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DIEL METABOLISM AND NUTRIENT DYNAMICS IN A SALT MARSH EMBAYMENT¹

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Abstract. Simultaneous measurements of the diel patterns of dissolved O₂, pH-CO₂, dissolved organic nitrogen, ammonia, nitrite, nitrate, dissolved organic phosphorus, phosphate, and silicate were made on four occasions in a shallow salt marsh embayment (Bissel Cove, Narragansett Bay, Rhode Island, USA) that was closed to tidal water exchanges for 24-h periods. In spite of high rates of community photosynthesis and respiration, there appeared to be little diel change in dissolved nutrient concentrations, especially with respect to inorganic nitrogen. During summer and early fall, inorganic nutrients appeared to cycle within the sediment-detritus system of the embayment bottom, rather than being released to the overlying water. This suggests that there would be little export of inorganic nutrients from the marsh during tidal exchanges with the estuary. The behavior of this marsh embayment contrasts with reports from other marsh areas where large net imports or exports of nutrients have been observed. The concentrations of dissolved organic phosphorus and nitrogen were higher than inorganic forms, and showed substantial variation over each diel sampling period. The relationship between photosynthetic or respiratory gas exchange and nutrient cycling in waters influenced by benthic community metabolism is subtle and complex, and cannot be adequately approximated by simple models such as the Redfield ratio.

Key words: *Diel; dissolved oxygen; metabolism; nitrogen; nutrients; phosphorus; Rhode Island; salt marsh; silica.*

INTRODUCTION

It has been over 35 years since Redfield (1934), Fleming (1940) and others first described the stoichiometry of nutrient cycling and energy flow in open ocean plankton ecosystems. While subsequent work has shown that the chemical composition of phytoplankton and zooplankton may change as a transient response to environmental and nutritional conditions, the classic Redfield ratio of 212 O:106 C:16 N:1 P by atoms continues to provide a useful description of large-scale, time-averaged conditions in the sea (Alvarez-Borrego et al. 1975). Until recently, the general applicability of the Redfield ratio or other stoichiometric relationships between biological metabolism and ambient water chemistry remained almost entirely unknown for other types of ecological systems. As part of the recent SYM-BIOS study of the coral reef at Eniwetok Atoll, Pilson and Betzer (1973) and Webb et al. (1975) compared upstream-downstream phosphorus and nitrogen changes in water flowing over the reef to those expected on the basis of O₂ changes and the Redfield ratio. Similarly, Rowe et al. (1975) and Nixon et al. (1975) compared nutrient fluxes measured *in situ* in coastal marine bottom communities with regeneration rates expected on the basis of their O₂ uptake. In both environments, the relationships between nutrient exchange and metabolic gas

exchange appeared quite different from that found in pelagic marine communities. With the exception of these papers, however, there have been few attempts to determine the relationship, if any, between nutrient exchanges and metabolism in marine or freshwater ecosystems. While there have been numerous measurements of total system metabolism in a variety of environments (Odum and Hoskin 1958, Odum et al. 1959, Odum and Wilson 1962, Beyers 1963, Cooke 1967, Nixon et al. 1971, Cooper and Copeland 1973), there have been few attempts to measure diel changes in dissolved nutrient concentrations (Newcombe and Lang 1939, Ryther et al. 1961, Beers and Kelly 1965). Simultaneous time-series measurements of both parameters have only occasionally been reported (Bruce and Hood 1959).

In a previous study (Nixon and Oviatt 1973), we were able to exploit the hydrography of a shallow salt marsh embayment to carry out detailed measurements of diel oxygen metabolism in the embayment over an annual cycle. The major advantage of the Bissel Cove embayment (Narragansett Bay, Rhode Island, USA), a 6,000-m² area surrounded by *Spartina* marsh, is that all of the tidal flow enters and leaves through a single culvert. Thus, it was possible to stop the tidal flow for any desired period of time to maintain a resident water mass in the embayment for obtaining time-series measurements of O₂ changes. A much more complete description of the area and its ecology during the year has already been given (Nixon and Oviatt 1973, Welsh 1975).

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As an extension of this earlier work, the embayment seemed an ideal environment for obtaining simultaneous diel measurements of a variety of dissolved inorganic and organic nutrients, as well as dissolved O_2 and CO_2 . It was hoped that such a data set would yield information about the relationship between nutrient cycling and metabolism in very shallow marsh embayment waters with high rates of primary production and respiration, as well as organic inputs from the emergent marsh grasses. If diel nutrient curves could be obtained they could also be integrated to calculate the net uptake or output of nutrients from the embayment system in the same way that O_2 changes were used to calculate organic production, consumption, and export (Nixon and Oviatt 1973).

METHODS

An inflatable rubber and wooden plug was used to completely seal the culvert and stop tidal flow to and from the embayment for a 24-h period on four occasions in the summer and fall of 1974. According to the stage of the tide when the plug was inserted, mean depth in the embayment ranged from 45 cm to 85 cm on the study days in comparison with a mean low tide depth of about 25 cm (Nixon and Oviatt 1973). Duplicate samples of water were collected from a small wooden dock at \approx 3-h intervals during each 24-h period, including samples at dawn and dusk. These samples were then analyzed for dissolved O_2 (Strickland and Parsons 1972), pH, ammonia (Solorzano 1969), nitrate and nitrite (Strickland and Parsons 1972), dissolved organic nitrogen or DON (Kjeldahl digestion followed by determination of ammonia in the neutralized digestate by the phenolhypochlorite method [see Webb et al. 1975]), phosphate (Strickland and Parsons 1972), organic phosphorus (Menzel and Corwin 1965), and silicate (Strickland and Parsons 1972, with modifications by Fanning and Pilson 1973). Levels of precision ($\pm 1 s$) for the various determinations were as follows: $O_2 \pm 0.02$ mg l^{-1} ; pH ± 0.002 unit; $NH_3 \pm 0.07$ μM l^{-1} ; $NO_2 \pm 0.05$ μM l^{-1} ; $NO_3 \pm 0.15$ μM l^{-1} ; $DON \pm 1.7$ μM l^{-1} ; $PO_4 \pm 0.014$ μM l^{-1} ; $SiO_4 \pm 0.18$ μM l^{-1} . Water temperature and salinity were also measured at each interval. Incident solar radiation data were provided by the Eppley Laboratory in Newport, Rhode Island, from a roof-top pyrliometer. Changes in pH were converted to changes in CO_2 using the titration method of Beyers et al. (1963).

