

# PERSISTENT DINOFLAGELLATE BLOOMS IN A SMALL MARINE COVE

## II. Tidal Fluxes of Nutrients and Phytoplankton

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**ABSTRACT:** Pettaquamscutt Cove is unique among Rhode Island coastal waters for its persistent dinoflagellate blooms. A diel study of phytoplankton abundance, nutrients, temperature and salinity evaluated the hypothesis that circulation patterns provided a washout-reseeding mechanism which facilitates these dinoflagellate blooms. 22 samples were collected hourly over a 21 hr period covering two full ebb tide cycles and one-half full flood cycles. Diel freshwater inputs of inorganic nutrients from the major tributary were also examined. Observations supported the retention-reseeding hypothesis. About 50% of the population levels of the principal dinoflagellate species found then (*Glenodinium uncatenum* and *Scrippsiella trochoidea*) washed out of the inner basin (the site of the persistent blooms) on an ebb tide were reseeded into this basin on the ensuing flood tide. This physical mechanism supplements the potentially rapid growth rates reported for *Glenodinium uncatenum* and *Gymnodinium simplex* (another bloom species). These growth rates would appear adequate to compensate for expected tidally-induced, diel population washout rates based on Ketchum's model and cove flushing rates. Significant diel variations strongly characterized inorganic nutrient concentrations, influenced also by tidal inputs stage. Two contrasting trends occurred: inorganic nitrogen levels, particularly  $\text{NH}_4$ , were higher in flooding waters;  $\text{PO}_4$  and  $\text{SiO}_3$  concentrations were higher in ebbing waters. Significant levels of  $\text{NO}_3$  accreted into the inner basin from stream runoff were rapidly utilized during dinoflagellate growth and unavailable for tidal export to the outer basin. Two nitrogen pumps are thus operative within the inner basin of Pettaquamscutt Cove: freshwater delivery of  $\text{NO}_3$  and flood tidal inputs of  $\text{NH}_4$  remineralized in the outer basin. These nitrogen enrichment processes further contribute to the persistence, retention and blooms of dinoflagellates within the inner basin, and reveal that these blooms are also regulated by nitrogen availability. Another nutrient pump operative within Pettaquamscutt Cove is the tidal export of  $\text{PO}_4$  and  $\text{SiO}_3$  from the inner to outer basin despite considerable utilization within the inner basin. Diatoms were surprisingly insignificant within the inner basin despite the nitrogen pump mechanism and high reserves of  $\text{PO}_4$  and  $\text{SiO}_3$ -nutrient resources seemingly favorable to diatom growth in this shallow, well-mixed cove. This led to a relative under-utilization of  $\text{SiO}_3$  and its subsequent tidal export.  $\text{SiO}_3$  concentrations were strongly correlated with salinity ( $r^2=0.92$ ) at the diel, tidal monitoring station located at the sill separating the inner and outer basins, and over which tidal exchange occurred.  $\text{SiO}_3$  was therefore useful as a semi-conservative tracer of nutrient inputs and mixing. Tidal flux rates of the measured properties in the form of a general budget are presented. Available data on growth rates of some key dinoflagellate species, the circulation patterns and the nitrogen pump mechanisms provide reasonable explanations for the observed dinoflagellate blooms. An unresolved aspect of these unique blooms is the cause of the apparent repression of diatom growth. Possible explanations include: dinoflagellates outcompete the diatoms (=competitive exclusion); dinoflagellates secrete substances inhibitory to diatom growth (=allelochemic inhibition) and/or substances associated with freshwater runoff favor dinoflagellate growth over that of diatoms (=water quality effects). Comparisons are made between Pettaquamscutt Cove and other Rhode Island coastal lagoons, and further establish the locally unique aspects of this habitat.

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## Introduction

Dense, multi-specific persistent blooms of dinoflagellates occur year-round within Pettaquamscutt Cove, Rhode Island, U.S.A., a shallow (mean depth <1m), small (27 hectares), well-mixed cove of the tidal Pettaquamscutt River located near the mouth of Narragansett Bay (41°26.5'N, 71°42.8'W). This persistent dinoflagellate community is highly anomalous for Rhode Island coastal waters, in which diatoms are pre-eminent (Furnas *et al.*, 1989). In a previous paper we established that wind-induced and tidal circulation patterns regulated the distribution, washout and re-inoculation of dinoflagellates in Pettaquamscutt Cove (Furnas *et al.*, 1989). Application of Ketchum's (1954) plankton growth rate-tidal flushing model to a mid-summer event indicated that dinoflagellate growth rates of 1.8 to 2.1 divisions day<sup>-1</sup> were required to maintain steady state populations. Experimental data indicate that the predominant species at that time, *Glenodinium uncatenum* and *Gymnodinium simplex*, are indeed capable of such rapid growth under certain experimental conditions.

Pettaquamscutt Cove is divided by a narrow (~70 m), shallow sill (0.1m at low tide) into inner and outer basins of approximately equal areas, with the tidal prisms corresponding to 46% and 55% of the basin high tide volumes, respectively. Dinoflagellates are concentrated into patches within the inner basin where their growth is facilitated by nutrients accreted from Crying Brook. Dinoflagellate growth is less favored in the outer basin, but this region appears to be of fundamental significance to persistence of their blooms within the inner basin. The outer basin both buffers tidal flushing losses of the dinoflagellates displaced from the inner basin and, in turn, re-inoculates the inner basin with seed populations on the flooding tides.

Such physical regulation of dinoflagellate dynamics is well-known (Seliger *et al.*, 1970; 1971; Taylor and Seliger, 1979; Anderson *et al.*, 1982; Tyler *et al.*, 1982; Garcon *et al.*, 1986). However, in these deeper, stratified embayments a two-layer ebb flow system serves as the retention mechanism, sometimes facilitated by vertical migration patterns such as reported for *Chaltonella* blooms in Japanese embayments (Yoshida and Numata, 1982). Within the well-mixed Pettaquamscutt Cove, the physical exchanges between, and growth processes within the inner and outer basins appear to function as the retention mechanism in place of a two-layered system allowing the persistent

dinoflagellate blooms.

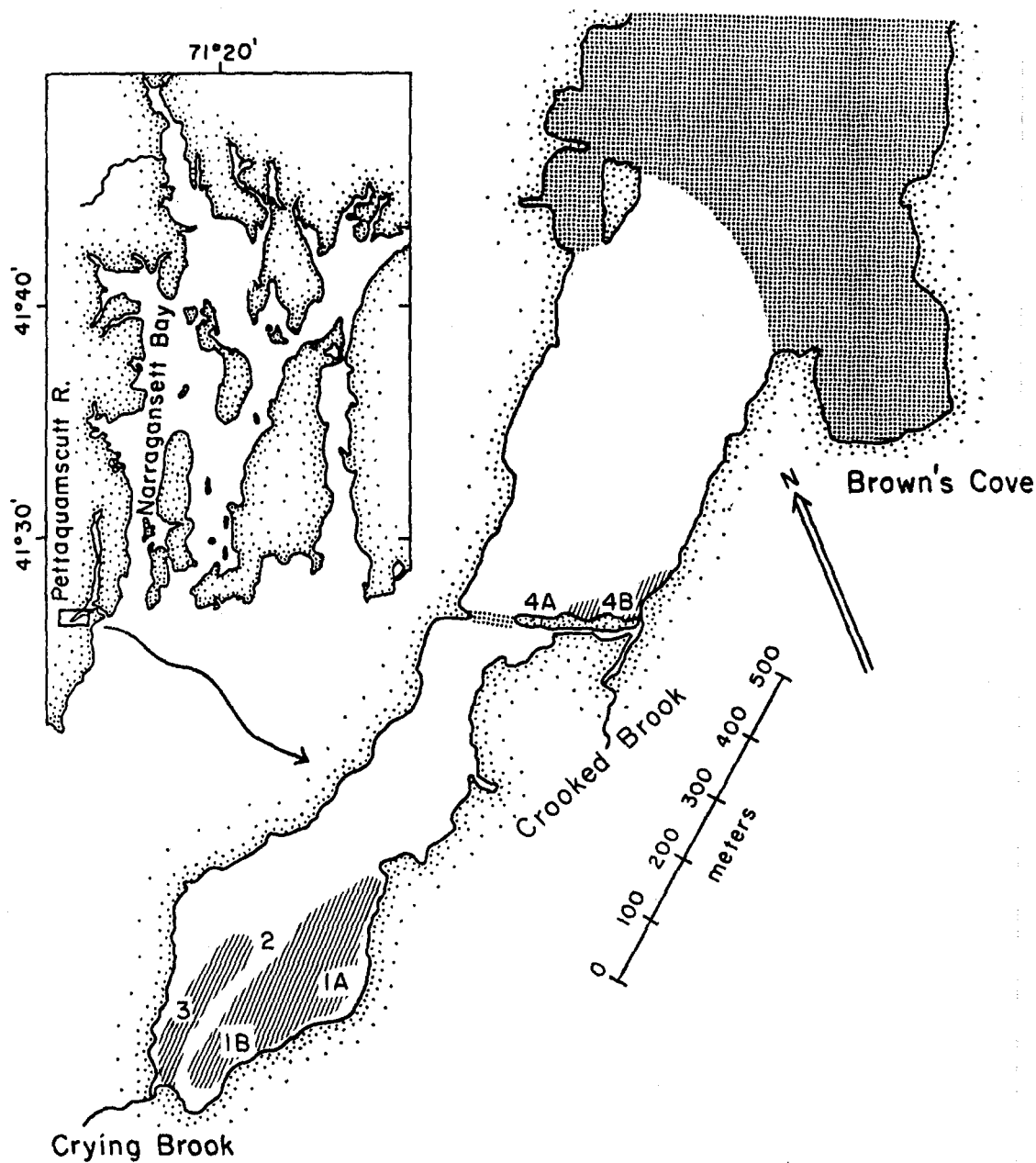
A surprising result of our study was the conspicuous unimportance of diatoms, notably *Skeletonema costatum*, despite high nutrient levels within the inner basin. This suggested to us that unknown factors limited diatom growth within Pettaquamscutt Cove, and that the resident dinoflagellate populations might be exploiting unique features of this cove.

To evaluate further these various conclusions, we undertook a diel study of the physical, chemical and phytoplankton characteristics of the water masses transported over the narrow, shallow sill sub-dividing Pettaquamscutt Cove into its inner and outer basins. Our intent was to establish the tidally-forced fluxes of nutrients and dinoflagellate populations between these two basins, and to construct tidal nutrient and phytoplankton budgets for the densely populated inner basin. Tidal budgets are commonly used to quantify nutrient and carbon fluxes between tidal embayments and coastal waters (Nixon, 1980; Chrzanowski *et al.*, 1982).

