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Red tide blooms of *Cochlodinium polykrikoides* in a coastal cove

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Abstract

Successive blooms of the dinoflagellate *Cochlodinium polykrikoides* occurred in Pettaquamscutt Cove, RI, persisting from September through December 1980 and again from April through October 1981. Cell densities varied from <100 cells L^{-1} at the onset of the bloom and reached a maximum density exceeding 3.4×10^6 cells L^{-1} during the summer of 1981. The bloom was mainly restricted to the mid to inner region of this shallow cove with greatest concentrations localized in surface waters of the southwestern region during summer/fall periods of both years. Highly motile cells consisting of single, double and multiple cell zooids were found as chains of 4 and 8 cells restricted to the late August/September periods. The highest cell densities occurred during periods when annual temperatures were between 19 and 28 °C and salinities between 25 and 30. A major nutrient source for the cove was Crying Brook, located at the innermost region at the head of the cove. Inorganic nitrogen (NH_3 and $NO_2 + NO_3$) from the brook was continually detectable throughout the study with maximum values of 57.5 and 82.5 μmol L^{-1}, respectively. Phosphate (PO_4-P) was always present in the source waters and rarely <0.5 μmol L^{-1}; silicate always exceeded 30 μmol L^{-1} with maximum concentrations reaching 226 μmol L^{-1}. Chlorophyll *a* and ATP concentrations during the blooms varied directly with cell densities. Maximum Chl *a* levels were 218 mg m^{-3} and ATP-carbon was >20 g C m^{-3}. Primary production by the dinoflagellate-dominated community during the bloom varied between 4.3 and 0.07 g C m^{-3} d^{-1}. Percent carbon turnover calculated from primary production values and ATP-carbon varied from 6 to 129% d^{-1}. The dinoflagellates dominated the entire summer period; other flagellates and diatoms were present in lesser amounts. A combination of low washout rate due to the cove dynamics, active growth, and life cycles involving cysts allowed *C. polykrikoides* to maintain recurrent bloom populations in this area.

Keywords: *Cochlodinium polykrikoides*; Harmful bloom; Narragansett Bay region

1. Introduction

Pettaquamscutt Cove, located at the southwestern region of the mouth of Narragansett Bay (Fig. 1), was the site of multispecies blooms of dinoflagellates during the period from May 1980 through November 1981. This cove, previously described (Furnas et al., 1989, 1990) as a shallow embayment at the lower reaches of the Pettaquamscutt River, which empties into the mouth of the Narragansett Bay, was heavily influenced by winds in the inner cove and winds and tides in the outer region. Furnas et al. (1989, 1990) speculated that the limited flushing rates of this region and rapid growth rates of the dinoflagellates resulted in the continuous bloom observed throughout their study period. Particularly notable was the presence of large populations of the dinoflagellate *Cochlodinium polykrikoides* appearing as large dark red patches common on the southern leeward shores of the cove and accompanied by visible accumulations of foam on windy days. Daily levels of dissolved oxygen remained continually supersaturated (>200%) during the early part of this bloom (Albert, RI DNR, personal communication). Although fish kills were not observed, local sport and commercial fishermen did not fish this cove during the summer of 1981. The bloom began earlier in the summer of 1980 and persisted from early September through late October, when the red coloration disappeared. From October to early December the waters were turbid, with a green discoloration that continued until the onset of winter when the cove became covered with ice. Blooms of *C. polykrikoides* reappeared in the summer of 1981 and persisted through November of that year.

The blooms observed in this region were attributed to the relative isolation of inner Pettaquamscutt Cove where the tidal

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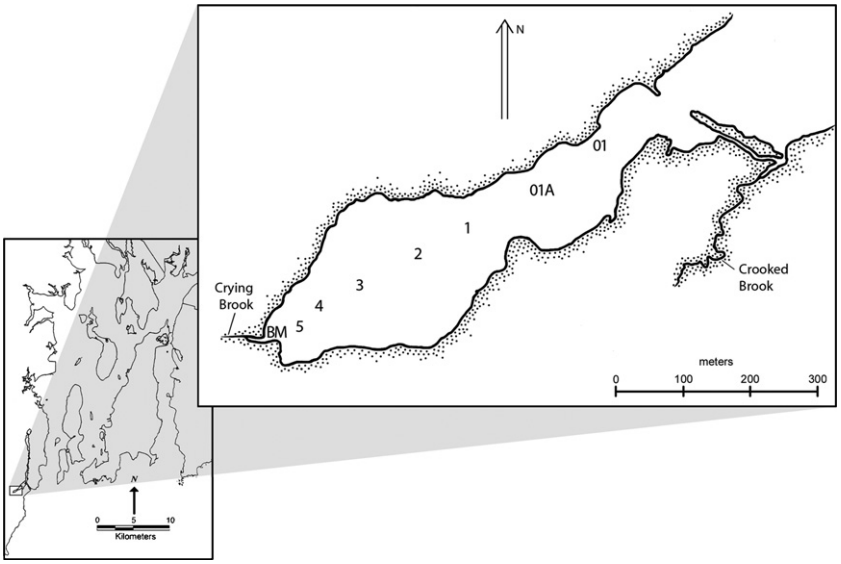

Fig. 1. Pettaquamscutt Cove, RI (large inset) site of *Cochlodinium polykrikoides* blooms.

prisms representing between 46 and 55% of the high tide volumes minimized flushing of this region (Furnas et al., 1989). A dominant feature of this region was the introduction of nutrients via two small brooks, Crying Brook, at the head of the cove and Crooked Brook located toward the outer regions of the cove (Fig. 1). The southern and western regions of the cove were lined with dwellings and a buffer area of *Spartina alterniflora* and *Phragmites communis* vegetation, while the northern shore had no domestic dwellings and was lined by a salt marsh meadow principally of *S. alterniflora*. The accretion of nutrients from the activities associated with these dwellings or the influx from Crying Brook at the mouth of the cove was not assessed during this study.

