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Survey of Environmental Conditions & Plankton Dynamics Along an Eutrophication Gradient in Narragansett Bay During An Annual Cycle

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Narragansett Bay Estuary Program

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FOREWORD

In 1985 the United States Congress directed the U.S. Environmental Protection Agency (US EPA) to conduct programs in four estuaries including Narragansett Bay, citing its concern for the "health and ecological integrity" of the nations's estuaries and estuarine resources. The Narragansett Bay Project (NBP) was established in 1985 under the joint sponsorship of the US EPA and the Rhode Island Department of Environmental Management with the mandate to direct a program of research and planning focussed on managing Narragansett Bay and its resources for future generations. The National Estuary Program was created by the amendments to the Clean Water Act in 1987; and Narragansett Bay was designated an "estuary of national significance" in 1988.

The NBP developed a draft Comprehensive Conservation and Management Plan (CCMP) in December 1991, which recommended actions to improve and protect the Bay and its natural resources.

The NBP has established the following seven issues of concern for Narragansett Bay:

- management of fisheries
- nutrients and potential for eutrophication
- impacts of toxic contaminants
- health and abundance of living resources
- land-based impacts on water quality
- recreational uses

The NBP is taking a watershed-based ecosystem approach to address these problems and has funded research that will help to improve our understanding of various aspects of these priority problems. The Project is also working to expand and coordinate existing programs among federal, state and local agencies, as well as academic researchers, in order to apply research findings to the practical needs of managing the Bay and improving the environmental quality of its watershed.

This report represents the technical results of an investigation performed for the Narragansett Bay Project. The information in this document has been funded wholly or in part by the United States Environmental Protection Agency through Cooperative Agreement #CX812680 to the Rhode Island Department of Environmental Management. The results and conclusions contained herein are those of the author(s), and as they do not necessarily represent the views or recommendations of the NBP, no official endorsement should be inferred. Final recommendations for management actions will be based upon the results of this and other investigations.

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EXECUTIVE SUMMARY

This study continued the investigation initiated on 25 July 1985 in response to the 1985 noxious brown-tide bloom of *Aureococcus anophagefferens*. Its dual purpose was to continue for a second year the on-line quantitative field measurements of phytoplankton - zooplankton - environment along the salinity - nutrient gradient in Narragansett Bay and to continue evaluation of the brown-tide dynamics, its environmental regulation and food-web consequences, should this bloom reoccur.

Water samples were collected from three depths at seven stations along a transect extending from the Providence River to Fox Island during 28 surveys from 2 July 1986 - 29 June 1987. The following variables were measured: temperature, salinity, Secchi Disc depth, NH_4, NO_3, SiO_2, PO_4, chlorophyll, ATP, phytoplankton numerical abundance and species composition, primary production, zooplankton numerical abundance, biomass and species composition, ctenophore abundance, and benthic larvae abundance. During the two years, 62 transects with 434 station visits and about 1300 discrete sample collections were made.

The principal findings during this second year of investigation were: failure of the *Aureococcus* "brown-tide" to develope during 1986 following a brief bloom in June; its absence in May - June 1987 --- the period when the early stages of its bloom development occurred in 1985 and 1986; and the return to "normal" plankton dynamics between July 1986 - June 1987.

Nutrients, particularly those accreted into the upper Bay *via* the Providence River and STP inputs, strongly regulated phytoplankton growth in Narragansett Bay. Progressive dilution and utilization progressively increases the downstream importance of *in situ* remineralization and nutrient advection from offshore. A shift in dominant nutrient flux mode from accretion in upper Narragansett Bay to remineralization in lower Narragansett Bay probably occurs in the region of the Narragansett Bay Sanctuary waters (Station 5). Mean annual primary production exhibited a strong inverse correlation with salinity and strong positive correlations with PO_4, NO_3+NH_4 and SiO_3 concentrations, similar to first-year results.

Mean annual biomass levels regressed against nutrient levels produced a "bell-curve" pattern. Mean annual biomass levels during 1986 - 87 were from 4.0 to 12.0 mg m^{-3} less than during 1985 - 86; annual mean production rates were similar, excluding a 33% higher rate adjacent to Sanctuary waters (Station 5) during 1986 - 87. Two mechanisms may be operative in suppressing a greater phytoplankton biomass development in response to high nutrient enrichment of the Providence River: growth repression due to chemical water quality and washout.

Mean 1986 - 87 zooplankton biomass and copepod numerical abundance generally exceeded 1985 - 86 levels, which were adversely effected by the "brown-tide" event. *Acartia tonsa* dramatically increased relative to 1985 - 86, and cladocerans reappeared. Mean zooplankton biomass was strongly correlated with mean surface phytoplankton biomass and mean annual primary production, similar to 1985 - 86.

Dynamics of the ctenophore *Mnemiopsis leidyi,* carnivorous on zooplankton, differed from its 1985 - 86 patterns, indicative of considerable inter-annual variability in dynamics and associated trophic interactions of this carnivorous, gelatinous zooplankter.

The results of the two-year study indicate considerable inter-annual variability occurs at both the phytoplankton and ctenophore trophic levels, with

associated effects on zooplankton dynamics. Nutrient enrichment of upper Narragansett Bay and downstream dispersal are stimulatory to increased phytoplankton biomass and production. Downstream encroachment of the nutrient-rich plume into Narragansett Bay Sanctuary waters, with associated increased biomass, primary production, red-tide blooms and anticipated bottom-water oxygen utilization is detectable. The phytoplankton flora of Narragansett Bay presently includes at least ten species associated with noxious and/or toxic blooms locally (*) and/or elsewhere within their distributional range: (*) *Aureococcus anophagefferens*, *Dinophysis acuminata*, *Dinophysis acuta*, *Dinophysis norvegica*, *Fibrocapsa japonica*, *Gymnodinium splendens*, (*)*Heterosigma akashiwo*, *Phaeocystis pouchetii*, *Prorocentrum minimum* and *Scrippsiella trochoidea*. Thus, there is large indigenous community of inimical species within Narragansett Bay with associated high potential of developing nuisance blooms. Bloom events of these species are unpredictable, and have been implicated in fish-kills, invertebrate die-offs, diarrhetic shellfish poisoning and fin-fish and shellfish recruitment failure. There is, as yet, no evidence for the occurrence of the paralytic shellfish poison species, *Alexandrium tamarense*, within Narragansett Bay, and which has spread into Long Island Sound.

The remarkable indifference of the Narragansett Bay Project and RIDEM to the need for, to nurture and their failure to support a continuous, adequate quantitative phytoplankton program within Narragansett Bay, given the commercially important shellfishery and occurrence of bloom species potentially detrimental to this industry and public health, is lamentable. The vulnerability of this shellfishery to noxious species and, potentially, anoxia accompanying red-tide bloom events and the need for consumer protection should be a major concern of the Narragansett Bay Project and RIDEM.

Four of the five anonymous reviewers of this report pointed out that this two years' study "-- provides an excellent base from which to monitor the progress of nuisance algal blooms"; that "-- much of the successes to date (in Narragansett Bay) would not have been achieved in most other areas where (similar) extensive time-series data sets -- are not available"; that "multi-year time-series have potential to provide insight into plankton - environmental synergisms and identify unusual factors related to nuisance blooms". Another reviewer expresses sorrow "-- to see the core of the work end and would counsel some skeletal portion of it to continue to preserve Smayda's long-term base continuity", and that "terminating this study is not wise". I concur with these evaluations and recommendations. Meaningful understanding of the dynamics, trophic consequences and environmental regulation of the phytoplankton based - benthically coupled ecosystem in Narragansett Bay requires quantitative investigation of bay-wide plankton dynamics. Without this quantification, management of this resource will be compromised, if not misguided. It is recommended that such studies be reinitiated.

SUMMARY

This study represents a continuation of the study initiated on 25 July 1985 in response to the "brown-tide" outbreak during the 1985 summer. The results of that study carried out during 34 transects between 25 July 1986 and 18 June 1987 were described in the Final Report submitted to the Narragansett Bay Project entitled: ENVIRONMENTAL CONDITIONS AND PLANKTON DYNAMICS IN NARRAGANSETT BAY DURING AN ANNUAL CYCLE CHARACTERIZED BY A BROWN-TIDE.

In addition, the following publications describing various aspects of the 1985 brown-tide event have been prepared:

1986	Smayda, T.J. Occurrence and Distribution of the 1985 Brown Tide in Narragansett Bay. <u>In</u>: Proceedings of the Emergency Conference on "Brown Tide" and Other Unusual Algal Blooms, pp. 7-8. N.Y. State Interagency Committee on Aquatic Resources Development, 1986.
1989	Smayda, T.J. & T. Villareal. An extraordinary, noxious "brown-tide" in Narragansett Bay. I. The organism and its dynamics. Pp. 127-130 <u>In</u>: Red Tides: Biology, Environmental Science and Toxicology, T. Okaichi, D.M. Anderson, and T. Nemoto (Eds.), Elsevier, N.Y. (See ANNEX #1)
1989	Smayda, T.J. & P. Fofonoff. An extraordinary, noxious "brown-tide" in Narragansett Bay. II. Inimical effects. Pp. 131-134 <u>In</u>: Red Tides: Biology, Environmental Science and Toxicology, T. Okaichi, D.M. Anderson, and T. Nemoto (Eds.), Elsevier, N.Y. (See ANNEX #2)

1989 Smayda, T.J. & T.A. Villareal. The 1985 "brown-tide" and the open phytoplankton niche in Narragansett Bay during summer. (in press; In E. Cosper (Ed.) Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms. Lecture Notes on Coastal and Estuarine Studies. Springer-Verlag, New York. (See ANNEX #3)

In addition, exclusive of symposia/workshops arranged by the Narragansett Bay Project, the following invited papers were presented at symposia:

Oct 1988 The 1985 "brown-tide" and the open phytoplankton niche in Narragansett Bay during the summer. Symposium on Novel Phytoplankton Blooms. SUNY Stony Brook, NY, 27-28 Oct.

Jan 1988 Phytoplankton Dynamics along the Nutrient Gradient in Narragansett Bay. AGU/ASLO Ocean Sciences Meeting, New Orleans, 18-22 Jan.

Nov 1987 An Extraordinary, Noxious "Brown Tide" in Narragansett Bay. I. The Organism and its Dynamics. International Symposium on Red Tides, Takamatsu, Japan.

Nov 1987 An Extraordinary, Noxious "Brown Tide" in Narragansett Bay. II. Inimical Effects. International Symposium on Red Tides, Takamatsu, Japan.

METHODS

Seven stations were established (Figure 1) along a salinity-nutrient gradient from lower Narragansett Bay (Station 7) to the entrance into the Providence River (Station 2). Stations 5 and 6 were in the region of the Narragansett Bay Sanctuary waters. Station 1 was located in Greenwich Bay, which supports a major quahog (*Mercenaria mercenaria*) shellfishery. The station grid was chosen to evaluate the environmental conditions in representative segments of Narragansett Bay and the effects of this regional environmental mosaic on plankton dynamics.

The sampling period extended from 2 July 1986 - 29 June 1987 and consisted of 28 transects. At each station samples were collected from the surface, mid and bottom depths independent of tidal phase. The average total depth (m) for the sampling period at the seven stations is given in Table 1:

Table 1

STATION:	1	2	3	4	5	6	7
	8.1 m	12.2	13.4	13.5	10.8	6.8	7.0

At each station, measurements of light transmission (Secchi Disc depth) and temperature were made upon arrival. Otherwise, the samples were returned to the laboratory for determination of salinity (by refractometer), nutrients, chlorophyll, ATP, phytoplankton and zooplankton.

Surface water samples were collected with a clean plastic bucket or by holding a clean plastic bottle just below the surface. Subsurface samples were collected with PVC Niskin® bottles or vacuum pump. Raw seawater samples were stored and transported to the laboratory in clean polyethylene bottles. (Bottles were cleaned between uses by repeated rinse with tap water and deionized water.) Upon return to the laboratory, subsamples were immediately filtered through precombusted (500°C - 1 hr) glass fiber filters (Gelman A/E). (After a suitable rinse with sample. these filters showed negligible leaching of the measured nutrients, including silicate. Samples were filtered within several hours after collection and stored in 2 oz. polyethylene bottles with polyethylene lined caps. When at all possible, nutrient analyses are run on freshly filtered samples. When samples were not immediately analyzed, they were deep frozen (-10°C) for periods of less than one month.

The concentrations of PO_4, NH_4, NO_3 and SiO_3 were measured using standardized methods for micronutrients in seawater (Strickland and Parsons, 1972), and carried out on a Technicon Autoanalyzer® using slight modifications of these methods. The analytical manifolds and reagents for ammonia, nitrate + nitrite and silicate analysis were as given by Friederich and Whitledge (1972), and the phosphate manifold and reagents as given by Grasshof (1966). Nutrient analyses were run in duplicate, and in triplicate on occasion.

Chlorophyll a and phaeophytin were measured using the fluorescent technique introduced by Yentsch and Menzel (1963), incorporating the modifications recommended by Lorenzen (1966) and ancillary procedures and steps recommended by an international committee (Joint Group of Experts on Determination of Photosynthetic Pigments (UNESCO, 1966).

Two types of counting chambers were used to enumerate the phytoplankton (live counts were made through 2 October 1987): Haemocytometer and Sedgwick Rafter Chamber. An Improved Neubauer Haemocytometer was used (Guillard, 1978) to assess nannophytoplankton (< 10 µm diameter) abundance when present in high abundance. The minimal number of cells detectable by this counting procedure is 1,000 cells ml^{-1}. The Sedgwick Rafter Chamber was used to enumerate the larger cells following the procedures of McAlice (1971). The Haemocytometer counts were pooled with the Sedgwick-Rafter counts to yield total phytoplankton numerical abundance.

Productivity measurements were made by the ^{14}C method (Steemann Nielsen, 1952) on a pooled sample containing equal proportions of the top, mid and bottom-depth samples. The productivity samples were incubated in 50 ml glass bottles (initially cleaned with hot Ultrex 0.1N HCl and rinsed with 18 megohm deionized H_2O) inoculated with 2µCi $H^{14}CO_3$. The samples were incubated under ambient temperature and light in an outdoor flow-through incubator through which Narragansett Bay water flowed. The flushing time of the incubator was 30 mins. The productivity samples, in duplicate, were exposed to 100%, 60%, 25%, 10% and 3% natural irradiance for 24 hrs. After 24 hours incubation, the material was filtered onto GF/F filters, rinsed with 20 ml of filtered seawater, placed in glass scintillation vials and treated with 0.1 ml of 0.1 N HCl to minimize isotope adsorption onto the filters (Lean and

Burnison, 1979). Activity was measured with a Beckman LS-150 scintillation counter to a minimum of 4000 cpm for each sample. Light intensity was monitored continuously during the incubation with Epply pyrheliometer located near the incubation platform.

The following procedures were used to assess the zooplankton community. Ctenophores and large medusae were sampled using a 1 m^2 square net with 1 mm mesh. The net was lowered to within 1 m of the bottom and hauled vertically, with the ship at rest. Replicate tows were made. The ctenophores, removed from the net with a spoon, were sorted and counted by size classes (> 1 cm, 1-2 cm, 2-4 cm, < 4 cm) using a gridded dish.

Two nets were used to sample the non-gelatinous zooplankton: a 153 µm mesh net fitted with a TSK flowmeter and a 64 µm mesh net fitted with a General Oceanics flowmeter. At station 7, a 20 µm phytoplankton net is towed in place of the 64 µm mesh net. All of these nets have a 0.305 m mouth diameter. A double oblique tow was made, during which the net was slowly lowered to within 1 m of the bottom and raised at a towing speed ot 1-2 knots. Each tow filtered 1 to 4 m^3 of water.

The 153 µm net samples were split in the laboratory using a sediment splitter. Half of the sample was sieved, rinsed with deionized water, dried for four weeks at 60°C in aluminum weighing pans, and the dry weights determined using a Mettler H-16 balance. The other half of the sample was preserved in 5% formalin for counting. The 64 µm net samples were preserved without splitting.

The most common planktonic forms, copepods, cladocerans, and more abundant benthic invertebrate larvae were identified to species; other forms to closest possible taxon. The 153 µm preserved sample was examined for macrozooplankton (chaetognaths, medusae, fish and decapod larvae), and also used to estimate the numbers of copepodite and adult stages of copepods and other organisms over 20 mm in width. The 64 μm net sample was used to estimate numbers of copepod nauplii and smaller forms of meroplankton.

RESULTS

Physical Oceanography

The temperature, salinity and density (σ_t) characteristics at the seven stations for the 28 transects surveyed between 2 July 1986 and 29 June 1987 are given in Appendix Tables 1, 2, 3.

A crisp surface salinity gradient characterizes Narragansett Bay. The mean surface values progressively decreased upbay from 29.4 ^{o}/oo (Station 7) to 21.2 ^{o}/oo (Station 2) in the Providence R. off Fields Pt. This gradient in mean salinity is virtually identical to that observed during 1985-1986 annual study (25 July 1985 - 18 June 1986): 30.3 ^{o}/oo (Station 7) to 20.7 ^{o}/oo (Station 2). The mean surface and bottom temperature and salinity levels were:

Table 2

STATION:	1	2	3	4	5	6	7
Surface °C	11.8	12.6	12.6	11.9	12.8	12.9	12.4
Bottom °C	11.5	12.5	12.0	11.9	12.9	12.8	11.5
Surface S ^{o}/oo	28.1	21.2	23.1	25.3	28.0	29.0	29.4
Bottom S ^{o}/oo	29.1	29.7	29.7	29.9	29.2	29.5	30.1

Mean bottom water salinities are higher, but similar; a feature consistent with a two-layer estuarine circulation pattern. Moreover, the mean salinities in 1986-87 were nearly identical with those observed in the 1985-1986 study. These mean salinity values and their vertical and horizontal gradients indicate the inter-annual persistence of the well-developed salinity gradient in Narragansett Bay. The strength of this gradient varies with the volume of freshwater input. This is reflected in the considerable range in surface salinity found at Stations 1 - 4, and to a lesser extent at lower Narragansett Bay Stations 5 - 7 (Table 3).

Table 3

	1986-1987			1985-1986		
STATION	Minimum	Maximum	Δ o/oo	Minimum	Maximum	Δ o/oo
1	20.2	30.1	9.9	17.1	31.7	14.6
2	6.8	26.5	19.7	10.9	28.6	17.7
3	11.4	28.0	16.6	11.8	28.6	16.8
4	11.6	29.6	18.0	16.5	30.7	14.2
5	23.3	31.7	8.4	24.4	30.7	6.3
6	25.4	30.7	5.3	27.5	31.7	4.2
7	23.9	31.7	7.8	28.6	31.7	3.1

Surface salinity at Station 2 exhibited a 19.7 o/oo range during 1986-87; a 16.6 o/oo range at Station 3, and 18.0 o/oo range at Station

4. Similar, pronounced oscillations also characterized this region of upper Narragansett Bay during the 1985-1986 surveys. The considerable distance of Stations 5, 6, 7 downbay from riverine inputs is reflected in the narrower annual range of fluctuation surface salinity evident at those stations. Considerable week-to-week and seasonal variations in the salinity gradient accompany the rainfall patterns. This oscillating gradient was particularly intense during the surveys carried out 15 April 1987 (Appendix Tables 2, 3). The annual minima in surface salinity recorded at all stations occurred on that date. Particularly intense freshening of the surface waters is commonplace at Stations 2 and 3 which contributes to pronounced vertical stratification of the watermass.

The horizontal salinity gradient is accompanied by a well-defined vertical salinity gradient, also evident in the vertical density (σ_t) profiles (Appendix Tables 2, 3). This vertical gradient influences water column mixing, the degree of vertical stratification and wash-out rate of the plankton. The σ_t Profiles (Appendix Table 3) indicate that Stations 1, 5, 6 and 7 are vertically mixed to the bottom throughout the year. In contrast, upper bay Stations 2, 3 and 4 are usually stratified year-round, with a distinct halocline present. The transitional area between the vertically mixed and stratified regions of the bay lies between Stations 4 and 5. This regional sub-division of hydrographic-mixing structure along the salinity gradient also characterized Narragansett Bay during the 1985-1986 surveys. As also found during the latter, at times of particularly voluminous freshwater inputs, and especially when facilitated by wind conditions, the entire bay may become stratified for a brief period, such as found during the

15 April 1987 transect (Appendix Table 3). Such bay-wide stratification, however, is just as infrequent as is the occurrence of vertical mixing to the bottom at Stations 2, 3, 4.

Stations 1, 5, 6 and 7 clearly reflect the influence of bottom water inflow into West Passage which continues upbay as a countercurrent to the offshore flow of the less saline, near-surface waters. The bottom water at Station 4, in contrast, is often clearly distinguishable from that at Station 5. The vertical temperature, salinity and σ_t patterns at Station 4 strongly point to an influx of bottom water different from that at Station 5. Using mean values (Table 1), the mean bottom water salinity (29.9 $^o/oo$) at Station 4 is 0.7 $^o/oo$ more saline than (29.2 $^o/oo$) at Station 5, and the mean bottom temperature 1.0°C lower. For the 1985-1986 surveys, the mean annual differences were +0.8 $^o/oo$ and +1.1°C greater at Station 4. Thus, the average bottom water at Station 4 is more saline and colder than at Station 5, characteristics inconsistent with an incursion of bottom water upbay from the latter station. Differences in the mean surface temperature between Stations 3, 4 and 5 are also conspicuous. The mean surface temperature (11.9°C) at Station 4 is 0.7 to 0.9°C colder than at Stations 5 and 3 (Table 1). Colder surface waters, on average by -0.5 to -0.8°C, characterized the 1985-86 surveys. Examination of the individual transect surveys (Appendix Tables 1, 2, 3) revealed that during the 1985-86 surveys Station 4 was frequently characterized by an influx of colder, more saline bottom, with an indication of periodic "upwelling" of this watermass to the surface. Such "upwelling" was not as evident during 1986-87. The periodic influx of a different watermass at Station 4 is also signaled as a core of warmer, more saline water during the winter, (see, for example, 8 and 17 December 1986; Appendix Tables 1, 2). Moreover, the bottom water characteristics at Station 3 suggest that this watermass periodically penetrates to that region.

It seems likely, then, that Station 4 frequently is influenced by incursions of bottom water from East Passage (Figure 1) in addition to inputs from West Passage. This region of Narragansett Bay represented by Station 4 may therefore be a particularly unique segment hydrographically along the transect gradient. It appears to be both a buffer zone and transitional region between the upper and lower bay stations with regard to freshwater input, water quality and mixing characteristics. It also exhibits a circulation pattern more complex than a simple two-layer estuarine flow. Both upwelling of bottom water and gyre flow may be occurring as a consequence of an influx of East Passage bottom water, together with an inflow of West Passage bottom water moving upbay. These physical features would be expected to influence plankton dynamics at Station 4 in several key ways, including enhancement of productivity. This will be examined elsewhere in this report. The foregoing physical oceanographic conclusions are similar to those reached by, and are reinforced by the 1985-86 survey results.

Light Penetration

The Secchi Disc measurements of light transmission are given in Appendix Table 4. Absorbance by suspended particles, chlorophyll and dissolved organic matter within the water column affect the *in situ* transmission of incident light. The relative contribution of these parameters to light transmission can not be determined from the available data. Since riverine input of particulate matter accompanies runoff, the general relationship between salinity and light transmission will be evaluated. The mean Secchi Disc measurements are given in Table 4.

Table 4

STATION:	1	2	3	4	5	6	7
1986-87							
Secchi Depth (m)	2.35	2.06	2.10	2.24	2.44	2.55	2.73
k (m^{-1})	0.61	0.70	0.69	0.64	0.59	0.56	0.53
1% Isolume Depth (m)	7.6	6.6	6.7	7.2	7.8	8.2	8.7
1985-86							
Secchi Depth (m)	1.90	1.71	1.80	1.88	2.12	2.20	2.42
k (m^{-1})	0.76	0.84	0.80	0.77	0.68	0.65	0.60
1% Isolume Depth (m)	6.1	5.5	5.8	6.0	6.8	7.1	7.7

The average Secchi Disc depths during the 1986-87 surveys ranged from 2.06 (Station 2) to 2.73 m (Station 7), with Secchi Disc depth progressively decreasing upbay along the salinity. Regression of mean Secchi Disc depth against mean surface salinity revealed a strong positive correlation ($r^2 = 0.85$), with all stations representing a single data cluster. This contrasts with the 1985-86 results, when the seven stations segregated into two distinct optical watermass types, each characterized by very strong positive correlations (the slopes of the regression lines differed significantly). The upper Narragansett Bay and Greenwich Bay stations (1, 2, 3, 4) comprised one optical group; the lower bay stations the other group. Their correlation coefficients were $r^2 = 0.98$ and $r^2 = 0.92$, respectively. These correlations suggested that increased turbidity accompanies decreasing salinity. This was further evaluated by regressing the mean extinction coefficients, k (Table 3), against mean salinity. Extinction coefficients per m^{-1} (k) were calculated from (Holmes, 1970):

$$k = 1.44/D$$

where D is Secchi Disc depth in m. A strong inverse correlation ($r = -0.95$) occurred between salinity and the extinction coefficient, with all stations grouping along the regression line, as the 1985-86 relationship ($r = -0.89$. Thus, the observed salinity gradient was accompanied by a gradient in the light transmission properties, with the extinction coefficient (= turbidity) progressively increasing upbay. This inverse relationship most likely is partly attributable to the associated increase in chlorophyll with decreasing salinity. The "bell-shaped" distribution of chlorophyll against salinity suggests also that terrigenous matter is particularly important in governing turbidity from Station 2 to 3, while the relatively high phytoplankton densities at "downstream" Stations 4 and 5 are a more significant determinant of turbidity and euphotic zone depth (see Figure 10; Tables 2, 4).