## Methods

**Physical Setting:** A detailed description of the morphology, tidal dynamics and circulation of Pettaquamscutt Cove is provided by Furnas *et al.* (1989). Fig. 1 shows that Pettaquamscutt Cove is subdivided into an inner and outer basin by an abandoned railway causeway located at its narrowest constriction approximately mid-way along its ~1.5 Km long axis. The inner basin comprises 48% of the total area ( $2.65 \times 10^6 \text{ m}^2$ ). The cove is a *cul-de-sac* separated by tidal flats from the main body of the Pettaquamscutt River which is located to the north of the cove and flows into Narragansett Bay. At high water, depths throughout much of Pettaquamscutt Cove slightly exceed 1 m. Tides are semi-diurnal, their range normally varying between 30 and 50 cm. A *Spartina* salt marsh fringes much of the cove.

Fresh water enters Pettaquamscutt Cove from several sources. These include a series of deep sink holes (>1.5m) and small springs located around the periphery of the cove, particularly along the western shore. Water from these springs flowed into the cove through a small brook. However, the largest visible source, Crying Brook, enters the inner basin at its head (Fig. 1). A smaller stream, Crooked Brook, discharges near the causeway, its flow entering both the inner and outer basins through a channel located at the eastern end of the causeway. This channel is one of two shallow breaches (30-35cm in depth) punctu-

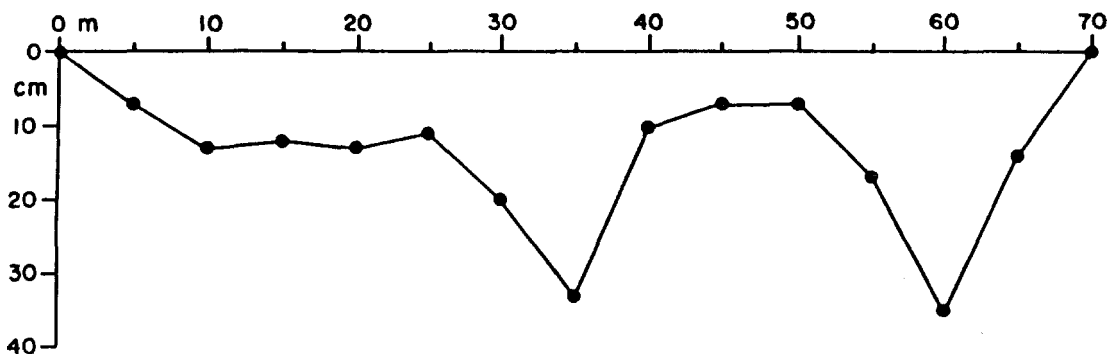


**Figure 1.** Pettaquamscutt Cove. Shaded areas show sill location separating inner and outer basins, and depict tidal area in outer basin separating it from the main tidal channel of Pettaquamscutt River. Striped areas represent dinoflagellate patches visibly detected on 6 July between 1115 and 1245hrs and sampled at the stations identified in the bloom patches.

ring the causeway, which forms a sill between the basins (Fig. 2). At high tide, the maximum channel depth in the breachway is 75-90cm. At low tide, sill depths across much of the channel are on the order of 10cm.

#### *Sampling the Breachway and Crying Brook:*

The diel survey began at 1130 hrs on 6 July 1981 during a flooding tide and continued through 0830 hrs (ebb) on 7 July. Near-surface water samples ( $n=$



**Figure 2.** Vertical cross section of the breach through the causeway separating Pettaquamscutt Cove into its inner and outer basins; diel sampling took place at the 60m breach opening.

22) of 1 L were collected hourly for 21 hours in the deepest channel through the breachway. Tidal height was measured at 30 min intervals at a tide stake located near the causeway. During the survey, winds were primarily from the south, estimated at 10-15 kts between 1115 and 1800 hrs on 6 July and  $\leq 5$  kts thereafter through 0830 hrs on 7 July. High tides occurred at 1340 hrs (6 July) and 0130 hrs (7 July); low tides at 2030 hrs and 0830 hrs, respectively. The period of flooding tide (7 hrs) exceeded the ebbing period (5 hrs).

Tidal heights at the time of sample collection were interpolated from tide stake readings. Instantaneous estimates of water volume inside the inner cove were calculated from the tidal height-cove volume relationship. For discrete time intervals between samples, changes in water volume inside the cove were calculated by difference. Phytoplankton populations were counted live in a Sedgwick-Rafter cell (McAlice, 1971). The unpreserved water samples used in the phytoplankton census were stored in the field on ice in the dark for up to eight hours before transmittal to the laboratory for processing. Aliquots of water for chlorophyll analyses were filtered in the field onto Gelman A/E glass fiber filters and frozen in liquid nitrogen until returned to the laboratory for storage in a deep freezer. Chlorophyll *a* and phaeophytin were measured fluorometrically (Yentsch and Menzel, 1963; Lorenzen, 1966). Samples for nutrient analysis were glass fiber-filtered into polyethylene bottles, stored on ice until returned to the laboratory, then deep frozen until analyzed. The concentrations of  $\text{NH}_3$ ,  $\text{NO}_3$ ,  $\text{PO}_4$  and  $\text{Si(OH)}_4$  were measured with a Technicon Autoanalyzer (Strickland and Parsons, 1972). Salinity samples, stored in 250ml screw-cap glass bottles, were measured with a Beckman inductive salinometer.

The area of the causeway channel was determined by trapezoidal integration of the area under the reference tidal height ( $9.95\text{m}^2$ ). Mean current speeds ( $\text{cm sec}^{-1}$ ) through the causeway between sampling times were calculated by dividing the change in cove volume ( $\text{m}^3$ ) by the mean area of the channel ( $\text{m}^2$ ). The resulting length (m) was converted to cm and divided by the number of seconds in the interval.

Nutrient and chlorophyll fluxes through the causeway between two sampling intervals were calculated by multiplying the change in water volume of the inner cove by the mean concentration of nutrient or chlorophyll during the given time interval. The mean nutrient or chlorophyll concentration was calculated from the values measured at each end of the time interval. Positive flux values indicate flow into the inner cove; negative fluxes indicate flow out of the cove. Each cm of tidal height represented  $1.3 \times 10^3 \text{m}^3$  of water in the inner basin and  $0.7 \text{m}^2$  of breachway cross-sectional area.

Freshwater flow in Crying Brook was estimated with a notch weir placed across an upstream culvert (Carter and Davidson, 1968). Stream flow ( $\text{m}^3 \text{hr}^{-1}$ ) is empirically related to water height above the base of the notch (*H*) by the equation:

$$Q = 251.8H^{5/2}$$

During the diel experiment, flow rates were measured hourly or near-hourly and water samples collected for dissolved inorganic nutrient determinations. Water samples were also collected from two freshwater springs in the saltmarsh to estimate groundwater nutrient concentrations.

## Results

During the three days preceeding the diel experi-

ment, there was a rainfall of 1.5cm; clear skies prevailed during the diel study, with 95% of the theoretical sunshine period achieved on 6 July (Anonymous, 1981). At the beginning of the sampling period, on the morning of 6 July, dense and distinct patches of dinoflagellates were observed in both nearshore and open water areas, including at the head of the inner basin and along the northern shore of the causeway (Fig. 1). Winds during this period were light and from the south. While water throughout the cove was noticeably discolored by dinoflagellates, boundaries of these patches on spatial scales of 5cm were readily discernable to the eye. Six regional phytoplankton samples were collected at the beginning of the diel study in the regions of visible discoloration (Fig. 1; Table 1). The dinoflagellate *Glenodinium uncatenum*, which overwhelmingly dominated (maximum of  $52,235 \text{ cells ml}^{-1}$ ), exhibited considerable regional variation in abundance, as did the other species. *Skeletonema costatum* was more abundant in the outer basin. Freshening southwesterly winds during late morning on 6 July stirred the inner basin and broke up the largest, dense patches of dinoflagellates into smaller patches which persisted within the inner basin. During the ebbing tide on the afternoon of 6 July, these patches were observed to exit the inner cove through the breachway. Some reformation of patches occurred in near-shore shallow areas during the night under calm air conditions, but not to the extent observed the first morning. (Observations by search light revealed patch and non-patch areas delineated on distance scales of 2-5cm.)

During the afternoon, bloom populations kept in a 1-L beaker actively swam to the bottom (5-10cm) forming dense, viscous agglomerations of cells within less than 15 mins. This behavior was not observed in the night samples or during the early morning of

7 July.

The experiment encompassed two ebb and one full flood tides. Virtually all of the water entering and leaving the inner basin passed through the breachway. A small, unmeasured flow passed through the narrow channel at the eastern end of the causeway (Fig. 1) where the current was considerably slower than through the main breachway. The marsh areas on both sides of the channel were flooded at high tide. However, direct flow across the marsh area was not observed; source waters flooded onto and ebbed from the marsh through the causeway channel. The maximal tidal range during this study of 50cm corresponded to inner basin tidal volumes of  $14.1$  and  $7.6 \times 10^4 \text{ m}^3$  on the high and low tide moments, respectively. Tidal prisms for the two ebb tides were 44 and 45 percent of the inner basin high tide volume.

The diel freshwater flow rates and nutrient concentrations in Crying Brook are given in Fig. 3. The corresponding freshwater and nutrient fluxes during discrete intervals of the tidal cycle are summarized in Table 2, and the flow rates and nutrient concentrations at other times during the early summer in Table 3. Brook flow during the experiment was relatively constant, ranging between  $42.2$  and  $36 \text{ m}^3 \text{ hr}^{-1}$ . On 21 July, a maximum flow rate of  $78 \text{ m}^3 \text{ hr}^{-1}$  was measured immediately after a cloudburst. Flows measured under non-rainy conditions on nine days between 30 June and 20 July ranged between  $11$  and  $49 \text{ m}^3 \text{ hr}^{-1}$ .

