

PERSISTENT DINOFLAGELLATE BLOOMS IN A SMALL MARINE COVE.

I. EFFECT OF WIND AND TIDAL CURRENTS

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ABSTRACT: Dense, multi-specific blooms of dinoflagellates persist year-round within Pettaquamscutt Cove, Rhode Island, U.S.A., a shallow embayment with a large tidal prism. Drogue tracking suggests that the retention of dinoflagellate patches (*Gyrodinium aureolum* and *Gymnodinium simplex*) during July is largely related to lateral mixing processes and exchange. Washout of dinoflagellate patches by tidal flushing is minimized by division of Pettaquamscutt Cove into an inner and outer basin, in which tidal prisms represent 46 and 55% of the high tide volumes, respectively. Surface water movements within the inner basin are largely controlled by winds; whereas in the outer basin both winds and tides contribute to circulation. The outer basin, under certain conditions, buffers tidal flushing losses of dinoflagellates from the more densely populated inner basin. During periods of strong, summer sea breezes from the southwest, irregularities in the shoreline and lee shores shelter bloom patches and further protect against their displacement from the cove. Application of Ketchum's model suggests that the dinoflagellate populations either are growing much more rapidly than expected from culture experiments and/or retention mechanisms are particularly well established in Pettaquamscutt Cove, and compensate for expected population washout rates through tidal flushing. The observations support the notion that the development and persistence of dinoflagellate blooms within small embayments are strongly determined by physical and chemical features specific to each embayment.

Introduction

Dense blooms of dinoflagellates and other flagellates commonly occur in coastal embayments (Pomeroy et al., 1956; Seliger et al., 1970; 1971; Taylor and Seliger, 1979; Anderson et al., 1982; Yoshida and Numata, 1982). Their development and persistence have been related both to conditions favoring rapid growth (Ragotzkie and Pomeroy, 1957) and to physical and biological processes enhancing the retention of motile cells and cysts within such embayments (Seliger et al., 1970; 1982; Tyler et al., 1982).

Ketchum (1954) modeled the interactions between plankton growth rates and their losses due to tidal flushing, processes which influence the retention of planktonic populations within estuaries. Below a critical growth rate,

populations inevitably will be flushed out; higher growth rates allow the populations to persist or even increase. Winds also influence water movements and the spatial distribution, retention and dissipation of plankton populations in shallow, enclosed waters (Ragotzkie and Bryson, 1953; Weisberg, 1976; Yoshida and Numata, 1982).

For two years, we followed the dynamics of dense, multispecific dinoflagellate blooms in Pettaquamscutt Cove, Rhode Island, U.S.A. (41°26.5'N, 71°28'W), a shallow, enclosed embayment near the mouth of Narragansett Bay (Fig. 1). Pettaquamscutt Cove is the southern arm of the Pettaquamscutt River, a drowned glacial valley connected by a narrow tidal channel to Narragansett Bay. This report evaluates the effects of winds and tides on water movements within this cove, and the influence of these

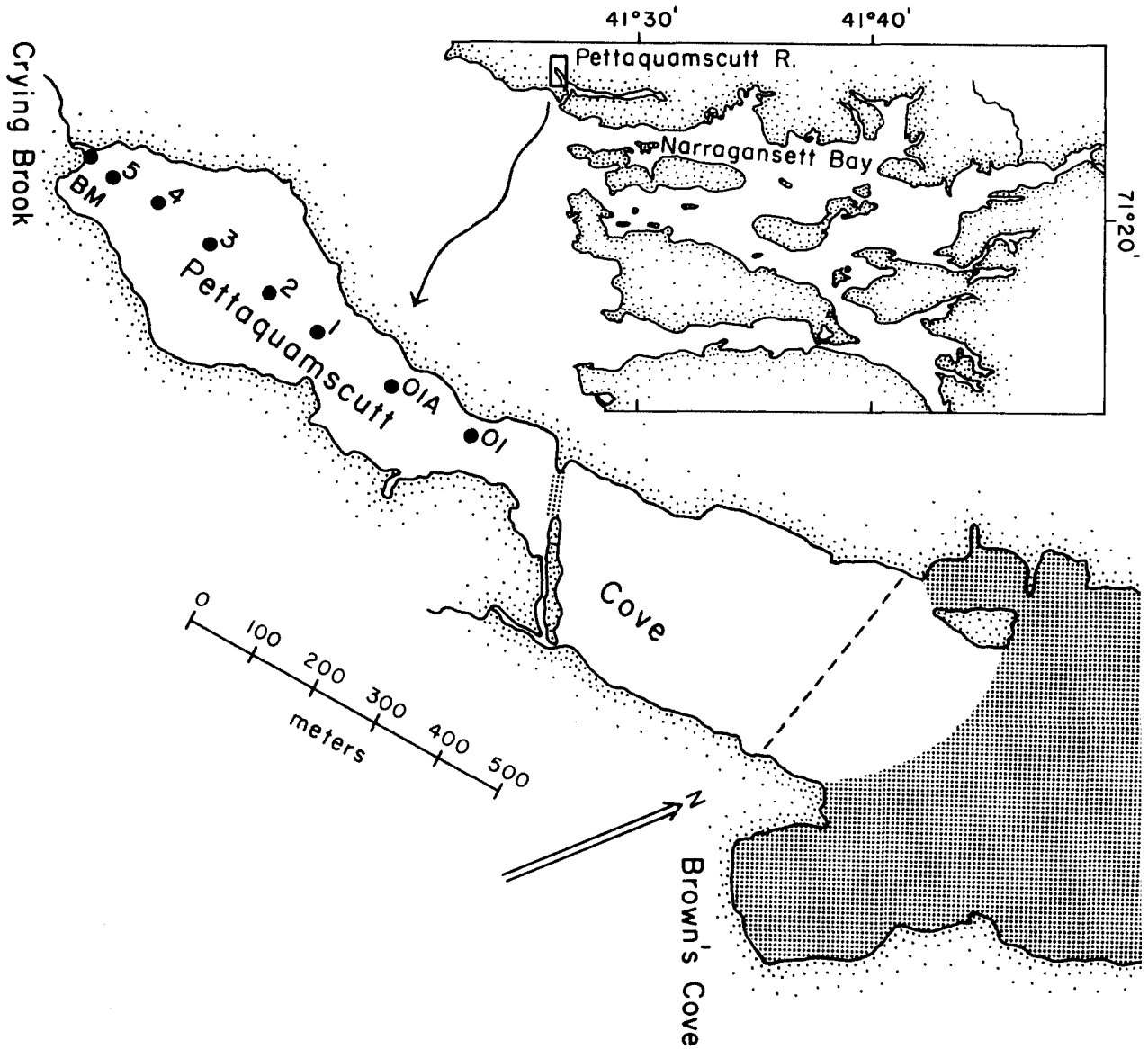


Figure 1. Pettaquamscutt Cove. Shaded areas show sill location separating inner and outer basins, and depict tidal area in outer basin separating it from the main tidal channel of Pettaquamscutt River; dashed line in outer cove locates bathymetric transect.

circulation patterns on the blooms, retention and spatial distribution of dinoflagellates. A diel study on the influence of tidal movements on fluxing of nutrients and

dinoflagellate populations in this small cove is evaluated by Furnas et al. (1989).