With a known water mass held in the marsh, the single diel curve method of Odum and Hoskin (1958) could be used to calculate total community metabolism in the embayment. Continuous diel dissolved O_2 measurements made previously with a Rustrak

190® oxygen-temperature meter indicated that the discrete sampling schedule used here gave a reasonable approximation of O_2 changes in the embayment. The diel curves were analyzed by integrating the rate of change in dissolved O_2 , CO_2 , or nutrients. The area under the positive portion of the oxygen rate of change curve (after correction for exchange with the atmosphere) represents apparent production during the day, while the area of negative change is equal to night respiration. In the case of CO_2 and nutrients, the curve is interpreted in the opposite way, with the area of negative rate of change indicating apparent production or uptake during the day. Exchange rates at the air-water interface had been measured previously in the system (Nixon and Oviatt 1973) using the floating plastic dome method (Cope land and Duffer 1964) as modified by C. Hall, J. Day and H. T. Odum (*personal communication*).

Samples of water were also taken and incubated for 24 h *in situ* during the diel curve to estimate the amount of production and nutrient flux associated with the pelagic phase of the community. Oxygen changes were followed in water taken from the same initial sample and incubated in glass bottles, while nutrient changes were followed in water taken from the same initial sample and incubated in a transparent plastic bottle. Since water circulation may play a role in regulating the metabolism of aquatic systems (Nixon et al. 1971), it is possible that confinement of the water in the embayment may have introduced errors leading to a probable underestimate of both production and respiration. However, it is felt that these artifacts, if present, would be small compared with similar problems long recognized in bottle experiments with plankton. Moreover, a careful examination of many diel curves over 3 yr has never revealed any trend in the time-series data that showed changes in the rate of production or consumption of O_2 associated with the amount of time the water had been held in the marsh, even for periods of 48 h.

As an ancillary part of this study, some attempts were also made to estimate the direct contribution of larger animals to nitrogen changes in the embayment. Several times during the year, fish, shrimp, crabs, snails, and bivalves were seined or collected by hand from the marsh and brought immediately to the laboratory. Varying numbers of animals (see Table 3) were placed in 3- to 5-replicate, 6- or 10-l tanks of embayment water, and incubated for 2-4 h at ambient field temperatures in the dark. Measurements of ammonia, nitrite, and nitrate were made at the beginning, middle, and end of the incubation. Rates were corrected for plankton metabolism using changes measured in control tanks containing embayment water without larger animals.

RESULTS AND DISCUSSION

Metabolism

The set of four simultaneous diel measurements is shown in Fig. 1. Although ambient temperatures and light inputs differed on each occasion, substantial diel oxygen changes were observed. Apparent production varied from 2.34 g O₂ m⁻² day⁻¹ to 8.06 g O₂ m⁻² day⁻¹, with ratios of daytime production to night respiration of 0.79–1.91 (Table 1). Measurements of pH also showed a strong diel curve that closely followed dissolved O₂ (Fig. 1). On the 2 days for which pH-CO₂ conversion curves were obtained, changes in CO₂ gave reversed diel rate of change curves that were compatible with O₂ changes in showing high rates of metabolism in the embayment (Fig. 2; Table 1). Ratios of ΔO₂ to ΔCO₂ were similar during day and night with community PQ values of 1.10 and 1.18 and RQ values of 0.73 and 0.88, respectively.

Simultaneous diel changes in O₂ and pH were also studied in Texas coastal waters by Park et al. (1958), who found anomalously low PQ and RQ values that were difficult to interpret because of methodological problems in their work. The diurnal ranges they observed were < 0.5 pH unit, though a number of diel pH measurements from other marine environments summarized in their paper showed ranges comparable to those reported here. The PQ values found in the marsh embayment are also well within the ranges expected on the basis of physiological measurements and the chemical composition of a variety of aquatic plants. Ryther (1956) discussed the utility of PQ measurements and calculated a range of expected PQ values from 1.09 to 1.48 with a mean of 1.20. Values at the upper end of the scale were associated with plants using nitrate instead of ammonia as the major nitrogen source for photosynthesis.

The low RQ values for the embayment suggest a metabolism involving fat and protein, as well as carbohydrate (Prosser and Brown 1950). This may seem surprising at first, since marsh embayments are often thought of in terms of cellulose metabolism based on inputs of dead *Spartina* grass. However, the PQ and RQ measurements reported here come close to a diel balance, suggesting that the more reduced material fixed during the day is the major substrate being respired at night. Previous work in this system supported the same conclusion because of a strong correlation between night respiration and apparent production the previous day (Nixon and Oviatt 1973). Our earlier work indicated that organic consumption in the embayment exceeds primary production by only ≈ 2% over the annual cycle. This deficit was met by the input of *Spartina* detritus from the emergent marsh.