Dissolved nutrient levels in brook waters were consistently high (Fig. 3). Nitrate was the principle inorganic nitrogen species; its mean concentration ( $29.6 \mu\text{g} \cdot \text{at } \ell^{-1}$ ) was about 7-fold that for  $\text{NH}_4$  ( $4.1 \mu\text{g} \cdot \text{at } \ell^{-1}$ ). The diel concentration range for  $\text{NH}_4$  ( $1.1$  to  $7.1 \mu\text{g} \cdot \text{at } \ell^{-1}$ ) exceeded (7-fold) that for  $\text{NO}_3$ , which ranged about 2-fold, from  $19.8$  to  $42.2 \mu\text{g} \cdot \text{at } \ell^{-1}$ .  $\text{NO}_3$  comprised between 81 and 96 percent of the instanta-

**Table 1.** Phytoplankton survey of 6 July sampled between 1115-1245 hr ( $\text{cells ml}^{-1}$ )

STATION:	1A	1B	2	3	4A	4B
<i>Glenodinium uncatenum</i>						
	12,701	52,235	14,839	17,516	6,390	3,296
<i>Cochlodinium heterolobatum</i>						
	56	1,575	304	236	135	79
<i>Scrippsiella trochoidea</i>						
	349	630	248	45	270	203
<i>Heterocapsa triquetra</i>						
	11	?	23	34	45	34
<i>Skeletonema costatum</i>						
	236	225	135	180	371	338

**Table 2.** Integrated fluxes of freshwater flow and inorganic nutrients from Crying Brook into Pettaquamscutt Cove during discrete intervals of the tidal cycle on July 6-7

	Time			
	*1130-1340	1340-2030	2030-0130	0130-0830
Direction	In	Out	In	Out
Freshwater(m <sup>3</sup> )	121	301	188	261
NO <sub>3</sub> +NO <sub>2</sub> (g-at)	4.49	8.24	5.71	6.56
NH <sub>4</sub> "	0.66	0.91	0.75	1.11
Total DIN "	5.15	9.15	6.46	7.67
PO <sub>4</sub> "	0.56	1.14	1.01	1.57
Si(OH) <sub>4</sub> "	17.71	36.50	34.27	44.62

\*incomplete cycle

**Table 3.** Representative freshwater flow rates and inorganic nutrient concentrations in Crying Brook on various days during June-July 1981

Date	Flow rate (m <sup>3</sup> hr <sup>-1</sup> )	NH <sub>4</sub>	NO <sub>3</sub> +NO <sub>2</sub> (μg · at ℓ <sup>-1</sup> )	PO <sub>4</sub>	Si(OH) <sub>4</sub>
30 June	16.2	4.0	40.3	4.9	163.1
1 July	28.2	6.9	52.8	4.9	168.3
2	30.0	4.6	42.1	4.3	157.5
3	33.8	4.1	39.7	3.6	160.4
5	49.3	4.5	39.1	5.0	179.6
8	31.9	4.4	27.1	8.6	216.5
15	31.9	6.7	11.7	5.3	219.1
20	31.9	6.9	14.6	10.4	201.0
21	77.8	—	—	—	—

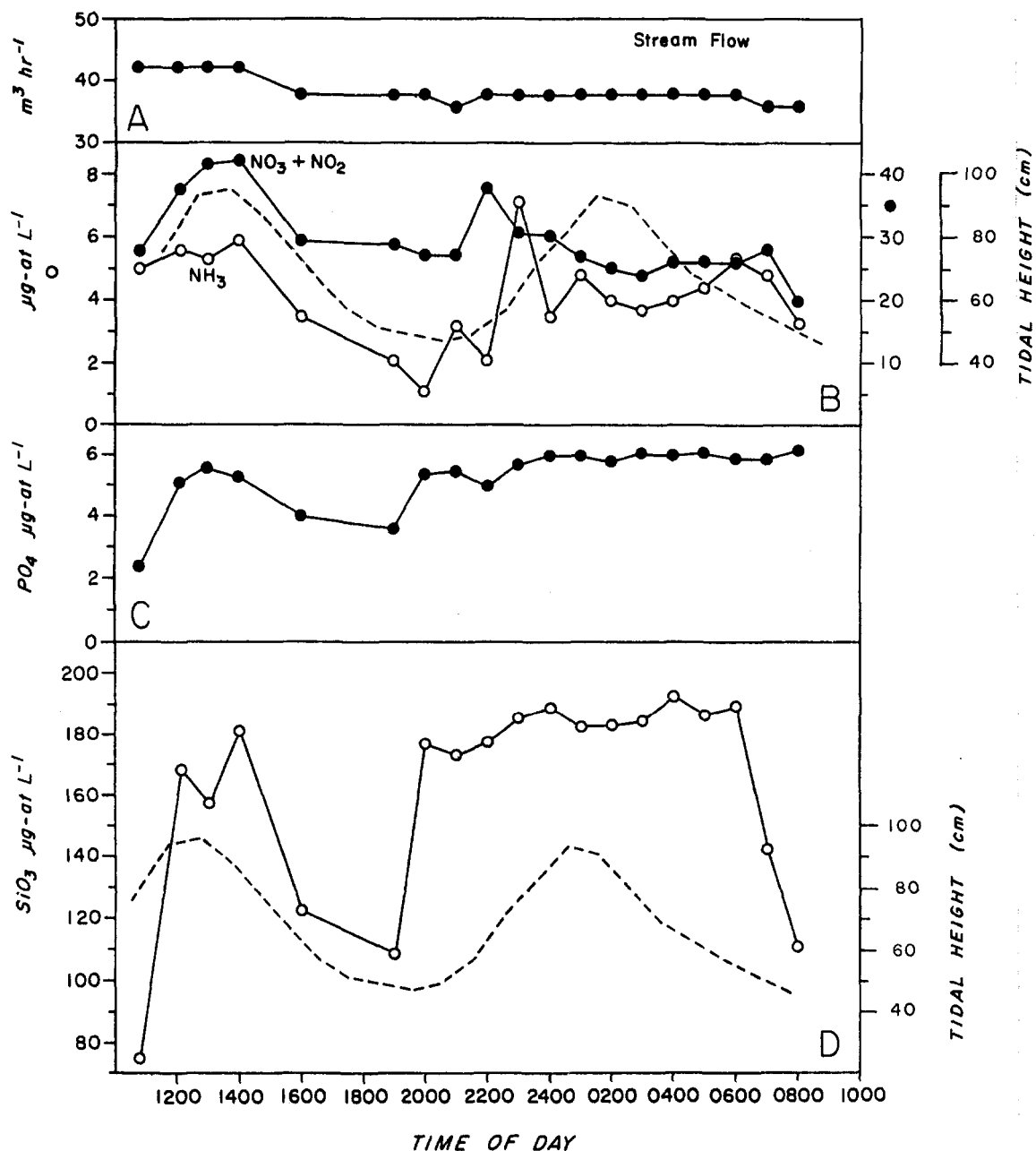
neous inorganic nitrogen flux. Silicate concentrations in the brook water exceeded 100 μg · at ℓ<sup>-1</sup> (with one exception), with a maximum of 192 μg · at ℓ<sup>-1</sup> and diel mean of 162.5 μg · at ℓ<sup>-1</sup>. Phosphate concentrations ranged between 2.4 and 6.2 μg · at ℓ<sup>-1</sup> with a diel mean of 5.3 μg · at ℓ<sup>-1</sup>. Groundwater nutrient levels (Table 4) were similar to those in the brook water. The pronounced difference between nitrate concentrations in the two springs only 3m apart is conspicuous. The diel cycling of nutrients in Crying Brook waters exhibited two distinct phases. NO<sub>3</sub>, PO<sub>4</sub> and SiO<sub>3</sub> concentrations were generally invariant between 2000 hrs and 0800 hrs. These nutrients and NH<sub>4</sub> then exhibited a maximum/minimum sequencing between 1100 hrs and 2000 hrs on 6 July which roughly trended with the tidal cycle. The significant observation, however, is that high nutrient concentrations characterize Crying Brook independent of tidal cycles. Their continuous discharge into the inner basin serves as a nutrient pump for phytoplankton growth independent of tidal phase or the diel exchange properties

between the inner and outer basins.

The ranges in physical, chemical and biological variables measured in the 22 water samples collected in the breachway during the twenty-one hour diel experiment are summarized in Table 5. The fluxes of fresh water, nutrients and phytoplankton biomass through the causeway breach during various tidal phases are given in Table 6. The diel patterns in tidal height velocity and other variables are shown in Figs. 5, 6, 7. A flooding tide was in progress when sampling commenced at 1130 hrs on 6 July; high tide occurred

**Table 4.** Salinities (‰) and inorganic nutrient concentrations (μg · at ℓ<sup>-1</sup>) of groundwater springs located in Pettaquamscutt salt marsh

	Salinity	NH <sub>4</sub>	NO <sub>3</sub> +NO <sub>2</sub>	PO <sub>4</sub>	Si(OH) <sub>4</sub>
Spring #1	4	5.8	16.5	7.4	213.4
Spring #2	2	4.1	70.2	4.6	132.9



**Figure 3.** A. Freshwater flow rates in Crying Brook during the July 6-7 diel experiment. B, C, D. Dissolved nutrient concentrations in Crying Brook; dashed line represents the diel tidal height pattern.

two hours later, ebbed during the afternoon-early evening, reached its lowest level at 2030 hrs, followed by high and low tides at 0130 hrs and 0830 hrs, respectively, on 7 July.

The maximum salinity (30.53 ‰) (Fig. 4) was observed at the initial high tide on the morning of 6 July. The minimum (29.4 ‰) coincided with the following

low tide. The lower salinity values observed on the second high tide suggest that freshwater flushed from the inner basin on the first ebb tide was partly retained in the outer basin and returned on the following flood. Water temperature ranged from an afternoon high of 28°C to 24°C during the evening and early morning (Fig. 4C). Mean current velocities calculated from

**Table 5.** Maximum and minimum values of physical, chemical ( $\mu\text{g} \cdot \text{at} \ell^{-1}$ ) and biomass ( $\text{mg m}^{-3}$ ) variables measured at the breachway between basins of Pettaquamscutt Cove on July 6-7, 1981

	Maximum	Minimum
Cove Water Volume	$1.41 \times 10^5 \text{m}^3$	$7.6 \times 10^4 \text{m}^3$
Salinity (‰)	30.53	29.42
Temperature ( $^{\circ}\text{C}$ )	28	24
Chlorophyll <i>a</i>	56.9	0.9
Phaeophytin	26.2	1.2
$\text{NO}_3 + \text{NO}_2$	1.0	0.0
$\text{NH}_4$	1.9	0.0
Total DIN	1.9	0.0
$\text{PO}_4$	2.23	1.54
$\text{Si}(\text{OH})_4$	47.6	27.4

**Table 6.** Integrated fluxes of freshwater, inorganic nutrients and plant pigments through the causeway breach during discrete tidal intervals. Freshwater fluxes were calculated relative to maximum salinity. Positive values indicate transport into inner basin; negative values transport from inner to outer basin