Materials and Methods

Bathymetric Mapping

Charts of Pettaquamscutt Cove were prepared from plat maps obtained from the towns of Narragansett and South Kingstown, Rhode Island. Ten bathymetric transects were established across the cove; nine within the inner basin, and one within the outer basin (Fig. 1). Stout, dacron twine graduated at 5 or 10 m intervals was stretched across the cove along each transect line. Two observers moved along each line in a small boat, measured the depth at each graduated mark with a meter stick, and noted the time. A third observer recorded tidal height versus time from a tide staff located within the cove. Tidal height on the staff was arbitrary and not leveled to an official datum. Additional depth measurements were made randomly throughout the outer basin during drogue studies. The positions of these depth measurements were determined with a sextant by measuring two adjacent angles between landmarks.

Depth measurements were corrected for tidal height at the time of measurement using the lowest observed tidal height as the reference level. Isobaths within the inner basin were contoured by linear interpolation. The outer basin has a flat bottom of nearly constant depth to within 10 m of the shore on all sides; therefore, it was not contoured. Total cove area and areas between isobaths were determined by the "cut-and-weigh" method. A *Spartina* saltmarsh lines the cove around most of its perimeter. The marsh edge is essentially vertical to depths below the reference tide level; thus, water volume changes in the cove could be computed by multiplying the total area of the cove by the change in tidal height.

Drogue Studies

Near-surface water movements were traced by drogues made from brightly colored latex balloons filled with fresh water (Nixon et al., 1980). The drogue-balloons floated at the water surface, with less than 1 cm projecting above the water line. Depending upon their size and shape, the drogues had drafts between 6 and 20 cm. Drogues made with heavy duty "punch" balloons were more durable than those made from "party" balloons; the latter eventually ruptured spontaneously after immersion.

To aid in their location, drogues were deployed in groups of two to four and followed by small boats. Two or three groups of drogues were generally followed at one

time. Each group (or individual drogue, if the group diverged) was gently approached and its position determined by taking bearings with a hand-held compass, or by measuring two adjacent angles between shoreline landmarks with a sextant.

Wind speed and direction in Pettaquamscutt Cove were noted throughout the day. Wind velocities inside the cove were either estimated by the observers, or measured with a hand-held wind speed gauge. A continuous record of wind speed and direction was obtained at a south-facing site 9 km north of the Pettaquamscutt Cove. Wind velocity measurements were also obtained twice daily from a wind-mill tower located 300 m east of Pettaquamscutt Cove.

Water Column Observations

At eight stations located along a 700 m transect within the inner basin, temperature, salinity and dinoflagellate abundance were measured (Fig. 1). Three depths were routinely sampled by water bottle at stations 1-5; surface samples only were collected at stations 01, 01A and BM (= mouth of Crying Brook). The surface sample (indicated as T in the Tables) was collected between the surface and 0.1 m. The depths of the mid- (M) and bottom (B) samples varied with tidal conditions in this shallow cove. The collection depths of the mid-depth samples varied from 0.25 to 0.55 m; the bottom samples from 0.51 to 1.1 m. Maximum recorded depths at these stations were about 1.1 m.

Dinoflagellates were counted live using a Sedgwick Rafter chamber. Details of the physical, chemical and biological investigations will be given in Tomas and Smayda (In prep.).

Results

Bathymetry and Tidal Prism

Fig. 1 is a map of Pettaquamscutt Cove. A broad, shallow tidal flat to the north of Pettaquamscutt Cove separates this cove from the main body of the Pettaquamscutt River and its tidal outlet. The cove is divided into inner and outer basins by an abandoned railroad causeway. Flow between these basins is largely restricted to the narrow (~70 m wide), shallow breach through this causeway, and primarily through a small opening at the eastern end of this channel. Low tide depths across much of the breach were approximately 10 cm, with a maximum depth of about 35 cm.

At low tide, virtually the entire inner basin is less than

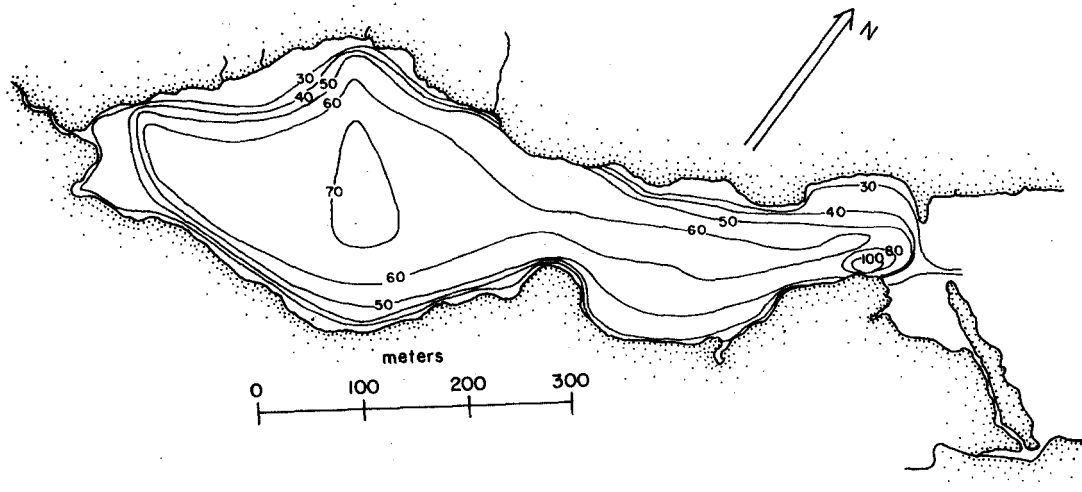


Figure 2. Bathymetric map of the inner basin. Depth contours are in centimeters relative to the reference tide level.

Table 1. Hypsometric data for the inner basin of Pettaquamscutt Cove at the reference tide level. Percentages are rounded to the nearest tenth

Depth Interval	Area $\text{m}^2 \times 10^4$	% of total	Volume $\text{m}^3 \times 10^4$	% of total
> 70 cm	0.62	4.7	0.44	6.7
70-60	4.38	33.5	2.81	43.0
60-50	3.41	26.1	1.88	28.7
50-40	1.47	11.2	0.66	10.1
40-30	1.35	10.3	0.47	7.2
< 30	1.86	14.2	0.28	4.3
Total	13.09		6.54	

1 m deep; depths greater than 1 m were found only in the channel just inside the causeway (Fig. 2). The maximum observed depth was 1.8 m. Hypsometric data for the inner basin are summarized in Table 1.

The outer basin is characterized by fairly steep slopes on all sides and a flat bottom (Fig. 3). The mean depth of the outer basin soundings (adjusted to the reference tide level) was $0.64 \pm .08$ m.