TABLE 1. Environmental conditions and total system metabolism during four diel measurements in a salt marsh embayment

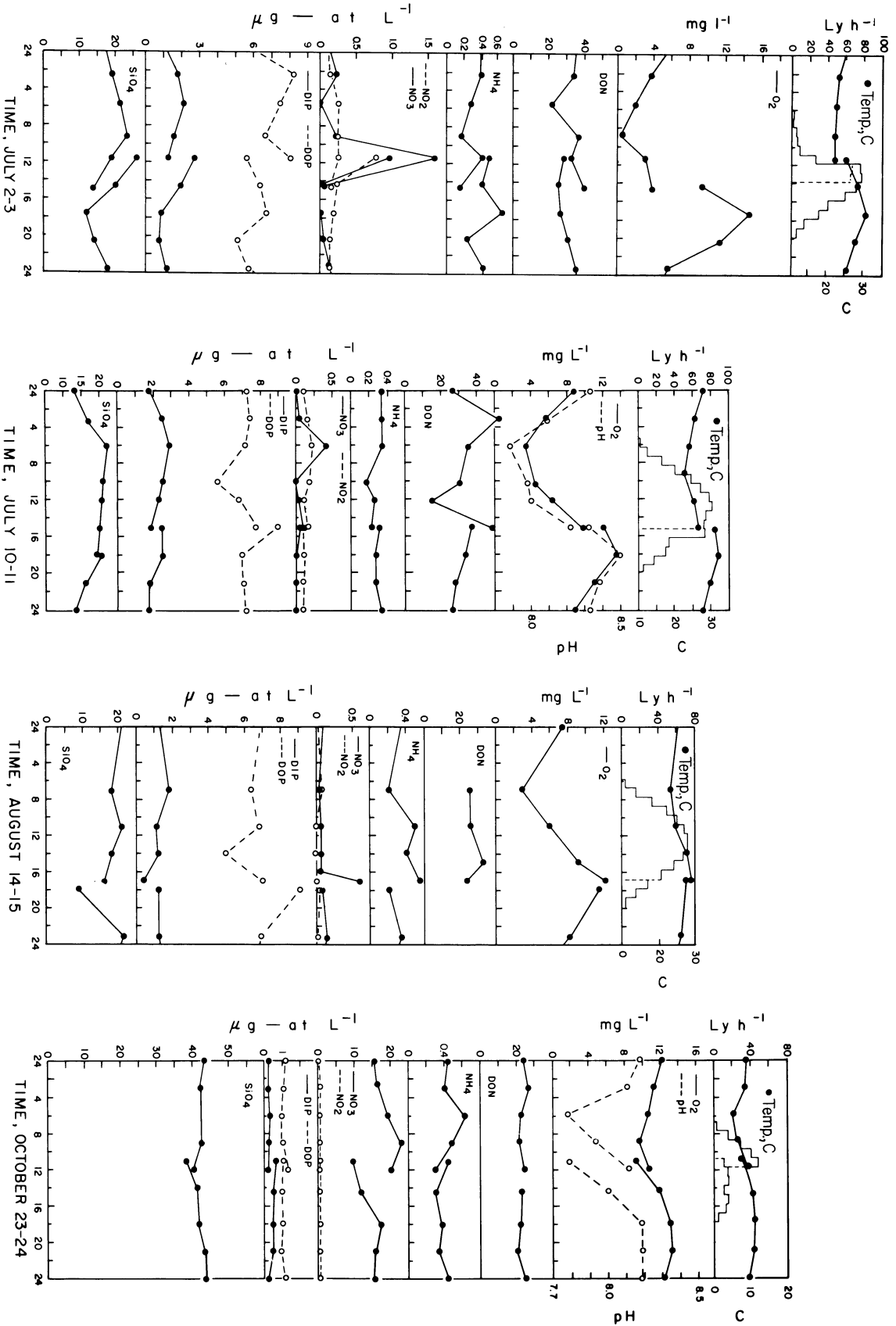
Date	Temp. range (°C)	Light energy (Ly ^c)	Salinity (%)	Depth (m)	Apparent production (mM O ₂ m ⁻² day ⁻¹)	Apparent production (mM CO ₂ m ⁻² day ⁻¹)	Apparent respiration (mM O ₂ m ⁻² day ⁻¹)	Apparent respiration (mM CO ₂ m ⁻² day ⁻¹)	P/R	PQ ^a	RQ ^b
2-3 July 1974	22.2-30.8	420.5	25.5	0.55	+174	----	-219	----	0.79	----	----
10-11 July 1974	22.7-32.0	673.0	28.5	0.78	+192	-162	-213	+189	0.90	1.18	0.88
14-15 Aug. 1974	23.6-29.0	553.9	29.5	0.85	+252	----	-159	----	1.58	----	----
23-24 Oct. 1974	5.2-16.3	218.8	21.5	0.74	+73	-66	-40	+29	1.91	1.10	0.73

^a +ΔO₂/−ΔCO₂.

^b +ΔCO₂/−ΔO₂.

^c To convert langley (Ly) to megajoules per square meter (MJ/m²), multiply by .04184.

FIG. 1. Simultaneous diel curves of dissolved O₂, pH, and major nutrients from Bissel Cove salt marsh embayment without tidal exchange.