	Time			
	*1130-1340	1340-2030	2030-0130	0130-0830
Direction	In	Out	In	Out
Cove volume ( $\times 10^4 \text{m}^3$ )	+2.60	-6.34	+5.95	-5.95
Fresh water ( $\text{m}^3$ )	+74.6	-1232.0	+953.0	-1476.3
$\text{NO}_3 + \text{NO}_2$ (g-at)	+6.67	-9.74	+25.76	-5.00
$\text{NH}_4$ $\nearrow$	+38.03	-31.69	+28.09	-13.23
Total DIN $\nearrow$	+44.70	-41.42	+53.85	-13.23
$\text{PO}_4$ $\nearrow$	+41.50	-123.25	+110.93	-131.21
$\text{Si}(\text{OH})_4$ $\nearrow$	+787.9	-2475.3	+2018.3	-2667.6
Chlorophyll <i>a</i> (g)	+39.3	-2308.6	+603.8	-458.1
Phaeophytin $\nearrow$	+35.1	-969.2	+307.2	-238.4

\*incomplete cycle

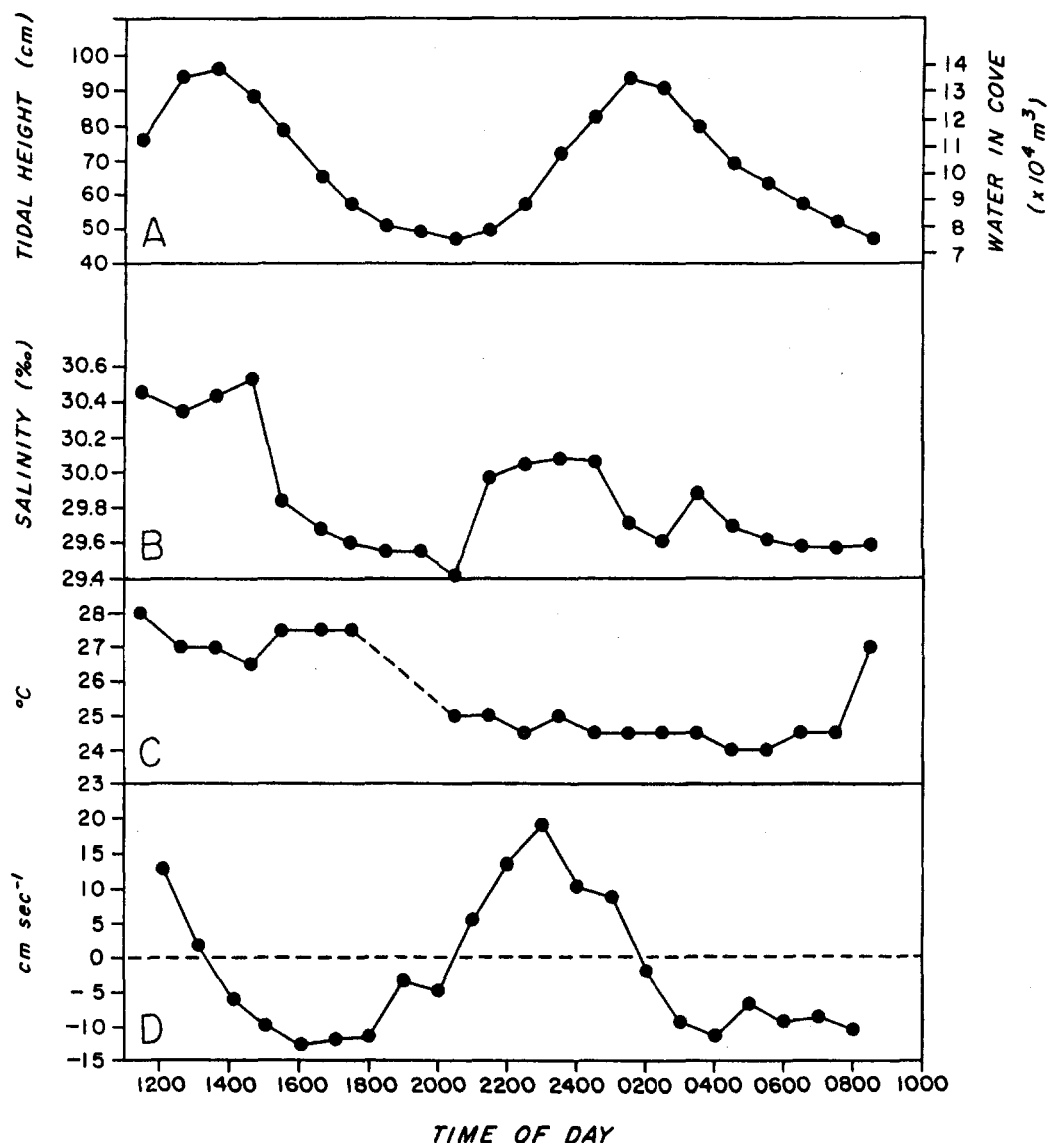
volume fluxes (Fig. 4) were relatively low despite the restricted area of the breachway channel. Attempts to measure current velocities directly were unsuccessful because the flow rates were below the instrument threshold.

If water of the lowest diel salinity (29.547 ‰) was evenly mixed throughout the inner basin and the maximum salinity (30.53 ‰) is taken as the offshore mixing end-member, freshwater comprised 3.2 percent of the inner basin volume. At the maximum flow rate ( $77.8 \text{m}^3 \text{hr}^{-1}$ ) recorded for Crying Brook (Table 3), it would take 32 to 59 hours to deliver this volume of freshwater to the inner cove. Since this estimate ignores tidal flushing, flow rates in Crying Brook must have been substantially higher during and immediately after the rainstorm in the three days preceding

the diel study, or substantial ground water inputs also took place.

Inorganic nutrient concentrations exhibited considerable diel variations which were strongly influenced by tidal stage (Fig. 5). Two contrasting trends were found: inorganic nitrogen levels, particularly  $\text{NH}_4$ , were higher in flooding waters, whereas  $\text{PO}_4$  and  $\text{SiO}_3$  concentrations were higher in ebbing waters. That is, over the tidal cycle the inner basin imported nitrogen from the outer basin, but exported  $\text{PO}_4$  and  $\text{SiO}_3$ . Maximal  $\text{NH}_4$  concentrations at the two flood tides ( $1.9$  and  $1.2 \mu\text{g} \cdot \text{at} \ell^{-1}$  respectively) decreased to non detectable levels during the ebb phases (Fig. 5A).  $\text{NO}_3$  concentrations were below  $0.4 \mu\text{g} \cdot \text{at} \ell^{-1}$  in 21 of the 22 samples and, in contrast to Crying Brook (Fig. 3B), similar to  $\text{NH}_4$  concentrations.  $\text{NO}_3$  and  $\text{NH}_4$  con-

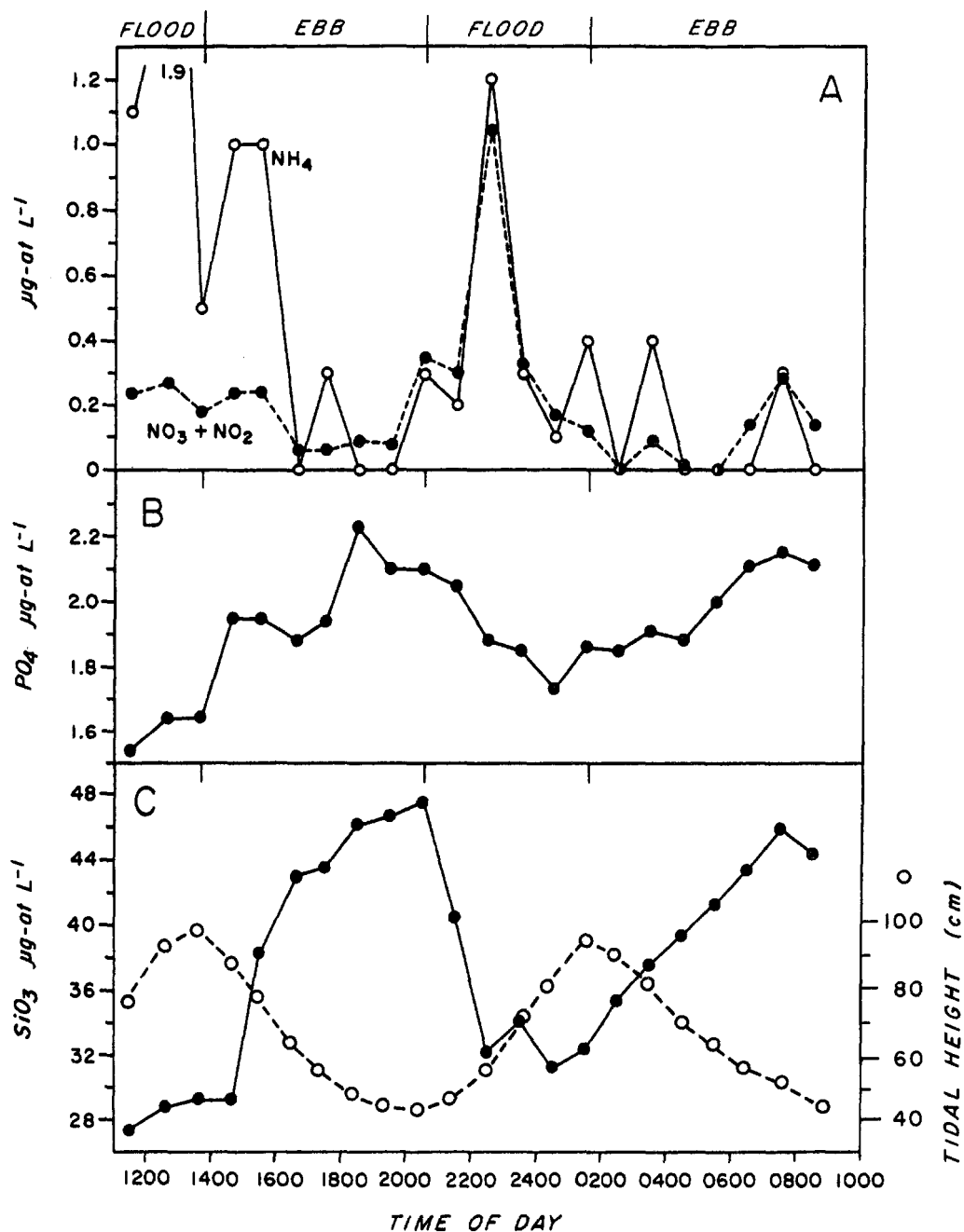




**Figure 4.** A. Tidal height in Pettaquamscutt Cove during the July 6-7 diel experiment relative to tide stake; B. Surface salinity and C. Surface water temperature in the causeway breach; D. Computed mean flow rates through the causeway breach.

centrations were considerably higher in Crying Brook and in groundwater (Table 4), both sources serving as inorganic nitrogen pumps to the inner basin. The very low  $\text{NO}_3$  concentrations in the waters ebbing from the inner basin reveal that its accretion from freshwater sources is very rapidly taken up by the phytoplankton within the inner cove. Thus, two nitrogen pumps are operative within the inner basin of Pettaquamscutt Cove: freshwater delivery of  $\text{NO}_3$  and tidal inputs of  $\text{NH}_4$  remineralized in the outer basin.