Pettaquamscutt Cove has an overall area of $2.69 \times 10^5 \text{ m}^2$ (~27 hectares), of which the outer basin comprises 52 percent. At the reference low tide level, the water volume of the inner and outer basins is 6.43 and $8.94 \times 10^4 \text{ m}^3$, respectively. The tidal prism volumes for the inner and outer basins at the maximum observed tidal

range of 55 cm are $7.04 \times 10^4 \text{ m}^3$ and $7.74 \times 10^4 \text{ m}^3$, respectively. These tidal volumes correspond to 52 and 46 percent of the respective high tide volumes. Tidal prism volume of the inner basin is 91 percent of the outer basin prism volume.

Temperature and Salinity Distributions

Temperature and salinity distributions at the 8 stations along the 700 m transect in the inner basin were determined on five occasions between 30 June and 28 July 1981 (Table 2). Measurements on 30 June and 20 July were made during high tide conditions; during a mid-flood tide on 14 July; a mid-ebbing tide on 28 July and during a low tide on 8 July. The salinity gradients generally

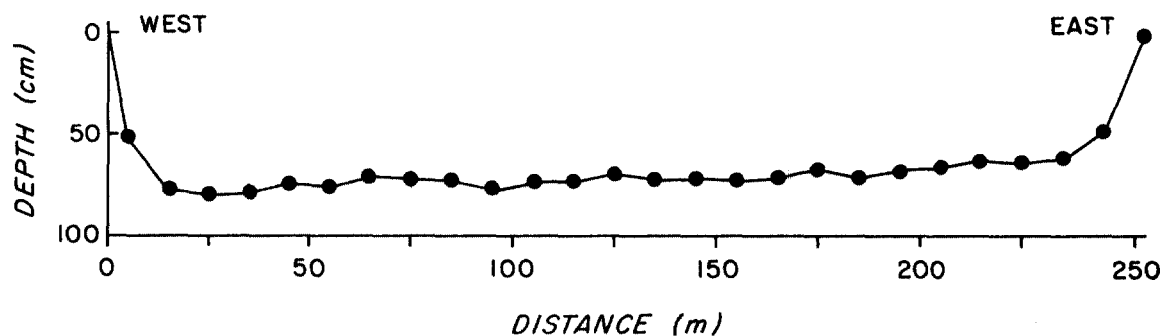


Figure 3. Depth profile across the outer basin of Pettaquamscutt Cove at transect location shown in Fig. 1.

Table 2. Temperature and salinity conditions in inner Pettaquamscutt Cove between 30 June and 28 July 1981. T, M, B = surface, mid and bottom depths, respectively. BM = Crying Brook mouth. Location of stations shown in Figure 1

Time:	1000		0930		0940		1004		0913	
	30 June		8 July		14 July		20 July		28 July	
Sta.	°C	S ‰	°C	S ‰	°C	S ‰	°C	S ‰	°C	S ‰
01	23.0	29.0	27.5	28.0	24.5	29.0	28.0	30.0	25.0	29.0
01A	23.5	29.0	27.5	28.0	26.0	29.0	28.0	30.0	25.0	29.0
1T	23.5	29.0	27.8	28.0	26.5	29.0	28.0	30.0	25.0	28.0
M	23.0	29.0	28.0	28.0	26.0	29.0	27.5	30.0	24.8	28.0
B	22.0	29.0	28.0	28.0	25.8	29.0	27.5	30.0	24.8	29.0
2T	22.5	29.0	27.2	28.0	26.5	28.0	28.0	30.0	25.0	25.0
M	22.5	29.0	27.2	28.0	26.0	29.0	28.0	30.0	25.2	25.2
B	22.5	29.0	28.2	28.0	26.0	28.0	27.5	30.0	25.2	25.2
3T	23.5	29.0	27.5	28.0	26.8	28.0	28.0	30.0	25.5	25.5
M	23.0	29.0	27.5	28.0	26.5	28.0	28.0	30.0	25.5	25.5
B	23.5	29.0	28.5	28.0	26.2	28.0	27.5	30.0	26.0	26.0
4T	23.5	29.0	28.0	28.0	26.0	28.0	28.0	30.0	25.5	25.5
M	23.0	29.0	28.0	28.0	26.2	28.0	28.0	30.0	25.8	25.8
B	23.0	29.0	27.5	28.0	26.2	28.0	27.5	30.0	26.0	26.0
5T	24.0	29.0	28.0	28.0	26.5	28.0	27.5	28.5	26.0	26.0
M	23.5	29.0	28.0	28.0	26.5	28.0	28.0	30.0	26.0	26.0
B	23.5	29.0	28.0	28.0	26.5	28.0	28.0	30.0	26.0	26.0
BM	21.0	24.0	28.5	22.0	26.0	26.0	26.0	28.5	22.0	8.0

reflected these tidal conditions. The significant features of the temperature and salinity distributions are the generally well-mixed waters of the inner basin, and the responsiveness of this shallow basin to solar irradiance. For example, inner basin temperatures increased 4° to 5°C

throughout the water column over the 8-day sampling period from 30 June to 8 July, then decreased about 1.5°–2°C during the following 6 days.

Drogue Studies

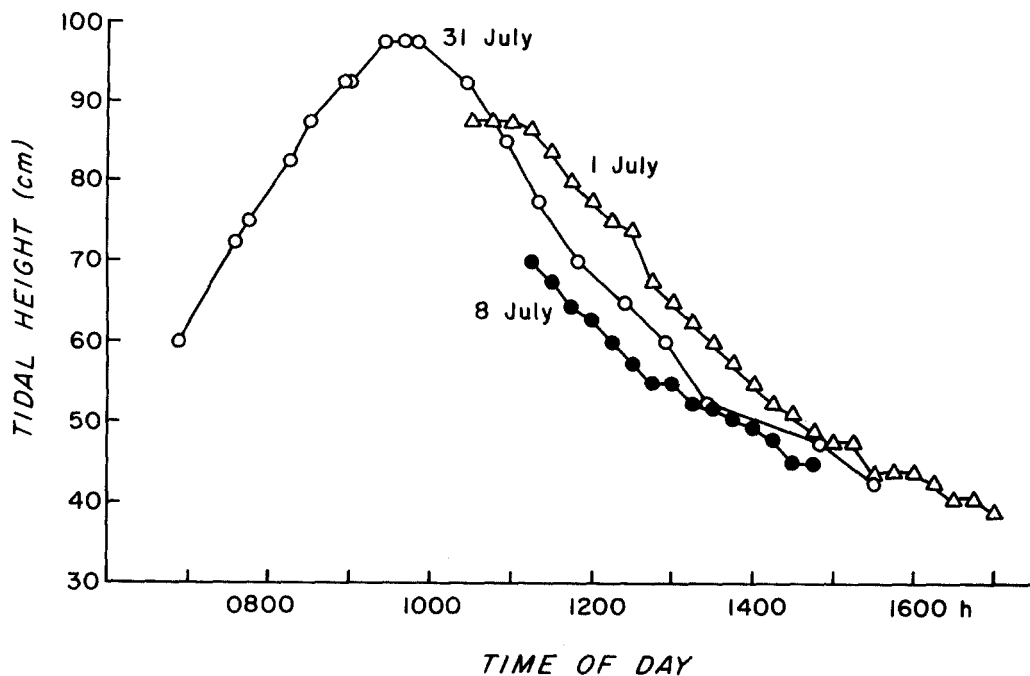


Figure 4. Tidal height vs. time of day during three drogue experiments.