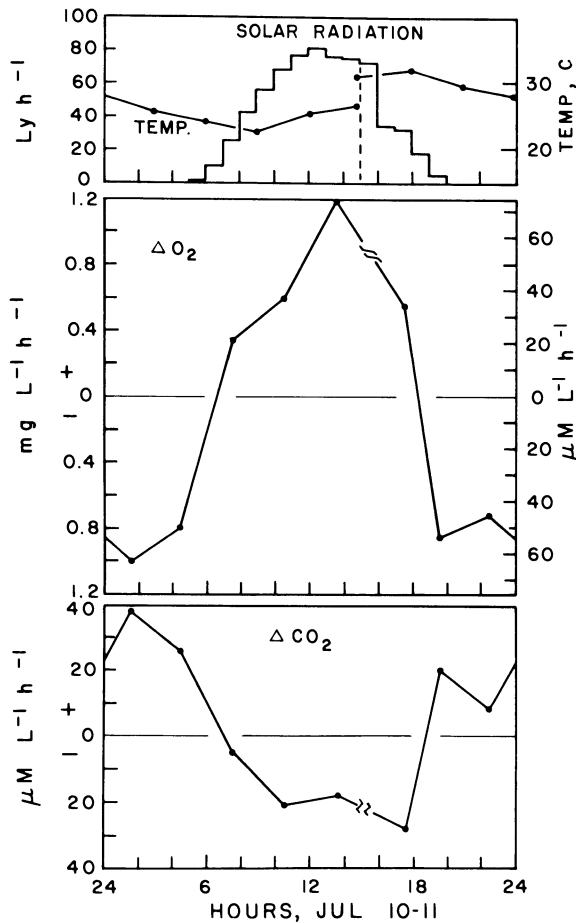


FIG. 2. Simultaneous rate of change curves for dissolved O_2 and CO_2 in Bissel Cove marsh embayment.

As expected on the basis of its shallow depth, the metabolism of the system was dominated by the bottom sediments and attached algae and epifauna. Patches of *Ulva* and a few scattered seaweeds were the only macrophytes present. Oxygen changes in the plankton bottles ranged from -1.87 to $+2.66$ $mg\ l^{-1}$ over 24 h (Table 2), and the metabolism of the water was not necessarily correlated with the activities of the embayment as a whole. For example, while O_2 changes in the incubated water samples on 14–15 August showed a reduction

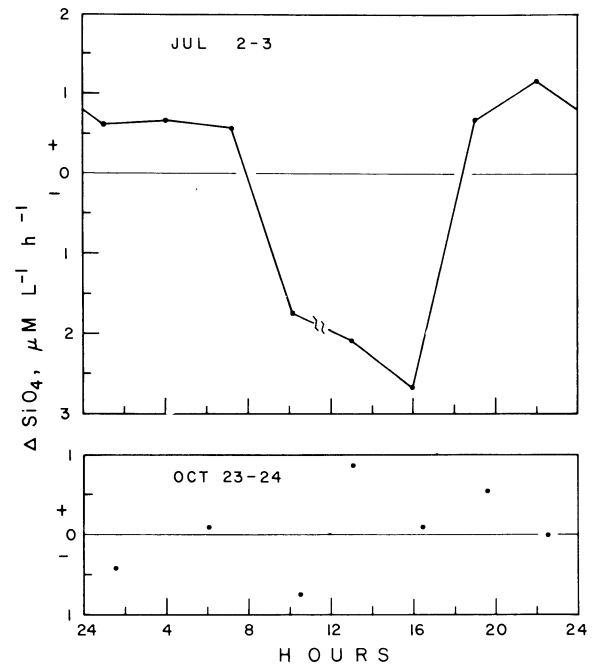


FIG. 3. Diel rate of change in dissolved silicate on the 1 day in which a clear diurnal pattern was observed. October 23–27 is shown as representative of the 3 other days during which no pattern was recognized.

equivalent to -1.59 $g\ m^{-2}\ day^{-1}$, free water changes in the embayment showed a net production (apparent production – apparent respiration) of 2.98 $g\ m^{-2}\ day^{-1}$ (Table 1).

Nutrient dynamics

Silica.—Dissolved silicate showed variations of about $10\ \mu M\ l^{-1}$ during each of the 24-h periods (Fig. 1). However, a regular diel curve showing a rather constant rate of silica release during the night and uptake during the day was found only on 2–3 July (Fig. 3). On the other 3 days, the changes varied in magnitude and direction throughout the sampling period. The silicate changes observed during the night of 2–3 July corresponded to a flux rate of $\approx 350\ \mu M\ m^{-2}\ h^{-1}$, which is somewhat lower than the 500 – $600\ \mu M\ m^{-2}\ h^{-1}$ release rates measured

TABLE 2. Net changes in dissolved O_2 and nutrients in isolated samples of embayment water incubated *in situ* during diel curves

Date	Net changes in 24 h, $\mu M\ l^{-1}$							
	O_2	NH_3	NO_3	NO_2	DON	PO_4	DOP	SiO_4
2–3 Jul.	–0.09	–0.96	–0.49	–1.7	–0.92	0	–12.2
10–11 Jul.	–0.6	+0.44	0	0	–2.9	–1.16	–1.3	–14.6
14–15 Aug.	–58.4	+0.09	+0.14	0	–3.3	–0.55	–8.1
23–24 Oct.	+83.1	–3.17	–1.22	0	–2.4	–0.39	0	–7.2