The crisp, diel cycles of  $\text{PO}_4$  and  $\text{SiO}_3$  synchronous with the tidal flow at the breachway are evident (Figs. 5B, C).  $\text{PO}_4$  maxima for the two ebb tides were 2.23 and  $2.15 \mu\text{g} \cdot \text{at } \ell^{-1}$  respectively, whereas the full flood tide concentrations were 1.64 and  $1.86 \mu\text{g} \cdot \text{at } \ell^{-1}$ . Thus, while the concentration differences between tidal maxima/minima for  $\text{PO}_4$  were modest, the progressive increases and decreases in  $\text{PO}_4$  concentrations in ebbing waters and flooding waters, respectively, crossing the causeway are evident. This tidal pattern



**Figure 5.** Surface concentrations of: A. Nitrate (○) and ammonia (●); B.  $\text{PO}_4$ ; C.  $\text{Si(OH)}_4$  in the causeway breach, along with the diel tidal height pattern during the July 6-7 diel experiment.

is even more conspicuous for the  $\text{SiO}_3$  diel cycle: the two ebb tide maxima of 47.6 and 45.9  $\mu\text{g} \cdot \text{at} \cdot \ell^{-1}$  contrast with the flood tide maxima of 29.3 and 32.4  $\mu\text{g} \cdot \text{at} \cdot \ell^{-1}$  respectively.

$\text{PO}_4$  and  $\text{SiO}_3$  concentrations are higher in Crying Brook (Fig. 3) and groundwater (Table 4), freshwater

inputs which result in much higher residual levels of these nutrients within the inner basin than found in the outer basin. Despite considerable utilization of  $\text{PO}_4$  and  $\text{SiO}_3$  by phytoplankton within the inner basin, a considerable surplus remains, unlike for inorganic nitrogen, available for export to the outer basin during

ebb flow. The considerable uptake of  $\text{PO}_4$  and  $\text{SiO}_3$  in the outer basin is revealed by their significantly lower concentrations in waters flooding inwards from the outer basin. Tidal export of  $\text{PO}_4$  and  $\text{SiO}_3$  from the inner to the outer basin, therefore, represents another nutrient pump operative within Pettaquamscutt Cove.

### Chlorophyll and Phytoplankton

Diel chlorophyll concentrations varied significantly from 0.9 to  $56.9 \text{ mg m}^{-3}$ , a range which occurred between 1130 and 1730 hrs on 6 July (Fig. 6). There was a clear initial association between chlorophyll concentration and tidal cycle. Maximal chlorophyll concentrations were measured during the late-afternoon ebb tide on 6 July; a strong ( $15\text{--}35 \text{ m sec}^{-1}$ ) southwesterly breeze then blew along the cove axis. Distinct patches of dinoflagellates were observed to leave the inner basin through the breachway and to move northward across the outer basin. (No attempt was made to sample in or outside of these patches). The high pigment concentrations observed in the afternoon were not observed in the final ebb tide samples, or subsequently. Thus, the diel variations in chlorophyll levels transported across the causeway were related to both tidal and wind conditions. Chlorophyll levels surged to a lesser extent over a 4 hr period during the ebbing tide on 7 July, from 3.5 to  $19.8 \text{ mg m}^{-3}$ .

The ebbing and flooding tidal phase chlorophyll concentrations are useful indicators of phytoplankton biomass in the inner and outer basins, respectively. Their tidal dynamics confirm the higher biomass levels in the inner basin expected from the diel nutrient cycles and freshwater nutrient inputs.

The diel chlorophyll cycle also indicates that re-inoculation of the inner basin occurs during tidal flooding by cells previously washed-out into the outer basin. Thus, during the flooding period from 2130 to 0130 hrs, chlorophyll levels decreased from 17.1 to  $7.1 \text{ mg m}^{-3}$ . That is, during the initial flooding stages, dinoflagellate cells most recently advected from the inner to outer basin were re-inoculated first. The lower biomass concentrations during the later flooding stages reflect both dilution of cells washed-out during the early stages of the previous ebb cycle and the lower populations characteristic of the outer basin.

Dinoflagellates dominated the diel phytoplankton communities at the breachway, with *Glenodinium uncatenum*, *Scrippsiella trochoidea*, *Cochlodinium heterolobatum*, *Heterocapsa triquetra*, *Prorocentrum triangulatum* and *Prorocentrum redfieldii* most prominent. *Skeletonema costatum*, the primary diatom, and a euglenid community were also present. *Glenodinium uncatenum* overwhelmingly dominated the community; its diel cycling is shown in Fig. 7. A conspicuous wash-out of *Glenodinium* from the inner basin occurred on eb-

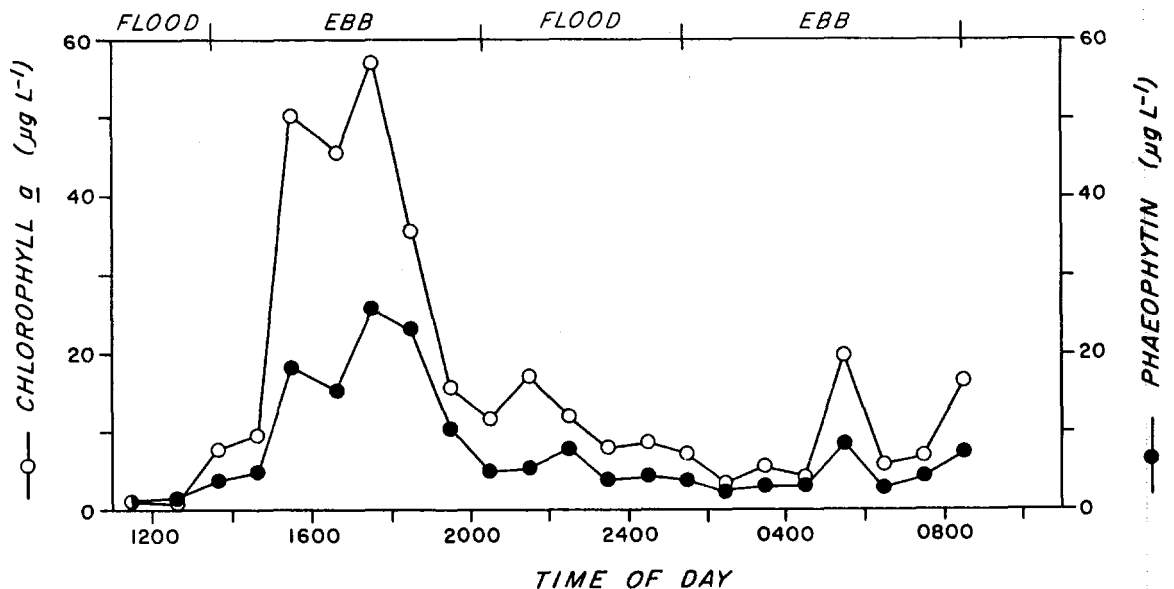
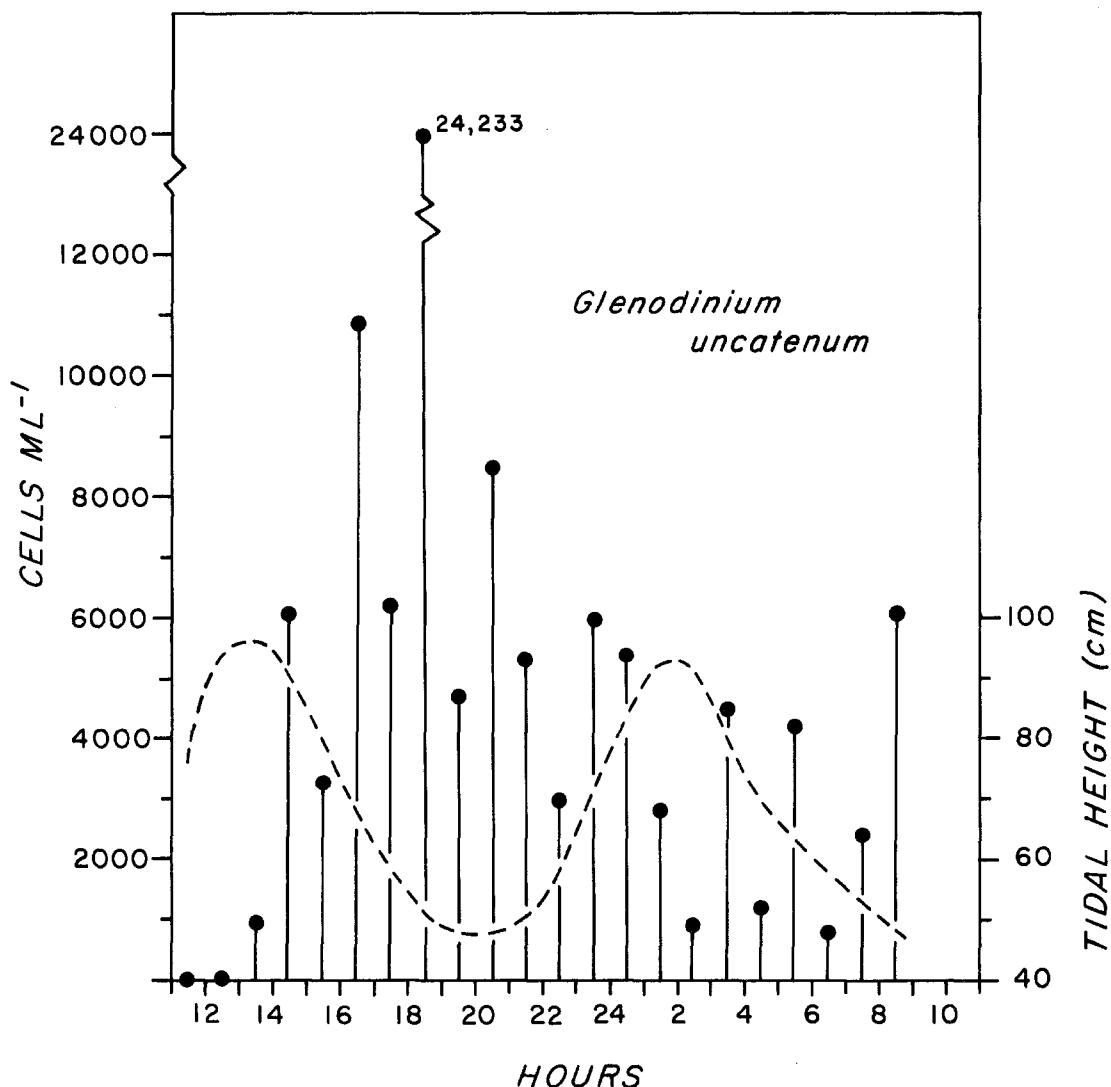


Figure 6. Surface chlorophyll *a* (○) and phaeophytin (●) concentrations in the causeway breach during the July 6-7 diel experiment.