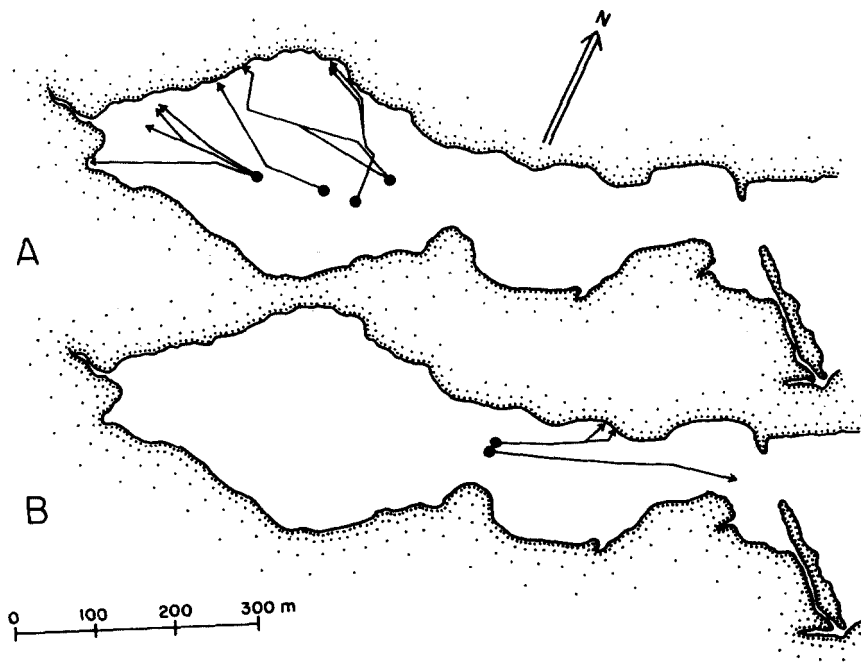


Figure 5. Drogue movements within the inner basin during easterly (A) and southwesterly (B) winds. Dark circles indicate launch points.

Three drogue experiments were carried out during July 1981 under various wind and tidal conditions. Experiments 1 and 2 in the inner Pettaquamscutt Cove were conducted on ebb tides (Fig. 4) ; drogue experiment 3 was carried out in the outer basin during both flood and ebb tides. During the 1 July experiment, winds blew steadily from the east at approximately 10 m sec^{-1} and intensified somewhat during the afternoon. During the second experiment on 3 July, southeasterly winds predominated; velocities increased from $5\text{--}10 \text{ m sec}^{-1}$ during the morning to $10\text{--}20 \text{ m sec}^{-1}$ during the afternoon as a southwesterly sea breeze developed. In both ebb tide experiments within the inner basin, the drogues moved before the wind regardless of stage of the tidal flow (Fig. 5). With the wind coming from the east, the drogues moved to the head of the cove and grounded against the western shore (Fig. 5A). With southwesterly winds, the drogues moved toward the causeway (Fig. 5B). Drogue velocities between position fixes generally were between 2 to 10 cm sec^{-1} (Fig. 6) ; the maximum velocity was 27 cm sec^{-1} . Drogues entrained in the outgoing flow accelerated near the causeway constricting Pettaquamscutt Cove into its inner and outer basins (Fig. 1), particularly before a southerly wind.

In Experiment 3 in the outer basin (31 July), drogues were deployed on both incoming and outgoing tides. A dead calm prevailed during early morning, followed by stiff ($10\text{--}15 \text{ m sec}^{-1}$) southeasterly winds during late morning and early afternoon. During late afternoon the winds shifted to the southwest, and blew down the main axis of the cove at $10\text{--}20 \text{ m sec}^{-1}$. Drogues moved in response to both winds and tides. During still morning air and flooding tide, surface water from virtually the entire outer basin area flowed into the inner basin (Fig. 7A). Drogue velocities in this flow averaged nearly 8 cm sec^{-1} . Drogues deployed in the northeast corner of the outer basin initially drifted toward, then eastward along the causeway, then ended up in the southeast corner of the outer basin where a dense dinoflagellate patch was observed. During this experiment, incoming drogues penetrated less than a fifth of the length of the inner basin.

During the ebbing tide experiments, with easterly (Fig. 7B) and southeasterly (Fig. 7C) winds, water flowed outwards along the western shore of the outer basin. Drogues entrained within this flow moved against, or across the prevailing wind (Fig. 7B). The outward movement of these drogues slowed considerably when moving against the

wind; eventually, they grounded against the western shore.

Drogues released in the center of the outer basin during moderate southeasterly winds ($8\text{--}5 \text{ m sec}^{-1}$) moved westward initially, parallel to the causeway and toward the breachway (Fig. 7C). These southerly winds intensified during the afternoon ($10\text{--}20 \text{ m sec}^{-1}$), but water continued to flow northward along the western shore (Fig. 7D). Drogues deployed in the southeast corner and along the eastern bank at that time (Figs. 7C, D) moved directly across the outer basin, then entered the outgoing flow along the western shore.

Drogues deployed along the eastern shore during strong southwesterly winds (Fig. 7E) moved parallel to the shore, then exited Pettaquamscutt Cove over the shallow flats north of the outer basin. Concurrent observations of flotsam and dinoflagellate patch movements suggested that virtually all of the surface water in the outer basin was displaced northward by the wind. Dinoflagellate patches emanating from the inner basin and the southeast corner of the outer basin moved northward along both sides of the outer cove.

Most wind-driven and tidal current velocities in the outer basin ranged from $4\text{--}10 \text{ cm sec}^{-1}$ (Fig. 6). Maximum velocities between successive positions in the individual experiments ranged between 8 and 33 cm sec^{-1} . At these velocities, dinoflagellate patches and drogues could move across either the inner or outer basin within 2-4 hours.

Distribution of Dinoflagellate Patches

Dinoflagellate blooms occur in Pettaquamscutt Cove from mid-June through November (Tomas and Smayda, in prep.), a period when a variety of wind regimes affect water movements and the entrained dinoflagellate populations. Throughout the summer, a stiff ($10\text{--}20 \text{ m sec}^{-1}$) west-southwesterly sea breeze commonly develops in the early afternoon and blows directly down the major axis of the cove. Summer winds during late-night and early-morning are generally light and variable in direction. During autumn (mid-September to November), winds from the northwest become increasingly important. However, Pettaquamscutt Cove is sheltered from direct northwesterly winds by a ridge line which runs parallel to the major axis of the cove along its western shore. Summer and fall storms are often characterized by strong ($> 20 \text{ m sec}^{-1}$) northeasterly, easterly or southeasterly winds.

