually attached to the benthic substrate. Water movements, caused by tides, wind, and currents, and changes in water sources caused by weather, seasons, and upwelling, expose fixed algae to constantly changing water chemistry and hydrology, providing daily and seasonal cycles in environmental conditions, that are useful in testing hypotheses about estuarine nutrient cycling. In addition, macroalgae are located between the sediment and the water column, suggesting that macroalgae might intercept sediment-regenerated nutrients before they reach the water column.

Field studies of macroalgal metabolism in estuaries have shown that Ulva and Enteromorpha spp. (important macroalgal genera in Pacific Northwest estuaries) can have a measurable effect on nutrient cycles. Welsh (1980) reported that ammonium and phosphate uptake rates in intertidal beds of Ulva lactuca varied diurnally, and were the same

order of magnitude as microalgal rates and bare sediment exchange. Ammonium uptake rates in <u>Enteromorpha</u> spp. vary seasonally: maximum uptake occurs in summer and less uptake in spring and fall (Owens and Stewart 1983). <u>Enteromorpha</u> is also an important source of organic matter in an intertidal mudflat, supplying enough carbon to the sediment to support all benthic secondary production (ibid.).

Although these system-wide studies provide broad measurements of macroalgal influence, a thorough interpretation of the potential that macroalgae represent for nutrient uptake and cycling is difficult to achieve. Macroalgal nutrient uptake kinetics are not well known. However, a combination of the kinetic data available with a certain amount of speculation could provide a basis for comparison with new field results.

Because macroalgal uptake and assimilation of different forms of nitrogen interact, a study of nitrate uptake alone would not represent the true response of any system to nitrogen loading. All forms of inorganic nitrogen must be included in the analysis, and macroalgal response to each should be considered.

Most macroalgae probably can take up several forms of available nitrogen simultaneously (McCarthy 1980). The response to each form will not necessarily be the same. Ammonium uptake is usually faster and more prevalent than nitrate uptake. In some instances, nitrate uptake may be suppressed by ammonium availability. Nitrite can be toxic to macroalgae at lower concentrations than other forms of nitrogen. In <u>Agardhiella</u> <u>subulata</u>, there is a preferred heirarchy for the uptake of nitrogen species. DeBoer (1978) found the sequence is ammonium first, followed by sewage (his term), nitrate, and urea.

Characteristics of nutrient uptake by macroalgae can be studied by using nutrient kinetic curves that yield specific constants describing uptake capabilities (see Raun 1983 for a general discussion). Half-saturation constants (K) for ammonium and nitrate are nearly equal at 2-13 micromolar with maximum uptake rates (V_{max}) from 8-25 micromoles $gdw^{-1} h^{-1}$ (DeBoer 1981). The uptake mechanism for nitrate is probably carrier-mediated, but ammonium may have a dual uptake mechanism: carrier-mediated at low concentrations, and diffusion-limited at higher concentrations (ibid.).

Phosphorus uptake dynamics are simpler than for nitrogen because most inorganic phosphorus is present in seawater as reactive orthophosphate. Phosphate uptake by many macroalgae is also saturation-limited, so is probably accomplished by active transport. Half-saturation constants and maximum uptake rates are around 0.4 micromolar and 0.47 micromoles $gdw^{-1} h^{-1}$ respectively (O'Gorman unpub. from DeBoer 1981). Phosphate monoesters can be taken up by some macroalgae when alkaline phosphatase enzymes are present in the cell membrane (McCarthy 1980), but their importance in the natural environment is unknown.

In this study, Ulva spp., and less frequently Enteromorpha spp., were the dominant algae found on the mudflats. Some specifics of nutrient uptake for each of these genera have been measured. Ulva fasciata has higher growth rates when grown on urea than on nitrate or ammonium (Mohsen et al. 1974). In Ulva lactuca, ^{14}C fixation is stimulated by orthophosphate additions up to 25 micromolar (Waite and Mitchell 1972). Enteromorpha is known to accumulate polyphosphates

(Kuhl 1974). In one study, K and V_{max} for phosphate uptake in Enteromorpha compressa were 59 micrograms per liter and 515 micrograms $gdw^{-1} h^{-1}$ respectively (Kautsky 1982). Kinetic constants of K=16.6 micromolar, and V_{max}=129.4 micromoles $gdw^{-1} h^{-1}$ have been reported for nitrate uptake in Enteromorpha spp. (Harlin 1978). Ammonium uptake kinetics have been studied in Enteromorpha compressa, and Kautsky (ibid.) reported K=31 micromolar and V_{max}=336 micrograms $gdw^{-1} h^{-1}$. Owens and Stewart (1983) measured uptake rates that varied from .003 to 15.5 microgram-atoms ammonium-N $gdw^{-1} h^{-1}$ for Enteromorpha spp. in the field. The discrepancies between laboratory and field results illustrate the problems of extrapolating laboratory rates for field studies.

Because the uptake of inorganic nitrogen and phosphorus requires energy, I would not expect the internal stores of inorganic ions thus accumulated to be given up easily. This expectation is not fulfilled, however, when sufficient internal stores are accumulated. Macroalgae are actually quite "leaky" and will release inorganic nitrogen and phosphorus unless growth is nutrient-limited (M.W. Davis pers. comm.). Little work has been done on this release, probably because it happens when the algae are not nutrient limited.

Organic forms of nitrogen and phosphorus, however, are often released by macroalgae for specific purposes: growth regulation, inhibition of other species, and coordination of plasmogamy are some of the functions studied (Hellebust 1974). Measuring and interpreting this organic release is complicated by the potential for bacterial interference. For example, in a non-axenic macroalgal culture with urea as the nitrogen source, the disappearance of urea does not

necessarily indicate urea uptake by the alga. Bacteria could break down the urea into ammonium, which is then taken up by the plant (Lobban et al. 1985). Compared to ambient concentrations of inorganic nitrogen, extracellular releases of organic nitrogen by macroalgae are not expected to be significant losses from intracellular nutrient pools (Pregnall 1983).

Intracellular nutrient pools are more closely related to cell growth rate than extracellular nutrient concentrations (Droop 1974). When ambient nutrient supplies exceed metabolic demands, nitrogen and phosphorus can be accumulated within macroalgal cells. Nitrogen can be stored as pigments or as unused nitrate kept in vacuoles (DeBoer 1981). Phosphorus can be stored as polyphosphates (Kuhl 1974) or as phosphate in vacuoles (Healey 1973). These excess nutrient stores are thought to be used when extracellular nutrient availability decreases below sufficient levels. The degree and duration of any such deprivation will determine whether the stored nutrients will forestall a growth crisis, or the plant will have to respond with conservation measures when nutrients are in short supply.

When nutrient availability limits algal growth and internal stores of nutrient are exhausted, macroalgae may decrease the amount of photosynthetic pigments, increase storage of carbon-rich compounds such as carrageenan and agar, and decrease the concentration of proteins and nucleic acids (Healey 1973). In addition, uptake mechanisms can be changed to take up nutrients from the environment in spite of their low concentrations. When nitrogen deficient, the plant may switch from a scarce form of nitrogen ion to an abundant one.

Even though internal nutrient concentrations are more critical for plant growth than external concentrations, ambient nutrient concentration is a critical factor for macroalgal growth: one that interacts with other characteristics of the environment. For example, if water movement is slow enough to allow a boundary layer to develop, macroalgal nutrient uptake will be more limited by diffusion than by ambient concentration. Other environmental factors, such as previous light exposure, temperature acclimation, and previous nutrient supply predetermine the macroalgal response to nutrient levels by affecting internal nutrient pools and metabolic rates.

The net elemental composition of macroalgae can change in response to all of the variables discussed above. Ratios of elements found in macroalgal tissues thus provide a measure of the plant's physiological state. Redfield's ratios (Redfield et al. 1963) of C:N:P=106:16:1 have long been used as an ocean-wide average against which to compare such diverse processes as phytoplankton nutrient uptake, geochemical sources and sinks, and sediment regeneration of nutrients. Recently, Atkinson and Smith (1983) compiled an exhaustive list of macrophyte C:N:P ratios from the literature. Their median result was 550:30:1, quite different from Redfield's ocean average. Redfield ratios are based on open-ocean plankton composition, whereas Atkinson and Smith's ratios are based only on macroalgal tissue composition. The newer macrophyte ratios are more appropriate than Redfield's for predicting changes in nitrogen and phosphate ratios based on oxygen production by macroalgae, and hence were used in analysis of data for this thesis.

IV.   Sediment Metabolism: Oxygen Demand and Nutrient Regeneration

Estuarine nutrient concentrations are a result of allocthonous supplies and an estuarine recycling process: sediment metabolism. "New" nutrients come from the breakdown of allocthonous organic matter or from outside sources such as river flow. Degradation products from autochthonous organic matter are "recycled" by sediment and water-column metabolism, and will not contribute to increases in system biomass. Heterotrophic metabolism in marine sediment converts organic matter into inorganic nutrients, carbon dioxide, and refractory organic matter, while consuming oxygen. The net result of sediment metabolism is often a release of regenerated nutrients from the sediment (Rowe et al. 1975, Nixon et al. 1976, Elderfield et al. 1981, Nixon 1981). Whether or not these releases reach overlying water may depend on other factors such as interaction with particulates (Pomeroy et al. 1965, Balzer 1984), sediment-associated microalgal uptake (Davis 1981), and macroalgal growth.

Measuring the amount of organic matter deposited in an estuary, and thus available as fuel for sediment metabolism, is difficult. Possible sources include freshwater inflow, seawater exchange, and local primary and secondary production. Direct measurements using sediment traps do not provide meaningful results because sediment is often resuspended in estuaries. River input of organic matter can be measured (Naiman and Siebert 1978), but to determine how much material is retained in the estuary, throughput must also be measured. Naiman and Siebert (1978) point out the difficulties of measuring throughput, concluding that it may be one of the last parameters known for an

estuary. Measuring seawater exchange is as difficult as measuring throughput, and has only been attempted by modeling (Kremer and Nixon 1978). Primary and secondary production can be estimated from oxygen production and field sampling (Frolander et al. 1973, Deason 1975, Smith 1978, Nixon 1981) and may be the most constrained measurements of the possible sources.

When organic matter input exceeds the regeneration capabilities of the sediment, sediment metabolism depletes the dissolved oxygen in the water column, setting off a chain of events that can lead to eutrophication. In the Yaquina River Estuary, in spite of the high winter nitrate loading, this does not occur because bottom water remains oxygenated throughout the year (Garber et al. 1984, Butler 1986).

Marine sediment oxygen demand is widely studied (Hargrave 1969), and is known to respond to many variables: organic loading (Nixon 1981), temperature (Hargrave 1969), infaunal metabolism and density (Kelly 1983), and sediment-associated microalgal primary production (Davis 1981). Recent studies show that some shallow-water sediment communities may consume more organic matter than they produce (Nowicki and Nixon 1985a), indicating that imported organic material is necessary to maintain benthic productivity. To complicate matters further, sediment oxygen demand varies with water depth (Kemp and Boynton 1981). As a result, a complete model of sediment oxygen demand and consequent nutrient regeneration should include the influence of all of these variables.

By using expected stoichiometric ratios (e.g. Redfield et al. 1963), sediment oxygen uptake can be used to predict how much inorganic nitrogen and phosphorus the sediments are expected to produce. These sediment-water nutrient fluxes can be extremely variable spatially, but overall, often follow the expected stoichiometry (Nixon 1981). Sediment-associated nutrient remineralization can supply an important fraction of plant nutrient demand (Furnas et al 1976, Garber 1982, Hopkinson and Wetzel 1982). Other features of the coupling between sediment metabolism and nutrient dynamics were reviewed by Zeitschel (1980).

With the development of new techniques in the past five or six years, attention has been increasingly focused on denitrification in marine sediments (Seitzinger et al. 1980). A major reason for this increased popularity is that denitrification offers a new explanation to an old problem. When budgets for sediment-regenerated nutrients are compiled and compared to expectations based on stoichiometric ratios, a portion of nitrogen is consistently missing. Denitrification rates are large enough to suggest that the missing nitrogen may be converted to atmospheric nitrogen or nitrous oxide. The highest reported denitrification rates were found in an estuary (Nishio et al. 1982).

Because the substrate for denitrification is usually nitrate, sediment uptake of nitrate is strong evidence for denitrification. Smith et al. (1985) found a correlation between river nitrate input and measurements of denitrification rate in a turbid estuary. With nitrate as the main focus of this study, sediment-water fluxes may provide some insight into the denitrification process in the Yaquina River Estuary.

V.   Other Factors Influencing Estuarine Metabolism

Numerous factors in addition to those discussed above may exert significant influence on estuarine metabolism and nutrient cycling. In this study, probably none of these is more important than the hydrodynamics of water flow over the mudflats. Welsh's (1980) study of material movement through the intertidal zone in an estuary demonstrates how important hydrodynamics can be to interpretation of estuarine function. Imberger et al. (1983) removed the influence of flow oscillations by combining calculations of variance components with sampling design. A refined analysis of this study would include the hydrodynamic aspect of intertidal water flow.

Among the remaining factors, interaction between particulates and phosphate may be second only to hydrodynamics in implications for this thesis. Phosphate can be scavenged from the water column by sediment floc (Balzer 1984) and can be bound by iron oxides that are sorbed onto clay minerals (Nixon et al. 1979). If the sediment environment changes from oxidizing to reducing, the iron becomes more soluble, releasing bound phosphate (ibid.). This physico-chemical process is a major concern in phosphorus-limited systems because it is an integral part of the eutrophication process. The related sequence of events is:

1) As eutrophication begins, some of the initial loading of phosphate is sequestered by combination with iron oxides in suspended particles and sediment.

2) Increased nutrient loading causes increased productivity and

accumulation of organic matter in the sediment.

3) Sediment oxygen demand increases as the organic build-up is decomposed.

4) As sediment anoxia develops, the sediment chemical environment changes from oxidizing to reducing, dissolving some of the iron-phosphate complex removed previously and releasing phosphate into an already eutrophic, phosphorus-limited system.

Thus, eutrophic freshwater systems have a built-in phosphate reservoir that can accelerate the deterioration of water quality as the process progresses. Luckily, decreasing the phosphate loading can demonstrably reverse the secenario (Jaworski 1981).

Primary production in an estuary is usually dominated by plankton or attached macrophytes. For this reason, most studies of estuarine production have focused on these portions of the plant community (Mann 1980). As explained above, the macroalgae can play a major role during particular seasons, as can the sediment-associated microalgae. In winter, sediment-associated diatoms dominate benthic plant biomass in Yaquina and Netarts Bays (M.W. Davis pers. comm.). The microalgal communities in Yaquina Bay respond to increased nitrogen, but are not nitrogen-limited (Cardon 1982). Graneli and Sundback (1985) have also shown that microalgae can be an important nutrient sink in shallow water.

The water column can be a source of nutrients as well as a sink. Zooplankton excretion can be an important nutrient source for the phytoplankton (Smith 1978), but this is not a source of new nutrients. Zooplankton excretion products represent nutrients originally provided in the plankton consumed (Vargo 1979). Pelagic regeneration can also

supply nutrients in the water column, but is not likely to be significant in shallow water, compared to sediment regeneration (Nixon 1981).

METHODS AND PROCEDURES

I. Description of the Study Sites

The Yaquina River drains 627 km^2 of coastal mountain range in
west-central Oregon and reaches the Pacific Ocean via the Yaquina River
Estuary. Weather in this region is characterized by dry summers and
rainy winters. Salinity in the bay varies from 10 to 34, depending
primarily on the amount of freshwater input. High rainfall in the
watershed is accompanied by increased riverflow and lowered salinities
throughout the estuary. Seasonal winds that accompany the summer
weather pattern cause upwelling, providing cold, nutrient-rich water
along the coast. Exchange of bay water with this coastal water
moderates bay temperature, keeping it lower in summer than insolation
would otherwise produce. Central bay temperature remains near 12
degrees C year-round, but variation is greater in shallow water because
of insolation. Mean diurnal tide range is 2.4 m with a maximum range
of 3.8 m. Mean freshwater input from the Yaquina River varies from
0.34 m^3 s^{-1} in August to 20 m^3 s^{-1} in December, and averages 7.1 m^3 s^{-1}
annually (Friday and Miller 1984). Vigorous tidal flushing in the bay
produces a well-mixed water column in the summer although some
stratification occurs in the winter.

Two sites were sampled (Figure 1), both exposed at mean low
water. Site 1 is exposed to more saline water than Site 2. Each site
was sampled five times: Site 1 on 22 Sept. 1984, 6 Oct. 1984, 4 Dec.
1984, 19 April 1985, and 1 July 1985; Site 2 on 9 Sept. 1984, 7 Oct.
1984, 13 Jan. 1985, 8 Mar. 1985, and 30 June 1985. Sampling dates were

Figure 1:   Study sites in Yaquina Estuary.   Intertidal areas are shaded.   (from Cox, 1973).   YAQ=Yaquina Bay Study Sites, 1983-84; SAF=sites from this study, 1984-85.

Figure 1

YAQ Station 2

SAF
Site 1

SAF
Site 2

YAQ Station 4

TIDELAND MAP
OF
YAQUINA BAY

STATE OF OREGON
DIVISION OF STATE LANDS
SEPTEMBER 1972
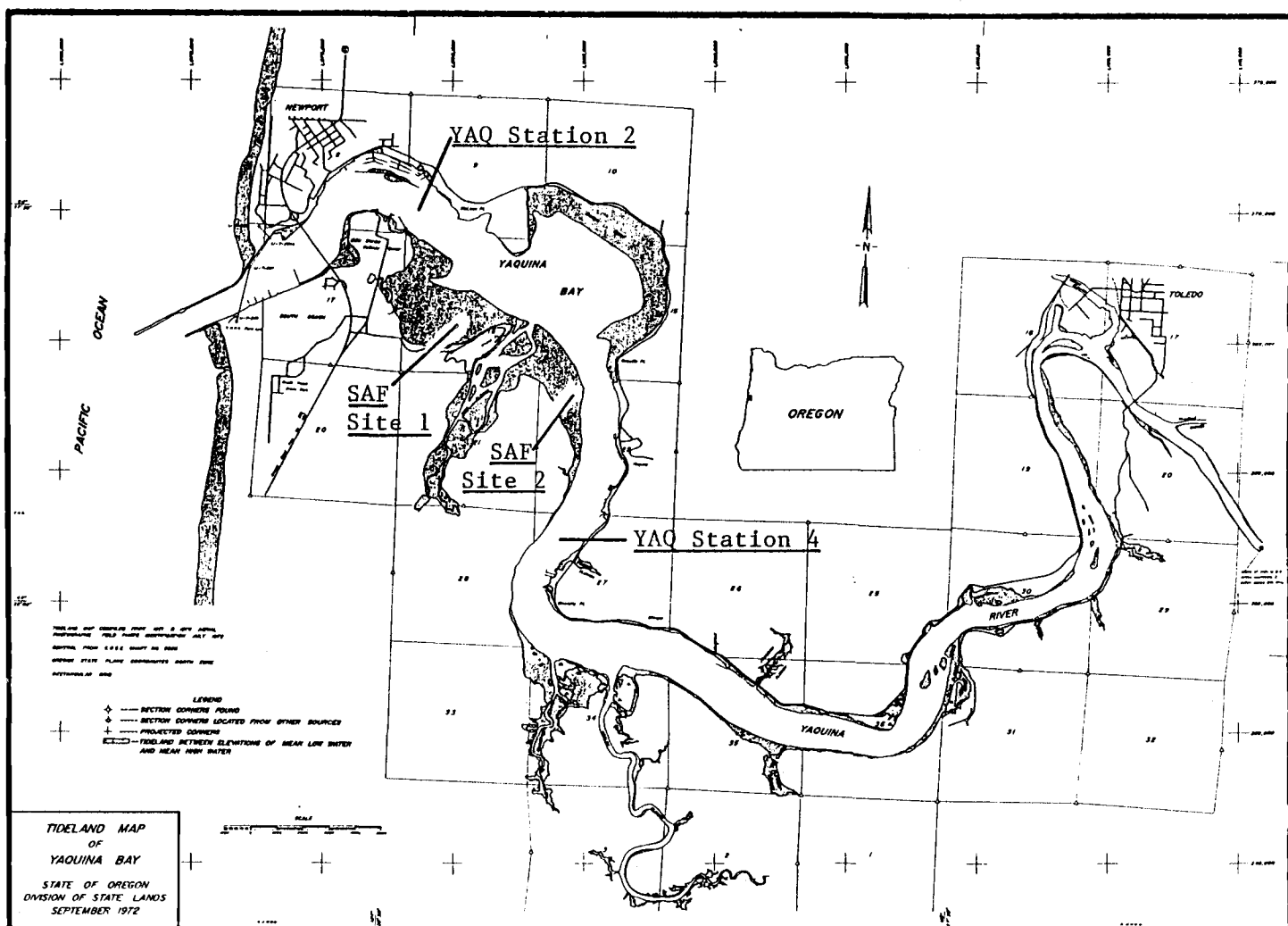
determined by tidal cycles and time required to complete data analysis.
Relative positions of sampling locations are shown in Figure 2. The
sediment at each of these sites was described by Kulm (1965). At Site
1, sediment was classified as fine and medium sand to silty sand, with
organic matter measured as 2.92%. Site 2 sediment was silty sand with
undetectable amounts of organic matter. Median diameters of surface
sediments range from 2.3 to 3.6 phi for both sites.

II. Experimental

Net fluxes of dissolved oxygen and nutrients at the two sites
were measured using a stirred bell-jar technique with 8 water-tight
cylindrical acrylic chambers (4 clear, 4 opaque). The chambers were
designed and built by M. Kentula (1983).

Field experiments were done when higher high slack tides
occurred between 1000 h and 1300 h local time. The chambers were
deployed two hours before high slack water. Each was pressed into the
sediment to a depth of 30 cm, enclosing a sediment surface area of
.0128 m^2 and 5.7 liters of water above the sediment surface. Two light
and two dark chambers were placed over macroalgae, the other four were
pressed over sediment with no visible macroalgal cover. Macroalgal
fronds that were bright green, not in a large clump of algae, and
appeared to be smooth and uniform in texture were selected for use.
Algae with these characteristics were assumed to be relatively young
and photosynthetically active. The sediment surface was disturbed as
little as possible while the chambers were being placed. As the tide

Figure 2: Location of sampling sites for each sampling date; relative
to water depth. Each site is identified by one or more
sampling dates. MHHW=mean higher high water (water
depth=2.44 m); MLLW=mean lower low water (water depth=0 m).
Not to scale.

Figure 2

Intertidal Sediment Surface

2.5

2.0   6 Oct. 1984
                                             1 July 1985

1.5   4 Dec. 1984

1.0   22 Sept. 1984
                                                       19 Apr. 1985

0.5

0

0   300   600

Water depth (m)

Site 1

9 Sept. 1984

13 Jan. 1985

7 Oct. 1984

30 June 1985

8 Mar. 1985

0   300

Site 2

Linear distance between MHHW and MLLW (m)
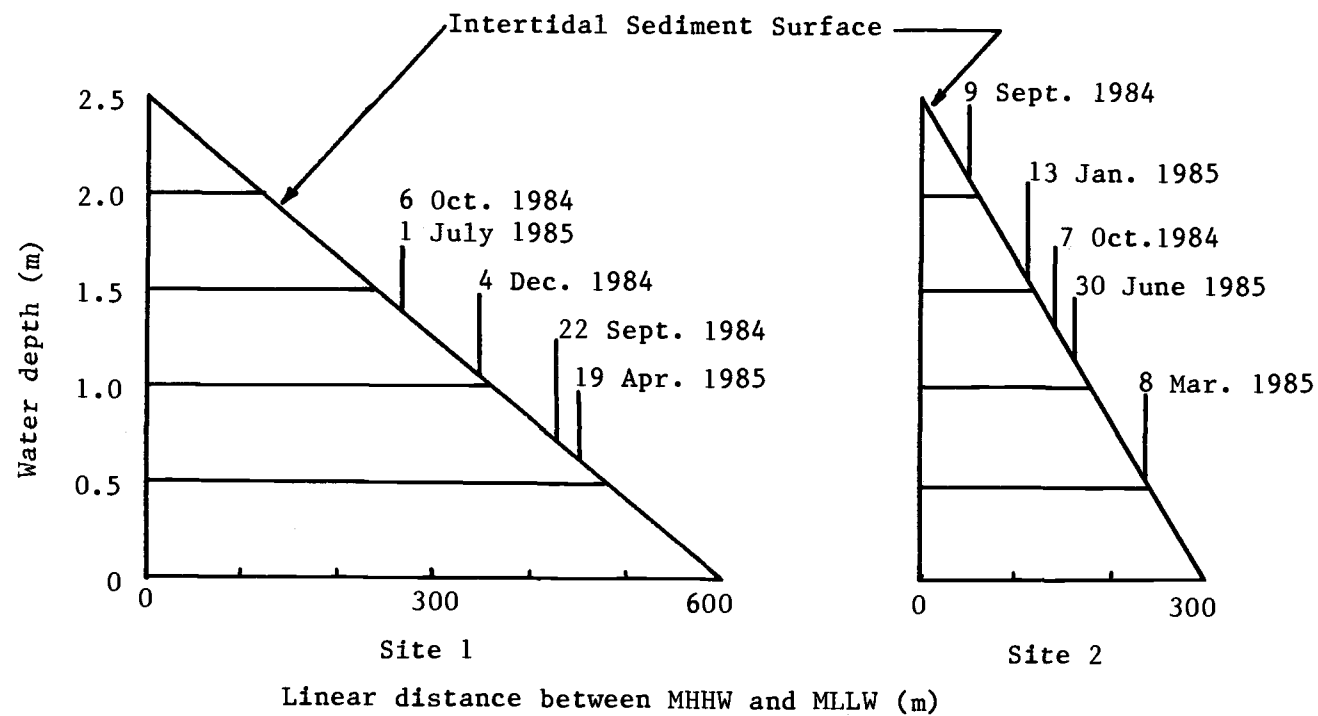
rose, the chambers filled with surrounding bay water through a small port in the chamber wall. When the chambers were nearly full, initial dissolved oxygen and nutrient samples were taken from inside the chamber and the chambers were sealed. Water in the chambers was gently stirred during the entire incubation period by an enclosed, battery-driven impeller. The rising tide completely covered the chambers. Final samples were taken approximately two hours after high slack tide.