**Figure 7.** Diel variations in numerical abundance of *Glenodinium uncatenum* at the causeway sampling site, and in tidal height pattern.

bing tides. A maximum of 24,233 cells ml<sup>-1</sup> occurred at 1830 hrs on 6 July; the huge populations during the ebb phase being consistent with measured chlorophyll levels (Fig. 6). Excluding the 1830 hr abundance level, the mean ebb flow abundance of *Glenodinium* on 6 July (1435 to 2030hrs) was 6,621 ml<sup>-1</sup>, whereas the mean flood population level on 6-7 July (2130 to 0130 hrs) was 3,069 ml<sup>-1</sup>. That is, about 46% of the cells washed out from the inner basin on an ebbing tide were reseeded on the ensuing flood tide. The mean ebbing population on 7 July (0330 to 0830 hrs) was 3,210 ml<sup>-1</sup>, about 50% lower than during the 6 July ebb phase. The conspicuously lower abun-

dance of *Glenodinium uncatenum* at the causeway during the flood tide peak is evident (Fig. 7). The mean levels on 6 and 7 July were 473 ml<sup>-1</sup> and 1,884 ml<sup>-1</sup>, respectively; i. e., considerably below the mean ebb and mean flood populations.

The diel patterns of *Scrippsiella trochoidea* and *Cochlodinium heterolobatum* were similar to that for *Glenodinium uncatenum* (Figs. 8A, B). A strong wash-out of *Scrippsiella* occurred during ebb flow, its maximum abundance of 518 cells ml<sup>-1</sup> recorded at 1932 hrs on 6 July just prior to the ebb maximum. The mean ebbing populations on 6 and 7 July were similar: 279 and 388 ml<sup>-1</sup>, respectively. The mean flood population

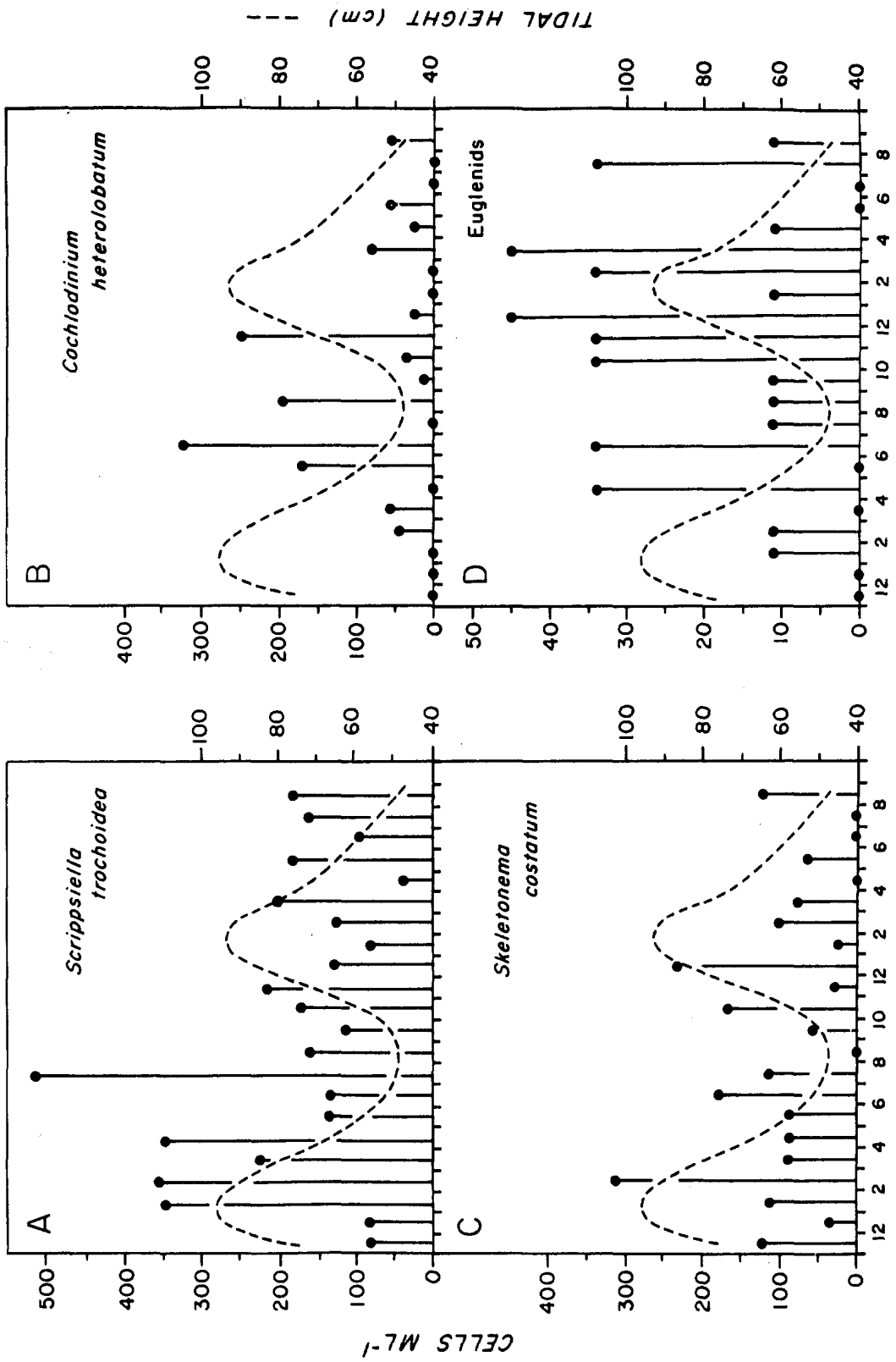


Figure 8. Diel variations in numerical abundance of: A. *Scrippsiella trochoidea*; B. *Cochlodinium heterolobatum*; C. *Skeletonema costatum*, and D. Euglenid community at the causeway sampling site, and tidal height pattern.

on 6 July (2130 to 0030 hrs) was  $155 \text{ ml}^{-1}$ . This indicates a 56% return of cells washed out from the inner basin during the ensuing flood tide, a reseeded percentage similar to that for *Glenodinium uncatenum*. The low abundance of *Scrippsiella* at, or near the flood peaks ( $84$  and  $143 \text{ ml}^{-1}$ ) is conspicuous. The maximal abundance of *Cochlodinium heterolobatum* ( $326 \text{ ml}^{-1}$ ) near the ebb peak coincided with that for *Glenodinium uncatenum*, and preceded that for *Scrippsiella trochoidea*. The progressive increase in abundance with ebb stage during 6 July from 1340 to 1930 hrs is conspicuous.

These three major dinoflagellates were advected from the inner basin during ebb flow and reseeded into this basin during flooding tides. In contrast, the diel cycle of the diatom *Skeletonema costatum* was somewhat confused (Fig. 8C). Excluding the maximum concentration of  $315 \text{ cells ml}^{-1}$  at 1435 hr on 6 July, the mean cellular concentrations during ebb and flood flow were similar:  $97$  and  $101 \text{ cells ml}^{-1}$ , respectively. *Skeletonema* abundance appeared to decrease progressively with stage of the ebb tide expressed relative to the maximal ebb tidal level. *Skeletonema* was not clearly advected into the outer basin in the manner described for the dinoflagellates. This is further evidence for the unexpectedly poor diatom growth within the inner basin commented upon previously. In fact, the diel cycle partially suggests that transport occurs primarily from the outer to inner basin. The diel cycling of the modestly abundant euglenid community shows no apparent correlation with the tidal cycle.

### Tidal Fluxes

The diel fluxes of nutrients and chlorophyll through the breachway are shown in Fig. 9; with integrated fluxes calculated for four distinct tidal intervals summarized in Table 6. The initial period (1130-1340) comprised only a small portion of a complete incoming tidal phase, and will not be emphasized. Nonetheless, inward fluxes of nitrogen, principally  $\text{NH}_4$ , and phosphorus took place on this incoming tide. Comparison of the fluxes for the single full incoming tide segment relative to the two complete ebb tide events indicates that the inner basin exported fresh water, phosphate, silicate, and pigments, but imported inorganic nitrogen. Chlorophyll exports (Fig. 9C) were most pronounced during the afternoon ebb tide (1340-2030) when southerly sea breezes accelerated the outward flow. At night, under low wind conditions, a portion of this biomass was returned to the inner basin and retained.