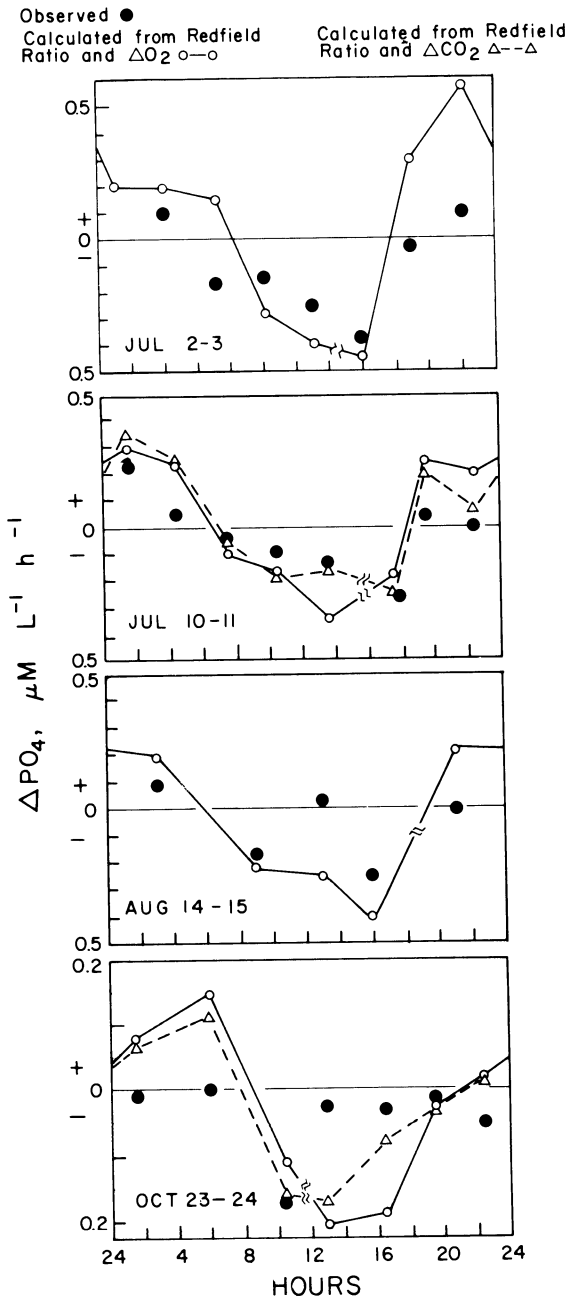


FIG. 4. Comparison of observed rates of change in phosphate with rates calculated from the Redfield ratio (212 O : 106 C : 16 N : 1 P by atoms) and the observed changes in dissolved O₂ and CO₂.

in situ from the bottom of Narragansett Bay (Hale 1974, S. W. Nixon, C. A. Oviatt, and S. S. Hale, *personal observation*).

In the isolated water samples, a substantial net uptake of silica occurred each day, even when net O₂ changes were negative (Table 2). This apparent conflict may result from active diatom growth and

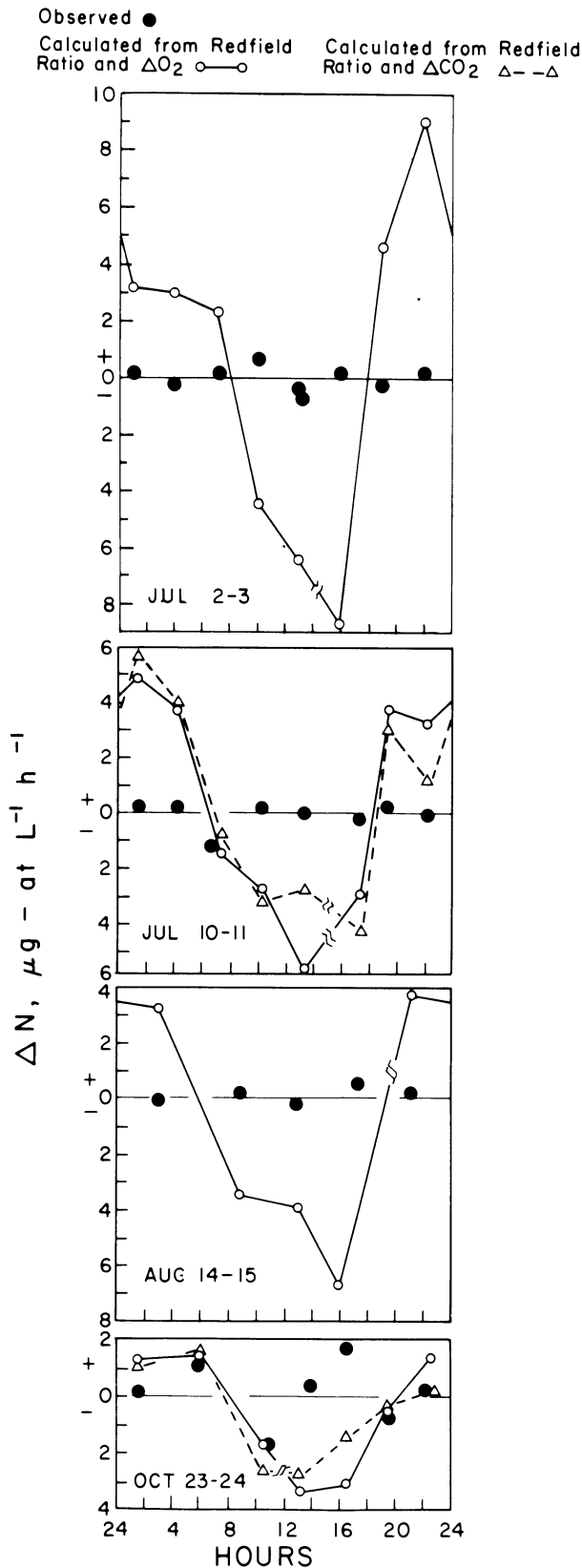
accompanying silica uptake during the light, even when the total respiration of the plankton (including phytoplankton, zooplankton, pelagic bacteria, and detritus) exceeded photosynthesis over 24 h.

Phosphorus.—The levels of reactive and dissolved organic phosphorus (DOP) in the embayment varied, with DOP averaging about 4× higher than phosphate on all days (Fig. 1). On 2 of the 4 sample days, a marked diel pattern of phosphate was found in the embayment (Fig. 4). Both of these days (2–3 July and 10–11 July) were characterized by a P:R ratio of < 1.0 (Table 1). On the two other sampling days, apparent production substantially exceeded night respiration, and phosphate varied irregularly (14–15 August), or was taken up continuously (23–24 October; Fig. 4).