Cochlodinium polykrikoides was originally described by Margalef (1961) as a bloom species from Phosphorescent Bay (Bahía Fosforescente), Puerto Rico. In U.S. coastal waters, in addition to Pettaquamscutt Cove, blooms exceeding 10^7 cells L^{-1} were noted for Point Judith Pond, RI (Hargraves and Maranda, 2002). Blooms were reported from Barnegat Bay, NJ, as *C. heterolobatum* (=*C. polykrikoides*) (Sousa e Silva, 1967); from Peconic Estuary, NY (Nuzzi, 2004), Chesapeake Bay (Marshall, 1995), York River, VA (Zubkoff and Warinner, 1975), as well as New River, NC and Palma Sola (Sarasota), FL (Tomas, unpubl. data).

Elsewhere on the American continent, blooms were reported at Vancouver Island, British Columbia, Canada (Whyte et al., 2001), Gulf of California (Garate-Lizárraga et al., 2004), Costa Rica (Viques and Hargraves, 1995; Vargas-Montero and Freer, 2005) and Guatemala (Rosales-Loessener et al., 1996). In the Mediterranean, blooms of *C. polykrikoides* were reported from four sites in the Gulf of Olbia, Sardinia (Italy) where summer blooms were common (Sannio et al., 1997). Along the Ukrainian coast of the Black Sea, *C. polykrikoides* was noted from regions associated with mussel/oyster cultivation (Vershinin et al., 2004, 2005).

Reports of *C. polykrikoides* blooms associated with fish kills in the Inland Sea of Japan were given by Yuki and Yoshimatsu (1989) and by Yamatogi et al. (2002) for Usuka Bay, West Japan. In China, blooms in Zhujiang (Pearl River) estuary were also noted (Huang and Dong, 2000). Fish death, oxygen depletion and choking of fish gills were reported for the Malabar Coast, India by Ramaiah et al. (2005), where *C. polykrikoides* was implicated in extensive fish kills.

The most extensive studies of *C. polykrikoides* blooms are those for Korean waters and are a major effort of this issue of *Harmful Algae*. Presently the entire southern Korean coast is involved with seasonal blooms having extreme impacts on the survival and fisheries of the region. The factors affecting the outbreaks of *C. polykrikoides* in Korea are complex (Yoon, 2001) and linked to coastal nutrient enrichment, primarily nitrate from seasonal rainfall along with intrusions of warm water from the Tsushima Current carrying seed populations of *C. polykrikoides* (Lee, 2006; Lee and Lee, 2006). The bloom dynamics of *C. polykrikoides* for Pettaquamscutt Cove presented here can serve as a comparison to those from open coastal areas where different dynamics may govern them.

2. Methods

Pettaquamscutt Cove, a portion of the Pettaquamscutt River estuary, is located at 41°25′20″ N and 71°28′14″ W due west of the mouth of Narragansett Bay, Rhode Island (Fig. 1). The cove (area = 0.788 km^2) is divided into two natural subsections by the constricted shallow passages at Sedge Island and an abandoned causeway (Gaines, 1975). The inner cove, with an area 0.128 km^2 and depths of 1 m or less at mean low water, is flanked by a fringing salt marsh except at the southern region where domestic dwellings are located near the shore. Freshwater inputs to the inner cove occur through Crying Brook located at the head of the cove, and Crooked Brook located near

Table 1
Physical–chemical data for Crying Brook, Pettaquamscutt Cove, RI, at surface for the *Cochlodinium polykrikoides* bloom period during 1981 and 1982

Date	Temperature (°C)	Salinity	μmol L^{-1}			
			NH_3	$NO_2 + NO_3$	PO_4	Si
1980						
9/10	17.5	0.0	2.90	>50.00	0.40	>80.0
10/07	16.0	2.0	2.52	64.00	1.44	51.2
10/09	16.0	0.0	3.42	0.78	2.31	51.0
10/14	15.0	0.0	2.59	56.80	0.79	90.5
10/15	14.0	0.0	2.15	60.70	0.79	85.9
10/17	14.0	0.0	2.17	60.10	0.63	83.4
10/20	12.0	0.0	2.30	50.00	0.70	93.3
10/22	11.0	1.0	2.12	50.80	4.01	139.9
10/24	9.5	13.0	25.20	9.40	2.78	67.7
11/13	0.0	5.6	57.50	1.28	12.09	–
11/17	–	0.0	7.29	63.30	1.37	138.8
11/26	4.8	0.0	4.82	45.30	4.46	169.4
12/09	5.5	1.0	4.43	82.50	5.11	126.0
1981						
04/28	13.2	24.0	9.48	1.79	1.28	37.0
05/07	14.8	12.0	35.6	1.84	4.04	106.0
05/13	15.0	24.0	4.92	2.79	1.12	25.3
05/19	14.5	24.0	8.47	0.06	1.74	37.5
05/27	–	–	11.60	1.41	2.69	66.3
06/02	16.5	14.0	32.70	2.20	4.91	109.5
06/16	21.0	21.0	22.00	3.20	3.16	113.2
06/24	20.0	4.0	38.40	4.10	4.65	183.5
07/08	28.5	22.0	3.90	0.90	4.74	59.3
07/20	26.0	28.0	0.38	0.44	5.42	87.7
07/28	22.0	8.0	5.98	4.74	6.90	178.4
08/04	25.5	0.0	17.90	6.20	10.20	226.0
08/12	26.0	22.0	0.26	0.66	6.20	98.3
08/18	23.0	28.0	0.00	0.41	4.21	75.9
08/25	20.0	30.0	0.16	0.19	2.91	51.1
09/03	19.5	–	0.40	0.83	4.77	115.3
09/09	23.5	29.0	0.26	0.97	3.71	79.6
09/15	23.0	30.0	0.11	0.58	2.86	61.7
09/24	15.5	22.0	5.12	3.95	2.59	80.0
09/29	16.3	22.0	0.63	0.77	2.84	32.3
10/06	14.5	26.0	4.45	7.29	2.78	54.7

(–) Data not available.

the abandoned causeway. Numerous shallow drainage ditches also empty water from the pannes and salt marshes at various points along the shore. A detailed description of the morphometry and hydrography is presented by Furnas et al. (1989, 1990).