Four light and four dark water-filled bottles (1-liter pyrex "Fleakers" with rubber stoppers) - 2 with and 2 without macroalgae - were incubated with the chambers for two to three hours. These bottles were suspended just above the sediment surface on a octagonal framework of PVC pipe that was designed by J. Garber. Each bottle was suspended by a nylon cord on a brass swivel, and contained a glass marble that agitated the bottle contents as the current buffeted the bottles. Initial oxygen and nutrient samples were taken from the bay water used to fill the bottles. Final samples were taken from each bottle at the end of the incubation period.

On 3 December and 12 January, the relation of daylight to tidal cycle would not allow field experiments, so sediment cores were brought to laboratory tanks. Chambers were deployed as described above. Then, with as little disturbance as possible, chambers were dug out of the surrounding sediment and capped for transport. In the laboratory, the chambers were set in outdoor tanks supplied with a continuous flow of bay water. Chambers filled with bay water as the tank filled, and were left overnight to decrease the trauma of transportation. Chambers and control bottles were placed to be in direct sunlight throughout the

incubation period. Incubations began the following day: initial water samples were taken from each chamber and the chambers sealed; algae collected on the mudflats the day before and kept in a bucket of seawater overnight were used in the bottle experiments; bottles were filled with water from the outdoor tank. All other procedures were the same for both tank and field experiments.

Field environmental conditions were measured hourly during each experiment. Salinity and temperature were measured at the water surface and sediment surface over the mudflat using a conductivity-thermistor probe (Montedoro-Whitney CTU-3). Salinity was also checked in the laboratory with an A/O refractometer. Light intensity at the water surface and the sediment surface was measured with a LiCor quantum photometer during all incubations.

Macroalgae from both chambers and bottles were sealed in foil at the end of the incubations, kept on ice, and brought back to the laboratory for weighing and elemental analyses.

III. Analytical

Nutrient samples were collected in 250 ml polyethylene bottles, and kept on ice until returned to the laboratory, where they were filtered (Whatman GF/C) and subdivided into portions for three analyses: automated analysis of nitrate, nitrite, and phosphate (Calloway et al. 1972), manual ammonium analysis (Solórzano 1969), and an automated modification of D'Elia's (1977) dissolved organic nitrogen (DON) analysis. Oxygen samples (in clear, 300 ml. BOD bottles) were

fixed (basic iodide and manganous reagents) immediately in the field and were analyzed by Winkler titration (Strickland and Parsons 1972) as soon as they were returned to the laboratory. Ammonium samples were analyzed as soon as subsampling was completed. Inorganic and organic nutrient samples were refrigerated and analyzed within a day if possible, or frozen for two days to two weeks in acid-cleaned, acetone-rinsed poly bottles. Total dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite, and ammonium concentrations. Precision of each chemical analysis is given in Table 2.

In the laboratory, algal samples were rinsed briefly with distilled water, freeze-dried, weighed, ground to a fine powder and kept in a dessicator for further analysis (Davis 1981). Some algal samples were kept frozen for several weeks before freeze-drying.

Sediment samples were taken during some field experiments. These were kept frozen until they could be subsampled, filtered and rinsed with distilled water to remove salt. Soaking sediment samples in 6N HCl removed carbonate. After rinsing and filtering again, the samples were dried at 60 degrees C, ground to a fine powder, and kept in a dessicator until analyzed.

Algal and sediment samples were analyzed for total insoluble carbon and total insoluble nitrogen by high-temperature combustion (Perkin-Elmer 240 Elemental Analyzer).

IV. Calculations

Flux calculations for each chamber are based on changes in concentration of chemical constituents in the water overlying the

Table 2: Precision of chemical determinations.

Analyte	Method	Precision	Reference
Nitrate + Nitrite	Colorimetric - automated	+0.1 μM	Callaway et al. (1972)
Phosphate	Colorimetric - automated	+0.01 μM	Callaway et al. (1972)
Ammonium	Colorimetric - manual	+0.06 μM	Solórzano (1969)
Dissolved Organic Nitrogen (DON)	Persulfate Digestion	+0.1 μM	D'Elia et al. (1977)
Dissolved Oxygen	Winkler Titration	+3.0 μg-at O liter	Strickland and Parsons (1972)

sediment cores. Adjustments were made for chamber volume, net plankton production and respiration (bottle experiments), sediment core surface area, incubation time and macrophyte dry weight. The basic form of the equation used to calculate fluxes was:

$$\text{Flux (moles m}^{-2}\text{ h}^{-1}) = \frac{(F - I - C)V}{A * T}$$

F = final concentration of analyte
I = initial concentration of analyte
C = control bottle final concentration minus initial concentration: may be positive, negative, or zero
(Note that opaque bottles without macroalgae were the controls for the opaque chambers, and transparent bottles without macroalgae were the controls for the transparent chambers.)
V = volume of water in the chambers (5.7 liters)
T = incubation time in hours
A = surface area of sediment within chamber (m^2)

Macrophyte production and benthic oxygen uptake were determined by comparing fluxes in light and dark. Oxygen flux was converted to carbon by using a photosynthetic quotient of 1.2 (i.e. mg C = 5 x mg-at O) (Ryther 1956).

The influence exerted by macroalgae on sediment-water exchanges of oxygen and nutrients was calculated in two ways. One aproach normalized the flux to the biomass of macroalga in the chamber, the other expressed fluxes on an areal basis without the biomass influence. Comparisons of the two approaches were used to determine whether seasonal patterns of fluxes and correlations between them were more dependent on macroalgal biomass or sediment processes.

By measuring flux in transparent chambers both with and without macroalgae, the net influence of macroalgal growth was calculated. The

two ways of calculating flux attributable to macroalgal growth are as follows:

Method 1: moles gdw^{-1} h^{-1} = $\dfrac{[(L+)-(\bar{L}-)]A}{gdw}$

Method 2: moles m^{-2} h^{-1} = $(L+)-(\bar{L}-)$

L+ = total sediment community including algae, individual
    transparent chambers (moles m^{-2} h^{-1})
$\bar{L}-$ = total sediment community without algae, mean of two
    transparent chambers (moles m^{-2} h^{-1})
A = surface area of sediment in each chamber (m^2)
gdw = dry weight of macroalgal tissue (g)

Significance tests in correlation included an adjustment for bias at low sample size (Sokal and Rohlf 1981).

RESULTS

I. Environmental Conditions

During 1983-1984, a series of transects along the Yaquina
Estuary established baseline data of nutrient concentrations for the
low tide mixing regime in the estuary (Garber et al. 1984, Butler
1986). These data provide a convenient basis for comparison with field
conditions encountered during this study and provide some sense of the
scale of interannual variability in the bay. It is important to note
that the data from 1983-1984 (hereafter referred to as YAQ data) were
taken in mid-channel around low slack water, while field conditions in
this study (hereafter referred to as SAF, Sediment-Algal Flux, data)
were measured over mudflats. Only data from the two YAQ stations
closest to SAF study sites will be used for comparison. YAQ Station 2b
was located in mid-channel, on the bottom, but close to SAF Site 1, and
represents high-salinity estuarine water. YAQ Station 4s was also in
mid-channel, but was at the surface close to SAF Site 2 and represents
more brackish estuarine water. YAQ and SAF upstream stations are more
influenced by river flow, whereas downstream stations are more
influenced by mixing with offshore coastal water.

A. Physical Variables

Temperature readings at the two YAQ stations closest to SAF
study sites were similar except during the period from June to October
(Figure 3). The seasonal difference is probably caused by higher-

Figure 3: Seasonal variation of a. ambient temperature b. ambient salinity in Yaquina Estuary. Open boxes=SAF Site 1, closed boxes=SAF Site 2, crosses=YAQ Station 2b, diamonds=YAQ Station 4s. SAF data from 1984-85 (this study). YAQ data from 1983-84 (Garber et al. 1984, Butler 1986).

Figure 3

a. AMBIENT TEMPERATURE
YAQ and SAF Data
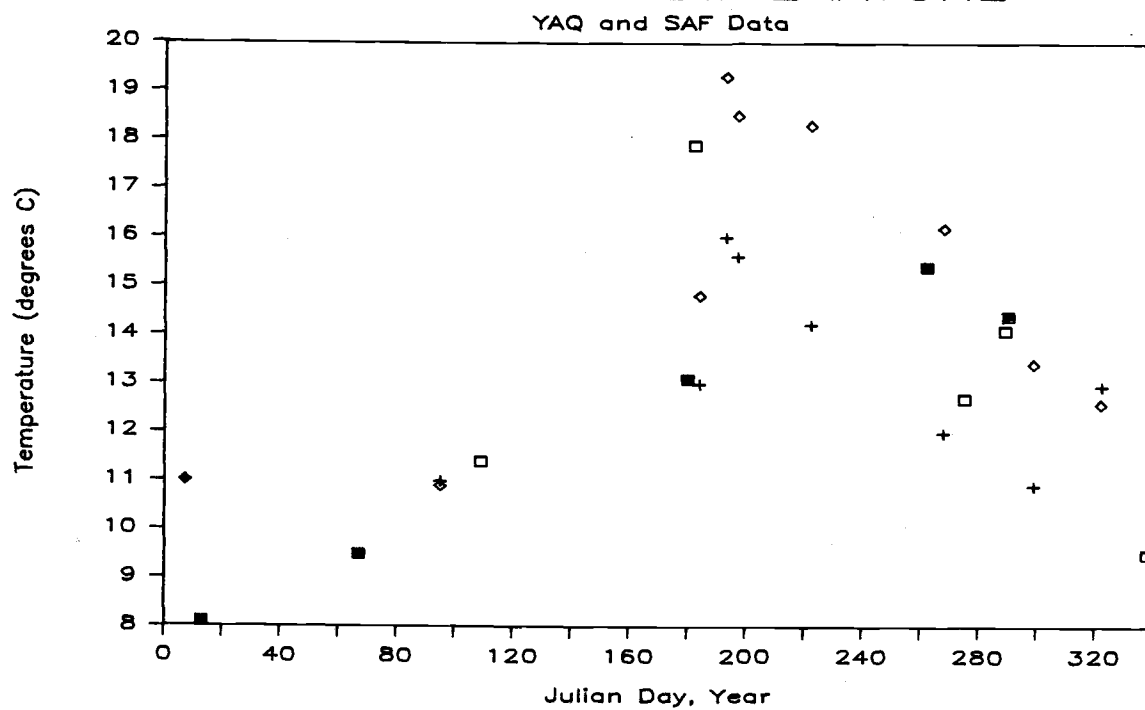
b. AMBIENT SALINITY
YAQ and SAF Data
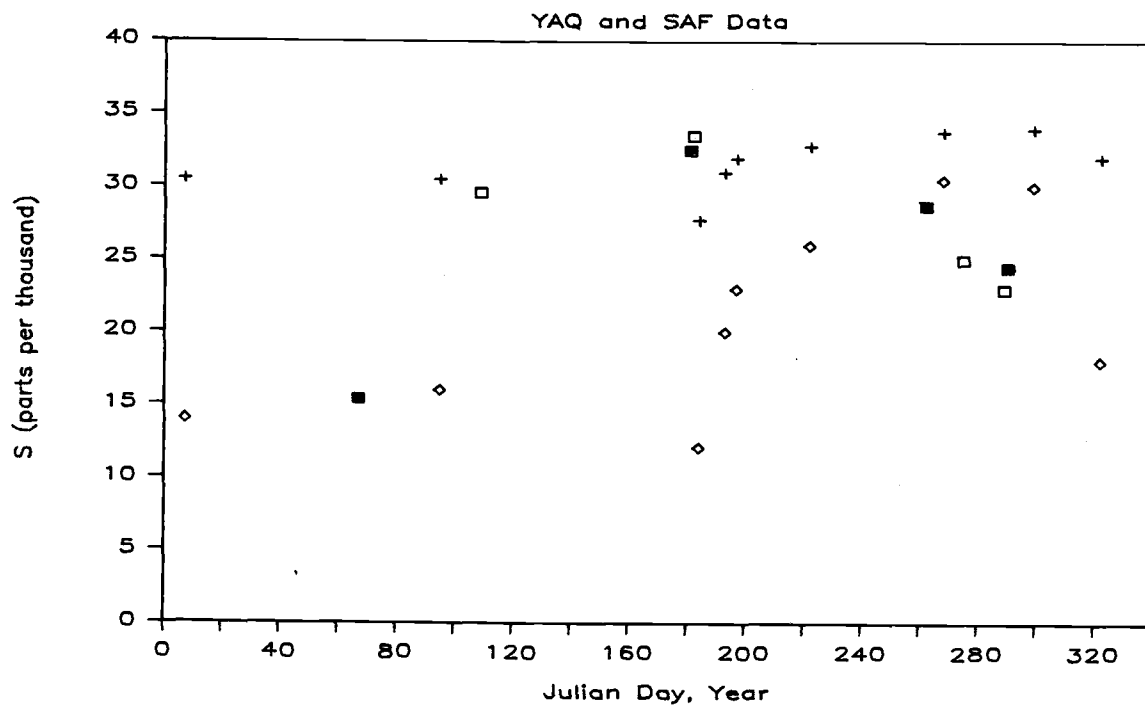
temperature river water during summer low-flow periods. Also, coastal upwelling introduces offshore water that will be colder in summer than winter. Temperatures at the SAF sites were generally similar, probably because in shallow water, no matter what the season, solar heating of the sediment dominates the temperature structure of the environment.

Light conditions were not measured during the YAQ cruises, so the data discussed here are SAF measurements only. Measurements of light intensity at the water surface and the sediment surface are shown in Figure 4. Light penetration decreased during the winter. Increased turbidity caused by high runoff was the probable cause. The photoperiod ranged from 12.7 hours in June to 6.1 hours in December.

B. Sediment Analysis

Measurements of organic matter in sediment differed from Kulm's (1965). Organic matter was detectable at both sites, and varied with season. There was no significant difference between the sites on this basis. Percent insoluble carbon and percent insoluble nitrogen ranged from 0.12 and 0.01 in September to 3.4 and 0.19 in March respectively.

Ratios of carbon to nitrogen by atoms in sediment samples increased from 10.2 in September to 21.9 in March, then dropped to 13.5 in April. Interstitial diatoms are the dominant intertidal plants from January through March (M.W. Davis pers. comm.). Changes in microalgal biomass were undoubtedly an important part of this seasonal variation.

Figure 4: Seasonal variation of light intensity at water surface
           (boxes) and sediment surface (crosses). For SAF field work.

Figure 4 AMBIENT LIGHT INTENSITY
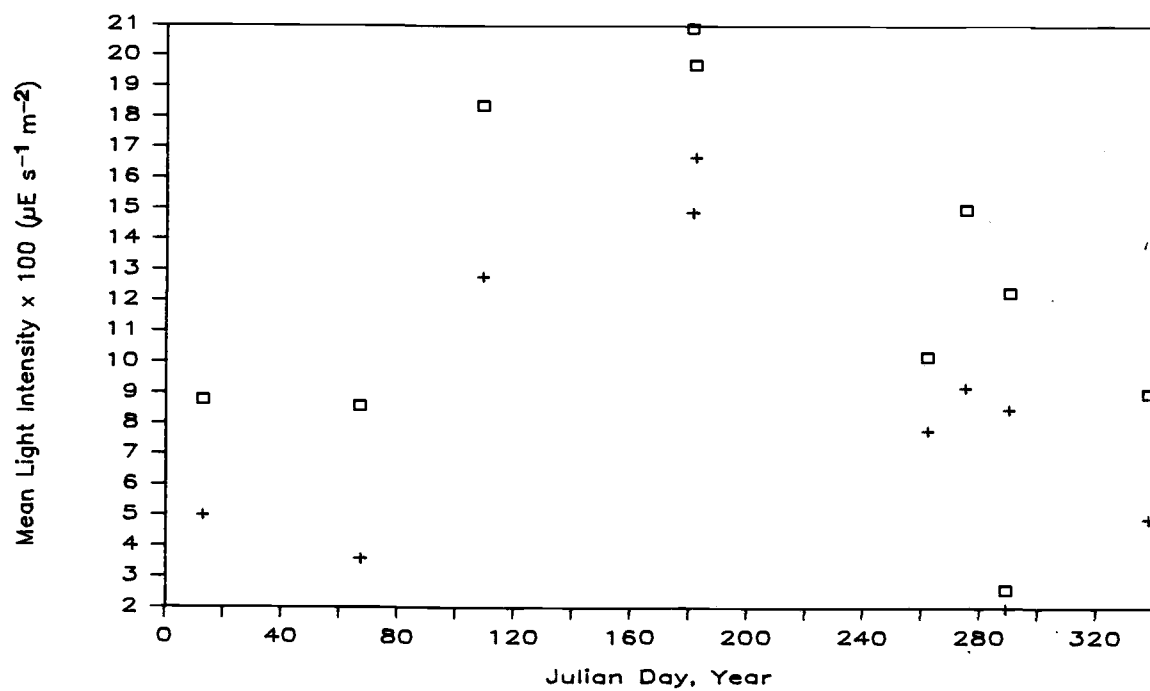
C. Nutrient and Dissolved Oxygen Concentrations

Seasonal patterns were evident in the ambient concentrations of nitrate, phosphate, and dissolved oxygen. Ammonium (Figure 5a) and nitrite (Figure 5c) remained relatively constant throughout the sampling period.

The most obvious seasonal feature of the dissolved nutrient distributions was high nitrate concentration in winter, spring, and summer (Figure 5a). In late summer and fall, the nitrate concentration decreased. Nitrite remained a minor component of total dissolved inorganic nitrogen (DIN) inventories throughout the study. DIN was highest in winter when it was dominated by nitrate, and then decreased in spring to a minimum in late summer or early fall, when ammonium concentrations were a larger percent of the DIN pool. Phosphate followed a pattern opposite to that found for DIN: minimum phosphate concentrations occurred in winter and highest concentrations in summer and early fall (Figure 5b).

With the exception of measurements taken in July, ambient dissolved oxygen concentrations were correlated with temperature [$r^*=.784$ (bottles, n=10), =.616 (chambers, n=10)], indicating that atmospheric equilibration is the major factor in determining ambient dissolved oxygen concentrations. The July results are unusual because all oxygen concentrations measured were above 160% saturation (Figure 6). This might have been caused by high algal productivity combined with an onshore wind that decreased mixing between slough water and channel water. With the exception of the July results, dissolved oxygen exhibited a winter maximum and summer-fall minimum (Figure 5b).

Figure 5:   Seasonal variation of ambient concentration of inorganic
            nutrients and dissolved oxygen during SAF field work.
            a. Nitrate (boxes), Ammonium (crosses), and DIN (diamonds).
            b. Phosphate (boxes) and Dissolved Oxygen (crosses).
            c. Nitrite

Figure 5 SAF AMBIENT CONCENTRATIONS

a. Nitrate, Ammonium, DIN

b. Phosphate and Dissolved Oxygen

Figure 5 (cont)


c.   Nitrite
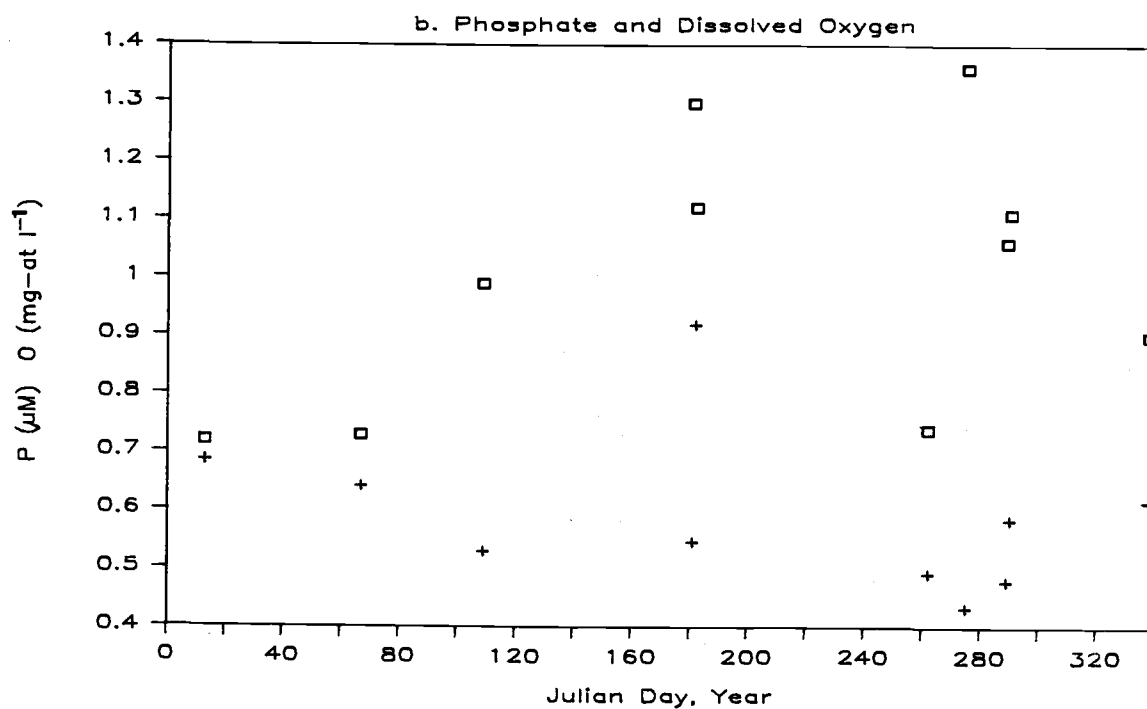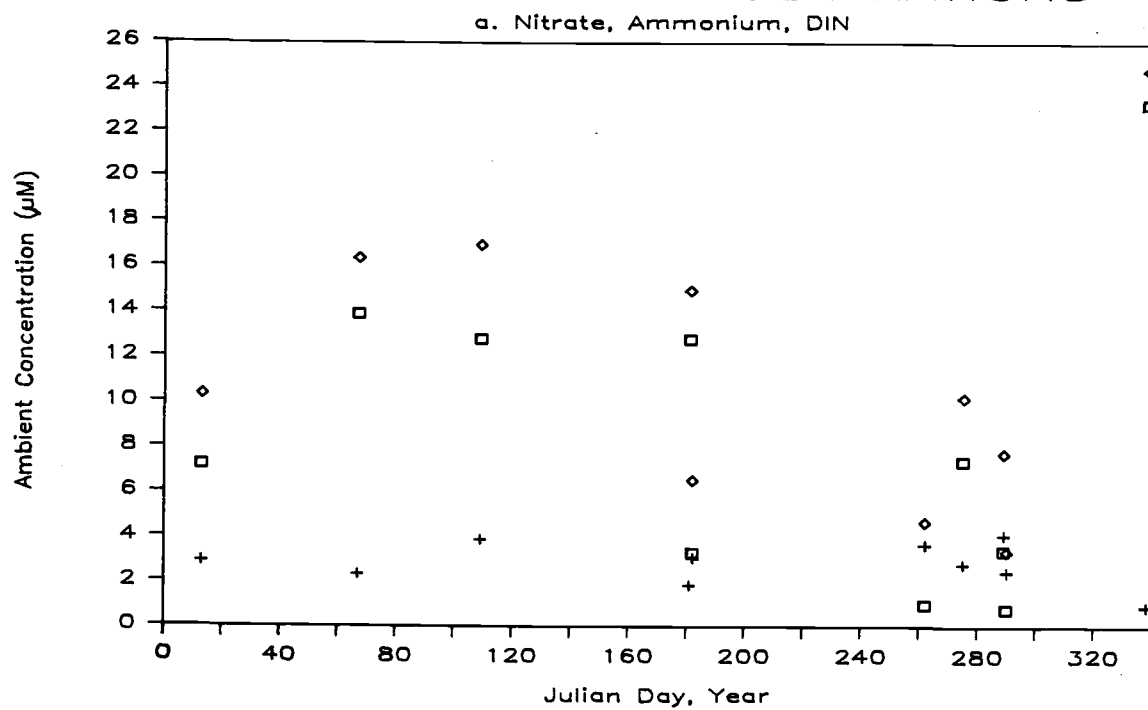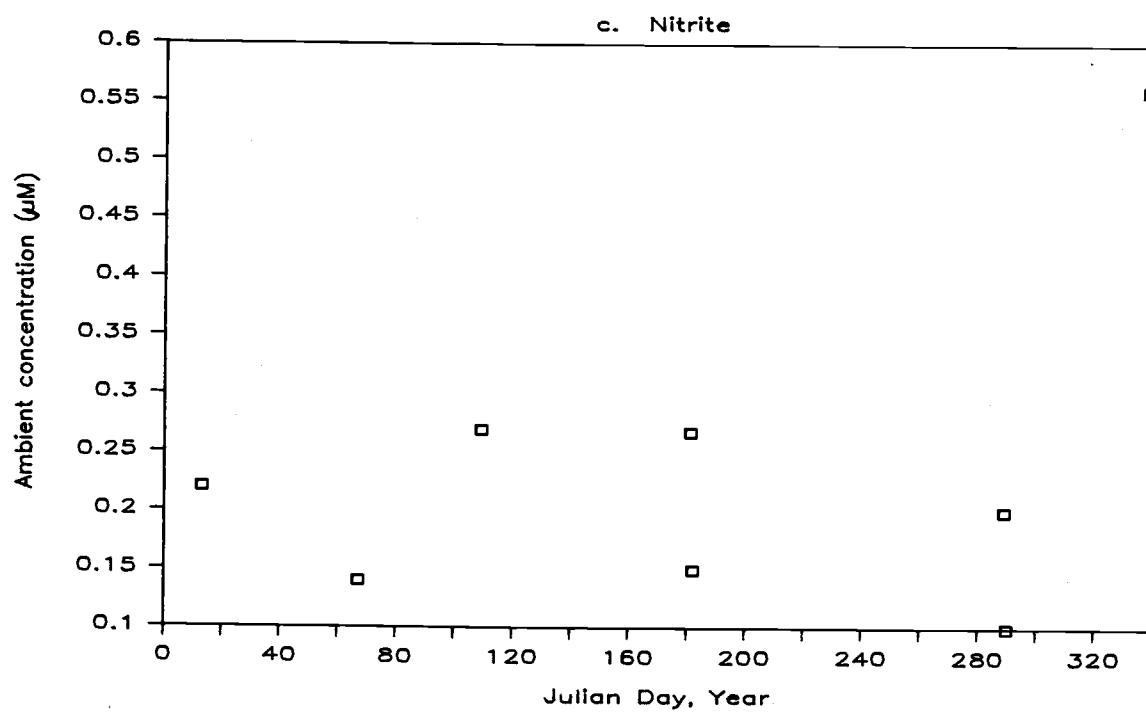
Figure 6: Ambient dissolved oxygen as percent saturation.