While diel phosphate curves have been reported in the past for a station in Chesapeake Bay (Newcombe and Lang 1939), for some shallow bays in Texas (Bruce and Hood 1959), and for the Sargasso Sea (Ryther et al. 1961), the results have always been somewhat ambiguous, especially in terms of their interpretation with regard to metabolism. For example, the Chesapeake Bay data was taken at a fixed station with tidal influence. Similarly, the samples in Texas and the Sargasso Sea may have been influenced by horizontal and vertical water transport as well as by ship drift. In none of these cases was it possible to show a consistent relationship between phosphate changes and community photosynthesis or respiration. A more rigorous attempt to explore the possible relationship between phosphate change and community metabolism was also made by Pilson and Betzer (1973) using upstream-downstream measurements across a coral reef at Eniwetok Atoll. They found essentially no change in the reactive or organic phosphorus content of water flowing over the reef, in spite of measurements documenting substantial changes in dissolved O₂. In contrast, our results indicate that a clear diel phosphate pattern was developed on some, but not all occasions in the highly metabolic marsh embayment. When present, the diel phosphate changes appeared smaller than expected on the basis of the Redfield ratio and dissolved O₂ or CO₂ changes (Fig. 4).

There did not appear to be any relationship between the ambient concentration of phosphate and changes in its concentration as suggested for Georgia marsh waters by Pomeroy et al. (1965). This is consistent with the results of a large number of *in situ* sediment-water nutrient flux measurements made in Narragansett Bay, in which phosphate release was highly correlated with O₂ uptake but showed no negative correlation with ambient phosphate concentration (Hale 1974, Nixon et al. 1975).

The phosphate changes observed in the isolated



water samples were always negative (Table 2), and ranged from -175 to $-900 \mu\text{M m}^{-2} \text{day}^{-1}$. On each of the two days in which "regular" diel phosphate curves were observed there was a similar net uptake of phosphate by the embayment amounting to -720 and $-570 \mu\text{M m}^{-2} \text{day}^{-1}$. Thus, even though a well defined and reasonable diel phosphate pattern could be obtained, on both occasions the integrated 24-h nutrient curve indicated net uptake, while O_2 and CO_2 data showed respiration exceeding production over the same time period (Table 1). It is clear that this phosphate uptake did not imply net primary production. In such a complex system it is quite possible that the phosphate is in fact being taken up by bacteria, entering into sorption reactions with sediments, or forming complexes with iron. Even with clear, well-developed diel patterns, the net flux of phosphate does not seem to reveal much about the magnitude of photosynthesis and respiration in the system.

While changes in DOP were also found (Fig. 1), they never showed any pattern that could be related to light, temperature, metabolism, or changes in other nutrients. This lack of a clear trend may reflect a distribution of organic phosphorus compounds that is patchy in terms of amount or susceptibility to the oxidation process used in analysis. A number of other possibilities may also be suggested, including lysis of plankton or bacterial cells during filtrations. In any case, we did not feel it appropriate to attempt to estimate any sort of diurnal DOP flux by integrating such erratic curves with a 3-h sample interval.

Nitrogen.—The levels of inorganic nitrogen were relatively low during the summer sampling days, but increased substantially by the time the last diel samples were taken in October (Fig. 1). While some small erratic changes in nitrate, nitrite, and ammonia were observed during the summer diel sampling, they could not be related in any way to changes in dissolved O_2 , CO_2 , or phosphorus. In spite of the very high rates of photosynthesis and respiration shown by the O_2 and CO_2 changes, and in spite of the fact that the measured PQ and RQ values indicated that protein and fat as well as carbohydrate were being metabolized, the levels of inorganic nitrogen in the water over the sediments showed essentially no change (Fig. 5). During the fall, when the concentration of nitrogen was much higher, significant changes in the levels of ammonia and nitrate were found between sampling periods (Figs. 5 and 6). However, their interpretation is difficult, since

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FIG. 5. Comparison of observed rates of change in inorganic nitrogen (NH_4 , NO_2 , NO_3) with rates calculated from the Redfield ratio and the observed changes in dissolved O_2 and CO_2 .

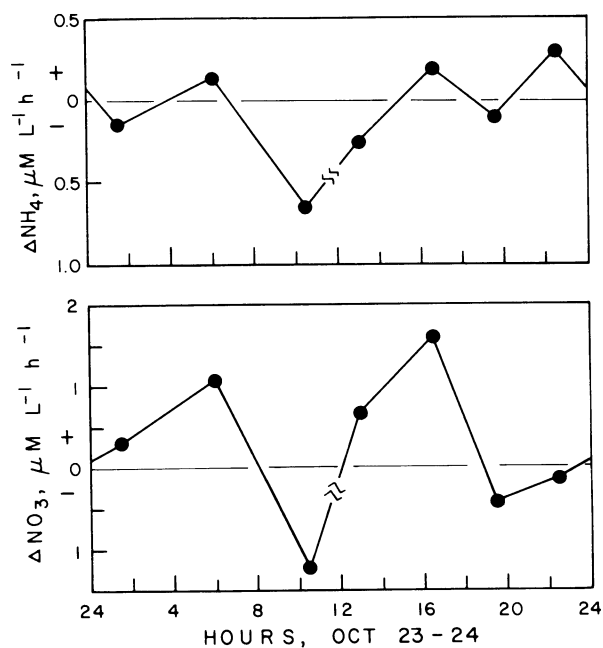


FIG. 6. Observed rates of change in ammonia and nitrate on the 1 day in which significant inorganic nitrogen changes were observed. There were no detectable changes in nitrite.

they did not follow the O_2 patterns in any straightforward way and the levels of all nitrogen containing compounds in the embayment are determined by the net effects of fixation, assimilation, denitrification, regeneration, and other processes in the complex nitrogen cycle.