The 1% isolume depth, commonly believed to define the depth of the euphotic zone, was calculated based on the equation for the penetration of light in sea water:

$$I_z = I_o e^{-kz}$$

where I_z is the irradiance at a given isolume depth (z), I_o is the incident irradiance and k is the extinction coefficient.

The 1% isolume depth varied from 6.6 to 8.7 m (Table 3). Relative to the station water column depths at Stations 6 and 7, photosynthetic carbon production (i.e., the euphotic zone) extended to the bottom sediments. At Stations 5 and 1, the euphotic zone ranged from 70 to 90% of the water column and at the upper bay stations (2, 3, 4) roughly the upper half of the water column.

The salinity gradient therefore influences light transmission and the depth of the euphotic zone. The proportion of the total water column depth in which photosynthesis could occur decreased with salinity.

Relative to the 1985-86 surveys the average transparency of the watermass increased at all stations during the 1986-87 surveys. At Station 2, which had the poorest light penetration, the euphotic zone depth (1% depth) increased by 20%, from 5.5 to 6.6 m; at Station 7, the least turbid station, mean euphotic zone depth increased by 13%, from 7.7 to 8.7 m, with the greatest percentage increase (25%) occurring at Station 1. Along the entire transect, the mean euphotic zone depth increased by about 1.0 to 1.5 m between annual surveys, a relatively significant increase in these relatively shallow waters.

Nutrients

The concentrations of PO_4, NH_4, NO_3 and SiO_3 are given in Appendix Tables 5, 6, 7, 8. Text Table 5 summarizes the mean concentrations and maximal and minimal nutrient levels at the surface.

All nutrients exhibited a conspicuous range in concentration, even at Station 2 (Providence R.) where pronounced accretion resulted from both riverine and sewage effluent inputs. Station 2 is within, or adjoins the zone of initial dilution of the Narragansett Bay Commission sewage treatment plant (STP) at Fields Point in the Providence River (Figure 1). Stations 3 and 4 lie within the region directly subjected to STP inputs during downstream flow of the enrichment plume. The maximal surface concentrations of PO_4, NH_4, NO_3 and SiO_3 at Station 2 were 8.2, 56.3, 37.9 and 146.7 mg-at m^{-3}, respectively. At Station 7 in lower Narragansett Bay, these values were 2.5, 8.9, 12.2 and 45.9 mg-at m^{-3}, respectively. Maximal PO_4, NO_3 and SiO_3 surface concentrations in the Providence River were about 3- to 4-fold greater; NH_4 concentrations about 6-fold greater. The minimal concentrations at Station 2, which reflect reduced input and/or phytoplankton utilization, were significantly lower than the maximal concentrations, and even below maximal levels recorded at Station 7. The data collectively indicate that a distinct nutrient gradient occurs.

The seasonal cycles and dynamics for each nutrient were generally similar at all stations. (The surface concentrations will be used to illustrate this.) The annual maxima in PO_4 (Appendix Table 5) did not occur synchronously along the transect. Recorded maxima occurred in late July at Station 2; August at Station 5; mid-September at Stations 1, 3 and 6, and December at Stations 4, 7. (The data on 17 September at Station 6 are suspect; more likely, the maximum occurred in late November/early December, as at Station 7.) A conspicuous decrease to $\leq$ 0.4 mg-at m^{-3} occurred simultaneously between 24 February and 2 March 1987 at Stations 1, 5, 6 and 7 during the winter-spring bloom, and dropped below 1 mg-at m^{-3} at Stations 3 and 4 after mid-April. The annual PO_4 maxima during the 1985-86 surveys, in contrast, occurred during the summer brown-tide event at Stations 1, 5, 6 and 7. Upper bay Stations 2, 3 and 4 exhibited maximal levels during mid-September during the "brown-tide" event.

The NH_4 maximum (Table 5; Appendix Table 6) exhibited a conspicuous downbay shift in time of its occurrence: mid-September at upper bay Stations 2, 3 and 4; late October at Station 1 (Greenwich Harbor); early November at Station 5, and late November at lower bay Stations 6 and 7. At Stations 2, 3 and 4, conspicuous differences between surface and bottom concentrations generally occurred throughout the annual cycle. During the mid-September maxima, surface concentrations were about 3.7- to 8-fold greater. In contrast, at Station 5 the difference was 1.6-fold; at the lower bay Stations 1, 6 and 7, surface and bottom concentrations were similar during the annual maxima. The occurrence of an extremely rich NH_4 surface layer relative to deeper waters was a persistent characteristic at Stations 2, 3 and 4 from November through May. These different patterns in the vertical concentration gradient reflect the highly stratified conditions present year-round in the upper bay, the well-mixed water-column characteristic of the lower bay throughout the year, with Station 5 located in the transitional region between these two hydrographic extremes. The significant and variable surges in NH_4 concentrations occurring between sampling periods is an additional characteristic of the NH_4 cycle. For example, at Station 3 (Appendix Table 6) during September 1986, the surface concentrations were 18.1, 9.4 and 40.2 mg-at m^{-3} during 3, 10 and 17 September, respectively. Such transect-to-transect surges particularly characterized the upper bay stations which are influenced more directly by Providence R. and Fields Pt. sewage treatment discharges than are the lower bay stations.

Significant NH_4 levels occurred throughout the annual cycle at Stations 2 and 3. At Station 2, the minimum recorded value was 8.3 mg-at m^{-3} (Table 6); surface levels (n = 26) were otherwise always > 12 mg-at m^{-3}. At Station 3, where the minimum surface concentration was 2.8 mg-at m^{-3}, surface levels exceeded 9.0 mg-at m^{-3} during 24 of the 28 transects. At the other stations, the effect of phytoplankton growth on NH_4 concentrations was much more evident (Table 5, Appendix Table 6), particularly during the winter-spring bloom growth in January and thereafter. The NH_4 annual cycles during the 1985-86 and 1986-87 survey years were generally similar.

The NO_3 maxima (Appendix Table 7) at Stations 2, 3 and 4 in mid-September coincided with the NH_4 maxima. At lower bay Stations 5, 6 and 7, the annual NO_3 maxima occurred in late November, and in mid-December in Greenwich Bay (Station 1). These two distinct maximal NO_3 peaks contrast with the downbay shift in time of occurrence described for the NH_4 maxima. The conspicuously higher NO_3 levels in the surface waters at Stations 2, 3 and 4 relative to deeper layers led to sharp differences in the vertical NO_3 gradients and surges between sampling transects, similar to the NH_4 patterns. A sharp decrease in NO_3 concentrations occurred at all stations in February accompanying the winter-spring bloom. These decreases coincided with those for NH_4 at Stations 1, 5, 6 and 7.

The SiO_3 maxima (Table 5; Appendix Table 8) occurred in July at Stations 1, 4, 6, 7, and in January at Stations 2, 3. (While very high SiO_3 concentrations also occurred in July at Station 5, the recorded surface maximum (52.1 mg-at m^{-3}) in early December slightly exceeded maximal July levels (48.2 mg-at m^{-3}). Levels were persistently high throughout the year, although a conspicuous decrease occurred at Stations 1, 4, 5, 6 and 7 in February (coincident with the sharp decreases in NH_4 and NO_3.) Levels then continued to decrease: to ca. 1 mg-at m^{-3} at lower bay Stations 1, 5, 6, 7; to about 6 mg-at m^{-3} at Stations 3 and 4. The minimum at Station 2 (25.1 mg-at m^{-3}) exceeded the mean concentration at the other stations exclusive of Station 3 (Table 5).

Table 5

STATION:	1	2	3	4	5	6	7
PO_4							
Mean	1.7	4.1	3.0	2.3	1.5	1.7	1.2
Min	0.0	0.6	0.1	0.1	0.1	0.0	0.0
Max	6.1	8.2	6.6	5.4	3.2	10.8	2.5
NH_4							
Mean	3.6	29.6	17.4	10.6	4.2	3.5	2.4
Min	0.2	8.3	2.8	0.8	0.3	0.1	0.4
Max	11.5	56.3	40.2	45.3	16.3	13.5	8.9
NO_3							
Mean	4.3	21.2	14.4	9.1	5.3	4.5	3.5
Min	0.2	8.7	1.3	0.0	0.1	0.1	0.0
Max	18.5	37.9	27.8	29.5	17.6	15.9	12.2
NH_4+NO_3							
Mean	7.9	50.9	31.8	20.3	9.5	8.0	5.9

SiO_3

Mean	20.9	49.4	37.7	24.7	20.8	19.0	17.4
Min	1.2	25.1	6.8	5.7	1.1	1.0	1.0
Max	>60.0	164.7	84.5	49.0	52.1	50.5	45.9

As during the 1985-86 annual surveys: in 1986-87 the highest nutrient concentrations occurred in upper Narragansett Bay; the region between Stations 4 and 5 was transitional to the lower nutrient environment of lower Narragansett Bay; these regional nutrient distributions were strongly coupled to the salinity gradient. Nearly perfect inverse correlations occurred between the mean PO_4, NH_4, NO_3, NH_4+NO_3 and $Si(OH)_4$ concentrations and salinity at the surface (Figures 2, 3, 4, 5, 6; Table 8). This reflects both the significant accretion of nutrients into upper Narragansett Bay accompanying runoff and sewage discharge and the progressive dilution and utilization of these nutrients along the downbay axis. These distributions also indicate that two significantly different nutrient input mechanisms occur along the nutrient-salinity gradient. In the upper bay: riverine, STP and urban inputs represent a nutrient pump. At the entrance into lower Narragansett Bay: "new" nutrient is introduced via the advection of nutrients accompanying inflow of bottom water. Supplementing these two mechanisms, nutrient recycling accompanying food web dynamics occurs along the entire gradient accompanying food web dynamics. Along the salinity gradient, the relative importance of these mechanisms changes, with <u>in situ</u> recycling and offshore nutrient inputs progressively becoming more important downbay. The persistence of extremely high nutrient concentrations at Stations 2 and 3, and the low concentrations at Station 7, with intermediate characteristics at Stations 1, 4, 5, 6, is a manifestation of these differing mechanisms.

Table 6 compares mean surface concentrations during the 1986-87 surveys to those during 1985-1986. Regression of the mean 1986-1987 NH_4, NO_3 and $NH_4{+}NO_3$ levels against salinity indicates almost perfect agreement with the 1985-86 series (Figures 2, 3, 4). The primary difference is in mean concentrations (Table 6). Mean NH_4 levels during 1985-86 at Stations 2 and 3 were ca. 3.7 to 6.9 mg-at m^{-3} greater than those in 1986-87, i.e., corresponding to differences in mean loading of 13% and 39%, respectively. At the other stations, mean concentrations were similar during both annual surveys. Mean NO_3 concentrations, in sharp contrast to NH_4, were considerably greater (by +1.27 to +2.67 mg-at m^{-3}) at Stations 1, 4, 5, 6, 7. This represented a 2.4- to 2.6-fold increase in average NO_3 concentrations at lower bay Stations 1, 6 and 7 over 1985-86 levels. In contrast, mean NO_3 concentrations at upper Narragansett Bay Stations 2 and 3 were approximately equivalent during the two annual surveys.

Differences in mean concentrations of $NH_4{+}NO_3$ were clearly evident between years. Mean concentrations at Stations 2 and 3 during 1985-86 were ca. 3 to 6 mg-at m^{-3} greater than in 1986-87. These differences of about 6% and 19%, respectively, were modest relative to the very high mean $NH_4{+}NO_3$ concentrations found at these stations. In contrast, the mean combined inorganic N levels at the other stations during 1986-87 were from +1.45 to +3.57 mg-at m^{-3} greater than those during 1985-86. At Stations 1, 6 and 7 the 1986-87 mean levels were about 80% higher.

Table 6

STA.	1	2	3	4	5	6	7
NH_4							
1986-87	3.56	29.63	17.37	10.62	4.20	3.47	2.39
1985-86	2.66	33.34	24.22	11.07	4.26	2.70	1.94
△	+0.90	-3.71	-6.85	-0.45	-0.06	+0.77	+0.45
NO_3							
1986-87	4.31	21.23	14.41	9.07	5.34	4.52	3.47
1985-86	1.64	20.70	13.70	7.80	3.70	1.90	1.30
△	+2.67	+0.53	+0.71	+1.27	+1.64	+2.62	+2.17
$NH_4^+NO_3$							
1986-87	7.87	50.86	31.78	20.32	9.54	7.99	5.86
1985-86	4.30	54.04	37.92	18.87	7.96	4.60	3.24
△	+3.57	-3.18	-6.14	+1.45	+1.58	+3.39	+2.62
PO_4							
1986-87	1.67	4.08	3.01	2.27	1.54	1.34	1.20
1985-86	1.36	5.43	4.14	3.56	1.49	1.55	1.02
△	+0.31	-1.35	-1.13	-1.29	+0.05	-0.21	+0.18
$Si(OH)_4$							
1986-87	20.94	49.38	37.65	24.72	20.75	18.97	17.43
1985-86	16.51	34.76	28.39	17.59	13.07	12.23	10.69
△	+4.43	+14.62	+9.26	+7.13	+7.68	+6.74	+6.74

The annual mean PO_4 concentrations were similar during both surveys, excluding the upper bay stations. 1986-87 mean levels at Stations 2, 3 and 4 were about 33% to 57% higher. The $Si(OH)_4$ mean levels, similar to NO_3, were generally higher during the 1986-87 survey. Mean values exceeded 1985-86 levels by +4.4 to +14.6 mg-at m^{-3}. In contrast to the reduced mean levels of PO_4 and NH_4 at Stations 2, 3 and 4, mean $Si(OH)_4$ concentrations were about +7.0 to +14.6 mg-at m^{-3} higher; 33% to 42% above 1985-86 levels. At Stations 5, 6 and 7, 1986-87 levels (ca. +7.0 mg-at m^{-3}) were 55% to 63% higher than 1985-86 levels.

It is evident, then, that significant inter-annual differences in mean nutrient levels occurred during the 1985-87 surveys. At Stations 2, 3 and 4, mean PO_4, NH_4 and (at 2, 3) NH_4+NO_3 concentrations were lower in 1986-87; $Si(OH)_4$ levels were substantially higher. During 1986-87, NO_3 and $Si(OH)_4$ levels were elevated baywide. The major similarity between annual surveys was the progressive increase in nutrients along the salinity gradient, and reflected in the strong inverse coupling between these variables (Figures 2-6).

Nutrient ratios (by atoms) also varied along the salinity gradient reflecting differing inputs, and those for N:P and N:Si were highly correlated with mean salinity (Figures 7,8; Tables 7, 8). The mean ratios of N:Si and N:P, by atoms, were strongly and inversely correlated with mean salinity ($r = -0.97$). The mean N:Si ratio (using both NH_4+NO_3) progressively decreased from 1.0:1 at Station 2 to 0.3:1 at Station 7, following a pattern similar to that observed in 1985-86. However, the considerably elevated $Si(OH)_4$ levels during 1986-87 resulted in a 25% to 37% reduction in the N:Si ratio at upper bay Stations 2, 3, 4 and 5 (Table 7). The mean N:P ratio progressively decreased from 12.5:1 at Station 2 to 4.9:1 at Station 7. The mean N:P ratio increased substantially at all stations, from +0.9 to 3.7 in absolute units, which corresponded to increases in the amount of nitrogen available to phosphorus by 53% (Station 7) to 70% (Station 7) in the lower bay; 47% in Greenwich Harbor (Station 1) and 15% to 25% at the other stations. Regression of the mean N:P ratios against mean salinity for both surveys (Fig. 7) yielded a highly significant correlation (r = -0.97; Table 8). However, the observed distribution suggests three distinct zones of mean N:P ratios characterize the salinity-nutrient gradient. Stations 2 and 3 are characterized by mean N:P ratios varying from about 9 to 10:1; Stations 4, 5 by ratios of about 5:1 (i.e., there is about 50% less N available per unit P), and lower by Stations 1, 6 and 7 by N:P ratios of about 3:1. This clearly indicates the progressively greater availability of N relative to P along the salinity gradient upwards into Narragansett Bay.

Table 7

STA.	1	2	3	4	5	6	7
N:P							
1986-87	4.7	12.5	10.6	9.0	6.2	6.0	4.9
1985-86	3.2	10.0	9.2	5.3	5.3	3.6	3.2
Δ	+1.5	+2.5	+1.4	+3.7	+0.9	+2.4	+1.7
N:Si							
1986-87	0.38	1.03	0.84	0.82	0.46	0.42	0.34
1985-86	0.26	1.56	1.33	1.08	0.61	0.38	0.30
Δ	+0.12	+0.53	-0.49	-0.26	-0.15	+0.04	+0.04
Si:P							
1986-87	12.5	12.1	12.5	10.9	13.5	14.2	14.5

1985-86	12.1	6.4	6.9	4.9	8.8	7.9	10.5
△	+0.47	+5.7	+5.6	+6.0	+4.7	+6.3	+4.0

The relationship between the Si:P ratio and mean salinity, in contrast, not only differed from the N:P and N:Si ratios, but also differed significantly between surveys (Fig. 9; Tables 7, 8). In 1985-86, the stations were clustered into two subgroups: Stations 1, 2, 3 and Stations 4, 5, 6, 7. The mean ratios for each group were strongly correlated with mean salinity, but *directly* rather than inversely. The correlations were 0.95 and 0.89, respectively, which decreased to 0.58 when all stations are pooled. Therefore, unlike the N:Si and N:P ratios, the Si:P ratios increased downbay with mean salinity. For the 1986-87 surveys, the mean Si:P ratios (10.9 to 14.5:1) were substantially higher than 1985-86 ratios. At the various stations, during 1986-87 there was from about 122% more $Si(OH)_4$ available per unit P; about 80% more at Stations 2, 3, 6; 53% more at Station 5; 30% more at Station 7 and unchanged at Station 1. This significantly increased availability of Si relative to both P and (at Stations 2, 3, 4, 5) N reflects the increased mean loading of $Si(OH)_4$ during the 1986-87 surveys. The correlation coefficient ($r = +0.67$) for all stations primarily reflects the strong correlation ($r = 0.92$) for Stations 1, 4, 5, 6, 7, which are clustered.

Table 8

	1986-87	1985-86	1985-87
PO_4 vs S ^{o}/oo	r = -0.97	-0.98	-0.93
NH_4 vs S ^{o}/oo	r = -0.97	-0.98	-0.97
NO_3 vs S ^{o}/oo	r = -0.97	-0.99	-0.98
$NH_4{}^{+}NO_3$ vs S ^{o}/oo	r = -0.97	-0.99	-0.98
$Si(OH)_4$ vs S ^{o}/oo	r = -0.96	-0.98	-0.91
N:P vs S ^{o}/oo	r = -0.97	-0.95	-0.92
N:Si vs S ^{o}/oo	r = -0.97	-0.95	-0.89
Si:P vs S ^{o}/oo	r = +0.67	+0.58	

An additional aspect of the salinity-nutrient gradient which characterized both surveys is the occurrence of a crisp gradient in nutrient ratios, and in which N becomes increasingly more available relative to both P and Si with decreasing salinity. The stoichiometry between Si and P is more complex, with subgroups of stations occurring. However, there is a general trend in which Si becomes less abundant relative to P with decreasing salinity. Such nutrient resource ratios can be expected to influence phytoplankton community structure.

Appearance and failure of the "brown-tide" in 1986:

Aureococcus anophagefferens, the species responsible for the "brown-tide" outbreak during the 1985 summer was detected in great numbers at the transect stations on 14 May 1986. Surface populations

(T) ranged from 53 to 180 million cells L^{-1}, and bottom populations from 106 to 254 million cells L^{-1}. The bottom populations (B) were from 18% to 236% greater than surface populations, excluding Station 7 where a homogeneous vertical distribution occurred. The phytoplankton community was otherwise depauperate and dominated by Skeletonema costatum (< 0.5 million cells L^{-1}) and, secondarily, by Chaetoceros socialis.

Abundance (cells ml^{-1}) of Aureococcus on 14 May and its subsequent abundance patterns at the surface were:

STATION:	1	2	3	4	5	6	7
14 May	101,101	79,992	53,328	94,435	107,767	79,992	104,434
21	394,415	103,323	92,213	155,540	35,552	105,545	81,103
28	211,090	138,875	211,090	116,655	126,654	97,768	95,546
4 June	114,433	32,219	58,880	71,104	102,212	126,654	102,212
18	93,324	44,440	78,881	53,328	59,994	109,989	176,649

During July, Aureococcus continued to decline making up a progressively decreasing proportion of the nannophytoplankton community, now dominated by other species:

STATION:	1	2	3	4	5	6	7
2 July	101,101	112,211	141,097	193,314	108,878	127,765	141,097
10	102,212	9,999	95,546	186,648	92,213	52,217	106,565
16	167,761	69,993	62,216	149,985	146,652	246,642	178,871
23	203,313	102,212	89,991	61,105	129,987	102,212	85,547
20 Aug	83,325	4,995	38,885	77,770	42,218	105,545	79,992

Clearly, *Aureococcus* failed to develop into a nuisance bloom event, despite its reappearance in May, as during 1985, and accelerated and abundant growth during June. By July its abundance began to wane and was then out-competed by other nannoplanktonic and picplanktonic species which did not achieve significant abundance levels.

A significant difference from 1985 in community structure was the appearance and persistence in great abundance during 1986 of heterotrophic (= holozoic) dinoflagellates capable of feeding on particles in the size range (~ 2 μm) of *Aureococcus*. Such holozoic dinoflagellates were initially insignificant during the 1985 brown-tide. The abundance (cells ml^{-1}) of these heterotrophs was:

STATION:	1	2	3	4	5	6	7
14 May	17	2	-	-	2	-	4
21	17	4	8	51	21	11	19
28	105	2	41	191	21	30	111
18 June	417	6	163	270	?	293	11
2 July	28	21	529	315	158	360	34
16	330	6	4	585	621	889	47
10 Sept	11	-	6	2	39	8	5
17	8	4	4	11	-	8	-

The heterotrophic flagellate community achieved great abundance concurrent with the demise of *Aureococcus anophagefferens*. The data suggest that predation of *Aureococcus* by the holozoic dinoflagellates regulated its abundance and contributed to failure of *Aureococcus* to form a "brown-tide" outbreak during the 1986 summer.

The principal phytoplankton event was the red-tide blooms of *Olisthodiscus luteus* and *Prorocentrum redfieldii* during early summer. Abundances (cells ml^{-1}) in early July were:

STATION:	1	2	3	4	5	6	7
Olisthodiscus luteus	489	15	90	214	4,084	1,294	529
Prorocentrum triangulatum	6	21	24	73	42	13	99

This community was replaced in mid-July by a bloom of the diatom *Skeletonema costatum*; *Prorocentrum redfieldii* and heterotrophic gymnodnioid dinoflagellates were also prominent:

STATION:	1	2	3	4	5	6	7
Skeletonema costatum	71	839	17,750	12,159	32,994	12,110	213
Prorocentrum redfieldii	13	4	23	96	146	108	64
Gymnodinioids	326	6	4	585	619	878	45

Diatoms continued to predominate during the summer, and by mid-September the small centric diatom *Thalassiosira pseudonana* co-dominated with *Skeletonema costatum*, with *Rhizosolenia fragilissima* of secondary importance; Gymnodinioids were unimportant:

STATION:	1	2	3	4	5	6	7
Skeletonema costatum	111	759	9,540	6,206	640	40	27
Thalassiosira pseudonana	22,380	619	11,414	3,425	2,008	669	96
Rhizosolenia fragilissima	15	81	759	332	178	258	439
Gymnodinioids	11	-	2	-	39	8	-

The diatom bloom continued into October, dominated by *Skeletonema costatum* and a diverse diatom and dinoflagellate community, including:

STATION:	1	2	3	4	5	6	7
Skeletonema costatum	827	645	2,633	1,148	1,350	1,333	140
Rhizosolenia fragilissima	259	45	?	231	338	186	54
Thalassionema nitzschioides	94	-	24	26	90	86	46
Prorocentrum redfieldii	11	13	26	24	6	-	-
Heterocapsa triquetra	4	8	6	9	8	-	-
Massartia rotundata	45	15	-	34	23	23	-

Thereafter, the phytoplankton community declined to its winter nadir, followed by a winter-spring bloom beginning in February 1987 in which *Detonula confervacea*, *Thalassiosira nordenskioeldii* and *Skeletonema costatum*, the normal winter-spring components dominated.

Exclusive of the 1985 brown-tide bloom of *Aureococcus anophagefferens*, the most distinctive aspect of summer phytoplankton dynamics during 1986 was the absence then of the anomalous flagellate blooms recorded in 1985. October and November blooms of *Prorocentrum* spp. and *Massartia rotundata*, respectively, were not encountered. Nor did the October-November "green-water" blooms of Euglenids develope, *Fibrocapsa japonica* was not encountered during 1986, nor were *Pyramimonas* sp. blooms. Rather, the phytoplankton flora, its abundance and cycles were more or less representative of the well-established trends for Narragansett Bay, in contrast to the 1985 summer events described in detail in the report on the 1985-86 survey previously submitted.

Phytoplankton Biomass Levels and Dynamics

Phytoplankton biomass as chlorophyll and carbon (based on ATP) exhibited significant regional variations (Appendix Tables 9, 10). The mean annual chlorophyll concentrations (mg m^{-3}) at the seven stations are given in Table 9.

Table 9

1986-87 STN	Chl	1985-86 STN	Chl	
3	13.6 mg m^{-3}	3	21.0	+ 7.4
4	12.9	4	24.6	+11.7
5	12.5	5	20.5	+ 8.0
6	9.8	1	16.2	+ 6.4
1	9.3	6	13.9	+ 4.6
2	7.2	2	13.9	+ 6.7
7	7.1	7	11.2	+ 4.1

Mean annual levels varied among stations by about 2-fold; with the maximum/minimum levels found at Stations 4/7.