Figure 6　AMBIENT DISSOLVED OXYGEN

Percent Saturation
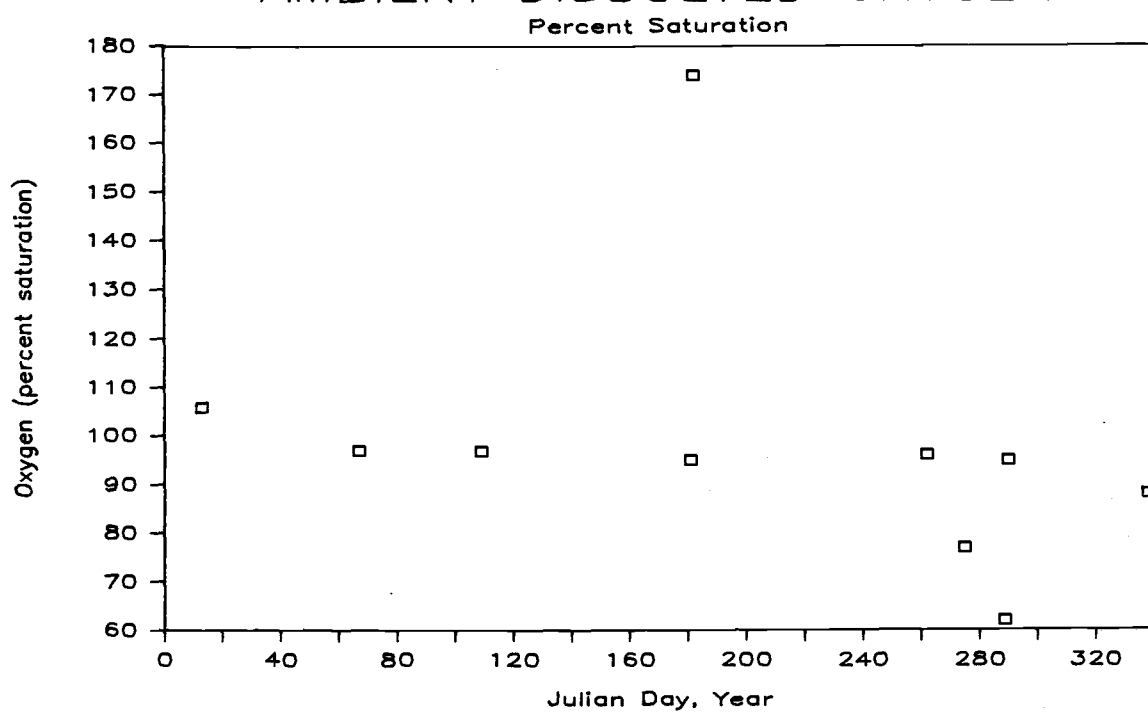
The ratio of available DIN to available phosphorus shows strong seasonal patterns as a result of the interaction of the seasonal cycles discussed above. Nitrogen availablity relative to phosphorus is greatest during the winter flush of nitrate, and least during summer and fall (Figure 7).

Inorganic nitrogen forms followed similar seasonal cycles in 1983-84 as in 1984-85, but with changes in timing and magnitude. The maximum nitrate peak occured later during 1983-1984 (Figure 8a,b), and mid-channel concentration at YAQ Station 4s was higher than mudflat concentration at SAF Site 2 in 1984-1985. The timing of the nitrate peak was probably related to differences in rainfall between the two study periods. DIN concentrations followed the nitrate peak as in SAF data, with ammonium a more significant percent in summer and fall. An interesting feature of the YAQ data was the difference in magnitude of the nitrate concentration between the two YAQ sites. It is clear that river water, high in nitrate, was diluted by ocean water that is poorer in nitrate. As in the SAF data, nitrite and ammonium remained relatively constant and low compared to nitrate throughout the YAQ study period.

Phosphate and dissolved oxygen concentrations at YAQ stations 2 and 4 followed seasonal patterns similar to those found in the SAF data (Figure 8c,d), with a few differences in magnitude (compare to Figure 5b). Oxygen concentrations from the YAQ study were also correlated with temperature ($r^*=.784$, n=16). Phosphate concentrations at the two YAQ stations were very similar. This is in contrast to nitrate concentrations, which were generally higher at the upstream station.

Figure 7: Seasonal variation of the ratio ambient DIN/ambient
phosphate. Symbols and sources as in Figure 3.

Figure 7 AMBIENT DIN/PHOSPHATE

YAQ and SAF Data
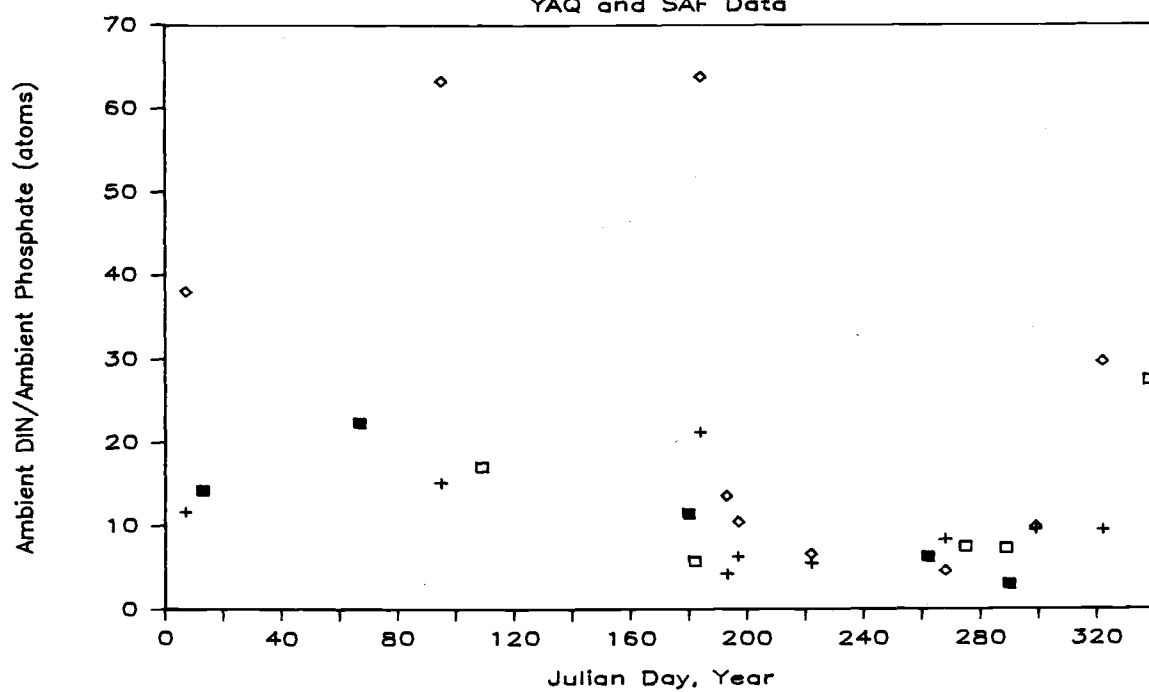
Figure 8: Seasonal variation of ambient concentration of inorganic
nutrients and dissolved oxygen during YAQ field work 1983-84
(Garber et al. 1984). Symbols for a. and b. as in Figure
5a; symbols for c. and d. as in Figure 5b.

Figure 8 YAQ AMBIENT CONCENTRATIONS

Figure 8 (cont.)

c. Station 2b, Phosphate and Oxygen

d. Station 4s, Phosphate and Oxygen
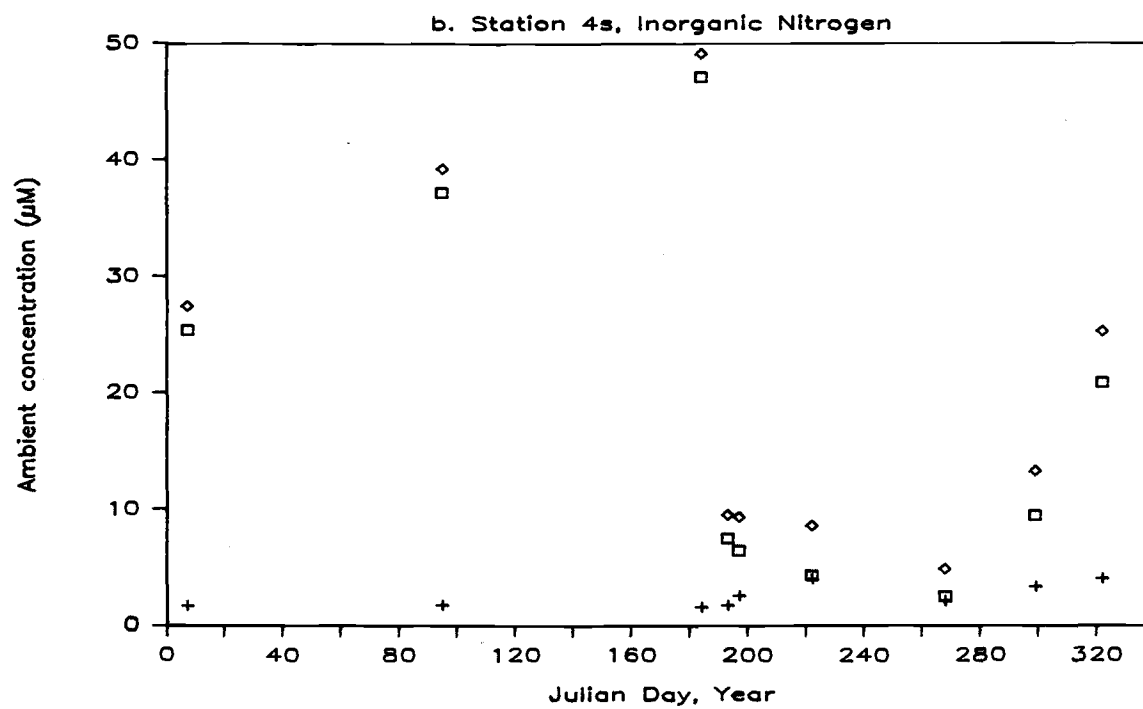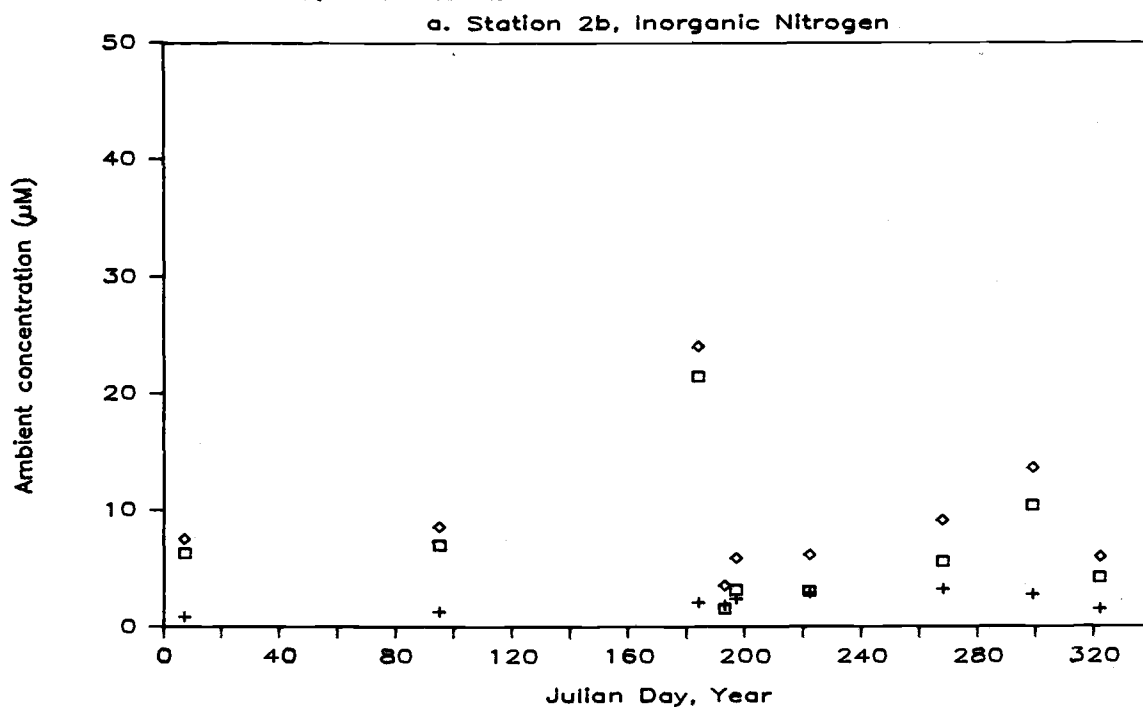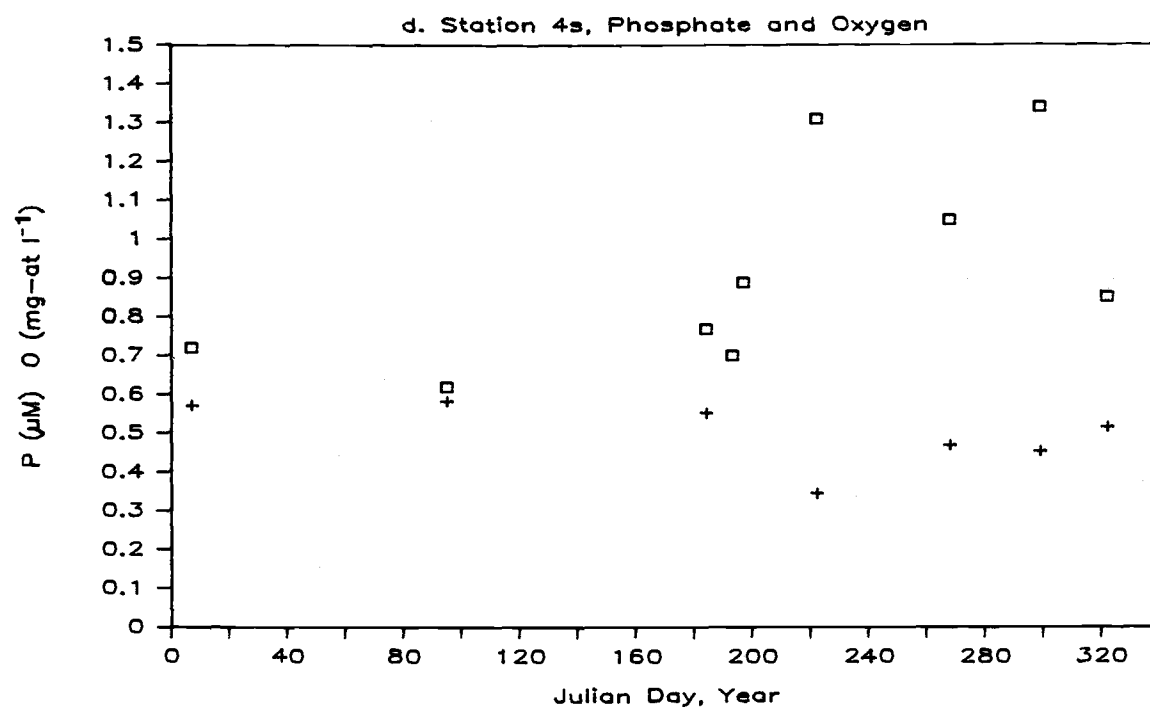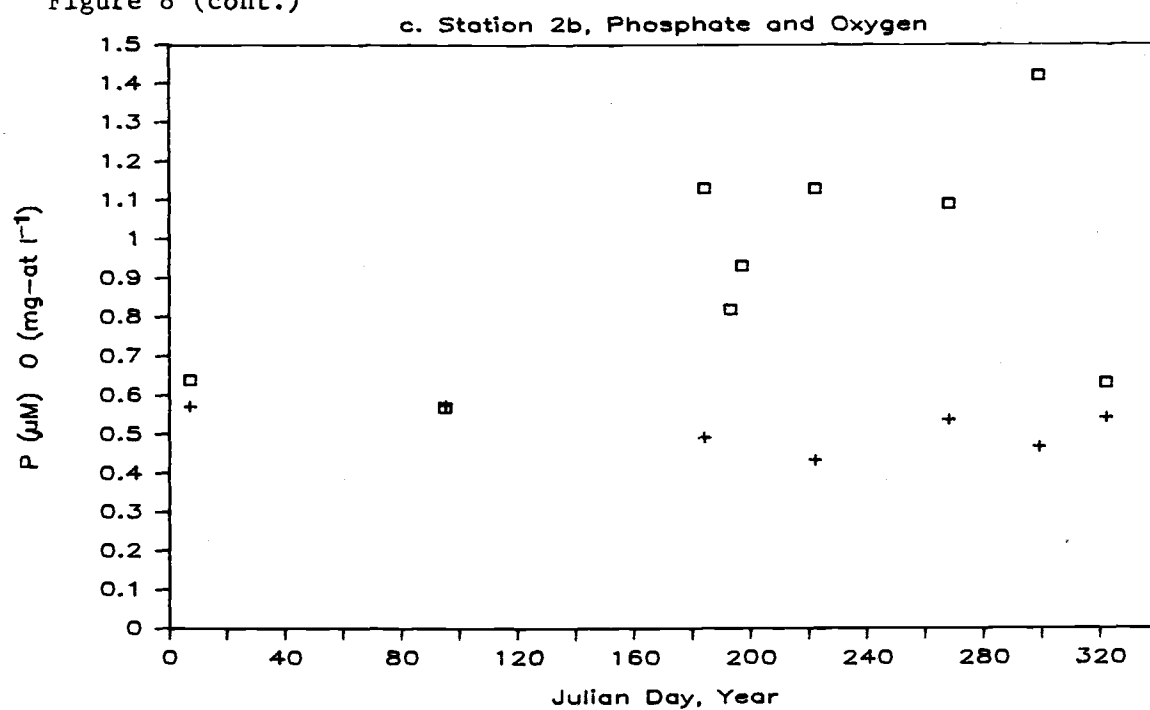
Phosphate concentration apparently remained more constant along the salinity gradient than nitrate.

The DIN:phosphate ratio of the SAF and YAQ data followed similar patterns with much higher ratios at the upriver YAQ station, reflecting higher nitrate concentrations (Figure 7b). The timing of the peak in DIN:P coincided with the nitrate peak for both data sets.

The YAQ data for endmembers of the mixing curve show that ocean water is indeed a source of phosphate to the bay in summer. In fact, except for November during the YAQ sampling period, phosphate concentrations in ocean water were always higher than in the river.

Differences in nitrate concentration between the YAQ stations suggest that SAF Site 2 may receive stronger pulses of nitrate from river water than SAF Site 1.

The comparison between the YAQ and SAF data illustrates interannual variability in timing and magnitude of nitrate delivery to the bay. It also shows there may be differences in the amount of nitrate delivered to the two SAF sites. The seasonal patterns of dissolved oxygen, nitrite, ammonium, and phosphate concentrations show that these analytes exhibit much less interannual variability than nitrate.

II. Sediment Metabolism: Intertidal Oxygen Demand and
     Nutrient Exchange Without Macroalgal Influence

In this and following sections, any nitrogen flux comprising half or more of the DIN flux is described as "dominant". Note also that "uptake" (a negative flux) refers to a net flux of analyte from the water to the sediment or algae, and "regeneration" (a positive flux) refers to net flux of analyte from sediment to the water.

I have assumed linearity of exchange and production rates with time during the incubation period. This assumption may not always hold for sediment regeneration processes (Hopkinson and Wetzel 1982) or for algal growth experiments (DeBoer 1981). For example, in the bottle experiments during September, final concentrations of nitrate and phosphate were undetectable, indicating that the algae may have removed all available nutrients before the experiment ended. According to Nixon et al. (1979), linearity is more likely in dark chambers than in light, and with ammonium flux than oxygen flux in dark chambers.

Nixon et al. (ibid.) have shown that phosphate regeneration in the sediment is usually linear with temperature, and inversely correlated with sediment oxygen demand. Comparing the relation between these variables for experiments done in laboratory tanks against those done in the field, I found no important differences. Consequently, I concluded that transporting sediment cores from mudflat to laboratory did not change the sediment-water fluxes enough to consider the tank experiments separately from the field experiments. Therefore, laboratory tank experiments and field experiments are combined in the following discussion.

Fluxes of nitrate, DIN, and phosphate differed in magnitude and seasonal pattern at the two study sites. Sediment oxygen demand, however was not significantly different between the sites. Magnitude and seasonal variation of these fluxes are reported in Appendix A.

Nitrate and ammonium fluxes generally dominated the DIN flux, but shifted in dominance between sites and with seasons. At Site 1, nitrate uptake and ammonium regeneration were the dominant nitrogen exchanges in the sediment at low and high temperatures, respectively. As temperature increased at Site 1, ammonium regeneration increased to a maximum of 204 microgram-atoms $N \: m^{-2} \: h^{-1}$ and nitrate uptake decreased (Figure 9a). Nitrate uptake clearly dominated DIN flux at Site 1 during December when it reached a maximum of -208 microgram-atoms $N \: m^{-2} \: h^{-1}$. During July, September, and October, when water temperatures were higher, ammonium regeneration in the sediment determined the direction of DIN flux at Site 1.

At Site 2, processes opposite to those operating at Site 1 dominated DIN fluxes (Figure 9b). That is, nitrate was usually regenerated instead of taken up, and ammonium was taken up as often as regenerated. Nitrate and ammonium fluxes almost always occurred in the same direction at Site 2; whenever the mean nitrate flux was positive, so was the mean ammonium flux. Net nitrate and ammonium regeneration increased from winter to summer, with nitrate the larger of the two. There was no seasonal pattern evident in fall.

Several generalizations emerged from the nitrate and ammonium flux data. At Site 1, DIN flux was dominated by ammonium regeneration during fall and summer, and by nitrate uptake in winter and spring. At Site 2, DIN flux was dominated by ammonium - both regeneration and

Figure 9: Seasonal variation of flux between sediment and water:
nitrate (boxes) and ammonium (crosses) during SAF field
work. a. Site 1, b. Site 2.