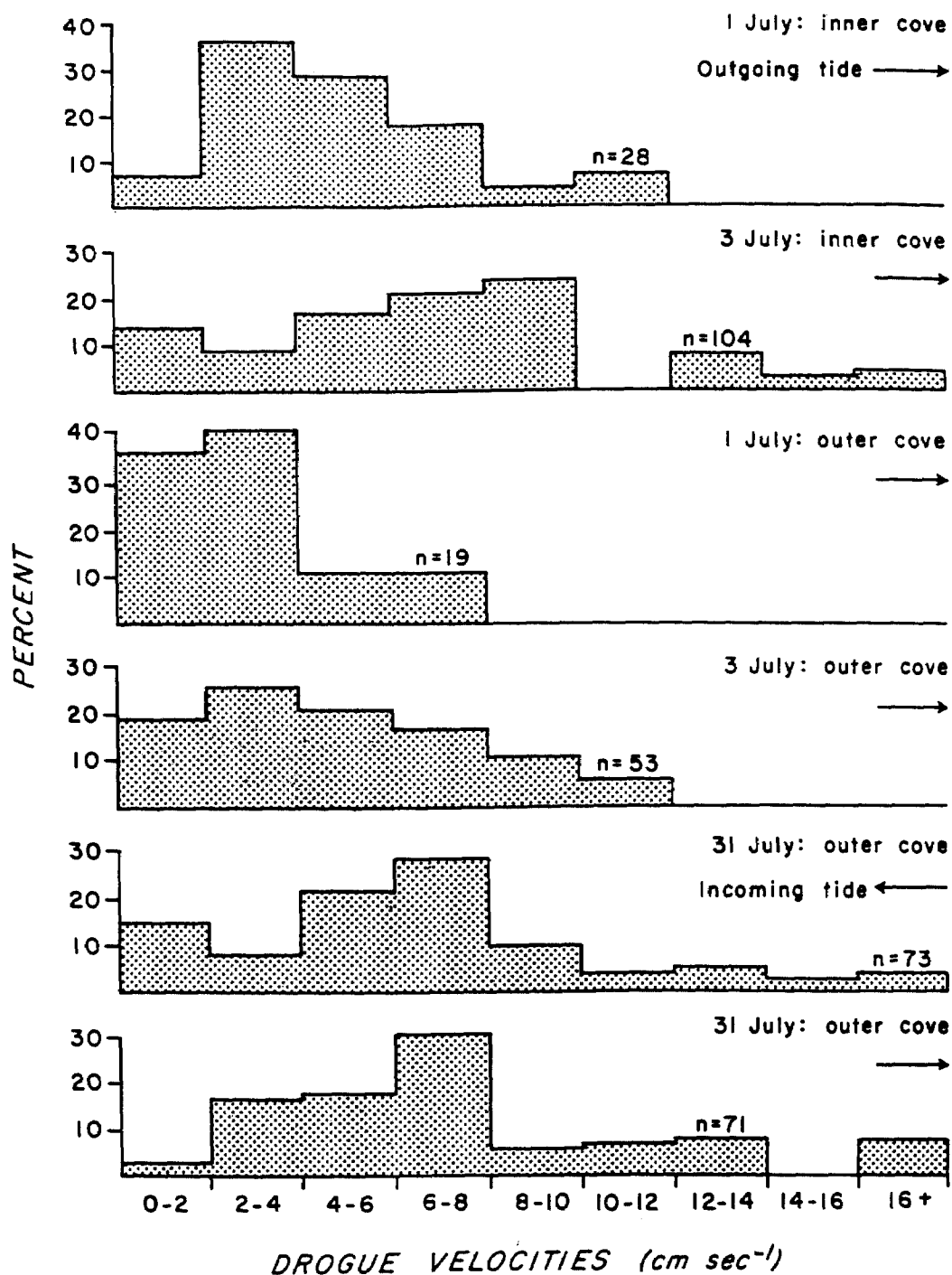


Figure 6. Frequency distribution of drogue velocities measured in the inner and outer basins during drogue experiments. Velocities are 0-2, 2.1-4 cm sec^{-1} , etc.

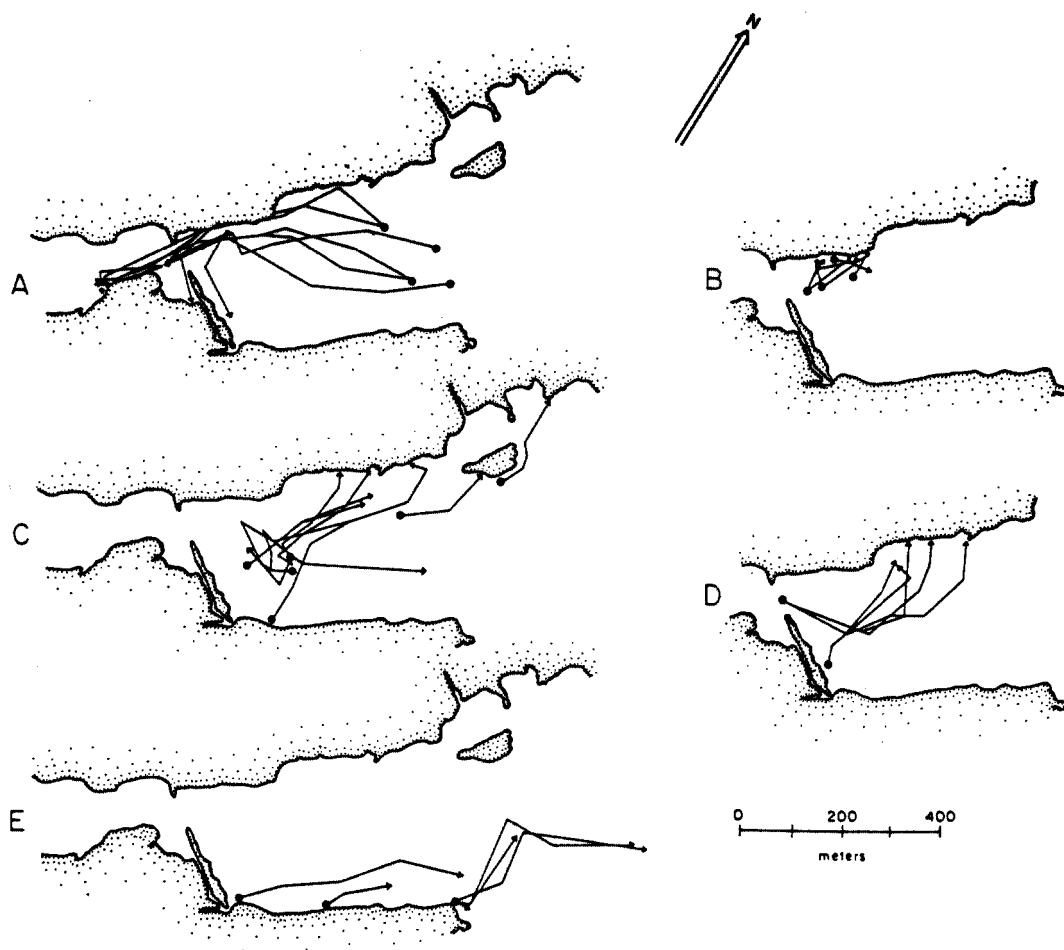


Figure 7. Drogue movements within the outer basin during: A. Still air and incoming tide; B. Easterly winds, outgoing tide; C. Southeasterly winds, outgoing tide; D. Southeasterly winds, outgoing tide, and E. Southwesterly winds, outgoing tide. Dark circles indicate launch points.