Several patterns in biomass dynamics are evident. The average surface chlorophyll level (11.6 mg m^{-3}) in upper Narragansett Bay (Stations 2, 3, 4, 5) was about 33% greater than than (8.7 mg m^{-3}) in the lower Bay (Stations 1, 6, 7). During the 1985-86 surveys, the corresponding means were 20.2 and 13.8 mg m^{-3}, respectively. During the 1985-86 surveys the mean upper bay chlorophyll level was approximately 2-fold greater; in the lower bay, it was about 60% greater.

A gradient in mean station levels occurred: $3 > 4 = 5 > 6 > 1 > 2 = 7$, as during the 1985-86 surveys. The chlorophyll distributions during the individual transect surveys (n = 31) are consistent with this average condition (Appendix Table 9). Figure 10 shows the relationship between mean annual surface chlorophyll levels and mean annual surface salinity. A conspicuous bell-shaped relationship with salinity is evident for both surveys. Mean chlorophyll levels increased significantly between the Providence River (Station 2) and the phytoplankton biomass epicenter in the region between Gaspee Pt. (Station 3) and Providence Pt. (Station 5). Mean chlorophyll levels progressively decreased downbay from Station 4 along the increasing salinity gradient. The conspicuously greater mean chlorophyll levels during the 1985-86 surveys reflect the "brown-tide" event. The mean chlorophyll levels at the 7 transect stations were then from ca. 4.0 to 12.0 mg m^{-3} greater than mean 1986-87 levels (Table 9).

The annual biomass cycle is evident from Table 10 which presents the maximal monthly chlorophyll levels found at the transect stations from July 1986 - June 1987. Intense summer blooms occurred baywide. At Station 4, intense growth ranging from ca. 20 to 30 mg m^{-3} persisted from July - October. At Station 3, the bloom (ca. 43 to 56 mg m^{-3}) persisted from July - September; at Station 5, the maximum recorded bloom event (ca. 173 mg m^{-3}) occurred in August. Excluding this latter event, the maximal summer blooms recorded at the individual stations exhibited a 3-fold range, from 18.1 (Station 7) to 55.6 mg m^{-3} (Station 3). A conspicuous bay-wide demise in phytoplankton abundance occurred in October/November; this nadir persisted through January. Maximal chlorophyll concentrations at the stations then ranged from 1.0 to 2.0 mg m^{-3}.

Table 10

STATION	1	2	3	4	5	6	7	
July '86	27.0	30.7	55.6	29.4	51.5	25.3	18.1	mg m^{-3}
Aug	8.8	3.9	47.0	25.8	172.6	3.7	5.3	
Sept	20.3	18.4	43.4	21.7	21.2	13.2	12.2	
Oct	7.3	5.5	12.3	23.8	11.3	7.9	3.6	
Nov	4.0	1.1	0.8	1.1	1.4	1.4	1.2	
Dec	2.1	1.0	0.8	1.1	1.5	1.1	2.1	
Jan '87	6.4	2.8	2.4	2.4	2.8	3.3	2.9	
Feb	15.4	15.5	19.3	17.7	21.0	20.4	9.8	
Mar	19.3	26.2	28.9	23.5	15.9	15.9	18.6	
Apr	25.3	16.7	17.4	19.3	20.8	22.6	22.6	
May	9.6	9.8	9.8	8.5	12.0	13.3	8.1	
June	18.6	40.9	105.7	39.2	14.5	17.1	11.7	

The winter-spring bloom began in February, with maximal chlorophyll levels then ranging from about 10 to 20 mg m^{-3}. The bloom intensified and persisted through April. The winter-spring bloom terminated in May, characterized by a significant decrease in chlorophyll levels, although these levels were still quite high, ranging from about 8.0 to 13.0 mg m^{-3}. A strong resurgence then occurred in June, including the second major bloom event (106 mg m^{-3}) of the study which occurred at Station 5. During the winter-spring bloom, maximal chlorophyll concentrations were similar at the different stations. Maximal levels ranged only 1.4-fold, from 21.0 (Station 5) to 28.9 mg m^{-3} (Station 3). This contrasts with the marked station-to-station differences in summer bloom maxima. Excluding the unique 20 August event (172.6 mg m^{-3}) at Station 5, the maximal summer levels ranged by 3-fold, from 18.1 (Station 7) to 55.6 mg m^{-3} (Station 3). Lower bay Stations 1, 6 and 7 produced summer and winter-spring blooms of similar biomass concentrations; the ratio of summer: winter/spring chlorophyll maxima ranging from 0.80 to 1.12. In contrast, the summer biomass maxima at the upper bay Stations 2, 3, 4, 5 were significantly greater, the ratio ranging from ca. 1.6- to 2.5-fold.

The primary seasonal bloom events appear to be synchronized. That is, the winter-spring bloom in 1987 began baywide in February and the annual baywide demise in 1986 began in October/November with a December nadir. Within this general pattern, the stations diverged somewhat, notably during the summer, in variable week-to-week, transitory surges in bloom events. During the 1985-86 survey, the winter-spring bloom began simultaneously at all stations in early January. Bloom intensity was initially greatest in the lower Bay, including Greenwich Bay, and progressively moved upbay during the next two weeks. During the 1986-87 surveys, the winter-spring bloom intensity was initially greatest at lower bay Stations 6 and 7, and progressively moved upbay, reaching its maximum intensity five weeks later (30 March) at Stations 2, 3 and 4 and eight weeks later (27 April) in Greenwich Bay (Station 1; Appendix Table 11). This occurrence of a simultaneous baywide bloom during the 1985-86 and 1986-87 surveys, with bloom intensity progressing upbay, contrasts with Pratt's (1959) conclusion (based on cell number) that the winter-spring bloom begins upbay, then moves downbay.

Both surveys clearly show the considerable fertility of Narragansett Bay. Significant phytoplankton growth, particularly in upper Narragansett Bay, is a persistent feature. Using a surface concentration of 10 mg m^{-3} (quite high) as an indicator of bloom conditions, this level was exceeded during the 28 transect surveys at the various stations 25% to 57% of the year, frequencies 20% lower than during the 1985-86 surveys (Table 11).

Table 11

STATION	1	2	3	4	5	6	7
> 10 mg m^{-3}	43%	33	50	57	61	50	25
> 20 mg m^{-3}	11%	11	25	25	29	14	4

The frequency of blooms > 20 mg m^{-3} ranged from 4 to 29%, frequencies 12 to 19% lower than those during the 1985-86 surveys. For example, during the latter study blooms exceeding 20 mg m^{-3} chlorophyll occurred 40% of the year in Greenwich Bay (Station 1) and at nearby Station 5; 60% of the year near Conimicut Pt. (Station 4), and 25% to 33% elsewhere. The exceptional fertility of Stations 4 and 5 is evident.

These results also indicate that phytoplankton blooms are nearly continuous and most prolific in upper Narragansett Bay, with a significant downbay gradient in chlorophyll levels. This gradient in biomass is related to the regional variation and patterns in nutrient levels (Appendix Tables 5, 6, 7, 8). The mean annual surface concentrations of chlorophyll and nutrients are entered in Table 12.

Table 12

STATION:	1	2	3	4	5	6	7
Chl (mg m^{-3})	9.3	7.2	13.6*	12.9	12.5**	9.8	7.1
PO_4 (mg-at m^{-3})	1.67	4.08	3.01	2.27	1.54	1.34	1.20
$\sum NH_4^+NO_3$	7.9	50.9	31.8	20.3	9.5	8.0	5.9
SiO_3	20.9	49.4	37.7	24.7	20.8	19.0	17.4

(* exclusive of 6/29 bloom; ** exclusive of 8/20 bloom)

The relationships between mean surface annual chlorophyll levels and mean annual surface concentrations of PO_4, $NH_4^+NO_3$ and SiO_3 for the 1985-86 and 1986-87 surveys are shown in Figures 11, 12 and 13. For both surveys, chlorophyll regressed against each nutrient species shows a persistent, bell-curve pattern. Maximal chlorophyll levels occur at intermediate levels of either PO_4, $NH_4^+NO_3$ and SiO_3, i.e., at Stations 3, 4 and 5. Chlorophyll levels are depressed at higher (Station 2) and lower nutrient levels (Stations 1, 6, 7).

Regression of the mean chlorophyll level at each station against each of the concentrations of PO_4, $NH_4^+NO_3$ and SiO_3 indicates strong positive correlations for Stations 1, 4, 5, 6 and 7, with the two survey years distinguishable (Table 13).

Table 13

		PO_4	$NH_4{}^+NO_3$	SiO_3
STATIONS: 1, 4, 5, 6, 7				
1985-86	r =	0.84	0.90	0.79
1986-87		0.55	0.76	0.82
STATIONS: 2, 3, 4				
1985-86	r =	-0.97	-0.97	-0.94
1986-87		-0.87	-0.89	-0.79

That is, mean chlorophyll levels increased (in a statistically significant fashion) with mean ambient nutrients along the nutrient gradient extending upbay from Station 7 to Station 4. Further upbay, along this gradient from Station 4 into the Providence R. (Station 2 off Fields Pt.) and including Station 3 (off Gaspee Pt.), mean chlorophyll levels decreased with increasing ambient levels of each nutrient. The inverse correlations ranged from r = -0.94 to -0.97 during 1985-86, and from -0.79 to -0.89 during 1986-87. That this relationship between chlorophyll and nutrient level is independent of the mean absolute concentration is evident in Figures 11, 12, 13. Despite lower nutrient levels during the 1986-87 surveys, the "bell-shaped" relationship persisted, with the two stations clusters remaining distinctive and statistically correlated.

These correlations based on 59 transects over two years, indicate that mean phytoplankton biomass in Narragansett Bay increases with nutrient loading accompanying both riverine inputs and *in situ* processes in the region extending from Fox Island (Station 7) in lower

Narragansett Bay up to the region off Conimicut Pt. (Station 4). However, the progressively higher nutrient loadings accreted via the Providence R. in the region between Conimicut Pt. and Fields Pt. appear to repress biomass levels. It should be pointed out that the mean levels of chlorophyll and nutrients represent residual values. That is, the levels of chlorophyll are those remaining above grazing, sinking and advective losses at the time of sampling, and the nutrient levels are those yet to be used. Moreover, use of mean values blur significant day-to-day events which influence the biomass-nutrient availability relationship. Nonetheless, the strong statistical correlations suggest that these apparent beneficial and negative effects of nutrient inputs into Narragansett Bay along its gradient are major, general features.

Primary Production

Primary production rates at the surface based on ^{14}C measurements during 28 transects are given in Appendix Table 11. A distinct regional gradient characterizes the mean annual rates (g C m^{-3} $year^{-1}$) in Table 14.

Table 14

STATION:	1	2	3	4	5	6	7
1986-87	116.7	123.0	284.0	207.7	201.6	127.2	64.5
1985-86	120.5	159.0	261.3	231.1	151.5	112.7	76.5
Δ	-3.8	-36.0	+22.7	-23.4	+50.1	+14.5	-12.0
% Δ	-3%	-23%	+9%	-10%	+33%	+13%	-16%

The maximal rate observed at Station 3 exceeded by about 4.5-fold the minimal rate at Station 7. During the 1985-86 surveys, the maximal and minimal production rates, also found at these stations, differed by 3.5-fold. The most productive region encompasses the area between Gaspee Pt. (Station 3) and Providence Pt. on Prudence Island (Station 5). Annual rates upbay of this region in the Providence R. (Station 2) and in the lower Bay (Stations 1 and 6) relative to Station 3 were about 60% lower. Station 7 was about 75% lower. This 4.5-fold regional variation in primary production was greater than that found for standing stock: ca. a 2-fold difference occurred between the maximal/minimal mean phytoplankton biomass (as chlorophyll), similar to the 1985-86 survey.

The annual mean rates for the 1985-86 and 1986-87 surveys were remarkably similar (Table 14). The major difference was the 33% higher production level during 1986-87 at Station 5; at Stations 2 the annual mean was then 23% lower. At the other stations the mean annual differences were less than about ± 15%. The similarity in mean production rates between years is striking, given the considerably lower biomass levels during the 1986-87 surveys (Table 9). The mean daily Assimilation Numbers (the mean daily Carbon fixation rate per mean daily chlorophyll level) are presented in Table 15.

Table 15

STATION:	1	2	3	4	5	6	7
1986-87	34.3	46.8	57.2	44.1	44.2	35.6	24.9
1985-86	20.4	31.3	34.1	25.7	20.3	22.2	18.7
% △	68%	50%	68%	72%	118%	60%	33%

Mean Assimilation Numbers during 1986-87 ranged 2.3-fold, from 24.9 to 57.2 mg C fixed [mg $chl^{-1}] \cdot d^{-1}$, and about 1.8-fold (18.7 to 34.1) during 1985-86. The mean Assimilation Numbers were considerably higher during 1986-87; at Station 5 it was 2.2-fold higher. At the other stations, assimilation was 33% to 72% higher. The reasons for the greater production per unit chlorophyll during the 1986-87 surveys are obscure. Should the brown-tide species, _Aureococcus anophagefferens_, have less photosynthetic capacity per unit chlorophyll, the reduced Assimilation Numbers characterizing the 1985-86 surveys would be partly explained.

The statistical relationships between the regional variations and gradients in primary production, salinity and nutrients were evaluated. The relationship between mean surface salinity and mean annual surface production is shown in Figure 14. Primary production at Stations 1, 3, 4, 5, 6, 7, similar to 1985-86, exhibited a strong inverse correlation ($r = -0.90$) with salinity. In fact, the mean production rates at these stations for the 1985-86 and 1986-87 surveys fall along the same regression line, yielding a correlation coefficient of $r = -0.93$. This well-defined, progressive increase in primary production inwards along the gradient of decreasing salinity is abruptly altered below 23 $^{o}/oo$ salinity. Primary production at Station 2 located in the Providence River was significantly depressed during both surveys when the mean surface salinity was 20.3 $^{o}/oo$ and 21.2 $^{o}/oo$, respectively. Over the approximately 1.5 km distance between Stations 2 and 3, mean surface salinity and mean annual surface production during 1985-86 increased by 3.4 $^{o}/oo$ and 102 g C m^{-3} yr^{-1}, respectively, and by 1.9 $^{o}/oo$ and 161 g

C m-3 yr-1 during 1986-87.

The mean annual production rates were strongly correlated with PO_4, NH_4+NO_3 and SiO_3 concentrations (Table 16; Figures 15, 16, 17), as during the 1985-86 surveys. Carbon production and mean PO_4 at Stations 1, 3-7 were linearly correlated ($r = 0.88$). The correlation coefficient for the 1985-86 data was $r = 0.97$, and combining both surveys yields a highly significant $r = 0.85$. During both surveys Station 2, characterized by the highest mean PO_4 concentration (> 4 mg-at m-3), deviated from this relationship, as also found for the production-salinity relationship (Figure 14). Station 2 also deviated from the other stations in the regressions of primary production against NH_4+NO_3 and SiO_3 concentrations (Figures 16, 17). Whereas production was linearly correlated to PO_4 concentrations, hyperbolic relationships appeared to characterize the production- $\sum N$ and production-SiO_3 relationships.

Table 16

	PO_4	NH_4+NO_3	SiO_3
STATIONS 1, 3, 4, 5, 6, 7			
1986-87	r = 0.88	0.89	0.86
1985-86	0.97	0.92	0.87
1985-86-87	0.85	0.89	-

Annual production rates progressively increased with $\sum$ N availability up to about 16 mg-at m-3 at Stations 1 and 5-7. Higher $\sum$ N concentrations (Stations 3, 4) were characterized by reduced rates of increased production suggestive of a saturation effect. Nonetheless, the linear regressions on all stations (exclusive of Station 2) yielded high correlation coefficients (r = +0.89 to +0.92), including the combined data from both surveys (Table 16).

Similar hyperbolic relationships are suggested by the regressions of production against silica availability. Highly significant, strong correlation coefficients (r = +0.86) characterized both surveys (excluding Station 2). However, unlike for the PO_4 and $NH_4{+}NO_3$ regressions, combining the 1986-87 and 1985-86 data led to a poor correlation. Mean silica concentrations during 1986-87 were generally higher than 1985-86 levels, yet production was not commensurately increased (Table 14). This suggests that other factors influenced the production-silica relationships resulting in the clear distinctions between the 1986-87 and 1985-86 surveys (Figure 17).

These correlations clearly indicate that primary production increases upbay along the salinity gradient, which is related to increased nutrient availability. Moreover, the relationships suggest a classical yield-dose response, with both linear (PO_4) and hyperbolic ($\sum N$, SiO_3) patterns evident. Surprisingly, an apparent repression occurred at the highest nutrient levels (Station 2) (Figures 15, 16, 17).

Given the strong inverse correlations between mean nutrient levels and salinity (Figures 2, 3) and between production and salinity (Figure 14), it might be argued that the increased surface production along the upbay gradient might really be regulated by salinity. That is, the apparent correlations with nutrients are merely indicative of parallel patterns. This potential importance of salinity *per se* seems highly unlikely, given the strong euryhaline nature of the phytoplankton.

Nonetheless, independent confirmation of this apparent regulation by nutrients was tested by evaluating the effect of nutrient levels on carbon turnover. Carbon turnover was defined as the mean carbon production per mean unit of phytoplankton standing stock expressed as chlorophyll, i.e., the Assimilation Number. The regressions of carbon turnover [mg C produced$\cdot m^{-3}$ per mg chlorophyll$\cdot m^{-3}$] against PO_4, $\sum N$ and SiO_3 revealed strong, positive linear correlations in every instance, ranging from 0.68 to 0.71, respectively. Station 2 was less deviant, although hyperbolic trends with $\sum N$ and SiO_2 regulation persisted. Regression of the 1985-86 data, in contrast, indicated that Station 2 was neither deviant, nor were hyperbolic trends evident with $\sum N$ and SiO_3 regulation. The correlation coefficients ranged from $r = 0.96$ to 0.98. Omitting Station 2 from the regressions for the 1986-87 data yielded a correlation coefficient (r) of 0.89 for PO_4, $\sum N$ and SiO_3, respectively. Collectively, these analyses reaffirm the evidence that nutrient levels regulated primary production along the salinity gradient rather than salinity.

Mean carbon growth rates were also calculated and related to nutrient levels. The carbon equivalent of the mean chlorophyll biomass was calculated using a C:chlorophyll ratio of 50:1, the ratio routinely used by phytoplankton ecologists. Growth rate (k) was determined from

$$k = \ln \frac{C_p+C_b}{C_b} \left(\frac{t}{1 \ln 2}\right)$$

where C_p is the mean daily carbon production rate ($mg\ C\cdot m^{-3}\cdot d^{-1}$) and C_b is the mean daily phytoplankton carbon standing stock ($mg\ C\cdot m^{-3}$). The mean daily growth rates (k) are given in Table 17.

Table 17

STATION:	1	2	3	4	5	6	7
1986-87							
k d^{-1}	0.75	0.95	1.10	0.91	0.91	0.78	0.58
1985-86							
k d^{-1}	0.49	0.70	0.75	0.60	0.49	0.53	0.46

The mean daily carbon growth rates ranged from 0.58 (Station 7) to 1.10 d^{-1} (Station 5). Upper bay Stations 2-5 exhibited more rapid growth rates, nearly one carbon doubling per day (x = 0.97 d^{-1}), than lower bay Stations 1, 6, 7 (x = 0.70) where, on average, carbon doubled every 34 hours. The mean carbon doubling rates at all stations during 1986-87 exceeded those during 1985-86, ranging from 0.46 d^{-1} (Station 7) to 0.75 d^{-1} (Station 3). At Station 3, for example, during 1986-87, carbon doubled every 22 hours; in 1985-86, every 32 hours. The rank ordering of the stations by growth rate was identical during both years.

A hyperbolic relationship occurred between mean daily growth rate and mean NH_4+NO_3 concentrations during both surveys (Figure 18). Below 12 mg-at m^{-3} (Stations 1, 5, 6, 7) growth rates for both years lie along the same regression line (r = +0.81). Above this concentration (Stations 2, 3, 4), mean daily growth rate was more or less invariant up to about 55 mg-at m^{-3} NH_4+NO_3. The higher growth rates during 1986-87 at the upper bay stations are evident. Hyperbolic relationships also characterized the plots of mean daily carbon growth rates and the concentrations of PO_4 and SiO_3 (Figures 19, 20). Mean daily phytoplankton growth rates increased significantly along the nutrient gradient. The average generation time (= doubling time), calculated from (1/k), decreased from 1.7 to 0.9 day between Stations 7 and 2 during 1986-87, and from 2.2 to 1.3 days during 1985-86. This further indicates that the increased productivity upbay along the salinity gradient is attributable to an increased nutrient flux. Moreover, the second highest growth rates and assimilation numbers were obtained for Station 2 in the Providence R. This suggests that the low phytoplankton levels (as chlorophyll) at that station during both surveys, and lower than expected from the relationship between standing stock and nutrients, were not completely attributable to water quality. Washout in this rapidly flushed region and possibly grazing (secondarily) may have prevented an accumulation of phytoplankton biomass commensurate with its production.

Thus, at Station 2, two mechanisms may be operative in causing the apparent suppression of biomass development associated with the high nutrient levels characteristic of that area: repression of phytoplankton growth due to chemical water quality (e.g. nutrient concentrations, their ratios and toxicants) and the physical mechanism of washout. Resolution of the contribution of these and other processes to the apparent suppression of a phytoplankton biomass in upper Narragansett Bay Station 2 requires experimental evaluation.

The data indicate, therefore, that nutrients, particularly nutrients accreted into upper Narragansett Bay via the Providence R., and STP inputs strongly regulate phytoplankton growth in Narragansett Bay. Along the downstream gradient this effect would be greatest in upper Narragansett Bay. The progressive dilution and utilization by phytoplankton would progressively diminish this input downstream and increase the importance of in situ remineralization and offshore inputs to nutrient flux. This suggests that two primary nutrient pumps are operative in Narragansett Bay which regulate phytoplankton growth: nutrient accretion in upper Narragansett Bay and in situ remineralization/advection in lower Narragansett Bay.

The Redfield Ratio expresses the stoichiometry between carbon production and N and P utilization: C:N:P = 106:16:1 (by atoms). It was used to convert the mean daily carbon estimates to equivalent N and P production rates (i.e. supply rates), to which the residual N and P concentrations were added. This sum represents the average daily availability of N and P before production (= utilization). The percentage of the concentration used in daily production when plotted against the residual concentration showed a strong inverse curvilinear correlation for all nutrients. For $\sum$ N, the mean daily percentages of the available nitrogen used in carbon production are given in Table 18.

Table 18

STATION:	1	2	3	4	5	6	7
1986-87	51%	8	31	35	73	55	38
1985-86	49%	10	19	30	40	46	45

Thus, along the gradient, from 8 to 73% and 10 to 50% of the surface nitrogen pool was used daily in primary production during the 1986-87 and 1985-86 surveys, respectively. Upper Narragansett Bay (Stations 2, 3, 4), on average, has a 3 to 10 days' supply of N to meet measured mean daily production rates; lower Narragansett Bay, a 2 to 2.5 day reserve. For PO_4, mean daily production requirements represented from 6 to 28% of the mean daily concentration during 1986-87, and from 6 to 22% during 1985-86. That is, mean daily concentration of the phosphorus pool represented a 3.5 to 16 daily reserve in support of surface production. This indicates that carbon production in lower Narragansett Bay is much more dependent on *in situ* nutrient recycling than in upper Narragansett Bay where nutrient flux is dominated by accreted inputs, and that the resupply rate of nitrogen is more critical than that for phosphorus. A shift in dominant nutrient flux mode, i.e., from accretion to remineralization, probably occurs in the region of the Narragansett Bay Sanctuary waters near Station 5.

Zooplankton

Appendix Tables P1-P2 present the zooplankton data. The zooplankton community was dominated by copepods, specifically *Acartia hudsonica* and *Acartia tonsa*. Their combined numerical abundance as a percentage of the mean total copepod abundance at each station varied from 64% (Station 2) to 82% (Station 5). The less abundant copepod species included *Pseudocalanus*, *Centropages*, *Oithona* and *Pseudodiaptomus*. Benthic larvae were the other major zooplankton group. Their annual mean numerical abundance at the 7 stations was about 20% of the copepod abundance at Stations 1, 3-6; 33% at Station 2 and only 12% at Station 7. However, on a given sampling date, notably from May-July, benthic larvae frequently represented a significant portion (> 30%) of the zooplankton community (Appendix Table P7), ranging from 13% to 56%. Table 19 summarizes the mean numerical abundance (m^{-3}) of these components and total zooplankton community biomass (mg dry weight m^{-2}).

Table 19

STATION	1	2	3	4	5	6	7
Copepods (m^{-3})							
1986-87	11293	9859	10295	12293	15220	12270	11756
1985-86	7964	4494	5448	6951	7394	8859	9814
Δ	+3329	+5365	+4847	+5342	+7826	+3411	+1942
% Δ	42%	119	89	77	106	39	20
Acartia hudsonica (m^{-3})							
1986-87	4801	1429	2150	4445	7282	5096	3562
1985-86	5985	1808	2968	3812	5345	6465	6774
Δ	-1184	-379	-818	+613	+1937	-1365	-3212
% Δ	-20%	-21	-28	+17	+36	-21	-47
Acartia tonsa (m^{-3})							
1986-87	4207	4901	4949	5093	5130	4314	5105
1985-86	939	1643	1645	2035	1276	1392	1945
Δ	+3268	+3258	+3304	+3058	+3854	+2922	+3160
% Δ	348%	198	201	150	302	210	162
Benthic larvae (m^{-3})							
1986-87	2355	3205	2366	2757	2564	2563	1440
1985-86	1669	2101	3069	2529	1581	1637	1321
Δ	+686	+1104	-703	+228	+983	+926	+119
% Δ	41%	53	-23	9	62	57	9

Biomass (mg m^{-2})

1986-87	407	597	640	807	710	447	310
1985-86	329	378	536	611	535	327	287
$\triangle$	78	61	104	196	175	120	23
% $\triangle$	24%	58	19	32	33	37	8

Acartia hudsonica dominates the zooplankton community during the winter-spring period. It is succeeded by *Acartia tonsa* during the summer, which then persists into early winter. *Acartia tonsa* usually appears during late-May to early-June. *Acartia hudsonica* usually disappears in late July to early August.