SEDIMENT NUTRIENT FLUX

Figure 9

a. Site 1, Nitrate and Ammonium
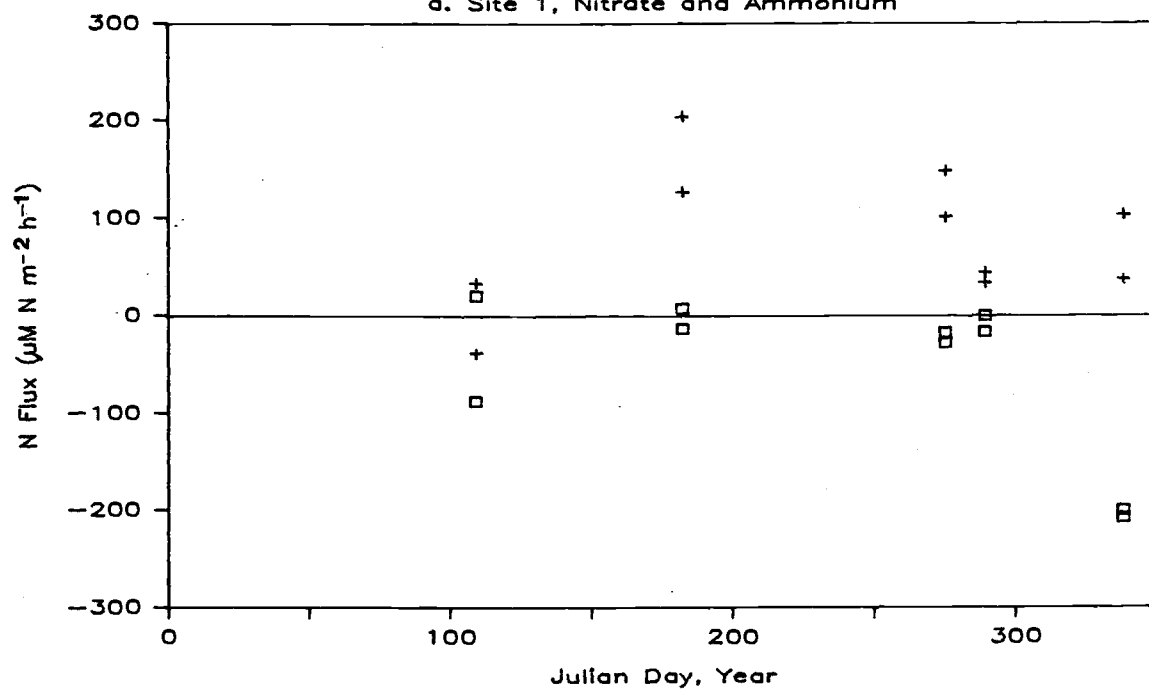
b. Site 2, Nitrate and Ammonium
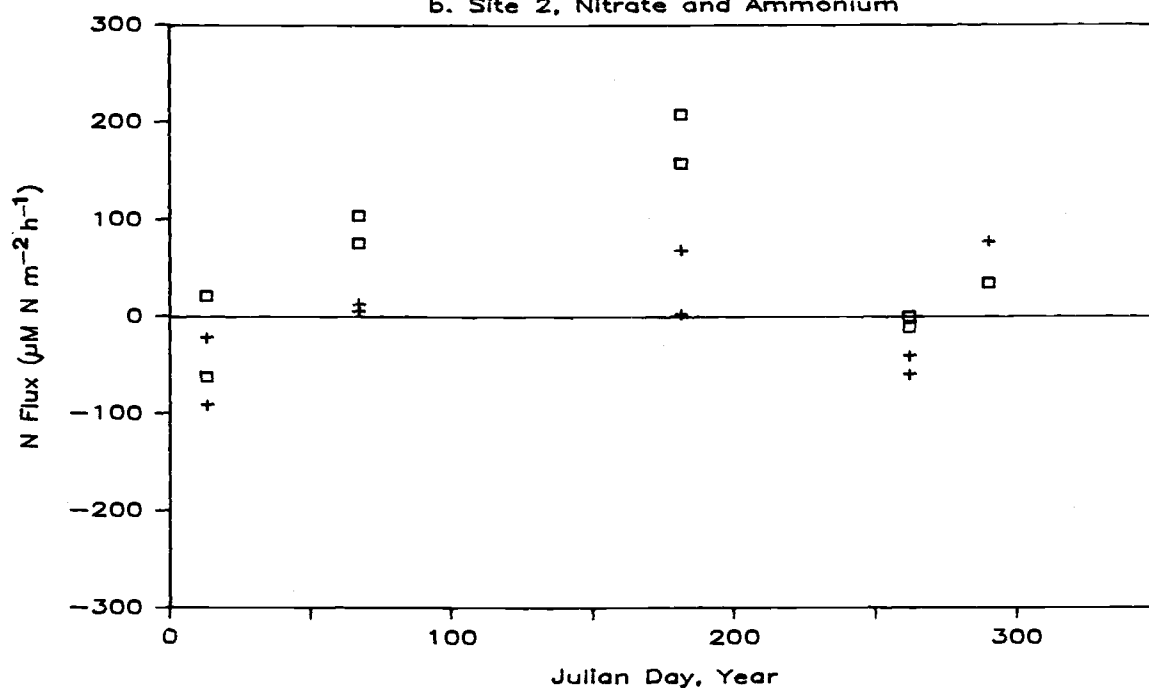
uptake - in fall and winter, and by nitrate regeneration in spring and summer.

DIN flux showed a more obvious seasonal pattern when both sites were considered together (Figure 10). Usually, sediment uptake of DIN occurred in winter and regeneration the rest of the year.

Phosphate was regenerated more often than taken up at both sites. Phosphate fluxes, calculated as the mean of duplicate chamber fluxes, showed a significant correlation with bottom water temperature at Site 1, but not at Site 2 (Table 3). However, when individual fluxes from both sites were combined (Figure 11), the overall relation with temperature was significant (Table 3). Phosphate regeneration was highest in summer and lowest in winter at both sites.

Sediment oxygen fluxes were generally negative, and were correlated with temperature (Table 3) at both sites, reaching a maximum oxygen uptake in summer (-8.9 mg-at O m^{-2} h^{-1}) and oxygen production ($+7.8$ mg-at O m^{-2} h^{-1}) in winter.

Significant correlations between temperature and nitrate, DIN, and phosphate fluxes were found only at Site 1 (Table 3). The only significant correlation to emerge at Site 2 was between oxygen flux and temperature. The correlation between oxygen and temperature at Site 1 was not statistically significant if all data points were used, but was significant ($P < .01$) if one outlier was omitted. The outlier occurred in July, when ambient oxygen concentration was 160% of saturation.

Phosphate fluxes based on individual chamber data showed no significant correlations with temperature at either site. However, if mean fluxes were used for each temperature, the correlation was

Figure 10: Seasonal variation of DIN flux between sediment and water during SAF field work, both sites.

Figure 10

SEDIMENT DIN FLUX
Both Sites
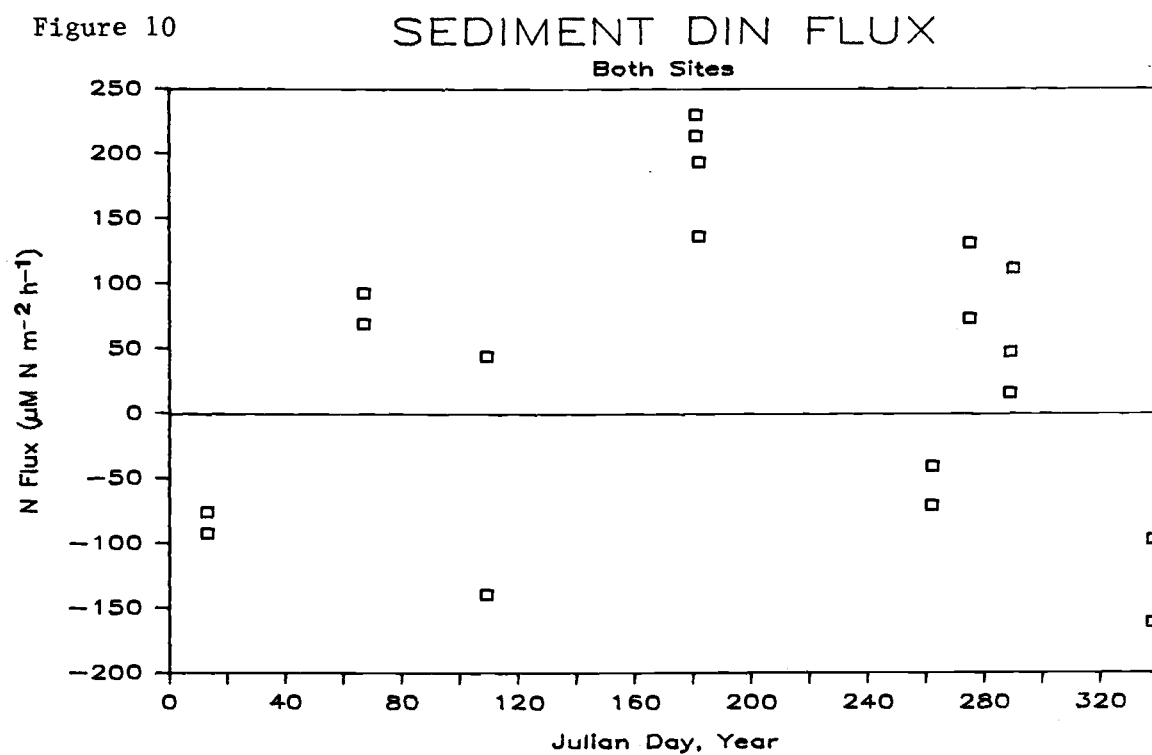
Table 3: Correlations of sediment flux data with temperature and other variables. Data considered here are from opaque sediment chambers without macroalgae and are expressed per square meter per hour. (*=P<.05, **=P<.01)

Relation	Significance	Element Ratios (by atoms)	r*	n
Site 1				
Nitrate vs Temp	*		.725	10
DIN vs Temp	**		.838	10
Phosphate vs Temp (means)	**		.973	5
Oxygen vs Temp	** (1 outlier omitted)		.853	9
Nitrate Flux vs Ambient Nitrate	**		.907	10
Ammonium vs Temp	P<.05=.632		.589	10
Site 2				
Oxygen vs Temp	**		.935	9
Both Sites				
Ammonium vs Temp	*		.489	19
Phosphate vs Temp	*		.567	19
Oxygen vs Temp	**		.734	19
Oxygen vs Phosphate	P<.05=.468	O/P=1650 C/P=825	.439	18
	**	O/P=1369 C/P=684	.641	15

Figure 11: Relation between sediment phosphate flux and water temperature at the sediment surface during SAF field work, both sites.

Figure 11

SEDIMENT PHOSPHATE FLUX
Both Sites
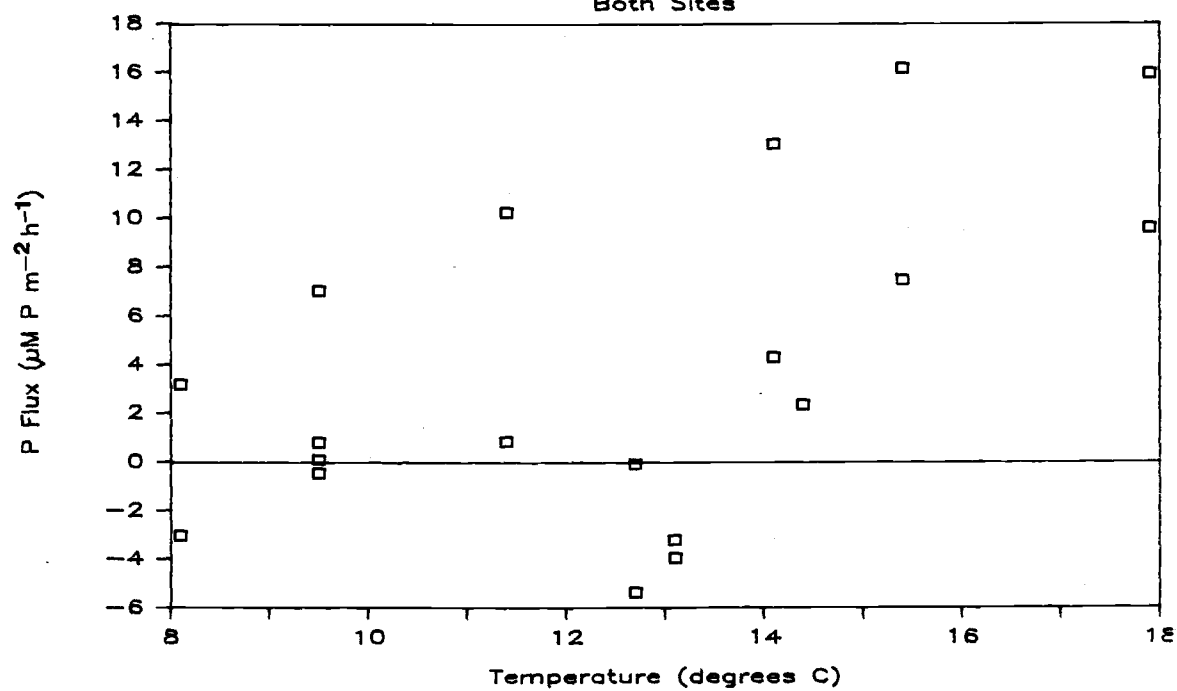
significant (P<.01) at Site 1. When individual chamber data (as opposed to means of duplicate treatments) from both sites were combined, ammonium, phosphate and oxygen also correlated significantly with temperature. The only analyte flux that correlated with ambient concentration was nitrate uptake, at Site 1.

The strong coupling between oxygen and phosphate fluxes and temperature prompted an attempt to correlate oxygen and phosphate. This correlation was not statistically significant. However, when only data points that combined oxygen production and phosphate uptake were used, the correlation was significant (P<.01) (Table 3). This correlation provided the only statistically significant relation for examining element ratios from sediment regeneration. Compared to Redfield ratios, that predict an O:P of around 276, these results indicate much less phosphate regeneration from intertidal sediments than would be expected from the observed levels of sediment oxygen demand. Interestingly, the ratio found in the intertidal sediment appears closer to Atkinson and Smith's (1983) average ratio for macroalgal tissue.

Nitrate fluxes exhibited curious between-site differences. Nitrate was nearly always taken up by the sediment at Site 1, but was nearly always regenerated at Site 2 (Figure 12). Uptake at Site 1 was correlated with both temperature and ambient nitrate concentration (Table 3). Neither of these relations was significant at Site 2.

Nitrite and DON fluxes showed no patterns or trends with temperature, season, or any of the other variables examined in this study.

Figure 12: Relation between sediment nitrate flux and water
temperature at the sediment surface during SAF field work:
a. Site 1., b. Site 2.

Figure 12 — SEDIMENT NITRATE FLUX
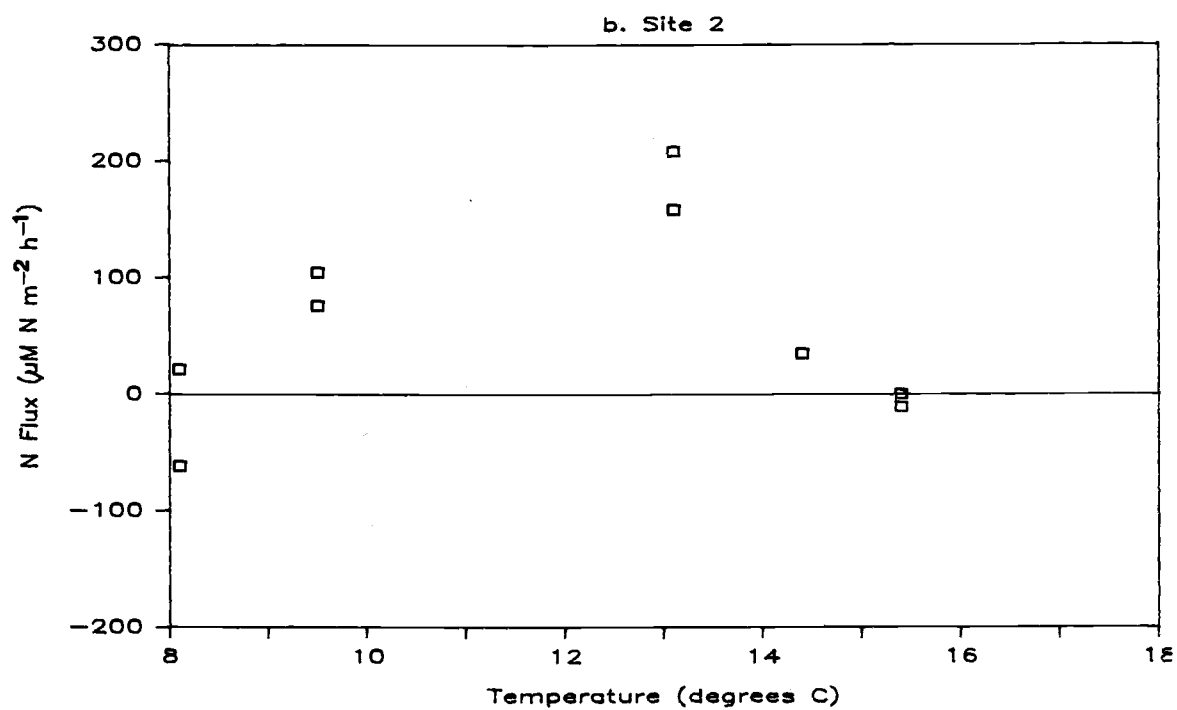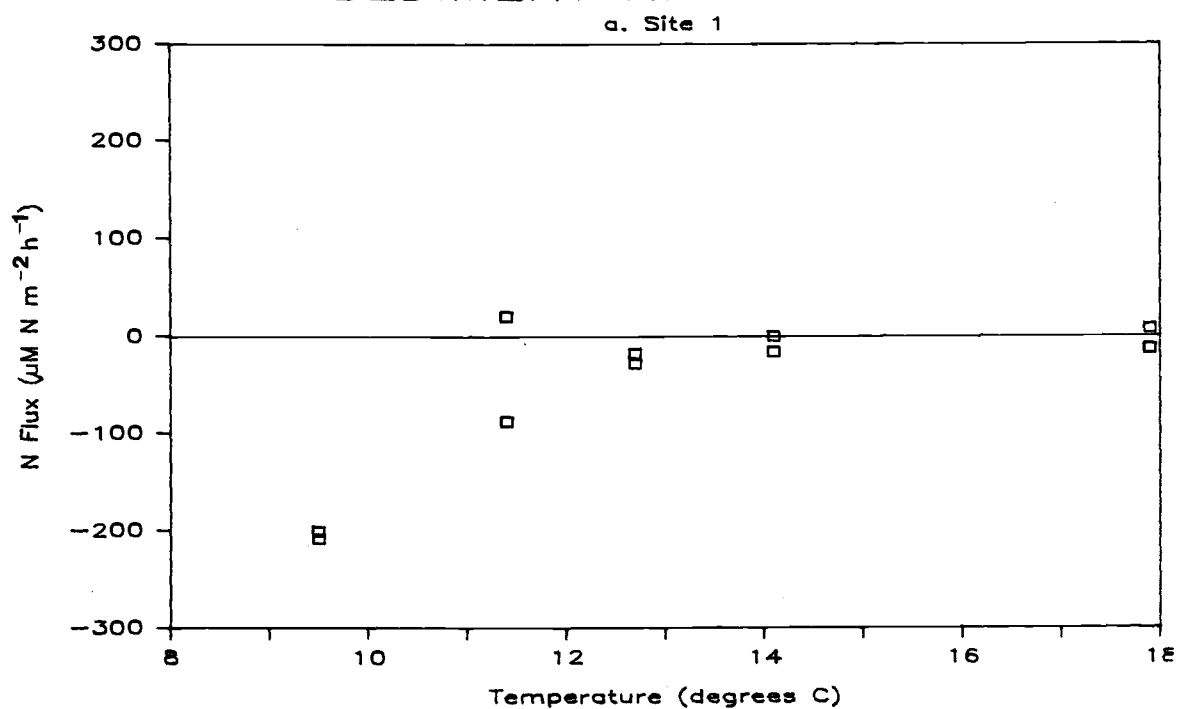
III. Macroalgal Influence on Sediment-Water Fluxes

Implicit in the flux calculations for the chambers is the assumption that bottle controls accurately reflect water-column nutrient processes. For most bottle experiments, the results from bottle duplicate treatments were similar, indicating this assumption is reasonable. By calculating the influence of macroalgae by difference between chamber fluxes of different treatments, I am assuming that a mean value of duplicate transparent chambers without macroalgae accurately represents community metabolism in the absence of macroalgae. From a comparison between bottles and chambers, the main source of variability in chamber fluxes appears to be a combination of sediment heterogeneity and variations in the amount of macroalgal tissue that was actively photosynthesizing. Consequently, I am more confident about conclusions of macroalgal productivity and nutrient uptake based on bottle experiments than any based on chamber experiments.

A. Macroalgal Biomass and Tissue Analysis

Except for experiments during September and October, only Ulva spp. was used for this study. In September and October, both Enteromorpha spp. and Ulva spp. were used in chamber and bottle incubations. When expressed as biomass per unit area, the algal tissue in the chambers showed a biomass peak during September and October (Figure 13), the time of maximum biomass and coverage for Ulva spp. (M.W. Davis, pers. comm.). This result showed that individual plants

Figure 13:   Seasonal variation of macroalgal biomass in sediment
             chambers during SAF field work.   Points are means ± 1 S.E.

Figure 13 CHAMBER MACROALGAL BIOMASS

Ulva spp. and Enteromorpha spp.
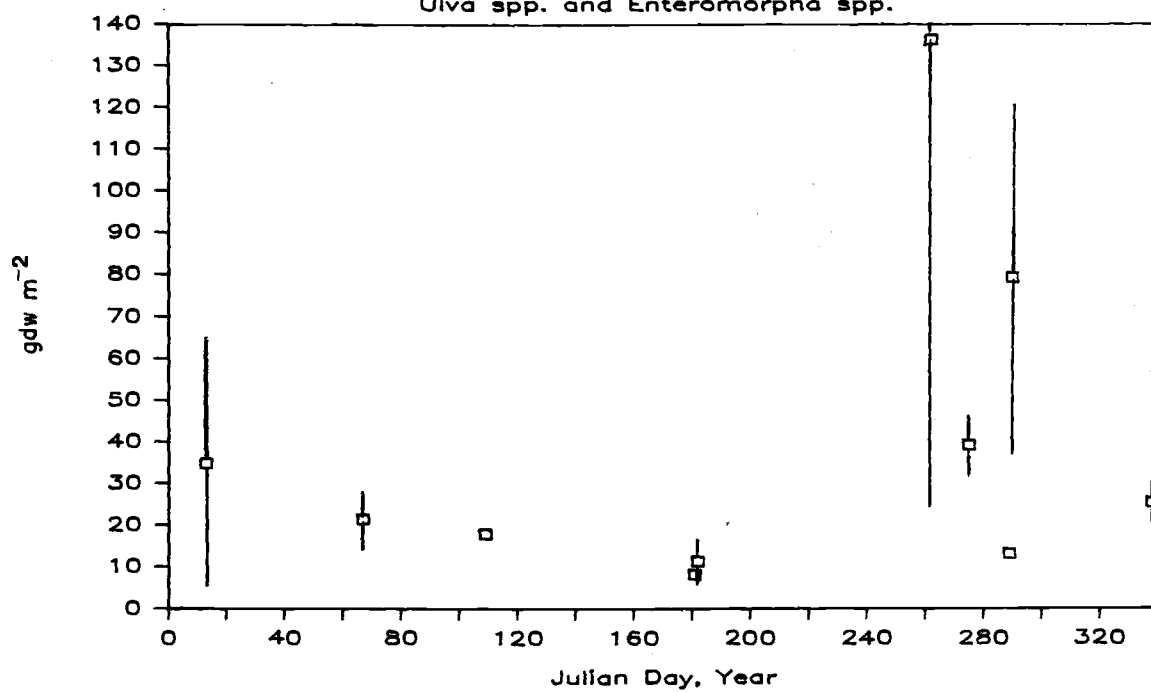
appeared to reach maximum size at the time of maximum biomass and coverage.

Seasonal changes were observed in macroalgal C/N ratios (Figure 14). The C/N ratio was greater than 10 in several plants collected in September and October at both sites, and in two plants collected in July at Site 1. The highest C/N measured was 12.6 in October at Site 2. The minimum value for the C/N ratio was 7.01 and occurred in March. Note the site difference in the spring: the ratio rises at Site 1, but not at Site 2. Similar seasonal changes occurred in percent nitrogen and percent carbon. Ratios of carbon to nitrogen (atoms) in macroalgal tissue that are greater than 10-15 indicate growth limitation by nitrogen (Hanisak 1983).

Macroalgal biomass measurements from chamber experiments may have included inactive or senescent tissue. If so, fluxes divided by the algal biomass would be lower than the actual uptake rate for active tissue. This source of variability may contribute to the weak coupling between algal growth and nutrient uptake that was found in chamber fluxes.

B. Net Macroalgal Productivity

Macroalgal growth was measured by short-term oxygen production. Short-term growth is more subject to variability than measurements of long-term growth (e.g. changes in standing stock), but short-term results will provide a better estimate of potential uptake rates in response to pulses of nutrient availability.

Figure 14:   Seasonal variation of C/N ratio (atoms) in macroalgal
              tissue.   Points are means $\pm$ 1 S.E.:   boxes=Site 1,
              crosses=Site 2.

Figure 14 — MACROALGAL TISSUE C/N RATIO

Figure 14
MACROALGAL TISSUE C/N RATIO

C/N Ratio (atoms) vs. Julian Day, Year
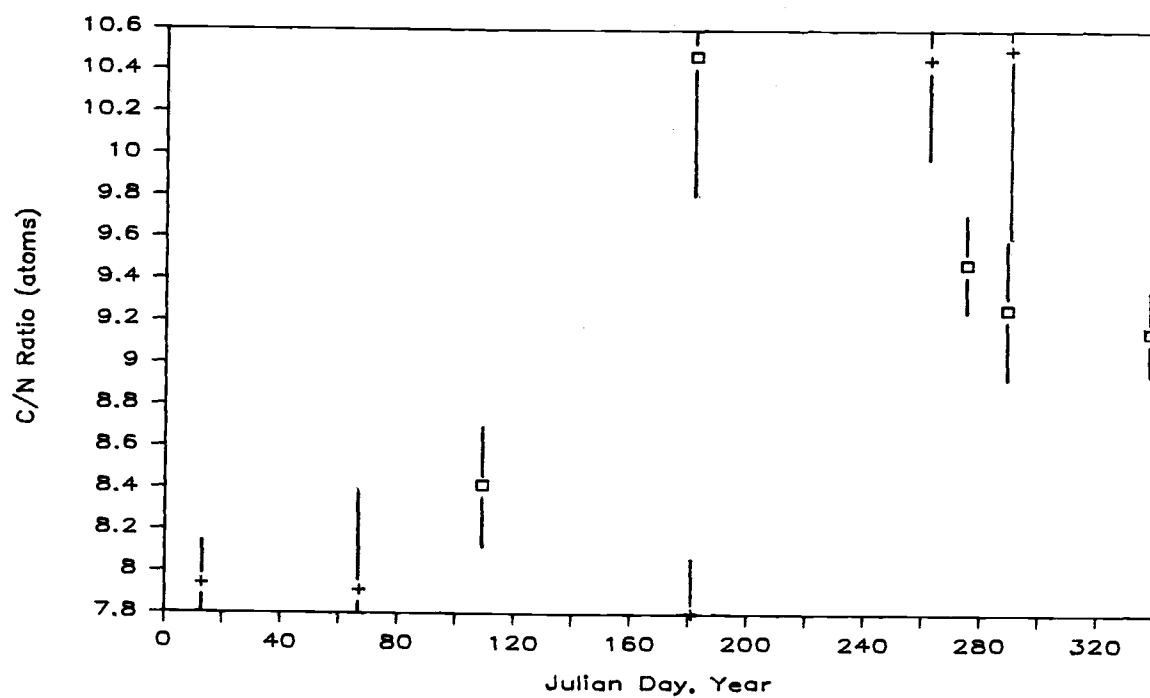
Net primary productivity was determined using results from both chambers and bottles. In both instances, a strong seasonal pattern emerged with a winter minimum and a summer maximum (Figure 15). Productivity increased from relatively low September values to another peak in October. Note that although the patterns are the same for bottles and chambers, the bottle productivity was much higher than that measured in the chambers. In addition, some chamber experiments produced negative values for net primary productivity, whereas all bottle results were positive.