A total of 34 samples were collected from 10 September to 9 December, 1980 and from 28 April until 6 October, 1981 at 8 locations (Fig. 1) within the inner cove and at the mouth of Crying Brook. The data presented here (Table 1) are the surface measurements made at the Crying Brook mouth throughout the study period.

Species identification and abundance were determined from live samples taken at each station. Cell counts were made using Sedgwick Rafter and 10 mL sedimentation chambers, at 10 or 20× magnifications, using a Wild M20 or Wild M40 inverted brightfield microscope. Photomicrographs were taken with a Zeiss Photomicroscope II using Kodak Techpan black and white film developed with dilute (1:3) Microdol X. Negatives were scanned with a Microtek Scanmaster scanner into digital files. All determinations were made usually within 1 h of collection upon return to the laboratory. Motile dinoflagellate samples were stabilized for counting with a few drops of Lugol's solution at the time of cell examination and counting.

Salinity was measured using a hand-held T/S refractometer. Ammonia, nitrate plus nitrite, phosphate and silicate were analyzed (filtered samples) using a Technicon Autoanalyzer II and methods described previously (Furnas et al., 1990). Chlorophyll *a* was determined fluorometrically using a Turner Fluorometer (Yentsch and Menzel, 1963; Holm-Hansen et al., 1967) and ATP following the procedures of Holm-Hansen and Booth (1966) as modified by Cheer et al. (1974). A ratio of 250:1 (Eppley et al., 1971; Sakshaug and Andresen, 1986) was used to convert phytoplankton ATP to carbon biomass.

Primary production determined from natural samples taken from the surface of station 4, on 9 of the 18 sampling days employed C^{14} techniques (Strickland and Parsons, 1968). One hundred milliliter aliquots of sample were inoculated with 1.5 μCi of C^{14}-bicarbonate and incubated for 24 h in a light

gradient chamber having intensities of 100, 60, 25, 10 and 3% incident solar radiation. Incubations were maintained at ambient Narragansett Bay temperatures by a continuous flow of sea water through the incubator.

ATP estimated living carbon (ATP × F = mg C m^3) and primary production measurements (as mg C m^3 d^{-1}) made on the same sample were used to estimate the percentage of carbon biomass produced during that day. This was calculated as (mg C m^3 d^{-1}/mg C m^3) × 100. Assuming that a doubling of carbon (e.g., 100%) for a day was required for one division d^{-1}, estimates of population growth of *C. polykrikoides* dominated communities could be made.

3. Results

3.1. Cell morphologies

Cochlodinium polykrikoides cells were present as unicells, 2 and 4 cell zooids and, rarely, as 8 and 16 cell chains (Fig. 2). The early stages of the bloom had small, single cells that gave rise to doublet zooids within a week of appearance. The greatest number of multiple cell zooids appeared in the mid-phases of the bloom and only for short (days) periods of time. The declining bloom population was again composed of single and few doublet cells. With respect to position in the water column, the majority of cells were found in the upper 10 cm during the mid-day samplings with some *C. polykrikoides* cells found at all depths at each station.

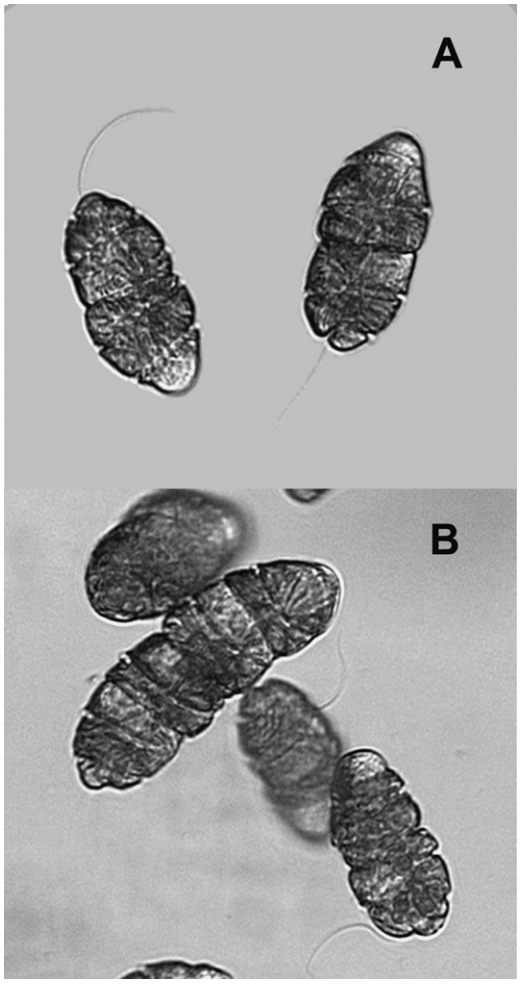

Fig. 2. *Cochlodinium polykrikoides* from bloom in Pettaquamscutt Cove, RI (A) Two cell zooids, (B) two and four cell zooids.