Mean total copepod numerical abundance during the 1986-87 surveys (Table 19; Appendix Table P2) was 20% (Station 7) to 119% (Station 2) greater than during the 1985-86 survey. Increased abundance was considerably greater (77% to 119%) in the upper bay (Stations 2, 3, 4, 5) than in the lower bay (Stations 1, 6, 7) - 20 to 42%. There were also significant differences in abundance of the two dominant congeners between survey years. Mean *Acartia hudsonica* abundance was lower during 1986-87 by about -20 to -30% at Stations 1, 2, 3 and 6; by -47% at Station 7, whereas mean abundance was greater at Stations 4 and 5; +17% and +36%, respectively. *Acartia tonsa* exhibited a dramatic increase in mean abundance during the 1986-87 surveys. Bay-wide, its abundance increased by 150% (Station 4) to 348% (Station 1) over mean 1985-86 levels. This remarkable difference between survey years appears to be linked to the 1985 summer "brown-tide" described in a previous report. This brown-tide coincided with the annual successional shift from *Acartia hudsonica* to *Acartia tonsa* dominance of the zooplankton community. Mean abundance of <u>Acartia</u> <u>tonsa</u> C_I - C_{VI} stages during the July - October period were about three times higher in 1986 than in 1985; nauplii were also generally more abundant in 1986. While the time-course of population growth was similar in 1985 and 1986, with initial appearances of <u>A</u>. <u>tonsa</u> in late May, <u>A</u>. <u>tonsa</u> abundance declined sharply by mid-August in 1985 and remained low until its disappearance in November. By contrast, in 1986, abundances remained high until late August/early September; declined sharply, and then recovered somewhat in mid-September before a late October or November decline. The data strongly indicate that the 1985 brown-tide development negatively influenced abundance of <u>A</u>. <u>tonsa</u>, consistent with experimental observations (Durbin and Durbin, in prep.). Mean abundance m^{-2} regressed against the mean number of brown-tide cells (m^{-2}) exhibited an inverse relationship, with the stations clustering into two subgroups: Stations 2, 3, 4 and Stations 1, 5, 6, 7; i.e., into upper and lower Bay groupings. A strong inverse correlation ($r = -0.91$) characterizes both groupings. Stations 2, 3 and 4 are distinguished from the others only in the higher <u>A</u>. <u>tonsa</u> standing stocks m^{-2}. The slopes of the two subgroups are not statistically different.

Excluding Station 3, where a 23% decrease in mean annual abundance in benthic larvae occurred during the 1986-87 surveys, larval numbers increased by about 40% to 60% at Stations 1, 2, 5 and 6, and by about 10% at Stations 4 and 7. The greater recruitment generally characterizing the 1986-87 results may also reflect, at least partly, adverse effect of the 1985 brown-tide.

Mean abundance during the 1985-86 surveys was inversely correlated (r = -0.58) with brown-tide cell numbers. Based on the six year inter-annual comparisons at Station 7, benthic invertebrate larvae were least abundant (857 m^{-3}) in 1985, following attainment of its greatest abundance (2385 m^{-3}) in 1984.

The most remarkable zooplankton modification accompanying the 1985 brown-tide outbreak was failure of the cladoceran community to develop. *Evadne nordmanni* and *Podon* sp., which normally exceed > 10,000 animals m^{-3} during June - August, failed to appear in 1985. Based on the six-year inter-annual comparisons at Station 7, the mean 1985 May - August abundance of only 80 m^{-3} was 10- to 75-fold lower than the means for the comparison years. During 1986, cladocerans appeared in the spring, and by mid-June reached abundances ranging from 2,000 to 29,000 animals m^{-3} at the transect stations. Cladocerans remained abundant through late-August, and then disappeared. In April, 1987 they reappeared, becoming moderately abundant (572 to 15,500 m^{-3}) by late June, when the 1986-87 survey terminated.

Mean zooplankton biomass (dry wt m^{-2}) during the 1986-87 surveys exceeded 1985-86 levels by 58% at Station 2; about 20 to 40% at Stations 1, 3-6, and 8% at Station 7 (Table 19). Maximal zooplankton biomass occurred at upper bay Stations 2-5; the mean of 689 mg m^{-2} exceeding by 1.8-fold that (388 mg m^{-2}) at the lower bay stations.

Collectively, these observations suggest that zooplankton and benthic larvae occurrence were influenced by the brown-tide development during the 1985-86 surveys, with a trend suggesting that adverse effects predominated. These include apparent reductions in animal abundance and biomass; suppression of cladoceran and *Acartia tonsa* occurrence, and recruitment of certain benthic larvae. It should be noted, however, that no correlation was found between zooplankton dry weight (biomass) and brown-tide cell numbers; both per m^{-2}. The 1986-87 surveys indicate that zooplankton community structure and dynamics returned to "normal" patterns following the anomalous 1985-86 annual cycle.

With regard to the annual zooplankton dynamics, *A. hudsonica* began to increase in response prior to the winter-spring diatom maximum, peaking to > 16,000 to 20,000 animals m^{-3} in February to early March at Stations 4, 5 and 6; a level of abundance not achieved until late March at Station 1. *Acartia hudsonica* was relatively depauperate at Stations 2 and 3 (Appendix Table P3; Table 18). At Station 5, *Acartia hudsonica* surged during April to about 50,000 animals m^{-3}, the maximal levels observed for this species. Mean abundance of *A. hudsonica* progressively decreased along the salinity gradient upbay during 1985-86, characterized by a very strong correlation with salinity ($r^2 = 0.96$). During the 1986-87 surveys, a similar trend occurred (Table 18), but was less strongly correlated ($r^2 = 0.56$).

As during the 1985-86 surveys, *A. tonsa* progressively decreased during the winter-spring diatom bloom, disappeared in mid-March, and reappeared in early June following sporadic, transient occurrences after mid-March (Tables P4, 18). The average abundance of *A. tonsa* during the 1985-86 survey (excluding Station 2) was 2- to 7-fold less than that for *A. hudsonica*; during the 1986-87 surveys, *A. tonsa* mean abundance exceeded that of *A. hudsonica* at Stations 2-4 and 7. Maximal abundance of *A. tonsa* occurred during July - August, ranging from about 21,000 to 49,000 animals m^{-3}. Unlike for *A. hudsonica*, mean abundance of *A. tonsa* was not correlated with salinity, its mean abundance at the stations ranging only 1.2-fold, from 4207 (Station 1) to 5105 animals m^{-3} (Table 18).

Benthic larvae made a surprisingly large contribution to the zooplankton community, both numerically and in percentage representation (Appendix Tables P6, P7). The mean abundance, similar to the 1985-86 surveys, ranged from about 1440 to 3205 larvae m^{-3}; this corresponded to 12 to 33% of the copepod abundance. During 1985-86, mean benthic larvae abundance generally exceeded that for _A_. _tonsa_ and _A_. _hudsonica_ at Stations 2, 3. In 1986-87, mean benthic larval numbers were subordinate to those for the _Acartia_ spp. Benthic larvae abundance progressively _decreased_ downbay during 1985-86, reflected in a strong inverse correlation with salinity ($r = -0.67$; -0.97 excluding Station 2). During 1986-87, the correlations were $r = -0.66$ and -0.40. Benthic larvae tended to be most numerous in the summer.

The inverse correlation between salinity and numerical abundance of _A_. _hudsonica_ was described previously. Zooplankton biomass is also strongly correlated with salinity, but the relationship is more complex (Figure 21). Mean biomass levels (dry weight m^{-2}) regressed against mean salinity were strongly and _positively_ correlated at Stations 2, 3, 4 ($r = 0.96$); but at Stations 4, 5, 1, 6, 7, strongly _negatively_ correlated ($r = -0.85$). Similar correlations characterized the 1985-86 survey results. In fact, the 1985-86 and 1986-87 data points at Stations 1, 4, 5, 6, 7 fell along the same regression line ($r = -0.85$). Therefore, along the salinity gradient from Fields Pt. (Providence R.) (= Station 2) to Conimicut Pt. (Station 4) mean zooplankton biomass increased. However, mean zooplankton biomass progressively decreased with increasing mean salinity along the gradient at the lower bay stations.

This relationship with salinity undoubtedly reflects a parameter running in parallel with salinity rather than primarily reflecting an osmotic effect. The relationships between nutrient concentrations and salinity were previously described. However, since zooplakton do not utilize inorganic nutrient, nutrients undoubtedly are not the parallel factor responsible for the correlation. Since the sampled zooplankton are mostly herbivorous, this prompted assessment of the relationship between zooplankton biomass along the salinity gradient and phytoplankton biomass (Figure 22) and production (Figure 23). Zooplankton biomass (m^{-2}) was strongly correlated with surface phytoplankton biomass (= chlorophyll) standing stock ($r = 0.74$). This was similar to that found during 1985-86 although a strong correlation occurred then ($r = 0.96$). The two annual regression lines did not overlap (Figure 22). Mean zooplankton biomass was strongly correlated with mean annual primary production during both surveys, with $r = 0.85$ and $r = 0.77$ for the 1985-86 and 1986-87 surveys, respectively (Figure 23). The mean zooplankton biomass at Station 3 during both surveys appeared to be depressed relative to expected levels, given the high annual production rates at that location. Eliminating Station 3 from the regressions increased the correlation coefficients for the 1985-86 and 1986-87 surveys to $r = 0.89$ and $r = 0.94$, respectively.

Ctenophores

The abundance of the ctenophore Mnemiopsis leidyi, a voracious grazer of copepods, is given in Appendix Table P8. Mean abundance varied about 3-fold, from 25 animals m^{-2} (Station 1) to 74 m^{-2} (Station

6). Mean abundances (m^{-2}) at the stations during 1986-87 and 1985-86 are given in Table 20.

Table 20

STATION:	1	2	3	4	5	6	7
1986-87	25	50	46	33	45	74	34
1985-86	50	60	95	66	67	33	15

Mean abundance during 1986-87 was ca. 50% lower at Stations 1, 3 and 4 than in 1985-86, but about 2- to 3-fold greater at Stations 6 and 7. Maximal abundance occurred in late August/early September, and ranged from 42 to 425 animals m^{-2} (Table P8). Thereafter, the population declined somewhat; resurged in November, with maximal abundances reaching their annual maxima in December-January, then disappeared in February. This cycle is in sharp contrast to that in 1985-86 when late fall-winter ctenophore levels were considerably lower in abundance. In 1986-87, as during the previous survey, Mnemiopsis reappeared bay-wide in May, and persisted in very low abundance, usually < 10 animals m^{-2}, through June 1987 when the survey was ended.

In 1985-86, mean ctenophore abundance significantly increased up the salinity gradient from Station 7 to Station 3, then decreased at Station 2 (60 m^{-2}), where its abundance was about 40% lower than that at Station 3 (95 m^{-2}). Excluding Station 2, a strong, inverse correlation then occurred between mean ctenophore numbers and salinity ($r = -0.92$). Thus, a strong gradient highly correlated with salinity characterized the nutrient, phytoplankton, zooplankton and ctenophore distributions in Narragansett Bay during 1985-86. For 1986-87, there was no correlation between Mnemiopsis mean abundance and mean surface salinity.

Previous studies in Narragansett Bay (Deason & Smayda, 1982) revealed that when ctenophores were very abundant, zooplankton numerical abundance decreased significantly, accompanied by a significant concurrent increase in phytoplankton abundance. This increased phytoplankton abundance during ctenophore pulses results from a relaxation of zooplankton grazing pressure accompanying their decimation by the carnivorous Mnemiopsis. That is, ctenophore abundance indirectly controls phytoplankton abundance through predation on zooplankton. The relationships between the standing stocks of phytoplankton, zooplankton and ctenophores at the transect stations were therefore examined.

There was no correlation in 1986-87 between mean Mnemiopsis abundance and mean numerical abundance of copepods. This contrasted with the 1985-86 survey results when, excluding aberrant Station 2, a near-perfect inverse correlation ($r = -0.99$) occurred between mean ctenophore abundance (m^{-2}) and mean numerical abundance of the copepods. This inverse relationship is consistent with previous field observations (Deason & Smayda, 1982) and grazing down of copepods by ctenophores. In 1985-86, regression of the mean zooplankton biomass (dry weight m^{-2}) against ctenophore abundance yielded a positive correlation ($r = 0.79$).

For the 1985-86 surveys, regression of phytoplankton standing stocks as carbon and chlorophyll against ctenophore abundance, again excluding aberrant Station 2, yielded positive correlations of $r = 0.81$

and r = 0.84, respectively. In 1986-87, there was no correlation. These 1985-86 correlations are consistent with previously observed field observations (Deason & Smayda, 1980), including the indirect regulation of phytoplankton abundance by ctenophores through their predation on herbivorous zooplankton. The lack of similar correlation during the 1986-87 surveys suggests significant inter-annual variation occurs in the phytoplankton-zooplankton-ctenophore nexus.

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Appendix Table 1. TEMPERATURE (°C) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	20.5	19.0	19.0	19.0	19.0	19.0	19.0
	M	20.0	18.0	17.5	18.5	18.0	18.0	19.0
	B	19.0	18.0	17.0	18.0	18.0	18.0	19.0
10	T	21.5	20.0	20.5	21.0	21.5	20.5	20.5
	M	20.5	18.0	19.0	19.0	20.5	20.0	20.5
	B	20.0	18.0	18.0	19.0	20.5	20.0	19.5
16	T	21.0	20.5	23.0	21.0	21.0	22.0	20.5
	M	20.0	19.5	18.5	18.5	19.5	21.0	20.5
	B	20.5	19.0	18.0	18.0	19.5	21.0	20.5
23	T	23.0	23.0	23.0	21.0	23.0	22.5	21.0
	M	22.5	20.5	21.0	21.0	22.0	22.0	20.5
	B	22.0	21.0	21.0	20.5	22.0	21.5	20.0
30	T	24.5	23.5	24.0	24.0	23.5	23.0	22.5
	M	24.0	22.0	21.0	21.0	22.5	21.5	22.5
	B	23.0	22.0	21.0	20.5	22.5	21.5	22.5
20 Aug.	T	23.0	23.0	22.5	22.5	23.0	22.0	21.5
	M	22.5	21.0	21.5	21.0	22.0	21.5	22.0
	B	23.0	21.5	21.0	21.0	23.0	23.0	21.5
3 Sept.	T	20.0	20.0	20.0	20.0	19.5	19.5	19.0
	M	20.0	19.0	18.0	19.0	19.5	19.5	19.0
	B	20.0	19.0	17.5	18.5	19.5	19.0	18.5
10	T	-	-	19.3	-	18.8	18.8	18.5
	M	-	-	18.5	-	19.0	19.0	18.0
	B	-	-	18.3	-	19.0	19.0	18.0
17	T	18.3	17.8	17.8	17.0	18.0	17.8	17.5
	M	18.0	18.5	17.8	17.8	18.0	18.0	17.1
	B	18.0	19.0	17.8	17.3	18.0	18.0	17.0
1 Oct.	T	19.5	20.3	20.0	19.5	19.0	18.5	18.0
	M	19.0	19.0	19.7	18.8	19.0	19.5	18.0
	B	19.0	18.5	18.3	18.0	19.0	19.5	18.0
22	T	13.0	15.0	14.5	13.8	14.0	14.0	13.3
	M	13.2	14.2	14.5	14.0	14.0	14.0	13.3
	B	13.3	14.2	14.3	14.0	14.0	14.0	13.3
5 Nov.	T	9.5	11.0	10.5	11.0	10.5	11.0	11.0
	M	9.0	11.0	11.0	10.5	10.8	11.0	10.5
	B	9.0	11.0	11.0	10.5	10.8	11.0	10.5

Appendix Table 1. (cont.)

24	T	6.5	6.5	7.5	7.5	7.0	-	7.0
	M	6.5	8.0	8.0	7.5	7.3	-	7.0
	B	6.5	8.0	8.0	8.0	7.3	-	7.0
8 Dec.	T	5.5	5.5	5.5	5.8	6.0	6.0	6.2
	M	6.0	7.2	7.0	7.0	7.0	6.0	6.2
	B	6.0	7.5	7.5	8.0	7.0	6.0	6.2
17	T	4.0	5.5	4.8	4.3	4.5	5.0	4.5
	M	4.3	6.0	6.0	5.5	5.0	5.3	5.0
	B	4.4	6.0	6.0	6.5	5.0	5.3	5.0
1987								
5 Jan.	T	2.5	3.5	3.5	3.4	3.5	4.5	4.5
	M	3.2	4.0	4.0	4.5	4.5	5.0	4.5
	B	3.2	5.0	4.5	4.5	4.5	5.0	4.5
12	T	3.0	4.5	4.0	3.8	3.5	4.5	3.5
	M	3.5	5.1	5.0	4.0	3.5	4.5	3.5
	B	3.5	5.5	5.0	4.0	3.5	4.5	4.0
2 Feb.	T	1.0	2.3	2.3	2.0	1.5	2.0	2.0
	M	1.5	2.9	2.5	2.5	2.0	2.5	2.5
	B	2.5	3.0	2.8	3.2	2.3	3.5	3.5
24	T	1.5	3.0	2.0	2.0	2.0	2.0	1.5
	M	2.0	3.0	3.0	2.5	2.0	2.0	1.5
	B	2.0	3.5	3.0	3.0	2.0	2.0	1.5
2 Mar.	T	3.0	-	2.5	3.0	3.2	3.0	3.0
	M	3.6	-	3.0	3.5	3.2	3.0	3.0
	B	3.6	-	3.0	3.5	3.2	3.0	3.0
16	T	3.0	4.0	4.5	3.5	4.0	3.5	3.5
	M	3.0	4.0	3.5	3.5	4.0	4.0	3.3
	B	3.0	4.0	3.5	3.5	-	4.0	3.3
30	T	8.5	9.0	9.0	8.0	7.5	7.0	7.5
	M	8.0	7.0	7.0	7.0	8.0	8.0	7.0
	B	7.5	6.5	7.0	7.5	7.5	7.5	6.5
15 Apr.	T	8.5	10.5	10.0	8.8	9.3	9.0	9.7
	M	7.5	7.0	7.0	8.0	8.2	8.3	7.5
	B	8.2	7.0	7.0	7.0	8.0	8.8	7.8
27	T	8.5	9.0	9.0	8.0	7.5	7.0	7.5
	M	8.0	7.0	7.0	7.0	8.0	8.0	7.0
	B	7.5	6.5	7.0	7.5	7.5	7.5	6.5
12 May	T	14.0	15.0	15.0	13.5	13.0	12.5	12.5
	M	12.0	11.0	10.8	11.2	12.8	12.0	11.5
	B	11.5	10.8	10.0	11.2	12.2	12.2	10.5

Appendix Table 1. (cont.)

26	T	14.6	14.6	14.7	15.0	15.5	14.5	15.5
	M	13.5	14.3	13.0	13.0	14.5	14.5	14.5
	B	13.3	14.3	13.5	13.0	14.5	14.5	14.0
15 June	T	20.0	21.0	22.0	20.5	20.5	20.5	19.0
	M	21.5	19.0	21.0	19.0	19.5	19.0	20.0
	B	20.0	19.0	19.0	18.5	19.0	19.0	19.0
29	T	19.2	19.5	21.5	19.0	18.5	18.5	18.5
	M	18.8	17.2	17.2	17.5	18.5	18.5	18.5
	B	19.0	17.2	17.2	17.2	18.5	18.0	18.5

Appendix Table 2. SALINITY LEVELS (o/oo) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	29.6	24.4	28.0	28.6	28.6	29.6	29.6
	M	29.1	28.6	29.6	29.6	28.6	29.6	29.6
	B	30.1	29.6	30.7	29.6	28.6	29.6	29.6
10	T	29.1	26.0	26.5	27.5	28.6	30.7	31.2
	M	29.6	29.1	29.6	30.1	29.6	30.7	31.2
	B	29.6	29.1	31.2	30.7	30.7	30.7	31.2
16	T	29.6	22.3	25.4	25.4	27.5	29.6	29.6
	M	29.6	28.6	30.7	30.7	30.7	30.1	29.6
	B	29.6	30.7	30.7	30.7	30.7	30.1	30.7
23	T	29.1	24.4	26.5	28.6	29.1	29.6	29.6
	M	29.6	29.1	29.6	29.6	29.6	29.6	30.1
	B	29.6	29.6	29.6	30.7	29.6	30.1	30.1
30	T	29.1	19.2	22.3	22.3	27.5	28.6	29.6
	M	29.1	27.5	30.1	29.6	29.6	30.1	29.6
	B	29.6	29.6	30.1	30.7	29.6	30.7	29.6
20 Aug.	T	28.6	19.7	23.3	24.3	27.5	29.6	30.1
	M	29.1	30.1	30.1	30.1	29.6	29.6	30.1
	B	29.1	30.1	30.1	30.1	29.6	29.6	30.1
3 Sept.	T	29.4	21.0	23.4	26.7	28.6	29.9	29.9
	M	29.4	28.6	30.7	28.8	28.6	29.4	30.4
	B	29.4	29.4	30.9	29.6	28.6	29.6	30.4
10	T	28.6	26.5	27.5	28.6	29.6	29.6	29.9
	M	29.6	28.3	29.1	28.6	29.6	29.6	30.1
	B	29.6	29.6	29.6	29.6	29.6	30.1	29.6
17	T	29.6	25.4	22.3	24.4	28.6	28.6	30.7
	M	29.6	29.1	28.6	28.6	28.6	28.6	30.7
	B	29.6	29.6	28.6	28.6	28.6	28.6	30.7
1 Oct.	T	30.1	25.4	26.5	28.6	30.7	30.7	31.7
	M	30.1	29.6	29.1	29.6	30.7	30.7	31.7
	B	30.1	30.7	30.7	30.7	30.7	30.7	31.7
22	T	29.6	25.4	27.5	29.6	29.6	29.6	30.6
	M	30.1	30.7	30.1	29.6	29.6	29.6	30.6
	B	29.6	30.7	30.1	31.7	29.6	29.6	31.2
5 Nov.	T	30.1	25.4	27.0	29.6	29.6	30.7	30.7
	M	30.1	28.6	29.1	29.6	30.1	30.7	30.7
	B	30.1	29.6	29.6	30.1	30.1	30.7	30.7

Appendix Table 2. (cont.)

24	T	27.5	11.8	22.3	26.5	27.5	28.6	30.1
	M	28.6	29.6	29.6	27.5	28.6	29.1	30.1
	B	28.6	29.6	29.6	29.6	29.6	29.6	30.1
8 Dec.	T	26.5	12.9	16.0	19.2	25.4	27.5	28.6
	M	27.0	25.4	25.4	26.0	26.5	27.5	29.6
	B	27.0	25.4	28.6	29.6	27.5	27.5	29.6
17	T	26.5	21.8	13.9	19.2	21.3	27.5	27.5
	M	28.0	29.6	28.9	28.6	27.5	28.6	28.6
	B	28.6	29.6	28.9	29.6	27.5	28.6	29.6
1987								
5 Jan.	T	27.0	18.1	22.3	24.4	24.4	28.0	28.0
	M	27.5	28.6	24.4	28.6	27.5	28.0	28.6
	B	27.5	29.1	27.5	28.6	27.5	28.0	28.6
12	T	28.0	24.4	24.4	23.9	28.0	29.1	29.1
	M	29.1	30.1	28.6	28.6	28.0	29.1	29.1
	B	29.1	31.7	30.7	30.7	28.0	29.1	-
2 Feb.	T	27.5	20.2	19.2	27.5	28.0	27.5	28.6
	M	27.5	28.6	28.6	28.0	28.0	28.6	29.6
	B	28.6	29.6	29.6	29.6	28.3	29.6	29.6
24	T	29.6	24.4	27.0	27.3	29.6	29.6	29.6
	M	29.6	26.2	28.6	29.6	28.6	29.6	29.6
	B	29.1	29.6	30.7	30.7	29.6	29.6	30.1
2 Mar.	T	28.6	-	17.1	24.9	29.6	29.6	30.1
	M	29.6	-	29.6	29.6	29.6	30.1	30.7
	B	29.6	-	30.1	30.1	29.6	30.7	30.7
16	T	28.6	22.3	23.3	22.0	28.6	29.4	28.8
	M	29.6	30.7	30.1	30.1	29.1	29.6	29.1
	B	29.6	30.7	30.7	30.1	-	29.6	29.6
30	T	27.8	18.6	23.3	26.5	29.1	29.6	29.6
	M	29.1	28.8	28.6	29.1	29.1	29.1	29.6
	B	29.6	29.6	29.6	29.1	29.6	29.6	30.7
15 Apr.	T	20.2	6.8	11.4	11.6	23.3	25.4	23.9
	M	25.4	28.6	29.1	26.0	26.5	26.5	28.6
	B	26.5	28.6	29.4	28.6	27.5	28.6	29.6
27	T	27.8	18.6	23.3	26.5	29.1	29.6	29.6
	M	29.1	28.8	28.6	29.1	29.1	29.1	29.6
	B	29.6	29.6	29.6	29.1	29.6	29.6	30.7
12 May	T	26.0	16.0	20.2	23.2	26.5	27.5	28.0
	M	28.6	28.6	29.6	27.5	28.0	28.0	29.1
	B	28.6	30.7	29.6	28.6	28.0	28.0	29.6

Appendix Table 2. (cont.)