The differences between productivity in bottles and chambers might have been caused by the difference in light transmissivity between the pyrex of the bottles and the plexiglass of the chambers. Another possible source of the discrepancy might be that macroalgae in the chambers may have been covered with a thin layer of silt that was resuspended when the chambers were pressed into the sediment. A third reason for apparently lower productivity in chambers than bottles might be increased diffusion of dissolved oxygen into the sediment as the concentration gradient increased with increasing production.

Oxygen production was correlated with bottom light intensity only at Site 2 for both the chambers and the bottles (Tables 4,7). These rates are similar to other measurements of macroalgal productivity in estuaries (Davis 1981, Thom 1983).

C. Macroalgal Influence on Nutrient Fluxes

Epiphyte influence was not partitioned from macroalgal influence in this analysis. Davis (1981) measured a growth rate of 0.26 g C m^{-2}

Figure 15: Seasonal variation of macroalgal net productivity as
            calculated from a. bottle experiments, b. chamber
            experiments. Open symbols=Site 1, closed symbols=Site 2.

Figure 15 MACROALGAL NET PRODUCTIVITY

a. Bottle Experiments

b. Chamber Experiments
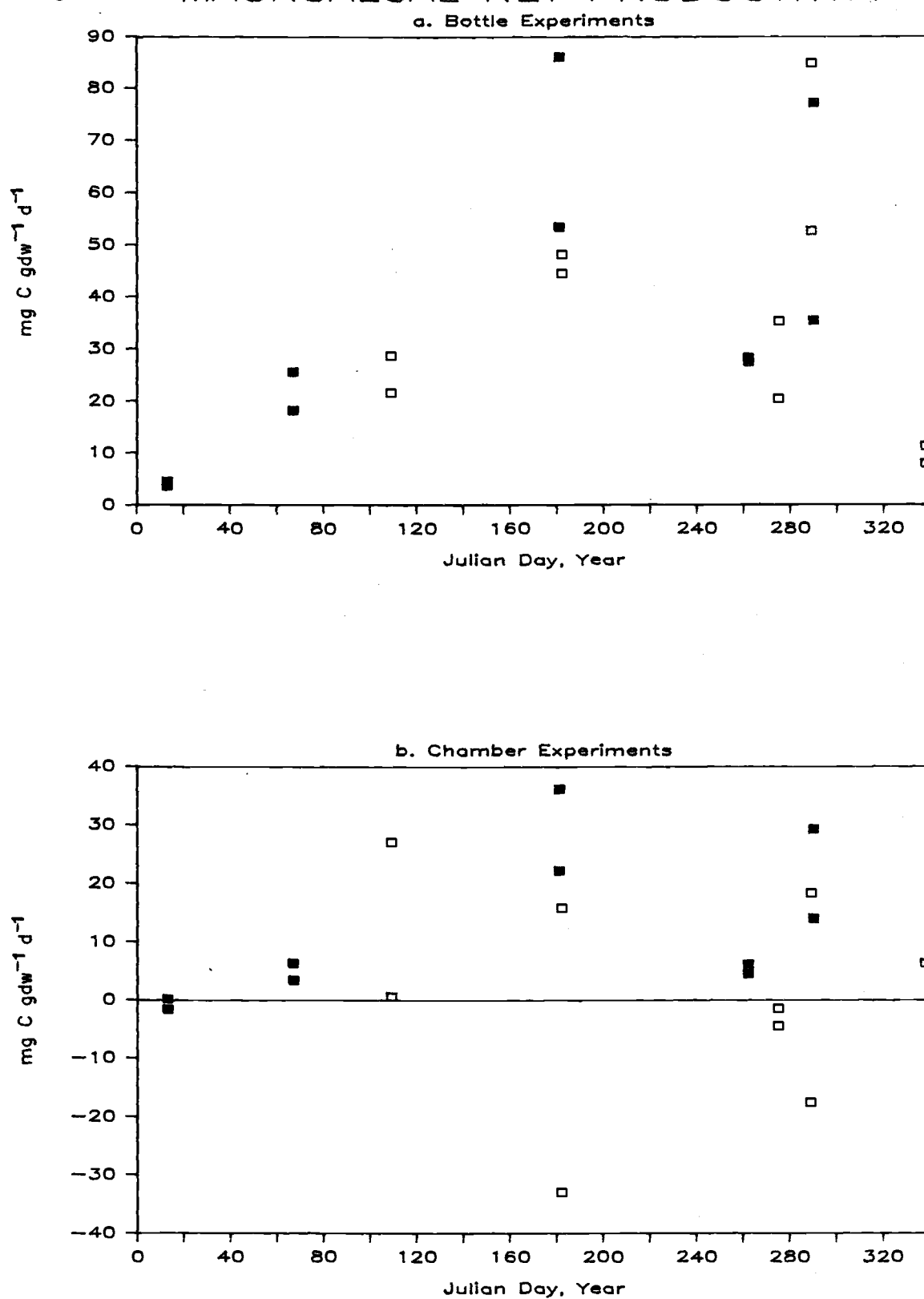
Table 4: Correlations of flux data expressed per gram dry weight of macroalgal tissue; from chamber experiments that included macroalgae. Element ratios from Chlorophyta growth are O:N:P= 1600:38:1 (modified from Atkinson and Smith 1983). Symbols as in Table 3.

Relation	Location	Signif.	Element Ratios (by atoms)		r*	n
Oxygen vs DIN	Both	**	O/N=28	C/N=12	.760	19
	1	**	O/N=26	C/N=11	.835	9
Oxygen vs Nitrate	Both	**			.727	19
	1	**			.814	9
Oxygen vs Ammonium	Both	**			.612	19
	1	**			.846	9
Oxygen vs Nitrite	1	*			.763	8
Oxygen vs Phosphate	Both	**	O/P=1958	C/P=816	.687	18
	1	*	O/P=2010	C/P=875	.829	8
Light vs DIN	2	*			.728	10
Nitrate	2	*			.679	10
Oxygen	2	**			.850	19

-1
d   for epiphytic diatoms. This rate is only 0.6% of the growth rate

measured here for macroalgae. Consequently, epiphytic diatoms probably

have little influence on nutrient cycling in the Yaquina Estuary.

Strictly speaking, the influence attributed to macroalgae in this study

includes the portion caused by epiphytes.

1.   Chamber Experiments: Fluxes Per Gram Dry Weight Macroalgal Tissue

Both release and uptake of DIN occurred in chambers containing

macroalgae and important differences between sites emerged. Macroalgae

removed nitrate consistently at Site 2, taking up more in the spring

and summer than in the fall and winter (Figure 16a). At Site 1, net

nitrate flux indicated release more often than uptake (Figure 16a).

The pattern for nitrite was similar to nitrate, with consistent uptake

at Site 2, and nearly constant release at Site 1 (Figure 16b).

Ammonium uptake and release occurred at both sites, but uptake in the

spring was lower than for nitrate at Site 2, although ammonium release

in the spring at Site 1 was equal to nitrate release (Figure 16c). Net

DIN flux reflected these patterns (Figure 16d). At Site 2, DIN uptake

was constant, increasing from winter to spring, and was low in the

fall. At Site 1, DIN was released more often than taken up. The

release was low from fall through winter and highest in the summer.

Overall, DIN was released almost as often as taken up.

Phosphate was released less frequently than DIN and was not

distinctly different between sites (Figure 16e). An unusual feature of

Figure 16: Seasonal variation of macroalgal net nutrient flux expressed per gram dry weight of macroalgal tissue from chamber experiments at Site 1 (open symbols) and Site 2 (closed symbols): a. Nitrate, b. Nitrite, c. Ammonium, d. DIN, e. Phosphate, f. DON.

Figure 16 NET NUTRIENT FLUX IN CHAMBERS

a. Nitrate

b. Nitrite

Figure 16 (cont.)

c. Ammonium

d. DIN

Figure 16 (cont.)

e. Phosphate


f. DON
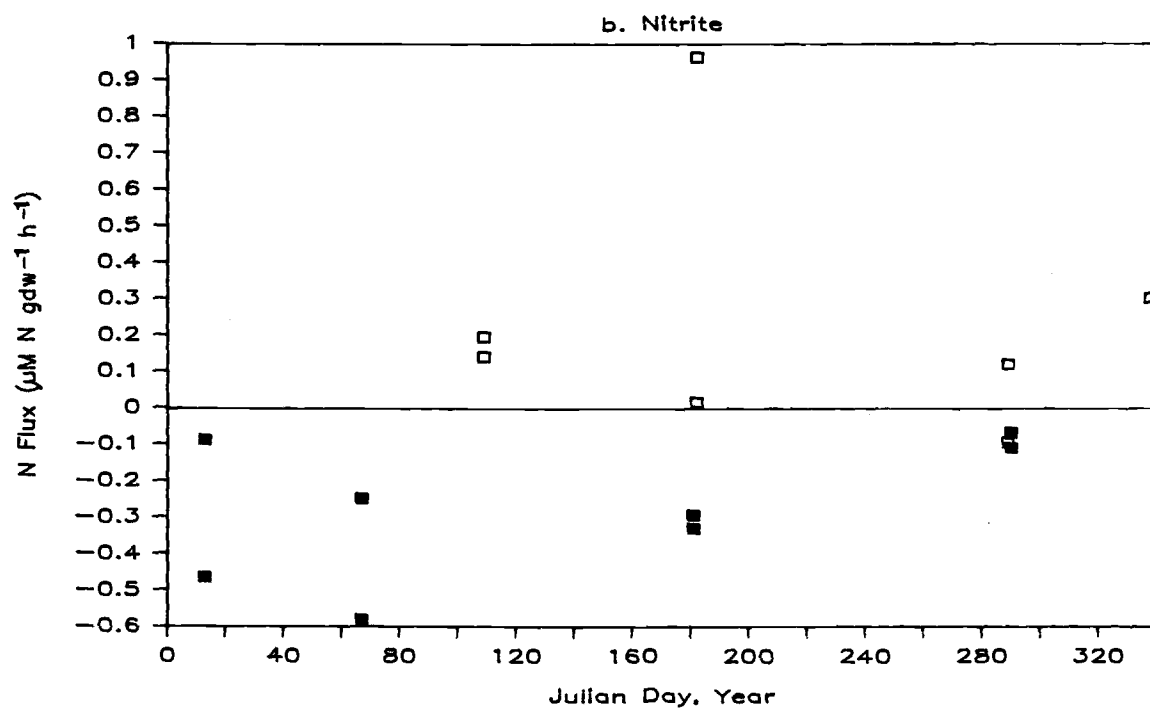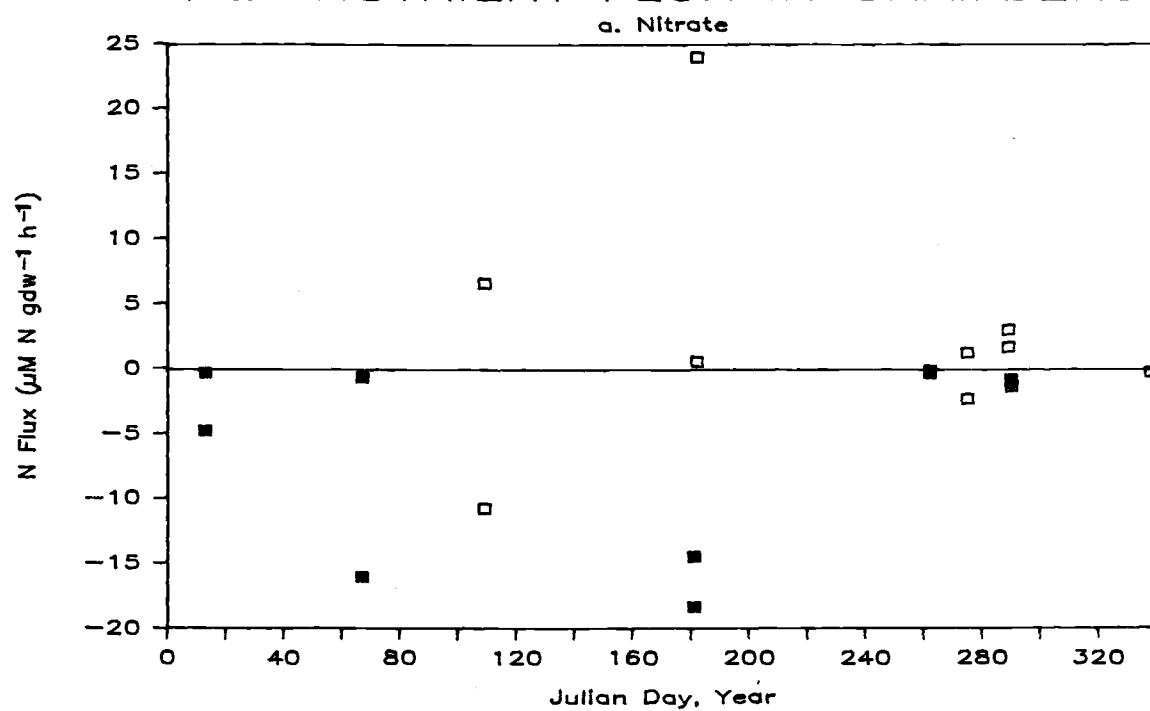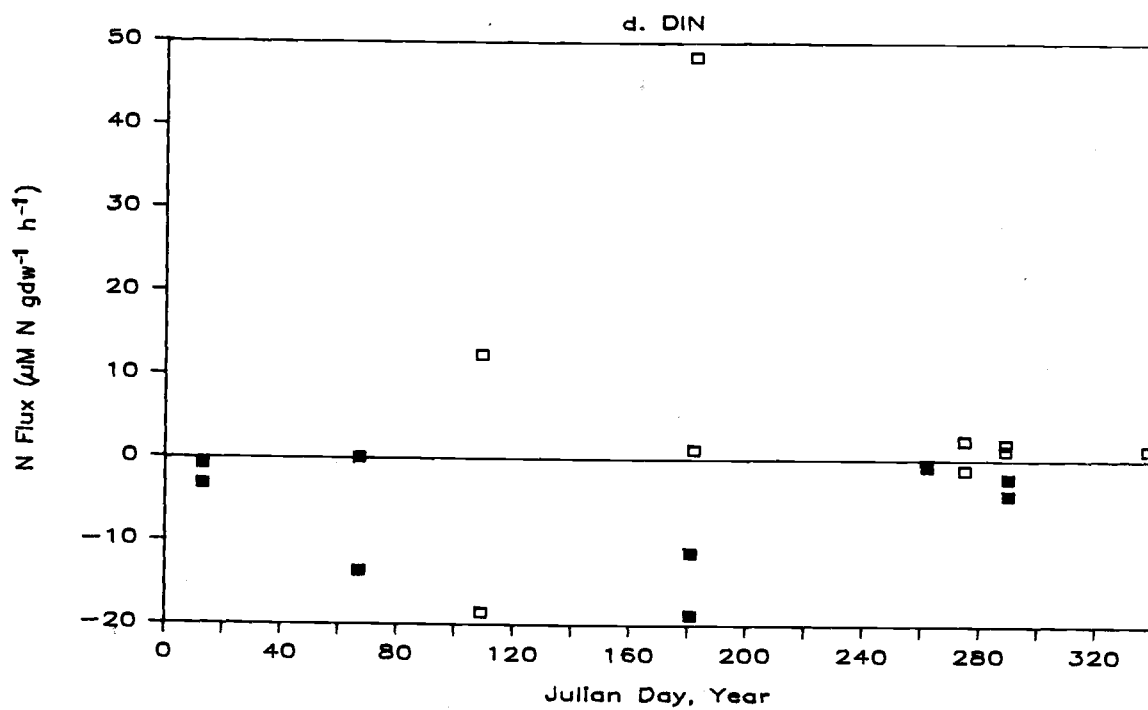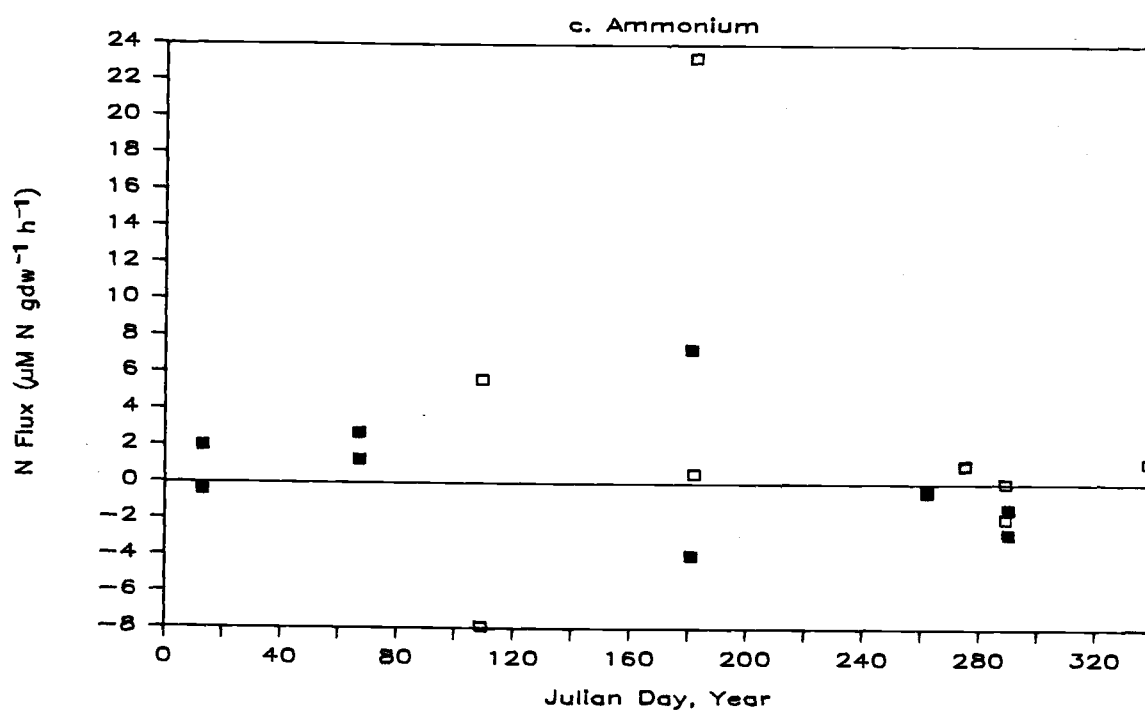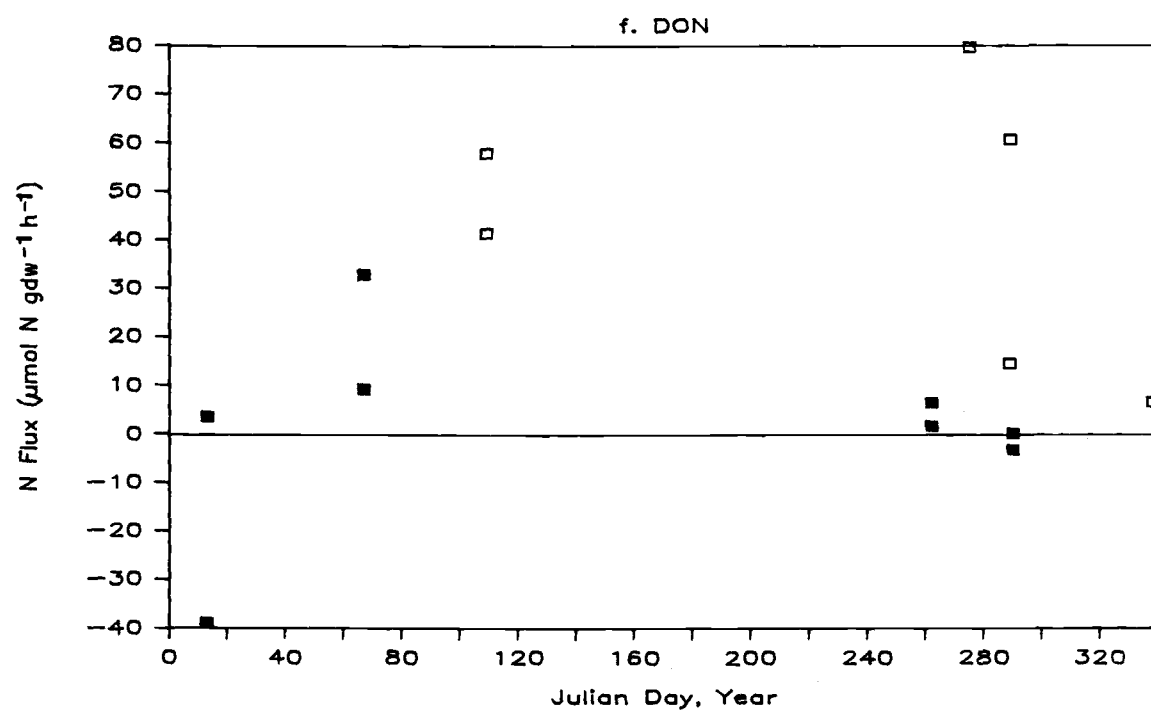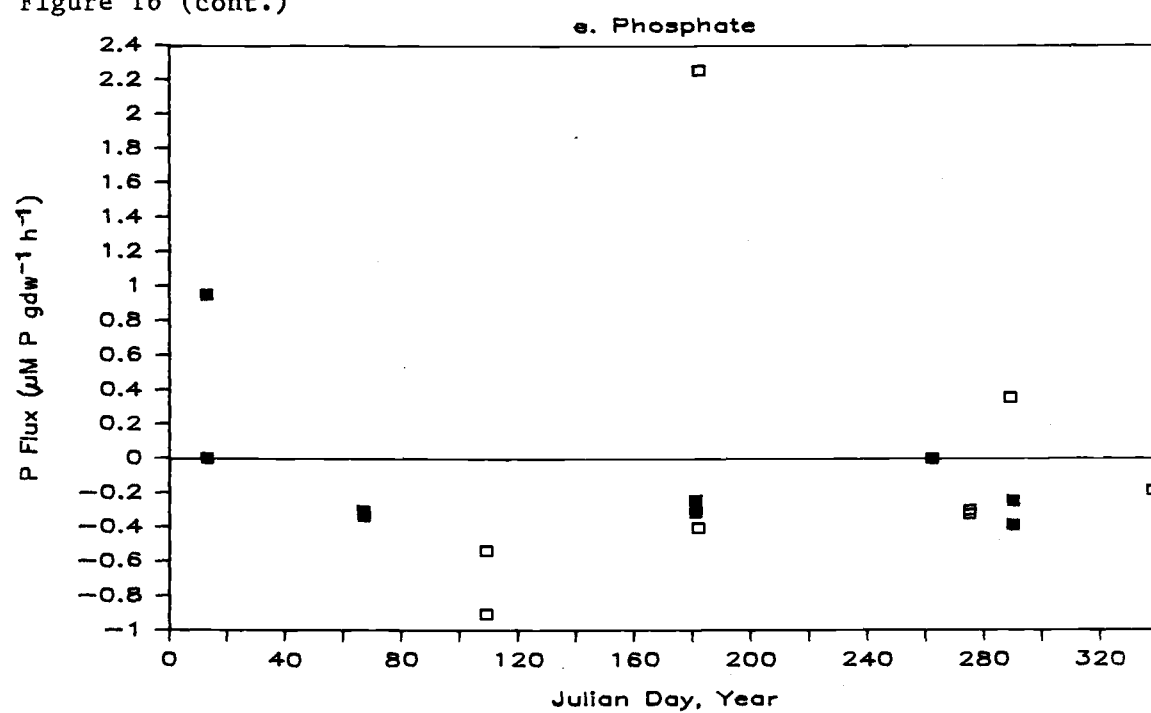
phosphate behavior is a high release at Site 1 in the summer, concident with high DIN release.

Although DON fluxes were not very different between sites, there was some seasonality to them (Figure 16f). They were nearly always positive, and reached a minimum in winter, with higher positive fluxes in fall and spring.

Correlation analysis was done to look for processes contributing to variations in the macroalgal-influenced nutrient fluxes. Table 4 shows that for fluxes expressed as per gram dry weight of macroalgal tissue, coupling seems strongest at Site 1 between oxygen and nitrogen forms, and between oxygen and phosphate. However, the correlation between light intensity at the sediment surface and nutrient fluxes, which is directly related to photosynthetic activity, is stronger at Site 2. In addition, net oxygen production occured in 89% of the chambers at Site 2, but only 56% at Site 1. As Table 5 shows, oxygen production coincides with inorganic nitrogen and phosphate uptake more often at Site 2 than at Site 1. Sediment-water fluxes of nutrients and oxygen appear to be coupled by macroalgal growth at Site 2 more than at Site 1.

Outliers in the data complicate interpretation of the correlation results. If outliers are omitted in Site 1 data, many of the correlations become insignificant. If outliers are omitted in Site 2 data, some of the correlations become significant. In a qualitative sense, Site 2 data show more of a trend, but outliers obscure any statistical significance, while Site 1 data show less trend but outliers cause significance. As a result, interpretations of the correlations based on these fluxes are equivocal.

Table 5: Agreement between oxygen production and inorganic
         nutrient uptake in chamber experiments that
         included macroalgae. Numbers given are percent
         of nutrient fluxes that indicated uptake when
         oxygen flux was positive.