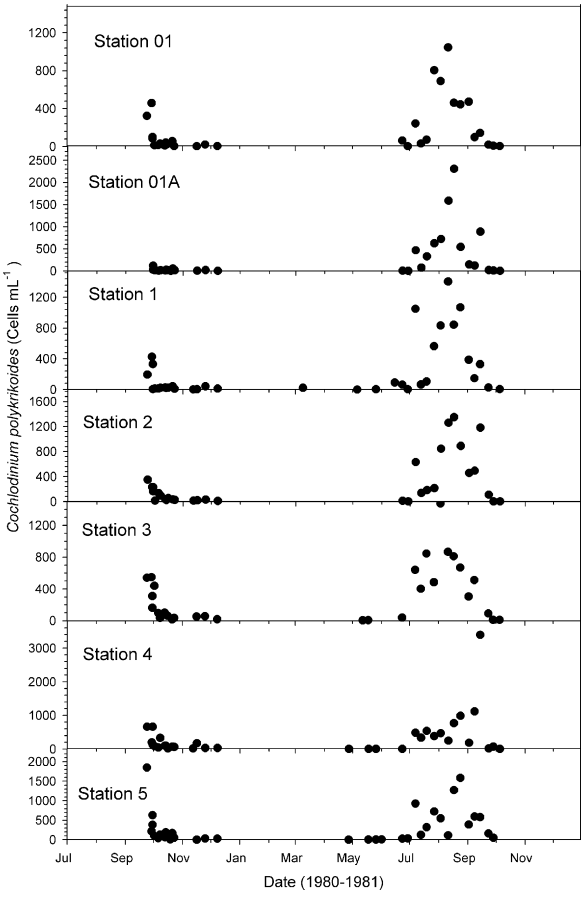

Fig. 3. *Cochlodinium polykrikoides* abundances at seven Stations in Pettaquamscutt Cove, Rhode Island during 1980 and 1981.

3.2. Cochlodinium polykrikoides abundance

The presence of *C. polykrikoides* at seven stations is presented in Fig. 3. At all locations, abundance rapidly declined during mid-September, reached low levels in November and *C. polykrikoides* disappeared by early December. No cells were observed until early May in the following year when *C. polykrikoides* was detected at 4 of the 7 stations (Fig. 3). Abundance remained low throughout June, but abruptly rose in July and August with maxima reached during September 1981. The highest concentrations were recorded in the mid-cove stations (stations 2–4) where abundances >1000 cells mL^{-1} occurred, but the bloom pattern was common to all stations. By mid-October and thereafter, *C. polykrikoides* was not observed.

With regard to temperature, *C. polykrikoides* (Fig. 4) was found between 3 and 28 °C, with elevated abundances mostly between 15 and 26 °C. Populations exceeding 1000 cells mL^{-1} occurred between 18 and 22 °C. Relative to salinity, *C. polykrikoides* was rarely present below a salinity of 25 and most

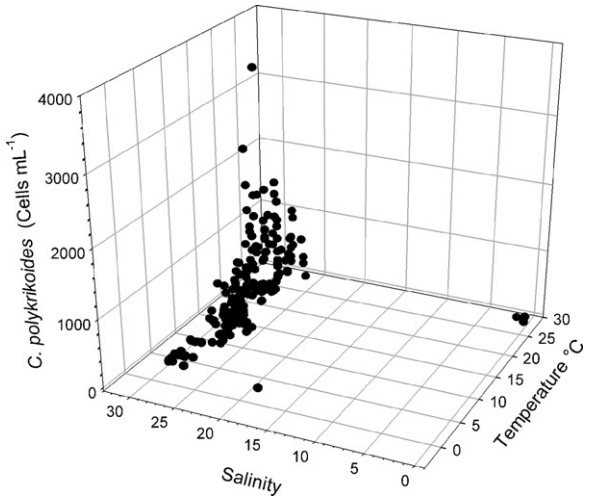

Fig. 4. Abundance of *Cochlodinium polykrikoides* in Pettaquamscutt Cove, RI as a function of temperature and salinity for the sampling period from Sept. 1980 through Oct. 1981.

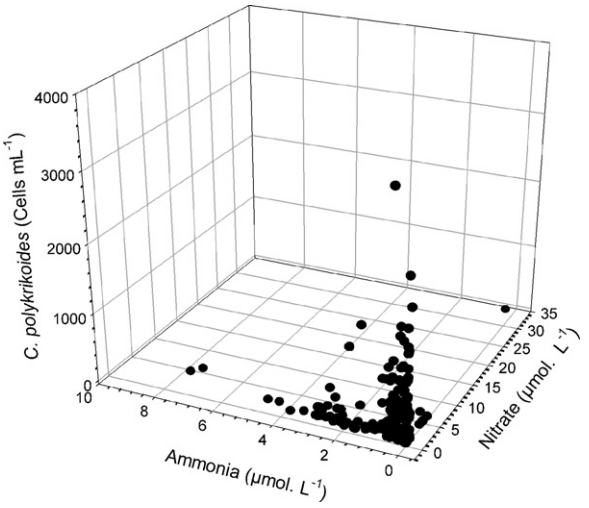

Fig. 5. Pooled *Cochlodinium polykrikoides* concentrations as a function of nitrate-N and ammonia-N concentrations for Pettaquamscutt Cove, RI, for Sept. 1980–Oct. 1981.

commonly between 28 and 31 (Fig. 4). Highest abundance was recorded at a salinity of 30. When combined, the temperature/salinity environment seemingly favored by *C. polykrikoides* was a relatively narrow temperature (15–28 °C) window and narrower salinity preference between 25 and 30 (Fig. 4).

3.3. Temperature and salinity

Water temperature at the brook mouth varied from 4.8 to 28.5 °C during the sampling period (Table 1). An initial warm period (>15 °C) persisted into mid-October when temperatures abruptly dropped to 9.5 °C and remained below 10 °C the rest of the winter. Warming resumed again by late-April with temperatures above 10 °C when *C. polykrikoides* reappeared, and increased to the annual maximum of 28.5 °C in early July. From June through September, temperatures remained above 20.0 °C. By the last sampling date (6 October) temperatures had decreased to 14.5 °C with declining dinoflagellate populations.

Salinity varied from 0 to 30 throughout the cove, but fluctuations were greatest at the Crying Brook mouth station where surface salinities from 0 to 28 were found (Table 1). Salinities for the 1980 samplings were mostly at 0 or <10, whereas the 1981 values were much higher, fluctuating mostly from 8 to 30.