26	T	26.5	21.3	23.3	25.4	27.5	28.6	27.5
	M	28.6	28.6	29.1	28.6	28.6	28.6	28.6
	B	28.6	28.6	28.6	28.6	29.6	28.6	28.6
15 June	T	27.5	26.5	27.0	28.0	31.7	32.2	30.1
	M	28.0	28.6	28.6	32.2	32.8	31.7	30.1
	B	28.6	31.7	28.8	32.2	31.7	30.1	29.6
29	T	29.1	24.4	25.4	28.6	29.6	29.6	29.6
	M	29.6	29.6	30.1	29.6	29.6	29.6	29.6
	B	29.1	29.6	30.1	30.1	29.6	29.6	29.6

Appendix Table 3. DENSITY (σ_t) DISTRIBUTION AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = surface, M = mid-depth, B = bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	20.6	17.0	19.7	20.2	20.2	21.2	21.2
	M	20.3	20.4	21.3	21.1	20.4	21.2	21.2
	B	21.3	21.2	22.3	21.2	20.4	21.2	21.2
10	T	19.9	18.0	18.2	18.8	19.5	21.4	21.8
	M	20.6	20.8	20.9	21.3	20.1	21.5	21.8
	B	20.7	20.8	22.4	21.8	21.4	21.5	22.0
16	T	20.6	15.0	16.7	17.3	18.8	20.2	20.6
	M	20.7	20.1	21.9	21.9	21.6	20.2	20.6
	B	20.6	21.8	22.0	22.0	21.6	20.2	20.6
23	T	19.5	16.0	17.5	20.2	19.5	20.0	21.0
	M	20.0	20.2	21.0	21.0	20.2	20.2	20.9
	B	20.2	20.4	21.0	21.4	20.2	20.7	21.1
30	T	19.1	11.9	14.1	14.1	18.2	19.1	20.0
	M	19.2	18.6	20.8	20.4	20.0	20.7	20.0
	B	19.9	20.2	20.8	21.4	20.0	21.1	20.0
20 Aug.	T	19.1	12.4	15.3	16.0	18.3	20.2	20.7
	M	19.6	20.8	20.7	20.8	20.2	28.7	20.5
	B	19.5	20.7	20.8	20.8	19.9	19.9	20.7
3 Sept.	T	20.5	14.2	16.0	18.5	20.0	21.0	21.2
	M	20.5	20.2	22.0	20.3	20.0	20.6	21.5
	B	20.5	20.8	22.3	21.0	20.0	20.9	21.7
10	T	-	-	19.3	-	20.2	21.0	21.3
	M	-	-	20.7	-	20.9	20.9	21.6
	B	-	-	21.1	-	20.9	21.3	21.2
17	T	21.1	18.0	15.7	17.4	24.5	20.5	22.1
	M	25.3	20.7	20.5	20.5	24.5	24.5	22.2
	B	25.3	20.9	17.3	20.5	24.5	24.5	22.3
1 Oct.	T	21.2	17.4	18.3	20.1	21.8	21.9	22.8
	M	21.3	20.9	20.4	21.0	21.8	21.6	22.8
	B	21.3	21.9	21.9	22.0	21.8	21.6	22.8
22	T	22.3	18.6	20.3	22.1	22.1	22.1	23.0
	M	22.6	22.9	22.3	22.1	22.1	22.1	23.0
	B	22.2	22.9	22.4	23.7	22.1	22.1	23.4
5 Nov.	T	23.2	19.4	20.7	22.6	22.7	23.5	23.5
	M	23.3	21.8	22.2	22.7	23.0	23.5	23.6
	B	23.3	22.6	22.6	23.1	23.0	23.5	23.6

Appendix Table 3. (cont.)

24	T	21.6	9.3	17.4	20.7	21.6	-	23.6
	M	22.5	23.1	23.1	21.5	22.4	-	23.6
	B	22.5	23.1	23.1	23.1	23.2	-	23.6
8 Dec.	T	20.9	10.2	12.7	15.2	20.0	21.7	22.5
	M	21.3	19.9	19.9	20.4	20.8	21.7	23.3
	B	21.3	19.9	22.4	23.1	21.6	21.7	23.3
17	T	21.1	17.2	11.1	15.3	16.9	21.8	21.8
	M	22.2	23.3	22.8	22.6	21.8	22.6	22.7
	B	22.7	23.3	22.8	22.5	21.8	22.6	22.7
1987								
5 Jan.	T	21.6	14.5	17.8	19.5	19.5	22.2	22.2
	M	21.9	22.8	19.4	22.7	21.8	22.2	22.7
	B	21.9	23.0	21.8	22.7	21.8	22.2	22.7
12	T	22.3	19.4	19.4	19.0	22.3	23.1	23.2
	M	23.2	23.8	22.7	22.8	22.3	23.1	23.2
	B	23.2	25.0	24.3	24.4	22.3	23.1	-
2 Feb.	T	22.1	16.2	15.4	22.0	22.4	22.0	22.9
	M	22.0	22.8	22.9	22.4	22.4	22.9	23.7
	B	22.9	23.6	23.6	23.6	22.6	23.6	23.6
24	T	23.7	19.5	21.6	21.9	23.7	23.7	23.7
	M	23.7	20.9	22.8	23.7	22.9	23.7	23.7
	B	23.3	23.6	24.5	24.5	23.7	23.7	24.1
2 Mar.	T	22.8	-	13.7	19.9	23.6	23.6	24.0
	M	23.6	-	23.6	23.6	23.6	24.0	24.5
	B	23.6	-	24.0	24.0	23.6	24.5	24.5
16	T	22.8	17.8	18.5	21.5	22.8	23.5	22.9
	M	23.6	24.4	24.0	24.0	23.2	23.5	23.2
	B	23.6	24.4	24.5	24.5	-	23.5	23.6
30	T	21.6	14.4	18.0	20.7	22.8	23.2	23.1
	M	22.7	22.6	22.4	22.8	22.7	22.7	23.2
	B	23.1	23.3	23.2	22.8	23.1	23.1	24.1
15 Apr.	T	15.7	-	8.7	8.9	18.0	19.7	18.4
	M	19.9	22.4	22.8	20.3	20.6	20.6	22.4
	B	20.6	22.4	23.1	22.4	21.4	22.2	23.1
27	T	21.6	14.4	22.2	20.7	22.8	23.2	23.1
	M	22.7	22.6	22.4	22.8	22.7	22.7	23.2
	B	23.1	23.3	23.2	22.8	23.1	23.1	24.1
12 May	T	19.3	11.4	14.7	17.3	19.9	20.7	21.1
	M	21.7	21.8	22.6	21.0	21.1	21.2	22.1
	B	21.8	23.5	22.8	21.8	21.2	21.2	22.7

Appendix Table 3. (cont.)

26	T	19.6	15.5	17.1	18.6	20.1	21.2	20.1
	M	21.4	21.2	21.9	21.5	21.2	21.2	21.2
	B	21.4	21.2	21.4	21.5	22.0	21.2	21.3
15 June	T	19.1	18.1	18.2	19.4	22.1	22.5	21.3
	M	19.1	20.2	19.7	22.9	23.3	22.5	21.1
	B	19.9	22.5	20.3	23.0	22.5	21.3	20.9
29	T	20.5	16.9	17.1	20.5	21.1	21.1	21.1
	M	21.0	21.4	21.7	21.4	21.1	21.1	21.1
	B	20.5	21.4	21.7	21.7	21.1	21.2	21.1

Appendix Table 4. SECCHI DISC MEASUREMENTS (m) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	1.75	1.0	1.75	1.75	1.25	1.25	2.0
10	1.25	2.75	2.0	2.0	1.0	2.0	2.25
16	2.0	2.0	2.0	1.75	1.75	1.5	1.75
23	1.5	1.0	1.75	2.5	2.5	1.75	2.0
30	2.0	1.75	1.25	1.5	1.5	2.5	2.25
20 Aug.	2.25	2.25	1.75	1.25	1.0	2.25	2.25
3 Sept.	1.5	1.75	1.75	1.0	1.75	2.0	2.25
10	1.75	2.25	2.0	2.0	2.25	2.25	1.75
17	2.5	1.75	2.5	2.5	2.75	1.75	2.25
1 Oct.	2.0	2.25	2.0	2.0	2.0	2.25	2.0
22	2.75	2.5	3.25	3.25	3.5	3.25	2.25
5 Nov.	2.75	3.0	2.5	2.5	3.0	2.5	2.25
24	2.5	1.25	2.0	2.75	3.0	3.0	3.5
8 Dec.	2.75	1.5	1.75	2.5	2.5	3.75	2.5
17	3.75	2.5	2.5	2.5	3.0	3.25	3.5
1987							
5 Jan.	3.25	2.75	2.0	2.75	3.25	3.5	3.75
12	2.75	1.75	2.5	2.5	2.5	3.0	4.25
2 Feb.	3.75	2.5	2.5	3.25	2.75	3.5	3.5
24	2.5	2.25	2.5	2.25	2.5	2.0	4.25
2 Mar.	3.25	-	1.5	1.75	3.25	4.0	4.25
16	2.75	2.5	3.25	3.25	3.5	3.5	3.5
30	2.0	2.0	1.75	2.0	2.5	2.25	2.5
15 Apr.	1.75	1.75	2.25	2.5	2.75	2.5	2.25
27	2.0	2.0	2.75	2.0	2.5	2.25	2.5
12 May	2.5	2.25	2.25	3.0	3.0	2.5	4.0
26	2.25	2.25	2.25	2.75	2.5	2.25	2.0
15 June	2.0	1.75	1.5	1.25	2.0	2.5	2.75
29	2.0	2.5	1.0	1.75	2.5	2.5	2.25

Appendix Table 5. PO$_4$ CONCENTRATION (mg-at m^{-3}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	3.3	4.1	3.9	2.4	2.0	1.3	1.5
	M	3.4	4.6	3.7	2.9	2.1	1.6	1.3
	B	4.1	4.4	3.2	3.1	2.3	1.4	1.2
10	T	2.2	3.2	5.9	3.1	2.4	2.1	1.2
	M	2.6	1.8	3.3	2.5	2.2	2.1	1.8
	B	2.7	1.4	2.6	2.5	2.3	1.8	2.0
16	T	3.3	4.8	3.5	4.6	1.8	1.7	1.8
	M	3.2	3.9	2.8	3.8	2.6	2.1	1.8
	B	3.2	3.5	2.8	3.5	2.7	2.1	1.7
23	T	3.0	4.7	3.1	4.0	1.8	2.1	1.8
	M	2.8	4.2	2.9	4.0	1.9	1.9	1.8
	B	3.1	5.0	2.9	3.4	1.7	1.9	1.9
30	T	2.5	8.2	2.1	-	2.2	1.8	1.8
	M	2.7	5.5	4.0	-	2.3	1.5	1.6
	B	2.8	3.4	7.1	-	2.4	1.7	1.6
20 Aug.	T	1.2	5.2	4.9	4.5	3.2	1.9	2.0
	M	3.1	3.2	2.5	1.0	2.7	2.5	1.6
	B	3.6	3.3	2.1	2.1	2.9	2.6	1.1
3 Sept.	T	1.9	5.0	3.8	1.0	1.0	1.7	0.9
	M	2.2	3.2	2.8	0.7	1.9	1.9	1.5
	B	1.9	2.2	2.8	1.6	1.6	1.1	1.1
10	T	1.6	5.9	3.1	2.9	1.5	1.1	1.0
	M	1.6	3.4	2.6	2.3	1.7	2.9	1.6
	B	2.1	3.1	2.4	1.8	1.5	1.3	1.6
17	T	6.1	4.0	6.6	3.9	1.9	10.8	1.8
	M	2.2	3.8	3.1	3.9	0.3	10.7	4.1
	B	3.0	3.8	2.7	1.7	1.0	3.1	6.5
1 Oct.	T	2.1	4.9	4.1	3.1	2.3	2.1	1.9
	M	1.9	3.6	3.4	2.3	2.1	2.2	1.8
	B	2.2	6.1	3.0	2.6	2.0	2.3	1.8
22	T	2.2	-	-	-	1.3	2.2	1.7
	M	1.0	2.3	2.1	1.2	2.0	2.2	1.1
	B	1.3	2.0	1.4	2.3	1.4	2.7	1.2
5 Nov.	T	1.5	6.2	5.3	3.6	3.0	2.5	2.2
	M	1.6	4.9	4.0	3.7	3.1	2.7	2.3
	B	1.7	4.0	3.8	3.1	3.1	2.8	2.3

Appendix Table 5. (cont.)

24	T	1.6	0.6	2.1	2.0	2.8	2.8	2.3
	M	2.2	2.4	2.1	3.0	2.7	2.5	2.4
	B	2.3	2.2	2.1	2.6	2.8	2.6	2.3
8 Dec.	T	2.7	-	-	-	2.9	2.7	2.5
	M	2.6	2.9	2.9	3.0	2.9	2.9	2.4
	B	2.4	3.0	4.7	2.7	3.0	2.8	2.2
17	T	1.8	5.4	0.8	5.4	1.8	1.7	1.6
	M	1.6	1.7	1.6	1.7	2.6	1.6	1.5
	B	1.5	1.8	2.4	1.4	1.6	1.6	1.3
1987								
5 Jan.	T	2.3	3.2	3.7	0.7	2.4	2.2	2.0
	M	2.3	2.2	2.3	2.3	2.3	4.3	2.2
	B	2.2	2.1	2.3	2.3	1.9	2.3	2.1
12	T	1.0	3.2	2.9	2.6	1.4	1.2	1.2
	M	1.0	1.2	1.4	1.3	1.4	1.1	1.1
	B	1.1	1.2	1.2	1.1	1.3	1.1	1.2
2 Feb.	T	1.0	3.5	2.5	1.5	1.1	1.0	0.9
	M	1.1	1.2	1.2	1.3	1.2	1.0	1.0
	B	1.1	1.3	1.2	1.0	1.2	1.0	0.9
24	T	1.4	5.4	5.4	2.1	1.4	1.4	1.4
	M	1.3	2.6	1.9	1.4	1.4	1.4	1.3
	B	1.4	1.6	1.5	1.5	1.4	1.4	1.4
2 Mar.	T	0.2	-	2.0	1.5	0.2	0.1	0.2
	M	0.1	-	0.5	0.3	0.2	0.1	0.2
	B	0.1	-	0.3	0.3	0.2	0.2	0.2
16	T	0.1	1.2	1.3	0.7	0.4	0.2	0.1
	M	0.1	0.7	0.4	0.4	0.2	0.2	0.2
	B	0.1	0.6	0.4	0.4	0.6	0.3	0.2
30	T	0.3	3.1	2.1	1.3	0.1	0.1	0.1
	M	0.1	0.2	0.9	0.2	0.1	0.1	0.2
	B	0.2	0.8	0.2	0.1	0.1	0.1	0.3
15 Apr.	T	0.2	5.4	1.8	1.0	0.4	0.2	0.1
	M	0.2	2.1	0.4	0.3	0.3	0.2	0.1
	B	0.2	1.5	0.4	0.4	0.4	0.1	0.3
27	T	0.1	-	-	-	0.3	0.0	0.0
	M	0.0	0.6	0.2	0.1	0.1	0.0	0.0
	B	0.1	1.7	0.2	0.1	0.1	0.1	0.3
12 May	T	0.0	3.1	0.6	0.4	0.1	0.0	0.0
	M	0.5	2.5	2.2	0.6	0.1	0.1	0.0
	B	0.5	1.1	3.6	0.5	0.2	0.1	0.1

Appendix Table 5. (cont.)

26	T	0.5	0.5	0.1	0.1	0.4	0.5	0.3
	M	1.0	3.2	1.3	0.9	0.6	0.5	0.3
	B	1.1	3.4	1.1	0.9	0.7	0.6	0.4
15 June	T	0.8	2.6	2.0	0.7	0.9	0.6	0.7
	M	0.7	4.0	1.9	1.5	1.0	0.7	0.7
	B	1.4	4.2	1.5	1.0	1.0	0.8	0.5
29	T	1.9	4.4	1.6	1.3	2.0	1.1	0.7
	M	2.0	3.5	2.0	1.8	1.8	1.0	0.6
	B	2.0	3.5	1.9	1.7	2.0	1.0	0.9

Appendix Table 6. NH_4-N CONCENTRATIONS (mg-at m^{-3}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	4.2	> 12.0	15.6	2.1	0.9	0.3	0.7
	M	4.3	6.8	11.1	5.3	1.2	0.5	0.9
	B	5.5	6.6	8.7	8.2	1.8	0.8	0.9
10	T	1.0	18.8	9.2	2.0	1.3	1.2	1.2
	M	1.1	9.6	5.5	1.4	1.4	1.2	1.2
	B	1.1	8.5	3.3	1.4	1.5	1.2	1.5
16	T	1.0	24.7	10.4	6.5	1.0	0.8	1.1
	M	8.2	13.8	11.2	8.4	8.9	2.1	1.0
	B	9.9	15.0	11.2	8.2	9.0	2.1	1.0
23	T	1.5	24.7	3.4	5.9	1.9	1.3	0.9
	M	2.1	15.8	10.6	8.0	6.3	1.7	1.5
	B	2.5	19.6	11.1	6.8	6.8	1.7	0.8
30	T	0.9	48.4	10.6	-	2.0	0.8	1.3
	M	1.9	22.9	9.9	-	6.3	1.0	1.7
	B	7.2	14.3	11.1	-	6.8	2.7	2.5
20 Aug.	T	11.5	32.7	22.2	7.1	10.4	9.8	4.4
	M	12.5	13.8	6.3	9.2	8.6	6.8	2.8
	B	11.4	7.5	9.6	10.7	10.7	6.7	0.1
3 Sept.	T	2.6	25.1	18.1	1.2	0.4	0.8	1.2
	M	2.0	9.0	7.2	5.8	2.1	1.1	2.7
	B	1.4	5.8	8.1	3.1	2.6	0.6	1.3
10	T	6.2	52.1	9.4	2.6	0.8	0.5	0.7
	M	1.0	11.0	6.1	0.6	2.2	0.7	3.3
	B	1.4	10.1	6.0	3.4	1.8	0.2	1.7
17	T	8.1	56.3	40.2	45.3	6.5	5.5	2.6
	M	3.3	14.1	15.9	6.7	7.0	4.6	2.8
	B	3.9	15.0	13.0	6.7	8.2	7.8	4.6
1 Oct.	T	7.3	31.7	29.6	6.7	4.1	5.9	3.3
	M	3.5	12.7	7.7	4.7	3.5	6.4	3.2
	B	6.3	18.2	10.7	8.0	3.1	5.7	3.6
22	T	11.1	35.8	24.9	35.9	8.9	9.6	6.0
	M	12.6	12.4	8.9	11.6	8.9	9.3	7.1
	B	12.0	11.7	15.3	11.3	10.6	10.2	11.2
5 Nov.	T	3.8	43.0	37.7	20.1	16.3	10.4	8.2
	M	3.6	32.6	21.5	20.1	14.1	10.5	8.0
	B	3.8	22.6	19.3	14.1	13.5	10.6	8.2

Appendix Table 6. (cont.)

24	T	8.0	35.5	28.5	19.8	15.0	13.5	8.9
	M	9.3	10.9	8.8	16.3	16.4	12.7	7.6
	B	8.4	10.9	7.9	14.7	14.2	12.0	7.9
8 Dec.	T	5.0	30.5	21.3	19.3	7.0	7.2	2.6
	M	3.2	7.4	7.7	7.2	6.2	4.9	3.3
	B	2.9	7.8	5.6	3.8	5.3	4.1	1.9
17	T	7.8	42.9	30.1	7.1	7.0	6.5	5.7
	M	5.1	10.4	6.4	5.5	22.6	6.7	4.6
	B	5.1	7.5	3.5	3.2	5.7	4.3	6.5
1987								
5 Jan.	T	2.1	8.3	17.2	15.8	4.7	1.6	0.3
	M	2.6	2.9	8.4	1.5	1.9	2.3	1.9
	B	1.8	2.6	3.5	1.4	0.3	2.4	2.6
12	T	1.1	20.5	13.0	13.2	4.6	2.2	2.3
	M	1.5	2.6	4.3	3.5	4.2	2.5	2.0
	B	1.6	1.5	2.5	6.7	4.0	2.0	2.1
2 Feb.	T	2.4	32.3	21.9	6.4	4.0	2.8	1.4
	M	2.5	5.7	4.2	4.6	3.7	2.6	1.8
	B	3.2	5.1	3.0	2.4	3.5	1.7	1.8
24	T	0.2	21.7	13.4	7.3	0.3	0.1	0.2
	M	0.2	25.5	5.5	0.5	0.2	0.1	0.1
	B	0.2	1.1	0.3	0.3	2.2	0.1	0.1
2 Mar.	T	0.2	-	23.0	14.8	1.0	0.4	0.4
	M	0.2	-	1.7	1.5	0.7	0.3	0.3
	B	0.5	-	0.8	0.3	0.9	0.2	0.5
16	T	0.4	12.9	12.7	4.4	1.8	0.8	0.4
	M	0.2	2.3	1.4	4.8	0.7	0.9	0.6
	B	0.8	1.8	1.6	1.1	1.1	0.8	0.2
30	T	8.2	32.8	3.5	3.6	7.5	9.4	7.2
	M	8.6	7.2	5.2	7.4	6.3	7.6	9.8
	B	9.0	6.2	7.2	5.2	8.1	7.8	10.8
15 Apr.	T	1.4	14.9	18.4	17.7	2.9	1.5	3.6
	M	1.9	3.9	1.0	1.0	2.7	1.3	2.4
	B	0.4	6.9	1.9	1.6	1.1	0.5	0.5
27	T	1.5	24.3	12.4	3.9	2.1	0.6	0.3
	M	2.5	2.3	1.0	0.6	0.6	0.3	0.3
	B	1.0	4.2	0.9	0.6	0.6	0.4	0.0
12 May	T	0.4	24.3	19.5	5.2	0.5	0.6	0.5
	M	1.0	5.1	4.5	1.7	0.8	0.7	0.2
	B	0.9	10.9	6.5	1.9	1.1	0.7	0.3

Appendix Table 6. (cont.)

26	T	0.8	47.5	18.5	5.8	0.4	1.2	0.4
	M	2.4	6.7	3.2	2.5	1.5	1.3	0.4
	B	2.5	6.9	2.9	2.5	2.1	1.4	1.0
15 June	T	0.4	35.2	7.8	0.8	0.8	0.5	0.7
	M	0.3	15.2	4.6	3.0	0.5	0.8	0.6
	B	1.3	11.9	4.1	2.7	0.9	1.1	0.6
29	T	0.7	38.2	2.8	6.2	3.5	1.4	0.4
	M	3.9	12.8	10.9	3.9	3.6	0.3	0.0
	B	3.2	12.1	10.7	4.2	4.1	0.5	1.5

Appendix Table 7. NO_3-N CONCENTRATIONS (mg-at m-3) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	0.3	8.7	6.3	0.5	0.1	0.1	0.1
	M	0.4	1.4	1.7	1.0	0.3	0.1	0.2
	B	0.4	0.9	0.7	1.1	0.3	0.2	0.2
10	T	0.3	10.5	9.3	2.5	0.3	0.2	0.2
	M	0.2	2.0	1.3	0.1	0.2	0.2	0.2
	B	0.2	1.0	0.7	0.2	0.2	0.2	0.3
16	T	0.3	25.8	15.3	11.0	0.3	0.4	0.2
	M	0.6	6.1	1.5	1.4	1.0	0.4	0.2
	B	0.7	1.2	1.1	1.2	0.9	0.4	0.2
23	T	0.1	14.7	7.1	1.6	0.4	0.2	0.1
	M	0.5	1.8	1.8	1.5	0.3	0.1	0.2
	B	0.5	1.1	1.6	1.3	0.3	0.2	0.2
30	T	0.2	26.9	1.3	-	0.6	0.2	0.2
	M	0.4	5.4	1.6	-	0.8	0.2	0.3
	B	0.7	1.7	7.8	-	0.9	0.5	0.5
20 Aug.	T	0.2	22.5	18.0	10.8	2.5	3.3	1.4
	M	3.2	3.4	2.8	1.1	2.5	3.0	2.4
	B	3.5	4.9	2.5	3.0	3.1	2.8	2.7
3 Sept.	T	0.7	26.6	22.2	0.2	0.1	0.2	0.3
	M	0.2	2.8	2.8	0.8	0.7	0.4	0.8
	B	0.0	3.2	3.1	2.0	0.6	0.3	0.2
10	T	0.2	13.7	9.1	1.1	1.1	0.1	0.1
	M	0.7	6.7	4.1	2.4	1.6	0.2	0.3
	B	0.7	3.5	3.4	3.1	0.9	0.1	0.4
17	T	1.9	37.9	27.8	29.5	4.2	4.2	1.1
	M	2.0	3.8	7.7	5.1	3.9	2.7	1.0
	B	1.4	3.5	6.1	2.7	3.1	3.1	1.0
1 Oct.	T	6.6	20.9	18.2	8.8	8.9	6.6	4.3
	M	6.4	9.5	12.2	8.3	7.2	6.7	4.0
	B	7.6	4.6	6.3	6.3	7.0	6.7	4.5
22	T	8.2	26.3	17.5	11.9	11.6	13.0	7.7
	M	11.9	12.5	14.2	12.3	12.4	12.4	8.8
	B	12.2	12.2	11.8	11.7	13.0	9.5	9.0
5 Nov.	T	7.8	24.8	22.1	15.0	13.3	11.3	8.6
	M	7.4	18.5	15.9	15.2	13.2	11.3	8.6
	B	7.3	16.0	14.7	12.2	13.4	11.5	8.7

Appendix Table 7. (cont.)