In the light of many *in situ* measurements showing a substantial flux of ammonia from heterotrophic subtidal bottom communities in adjacent Narragansett Bay (Hale 1974, Nixon et al. 1975), it was surprising that the high respiratory rates in the embayment did not result in a rapid increase in ammonia during the night. At summer temperatures, the bottom of the bay releases ammonia at rates of 150–250 $\mu\text{M m}^{-2} \text{h}^{-1}$, even with substantially lower rates of O_2 uptake. It was also thought that the often abundant shrimp and fish in the embayment might make a significant contribution of ammonia through excretion. Using the measured excretion rates of the most common animals in the embayment (Table 3) and population estimates for summer and fall from a previous study (Nixon and Oviatt 1973), it was possible to calculate an estimate of animal ammonia input. During the summer this amounted to about 0.5 $\mu\text{M l}^{-1} \text{day}^{-1}$, 80% of which could be attributed to the common mummichog. During fall the importance of the larger animals may increase substantially, with possible inputs of 4.5 $\mu\text{M l}^{-1} \text{day}^{-1}$ from grass shrimp and 4.3 $\mu\text{M l}^{-1} \text{day}^{-1}$ from fish, especially the common mummichog and sheepshead

minnow. When juvenile menhaden are present in the embayment (they did not appear to be on any of the days on which diel studies were conducted), they may add an additional 4–5 $\mu\text{M l}^{-1} \text{day}^{-1}$. The plankton in the embayment also regenerated substantial amounts of nitrogen on some occasions, though net uptakes were also observed (Table 2).

The fact that these inputs do not appear in the diel curves suggests that the marsh embayment is taking up nitrogen at a constant rate during the day and night, or at a rate that varies directly with the input. Moreover, the nitrogen being regenerated in the bottom sediments appears to be cycled tightly within the benthic community, rather than being exchanged with the overlying water. This behavior is quite different from that of other marine bottom communities studied by Hartwig (1974), Rowe et al. (1975), or Nixon et al. (1975), which were in much deeper water where organic inputs to the bottom come largely from sinking phytoplankton cells, zooplankton fecal pellets, and other pelagic detritus. In contrast, the bottom of the marsh embayment is partially autotrophic, with additional large organic inputs from *Spartina* detritus. Benthic diatoms and macroalgae may show a reduced, but still substantial uptake of ammonia at night (Eppley et al. 1971, M. Harlin, URI, *personal communication*), in addition to the uptake by bacteria and fungi growing on the *Spartina* detritus. The importance of heterotrophic nitrogen uptake in areas with large inputs of *Spartina* has been discussed by Thayer (1974). While organic material reaching the bottom of Narragansett Bay has a C:N ratio by atoms of ≈ 9.5 (Oviatt and Nixon 1975), the C:N ratio of dead creek bank *Spartina alterniflora* collected in winter before ice shear put it into the embayment was 55–60 (F and M model 185[®] CHN analyser, $n = 10$, C.V. = 3.1% for C and N). Since it has been well established that the nitrogen content of decomposing *Spartina* detritus is relatively low and increases over time in the water (Odum and de la Cruz 1967), it is clear that bacterial and fungal growth on the high carbon, low nitrogen substrate of dead grass should require a substantial nitrogen subsidy. Laboratory studies of the metabolism of *Spartina* detritus have shown increased rates of O_2 uptake when inorganic nitrogen and phosphorus were added to the water (Ustach 1969). A major factor limiting decomposition in the embayment may well be a lack of inorganic nitrogen.

As with phosphorus, the dissolved organic forms of nitrogen were much higher than the inorganic (Fig. 1), and the nature of the compounds involved is unknown. While relatively large changes were also found from sample to sample, it was again not possible to relate them to other activities in the system. It did appear that changes in DON were

TABLE 3. Ammonia excretion by marsh embayment animals

Species	(°C)	Salinity (%)	Size (mm)	N ^a	Excretion ($\mu\text{M g}^{-1} \text{h}^{-1}$) ^b
Common mummichog, <i>Fundulus heteroclitus</i>	4.0 19.5	14 31	50-60 45-55	12 5	0.80 ± 0.20 4.62 ± 1.29
Striped mummichog, <i>Fundulus majalis</i>	5.0 19.5 29.5	9 31 30	--- 65-70 75-80	1 6 1	0.50 3.88 ± 0.81 11.50
Silversides, <i>Menidia menidia</i>	30.0	30	35-40	3	12.82 ± 2.37
Sheepshead minnow, <i>Cyprinodon variegatus</i>	19.5 30	30 31	65-80 65-70	4 2	5.68 ± 1.33 14.05
Juvenile Atlantic menhaden, <i>Brevoortia tyrannus</i> ^c	16.5 20.5	--- ---	60-65 65-70	5 8	6.83 ± 2.74 7.91 ± 1.99
American eel, <i>Anguilla rostrata</i>	30	31	440	1	6.40
Grass shrimp, <i>Palaemonetes pugio</i>	5 12 30	9 14 31	--- --- ---	12 11 2	1.43 ± 0.60 3.90 ± 1.58 6.50
Blue crab, <i>Callinectes sapidus</i>	30	30	95-100	5	3.32 ± 0.85
Ribbed mussel, <i>Modiolus demissus</i>	21	29	75-80	9	3.58 ± 1.73
Mud snail, <i>Nassarius obsoletus</i>	15 30	--- 30	--- ---	9 3	0.49 ± 0.19 1.37 ± 0.35

^a Number of replicate rate determinations, each usually involving about 10 fish, 100 shrimp, 30 bivalves, or 100 snails.