3.4. Nutrients

Ammonia levels at the Crying Brook mouth station were between 0.26 and 4.8 μmol L^{-1} in 1980, except for 24 October and 13 November when values of 25.2 and 57.5 μmol L^{-1}, respectively, were measured (Table 1). Ammonia was higher in 1981, varying between 0.16 and 38 μmol L^{-1}. The period from May through early August 1981 had elevated ammonia levels that varied between 11.6 and 38.4 μmol L^{-1} while values from August through September were <5.0 and most often below 0.6 μmol L^{-1} (Table 1).

Levels of $NO_3 + NO_2$ were generally high within the 1980 samples, often exceeding 50 μmol L^{-1} up to 82.5 μmol L^{-1} for most of the sample dates (Table 1). This was in contrast to the following year when no sampling date had values >8 and levels as low as 0.06 μmol L^{-1} were measured. With inorganic

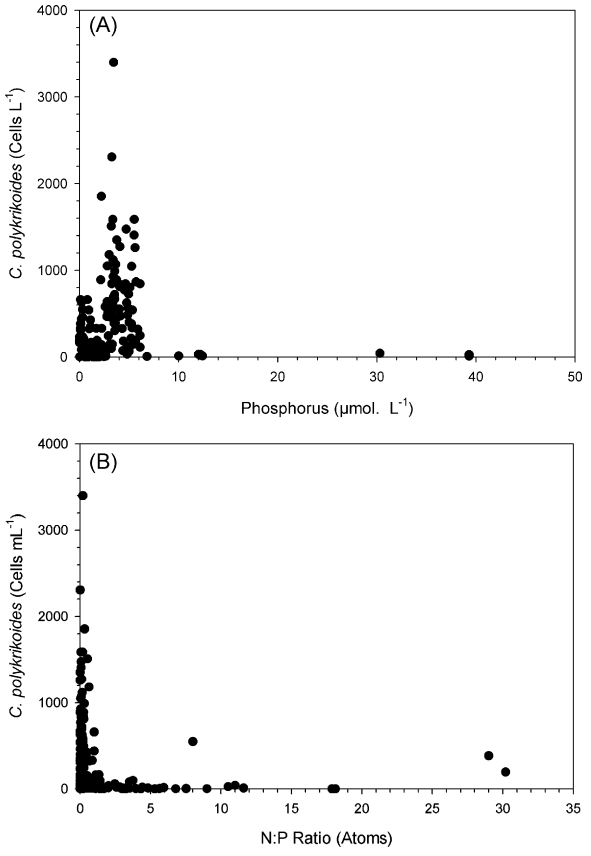

Fig. 6. Pooled data for *Cochlodinium polykrikoides* from Pettaquamscutt Cove, RI, for the period of Sept. 1980 through Oct. 1981. (A) Cell abundance as a function of phosphate – P and (B) cell abundance with N/P ratio (atoms).

nitrogen as nitrate + nitrite, *C. polykrikoides* cells were most prevalent at low $NO_3 + NO_2$ (Fig. 5) environments below 7 μmol L^{-1}, but were occasionally observed at levels above 15 μmol L^{-1}. The highest abundance occurred at <1.0 μmol L^{-1}, with >1000 cells mL^{-1} recorded between 0 and 4 μmol L^{-1} $NO_3 + NO_2$. A strikingly similar abundance pattern was observed with NH_3 (Fig. 5). Most elevated cell abundances were restricted to an ammonia concentration range between 0 to 7 μmol L^{-1}, with few cells above 7 μmol L^{-1}. The maximum abundances clearly indicated the predominance of *C. polykrikoides* in a nitrogen poor environment when NH_3 was below 2 μmol L^{-1} and NO_3 below 5 μmol L^{-1} (Fig. 5).

Dissolved phosphate concentrations were detected at all sampling dates during both years for Crying Brook (Table 1). During the 1980 bloom period, the lowest concentration detected was 0.23 μmol L^{-1} with values more commonly varying between 1.0 and 5.11 μmol L^{-1}. The highest value recorded was 12.09 μmol L^{-1} in November. Phosphate was again elevated in 1981, varying between 1.12 and 10.2 μmol L^{-1}, with values most commonly between 2.0 and 5.0 μmol L^{-1}.

While concentrations of phosphate nearing 40 μmol L^{-1} were observed during the study, *C. polykrikoides* was present and highest abundances were recorded at levels between 4 and 6 μmol L^{-1} (Fig. 6A) with the majority of cell abundances occurring at levels below 8 μmol L^{-1}. Cell abundance related to the N:P ratio (atoms) of DIN/PO_4, indicate routine presence at N:P ratios of 10 or below, with the highest abundance at N:P ratios ranging from 0.1 to 2.0 (Fig. 6B). This suggests that *C. polykrikoides* blooms consistently occurred or developed towards nitrogen limiting environments of N:P <15 and that this dinoflagellate rarely increased in abundance or occurred in phosphorus-limited environments i.e., at N:P >15.

There is no known requirement by *C. polykrikoides* for silica, thus it is not surprising that it was abundant at silica concentrations that ranged from 26 to >100 μmol L^{-1} (Fig. 7). Lower abundances at Si levels <25 μmol L^{-1} suggest periods of high silica consumption by diatoms resulting in a greater competitive stress on the dinoflagellates in general. There did not seem to be any relationship with cell abundance of *C. polykrikoides* and silica concentration.