Visibly distinct patches of dinoflagellates were observed frequently throughout Pettaquamscutt Cove during the drogue experiments. *Gyrodinium uncatenum* was the predominant species, with secondary blooms of *Gymnodinium simplex* (Table 3). The largest, densest patches consistently occurred along the southern and southeastern shorelines of the inner and outer basins (Fig. 8), particularly at the head of the inner basin. Raised banks or borders of trees lay along, or close to these shorelines. During southwesterly sea breezes, patches were also found behind irregularities in the shoreline and in small embayments along the eastern side of the inner cove (Fig. 8).

More quantitative features of the horizontal and vertical patterns in distribution and abundance of the dinoflagellates are presented in Table 3. On 30 June, the day before the first drogue experiment, the surface abundance of *Gyrodinium uncatenum* was maximal ($13,756 \text{ cells ml}^{-1}$) near the breachway at station 01 (Fig. 1), progressively decreased (by circa 10-fold) along the transect towards mid inner basin (station 3), then increased within the innermost region ($7,220 \text{ cells ml}^{-1}$) at station 5. The vertical distributions indicate that *Glenodinium* was more or less homogeneously distributed within the water column, although mid-depth populations tended to be lower

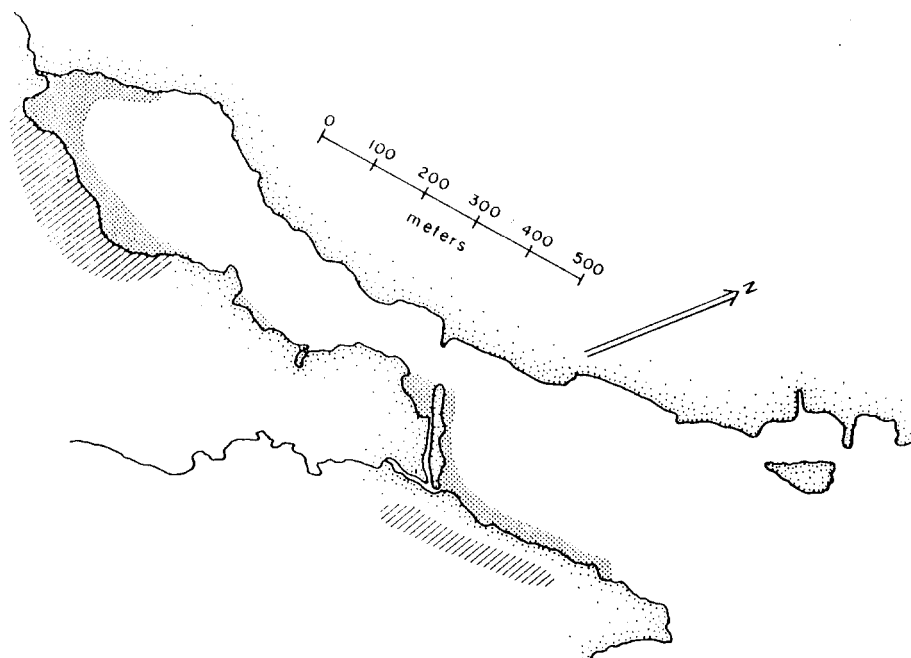


Figure 8. Region within Pettaquamscutt Cove where dense dinoflagellate patches consistently were found. Hatched areas indicate where shoreline banks and trees closely about the cove.

than surface and bottom levels. The surface populations of *Glenodinium* on 20 July, also sampled during high tide, ranged from about 11,000 to 18,000 cells ml^{-1} , significant increases over 30 June levels. *Gyrodinium* abundance progressively increased from the inner (station 5) to outer regions of the inner basin, with maximal abundance at station 2. In contrast, *Gymnodinium simplex* formed a distinct patch at stations 3 and 4, where its abundance equalled that of *Gyrodinium uncatenum*.

The ratios of surface abundance of *Gyrodinium uncatenum* at stations 01 and 5 on the two sampling dates were 1.9:1 and 1.6:1, respectively. On 14 July, sampled during mid-flood tide, this ratio was 1:1. An enormous concentration (68,839 cells ml^{-1}) of *Gyrodinium uncatenum* then occurred in the bottom water at station 5, located innermost near the mouth of Crying Brook; significant concentrations were also present at stations 3 and 4. *Gyrodinium* exhibited a marked vertical zonation at station 5, the population increasing significantly with depth. This trend in vertical distribution progressively weakened at stations 3 and 4, and was reversed at station 2 where the surface population (11,576 cells ml^{-1}) was about

twice that in the bottom layer.

These distributional patterns differed from those exhibited by *Gymnodinium simplex*, which became abundant on 14 July. Absent at the surface, it progressively increased to maximal abundance (ca. 1,000 to 3,000 cells ml^{-1}) in the bottom layers throughout the inner basin. It was most abundant in the innermost region.

The distribution and abundance of *Gyrodinium uncatenum* and *Gymnodinium simplex* on 30 June and 20 July indicate that their behavioral (= phototactic) properties manifested themselves despite the circulation patterns; that species-specific differences in distribution occurred, and that their distributional patterns were influenced by watermass circulation. Supporting evidence for these conclusions is available from samples collected on 8 and 28 July during a mid-ebb and low tide, respectively. The ratios of surface abundance at stations 01 and 5 were then 0.3:1 and 0.6:1, respectively. The enormous increase in *Gyrodinium uncatenum* on 8 July accompanied the 4° to 5°C increase. The aggregation of cells at stations 4 and 5, with their differing vertical zonation patterns, and their considerable reduction in abundance at station 3, where

Table 3. Cellular abundance (cells ml⁻¹) of *Gyrodinium uncatenum* and *Gymnodinium simplex*, (), in inner basin of Pettaquamscutt Cove between 30 June and 28 July 1981. T = top, M = mid and B = bottom depth