^b Expressed per gram dry wt for fish and shrimp, and per gram dry meat wt for shellfish and snails; $\bar{x} \pm 1 \text{ s.}$

^c Excretion data provided by A. G. Durbin.

smaller in the fall when the amount in the water was lower (Fig. 1). These changes may represent the same kinds of variability discussed with respect to organic phosphorus, or they may yet prove to have some significance (see Webb et al. 1975).

Net imports of inorganic nitrogen to marsh systems have been indicated by comparisons of nitrate levels in flood and ebb tidal waters in Delaware (Aurand and Daiber 1973) and by calculations of annual nutrient fluxes based on monthly concentrations and water transports in marsh creeks in Virginia (Axelrad 1974). Also, Valiela et al. (1973) found that large quantities of nitrogen applied to a New England marsh were not lost on ebbing tidal waters in inorganic forms. It should be pointed out that these findings and our work do not imply that marsh sediments are an infinite sink for nitrogen. Export of organic nitrogen exceeded the yearly net import of inorganic nitrogen in Axelrad's study. However, we did not find a consistent depletion of inorganic nitrogen accompanied by enrichment of organic forms as might have been expected if these processes were being mediated in the embayment sediments. It is clear that organic nitrogen must be figured in the total picture of nutrient dynamics in the marsh, but the composition and fate of this large store of nitrogen are not known. Nitrogen may also be lost from the system through denitrification, animal mi-

gration, and export of particulate matter following storms and winter ice shearing of emergent grasses.

Direct comparison of our results with the flux determinations cited earlier is difficult, since we did not feel it appropriate at this point to use the curves to estimate net daily flux of nitrogen. The diel samples do indicate that the time variation in concentration of dissolved nutrients within the marsh may be quite large and erratic, especially for organic forms. When imposed on the substantial variations in concentration that may be found on floodtide waters entering marshes (Axelrad 1974, Woodwell et al. *in press*), this behavior may make it risky to interpolate linearly between discrete samples that are collected over large (several hours) time gaps on ebb tides. The integration of such interpolated data for the construction of flux budgets is not warranted unless the interpolation can be shown to be a valid approximation with some intensive sampling over short time intervals.

It is also true that other marsh embayments may behave quite differently than Bissel Cove. For example, in an analysis of Flax Pond marsh on Long Island, Woodwell et al. (*in press*), have found substantial exports of ammonia during the summer. However, Flax Pond has a sandy bottom that may well support a dense infauna. Bissel Cove has a very soft substrate with a depauperate macrofauna (Nixon

and Oviatt 1973). Flax Pond also has a bed of blue mussels, *Mytilus edulis*, at its mouth (C. Hall, Marine Biol. Lab., Woods Hole, *personal communication*). Our studies of ammonia excretion by quadrats of healthy mussel bed in the laboratory with a flowing respirometer indicate that a bed of *Mytilus* may excrete 4–5 mM ammonia $m^{-2} h^{-1}$ at 15°C ($3.12 \pm 0.72 \mu M [g \text{ dry meat } wt^{-1}] h^{-1}$; $n = 9$). Thus, embayments with abundant mussel beds or other bivalves may well import particulate nitrogen and export large amounts of ammonia to offshore waters.

Nutrient cycling and system metabolism

In a recent review, Pomeroy (1970) contrasted the coral reef and the salt marsh as systems with different nutrient cycling "strategies." He speculated that nutrient cycling in reefs was closed, while marshes might be expected to show a greater exchange of nutrients with tidal waters. This view was certainly not unreasonable, since it would be difficult to find two more different marine ecosystems than the coral reef and the salt marsh—one exposed to a rather constant environment in oligotrophic tropical ocean waters, the other flooded by widely fluctuating eutrophic temperate coastal water. While the reef is often cited as the classic example of a very structured, highly diverse marine ecosystem, the salt marsh is the classic example of a highly stressed system with little biological structure and low diversity. While the reef shows high gross production and high respiration that lead to a near steady-state metabolism, the marsh system consists of emergent areas with high net production as well as creeks and embayments that are heterotrophic. In spite of these differences, however, some interesting similarities may emerge with regard to the overall behavior of major nutrients in the two systems.

The very complete cycling of phosphorus suggested by Pilon and Betzer's (1973) data from the reef at Eniwetok fits with the simple conceptual picture of how a reef ought to work. Yet at the same time, and over the same reef transects, Webb et al. (1975) found a substantial export of nitrogen. They also found high rates of nitrogen fixation that could provide about as large a nitrogen input to the reef as they observed being exported. As suggested by Odum (1967), stable systems such as coral reefs may be characterized by mechanisms that have evolved to conserve nutrients in short supply. Since there is no source of additional phosphorus input, the adaptive strategy in reef evolution may have been to put energy into mechanisms for phosphorus cycling. On the other hand, nitrogen fixation may be more efficient than nitrogen recycling. While high rates of nitrogen fixation are also found in salt marshes (Van Raalte et al. 1974, Jones 1974), substantial portions of the marsh also become anaerobic for

portions of the day. These anoxic regions of the marsh may contribute to high rates of denitrification capable of removing about as much nitrogen as fixed (W. Kaplan, Mar. Biol. Lab., Woods Hole, *personal communication*). The marsh embayment also receives large inputs of very high C:N ratio grass detritus that place a substantial nitrogen demand on the system. In this environment, the cycling of nitrogen within the sediments may be even more critical than phosphorous cycling, and there may be little or no exchange of nutrients with the overlying water.

The ultimate coupling of metabolism and mineral cycling is as much a constraint for systems with mud and marshes as it is for the plankton of the open sea. But as the spatial and biochemical complexity of the environment increases, time lags, intermediate transformations, and storages make it impossible for a simple relationship like the Redfield ratio to describe the exchanges between sediments and the overlying water. There is a stoichiometry of the ecosystem, but we must look beyond diel curves to understand the mechanisms of its more subtle cycles.

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