3.5. Biomass and primary production

Standing stock of Chl *a*, ATP-carbon and primary production were determined along with measurements of day length and carbon turnover (Table 2). Except for the very beginning and end of blooms, the day lengths varied between 10 and 15 h light (i.e., 10–15 L) with the highest cell concentrations occurring around 14 L. For the 1980 bloom period, Chl *a* ranged from 6.3 to 17.9 mg m^{-3} while in 1981 generally higher values occurred, exceeding 100 mg m^{-3} on three occasions. A direct relationship between Chl *a* and *C. polykrikoides* cells was observed for the combined data covering the full sampling period (Fig. 8). Correspondingly, ATP-carbon during 1980 varied from 853 to 4478 mg m^{-3}. As with Chl *a*, ATP-carbon levels the following year (1981) were

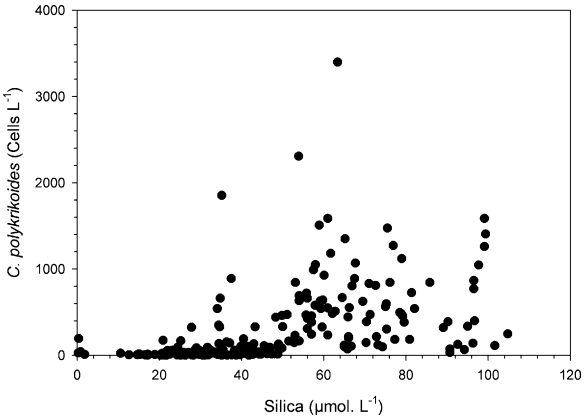

Fig. 7. Pooled data for *Cochlodinium polykrikoides* in Pettaquamscutt Cove, RI for the period from Sept. 1980 through Oct. 1981 as a function of silicate concentration.

more variable, ranging from a low of 610 to a maximum of 20,858 mg m^{-3}. Values exceeding 1000 mg m^{-3} were common for most of the 1981 sampling period. During this same period in 1980, primary production measured during the bloom varied from 85 to 1096 mg C m^3, with values exceeding 1000 mg C m^{-3} in 10 of the 24 samples measured in 1981.

The highest Chl *a*, ATP-carbon and primary production levels occurred in early October when *C. polykrikoides* dominated the phytoplankton. Elevated production rates, Chl *a* and ATP-carbon biomass persisted throughout 1980. The following year, Chl *a* >40 mg m^{-3} persisted from June 24 through September 3 when daily production values were between 1000 and 4321 mg C m^{-3} d^{-1} and ATP-carbon varied between 5013 and 10,498 mg C m^{-3} (Table 2). When compared to cell numbers both Chl *a* and ATP-carbon values agreed with the peak abundances of *C. polykrikoides* and the direct relationship between these two variables was clear (Fig. 9).

Percent carbon turnover calculated from the standing stock (i.e., ATP-carbon) and carbon fixation rates from primary production estimates (Table 2) consistently gave modest to low doublings and only once (10/03/80) was >100% carbon d^{-1}

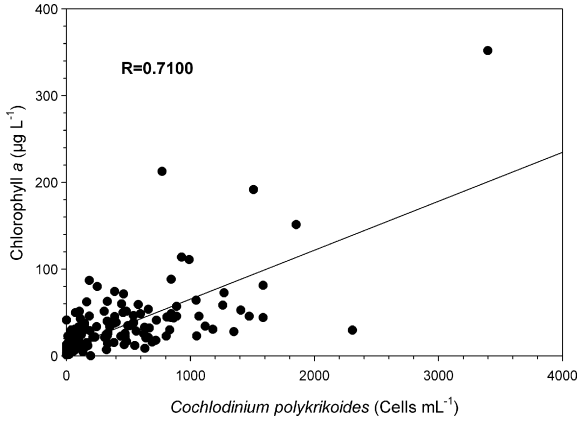

Fig. 8. Chl *a* concentration as a function of *Cochlodinium polykrikoides* in Pettaquamscutt Cove, RI from Sept. 1980 through Oct. 1981.

Table 2
Day length, Chl *a*, ATP-carbon and primary production and carbon turnover for samples studied at station 1, Pettaquamscutt Cove, RI during a *Cochlodinium polykrikoides* bloom

Date	Day length (h)	Chl *a* (mg m^{-3})	Primary Production (mg C m^{-3} d^{-1})	ATP-C (mg m^{-3})	C-turnover (%C d^{-1})
1980					
09/25	11.8	27.2	680	3030	22
10/03	11.4	13.7	1096	852	129
10/07	11.2	9.8	872	4477	19
10/15	10.8	17.9	419	3747	11
10/17	10.7	6.3	84	1352	6
10/20	10.6	10.5	148	1285	12
10/22	10.5	16.3	563	2835	20
11/17	9.5	13.7	351	–	–
12/09	9.1	11.3	458	2220	21
1981					
03/18	11.8	1.1	69	1032	7
05/07	14.1	3.8	420	610	69
05/13	14.3	2.7	201	1287	16
05/19	14.5	7.9	821	–	–
05/27	14.7	3.8	435	1730	25
06/02	14.8	1.6	143	860	17
06/10	14.9	26.0	1110	7662	14
06/16	15.0	22.6	953	4775	20
06/24	15.0	45.5	1313	8872	15
06/30	15.0	5.2	372	1435	26
07/08	14.9	51.2	1196	6562	18
07/14	14.8	28.5	993	4530	22
07/20	14.7	123.8	2185	20857	10
07/28	14.4	41.0	4321	6552	66
08/04	14.2	17.9	812	4660	17
08/12	13.9	106.7	2304	10497	22
08/18	13.7	54.1	2094	9355	22
08/25	13.3	44.6	1268	6945	18
09/03	12.9	42.5	1329	5012	27
09/09	12.6	34.2	947	5297	18
09/15	12.3	218.1	2329	6091	38
09/24	11.8	8.2	227	1723	13
09/29	11.6	4.7	308	2199	14
10/06	11.2	4.7	220	–	–

(–) Data not available. Daily total light, day length, primary production, Chl *a*, ATP-carbon, carbon turnover, daily production per Chl *a* and daily production per Chl *a* per light for *Cochlodinium polykrikoides* bloom periods in Pettaquamscutt Cove, RI during 1980–1981.

measured. The next highest values of 69 and 66% were observed on 5 May and 28 July of 1981 while all other values were at, or below 27% d^{-1}.