Fluxes expressed per gram dry weight of algal tissue

Analyte:	DIN	Nitrate	Ammonium	Phosphate
Site 1	11	22	22	50
Site 2	80	90	60	60

Fluxes expressed per square meter of sediment surface

Site 1	10	22	22	50
Site 2	80	90	60	60

Element ratios from macroalgal tissue were compared to elemental analysis of macrophyte tissue composition reported by Atkinson and Smith (1983). The correlations in Table 4 indicate that there is less phosphorus exchange relative to oxygen exchange, suggesting phosphorus limitation. Nitrogen exchange occurs in nearly the predicted ratio with oxygen, suggesting that nitrogen is cycling through the macroalgae in higher abundance than the predicted ratio in relation to oxygen and therefore may not be limiting.

In summary, seasonal changes in nutrient fluxes expressed per gram algal biomass are most obvious in phosphate and DON. Generally, all fluxes increase in magnitude in spring and summer, but net release of inorganic nitrogen is more prevalent at Site 1 than at Site 2. At Site 2, macroalgal uptake seems to predominate for all of the fluxes. Interpretations of correlations from these fluxes is complicated by outliers. The correlations indicate that oxygen flux is coupled more strongly with inorganic nitrogen and phosphorus fluxes at Site 1 than at Site 2. Light intensity at the sediment surface correlates with DIN, nitrate, and oxygen fluxes only at Site 2. Inorganic nitrogen uptake occurs with oxygen production more frequently at Site 2 than at Site 1. Element ratios from flux correlations indicate that phosphorus is more likely to be limiting than nitrogen.

2. Chamber Experiments: Fluxes Per Square Meter of Sediment Surface

Fluxes expressed in moles $m^{-2} h^{-1}$ showed the same overall seasonal patterns as fluxes expressed per gram dry weight of macroalgal

tissue. One new observation revealed by this method of analysis is that at Site 2, the DIN flux is dominated by ammonium removal in the fall, and by nitrate removal in the spring (Figure 17). Macroalgae may be shifting from fall ammonium uptake to spring nitrate uptake to capitalize on the most abundant ion. Phosphate removal seems more consistent overall than nitrogen removal, as in the fluxes per gram macroalga. DIN and phosphate uptake and oxygen production nearly always occur at Site 2, but are less consistent at Site 1. Thus, these fluxes lead to the interpretation that macroalgal metabolism may have a greater influence on sediment-water fluxes at Site 2 than at Site 1.

Results of the correlation analysis for these fluxes are given in Table 6. Correlations of oxygen with inorganic nitrogen and phosphate show coupling between the element fluxes, but no distinct difference between the sites emerges. The data points for the fall season at Site 2 showed two trends in the oxygen versus DIN fluxes (Figure 18). Consequently, the data were split and treated separately. Macroalgal biomass is correlated with oxygen flux only at Site 2. Based on the combination of these correlations, Site 2 seemed more under the influence of macroalgal metabolism than Site 1.

Seasonal differences in element ratios indicated a possible shift in the potential for nitrogen limitation from fall to spring. When all data points were considered, nitrogen was cycled less than would be expected by the oxygen measurements. When data points from fall at Site 2 were omitted, the ratio dropped, approaching the expected proportions of nitrogen and oxygen cycling. These ratios indicate that nitrogen is more likely to be limiting in the fall than

Figure 17: Seasonal variation of macroalgal net nutrient flux expressed per square meter of sediment surface from chamber experiments (Site 2 only): a. Nitrate, b. Ammonium.

NET NUTRIENT FLUX IN CHAMBERS

Figure 17

a. Site 2, Nitrate

b. Site 2, Ammonium
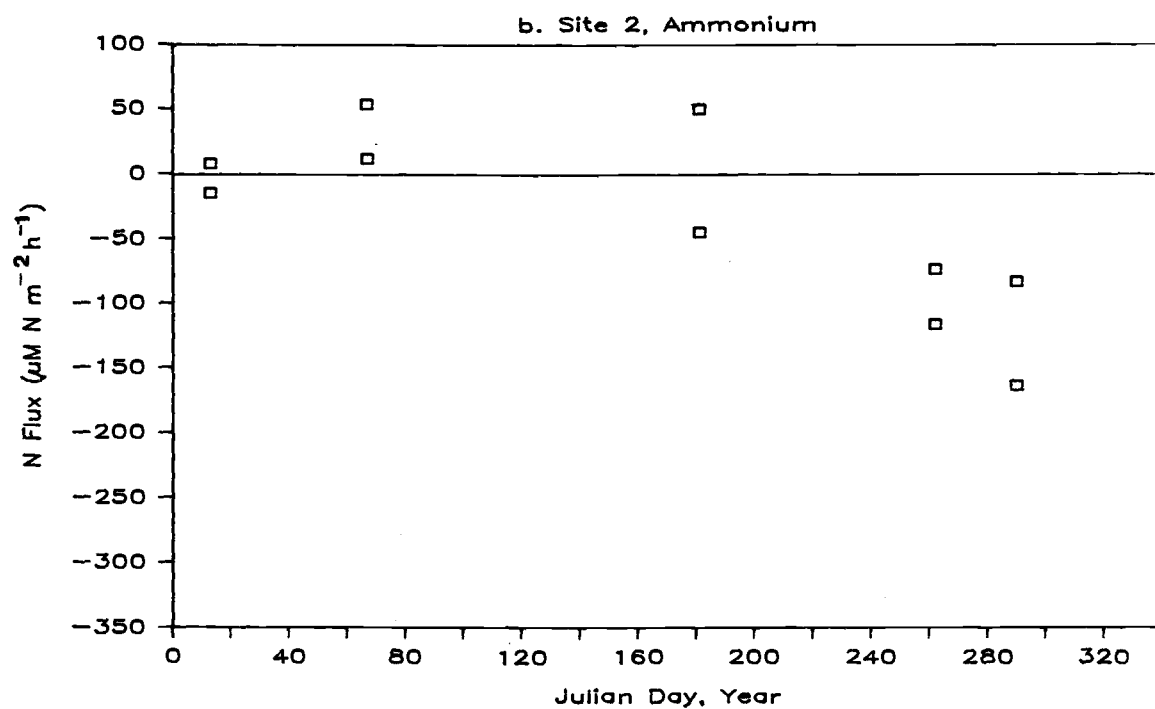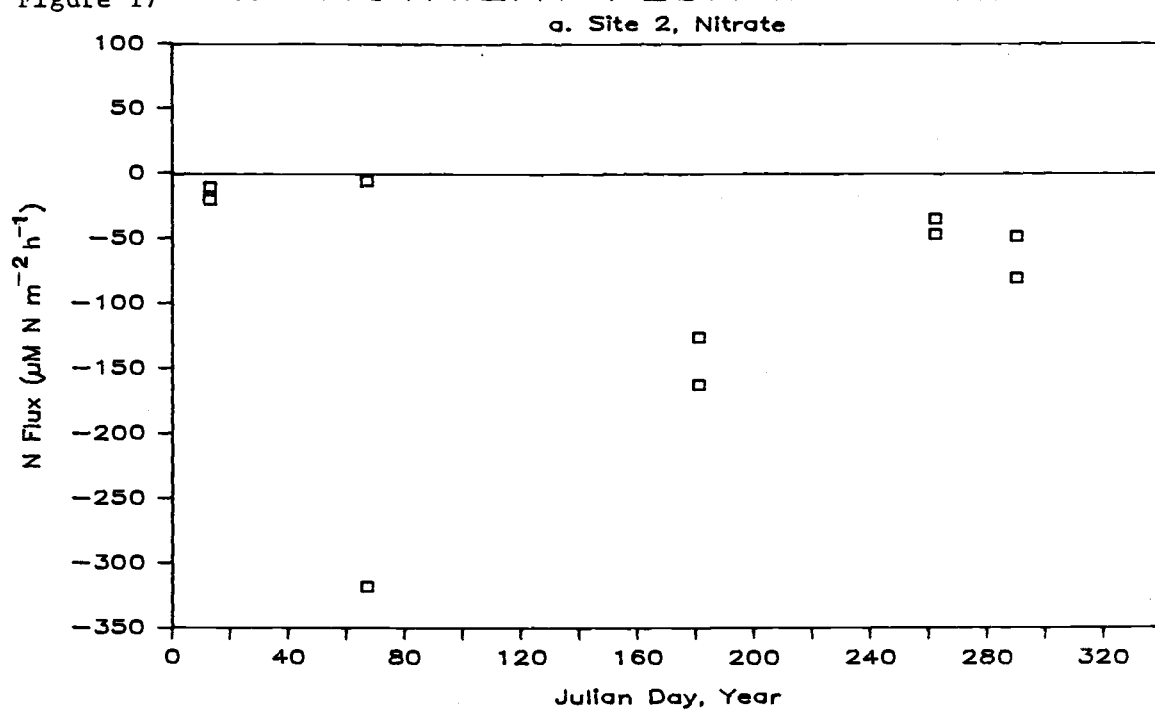
Figure 18: Relation between macroalgal net dissolved oxygen flux and macroalgal net DIN flux expressed per square meter of sediment surface from chamber experiments. Note the separate trend for 4 data points in the fall at Site 2 (closed symbols).

Figure 18   MACROALGAL INFLUENCE
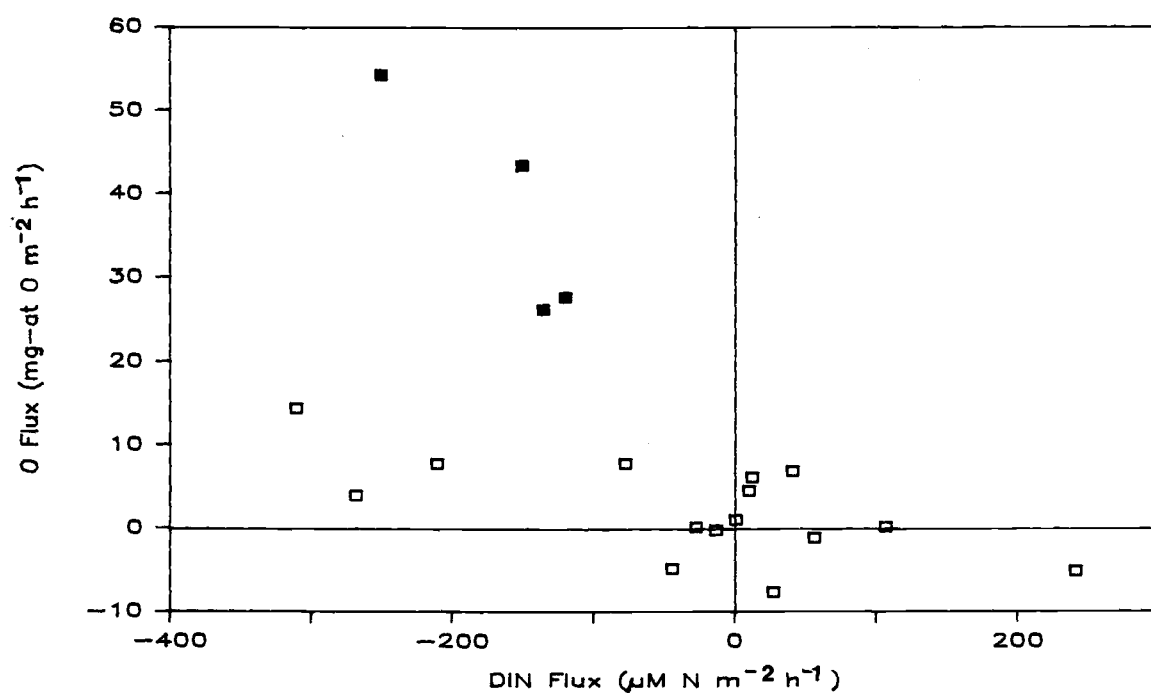
at any other time at Site 2. When Site 1 was considered alone, there seemed to be excess nitrogen being cycled.

Oxygen and phosphate fluxes were correlated at each site and when the sites were combined. There appeared to be sufficient phosphorus, but more was cycling relative to oxygen at Site 1 than at Site 2 (Table 6).

These two site differences - more nitrogen cycling at Site 1 than at Site 2, and more phosphorus cycling at Site 2 than at Site 1 - were the first indications found in this study for inter-site differences in potentially limiting nutrient.

The N/P ratio obtained by correlating DIN flux with phosphate flux indicates that over the entire sampling period, there is less nitrogen cycling than would be expected from the phosphate fluxes.

Both sets of chamber data, whether expressed as flux per gram macroalga or flux per square meter sediment area, showed seasonal changes in fluxes of inorganic nitrogen, phosphorus, and DON. Fluxes at Site 2 appeared to be more influenced by macroalagal metabolism than Site 1. Seasonal differences in element ratios suggest that nitrogen is more likely to be limiting in the fall than in the spring at Site 2, and that phosphorus is more likely to be limiting at Site 2 than Site 1. Overall, there appeared to be less nitrogen cycling relative to phosphorus than would be expected based on accepted stoichiometries.

Results from the chamber experiments showed that the potential for nutrient limitation in the Yaquina Estuary appears to vary spatially and seasonally. As the following discussion will explain, bottle experiments reinforce and further clarify this conclusion.

Table 6: Correlations of flux data expressed per meter squared of sediment surface; from chamber experiments that included macroalgae. Element ratios from Chlorophyta growth are O:N:P= 1600:38:1 (modified from Atkinson and Smith 1983). Symbols as in Table 3.

Relation	Location	Signif.	Element Ratios (by atoms)		r*	n
Oxygen vs	Both	**	O/N=71	C/N=30	.604	19
DIN	Both (1)	**	O/N=61	C/N=25	.682	16
	1	*	O/N=32	C/N=14	.707	9
Oxygen vs	Both (1)	*			.556	15
Nitrate	2 (2)	**			.917	7
Oxygen vs	Both	**			.831	19
Ammonium	1	*			.748	9
	2	**			.918	10
Oxygen vs	Both	**	O/P=1290	C/P=538	.579	19
Phosphate	Both (1)	*	O/P=1910	C/P=795	.568	16
	1	*	O/P=700	C/P=296	.711	9
	2	*	O/P=1470	C/P=613	.639	10
Phosphate vs						
DIN	Both	*	N/P=10		.560	19
Nitrate	2 (1)	*			.783	8
Ammonium	Both	**			.599	19
Nitrite	2	*			.774	8
Oxygen vs	2	*			.707	10
Biomass						

(1) Three points were omitted; see text.
(2) September, October, and near-zero fluxes

3. Bottle Experiments: Nutrient Uptake Per Gram Macroalgal Tissue

Bottle experiments duplicate the chamber experimental conditions without the contributions (and additional variability) of the sediment community. Consequently, the bottle experiments are a better indicator of isolated macroalgal metabolism than the chamber experiments.

Calculations of macroalgal influence based on bottle experiments showed that nitrate, ammonium and phosphate were always removed, and dissolved oxygen was always produced. The results of the bottle experiments clearly show the relation between macroalgal growth, element cycling, and changing environmental conditions.

Macroalgal uptake of nitrate, nitrite, ammonium, DIN, phosphate, and production of dissolved oxygen, exhibited seasonal patterns consistent with a minimum of macroalgal growth in December, January, and March and more growth during other months. As was found in the chamber fluxes not normalized to biomass, there was some indication of a shift in uptake from ammonium in the fall to nitrate in the spring. At Site 2, nitrate removal was greatest (-44 microgram-atoms N gdw^{-1} h^{-1}) in June (Figure 19a). At Site 1, ammonium removal was greatest in October (Figure 19c). DIN removal was higher in the summer than in the fall (Figure 19d), but phosphate removal (Figure 19e) was roughly equal in summer and fall. There was also an increase in dissolved oxygen production together with increased DIN and phosphate removal from September to October at both sites.

Nitrite concentrations aparently increased during the bottle experiments in December, January, and March. However, this result is

Figure 19: Seasonal variation of macroalgal net nutrient uptake in bottle experiments: a. Nitrate, b. Nitrite, c. Ammonium, d. DIN, e. Phosphate. Open symbols=Site 1, closed symbols=Site 2.

Figure 19 MACROALGAL UPTAKE IN BOTTLES

a. Nitrate

b. Nitrite

Figure 19 (cont.)

c. Ammonium

d. DIN

Figure 19 (cont.)

e. Phosphate
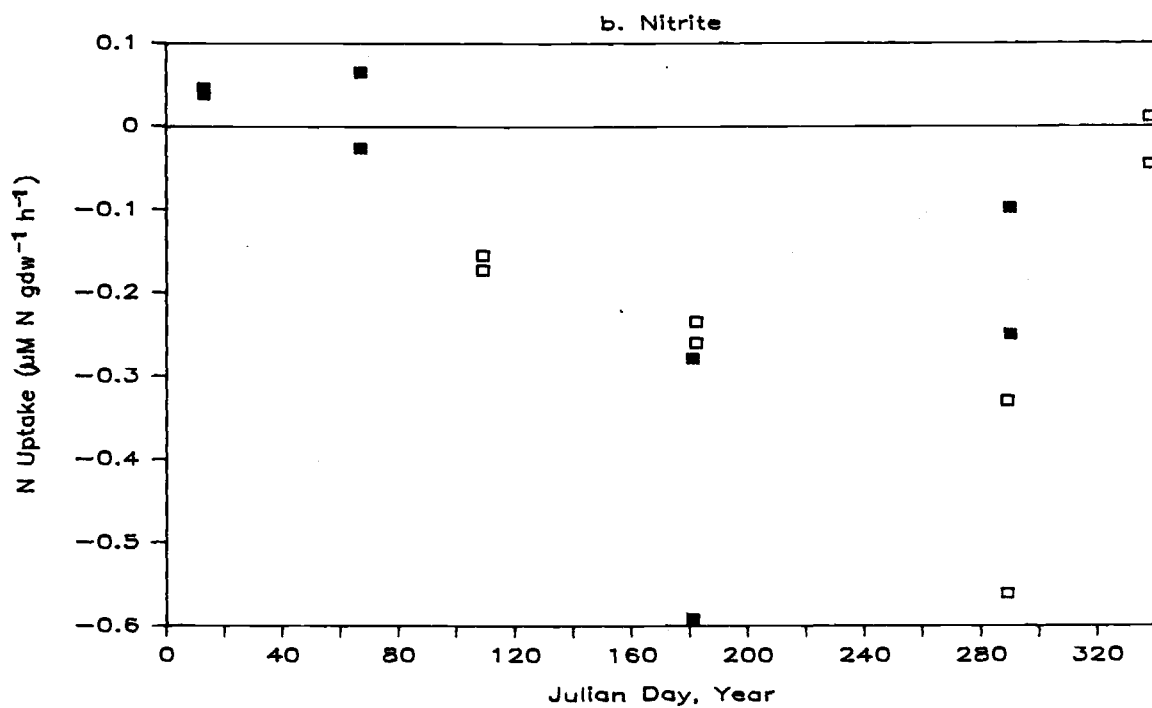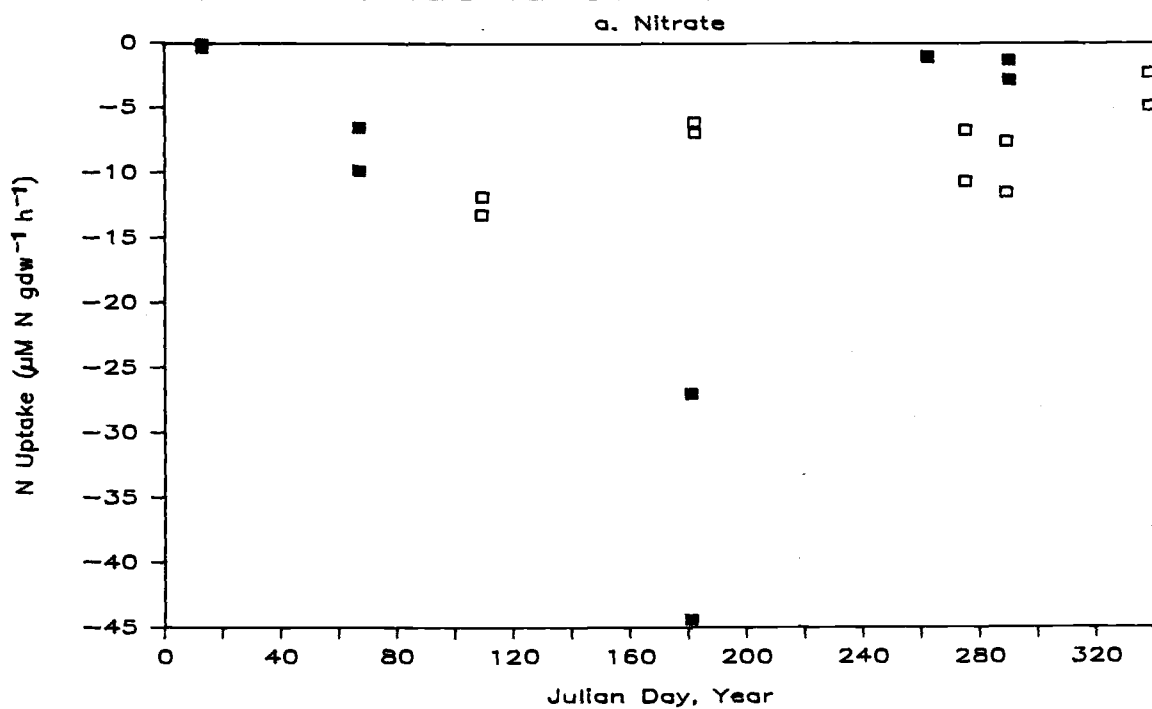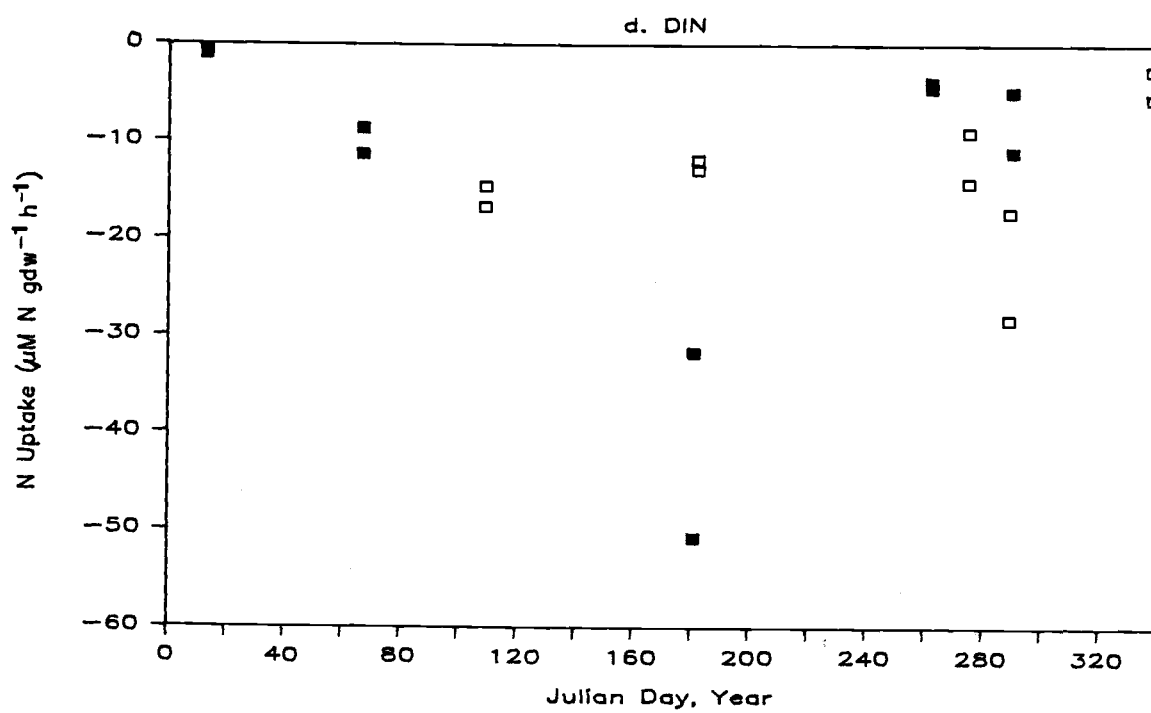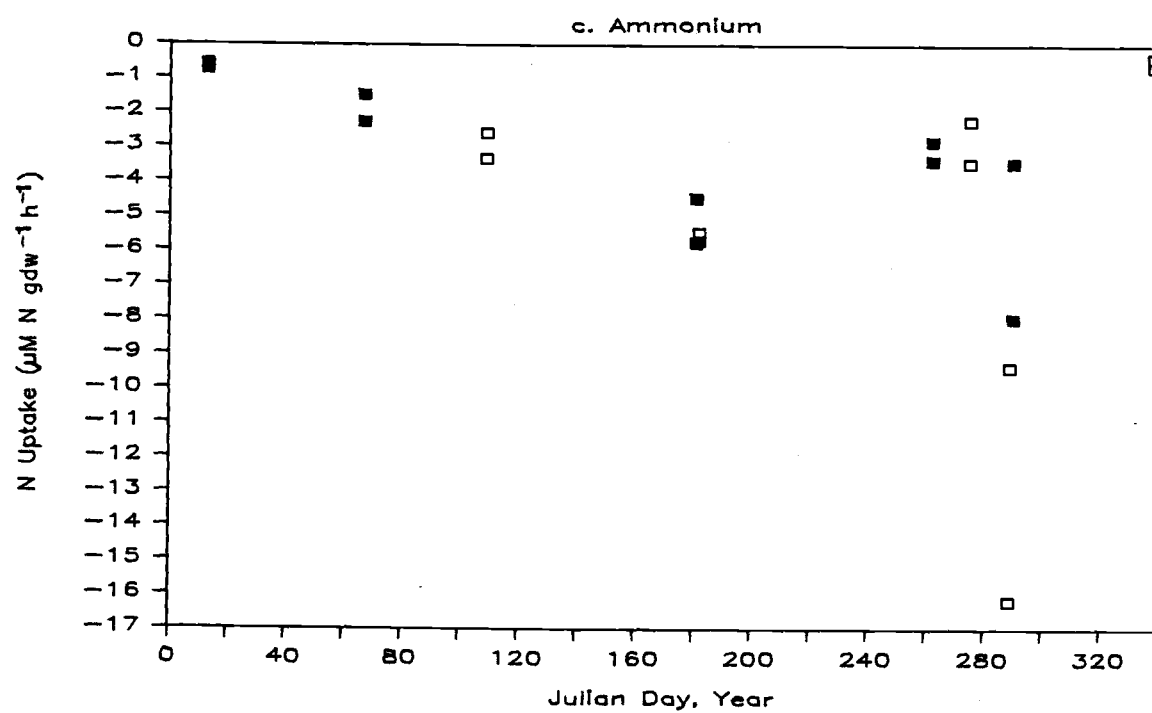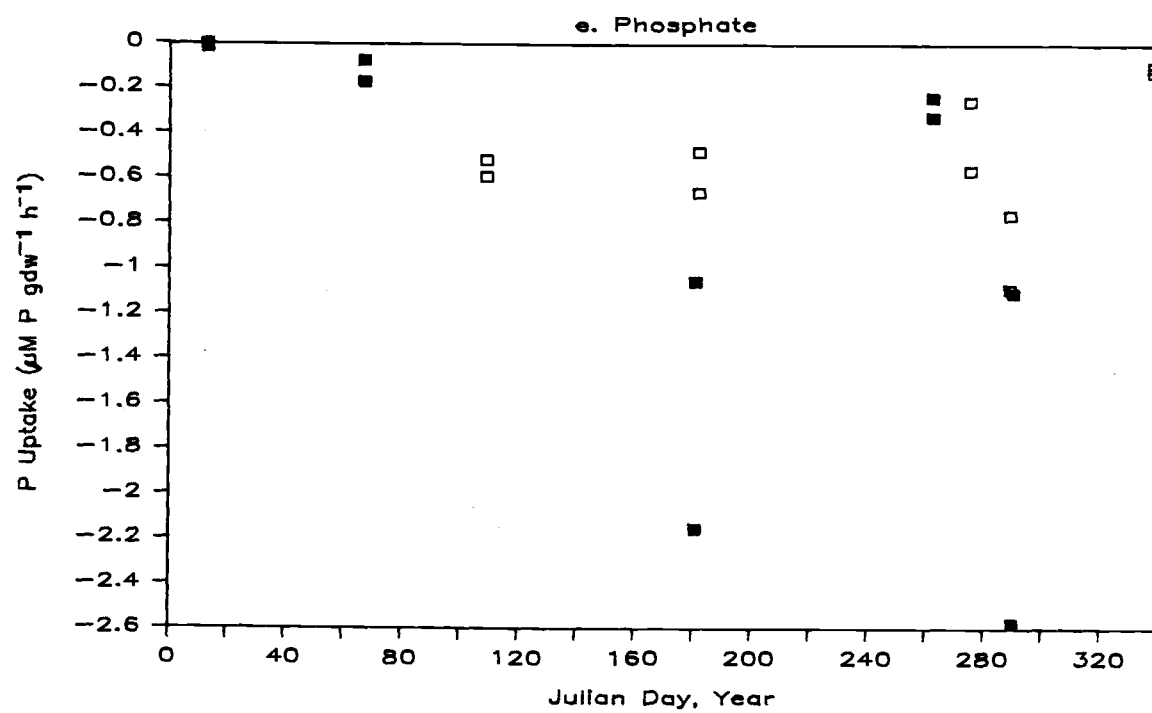
an artifact of calculation. Nitrite concentration changes in bottles containing macroalgae were equal to or less than changes in control bottles. Thus, there was no measureable nitrite uptake by the macroalgae in the winter.