STATION:		01	01A	1	2	3	4	5
Date	Depth							
30 June	T	13756	9960	6720	7078	1350	3875	7220
	M			9954	4102	723	1210	6303
	B			10040	6742	2358	1980	6780
8 July	T	12238	5073	9140	12448	5197	53298	41127
	M			11331	15680	11061	34342	43358
	B			10859	16954	24357	30726	35827
14 July	T	13464	10002	11366	11576	12136	6855	13211
	M			9757	9512	19270	15598	47842
	B			12380	5701	18640	17871	68839
	(T)	0	0	0	0	0	0	0
	(M)			283	912	1246	1001	1513
	(B)			1580	1068	2826	2203	2158
20 July	T	17941	11086	15388	20353	13324	11716	10981
	(T)	2448	3961	2937	3093	11191	12381	1335
28 July	T	8114	6470	7685	11692	6243	39407	13289
	(T)	378	534	378	823	579	2392	312

the population increased with depth, are notable. Considerable streaking of brownish patches circa 3 m from the shoreline was evident in the innermost regions. In the 28 July samples, collected 3 days prior to last drogue experiment, maximal surface abundance of *Gyrodinium uncatenum* and *Gymnodinium simplex* occurred in the innermost region at station 4. The *Gyrodinium* populations at stations 01 to 3 decreased by about 50% since the 20 July sample collected at high tide, but increased 3.5-fold at station 4.

The phytoplankton surveys made during the July surveys indicate that maximal levels of *Gyrodinium uncatenum* invariably occurred in the innermost region of Pettaquamscutt Cove at stations 4 and 5. Both the distributional data and visual observations of surface waters also indicate that patches of this dinoflagellate were moved by tidal and wind-induced currents. The limited data available for *Gymnodinium simplex* are in agreement.

Discussion and Conclusion

Dinoflagellates are the dominant phytoplankton component within Pettaquamscutt Cove, exhibiting a distinct seasonal successional pattern over an annual cycle (Tomas and Smayda, in prep.). The unimportance of diatoms is surprising, and in sharp contrast to contiguous Narragansett Bay (Smayda, 1973) and the upper regions of the Pettaquamscutt estuary (Smayda and Miller, 1989). The deeper, permanently stratified waters of the latter region are dominated by a nanno-diatom component (*Thalassiosira*; *Cyclotella*) and (at the oxic/anoxic boundary) by the euglenid *Euglena proxima*. Thus, environmental conditions within unpolluted Pettaquamscutt Cove conspicuously favor the growth, retention and predominance of dinoflagellates.

Circulation patterns within Pettaquamscutt Cove, strongly influenced by winds and tides, clearly influence the dispersion and aggregation of the dinoflagellate populations. The effects of winds and tides on circulation patterns, however, are regionally modified by local physiography and orientation of this small (27 hectares),

shallow (< 1 m) embayment, a cul-de-sac of the Pettaquamscutt River estuary. The southern and eastern shorelines, for example, are abutted by a forested, high bank which partly shields these regions from direct wind stress. Oceanic tides entering the tidal inlet also become locally distorted due to basin geomorphology and orographic differences in winds, resulting in erratic tidal effects (Gaines, 1975). The overall consequence is that the circulation patterns and their driving forces differ between the inner and outer basins. Within the inner basin surface water circulation, based on drogue movements, is primarily wind-driven; that in the outer basin is strongly influenced by both tides and winds.

Dinoflagellat aggregated into patches within the inner cove under conditions of still or light air, or when the sheltering banks protected the cove interior against wind-induced displacement of the watermass. The densest patches consistently were found (Table 3) at the head of the inner basin close to the mouth of Crying Brook (Fig. 1), where wind stress was minimized by shoreline topography, and tidal water movements were restricted. Pronounced advection of dinoflagellates from the inner cove occurred only during periods of stiff west-southwesterly sea breezes. The innermost dinoflagellate patches were then dispersed throughout the inner basin and transported toward the breachway. A positive, selective advantage accompanied the wind-induced aggregation of dinoflagellates in the innermost region of the inner cove. They tended to accumulate near the discharge site of Crying Brook which delivered nutrients, notably NO_3 , supporting continued dinoflagellate growth (Furnas et al., 1989). Thus, their periodic physical displacement inward towards a continuous nutrient source was analogous to a nutrient-pump effect.

Surface water movements in the outer basin of Pettaquamscutt Cove, in contrast, were strongly influenced by both tides and winds. Water ebbing into the outer basin from the inner basin generally flowed northward, exiting along the western shore of the outer basin. During a flood tide, when the air was calm or when easterly winds prevailed, water flowed southward into the outer basin along the eastern shore setting up a partial, transitory clockwise gyre open at the northern end of the outer basin. Thus, a considerable volume of "new" water enters the outer basin on each flood tide. Consistent with this, dinoflagellate patches were never observed in the shallow embayment (Brown's Cove) located just outside of the causeway (Fig.

1).

Drogues and dinoflagellate patches in response to southwesterly winds moved northward within the outer basin along its eastern and western shores, the drogue moving the entire length (~ 650 m) of this basin within 2–4 hours. This velocity indicates that within one tidal cycle wind-driven currents can exchange much of the surface water volume in the outer cove. However, dinoflagellate populations were not completely washed out when southerly or southwesterly winds prevailed. Dense patches commonly occurred in the extreme shallows along the shielded southern and easterly shores, and north of the causeway where relatively deep water lies close to the shore. Regions of the cove bordered by salt marsh, small embayments and other irregularities in the shoreline also sheltered small dinoflagellate patches in their lee.

Although these variable watermass movements within Pettaquamscutt Cove pose problems of dinoflagellate washout, their retention is clearly enhanced by the segmentation of Pettaquamscutt Cove into two basins. The outer basin restricts tidal flushing losses from the more densely populated inner basin, and therefore serves both as a buffer and inoculum source. Water and phytoplankton leaving the inner basin may be retained (to a variable degree) in the outer basin and drawn back into the inner basin on the following flood tide. Thus, the circulation pattern and physiographic features of Pettaquamscutt Cove provide a physical accumulation/dispersal mechanism facilitating dinoflagellate growth in the following manner. Their displacement and accumulation into the innermost regions of the inner basin provide access to accreted nutrients from Crying Brook (= nutrient pump). Their displacement into the outer basin disperses and dilutes the growing population, whose collective nutrient demands may exceed accreted nutrient levels. The incomplete washout, i.e., partial retention of the dinoflagellates in the outer basin, provides a seed population for their growth in the inner basin when transported back into the inner basin. While this may not be the decisive mechanism accounting for dinoflagellate predominance in Pettaquamscutt Cove, such a physical mechanism facilitates physical aggregation, access to nutrients, population growth, dispersion, and re-inoculation.