24	T	11.9	30.8	21.7	20.7	17.4	15.9	13.6
	M	17.7	13.0	12.3	16.9	15.8	15.5	13.9
	B	15.5	12.5	12.3	13.2	16.1	14.6	13.2
8 Dec.	T	16.2	26.9	19.7	21.3	17.6	14.8	10.4
	M	15.8	15.6	15.8	16.5	16.4	13.5	11.8
	B	14.1	14.9	13.2	13.0	15.4	14.6	11.6
17	T	18.5	27.6	23.5	11.0	15.9	15.3	15.4
	M	16.3	11.0	13.6	14.0	25.0	13.8	13.3
	B	16.3	12.0	13.1	11.2	15.8	13.4	12.9
1987								
5 Jan.	T	14.9	23.7	11.4	11.2	15.7	11.6	9.2
	M	13.4	11.1	15.7	11.3	12.9	11.9	10.7
	B	11.9	9.9	12.4	11.6	10.1	11.7	10.8
12	T	14.3	15.6	16.6	18.1	15.0	12.7	12.2
	M	12.1	9.1	12.2	12.4	14.8	12.8	11.5
	B	12.4	8.4	9.8	7.5	14.5	12.9	11.9
2 Feb.	T	11.3	24.1	22.7	12.8	11.4	11.2	8.9
	M	11.2	10.8	10.6	11.3	22.5	11.9	8.8
	B	11.1	10.5	9.2	8.8	22.5	9.0	8.5
24	T	0.2	13.0	6.9	7.9	0.1	0.1	0.3
	M	0.1	12.0	4.6	0.4	0.1	0.1	0.0
	B	0.1	1.6	0.7	0.3	0.9	0.1	0.0
2 Mar.	T	0.9	-	21.7	8.7	0.5	0.4	0.4
	M	0.2	-	1.6	1.0	0.5	0.2	0.2
	B	0.2	-	0.6	0.8	0.3	0.2	0.3
16	T	0.9	15.2	12.5	5.5	1.8	0.8	0.5
	M	0.3	1.5	1.2	0.9	0.8	0.6	0.5
	B	0.5	1.0	1.0	0.6	0.4	0.4	0.3
30	T	0.6	16.5	5.4	0.4	0.1	0.4	0.6
	M	0.2	0.3	0.4	0.3	1.9	0.3	0.5
	B	0.2	0.5	0.3	0.4	0.4	0.2	0.1
15 Apr.	T	0.9	26.2	20.3	19.0	5.5	1.2	0.6
	M	1.3	1.4	1.6	2.7	0.8	0.8	0.4
	B	0.2	1.0	1.5	1.3	1.0	0.2	0.5
27	T	0.9	13.6	9.5	3.8	2.5	0.4	0.0
	M	0.2	0.6	0.2	0.3	0.1	0.0	0.0
	B	0.3	1.2	0.3	0.5	0.2	0.2	0.0
12 May	T	0.4	18.5	11.6	4.9	0.5	0.2	0.2
	M	0.2	1.6	0.6	0.3	0.4	0.2	0.1
	B	0.2	0.3	0.5	0.9	0.4	0.2	0.1

Appendix Table 7. (cont.)

26	T	0.8	18.3	12.1	6.3	0.4	1.3	0.2
	M	1.2	1.2	1.1	1.2	1.0	1.1	0.2
	B	1.2	1.0	1.0	1.1	0.9	1.2	0.3
15 June	T	0.2	15.5	8.6	0.0	0.2	0.2	0.3
	M	0.2	2.1	0.9	0.5	0.4	0.1	0.2
	B	0.5	2.3	0.8	0.5	0.3	0.2	0.3
29	T	1.0	28.4	5.0	0.3	1.6	0.2	0.0
	M	1.6	4.7	2.2	1.6	1.3	0.1	0.0
	B	1.5	2.6	2.0	1.5	1.6	0.1	0.0

Appendix Table 8. SiO_3-Si CONCENTRATIONS (mg-at m-3) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)
(T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	>60.0	57.6	49.3	49.0	48.2	46.8	45.9
	M	>60.0	48.2	46.5	49.3	49.8	44.4	46.0
	B	>60.0	47.3	42.5	48.0	>60.0	45.3	45.3
10	T	26.8	45.7	59.6	47.9	45.8	50.5	43.8
	M	27.3	39.6	-	46.7	54.1	49.3	58.8
	B	26.8	38.5	96.1	49.7	43.5	48.4	49.1
16	T	41.8	50.2	37.2	47.6	24.4	18.9	32.2
	M	40.2	37.1	35.7	48.5	38.0	36.9	33.4
	B	40.8	35.6	36.0	46.8	38.3	37.7	35.7
23	T	36.9	37.7	30.3	36.7	33.1	35.3	32.1
	M	33.2	33.2	32.3	39.8	36.5	34.2	31.0
	B	37.8	34.7	32.6	38.7	39.3	36.8	30.5
30	T	36.4	72.4	24.6	-	27.5	28.5	29.4
	M	35.9	43.5	35.6	-	30.2	27.4	30.3
	B	34.3	43.5	13.6	-	30.5	27.8	30.8
20 Aug.	T	24.3	45.3	45.1	24.9	25.3	23.1	18.4
	M	27.3	27.1	21.3	19.3	25.0	24.1	16.6
	B	31.3	33.6	20.7	19.2	26.0	24.0	18.4
3 Sept.	T	18.4	44.2	26.2	8.1	9.4	17.9	18.1
	M	20.0	23.6	24.3	15.5	19.5	22.8	25.6
	B	19.6	24.2	25.0	19.4	18.8	20.0	19.2
10	T	7.6	30.6	19.3	8.1	10.8	9.9	11.6
	M	13.6	20.3	18.6	15.1	10.0	19.5	15.2
	B	15.8	21.1	17.1	11.1	16.8	12.3	22.5
17	T	18.6	25.1	46.0	25.4	13.9	15.3	14.1
	M	10.7	25.8	22.3	25.4	9.0	14.6	22.5
	B	27.2	25.6	18.1	11.1	11.3	15.6	14.9
1 Oct.	T	22.1	38.3	30.2	22.0	21.1	20.9	20.2
	M	22.2	26.1	22.3	19.4	18.3	20.6	19.8
	B	25.4	26.4	24.3	24.2	18.1	21.5	20.7
22	T	35.5	-	-	-	25.7	28.1	10.3
	M	27.9	26.8	27.7	25.7	24.2	27.9	26.3
	B	29.4	27.0	24.3	26.2	26.1	25.9	26.9
5 Nov.	T	28.9	40.3	35.5	28.4	26.9	26.6	21.9
	M	28.9	33.1	28.3	28.3	27.4	27.2	22.3
	B	28.6	29.3	28.1	25.1	27.5	26.8	22.2

Appendix Table 8. (cont.)

24	T	21.3	44.4	44.5	27.9	30.2	28.1	26.4
	M	30.2	25.9	24.6	29.7	27.3	27.4	26.4
	B	27.6	24.4	24.8	26.3	28.2	26.3	25.0
8 Dec.	T	37.4	-	-	-	52.1	37.7	26.2
	M	37.2	50.0	48.2	50.6	46.2	34.7	28.9
	B	33.8	49.9	41.4	35.5	42.1	36.5	29.0
17	T	34.4	44.7	44.7	44.7	29.9	29.1	29.8
	M	28.4	25.7	27.7	27.9	40.8	26.3	26.3
	B	27.5	26.3	26.9	23.9	30.2	25.8	25.2
1987								
5 Jan.	T	39.4	164.7	84.5	44.8	45.5	33.5	34.4
	M	37.6	32.2	49.9	33.2	38.1	35.2	31.6
	B	33.7	29.0	36.3	33.7	35.7	34.3	32.0
12	T	25.5	85.9	69.3	43.2	27.1	23.5	22.4
	M	22.8	18.5	23.4	22.9	26.5	23.2	21.6
	B	22.8	17.0	19.4	15.2	26.2	23.3	21.7
2 Feb.	T	17.3	57.5	58.4	20.8	17.6	16.0	13.7
	M	17.2	16.8	16.5	17.9	17.1	15.0	13.6
	B	17.1	17.0	14.9	13.8	17.0	12.6	12.9
24	T	7.0	44.9	6.8	6.3	6.6	6.9	6.4
	M	7.4	33.0	14.1	10.0	7.1	7.0	6.4
	B	6.7	8.2	7.4	7.4	7.9	6.8	6.5
2 Mar.	T	4.3	-	39.6	14.9	4.4	4.0	3.9
	M	4.0	-	5.0	4.3	4.0	3.8	4.3
	B	4.0	-	4.2	4.2	3.6	3.7	4.1
16	T	5.7	32.6	27.7	14.5	8.1	5.6	4.2
	M	5.0	6.1	5.6	5.4	5.5	5.3	4.7
	B	4.9	5.5	5.4	5.4	5.2	5.2	4.7
30	T	6.1	39.2	29.1	10.2	4.8	4.4	4.9
	M	4.3	4.5	4.4	5.1	6.9	4.1	4.8
	B	4.9	4.4	4.6	4.5	5.0	4.5	4.7
15 Apr.	T	5.8	44.8	44.8	44.8	13.9	5.9	2.3
	M	5.4	5.3	5.1	7.0	4.3	4.3	3.1
	B	4.4	5.2	4.6	4.3	4.1	3.1	3.1
27	T	1.5	-	-	-	7.6	2.6	1.6
	M	3.6	2.6	2.4	2.3	2.6	2.2	1.5
	B	2.0	3.2	2.5	2.9	2.1	2.2	2.7
12 May	T	1.2	43.1	29.1	16.2	1.2	1.0	1.0
	M	1.4	1.9	1.6	1.3	1.2	1.1	1.0
	B	1.4	43.2	1.8	1.4	1.2	1.0	1.2

Appendix Table 8. (cont.)

26	T	1.5	34.5	22.0	12.2	1.1	1.5	1.0
	M	2.4	3.1	2.3	2.0	1.8	1.6	1.1
	B	2.5	3.1	2.1	2.0	2.2	1.7	1.5
15 June	T	4.5	25.6	21.6	7.0	6.6	5.0	8.1
	M	4.5	16.0	11.0	11.4	7.3	6.3	9.1
	B	9.6	15.4	10.2	8.9	8.1	7.6	8.6
29	T	16.1	35.8	15.9	5.7	12.1	4.6	3.8
	M	14.5	20.0	16.6	14.4	11.9	3.9	3.5
	B	14.5	20.5	17.1	16.1	13.9	5.0	3.6

Appendix Table 9. CHLOROPHYLL LEVELS (mg m-3) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987) (T = Surface, M = Mid-depth, B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	5.3	4.2	9.8	14.4	35.8	15.0	7.6
	M	5.0	1.5	2.2	5.8	11.0	6.5	8.9
	B	1.3	0.6	0.9	1.6	4.7	7.6	8.9
10	T	13.6	4.0	9.8	18.6	51.5	20.2	8.7
	M	27.0	1.4	4.3	9.3	17.9	18.8	7.5
	B	9.8	1.1	2.9	7.1	6.8	11.2	5.4
16	T	13.3	6.4	13.9	17.3	25.0	25.3	8.7
	M	5.1	8.7	2.0	3.1	2.5	6.7	18.1
	B	2.0	6.0	-	1.3	2.4	6.7	7.5
23	T	9.1	30.7	16.7	6.0	3.7	9.5	8.4
	M	2.4	5.4	1.9	2.7	3.6	10.6	5.0
	B	1.9	2.8	1.9	1.8	2.6	3.9	2.8
30	T	12.5	13.2	55.6	29.4	33.0	16.1	8.9
	M	5.9	4.9	2.1	4.8	7.1	4.7	8.3
	B	2.5	2.8	3.2	4.9	3.2	4.0	8.9
20 Aug.	T	8.8	3.9	47.0	25.8	172.6	3.7	5.3
	M	1.5	1.8	2.8	3.3	3.1	1.7	2.2
	B	6.1	2.4	1.9	2.5	2.6	3.4	2.2
3 Sept.	T	14.5	18.4	43.4	-	21.2	13.2	4.1
	M	20.3	5.4	5.8	17.2	5.4	5.9	9.0
	B	16.9	4.1	4.4	12.5	7.4	9.3	12.2
10	T	10.1	4.6	27.6	21.7	11.3	10.1	11.3
	M	8.8	7.1	6.5	20.8	8.8	8.8	10.5
	B	3.1	2.8	4.9	8.6	8.3	10.1	10.1
17	T	2.8	1.9	1.8	3.4	2.1	2.5	2.4
	M	4.2	1.9	1.9	3.2	2.6	2.9	2.1
	B	3.3	2.2	2.9	1.5	1.7	2.8	2.2
1 Oct.	T	7.3	5.5	12.3	23.8	11.3	7.1	3.6
	M	6.1	4.9	6.8	10.1	11.2	7.6	3.9
	B	4.1	0.9	2.9	3.5	8.8	7.9	3.5
22	T	3.3	0.6	1.2	1.7	1.2	3.8	3.5
	M	1.3	1.2	1.2	1.5	1.3	2.8	2.4
	B	0.9	1.1	0.8	0.8	1.1	1.6	2.6

Appendix Table 9. (cont.)

5 Nov.	T	4.0	0.7	0.7	1.1	1.4	1.4	1.2
	M	4.2	0.8	0.7	1.1	1.1	1.7	1.2
	B	4.9	1.1	0.7	0.7	1.0	1.5	1.1
24	T	3.1	0.8	0.8	1.0	1.2	1.3	1.0
	M	2.1	0.4	0.6	0.7	1.0	1.2	1.0
	B	1.7	0.6	0.4	0.5	1.0	1.0	1.2
8 Dec.	T	2.1	0.6	0.7	0.7	1.1	1.1	2.1
	M	2.1	0.9	-	1.0	1.5	0.9	1.8
	B	2.2	1.0	0.8	1.1	1.0	0.9	1.2
17	T	0.3	0.5	0.3	0.4	0.3	0.8	0.5
	M	0.8	0.3	0.3	0.3	1.2	0.9	0.8
	B	0.8	0.5	0.3	0.5	0.9	0.6	0.9
1987								
5 Jan.	T	2.7	1.7	2.4	2.2	1.8	2.6	2.8
	M	3.5	2.2	1.9	2.4	2.8	3.3	2.9
	B	2.1	2.8	1.8	2.1	2.6	3.3	2.6
12	T	2.2	1.9	0.9	0.9	1.3	1.3	-
	M	6.4	2.0	1.6	1.4	1.3	1.4	1.1
	B	3.4	2.7	1.4	2.1	1.5	1.2	1.5
2 Feb.	T	5.3	1.1	0.8	1.2	2.1	2.2	2.7
	M	3.4	3.8	2.6	2.9	3.7	2.4	3.5
	B	4.2	3.5	2.6	2.8	3.0	5.9	4.1
24	T	12.0	11.5	19.3	15.7	21.0	20.4	9.8
	M	12.8	11.7	17.2	17.7	19.6	15.0	9.1
	B	15.4	15.5	15.2	12.3	17.2	16.9	9.8
2 Mar.	T	8.0	-	8.7	18.6	10.1	5.5	2.7
	M	8.4	-	13.6	-	9.9	4.3	2.6
	B	9.2	-	15.0	14.6	15.9	3.2	1.7
16	T	15.5	5.5	9.1	10.3	13.2	14.9	18.6
	M	18.8	13.2	12.8	13.7	14.0	15.9	16.7
	B	19.3	10.3	11.3	12.2	13.5	12.8	18.2
30	T	9.0	8.1	28.9	23.5	11.5	8.8	6.4
	M	11.5	26.2	31.2	14.5	10.1	8.8	6.4
	B	17.1	28.0	20.8	18.1	8.1	9.1	6.1
15 Apr.	T	19.8	0.6	1.4	0.5	12.2	19.1	19.9
	M	16.7	5.8	7.1	11.8	11.8	15.9	11.8
	B	11.5	6.8	6.3	6.8	9.1	9.5	6.9
27	T	25.3	5.9	12.8	19.3	20.8	18.8	22.6
	M	37.9	16.7	17.4	17.7	19.9	21.0	18.5
	B	23.0	16.6	16.1	15.2	15.9	22.6	12.7

Appendix Table 9. (cont.)

12 May	T	9.6	3.2	4.7	6.0	7.6	7.6	8.1
	M	7.4	9.8	9.4	7.6	7.6	1.8	2.0
	B	7.6	6.0	9.8	7.6	5.8	-	4.0
26	T	8.8	1.0	8.5	8.5	12.0	13.3	6.9
	M	3.6	1.2	1.9	2.2	4.4	6.8	7.1
	B	3.2	1.5	1.9	2.1	2.2	6.8	6.3
15 June	T	14.5	17.2	27.0	39.2	9.8	11.6	4.6
	M	15.0	2.7	4.5	2.0	14.5	8.3	6.0
	B	14.1	4.7	4.2	6.1	12.1	10.1	6.0
29	T	18.6	40.9	105.7	36.2	13.4	16.7	9.6
	M	8.8	7.1	8.1	14.2	10.5	17.1	11.3
	B	8.6	2.6	13.5	5.0	6.3	16.7	11.7

Appendix Table 10. ATP-C LEVELS (mg C m^{-3}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 15 April 1987) (T = Surface; M = Mid-depth; B = Bottom)

STATION:		1	2	3	4	5	6	7
1986								
2 July	T	775	458	1430	958	665	1318	413
	M	710	473	453	883	1063	968	408
	B	233	1910	203	280	598	1065	405
10	T	263	650	1688	3050	490	875	573
	M	483	305	535	675	308	235	388
	B	508	318	348	843	65	173	333
16	T	1295	563	1323	2528	3228	2373	1785
	M	498	978	285	380	263	755	1415
	B	210	343	305	335	338	678	905
23	T	1315	3278	2080	595	715	1530	330
	M	833	235	273	458	340	1198	88
	B	353	403	258	268	390	328	205
30	T	1003	715	3940	2768	1825	910	645
	M	543	513	95	503	553	178	460
	B	120	170	95	133	213	150	355
20 Aug.	T	1013	195	1683	1223	4368	273	220
	M	243	130	73	118	140	158	88
	B	398	173	1795	130	183	203	58
3 Sept.	T	918	1590	3788	5855	1520	888	500
	M	793	375	205	1088	273	665	123
	B	750	350	228	653	545	523	288
10	T	768	370	1738	1390	920	670	700
	M	713	505	265	1043	508	573	588
	B	648	205	273	520	585	888	540
17	T	400	153	245	425	353	293	203
	M	370	230	280	290	380	235	173
	B	338	178	250	265	288	255	160
1 Oct.	T	628	663	1040	1458	1075	653	288
	M	460	385	885	763	1050	578	280
	B	525	193	243	250	928	655	280
22	T	350	120	245	368	208	333	378
	M	250	155	115	295	130	355	190
	B	218	150	193	120	160	163	183
5 Nov.	T	578	130	105	165	168	173	113
	M	490	173	98	123	163	150	80
	B	490	130	65	65	1138	135	83

Appendix Table 10. (cont.)

24	T	175	20	10	50	93	108	93
	M	35	18	20	10	55	73	53
	B	73	5	10	13	108	113	58
8 Dec.	T	160	23	63	58	100	110	113
	M	160	13	88	70	95	155	130
	B	163	5	80	18	93	100	115
17	T	53	15	18	25	20	83	53
	M	55	25	20	33	105	88	63
	B	68	40	40	25	75	65	45
1987								
5 Jan.	T	68	40	20	53	13	65	38
	M	73	45	43	18	55	55	28
	B	33	23	25	53	63	83	28
12	T	78	20	20	3	10	80	48
	M	138	18	18	20	23	63	43
	B	53	40	53	48	40	68	-
2 Feb.	T	473	15	25	88	73	165	60
	M	558	118	158	135	228	68	148
	B	283	40	33	65	233	145	173
24	T	623	228	625	385	530	535	443
	M	550	288	588	358	460	720	438
	B	795	530	463	1210	663	630	355
2 Mar.	T	208	-	175	383	330	48	220
	M	270	-	445	413	330	113	8
	B	308	-	373	320	238	153	33
16	T	218	155	133	240	125	215	153
	M	63	8	75	65	240	-	190
	B	190	153	88	198	213	293	198
30	T	168	30	248	330	265	208	170
	M	100	368	328	390	143	178	203
	B	278	210	458	405	228	248	125
15 Apr.	T	290	83	50	53	73	353	275
	M	148	155	113	158	315	75	330
	B	220	155	118	120	150	98	125

Appendix Table 11. PRIMARY PRODUCTION RATES (mg C m^{-3} d^{-1}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION	% Light	1	2	3	4	5	6	7
1986								
2 July	100	325	109	577	412	796	144	33
	60	298	125	536	369	650	279	45
	25	197	85	397	191	713	301	46
	10	131	58	252	144	496	233	37
	3	59	17	86	83	265	358	25
10	100	217	377	1271	910	1008	396	192
	60	283	374	1289	846	1009	398	210
	25	265	227	1008	747	1015	403	213
	10	213	104	647	375	580	279	113
	3	138	72	237	317	470	210	112
16	100	422	461	2903	1993	2109	872	348
	60	485	638	2800	2095	2074	892	343
	25	439	465	2260	1454	1777	812	303
	10	330	310	1536	1046	1513	648	286
	3	185	149	840	532	1112	482	192
23	100	437	860	834	396	412	696	169
	60	434	961	880	376	502	717	202
	25	390	792	693	319	412	644	172
	10	293	402	484	192	280	474	134
	3	194	287	227	104	167	255	90
30	100	216	425	1418	823	985	691	104
	60	161	319	1002	641	817	508	90
	25	73	143	535	306	338	267	70
	10	48	77	244	163	180	120	41
	3	25	45	125	100	91	77	30
20 Aug.	100	396	148	907	373	2685	274	33
	60	360	151	700	308	2396	234	45
	25	227	91	421	206	1282	134	39
	10	120	40	266	108	800	60	33
	3	47	15	105	62	418	22	17
3 Sept.	100	576	666	1490	1566	830	314	119
	60	478	485	1390	1308	770	290	91
	25	346	376	1043	1062	636	268	66
	10	206	227	737	703	513	200	46
	3	149	127	454	431	332	122	31
10	100	804	432	2345	1631	350	796	253
	60	658	396	1930	1506	410	659	310
	25	533	269	1205	1109	300	507	259
	10	409	184	673	742	228	326	210
	3	250	109	286	443	125	150	139

Appendix Table 11.(cont.)

17	100	220	85	254	155	110	141	58
	60	232	88	263	193	78	148	70
	25	210	95	233	167	88	149	68
	10	148	63	144	124	90	111	58
	3	92	36	60	66	40	54	31
1 Oct.	100	288	174	735	495	671	588	78
	60	238	156	528	427	530	431	92
	25	190	114	305	308	328	287	74
	10	133	96	182	229	202	144	56
	3	87	61	91	149	103	87	39
22	100	82	50	43	77	66	183	160
	60	77	40	34	61	75	158	157
	25	60	36	27	55	55	116	106
	10	30	25	17	30	28	58	58
	3	17	8	11	11	9	19	24
5 Nov.	100	40	8	9	10	11	18	11
	60	35	6	7	8	8	14	12
	25	22	3	5	5	4	11	8
	10	12	1	2	2	4	6	3
	3	6	< 1	2	1	1	2	2
24	100	27	4	5	9	12	16	19
	60	20	4	5	8	14	18	17
	25	19	4	7	8	15	19	15
	10	20	4	7	8	14	17	12
	3	13	2	5	6	11	11	9
8 Dec.	100	39	5	9	12	18	27	35
	60	29	8	8	9	14	22	29
	25	17	2	6	7	10	14	14
	10	10	2	3	3	5	5	9
	3	5	1	2	1	2	3	5
17	100	6	< 1	3	5	5	7	8
	60	6	1	3	4	6	6	5
	25	4	< 1	4	3	4	5	7
	10	2	< 1	2	2	3	3	4
	3	< 1	0	1	1	2	2	3
1987								
5 Jan.	100	13	7	7	8	8	9	9
	60	20	11	9	10	13	13	14
	25	18	11	9	10	11	13	13
	10	14	10	9	10	10	11	10
	3	11	6	6	8	9	9	9

Appendix Table 11. (cont.)

12	100	73	8	14	14	17	21	16
	60	76	9	12	15	17	20	19
	25	66	9	13	12	19	26	18
	10	42	8	12	11	13	16	14
	3	27	6	9	8	9	10	8
2 Feb.	100	138	24	52	47	71	67	83
	60	141	30	43	47	68	71	80
	25	112	26	44	42	62	55	65
	10	76	17	27	28	41	43	42
	3	46	12	20	20	18	29	35
24	100	249	497	511	501	516	352	165
	60	348	493	538	505	574	511	145
	25	309	535	472	612	546	547	204
	10	369	382	475	472	484	463	169
	3	298	347	384	462	414	447	148
2 Mar.	100	50	-	177	252	118	30	15
	60	62	-	223	251	112	36	16
	25	70	-	217	258	143	42	16
	10	59	-	170	238	134	25	13
	3	50	-	119	211	113	40	13
16	100	460	159	141	238	373	312	396
	60	449	230	229	259	275	414	326
	25	444	199	212	348	414	300	186
	10	266	164	204	328	324	189	188
	3	257	108	138	242	198	155	115
30	100	252	402	589	469	87	127	72
	60	163	299	510	359	126	98	55
	25	114	207	315	241	74	73	33
	10	69	92	151	108	42	34	23
	3	32	57	113	80	21	22	7
15 Apr.	100	504	91	94	318	627	562	564
	60	654	147	80	292	593	785	522
	25	532	106	60	191	328	524	386
	10	345	69	45	109	211	212	226
	3	192	39	21	54	148	196	120
27	100	558	306	442	675	721	555	603
	60	511	295	439	565	541	523	453
	25	372	210	341	440	410	358	345
	10	311	157	200	289	305	313	270
	3	212	109	161	202	207	170	187
12 May	100	765	411	529	684	436	468	180
	60	743	454	571	588	435	571	177
	25	636	349	474	440	408	542	171
	10	595	302	404	476	329	439	144
	3	422	169	299	304	262	269	101

Appendix Table 11. (cont.)