Significant correlations between experimental variables were more numerous in the bottle experiments than in chamber experiments, reflecting tighter coupling of macroalgal production and nutrient uptake dynamics in the bottles (Table 7). Relations between oxygen production, ambient nitrogen, and ambient phosphate were particularly interesting. At Site 1, production was correlated with ambient nitrogen, but not with phosphate. The reverse was found at Site 2. The next set of correlations shows that nitrogen and phosphate removal and oxygen production were correlated with light intensity at the sediment surface when the sites are combined and at Site 2, but not at Site 1. Site 2 stands out again when removal of nitrate and phosphate correlate with ambient concentrations.

Usually, nitrogen and phosphate removal and oxygen production in the bottles were positively correlated. Note that there was a separate trend for the fall results at Site 2, just as there was in the chamber fluxes not corrected for algal biomass.

No correlation between oxygen production and nitrate removal was found at Site 1. Although this correlation was not significant, such a trend may be obscured by scatter in the data.

Element ratios from these correlations indicate that there may be less inorganic nitrogen and phosphate uptake in specific instances than stoichiometries predict. Using Atkinson and Smith's ratios (1983) as a guide, there appears to be a deficiency of nitrogen uptake

Table 7: Correlations of flux data expressed per gram
dry weight of macroalgal tissue; from bottle
experiments that included macroalgae. Element
ratios from Chlorophyta growth are O:N:P=
1600:38:1 (modified from Atkinson and Smith 1983).
Symbols as in Table 3.

Relation	Location	Signif.	Element Ratios (by atoms)		r*	n
Oxygen vs Ambient						
DIN	1	**			.789	10
Nitrate	1	*			.688	10
Ammonium	1	*			.706	10
Phosphate	Both	**			.578	20
	2	**			.745	20
vs Light						
DIN	2	**			.919	10
Nitrate	Both	*			.533	20
	2	**			.894	10
Ammonium	2	**			.645	10
Nitrite	2	**			.916	8
Phosphate	Both	*			.517	20
	2	*			.686	10
Oxygen	2	**			.799	10
Removal vs Ambient						
Nitrate	2	*			.640	10
Phosphate	Both	**			.564	20
	2	**			.851	10
Oxygen vs	Both	**	O/N=50	C/N=21	.782	20
DIN	Both (1)	**	O/N=56	C/N=23	.893	16
	Both (2)	**	O/N=226	C/N=94	.999	6
	1	**	O/N=90	C/N=38	.890	10
	2	**	O/N=43	C/N=18	.803	10
	2 (1)	**	O/N=51	C/N=21	.999	6
Oxygen vs	Both	**			.586	20
Nitrate	2	*			.717	10
	2 (1)	**			.999	6
	2 (2)	**			.998	6
Oxygen vs	Both	**			.852	20
Ammonium	1	**			.975	10
	2	**			.946	10
Oxygen vs Nitrite	Both	**			.928	16

Table 7:   (continued)

Oxygen vs Phosphate	Both	**	O/P=987	C/P=411	.869	20
	1	**	O/P=2200	O/P=926	.936	10
	2	**	O/P=898	O/P=375	.955	10
DIN vs Phosphate	Both	**	N/P=11		.648	20
	Both (1)	**	N/P=23		.972	18
	Both (2)	**	N/P=3.6		.974	6
	1	**	N/P=22		.970	10
	2	*	N/P=10		.642	10
	2 (1)	**	N/P=22		.992	6
	2 (2)	**	N/P=3.6		.974	6
Nitrate vs Phosphate	Both	*			.527	20
	Both (1)	**			.911	16
	1	*			.689	10
	2 (1)	**			.993	6
	2 (2)	**			.974	6
Ammonium vs Phosphate	Both	**			.583	20
	1	**			.924	10
	2	**			.952	10
Nitrite vs Phosphate	Both	**			.728	16
	1	**			.973	8
	2	**			.865	8
	2 (1)	**			.998	6
	2 (2)	**			.987	6
Algal Tissue C/N vs Ambient DIN	Both	**			.489	38
	2	*			.549	20
Bottle C/N vs Ambient						
Nitrate	Both	**			.636	20
DIN	Both	**			.670	20
Bottle C/P vs Ambient Phosphate	Both	**			.679	19
Bottle N/P vs Ambient						
Nitrate	Both	*			.507	19
DIN	Both	*			.510	19
Bottle N/P vs Ambient N/P	Both	**			.634	19

(1) Four points were omitted; see text.
(2) September, October, and near-zero fluxes

relative to oxygen production by the macroalgae at Site 1 during the entire sampling period and at Site 2 in the fall. Nitrogen uptake and and oxygen production appear in the predicted ratios at Site 2 in the winter, spring and summer. Although phosphorus uptake may have been low relative to oxygen production at Site 1, there appeared to be surplus phosphate uptake at Site 2 alone, and when data from both sites were combined.

Nitrogen and phosphate uptakes were significantly correlated in all possible combinations at each site, and with both sites combined. The ratios show that phosphorus uptake may be in excess of macroalgal demand, but nitrogen uptake may be less than demand. An interesting observation is that the N:P ratio from uptakes is the same at Site 1 year-round as at Site 2 only in the fall.

The correlations between algal tissue C/N and ambient DIN showed strong differences between sites. The C/N ratio in algal tissue correlated with ambient DIN only at Site 2.

The last correlations in Table 7 examined the relation between ratios of production to uptake and ambient nutrient concentrations. These relations may have some bearing on long-term macroalgal nutrient demand and will be discussed in the following section.

In conclusion, the bottle experiments show tight coupling between macroalgal production and the uptake of inorganic nitrogen and phosphorus. Strong seasonal patterns were also evident in macroalgal nutrient removal, indicating seasonal variation in macroalgal growth. Contrary to the results from chamber incubations, there was no evidence of net release of inorganic nutrients in the bottle incubations.

Differences between sites indicate 1) macroalgal nutrient uptake and photosynthesis may be more coupled to ambient nutrient concentrations at Site 2 than at Site 1 2) productivity is more coupled to ambient nitrogen at Site 1, but is coupled to ambient phosphorus at Site 2. Macroalgal uptake of nitrogen appears to shift from ammonium in the fall to nitrate in the spring. In the bottle experiments, ammonium uptake was greater than nitrate removal only in September, October, and January, and usually at Site 2. During all other months, nitrate uptake exceeded ammonium uptake. Element ratios produce a stronger argument for the potential of nitrogen limitation of macroalgal growth than phosphorus limitation, but there is evidence that both elements may at times be limiting.

DISCUSSION

I. Variability in Sediment-Water Fluxes: Differences Between Methods
    of Calculation

The four methods used in this thesis for expressing sediment-
water fluxes resulted in different conclusions about between-site
variation.   Coefficients of variation have been calculated to compare
variations between sites resulting from different methods of flux
calculations (Table 8).   When fluxes in chambers are based on sediment
surface area, coefficients of variation for nitrate and DIN fluxes
attributable to macroalgal growth show the greatest between-site
variability.   The between-site differences in ammonium fluxes appears
greatest for sediment regeneration processes.   Consequently,
differences in sediment processes may be responsible for variations in
inorganic nitrogen fluxes between sites.

Variations in phosphate, oxygen, and DON fluxes in chambers are
most different between sites when calculated on the basis of macroalgal
biomass.   For these fluxes, differences in macroalgal growth between
the sites appears to be a major source of variation.

However, bottle incubations produce the lowest variability
between sites, indicating that macroalgal growth is similar between
sites for all fluxes.

The variability in chamber fluxes may be a result of using the
difference between fluxes to describe macroalgal influence.   Flux
measurements are usually quite variable, and finding the difference
between two expressions of sediment-water nutrient flux compounds the

Table 8: Coefficients of variation for chamber and bottle fluxes as expressed in Appendix A.

	Nitrate	Nitrite	Ammonium	DIN	DON	Phosphate	Oxygen
Sediment Regeneration (per square meter of sediment surface)							
Site 1	155	742	88.9	498	231	118	108
Site 2	147	142	1110	256	116	336	729
Chamber Macroalgal Influence (per square meter of sediment surface)							
Site 1	42300	131	532	954	79.7	220	480
Site 2	112	40.8	194	77.2	169	171	114
Chamber Macroalgal Influence (per gram dry weight of algal tissue)							
Site 1	350	147	338	332	65.3	16800	1370
Site 2	131	67.7	834	119	1390	452	108
Bottle Macroalgal Influence (per gram dry weight of algal tissue)							
Site 1	42.7	81.2	96.6	53	174	58.6	64.5
Site 2	156	165	69.8	125	71.1	121	78

variability. Additional evidence for this arguement is the apparent release of nutrients observed in the chamber incubations, with no such release found in the bottle incubations. Bottle incubation results are generally less variable overall than either of the two calculated forms of chamber macroalgal fluxes (Table 8). Because coefficients of variation are usually lower and more similar between sites for the bottle incubations, a large part of the variability in chamber fluxes attributed to macroalgae may have resulted from using the difference method to determine these fluxes. This conclusion implies that interpretations of macroalgal growth and its influence on nutrient fluxes from chamber incubations are questionable. Results from bottle incubations were probably more reliable, and will be used to calculate removal capacity of the macroalgae in sections that follow.

II. Sediment Metabolism: Oxygen Demand and Nutrient Exchange

Measurements of oxygen demand and nutrient fluxes caused by sediment community metabolism in Yaquina Estuary were generally in the same range as other measurements from studies in coastal water (Table 9).

Table 9: Comparison of sediment-water flux measurements of inorganic nutrients and oxygen over bare sediment; this study with others. Units are micromoles m^{-2} h^{-1} except for oxygen, in mg-at O m^{-2} h^{-1}.

Ammonium	Nitrate+Nitrite	Phosphate	Oxygen	Ref
0 to 430	-95 to 38	-10 to 50	1 to 12	a
2.56 to 128	-0.97 to 9.07	-14.9 to 21.5	1.97	b
165	10	36.7	7.6	c
-90.8 to 204	-221 to 211	-5.35 to 16.2	-8.91 to 7.75	d

a) Nowicki and Nixon (1985a, b)
b) Rowe et al. (1975)
c) Hopkinson and Wetzel (1982)
d) this study

Oxygen demand was within the range found in other studies, as was the level of ammonium release. The phosphate flux from this thesis was also similar to other results, and illustrated the close coupling other workers have noticed with temperature and oxygen (Nixon et al. 1979).

The ratio of oxygen demand to regenerated phosphorus indicated that phosphorus limitation of macroalgal growth is possible because there is less phosphorus regenerated than stoichiometric ratios predict.

The greatest discrepancies between this study and others are in nitrate fluxes and ammonium uptake. No other studies have reported nitrate uptake or release by the sediments as high as those reported here. These measurements of sediment ammonium uptake are also higher than other reported rates.

Nitrate uptake by the sediment suggests that denitrification may be occurring in the sediment. Nitrate uptake is not correlated with

ammonium release at Site 1, showing that reduction to ammonium is not likely to be the cause of the sink. Nitrate uptake at Site 1 increases with ambient nitrate concentration, in spite of simultaneously decreasing water temperatures. Microbes responsible for denitrification processes can maintain high levels of ETS activity (a measure of microbial metabolism) at temperatures as low as 4 degrees C (Trevors 1985). This shows that denitrification may be proceeding in spite of the low temperatures.

Finding an explanation for the nitrate regeneration is not as easy. Nitrification could produce positive nitrate fluxes from the sediment. However, nitrification requires ammonium as the substrate, and ammonium uptake is not correlated with nitrate regeneration. The reasons for such a large flux of regenerated nitrogen remain a puzzle.

III. Autotropy and Nutrient Removal

Measurements of productivity in this study are comparable to other results for intertidal macroalgae (Table 10).

Table 10: Comparison of macroalgal productivity measurements: this study with others. Units are mg C gdw^{-1} h^{-1}. E = _Enteromorpha_ spp., U = _Ulva_ spp.

Productivity	Species	Location	Reference
7.5 to 19	U, E	Cos Bay, OR	a
9.5	E	Yaquina Bay, OR	b
10.3	U	Yaquina Bay, OR	b
0.02 to 10.8	E	Finland	c
0.575 to 13.6	U, E	Yaquina Bay, OR	d

a) Pregnall and Rudy (1985)
b) Davis (1981)
c) Kautsky (1982)
d) this thesis

Previous work (Davis 1981) indicates the light conditions encountered during this study are not likely to be limiting to macroalgal growth. Plots of nitrate and phosphate uptakes measured in bottle incubations against ambient nitrate and phosphate concentrations indicated that uptakes may become saturated at the higher ambient concentrations in this study. Phosphate uptake appeared to be saturated at 0.8 micromolar, and nitrate uptake at 10-15 micromolar. These approximations of V_{max} were similar to other measurements from intertidal macroalgae (see Introduction for references).

To relate a nutrient sink in Yaquina Estuary to macroalgal metabolism, the disappearance of nutrient measured during these experiments must be attributed to macroalgal metabolism. Correlations between oxygen production and nutrient uptake for chamber flux per gram, chamber flux not normalized to biomass, and changes in nutrient concentrations in bottle experiments have shown that this relation exists, albeit with variations between the methods of analysis. Therefore, it is reasonable to extrapolate from measured nutrient

uptake rates attributable to macroalgal metabolism to bay-wide estimates of nutrient removal capacity.

The calculations that will be discussed next were not the result of a complex model that included all pertinent factors. Rather, they represent a first attempt to set limits to the removal capacity of the macroalgal population in the bay. Among the factors that are not included are variations in macroalgal metabolism with water depth, age, and self-shading.

In addition, these calculations are based on several assumptions:

a. All nutrient loading from the Yaquina River is assumed to be available to the macroalgae for removal. This assumption is not accurate, because the hydrodynamics of flow in the estuary will not move all river water over the mudflats. Thus, calculations of removal capacity are maximum estimates until hydrodynamics are included. The difference between ambient nitrate concentrations at the two sites on June 30 (12.6 micromolar) and July 1 (3.5 micromolar) illustrates how different the hydrodynamics might be between the sites. The hydrodynamics of nutrient supply to the mudflats is probably the most important of the factors left unexplored in these calculations.

b. Nutrient concentrations in river water are assumed to be mean monthly concentrations. There is not sufficient data to know whether the concentrations used are representative of each month. It is possible that changes in nutrient concentrations over a few

days or a few hours may be large. Consequently, nutrient loading on the estuary may be more pulsed than indicated by these calculations.

c. Sediment regeneration and algal removal rates are also assumed to be monthly means, but may be more variable. Sediment uptake of nitrate may respond to pulsed river loading, just as luxury uptake by the algae may respond.

d. The interaction between photoperiod and inundation has been approximated using a mean value based on inundation for all months except December, when photoperiod is less than inundation period. A mathematical model has been used by Pregnall and Rudy (1985), and its use here would refine these calculations.

e. Macroalgal biomass (as used in the calculations of Appendix B), is based on conservative estimates of seasonal changes in maximum Enteromorpha spp. biomass measured in Yaquina Estuary by Davis (1981). Seasonal biomass measurements for both Enteromorpha and Ulva spp. should be used if available.

f. Macroalgal coverage (as used in Appendix B), is based on conservative estimates of seasonal changes in coverage of the maximum area available for macroalgal growth (30-40% of the Yaquina Estuary, M. W. Davis, pers. comm.).

Nitrate and phosphate supply to the bay were calculated based on river loading and sediment regeneration. Sediment regeneration or uptake of nitrate and phosphate were included as measured by chamber incubations. Not included in the calculations is a major phosphate source for the bay: seawater. Consequently, actual phosphate supply to the bay is higher than the figures used in removal calculations, making the phosphate removal factor somewhat high. A thorough

treatment of the oceanic phosphate source would also require modelling that is outside the scope of this investigation.

As a measure of how well the nutrient supply calculations account for the true nutrient sources, ambient nitrate and phosphate were correlated with nutrient supply estimates. Nitrate was significantly correlated ($r^* = .797$, $n = 10$) but phosphate was not. This shows that river supply and regeneration account reasonably well for the ambient nitrate concentration in the bay. Phosphate concentrations, on the other hand, are apparently regulated by other factors that probably include supply from coastal water.

Nutrient removal capacity attributable to the macroalgae was calculated using measurements of nutrient uptake in bottle experiments, macroalgal biomass and coverage, photoperiod, and tidal innundation. Results of these calculations are presented in Table 11. As the removal factor shows, the macroalgae could remove an order of magnitude more nitrate than was supplied to the estuary in the summer. In the fall, sediment uptake of nitrate was large enough to remove all of the nitrate supply. If sediment uptake were not included in these calculations, macroalgal demand could remove more than ten times the nitrate supplied. Consequently, fall nitrate supplies were far less than sediment and macroalgal demand, and may have been limiting to growth. When phosphate regeneration supplied nutrient to the water column, there seemed to be no shortage of phosphate for the macroalgae, except in the summer. However, ocean supply of phosphate would be greatest in summer, bringing phosphate supply closer to demand.

It is important to recall that with the shortcomings of these

Table 11: Removal factor for macroalgal uptake of nitrate and phosphate river loading on Yaquina Estuary. Removal factor describes the number of times that daily macroalgal growth could remove the amount of nitrate or phosphate brought into the estuary by river loading. See Appendix B for details of the calculations.

SAMPLING DAY	SUPPLY (mole d^{-1}) Nitrate	Phosphate	REMOVAL BY MACROALGAE (mole d^{-1}) Nitrate	Phosphate	REMOVAL FACTOR Nitrate	Phosphate
9-9-84	-971	4500	6960	1800		
9-22-84	-7560	-1010	56700	2640		0.4
10-6-84	-1170	3330	16000	1530		0.5
10-7-84	14900	20400	3500	3000	0.2	0.1
12-4-84	123000	1990	0	0	0	0
1-13-85	136000	696	0	0	0	0
3-8-85	123000	260	0	0	0	0
4-19-85	46400	2280	289	12.7	0.006	0.006
6-30-85	78100	-1280	61900	2830	0.8	
7-1-85	7580	4880	118000	10300	16	2.1

extrapolations, these removal factors are probably upper limits. Consequently, macroalgal growth may have been a significant sink for nitrate and phosphate loading in the fall, late spring, and summer, but it was out of phase with the rainy season responsible for delivering most of the nitrate to the estuary.

IV. Nutrient Limitation

If predictions of which nutrient were likely to be limiting had to be based on foregoing results alone, nitrate would undoubtedly be the choice. As explained above, macroalgal tissue analysis bore this out. Other information, however, pointed to phosphorus as well.

First, the carbon and nitrogen content of the macroalgal tissue from the chamber experiments were lowest in December (%C=17, %N=2.2) and highest in June and July (%C=35.7, %N=5.08). When these data were split by site, the percent nitrogen was 4.05% at Site 1 and 5.08% at Site 2. Each of these values wss a mean of four replicates, and the mean at Site 1 was significantly higher than at Site 2 (P<.01). Site 2 was the upriver site, closer to the river channel (and nitrate supply) than Site 1. Proximity of Site 2 to the main river flow could provide more nitrogen to the intertidal community than would be available to the mudflat at Site 1. At the times these algal samples were collected, ambient nitrate was 12.6 micromolar at Site 2 and only 3.6 micromolar at Site 1 even though the samples were taken on consecutive days. The difference between sites in algal tissue nitrogen was also apparent in the C/N ratios from the algae. The measurements were 7.8 in June at Site 2, and 10.5 in July at Site 1. The comparison between

these ratios indicated possible nitrogen limitation at Site 1, and showed that plants at Site 2 were richer in nitrogen than those at Site 1. The rise in C/N in the fall (Figure 14) showed that plants at both sites were lower in nitrogen than in winter or spring, when the nitrate flush was in progress.

Next, the last four relations in Table 7 showed significant correlations between a ratio of production to uptake, and ambient nutrient concentration. These relations supported the conclusion that production/uptake ratios responded to nutrient availability. Other correlations were significant:

Table 12: Correlations between elemental content of macroalgal tissue and nutrient sources. (see Appendix B for details of supply calculations) (**=P<.01)

Relation	Location	Significance	r*	n
Algal tissue C/N vs	Both	**	.551	38
Nitrate Supply	1	n.s.	-	-
	2	**	.751	20

That algal C/N was correlated with nitrate supply and ambient DIN at both sites, and at Site 2, but not at Site 1, showed that over the long term, tissue composition may have responded to nitrate supply in the estuary as a whole, and the coupling may have been tighter at Site 2 than at Site 1. In addition, ammonium regeneration was nearly constant during sampling at Site 1, but rarely found at Site 2. Because %N was not correlated with ambient DIN or nitrate supply, there was apparently little storage of nitrate at either site. The difference in ammonium regeneration between sites may have compensated for decreased access to

river nitrate at Site 1. Weight-specific ammonium uptake rates were greater in bottles at Site 1 than at Site 2 in October (Figure 19c). Together with the correlations in Tables 4, 6, and 7, these results showed that river nitrate may have been a more important source of nitrogen for macroalgae at Site 2 than at Site 1.

Taking this line of reasoning a step further, there was some evidence that phosphate limitation was more likely at Site 2 than at Site 1. Table 7 showed that algal productivity (oxygen production) was correlated with ambient phosphate at both sites together and at Site 2. Algal productivity at Site 1 was correlated with ambient DIN, nitrate, and ammonium. Considering that nitrate, the dominant form of available nitrogen was delivered primarily from upriver, and phosphate was delivered from the ocean, it is not hard to imagine a gradient between landward phosphate limitation and seaward nitrogen limitation.

Based on the correlations examined so far, both sites may have been nitrogen-limited under certain conditions in the fall, when river nitrate supply was lowest. More evidence for this speculation came from C/N ratios and %N in macroalgal tissue, as already discussed. Site 1 (the ocean site) was more likely to be nitrogen limited in the spring than Site 2, as shown by the lower %N in macroalgal tissue. This speculation may not be borne out in uptake ratios because sampling was not concentrated just in the spring. Site 2 (the river site) showed some evidence for phosphorus limitation, but no distinct seasonal difference.