While the horizontal circulation patterns of Pettaquamscutt Cove appear to favor such blooms, other factors which influence the retention and distribution of dinoflagellates in this embayment are: mixing, vertical

migration, and tidal dilution and/or enhancement of the populations. Because it is shallow, Pettaquamscutt Cove is generally well-mixed (Tomas and Smayda, in prep.; Table 2), although some vertical structure in nutrient distributions, temperature and salinity periodically occurs, principally at the head of the inner basin. However, persistent vertical gradients in salinity and density, such as observed in tropical phosphorescent bays (Seliger et al. 1970), are not found in Pettaquamscutt Cove. Vertical migration patterns of the dinoflagellate populations would also affect their patch movements and retention within the cove. Field sightings of dinoflagellates in undisturbed patches; populations observed in holding tanks, and enumeration of live samples collected along a gradient (Table 3) suggest that both *Gyrodinium uncatenum* and *Gymnodinium simplex* appear to undertake vertical migration despite the general absence of strong vertical, physical gradients. Both species-specific differences and regionally variable differences in the vertical distribution patterns of *Gyrodinium uncatenum* were observed during the same tidal phase. Vertical positioning of dinoflagellates through phototactic movements within the water column, however shallow, could minimize losses resulting from horizontal surface water displacements caused by winds and tides. For example, near-bottom populations entrained in an in-flow stream moving up-cove would replace populations entrained in water blown out of the cove. Likewise, upwelling along lee shores may also concentrate motile cells. Such vertical positioning and hydrodynamic events influence the retention of *Gyrodinium uncatenum* within Chesapeake Bay (Tyler et al., 1982) and other dinoflagellate populations in phosphorescent bays (Seliger et al., 1970) and in a New England coastal salt pond (Garcon et al., 1986). Similar interactions between wind-driven and tidal currents and vertical migration appear to be responsible for retention of dense *Chattonella* populations in two Japanese bays (Yoshida and Numata, 1982). However, the extent to which the vertical migratory behavior of dinoflagellates in Pettaquamscutt Cove, in interaction with horizontal flow and vertical mixing patterns, facilitates their retention within Pettaquamscutt Cove requires further study. Our initial assessment is that phototaxis is of secondary importance to dinoflagellate retention within Pettaquamscutt Cove, unlike in deeper, stratified coastal lagoons characterized by recurrent dinoflagellate blooms (Seliger et al. 1970; Garcon et al., 1986) and in Chesapeake Bay (Tyler et al., 1982).

The tidal prisms in the inner and other basins approximated 50 percent of their high tide volumes, based on the bathymetric and tidal range measurement. Tidal prism volumes in the inner and outer basins were approximately equal. The large tidal prism of Pettaquamscutt Cove and the almost daily displacement of surface waters by prevailing afternoon winds *a priori* require rapid *in situ* division rates to sustain the observed dinoflagellate populations (Table 3).

Ketchum (1954) proposed the relationship:

$$K = -\ln(1-R)$$

to estimate the minimum growth rate (K) required per tidal cycle to sustain a steady-state planktonic population within an estuary having a relative tidal prism (R). A coefficient of reproduction $K = 1.0$ corresponds to 1.44 cell divisions per tidal cycle. For Pettaquamscutt Cove, $R = 0.46-0.52$, which requires doubling rates on the order of 1.8 to 2.1 day⁻¹ to sustain a resident population in the inner basin. The Ketchum growth-rate flushing model indicates that estuarine plankton losses due to flushing and the growth rates needed to overcome such losses are reduced proportionately by the volume of reseeded water returned from downstream segments. Such tidal exchanges of phytoplankton occur between the inner and outer basins of Pettaquamscutt Cove. However, required growth rates calculated from tidal flushing characteristics alone are probably inaccurate, given the extreme variability in wind-forced displacements and movements of dinoflagellate populations between, and within the two basins of Pettaquamscutt Cove. Growth rates lower than those calculated from Ketchum's model probably would allow the observed retention and accumulation of the dinoflagellates during July in Pettaquamscutt Cove.

Growth rates of 1.8 to 2.1 divisions d⁻¹ are calculated to be required to maintain steady state populations of *Glenodinium uncatenum* and *Gymnodinium simplex* during the July tidal exchange rates in Pettaquamscutt Cove. Such high growth rates require that these species be rapid growers. Dinoflagellates generally are believed to be slow-growing, with a daily doubling rate of $K = 0.33$, i.e., equivalent to a generation time of 3 days (Smayda and Karentz, in prep.). This low growth rate is equivalent to a tidal prism of $R = 0.10$ in the Ketchum model, a flushing rate well below that observed in Pettaquamscutt Cove. Culture experiments indicate that both *Glenodinium uncatenum* and *Gymnodinium simplex* are indeed capable

of rapid growth, with rates approaching those based on Ketchum's model. The data available for *Glenodinium uncatenum* are somewhat contradictory, however. From data presented in Coats et al. (p. 356 in 1984), growth rates of 1.5 to 1.8 d⁻¹ at 20°C can be calculated. However, Tyler et al. (1982) report *Glenodinium uncatenum* grew at rates ranging from only 0.1 to 0.7 division d⁻¹ at various temperature-salinity combinations. Such slow growth suggests that *Glenodinium uncatenum* should quickly wash out of the inner basin, based on Ketchum's model. For *Gymnodinium simplex*, Thomas (1966) reports maximal rates of about 1.75 d⁻¹ at 23°-29°C, and Chan (1978) reported 1.25 d⁻¹ at 21°C. Thus, the pronounced red-tide blooms of *Gymnodinium simplex* in Pettaquamscutt Cove are consistent with their growth rate potential and the flushing characteristics of this small cove, whereas blooms of *Gyrodinium uncatenum* are enigmatic. A diel study of the flushing characteristics and entrained dinoflagellate populations, however, strongly indicates that the high growth rates required of *Glenodinium uncatenum*, and apparently reached under certain experimental conditions (Coats et al., 1984), are indeed achieved by the Pettaquamscutt Cove population (Furnas et al., 1989).

The following problem remains. Growth rates calculated from Ketchum's model are well within the range of division rates observed for summer diatom populations in Narragansett Bay (Furnas, 1982). Surprisingly, however, diatoms are not a dominant component of phytoplankton populations within Pettaquamscutt Cove, despite their high potential growth rates (Tomas and Smayda, in prep.). Dinoflagellates almost completely dominate the phytoplankton in Pettaquamscutt Cove. This indicates that unknown factors limit diatom growth within this cove, and suggests also that the resident dinoflagellate populations are exploiting unique features of this environment. Although the predominant current velocities in Pettaquamscutt Cove (Fig. 6) are similar to those (3-5 cm sec⁻¹) typical of a nearby coastal salt pond (Isaji et al., 1985), red-tide blooms are not a prominent feature there (Smayda, unpublished). Similarly, in nearby Pt. Judith Pond, where retention of winter flounder larvae is favored by the prevailing tidal movements (Crawford and Carey, 1985), dinoflagellate blooms are not conspicuous (Tomas, 1971). Thus, Pettaquamscutt Cove appears to represent a unique dinoflagellate habitat among Rhode Island coastal lagoons and Narragansett Bay. The dynamics of these red-

tide blooms and their environmental regulation will be evaluated in subsequent papers (Furnas et al., 1989).

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