26	100	555	30	424	518	523	572	358
	60	567	29	461	555	521	442	497
	25	451	33	400	482	373	516	372
	10	431	27	274	389	301	370	313
	3	245	18	171	246	228	193	268
15 June	100	571	1142	3333	1762	1303	732	343
	60	622	1231	3297	1650	1381	707	424
	25	587	1042	2947	1768	1570	871	361
	10	510	638	2209	1370	1132	754	380
	3	437	436	1410	1007	821	477	246
29	100	1123	3017	4007	1577	913	816	526
	60	959	2782	3766	1593	945	952	568
	25	1156	2168	3417	1440	653	791	586
	10	870	1428	2556	1115	486	540	536
	3	542	842	1988	-	318	444	383

Table P1. ZOOPLANKTON BIOMASS AS DRY WEIGHT (mg m^{-2}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	94	601	435	589	474	609	237
10	494	893	1197	1385	900	384	243
16	229	728	1099	614	679	604	198
23	670	1659	1659	662	719	1037	540
30	650	508	1245	1762	925	587	1235
20 Aug.	69	538	463	940	1268	417	482
3 Sept.	39	168	1124	-	754	103	175
10	178	182	632	345	342	458	-
17	840	346	374	1061	133	181	718
1 Oct.	494	105	118	109	500	375	366
20	148	65	180	167	237	560	260
5 Nov.	135	180	230	134	482	297	240
24	48	33	99	206	228	102	98
4 Dec.	-	-	-	-	-	-	-
17	34	-	191	103	206	218	68
1987							
5 Jan.	254	351	387	84	466	436	35
12	211	283	206	288	170	112	79
2 Feb.	877	223	359	1887	1014	313	487
24	442	682	464	2097	1216	978	270
2 Mar.	396	-	722	919	1441	783	238
16	409	261	483	1136	926	794	360
30	535	62	94	127	150	146	159
15 Apr.	248	343	541	860	1579	418	232
27	601	803	719	782	1064	156	215
12 May	330	300	124	395	194	139	208
26	285	397	284	897	880	325	434
15 June	1152	3181	1897	-	1241	1038	175
29	1125	2023	1591	2613	981	506	303

Table P2. COPEPOD ABUNDANCE (animals m-3) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	959	6861	8992	4694	7398	10680	9360
10	-	8893	8103	8208	7626	10317	25599
16	4745	12537	17028	17286	12782	20294	6150
23	24382	53000	32130	8139	17544	26640	20955
30	12638	13368	34720	56511	22518	32038	37976
20 Aug.	1368	17880	22197	20289	48375	27078	18696
3 Sept.	2255	5527	16022	8887	11208	3405	7187
10	4701	10407	15904	11412	10578	10162	23495
17	34991	33987	13723	22197	9668	8072	22646
1 Oct.	11557	6506	5290	4633	9894	11291	16981
22	6884	1068	5898	3093	8176	13389	3876
5 Nov.	3756	3262	3622	2857	7442	4595	12725
24	2615	707	908	3760	4495	3200	5090
17 Dec.	769	-	2342	2020	3646	2772	1635
1987							
5 Jan.	6957	3413	3471	4317	9865	12447	514
12	8685	1870	2856	3582	3575	3236	1820
2 Feb.	9796	1304	7964	18390	10613	6204	5946
24	10404	2492	3154	20302	25781	11240	6267
2 Mar.	4977	-	4771	6930	20825	21360	4232
16	12720	5927	8112	19025	16006	24354	13788
30	26442	1347	3195	9262	9647	15265	11721
15 Apr.	8157	6951	10428	21332	56575	15374	12640
27	12477	5594	16254	20738	36504	9393	8754
12 May	7523	3932	895	3793	2598	8132	7676
26	5831	7417	6090	6800	7214	6782	13857
15 June	36464	16910	12420	-	23084	21120	7651
29	31552	15587	11486	11172	7295	4611	10170

Table P3. *Acartia hudsonica* ABUNDANCE (animals m^{-3}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	738	3472	5928	3709	4932	8544	6120
10	-	2793	3996	3933	3936	5430	15582
16	1779	2965	1320	2193	4150	3796	1230
23	438	530	0	336	774	2590	1485
30	0	0	0	207	0	386	202
20 Aug.	0	0	0	0	0	0	0
3 Sept.	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0
17	92	0	0	0	0	0	0
1 Oct.	89	0	70	140	92	0	89
22	268	12	40	44	309	432	291
5 Nov.	303	196	149	178	399	1043	940
24	966	5	12	400	660	901	966
17 Dec.	250	-	72	334	1216	851	903
1987							
5 Jan.	5269	1302	1318	2616	8195	10135	199
12	7560	173	1372	2210	2616	2088	1484
2 Feb.	6399	870	6551	16490	9625	5788	4664
24	8247	554	1481	16080	20955	9422	4450
2 Mar.	4153	-	3916	6031	16541	16198	3099
16	11149	2778	4688	13780	9454	20295	9456
30	20709	692	2325	8001	8337	12996	8880
15 Apr.	6747	2543	5925	15594	49445	12594	8962
27	9263	2974	9042	14472	30888	6794	4906
12 May	6546	2549	769	2965	2200	6522	3838
26	3961	4230	4679	4816	5597	4329	10674
15 June	25016	6942	3864	-	11252	5040	2906
29	4872	143	546	1029	5049	1431	4859

Table P4. *Acartia tonsa* ABUNDANCE (animals m-3) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	98	2118	1976	379	1096	534	120
10	-	1330	1110	2394	2214	1810	1908
16	2504	5675	8580	7095	5976	5986	3595
23	22046	43990	26649	6209	10320	18870	14190
30	11926	3982	21917	48438	17658	20458	26260
20 Aug.	903	9720	17063	14567	41409	21236	14637
3 Sept.	2057	4973	11036	7342	9429	2534	6137
10	4109	8122	13076	9166	9505	9208	19795
17	32335	28004	11945	20536	8527	6612	20449
1 Oct.	10312	5161	4408	3978	9297	8979	13335
22	6079	871	5292	2652	6895	12093	3262
5 Nov.	2741	2446	3040	2234	5848	3086	9544
2[illegible]	1310	538	593	2740	3175	2109	3550
17 Dec.	284	-	1582	1161	2001	1188	561
1987							
5 Jan.	1243	1411	1426	1016	1096	889	100
12	441	921	812	432	130	209	90
2 Feb.	79	47	248	61	62	46	107
24	162	277	64	222	127	135	36
2 Mar.	0	-	71	0	0	0	30
16	0	46	60	0	0	0	0
30	0	10	0	0	0	0	0
15 Apr.	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0
12 May	0	0	0	0	0	0	0
26	0	0	31	30	58	0	0
15 June	1696	1602	690	-	464	180	119
29	9048	1287	1950	1764	3213	318	0

Table P5. COPEPOD ABUNDANCE (animals m-3) OTHER THAN *Acartia* spp. AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	123	1271	989	606	1370	1602	3120
10	-	4770	2997	1881	1476	3077	8109
16	462	3897	7128	7998	2656	10512	1325
23	1898	8480	5481	1595	6450	5180	5280
30	712	9386	12803	7866	4860	11194	11514
20 Aug.	483	8160	5134	5722	6966	5842	4059
3 Sept.	198	643	4986	1661	1779	871	1050
10	592	2285	2828	2246	1073	954	3700
17	2564	5549	1778	1510	1151	1460	2197
1 Oct.	1156	1345	812	515	505	2312	3557
22	537	208	566	397	972	864	323
5 Nov.	712	619	433	445	1195	466	2241
24	287	169	303	620	660	190	574
17 Dec.	235	-	688	525	429	733	171
1987							
5 Jan.	445	700	727	685	574	1423	215
12	684	776	672	940	829	939	246
2 Feb.	3318	387	1165	1839	926	370	1175
24	1995	1661	1609	4000	4699	1683	1781
2 Mar.	824	-	784	899	4284	5162	1103
16	1571	3103	3364	5245	6552	4059	4332
30	5733	645	870	1261	1310	2269	2841
15 Apr.	1410	4408	4503	5738	7130	2780	3678
27	3214	2620	7212	6221	5616	2599	3839
12 May	977	1383	126	828	398	1610	3838
26	1870	3187	1380	1956	1559	2453	3183
15 June	9752	8366	7866	-	11368	15600	4626
29	17632	14157	8970	8526	9186	2862	5311

Table P7. BENTHIC LARVAE AS PERCENTAGE OF TOTAL ZOOPLANKTON ABUNDANCE EXCLUDING NAUPLII AND CTENOPHORES AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	34.1	20.1	10.5	22.0	39.7	12.1	1.4
10	-	54.4	45.6	20.6	21.5	5.4	6.2
16	22.8	35.0	37.5	22.3	15.8	7.7	0.01
23	4.3	20.7	10.2	17.6	9.8	8.9	10.0
30	3.2	30.7	8.9	3.7	5.2	5.8	7.3
20 Aug.	10.3	7.2	3.9	2.0	4.9	6.8	12.2
3 Sept.	7.8	3.1	5.3	8.7	12.8	21.8	3.9
10	4.1	5.0	1.8	5.2	5.4	10.7	4.6
17	4.7	2.2	6.3	3.9	6.0	20.6	4.7
1 Oct.	4.5	5.5	6.6	25.0	10.4	15.8	5.4
22	2.1	4.7	9.9	22.8	7.9	4.0	0.8
5 Nov.	5.2	5.2	10.3	4.9	6.6	1.4	3.8
24	4.7	14.6	5.9	2.2	2.6	4.8	1.9
17 Dec.	4.7	-	2.2	1.5	1.4	1.1	1.4
1987							
5 Jan.	6.7	15.4	4.4	6.0	3.5	11.9	12.7
12	16.3	13.7	34.4	5.3	12.5	12.1	9.0
2 Feb.	36.1	13.6	7.3	19.2	8.5	10.7	48.1
24	17.2	39.0	30.5	9.6	10.6	18.5	21.4
2 Mar.	12.0	-	16.7	11.9	15.6	5.5	10.1
16	1.6	19.5	15.6	6.1	11.4	8.6	4.5
30	5.0	12.2	9.6	3.2	1.2	2.7	2.1
15 Apr.	12.4	20.4	17.6	14.0	5.4	9.0	11.7
27	54.4	39.1	13.0	12.5	4.3	9.0	7.5
12 May	34.8	59.1	59.3	34.3	28.9	28.6	19.7
26	24.1	21.1	24.0	15.6	29.0	32.3	5.6
15 June	16.6	36.9	27.8	-	17.2	22.5	25.3
29	15.2	25.0	40.4	68.5	36.0	42.3	27.3

Table P6. BENTHIC LARVAE NUMBERS (m^{-3}) AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	1285	2596	2477	3865	7538	4301	410
10	-	10615	7483	4492	4075	1650	2395
16	2958	7188	11533	5345	3656	3068	2
23	1561	15549	4035	2389	3388	5227	3970
30	931	6049	3487	2494	1498	2562	3259
20 Aug.	169	1385	926	423	2827	2517	2752
3 Sept.	197	179	899	850	1721	1010	295
10	207	552	299	634	623	1291	1154
17	1721	788	929	912	618	2113	1152
1 Oct.	545	378	374	1549	1151	2059	982
22	149	53	648	929	708	557	32
5 Nov.	214	182	314	148	533	66	505
24	131	123	59	200	127	166	104
17 Dec.	39	-	54	48	56	38	24
1987							
5 Jan.	503	653	162	279	366	1690	75
12	1700	302	1540	203	519	444	181
2 Feb.	5530	217	631	4392	988	741	5519
24	2156	1600	1388	2150	3048	2559	1709
2 Mar.	716	-	856	952	3689	1246	477
16	205	1437	1503	1245	2060	2337	640
30	1409	201	360	329	119	429	296
15 Apr.	1203	1806	2296	3558	3261	1575	1689
27	14959	3907	2571	3169	1660	961	714
12 May	5383	6221	1527	2534	1450	3567	2256
26	1911	1983	1986	1303	3074	3541	875
15 June	7654	10706	7045	-	5878	9004	3161
29	7801	5456	8491	27287	14604	14483	4253

Table P8. NUMERICAL ABUNDANCE OF THE CTENOPHORE *Mnemiopsis leidyi* (animals m^{-3}) AT NARRAGANSETT TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	-	0.04	0.12	0.57	0.05	0.21	0.14
10	0	0.35	1.68	0.16	0.27	0.39	0.07
16	0	0.28	0.43	0.08	0.19	0.35	0
23	0.10	0.08	0.03	0.27	0.05	0.07	1.14
30	0.10	0.94	3.20	0.18	0.37	0	0
20 Aug.	8.78	18.88	5.61	6.74	3.83	6.56	60.50
3 Sept.	14.57	12.07	6.32	2.97	3.50	6.21	11.50
10	6.91	5.20	2.95	3.66	2.65	0.90	1.71
17	2.92	34.51	1.54	7.92	1.54	3.21	16.71
1 Oct.	2.91	1.36	1.06	0.88	0.56	3.52	1.84
22	5.85	1.18	2.50	0.53	3.74	3.29	4.04
5 Nov.	0.99	2.17	3.07	2.85	9.53	16.51	19.07
24	19.88	0.57	8.69	5.91	2.80	4.07	1.58
17 Dec.	0.49	16.20	46.19	15.08	28.60	187.36	3.14
1987							
5 Jan.	5.93	6.18	2.28	10.80	41.84	50.67	1.49
12	7.62	0.68	2.52	3.81	7.26	0	0.64
2 Feb.	0.27	0.07	0	0.03	0.12	0.14	0
2 Mar.	0	-	0	0	0	0	0
16	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0
15 Apr.	0	0	0	0	0	0	0
27	0	0.17	0.03	0	0	0.15	0
12 May	0.65	1.44	0.21	0.11	0.08	0.16	0.33
26	0.10	0	0	0	0	0	0
15 June	0	0.42	0	0.27	0.08	0.26	1.05
29	0.10	0.42	0.47	0.77	0.31	0.21	0.33

Table P9. TOTAL ZOOPLANKTON ABUNDANCE (animals m-3), EXCLUDING NAUPLII, AT NARRAGANSETT BAY TRANSECT STATIONS (2 July 1986 - 29 June 1987)

STATION:	1	2	3	4	5	6	7
1986							
2 July	3772	12937	23462	17555	18967	35423	28429
10	-	19533	16403	21814	18924	30299	38448
16	12974	20531	30781	23944	23103	39484	18583
23	36087	75205	39619	13575	34481	58608	39883
30	29238	19705	39111	67750	28650	44214	44861
20 Aug.	1640	19269	23580	21247	57787	36842	22559
3 Sept.	2532	5733	16921	9805	13403	4633	7637
10	5036	11087	16205	12109	11539	12096	25204
17	36813	35034	14653	23164	10289	10281	24305
1 Oct.	12113	6885	5688	6182	11047	13050	18066
22	7034	1121	6546	4066	8930	13946	3911
5 Nov.	4077	3444	3937	3035	8108	4661	13306
24	2788	844	993	4060	4848	3484	5224
17 Dec.	837	-	2434	2102	3911	3309	1672
1987							
5 Jan.	7490	4239	3715	4651	10336	14144	589
12	10455	2200	4481	3811	4148	3682	2001
2 Feb.	15330	1601	8608	22917	11605	6951	11478
24	12571	4103	4553	22465	28836	13809	7980
2 Mar.	5968	-	5140	7992	23643	22788	4709
16	12966	7378	9647	20289	18083	27147	14361
30	27917	1643	3748	10195	9856	16123	12124
15 Apr.	9379	8835	13040	25476	60103	17404	14382
27	27484	9983	19775	25258	39036	10643	9477
12 May	15475	10529	2573	7369	5003	12458	11468
26	7931	9412	8288	8331	10597	10955	15742
15 June	46162	29049	25304	-	34113	40065	12485
29	51229	21808	21002	39811	40533	34256	15598

ANNEX # 1

AN EXTRAORDINARY, NOXIOUS BROWN-TIDE IN NARRAGANSETT BAY. I. THE ORGANISM AND ITS DYNAMICS

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ABSTRACT

A brown-tide bloom of a previously unknown chrysophyte *Aureococcus anorexefferens* (2 μm, autotrophic, non-motile) occurred from May-September 1985 reaching a maximum abundance of 1.2 x 10^9 cells L^{-1}. Mean abundance strongly correlated ($r = 0.98$) with salinity along the gradient. Its bloom dynamics do not suggest a response to eutrophication. Strong *inverse* correlations characterized mean abundance and NH_4+NO_3 ($r = -0.76$) and PO_4 concentrations ($r = -0.62$). Extensive blooms of diatoms, dinoflagellates, microflagellates and euglenids co-occurred. A highly anomalous sequence of euglenid blooms persisted through November, following termination of the brown-tide. The simultaneous occurrence of a similar brown-tide outbreak in Long Island and New Jersey coastal waters suggests a mesoscale phenomenon associated with complex climatologic and/or hydrographic conditions. Vernal increases in photoperiod and/or irradiance and phagotrophic flagellate abundance are considered to be potential bloom triggering factors. (Proof note: revised appelation *Aureococcus anophagefferens* now proposed [6]).

INTRODUCTION

The magnitude, duration, causative organism and ecosystem effects of this unusual brown-tide in Narragansett Bay (~41°30'N, 71°15'W) were extraordinary. Weekly phytoplankton analyses carried out since 1959 in lower Narragansett Bay did not previously record *Aureococcus*, although its small-size and/or limited abundance may have hindered earlier recognition. Maximal 1985 brown-tide concentrations (ca. 2 x 10^9 cells L^{-1}) exceeded by 8-fold previous red-tide bloom concentrations. Local red-tide blooms of dinoflagellates and *Olisthodiscus luteus* [1,2] usually last several weeks; the 1985 bloom persisted for 5-months. Blooms of the nuisance species *Phaeocystis pouchetii* [3] and *Olisthodiscus luteus* [1,2] within Narragansett Bay have not been associated with major deleterious ecosystem impacts, unlike the 1985 bloom, which adversely affected components of the zooplankton, benthos and nekton [4]. This extraordinary bloom occurred as part of a mesoscale phenomenon; similar blooms co-occurred in embayments on Long Island, New York and Barnegat Bay, New Jersey over a distance of *ca.* 500 km [5]. This implicates a regional climatologic and/or hydrographic event associated with development of the noxious 1985 bloom.

MATERIALS AND METHODS

Seven stations were sampled at three depths along a salinity-nutrient gradient at approximately weekly intervals beginning 25 July 1985 (Fig 1). St 7 is the long-term weekly sampling site. Measurements included: temperature, salinity, NH_4, NO_3, PO_4 and SiO_2; chlorophyll *a*; phytoplankton and zooplankton numerical abundance and species composition.

RED TIDES: BIOLOGY, ENVIRONMENTAL SCIENCE, AND TOXICOLOGY
Okaichi, Anderson, and Nemoto, Editors

RESULTS AND DISCUSSION

Concurrent, multiple blooms and a species succession characterized the brown-tide. Up to 27 x 10^6 cells L^{-1} of the diatom *Skeletonema costatum*; 14 x 10^6 L^{-1} of a small *Thalassiosira* sp.; mid-August blooms of the dinoflagellates *Prorocentrum redfieldii*, *P. scutellum* and *P. triangulatum* (>2 x 10^6 L^{-1}; anomalous euglenid blooms (≥ 2 x 10^6 L^{-1}), and an extraordinary August pulse (up to 140 x 10^6 L^{-1}) of the small diatom *Minutocellus polymorphus* occurred. The most abundant, persistent organism, however, was *Aureococcus anorexefferens*, described by Sieburth et al. [6] as a new chrysophycean genus and species (Fig 2). (Definitive experimental verification applying Koch's postulates that this organism was responsible for the observed ecosystem disruptions [4] is presently unavailable, although the circumstantial evidence is provocative.) This non-motile organism has resisted isolation into culture, or has appeared in mixed-cultures only [5]. Prominent features of *Aureococcus anorexefferens* are its minute size (~2 µm), exocellular polysaccharide layer, large, single chloroplast enclosing a distinctive pyrenoid and a voluminous nucleus (Fig 2).

The abundance cycle of *Aureococcus* at St 7 (Fig 3) shows its bloom began precipitously in mid-May (~10^9 cells L^{-1}), with a mid-July pulse (1.2 x 10^9 L^{-1}) followed by a prolonged curvilinear decrease (with a brief mid-August resurgence) until early October when it disappeared prior to hurricane GLORIA. *Aureococcus* was most abundant in Greenwich Bay (St 1), with large populations persisting in lower Narragansett Bay (St 6, 7). Mean surface populations at St 1 were twice those in the lower Bay and 3- to 3.5-times upper Bay levels. Regional variations in *Aureococcus* abundance were not correlated with water temperature. Mean abundance was invariant with mean salinity in the upper Bay between 24 and 27.6 °/oo (St 2, 3, 4), but increased from 0.2 to 0.7 billion cells L^{-1} along the salinity gradient (27.6 to 30.5 °/oo) from St 1, 4-7 (r^2 = 0.96; Fig 4). Salinity, *per se*, probably was not the causative factor of the regional variations in *Aureococcus* mean abundance, but reflected some factor(s) running in parallel with it. Mean *Aureococcus* abundance at 0 m was inversely and curvilinearly related to NO_3+NH_4 and PO_4 concentrations, progressively decreasing with increasing N and P levels along the gradient from St 1, 7, 6, 5 and 4 (Fig 5). Mean abundance was generally invariant between St 4, 3 and 2. This *decrease* in mean cellular abundance with increasing NO_3+NH_4 and PO_4 concentrations suggests that the brown-tide development was not fundamentally a response to nutrient enrichment. In fact, high nutrient loadings appeared to suppress *Aureococcus* abundance.

Following maximal abundance on 25 July, *Aureococcus* declined baywide following the pattern depicted for St 7 (Fig 3), and suggestive of a general population control mechanism. Lytic virus infections were commonplace within *Aureococcus* cells during the bloom peak [6], but did not correlate with the bloom demise. A significant surge in phagotrophic flagellates occurred baywide in mid-August and persisted through September, with maximal abundances ranging from ca. 20 to 44 x 10^9 m^{-3}. The coincidence of the decline in *Aureococcus* abundance and increase in phagotrophic flagellates may be causal. A statistically significant direct correlation was found (r = + 0.66).

Aureococcus was last observed on 2 October. Significant decreases in temperature (1.7 to 3.2°C), nutrient concentrations and phytoplankton abundance, and increased zooplankton numerical abundance occurred between then and 9 October. Thereafter, an anomalous phytoplankton community persisted through November characterized by an unique flagellate successional pattern: baywide Euglenid blooms (up to 2.7 x 10^6 L^{-1}) in mid-October causing local green-water displays; October and November blooms of the dinoflagellate *Massartia* rotundatum; September - October blooms of an organism similar to *Fibrocapsa* cf. *japonica* (up to 0.4 x 10^6 L^{-1}); and a brief October bloom of *Olisthodiscus luteus*, the locally common red-tide producer conspicuously absent during the brown-tide.

The winter-spring bloom in early January was typical of Narragansett

Bay. On 14 May 1986, *Aureococcus* precipitously reappeared in great abundance (53 to 180 x 10^6 cells L^{-1}), but a brown-tide did not develop ; by late June it disappeared. The most significant difference from the 1985 outbreak (comparisons possible only for St 7) was the large population ($\sim$0.5 x 10^6 L^{-1}) of heterotrophic dinoflagellates during 1986. The potential role of grazing as a regulator of *Aureococcus* blooms is considered by Smayda and Fofonoff [4].

Remarkably, *Aureococcus* or a similar brown-tide species also reappeared during May/June in Long Island embayments [5]. These regional May bloom-inceptions suggest vernal increases in photoperiod and/or irradiance as potential triggering factors, particularly if an epibenthic stage is present, as found in certain motile chrysophytes [7]. A two-step triggering event would then be required: initially, induction of the morphogenetic transition of the benthic aggregate into its non-motile, planktonic phase, followed by vigorous vegetative growth of the latter regulated by other factors.

ACKNOWLEDGEMENTS

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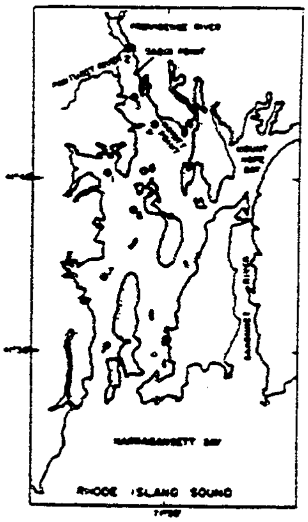

Fig. 1. Station locations in Narragansett Bay sampled during the "brown-tide" study. St 7 site of the long-term station sampled at weekly intervals.

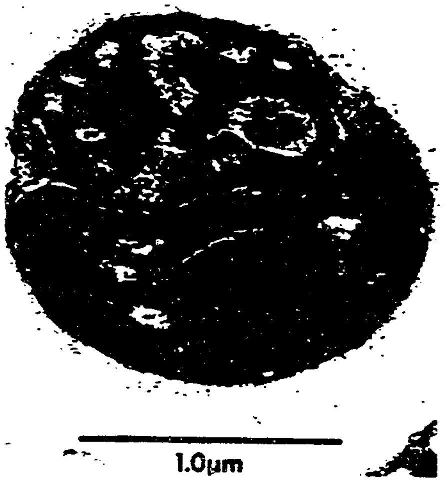

Fig. 2. Ultrastructure of the "brown-tide" organism *Aureococcus anorexefferens* as shown by transmission electron micrograph of a thin section; magnification 37,000X. (Micrograph courtesy of Prof. J.M. Sieburth and Mr. P.W. Johnson.)