4. Discussion

The blooms of *C. polykrikoides* in Pettaquamscutt Cove during 1980–1981 represented a unique series of events. This species, not reported in the long-term data set for adjacent Narragansett Bay or from the upper Pettaquamscutt River Estuary where *Akashiwo sanguinea* (=*Gymnodinium splendens*) and monads dominated (Miller, 1972), was able to establish itself at sustaining densities of 10^5 to 10^6 $cells^{-1}$ and form recurrent blooms over the two year period of our study. The blooms, which began in early summer, dominated the phytoplankton community composed primarily of dinoflagellates and declined with decreasing day lengths and temperatures. The distribution of *C. polykrikoides* in the inner cove regions was heavily influenced by wind, to a lesser extent by tides (Furnas et al., 1989, 1990), and by limited exchange with the outer cove. This wind and tidal action tended to harbor populations from excessive advective losses. *Cochlodinium polykrikoides* is known to undertake vertical migrations (Park et al., 2001), which in this shallow inner cove, together with the

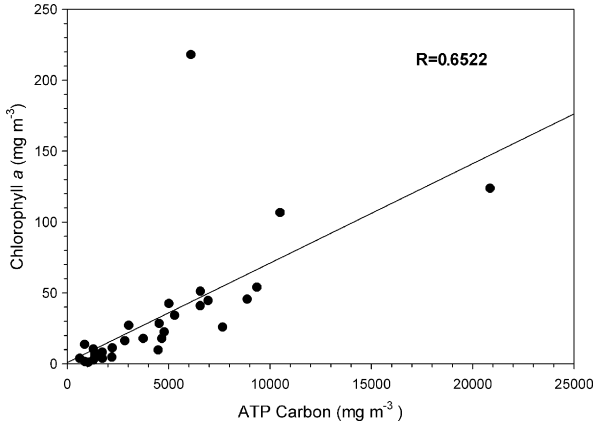

Fig. 9. Chl *a* concentration as a function of ATP-carbon during *Cochlodinium polykrikoides* blooms in Pettaquamscutt Cove, RI during 1980–1981.

displacement of surface layers by the prevailing northwest winds, resulted in the dense accumulations of cells observed in the southwestern regions of the cove. This cove is too shallow and well-mixed to infer any nutrient gathering advantage as was postulated for other catenate species such as *Gymnodinium catenatum* in the Atlantic upwelling regions of Spain or in Tasmania (Hallegraeff and Fraga, 1989). However, sizable populations of *C. polykrikoides* occurred where ambient nitrogen was at low levels (Fig. 5), inferring heavy nitrogen utilization and possibly tight coupling with nitrogen cycling was required to sustain these populations.

Cochlodinium polykrikoides was highly motile, appearing as single, double, four and eight cell zooids. When enclosed in experimental bottles, dense populations would often migrate to the bottom of the container where they formed non-motile gelatinous masses. Similar clusters were seen in the cove and in production bottles as well. Formation of such clusters in production bottles may have resulted in our underestimation of photosynthesis. In less dense populations, surface aggregations were observed. This life-form characteristic may be important in promoting the patchy distribution observed in the cove and a mechanism important in its spatial concentration and movement by wind (Seliger et al., 1971). In this regard, *C. polykrikoides* differed from *Heterocapsa rotundata*, the species that appeared subsequently in the cove and which did not show similar aggregation or bottom-clumping. The ability of *C. polykrikoides* to form recurrent blooms suggests a cyst-type overwintering stage. Temporary cysts in Pettaquamscutt Cove bloom samples were observed as hyaline membranes covering single motile cells. Similar cysts of *C. polykrikoides* were observed to survive up to 6 months at 4 °C in the dark (Kim et al., 2002) and regenerate motile cells when returned to 20 °C, fluence fluxes of 40 μm photons m^{-2} s^{-1} and a 14 h light–dark photoperiod. Hyaline coatings of cell chains were also reported (Kim et al., 2007) as potential cysts. Remains of thecate cells in *C. polykrikoides* cultures reported by Kim et al. (2007) were not observed in the cove samples. The survival period and germination conditions are well within those expected from the end to the beginning of the following *C. polykrikoides* blooms in the cove and may serve to allow recurrent blooms there. The conditions for regeneration of motile cells also agreed well with those when *C. polykrikoides* was abundant in the cove (Fig. 4, Table 2). The optimal temperature and salinity environment (Figs. 4, 5 and 6) for *C. polykrikoides* in Pettaquamscutt Cove agreed well with that reported by Kim et al. (2004) where maximum growth (0.41 doublings d^{-1}) occurred at 25 °C and a salinity of 36. Similar conditions were reported by Yamatogi et al. (2002) for Imari Bay, Japan, where 27.5 °C and salinity of 32 were given as optimal conditions giving growth rates (μ) of 0.90 d^{-1}.

The influence of continuous supply of nutrients (particularly nitrogen) contributed by Crying Brook waters cannot be underestimated. This brook delivered nitrogen, as ammonia, nitrate plus nitrite, phosphate and silica to the cove area. Urea was not determined. Furnas et al. (1990) asserted that there was a net export of both phosphorus and silica from the inner cove, suggesting that the blooms were not phosphate-limited. This is in agreement with that of Park et al. (2001) who reported that growth of *C. polykrikoides* was controlled by phosphate, not nitrate, in Korean coastal waters. Elevated *C. polykrikoides* densities were associated with periods of heavy rainfall and nutrient input, mainly nitrogen in Korean waters (Lee and Lee, 2006). The addition of f/2 nutrients to natural populations did not promote growth of *C. polykrikoides*, causing these authors to suggest that along with nutrients, growth promoting substances delivered in the rain water runoff stimulated the blooms. Although rich in humic substances, the role of humics stimulating phytoplankton growth in Pettaquamscutt Cove was not tested. The influence of these substances, as well as those potentially excreted by *C. polykrikoides*, in preventing the development of large diatom blooms commonly found in nearby adjacent waters still remains an open question.