Ratios of C:N:P from bottle incubations showed seasonal variations in uptake and productivity that illustrated the potential

for a seasonal shift from potential nitrogen limitation to potential phosphorus limitation. Figure 20a shows the ratio of growth (in terms of carbon) to nitrogen uptake. Keeping in mind the predicted ratios from Atkinson and Smith (15) and Redfield (6.6), it appears that nitrogen may have always been limiting. This conclusion may be related to the choice of photosynthetic quotient for these calculations. Nitrogen limitation was not likely in the winter because of the nitrate flush.

Nevertheless, seasonal changes in this ratio corresponded somewhat to changes in tissue composition. The ratio remained about the same at Site 1 until the summer, when it rose, suggesting that nitrogen was limiting. This rise corresponded to the rise in tissue C/N observed in Figure 14a. At Site 2, the ratio was highest in the fall, corresponding to the high C/N found in Figure 14b. Why the algal growth/uptake ratio is not higher at Site 1 in the fall is a mystery.

Figure 20b compares growth (carbon) to phosphate uptake. Critical ratios from Atkinson and Smith and Redfield are 488 and 106, respectively. The "baseline" for C/P was closer to the expected ratios in this graph, and again showed a seasonal change in likelihood that phosphorus may be limiting in the estuary. The ratio at Site 1 changed little throughout the year. This may have been a result of ample phosphate availability from more mixing of ocean water with estuarine water at Site 1 than at Site 2. Nutrient concentrations from the YAQ data of 1983-84 showed that higher-salinity water reached the main channel in the estuary even in the winter when river flow was highest. Salinity reached 30.5 and 27.7 in bottom water at YAQ Station 2 in April and June, respectively. On the same sampling dates, salinity was

Figure 20: Seasonal variation of the ratio a. growth (carbon
assimilation)/DIN uptake   b. growth (carbon
assimilation)/phosphate uptake   c. DIN uptake/phosphate
uptake.   All from bottle experiments.   Open symbols=Site 1,
closed symbols=Site 2.

Figure 20 ATOMIC RATIOS: BOTTLES
a. C/N

b. C/P

Figure 20 (cont.)

c. N/P
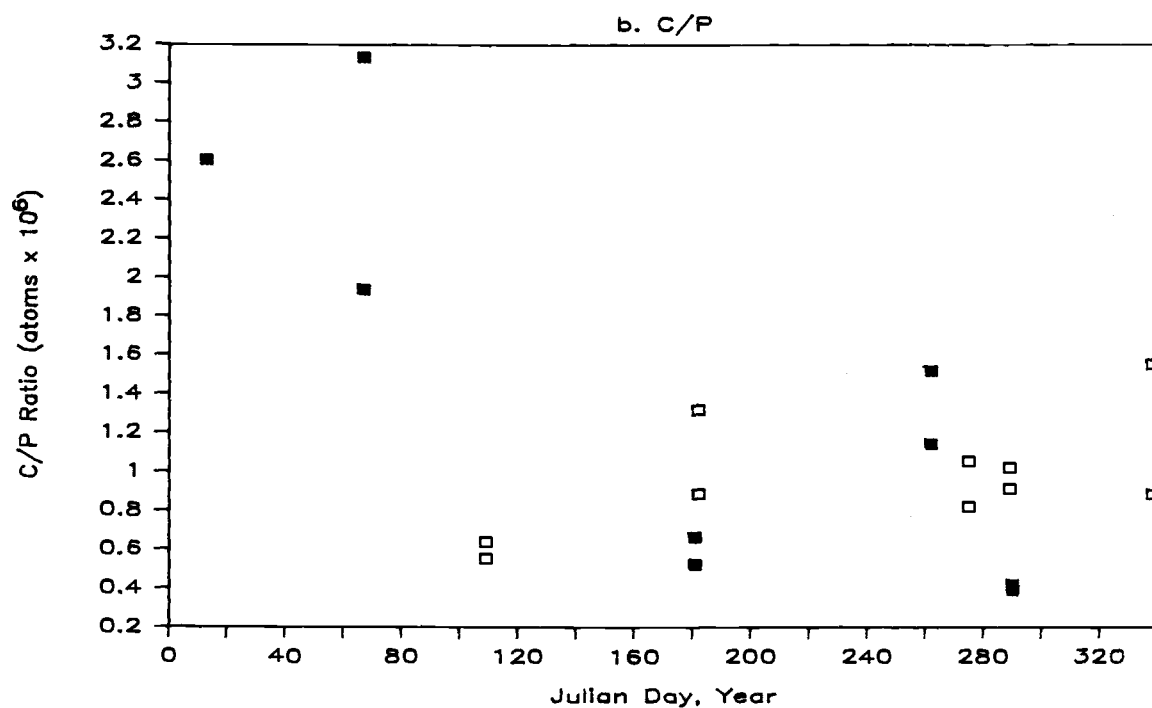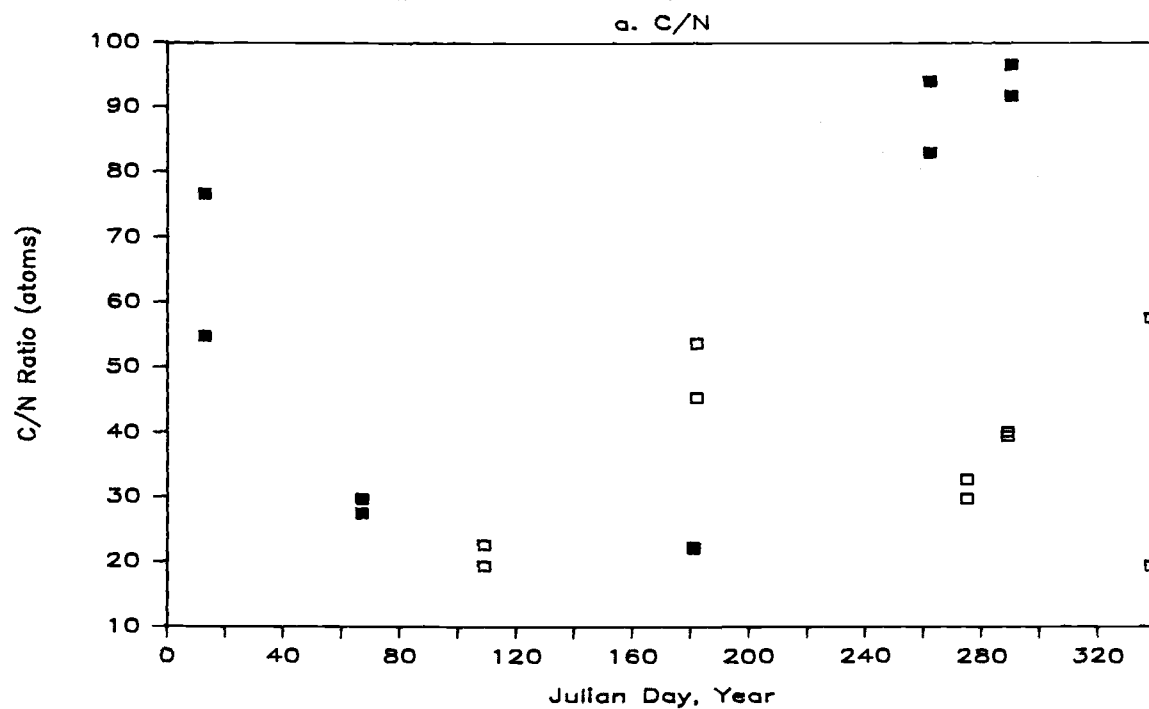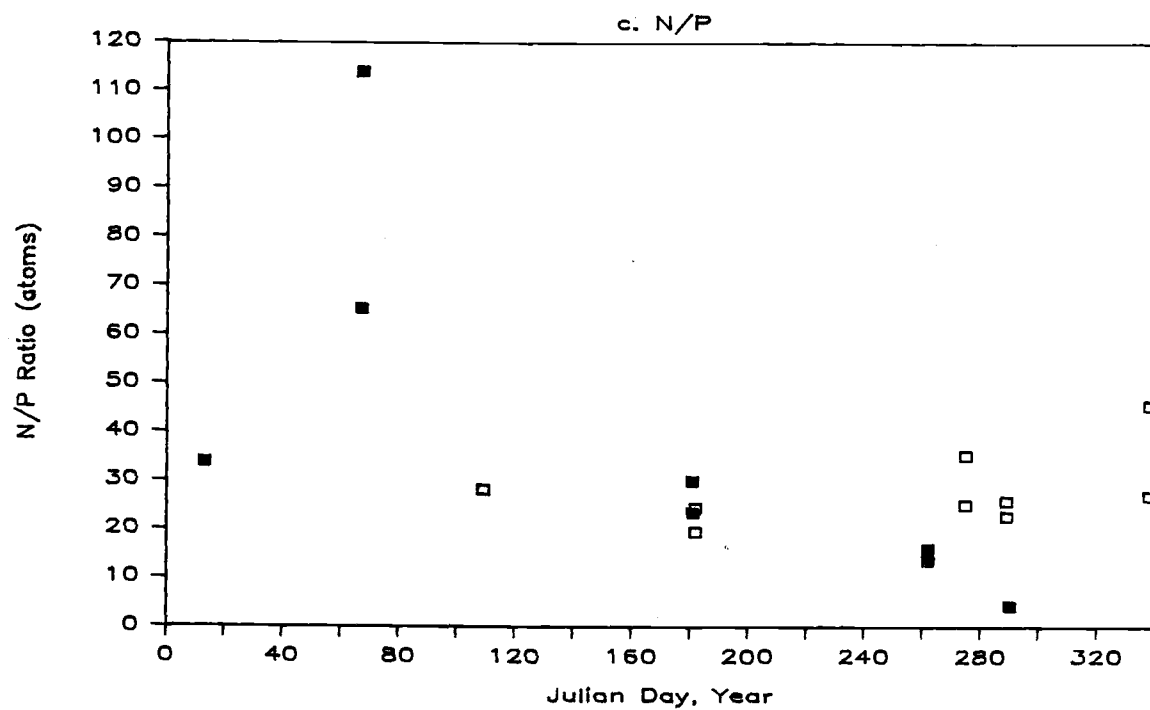
19.2 and 13.6 in bottom water at YAQ Station 4. Thus, at Site 2, bottom water salinity in the main channel showed that there was less mixing of high-phosphate water with the incoming river water. The growth/uptake ratio at Site 2 showed decreased uptake of phosphate compared to productivity in the winter. High winter river flow may have prevented penetration of seawater into the estuary, decreasing the phosphate availability at Site 2 more than at Site 1.

The comparison between nitrogen and phosphate uptake (Figure 20c) agreed with predicted ratios (Atkinson and Smith: 33, Redfield: 16) better than the previous two relations, implying that the photosynthetic quotient used to convert oxygen production to carbon incorporation may not accurately reflect the growth process. No such conversion is necessary with N/P ratios. The patterns were different between the sites, with Site 1 showing little variation from the expected value of 33. It is possible that supplies of phosphate from seawater satisfied the algal demands for phosphorus at Site 1. In spite of the nitrate uptake by the sediment, ammonium regeneration was more frequent at Site 1, and may have helped satisfy the nitrogen demand.

At Site 2, however, the fall drop in N/P indicated that nitrogen was more likely to be limiting than phosphorus. In the fall, river supply of nitrogen was at its lowest, and there was little ammonium regeneration at Site 2. Higher-phosphate seawater from offshore upwelled water may have mixed farther up into the estuary. In the spring, the ratio reached a peak, because nitrate was abundant, and phosphate may have been limiting. It seemed that the two sites used

in this investigation may have spanned the nutrient limitation

gradient, providing a glimpse of the spatial and temporal variations

that characterize this estuarine phenomenon.

V. Ratios of Elements Required for Macroalgal Metabolism

Expected macroalgal nutrient demand was calculated by using

ratios of elements in macroalgal tissue and measurements of plant

oxygen production. These predictions were then compared to measured

nutrient uptakes.

Ratios of element composition based on Atkinson and Smith's data

(1983) for marine macrophytes were more accurate in predicting nutrient

uptake in macroalgae than Redfield ratios that apply to phytoplankton-

based systems. Figure 21 shows a comparison of the nutrient demand

calculated from Atkinson and Smith's ratios and Redfield ratios.

Perfect agreement between the predictions and the measurements would

produce a ratio of one. It is clear that the macroalgae behaved

differently than phytoplankton and their nutrient demands were more

accurately predicted by Atkinson and Smith's ratios than Redfield's.

Figure 21: Ratio of predicted a. inorganic nitrogen, b. inorganic
phosphorus uptake to measured uptake in bottle experiments.
Predictions are based on oxygen production and ratios from
Atkinson and Smith (1983) (boxes) and Redfield et al.
(1963) (crosses).

Figure 21 NUTRIENT UPTAKE PREDICTIONS

a. Predicted Nitrogen Uptake

b. Predicted Phosphorus Uptake
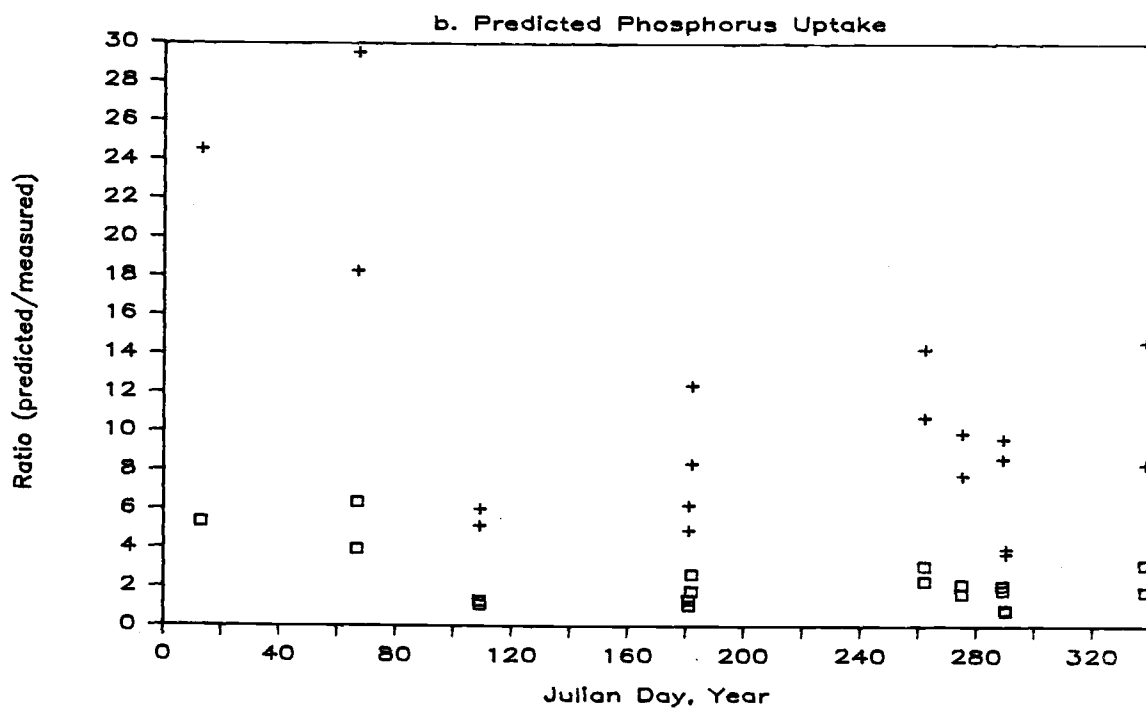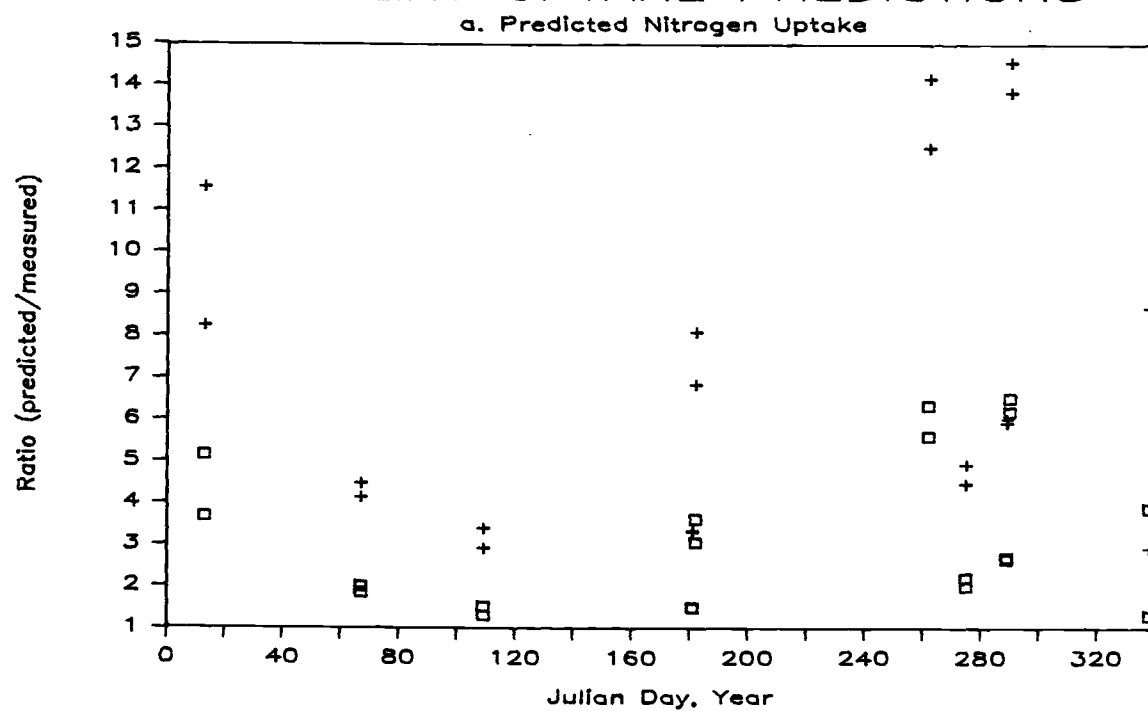
CONCLUSIONS

1. Between-site differences in chamber fluxes were probably attributable more to sediment heterogeneity between sites and within sites, than to differences in macroalgal metabolism.

2. Macroalgal growth in bottle incubations showed tight coupling between net primary productivity and uptake of inorganic nitrogen and inorganic phosphate.

3. The potential for macroalgae to be a sink for nitrate and phosphate was limited to the growing season, and was therefore out of phase with the main flush of nitrate to the estuary. Macroalgal growth may be responsible for some of the nitrate sink observed in mixing curves during the macroalgal growing season.

4. Seasonal differences in nutrient availability between sites indicated the possibility of a gradient from nitrogen limitation in the lower estuary to phosphorus limitation in the upper estuary. The likelihood for nitrogen limitation increased from summer through fall, becoming likely earlier in the lower estuary than in the upper estuary. Phosphorus availability may limit growth in the upper estuary in spring when high rainfall and runoff prevent circulation of higher-phosphate seawater into the upper estuary. Element ratios from this study indicated that both nitrogen and phosphorus could have been limiting at different times and places.

5. There was some evidence for a shift in preferred nutrient for the macroalgae from nitrate in the spring and early summer to ammonium in the fall.

6. Element ratios proposed by Atkinson and Smith were better predictors of macroalgal nutrient demand than Redfield ratios.

7. Sediment fluxes indicated the potential for denitrification at Site 1, and nitrification at Site 2. Denitrification may be the next logical suspect for the observed nitrate sink in the estuary.

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Appendices

Appendix A: Ranges and mean values for each analyte flux attributable to sediment exchanges or macroalgal growth in chambers and in bottles. Units for sediment regeneration and macroalgal influence per square meter of sediment surface area are μM m^{-2} h^{-1}; for macroalgal influence per gram macroalgal dry weight (bottle and chamber experiments) are μM gdw^{-1} h^{-1}; and for oxygen production as above except in mg-at instead of μM.

		Nitrate	Nitrite	Ammonium	DIN	DON	Phosphate	Oxygen
Sediment Regeneration (per square meter of sediment surface)								
Site 1	minimum	−208	−13.8	−38.5	−161	−469	−5.35	−7.71
	maximum	20.5	7.91	204	194	2650	15.9	1.29
	mean	−54.3	−0.995	79.4	24.3	531	5.63	−2.79
Site 2	minimum	−61.7	−19.8	−90.8	−92.4	−443	−3.93	−8.91
	maximum	208	3.24	77.6	230	2370	16.2	7.75
	mean	58.8	−6.69	−5.00	48.6	945	2.04	−0.846
Chamber Macroalgal Influence (per square meter of sediment surface)								
Site 1	minimum	−181	−0.998	−132	−311	0	−9.01	−7.63
	maximum	120	10.2	116	241	1150	11.3	14.4
	mean	0.203	2.83	12.5	15.3	486	−3.08	1.48
Site 2	minimum	−317	−6.39	−164	−268	−194	−22.8	−0.224
	maximum	−5.77	−1.96	54.0	0.577	916	4.04	54.2
	mean	−85.2	−3.93	−37.0	−125	238	−4.74	17.2
Chamber Macroalgal Influence (per gram dry weight of algal tissue)								
Site 1	minimum	−10.8	−0.0945	−7.89	−18.5	6.48	−0.903	−1.04
	maximum	24.0	0.965	23.3	48.2	79.6	2.26	0.857
	mean	2.65	0.235	2.53	5.40	43.4	−0.00582	0.0426
Site 2	minimum	−18.3	−0.580	−4.00	−18.8	−38.9	−0.389	−0.0530
	maximum	−0.114	−0.0673	7.31	0.0610	32.8	0.956	1.14
	mean	−5.71	−0.272	0.382	−5.55	1.42	−0.0877	0.380
Bottle Macroalgal Influence (per gram dry weight of algal tissue)								
Site 1	minimum	−13.2	−0.561	−16.2	−28.3	−103	−1.09	0.260
	maximum	−2.32	0.0110	−0.375	−2.68	6.5	−0.0992	2.68
	mean	−8.198	−0.218	−4.93	−13.3	−22.0	−0.513	1.12
Site 2	minimum	−44.4	−0.591	−7.96	−50.8	0.850	−2.58	0.115
	maximum	−0.0922	0.0654	−0.580	−0.627	8.357	0	2.72
	mean	−9.45	−0.137	−3.29	−12.8	3.91	−0.773	1.14

Appendix B: Nitrate and phosphate supply to Yaquina Estuary via remineralization and riverine input, and removal capacity as calculated for macroalgal uptake.

SAMPLING DATE	RIVER DISCHARGE ($l\ s^{-1}$)	CONCENTRATIONS IN RIVER WATER (μM)		LOADING (mole d^{-1})	
		Nitrate	Phosphate	Nitrate	Phosphate
9-9-84	425	31.9	0.57	1170	20.9
9-22-84	425	29.4	0.51	1080	18.7
10-6-84	935	24	0.44	1040	35.5
10-7-84	935	24	0.44	1040	35.5
12-4-84	20000	116	0.54	200000	933
1-13-85	16200	103	0.47	144000	658
3-8-85	11300	91	0.34	88800	332
4-19-85	8020	85.3	0.28	59100	194
6-30-85	1420	71.1	0.54	8720	66.2
7-1-85	1420	71.1	0.54	8720	66.2

	SED REGENERATION RATE ($\mu mol\ m^{-2}\ h^{-1}$)		BAY-WIDE REGENERATION (mole d^{-1})		SUPPLY: LOADING +SED REGEN (mole d^{-1})	
	Nitrate	Phosphate	Nitrate	Phosphate	Nitrate	Phosphate
9-9-84	-5.65	11.8	-2140	4470	-971	4500
9-22-84	-22.8	-2.72	-8640	-1030	-7570	-1010
10-6-84	-8.2	8.7	-3110	3300	-1170	3330
10-7-84	34.1	53.6	12900	20300	14900	20400
12-4-84	-204	2.8	-77400	1060	123000	1990
1-13-85	-20	0.1	-7580	37.9	136000	696
3-8-85	90.1	-0.19	34200	-72	123000	260
4-19-85	-33.3	5.5	-12600	2080	46400	2280
6-30-85	183	-3.56	69400	-1350	78100	-1280
7-1-85	-3.02	12.7	-1140	4820	7580	4880

	REMOVAL BY MACROALGAE ($\mu mole\ gdw^{-1}\ h^{-1}$)		EFFECTIVE PHOTOPER & INNUNDATION (h)	ALGAL BIOMASS (gdw m^2)	ALGAL COVERAGE (m^2)	REMOVAL BY MACROALGAE (mole d^{-1})	
	Nitrate	Phosphate				Nitrate	Phosphate
9-9-84	-1.08	-0.28	6.34	334	3040000	6950	1800
9-22-84	-8.8	-0.41	6.34	334	3040000	56600	2640
10-6-84	-9.6	-0.92	6.34	170	1550000	16000	1540
10-7-84	-2.1	-1.8	6.34	170	1550000	3510	3000
12-4-84	-3.6	-0.11	6.1	0	0	0	0
1-13-85	-0.23	-0.009	6.34	0	0	0	0
3-8-85	-8.2	-0.12	6.34	0	0	0	0
4-19-85	-12.5	-0.55	6.34	20	182000	288	12.7
6-30-85	-35	-1.6	6.34	175	1590000	61700	2830
7-1-85	-6.5	-0.57	6.34	560	5100000	118000	10300

	PERCENT OF SUPPLY REMOVED BY ALGAE		REMOVAL FACTOR		REGENERATION > 0	
	Nitrate	Phosphate	Nitrate	Phosphate	Nitrate	Phosphate
9-9-84		40.1		0.4		+
9-22-84						
10-6-84		46		0.5		+
10-7-84	25.1	14.8	0.2	0.1	+	+
12-4-84	0	0	0	0		+
1-13-85	0	0	0	0		+
3-8-85	0	0	0	0	+	
4-19-85	0.6	0.6	0.006	0.006		+
6-30-85	79.2		0.8		+	
7-1-85	1550	211	16	2.1		+