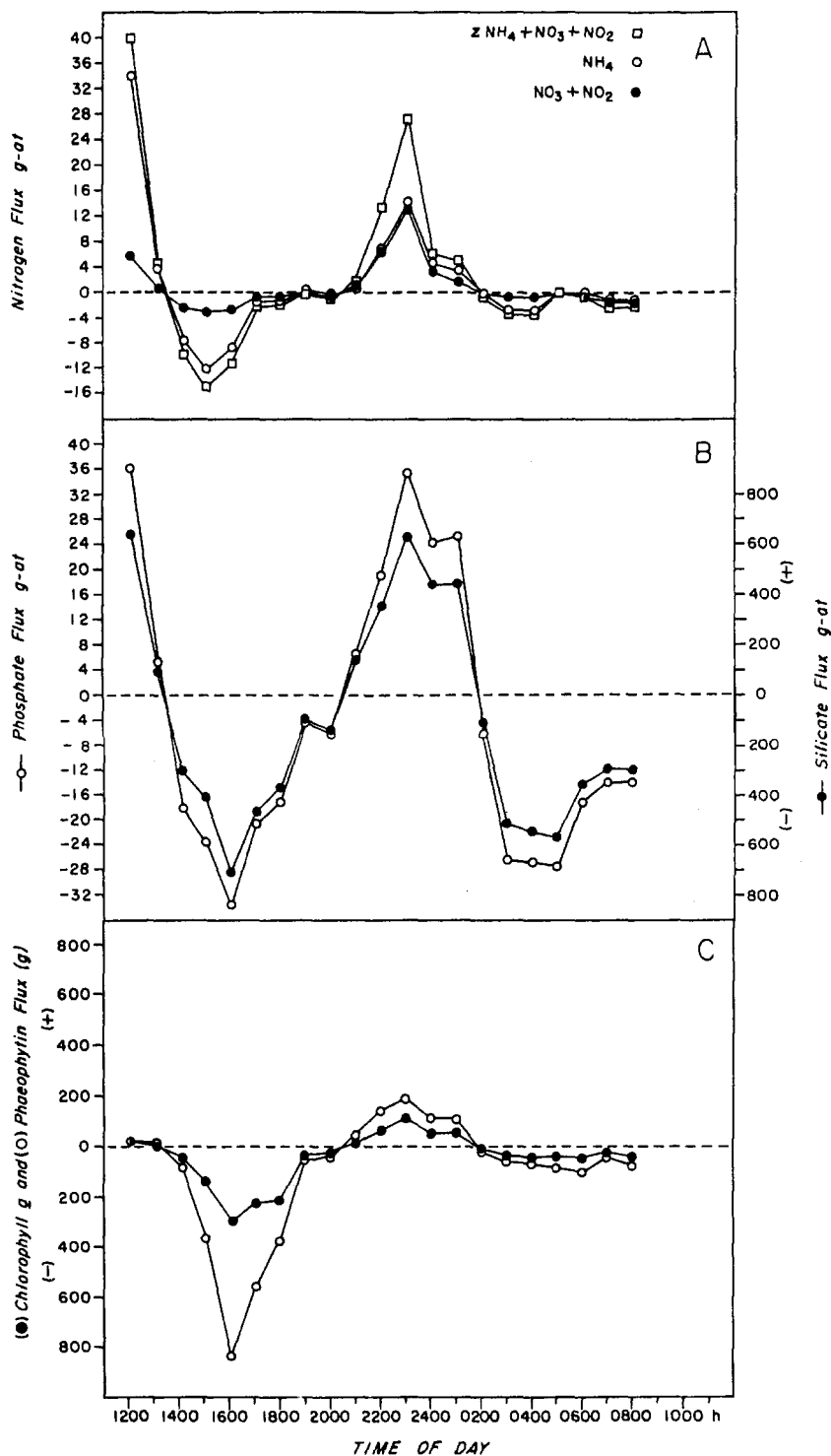
Nutrient and freshwater fluxes were not coupled, either prior to, or during the study. The surprising lack of diatoms within the inner basin contributed to the relative under-utilization of  $\text{SiO}_3$  and its tidal export. It can therefore be used as a semi-conservative tracer of nutrient inputs and mixing. Silicate concentrations in the breachway samples (Fig. 10) were linearly related to salinity ( $r^2=0.92$ ), suggestive of conservative mixing between fresh and saltwater end members. Extrapolation of the mixing line to 0‰ salinity yields an inferred silicate concentration in Crying Brook water ( $596 \mu\text{g} \cdot \text{at} \cdot \ell^{-1}$ ) nearly three times measured levels (Table 2). Net tidal silicate exports over the two tidal cycles were 8.5- and 6.4-times those expected from estimated freshwater exports and the maximum Crying Brook silicate levels. Silicate concentrations in the groundwater samples (Table 4) are insufficient to account for the difference. Net phosphate fluxes showed a similar discrepancy.

In contrast, the inner basin was a net importer of inorganic nitrogen supplied from freshwater runoff and the outer basin. Although nitrate and ammonia concentrations were generally low in both basins, their concentrations at high (=incoming tides) were consistently higher than in outgoing tides.  $\text{NO}_3$  and  $\text{NH}_4$  entering the inner basin from Crying Brook were rapidly utilized by dinoflagellate populations at the head of the cove. Enhanced inorganic nitrogen concentrations were rarely observed within 100m of the brook mouth. The pronounced exports of phytoplankton pigments (Fig. 6) indicate that much of the nitrogen entering the inner basin is exported as organic nitrogen.

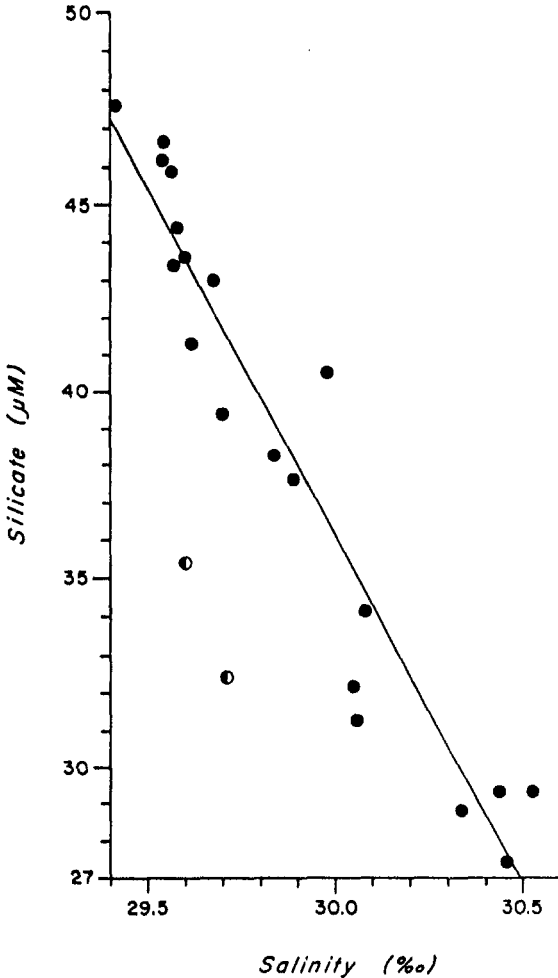
### Discussion

Within the brief 21 hr study period, during which 22 samples were analyzed, the Pettaquamscutt Cove system responded to nutrient loading from prior freshwater runoff following a rainstorm; to semi-diurnal tidal flushing, and to diel changes in wind stress which strongly influenced tidal flushing dynamics. The wind stress patterns, concentrations of nutrients, and distribution of dinoflagellate populations reported here are typical of summer conditions (Tomas and Smayda, in prep.). To a degree, therefore, our diel observations represent a snapshot of tidal flux processes normally at work in Pettaquamscutt Cove.

This diel study was undertaken principally to evaluate our conclusion (Furnas *et al.*, 1989) that the circulation patterns facilitated the persistent dinoflagellate blooms within Pettaquamscutt Cove, providing



**Figure 9.** Transport rates through the causeway breach into (+) and out of (-) the inner basin during the July 6-7 diel experiment for: A. Dissolved nitrate + nitrite (●), ammonia (○) and total DIN (□); B. Phosphate (○) and Silicate (●), and C. Chlorophyll *a* (●) and Phaeophytin (○).



**Figure 10.** Relationship between silicate concentration and salinity in diel water samples collected at the causeway breach. Equation for the regression line is  $Y = -18.61 \times -594.4; r^2 = 0.92$ . The piebald symbols at 0130 and 0230 hrs were not included in the regression calculation.

a washout-reseeding mechanism favorable to dinoflagellate persistence and growth. This conclusion is supported by the diel study. About 50% of the population levels of the principal dinoflagellates *Glenodinium uncatenum* and *Scrippsiella trochoidea* washed out of the inner basin on an ebbing tide were reseeded into this basin on the ensuing flood tide. Thus, the annually persistent dinoflagellate blooms in Pettaquamscutt Cove, unique to Rhode Island coastal waters and lagoons, are partly attributable to the physiographic and circulation patterns of this shallow cove. *Glenodinium*

*uncatenum* also forms massive blooms in Chesapeake Bay and its tributaries (Tyler *et al.*, 1982), where its retention is also related to circulation in combination with its migration and encystment patterns. Strong, positively phototactic migration patterns of *G. uncatenum* induce its diel migratory excursions into and out of the onshore/offshore currents present in that two-layered system. Its retention within that estuary is facilitated by this "conveyor belt" routing. Cyst induction near the end of its bloom period is accompanied by their deposition into sediments at frontal convergences; excysted cells then reseed the population during its next growth period.

In reality, this retention mechanism represents two different aspects of the seeding problem. (We have not looked for cysts in the sediments of Pettaquamscutt Cove.) Encystment-excystment processes are more relevant to the maintenance of indigenous populations. That is, their role is to reseed at the beginning of a growth period, which differs from the need for viable cells during the active growth period following excystment. The ratio of washout to advective reseeded of vegetative cells then becomes the more important determinant of continued growth. Although a two-layered system is not present in shallow, well-mixed Pettaquamscutt Cove, the diurnal tidal flux provides a suitable retention mechanism. Obviously, in deeper, stratified estuarine systems a two-layer transport mechanism, such as described by Tyler *et al.* (1982), is a more effective retention mechanism than the diurnal tidal mechanism operative in Pettaquamscutt Cove: The occurrence of strong, positive phototaxis by *Glenodinium uncatenum in situ* reported by Tyler *et al.* differs from the strong negative phototaxis exhibited in carboys by the Pettaquamscutt Cove populations.

The regulatory role of tidal fluxes as a retention mechanism for the persistent red-tide blooms in the inner cove is modified by wind-patterns. Concurrent drogue studies showed that surface water movements within the inner basin were largely determined by the prevailing winds (Furnas *et al.*, 1989). Under favorable conditions, the inner basin concentrates dinoflagellate populations over several days, or tidal cycles. Easterly or northerly winds pushed dinoflagellates to the head of the cove, regardless of the tidal direction. In the absence of southwesterly sea breezes, the dense patches found at the cove head remained there, relatively immune to tidal flushing losses. Under still air or northerly wind conditions, much of the water ebbing from the inner basin was retained in the outer basin and



returned on the following flood. Afternoon southwesterly sea breezes were a major factor regulating tidal flushing of phytoplankton from the inner basin. These winds, often daily in occurrence, dispersed phytoplankton patches within the inner basin, and pushed surface waters through the mouth (breachway) of the inner basin into the outer cove. There, the water parcels continued to flow northwards toward the tidal channel connecting the Pettaquamscutt River with Narragansett Bay. Northward displacement of surface waters from the relatively unprotected outer basin occurred frequently during the summer, and led to a net loss of biomass from the cove system.

The magnitude, direction and timing of chlorophyll fluxes between cove basins were strongly related to the diel cycle of wind stress and its interaction with the tidal cycle. The difference between exports of chlorophyll during the afternoon and late-night ebb tides illustrates the extremes in tidal fluxes of phytoplankton between basins. Over 90 percent of the chlorophyll from the inner cove left during the five hour interval between 1400 and 1900 hr on 6 July.