Cochlodinium polykrikoides is capable of mixotrophy in addition to its photosynthetic capacity (Jeong et al., 2004a: Jeong et al., 2005). Using a variety of prey items, *C. polykrikoides* growth rates rose with mean prey densities, primarily with a cryptophyte flagellate, increasing the daily rate from 0.17 without prey to 0.32 doublings d^{-1}, with prey. Ingestion and growth rates of dinoflagellates including *C. polykrikoides* were measured using *Synechococcus* sp. as prey indicating that growth rates of the photosynthetic *C. polykrikoides* were comparable to those measured from heterotrophic nanoflagellates and ciliates (Jeong et al., 2005).

In order for *C. polykrikoides* to establish and maintain a population in Pettaquamscutt Cove, losses due to advection and predation would have to be compensated by active growth. The physical dynamics of the cove (Furnas et al., 1989, 1990) favor maintaining populations within its inner regions. Estimates of *C. polykrikoides* expressed as cell number, chlorophyll *a* and ATP-carbon (Fig. 3, Table 2) indicated that a significant portion of the population accumulated in the cove and that cellular dynamics were capable of maintaining this population. Our estimates using percent carbon turnover d^{-1} (Table 2) suggested that doublings on the order of one per day could occur, but that growth was more commonly half that value, or less. As mentioned previously (Furnas et al., 1989), doubling times in excess of 1.8–2.1 division d^{-1} per tidal cycle were needed to sustain the resident population in the inner cove. Laboratory studies measuring growth of *C. polykrikoides* showed lower rates between 0.13 and 0.91 doublings d^{-1} (Kim et al., 2004). For the blooms to develop and increase in the inner Cove, growth had to be greater than that estimated in this study. Potential errors in our measurements could derive from a variable instead of a constant ATP/C ratio and from underestimates of production due to *C. polykrikoides* populations in bottles settling to the bottom and forming immobile masses.

Losses due to predation on *C. polykrikoides* are difficult to assess. While predation of *C. polykrikoides* occurs, it was not readily evident from direct observations of the common ciliates and rotifers. Studies on ingestion by the mixotrophic thecate dinoflagellate *Fragilidium* cf. *mexicanum* demonstrated feeding on a number of dinoflagellates, but not *C. polykrikoides* or *Amphidinium carterae* (Jeong et al., 1999a). The ciliate *Strombidinopsis* sp. provided with five different dinoflagellates

as prey, grew best (1.38 doublings d^{-1}) on *C. polykrikoides* (Jeong et al., 1999b). Larvae of the mussel *Mytilus galloprovincialis* were able to feed on dinoflagellates including *C. polykrikoides*, only after 9–13 days post fertilization, as opposed to 5 days with an *Isochrysis* control. The ingestion rates for these larvae, however, were higher than those observed for other ciliates (Jeong et al., 2004b). Although larger zooplankton was not sampled in our study, *Tintinnus*, *Tintinnopsis*, *Mesodinium*, and rotifers were noted during normal cell counting. No direct relationship could be discerned from their abundance and that of *C. polykrikoides*. Recent studies of egg production, viability and fecal pellet production reported for *Acartia omorii* (Shin et al., 2003) showed that among dinoflagellate and diatom-based diets, those of dinoflagellates tested, with the exception of *C. polykrikoides*, gave results superior to the diatom-based diets. When the *C. polykrikoides* dominated community changed over (Oct.-Nov.) to the *Heterocapsa rotundata*, extensive populations of *Mesodinium* and rotifers appeared. Similar herbivores were noted by Seliger et al. (1975) and Burkholder et al. (1967) to be important grazers on microflagellates in the succession to dinoflagellate-dominated communities. *Mesodinium* and rotifers may play a similar function in Pettaquamscutt Cove in driving the succession from one dinoflagellate species to another.

The toxicity associated with *C. polykrikoides* blooms appears complex and reminiscent of that described for the Raphidophyceae. In Pettaquamscutt Cove, no major fish kills were observed although anecdotal evidence from local fisherman was that they no longer fished the cove during the summer when blooms were present. Fish were then absent from the area, seen porpoising in surface waters, or not responding to baited traps. Similar observations were made of Atlantic Salmon (*Salmo salar*) behavior in Vancouver, British Columbia (Canada), where the fish stopped feeding when *C. polykrikoides* counts exceeded 500 cells mL^{-1}, with mortality appearing when the densities exceeded 2000 cells mL^{-1}. S. *salar* smolts died within 27 min of exposure to 7200 cells mL^{-1} (Whyte et al., 2001). Cell densities of this order were found during both blooms in Pettaquamscutt Cove. As for the active agents in the toxicity, and again similar to Raphidophytes, reactive oxygen species (Kim et al., 1999), hemolytic toxins (Kim et al., 2001), long chain polyunsaturated fatty acids (PUFAs) (Lee, 1996) appear all to play some role in the toxicity leading Kim et al. (2002) to conclude that toxicity was a function of multiple factors. The exact mechanism remains elusive and will take further efforts to define clearly.

While the bloom of *C. polykrikoides* in Pettaquamscutt Cove appeared to be a singular isolated event, it is not known if the blooms have persisted. Moreover, the question as to how the bloom was first initiated in that small, isolated cove remains an open question. The ecological and physiological evidence, however, agrees as to temperature and salinity preferences given for *C. polykrikoides* blooms elsewhere. The question regarding the origin may be in part answered by molecular studies on blooms in coastal U.S. and those from the type location (Phosphoresecent Bay, Puerto Rico). While some inroads have been made regarding the mode of toxicity characterizing *C. polykrikoides* by identifying reactive oxygen species (Kim et al., 1999) and hemolytic activity (Tomas, unpubl. data) by the lysis of human erythrocytes, the precise mechanism governing its toxicity and virulence *in situ* remains to be discovered.

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