A conspicuous feature accompanying the persistent dinoflagellate blooms in Pettaquamscutt Cove was revealed by the diel study: the net export of silicate, phosphate, freshwater and phytoplankton biomass from the inner to outer basin, and net import of inorganic nitrogen into the inner basin. Following their accretion from freshwater sources, silicate and phosphate were passively flushed from the system by tidal action. In contrast, nitrogen pulsed into the cove was taken up by the resident dinoflagellate population. A proportion of this, as particulate nitrogen, was actively washed-out by factors affecting the removal of cells. Fluxes of silicate and phosphate were coupled to freshwater movements through the cove, although this coupling was neither direct, nor simple. Silicate served as a useful water tracer. Since diatoms, unexpectedly, were not an important component within the inner basin, their uptake of silicate there was minimal. Silicate entering this cove was therefore flushed through as a conservative tracer. Extrapolation of an estuarine mixing line for silicate to 0% indicates incoming brook and groundwater would contain up to  $600 \mu\text{g} \cdot \text{at} \ell^{-1}$ ; measured concentrations were approximately  $200 \mu\text{g} \cdot \text{at} \ell^{-1}$ . Silicate levels in water exiting the inner cove on ebbing tides considerably exceeded (by 2-3 fold) predicted levels, based both on the volume of freshwater remaining within the inner cove and on the concentrations measured in brook and ground waters. This discrepancy suggests that nutrient

levels in the runoff entering the cove following the rainfall event of 3-5 July were considerably higher than those measured during the diel experiment on 6-7 July. Valiela *et al.* (1978) estimated the amount of freshwater and groundwater passing through the Sippewissett Marsh system from changes in salinity. Our results indicate such analyses can give misleading results in systems where transient events introduce disproportionate amounts of nutrients in short time intervals.

It seems unlikely that groundwater accounted for the short-term differences in nutrient fluxes in Pettaquamscutt Cove, although groundwater nutrient fluxes may dominate overall fluxes in estuarine or coastal systems (Johannes, 1980), including other Rhode Island coastal lagoons (Nowicki and Nixon, 1985). Our nutrient analyses of the two groundwater springs accessible through the Pettaquamscutt salt marsh (Table 4) differ considerably from Nowicki and Nixon's (1985) groundwater analyses ( $n=150$  drinking wells) surrounding Rhode Island coastal lagoons. Their mean value of about  $200 \mu\text{M NO}_3$  was about 3-to 13-fold higher than the 16 to  $70 \mu\text{M}$  range found by us; whereas they did not detect  $\text{PO}_4$ , we measured from about 4 to  $7 \mu\text{M PO}_4$ . The salinity values of 2 to 4.0‰ in our samples suggest, however, partial contamination by saline waters.

Significant freshwater levels of inorganic nitrogen, notably  $\text{NO}_3$ , are present in Crying Brook, which flows into the innermost region of the inner basin. Groundwater levels of nitrogen are also relatively high. Rhode Island coastal lagoons generally are recipients of significant groundwater flow, with  $\text{NO}_3$  accretion in this flow representing 70 to 90% of the total nitrogen loading into six coastal lagoons (Lee and Olsen, 1985). Thus, freshwater delivery of  $\text{NO}_3\text{-N}$  into inner Pettaquamscutt Cove represents a significant source of nitrogen for phytoplankton growth. Dissolved inorganic nitrogen concentrations within the inner cove, however, are low throughout the summer (Tomas and Smayda, in prep.). Elevated nitrogen levels are generally confined to the area in, or near the mouth of Crying Brook, i. e., the region of the most extensive dinoflagellate blooms. Inorganic nitrogen entering the inner cove via brooks and groundwater apparently is utilized within a few meters of the accretion sites (Tomas and Smayda, in prep.), and partially accounts for the luxuriant dinoflagellate growth and high biomass.

Phytoplankton chlorophyll levels in other Rhode Island coastal lagoons during the summer generally

average 3 to 5 mg m<sup>-3</sup> (Lee and Olsen, 1985), in contrast to the maximum of 56.9 mg m<sup>-3</sup> measured during the diel study. This further indicates the uniqueness of Pettaquamscutt Cove, relative to other Rhode Island coastal lagoons, in terms of persistent dinoflagellate blooms of high biomass level. This luxuriant growth, facilitated by accreted NO<sub>3</sub> from freshwater inputs, is further supported by the diel fluxes of inorganic nitrogen (NH<sub>4</sub>) accompanying flooding tides. This is clearly indicated by the mass balance calculations revealing a net import of NH<sub>4</sub> during the diel study, in contrast to the diel export of SiO<sub>3</sub>, PO<sub>4</sub> and chlorophyll. The muddy sediments of Pettaquamscutt Cove undoubtedly release remineralized NH<sub>4</sub> (rates were not measured) similar to other Rhode Island coastal lagoons (Nowicki and Nixon, 1985). Despite these freshwater sedimentary and tidal sources of inorganic nitrogen, their supply of nitrogen is inadequate to support the dinoflagellate populations within the inner basin. This is clearly demonstrated by the result that the inner basin was a net importer (=sink) of nitrogen during the diel cycle. That is, inorganic nitrogen was the limiting nutrient regulating dinoflagellate growth in the inner basin. This contrasts with Potter Pond, another shallow (mean depth = 0.68 m) Rhode Island coastal lagoon which Nowicki and Nixon (1985) concluded might be phosphorus-limited rather than nitrogen-limited. This situation in Potter Pond appears to reflect a large input there of groundwater having high NO<sub>3</sub> and low PO<sub>4</sub> concentrations, and low PO<sub>4</sub> release rates from ubiquitous sandy sediments.

We did not establish the extent to which nitrogen was exchanged between the *Spartina* salt marsh fringing Pettaquamscutt Cove and cove waters. Valiela *et al.* (1978) found a net uptake of inorganic nitrogen by salt marsh plants during the early summer in nearby Sippewissett Marsh (Massachusetts). The Sippewissett Marsh and Pettaquamscutt Cove systems, however, differ in that the dinoflagellate populations resident within Pettaquamscutt Cove were sufficiently abundant to take up added nitrogen fully, and thereby outcompete the surrounding marsh for nutrient. A general coupling occurred between the magnitude, timing and direction of flow and the nutrient and dinoflagellate concentrations during the semi-diurnal tidal cycles, with the difference that SiO<sub>3</sub>, PO<sub>4</sub> and dinoflagellate concentrations were higher in ebbing waters and NH<sub>4</sub> concentrations in flooding waters. These nutrient dynamics contrast with those in nearby Bissels Cove, a small, shallow (0.45-0.85m) tidal inlet

of Narragansett Bay surrounded by a salt marsh (Nixon and Oviatt, 1973; Nixon *et al.*, 1976). Diel studies of productivity, metabolism and nutrient dynamics were made on four occasions after cutting off tidal exchange with Narragansett Bay. There was little diel change in NH<sub>4</sub>, NO<sub>3</sub>, PO<sub>4</sub> and SiO<sub>3</sub> concentrations (particularly in inorganic nitrogen) despite high rates of production and respiration. The inorganic nutrients appeared to cycle primarily within the sediment-detritus system on the cove bottom, suggesting little export of inorganic nutrients occurs during tidal exchanges with Narragansett Bay. Dinoflagellate blooms similar to Pettaquamscutt Cove were not reported. The diel patterns in Pettaquamscutt Cove also contrast with results from a sub-tropical lagoon-San Quentin Bay, Mexico (Lara-Lara *et al.*, 1980). The ebb- and flood-flow mean levels of inorganic nutrients and phytoplankton did not differ in twice-daily measurements made over an 18-day period. In another Mexican lagoonal system, the Barrier Island lagoons of the Gulf of California, an even more divergent result was reported (Gilmartin and Revelante, 1978). There, positive correlations occurred between lagoonal flushing rates and PO<sub>4</sub> concentrations, chlorophyll biomass, and primary production, i. e., increased flushing stimulated phytoplankton dynamics rather than diluted output via wash-out. Gilmartin and Revelante suggested that this provocative finding was somehow related to the nutrient-trapping properties of this lagoonal system and/or eutrophication.

The presence of extensive dinoflagellate populations in inner Pettaquamscutt Cove also represents a constant (and exportable) sink for nutrients. Although such blooms dampen diel fluctuations, the observed diel fluctuations in nutrient levels were strongly in phase with tidal water movements. The low N/P ratios of inorganic nutrients within the cove and diel nitrogen import strongly indicate that the resident dinoflagellate populations were nitrogen-limited, if not stressed. Whether utilized by dinoflagellates, *Spartina* or benthic algae, any nitrogen entering the inner cove is rapidly removed from the soluble inorganic pool (Tomas, Smayda and Furnas, in prep.) and converted into particulate nitrogen, a variable proportion of which is subsequently advected as particles into the outer basin. Thus, a complex nutrient pump exists within Pettaquamscutt Cove. The inner basin exports dissolved inorganic PO<sub>4</sub> and SiO<sub>3</sub> into the outer basin where it is available to other trophic levels. The outer basin, in contrast, exports remineralized NH<sub>4</sub> into the inner basin which, combined with accreted NO<sub>3</sub> from

freshwater inputs and recycled  $\text{NH}_4$  from the sediments, supports the persistent dinoflagellate blooms. Given the high silicate and phosphate levels; the expected rapid inorganic nitrogen turnover, and the irradiance, temperature and mixing characteristics, it is remarkable that diatoms are so unimportant. Their relative insignificance in the inner basin compared to dinoflagellates is reflected in a regional survey undertaken on 3 July. A progressive 10-fold increase in abundance of *Skeletonema costatum* from 113 to 1238 cells  $\text{ml}^{-1}$  occurred in the outer basin along a 600m gradient of four stations sampled between the breachway separating the basins and the island situated in the northwest edge of the outer cove (Fig. 1). In contrast, inner cove populations ranged from 73 to 113 cells  $\text{ml}^{-1}$ . Thus, an unresolved aspect of the unique dinoflagellate blooms characterizing Pettaquamscutt Cove is the cause of the apparent repression of diatom growth. It is unknown whether *Glenodinium uncatenum*, *Scrippsiella trochoidea*, *Gymnodinium simplex* and *Cochlodinium heterolobatum* are simply outcompeting *Skeletonema costatum*, for example; whether the dinoflagellates are secreting substances inhibitory to diatom growth (Iwasaki, 1979), or whether substances associated with freshwater runoff have water quality effects consequential to the competition between dinoflagellates and diatoms within Pettaquamscutt Cove.

Finally, these admittedly incomplete diel observations illustrate some basic features of nutrient phytoplankton fluxes and dynamics within the Pettaquamscutt Cove system. In common with other salt marsh and small estuarine systems (Chrzanowski *et al.*, 1982), long-term (weeks to months) fluxes of nutrients and biomass are the summation of many short term or transient events (hours to days) affecting individual nutrient or biomass levels and species dynamics.

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