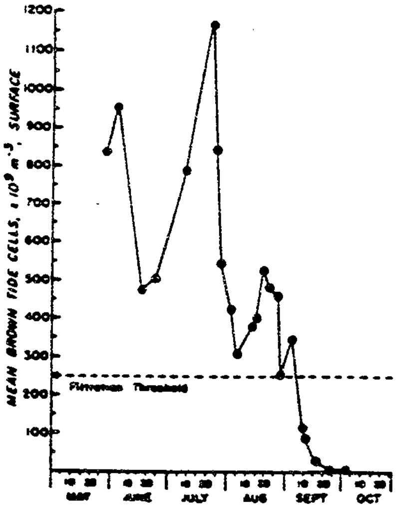

Fig. 3. Abundance of *Aureococcus anorexefferens* at 0 m at St 7. Filtration threshold designates *Aureococcus* population density at which filtration by the mussel *Mytilus edulis* was inhibited.

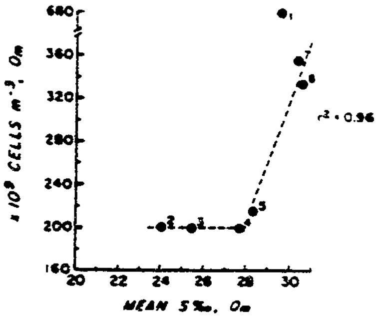

Fig. 4. Mean concentration of *Aureococcus anorexefferens* at 0 m vs. mean salinity at the seven sampling stations during the "brown-tide" bloom.

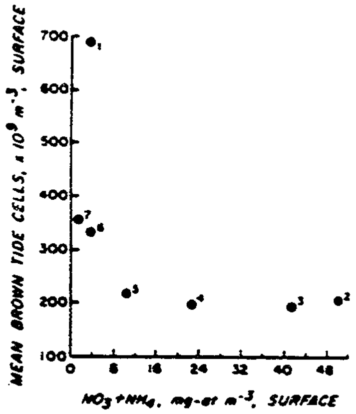

Fig. 5. Mean concentration of *Aureococcus anorexefferens* at 0 m vs. mean concentrations of NO_3-NH_4 at the seven stations during the "brown-tide" bloom.

ANNEX # 2

AN EXTRAORDINARY, NOXIOUS BROWN-TIDE IN NARRAGANSETT BAY. II. INIMICAL EFFECTS

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ABSTRACT

A bloom of *Aureococcus anorexefferens* had significant inimical effects on zooplankton, the edible mussel *Mytilus edulis*, benthic larval abundance, anchovy fecundity, and on kelp beds. Numerical abundance of the predominant copepod *Acartia tonsa* inversely correlated ($r = -0.91$) with *Aureococcus* abundance. Adult females fed *Aureococcus* had lower rates of feeding, egg production and reduced body weight. Mean cladoceran (*Evadne* sp., *Podon* sp.) abundance was 60-fold lower than during the 1984 and 1986 summers. Natural mussel beds exhibited 30% to 100% mortality, which appeared to reflect starvation. Laboratory-reared mussels ceased to filter when *Aureococcus* abundance exceeded 500×10^6 cells L^{-1}. A kelp die-off occurred when euphotic zone mussels, to which laminarians were attached, died, lost byssal contact and sank into the aphotic zone. Benthic larval numbers inversely correlated ($r = -0.58$) with *Aureococcus* abundance. Polychaete and bivalve larvae were 1.5- and 3.6-fold lower, respectively, than previous minima. Egg numbers of the bay anchovy *Anchoa mitchilli* were about 10-fold lower than in comparison summers. The intensity and prolongation of the *Aureococcus* bloom seem attributable to a reduction in zooplankton and benthic grazing.

INTRODUCTION

Phagotrophic flagellates increased dramatically during the *Aureococcus* bloom decline; their mean abundance during the brown-tide correlated directly with *Aureococcus* [1]. Holozoic dinoflagellates were abundant during the brief resurgence of *Aureococcus* in May 1986; a brown-tide did not develope subsequently. These heterotrophic dinoflagellates were sparse during the initial stages of the *Aureococcus* bloom in May 1985; a brown-tide subsequently developed. These associations suggest that phagotrophic, naked flagellates and dinoflagellates actively grazed *Aureococcus*. This predator-prey relationship contrasts with apparent inimical effects of *Aureococcus anorexefferens* cells and/or population levels on the feeding, growth, fecundity and viability of certain zooplankters, benthic feeders, and a fish.

RESULTS

There is no field evidence that the *Aureococcus* bloom was antagonistic to other phytoplankton species. The conspicuous absence of *Olisthodiscus luteus* may merely reflect inter-annual variability in its red-tide patterns [2]. However, experimental data to evaluate potential antagonistic interactions such as described by Iwasaki [3] are unavailable. The general impression is that the *normal* summer phytoplankton assemblages thrived in Narragansett Bay during the anomalous and extraordinary brown-tide bloom of *Aureococcus anorexefferens*.

Total zooplankton community biomass regressed against surface abundance

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of *Aureococcus* revealed two regional subgroupings, both *positively* correlated, in which zooplankton biomass increased with brown-tide abundance (Fig 1). Zooplankton levels were considerably lower (≤ 150 mg dry wt m^{-2}) at lower Bay stations [1] (1, 6 and 7) where mean brown-tide abundance exceeded 300 billion cells m^{-3}. In the upper Bay, where *Aureococcus* levels were $\leq$ 200 billion cells m^{-3}, zooplankton dry weight was considerably greater. For individual zooplankton components, however, a different pattern emerges. *Acartia tonsa* was the dominant copepod during the brown-tide, the result of the normal successional pattern [4]. Strong *inverse* correlations occurred between mean numerical abundances of *Acartia* and *Aureococcus* integrated over the water column (Fig 1). Two distinct regional subgroups are evident: upper Bay St 2, 3 and 4 and lower Bay St 1, 5, 6, 7; $r^2 = 0.83$ for both clusters. *Acartia* was about 2-fold more abundant per unit of brown-tide cellular abundance at the upper Bay stations than in the lower Bay, i.e., the negative affect of *Aureococcus* on *Acartia* numbers was more pronounced in the lower Bay where the brown-tide was most intense. Durbin and Durbin [5] confirmed experimentally that *Aureococcus* was inimical to *Acartia tonsa*. Adult females incubated in the presence of *Aureococcus* had much lower rates of grazing, egg laying, and body carbon development compared to animals fed other phytoplankton species. Daily egg production and body carbon in adult female *Acartia* exposed to *Aureococcus* were about 40% of rates with other phytoplankton diets. Only 44% of the daily body weight was ingested in the presence of *Aureococcus* and 174% with other phytoplankton diets.

Failure of the cladoceran community to develop was the most remarkable zooplankton modification accompanying the brown-tide outbreak (Fig 2). *Evadne nordmanni* and *Podon* sp., which normally exceed 10,000 animals m^{-3} during June - August, failed to appear in 1985. Based on the six-year interannual comparisons at St 7 [1], the mean 1985 May - August abundance of only 80 m^{-3} was 10- to 75-fold lower than the means for the comparison years. The strong recovery during 1986 when a brown-tide did not develope is notable.

The mean depth (9 m) and strong year-round mixing in Narragansett Bay result in a strong benthic-pelagic coupling [6] in which the clam *Mercenaria mercenaria* and mussel *Mytilus edulis* are important benthic filter feeders. Field studies during the brown-tide revealed reproductive failure of gravid mussels and massive Bay-wide mortality approaching 100% by mid-August [7]. In laboratory experiments [7], *Mytilus edulis* actively filtered 2 µm *Synechococcus* in contrast to drastically reduced filtration rates at *Aureococcus* (2 µm) concentrations between 250 to 500 x 10^6 cells L^{-1}, even when provided in combination with *Isochrysis galbana*. Fig 1 in [1] suggests potential feeding inhibition from May - August in the lower Bay. Above 500 x 10^6 cells L^{-1}, marked feeding inhibition occurred, leading Tracy [7] to conclude that starvation stress of the pre-spawning mussels caused the die-off, accelerated by high summer temperatures. However, it is unresolved whether starvation resulted solely or primarily from dense accumulations of unpalatible *Aureococcus* cells. Histopathological examination of field collections during the brown-tide revealed mussel gill filaments were often swollen; the food groove packed with yellow-brown granules; sloughed off mucous; exhibited necrotic foci, and were packed with amoebocytes [8]. The possibility of a supplemental contact-toxin effect of the *Aureococcus* cells, which have a prominent exocellular polysaccharide layer (see Fig 2 in [1]), needs to be evaluated. The mortality of kelp populations (*Laminaria saccharina* and *L. digitata*) was a remarkable side-effect of the mussel die-off [9]. Laminarians attached to mussels sank into the aphotic zone when the dead mussels lost byssal contact and slumped to depth.

Benthic larval abundance and *Aureococcus* abundance were inversely correlated ($r = -0.58$)(Fig3). Mean larval abundance at St 7 during 1985 was the lowest observed during the comparison years (1981-1986). Mean abundances of polychaete larvae and bivalve veligers were 1.5-fold and 3.6-fold lower, respectively, than the 6-year minima. Nonetheless, there is no convincing statistical evidence based on larval abundance that benthic recruitment (excluding *Mytilus edulis*) was impaired by the brown-tide.

An inimical effect at the nekton level was also found. Eggs of the anchovy *Anchoa mitchilli* were conspicuously sparse during the brown-tide (Fig 4); mean abundance levels were about 10% those during the comparison years. Their strong comeback in 1986 similar to cladocerans (Fig 2) is notable.

DISCUSSION

Contemporaneous blooms of *Aureococcus anorexefferens* in Long Island coastal embayments during 1985 were also accompanied by inimical shellfish effects. Adult bay scallop, *Argopecten irradians*, exhibited a considerable weight loss; larval bay scallops 100% mortality; oyster mortality also occurred during *Aureococcus* blooms [10]. Moreover, light attenuation by the brown-tide reduced the distribution and abundance of eel grass meadows of *Zostera* marina, a loss which reduced the nursery grounds and habitats for scallops and juvenile fishes [11]. Clearly, *Aureococcus anorexefferens* is an incomparable, broad-spectrum, nuisance phytoplankter, seemingly without parallel to date. Its blooms appear capable of negatively impacting, directly or indirectly, all major trophic levels, including members of the zooplankton, benthos (bivalves particularly), certain fishes, macroalgae, and even phanerogams. The causes of its extraordinary blooms during the summer of 1985 in Narragansett Bay, the Long Island embayments (in 1986 and 1987 as well) and Barnegat Bay [1] are obscure. The accompanying inimical effects within Narragansett Bay suggest that the intensity and duration of its 1985 bloom were partly attributable to a reduction in grazing by zooplankton and benthos. This grazing impact is in addition to the potential role ascribed [1] to phagotrophic flagellates in influencing the initiation and buildup of *Aureococcus* blooms. Are such multiple grazing effects a useful general paradigm for evaluating regulation of nuisance algal blooms in the sea?

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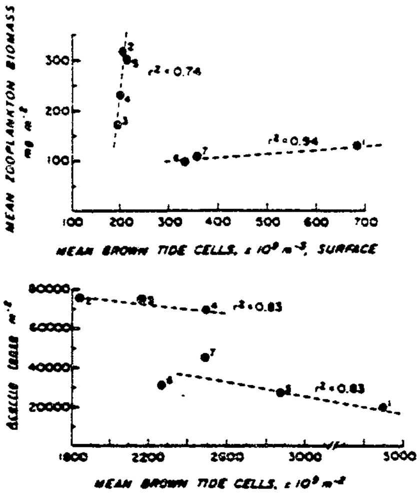

Fig. 1. Mean zooplankton biomass as dry weight during the "brown-tide" bloom vs. mean abundance of Aureococcus anorexefferens at the seven stations (upper panel) and (lower panel) mean numerical abundance of the copepod Acartia tonsa vs. mean abundance of Aureococcus anorexefferens integrated for the water column.

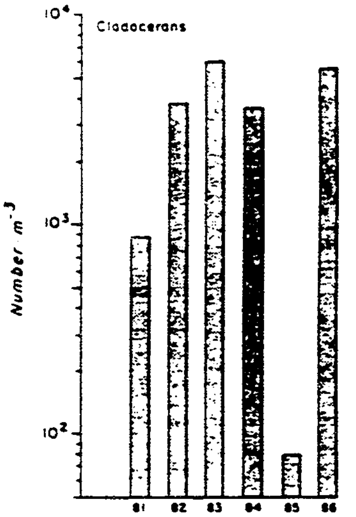

Fig. 2. Mean abundance of the cladocerans Podon sp. and Evadne nordmanni during their summer occurrences at St 7 from 1981 - 1986.

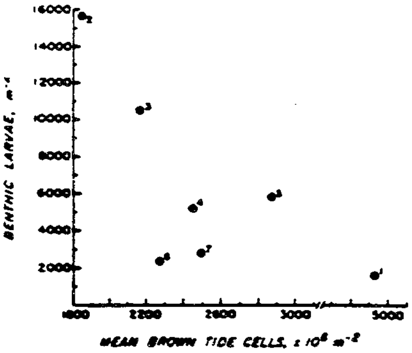

Fig. 3. Mean numbers of benthic larvae vs. mean abundance of Aureococcus anorexefferens integrated for the water column at the seven stations during the "brown-tide" bloom.

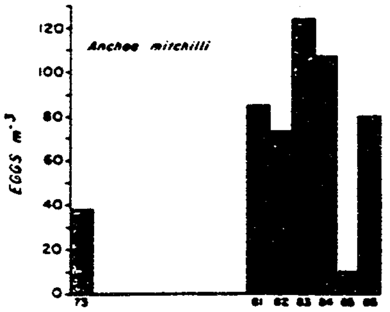

Fig. 4. Mean egg abundance for the anchovy Anchoa mitchilli at St 7 during its summer occurrences in 1973 and from 1981 - 1986.

ANNEX #3

THE 1985 "BROWN-TIDE" AND THE OPEN PHYTOPLANKTON NICHE IN NARRAGANSETT BAY DURING SUMMER

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INTRODUCTION

The unprecedented mesoscale bloom of the chrysophyte *Aureococcus anophagefferens* Sieburth, Johnson et Hargraves during the 1985 summer in Narragansett Bay (Smayda & Villareal, 1989; Smayda & Fofonoff, 1989; Sieburth et al., 1988), Long Island coastal embayments (Cosper et al., 1987) and Barnegat Bay, New Jersey (Olsen, 1989) probably was partly triggered and maintained by a regional climatological and/or hydrographical event. However, the apparent absence of a similar bloom in the contiguous waters of Buzzards Bay, located immediately east of Narragansett Bay, and in Delaware Bay, just south of Barnegat Bay, is noteworthy. *Aureococcus* was either absent in those areas, or its niche was not locally favored despite similar regional characteristics. Thus, the *Aureococcus anophagefferens* bloom was probably regulated on two levels: by events operative on both regional and local scales. These simultaneous bloom events in Narragansett Bay, the Long Island embayments and Barnegat Bay indicate that the Aureococcus niche opened up concurrently in three widely separated environments: a most remarkable happening.

Within Narragansett Bay, however, the appearance of flagellate or other non-diatomaceous bloom components during May-June followed by their summer bloom events is not unusual. The salient feature of this successional shift is that the bloom-species are unpredictable; i.e., an "open" phytoplankton niche appears to occur during the summer within Narragansett Bay. Since a complicated interaction of physical, chemical and biological factors determines which species will bloom (Smayda, 1973), there is a poor predictive capability as to which species will fill and predominate within this open-niche. Predictability is also compromised by significant inter-annual variations in key determinants of niche availability and occupancy, such as factor-interactions and hysteresis effects from winter-spring diatom bloom dynamics. When a regional event is superimposed upon this situation, as appears to be the case with the 1985 Aureococcus bloom, predictability becomes even more tenuous.

In order to quantify those factors regulating unusual phytoplankton blooms, an adequate description of the bloom niche(s) is required. This requires proper description of the phytoplankton community participating in the bloom event. Significant insights can be obtained from an analysis of community structure, particularly where there is good autecological data. A species' autecological and niche requirements are aspects of the same issue: species-specific dependencies on the occurrence and maintenance of a suitable biotope allowing its cellular and population growth. Unfortunately, conspicuous phytoplankton bloom events generally are inadequately described. Inevitably, the focus is on the primary bloom organism(s). We usually are not provided with clear information as to whether the bloom was primarily a mono-specific event; whether several species with the normal successional sere bloomed concurrently, or whether the bloom event followed the incursion of a seasonally variable, allochthonous community or new immigrant species. These three different situations (more could be added) represent different types of bloom episodes, each accompanied by their specific regulatory factors and unique ecosystem effects.

The great attention given to the "brown-tide" has focused on Aureococcus as though it represented a mono-specific bloom. In this paper we will assess overall phytoplankton community structure during the 1985 bloom in Narragansett Bay, and evaluate those general factors contributing to the occurrence of an "open" phytoplankton niche during the summer in this bay.

METHODS

A long-term station sampled weekly has been maintained (Station 7) in lower Narragansett Bay (Fig. 1). Routine observations (Smayda, 1984; Smayda & Villareal, 1989) include microscopic counts of phytoplankton abundance and species composition using live material. Abundance of Aureococcus anophagefferens and other picoplankters was established using an Improved Neubauer Haemocytometer (Guillard, 1978) under 430X (43X objective x 10X ocular) magnification. Larger cells were enumerated in a Sedgwick-Rafter Chamber following the procedures of McAlice (1971). The 1985 bloom dynamics at Station 7 are presented in Figure 2.

Following the bay-wide development of the "brown-tide", six additional stations were surveyed at approximately 10-day intervals, beginning on 25 July. Bloom dynamics at Station 4 (Figs. 1, 3-7) will be presented to convey the successional trends and individual species' bloom events representative of Narragansett Bay during the 1985 summer "brown-tide" event.

RESULTS AND DISCUSSION

Figure 2 illustrates Aureococcus dynamics at Station 7 during May - October 1985. A series of four peaks is evident, with maximal surface abundance (1.2 x 10^9 cells L^{-1}) occurring in mid-July. Thereafter, numerical abundance progressively declined (reminiscent of a washout curve), interrupted by brief, minor population surges in August and September. Bloom termination pre-dated the occurrence of hurricane GLORIA. This seasonal pattern is remarkably similar to that found by Nuzzi and Waters (1989) in the Peconic embayments in eastern Long Island. Within Narragansett Bay, the Aureococcus bloom was remarkable for its numerical intensity, duration and negative impact upon higher trophic levels (Smayda & Fofonoff, 1989). This species joins Olisthodiscus luteus (Tomas & Deason, 1981; Verity & Stoecker, 1982) and possibly Phaeocystis pouchetii as nuisance species in Narragansett Bay. However, the maximal (< 35 mg m^{-3}) and mean (22 mg m^{-3}) biomass (chlorophyll) during the bloom were similar to those during the winter-spring diatom bloom.

The seasonal bloom pattern of Aureococcus generally was similar at all stations. Maximal abundance occurred during the first regional survey (25 July), ranging from 0.8 (Station 4) to 1.5 billion cells L^{-1} (Station 1), and then decreased more or less progressively between 25 July and 2 October. Cells were not recorded during the 9 October survey. Within Narragansett Bay, its abundance varied regionally. Its seasonal mean and maximal abundance levels were generally greatest in Greenwich Bay (Station 1); its occurrence there was part of a conspicuous plume of elevated abundance in West Passage which extended to Stations 6 and 7 (Fig. 1). *Aureococcus* was less abundant in upper Narragansett Bay (Stations 2, 3, 4 and 5). Mean surface population abundance in Greenwich Bay (0.7 billion L^{-1}) was twice that in lower Narragansett Bay and 3 to 3.5-fold greater than that in the upper bay.

The successional and abundance trends of other phytoplanktonic species which co-occurred with *Aureococcus anophagefferens* will be illustrated for Station 4 (Fig. 1). Station 4 was selected as an intermediate location generally representative of the 1985 *Aureococcus* bloom event. Significant growth and blooms of the diatoms *Minutocellus polymorphus* (Hargraves et Guillard) Hasle, von Stosch et Syvertsen (> 10^9 cells L^{-1}), *Skeletonema costatum* (Grev.) Cleve (> 10^7 cells L^{-1}) and *Thalassiosira* cf. *pseudonana* (10^6 cells L^{-1}) co-occurred with *Aureococcus anophagefferens* (Fig. 3). The prodigious *Minutocellus* bloom was restricted to August; the *Skeletonema* and *Thalassiosira* blooms persisted through mid-October. Significant dinoflagellate growth, abundance and species succession accompanied the *Aureococcus* bloom and continued after its demise. A *Prorocentrum* assemblage comprising *P. triangulatum* Martin (= *P. minimum* Pavillard (Schiller), *P. redfieldii* Bursa and *P. scutellum* Schröder persisted from September through mid-November, as did heterotrophic gymnodiniaceans (Figs. 4, 5). The sudden bloom of *Scrippsiella trochoidea* (Stein) Loeblich III coincided with the disappearance of *Aureococcus*. The diminutive *Katodinium (= Massartia) rotundatum* (Lohmann) Loeblich suddenly appeared in bloom proportions in late October, declined and bloomed again in late November (Fig. 5).

In addition to these diatom and dinoflagellate blooms co-incident with the *Aureococcus* bloom, extensive blooms of various phytoflagellate species representative of several phylogenetic groups also coincided with, and followed the Aureococcus bloom (Fig. 6). The chlorophyte Pyramimonas sp. appeared in late August and bloomed in late October. A remarkably persistent and unusual bloom of the raphidophycean Fibrocapsa japonica Toriumi et Takano occurred; this species was previously recorded only sporadically and in relatively low abundance in Narragansett Bay (Smayda, unpublished). Following its sudden bay-wide appearance in late August, it proliferated through early October, reaching maximal populations of 0.2 million cells L^{-1} (0.3 million L^{-1} at Station 6), and then persisted through mid-November. The autotrophic Cryptomonas amphioxeia Conrad bloomed during October and November. The raphidophycean Olisthodiscus luteus Carter, absent throughout the summer, bloomed suddenly in mid-October (notably at Stations 3, 4 and 5), then abruptly disappeared.

A remarkable euglenid bloom developed during the "brown-tide", and persisted until late November following the early October collapse of the latter. Euglenids appeared suddenly at all stations on 15 August; by August 28, maximal populations reached 1.9 million cells L^{-1} at Station 2 and between 0.23 and 0.34 million cells L^{-1} at Stations 3 and 4, respectively (Figs. 1, 6). The bloom was then centered in this region of upper Narragansett Bay, abundance decreasing precipitously at Station 5 (15,000 L^{-1}) and at lower Narragansett Bay Stations 6 and 7 (< 5,000 L^{-1}). On 2 October, the population pulsed in the latter region, attaining 0.5 and 0.12 million cells L^{-1} in the surface waters at Stations 6 and 7. The euglenid population remained fairly high at these stations; elsewhere it continued to proliferate. By mid-October, "green water" was reported both from Bristol Harbor (Hunt, personal communication), located south of Nayatt Point (Fig. 1), and also to the west of Station 7, and again during the 30 October transect at Stations 3 and 4. The euglenid population in the surface water at these stations reached 2.7 million cells L^{-1}; 1.5 million L^{-1} at Station 5; 0.9 million L^{-1} and 0.65 million L^{-1} at Stations 1 and 6, respectively. The previous week (23 October) 1.3 million cells L^{-1} were recorded at Station 7, where 1.2 million cells L^{-1} were recorded on 13 November. The euglenid population at Stations 1, 5 and 6 was then about 0.5 million L^{-1}; 0.3 million L^{-1} at Station 4, and considerably lower at Stations 2 and 3. Thus, maximal bloom occurrence shifted from upper Narragansett Bay during the "brown-tide" outbreak to lower Narragansett Bay in November. The population collapsed precipitously by the time of the 4 December transect.

Successional Trends

Clearly, the 1985 "brown-tide" bloom of Aureococcus anophagefferens was accompanied by several co-occurring blooms of diatoms, dinoflagellates and other flagellates (Fig. 7). (The data plotted in Fig. 7 are from Station 4.) This bloom was not a mono-specific event; rather, a succession of significant bloom events involving 14 additional taxa occurred. These bloom patterns exhibited both normal and anomalous characteristics. The unprecedented Aureococcus bloom was accompanied by equally novel blooms of Minutocellus polymorphus and Fibrocapsa japonica. Neither of these species was recorded previously at Station 7 (Fig. 1) during the weekly surveys carried out since 1959 (Smayda, unpublished). These species, similar to Aureococcus anophagefferens, may indeed have been a normal, long-term component of the rarified "hidden flora". Of greater interest is their sudden detection, emergence and proliferation (= niche exploitation) during 1985, accompanied by anomalous floristic, successional and bloom dynamics. The occurrence of the cyst-producing Fibrocapsa japonica is notable, since in Japanese coastal waters this (or a related species) may produce an ichthyotoxin (Hara & Chihara, 1985;

Yoshimatsu, 1987). Another anomalous characteristic of the 1985 summer relative to previous studies in Narragansett Bay is the unusual flagellate blooms following the Aureococcus collapse (Pratt, 1959; Smayda, 1957; 1973; unpublished). Olisthodiscus luteus frequently causes local "red-tides" during the summer (Pratt, 1966), followed by a brief resurgence in October (Tomas, 1980). Its modest October 1985 bloom (unusual for its occurrence without a preceding summer abundance) is noteworthy. The restriction of its 1985 bloom to October following the disappearance of Aureococcus anophagefferens suggests that its summer niche was filled by Aureococcus.

The October blooms of Prorocentrum redfieldii, Scrippsiella trochoidea and Massartia rotundata in early October following the disappearance of Aureococcus anophagefferens are also notable anomalies. Dinoflagellate blooms so late in the annual cycle are unusual in Narragansett Bay, based on the long-term phytoplankton data set (Smayda, unpublished).

The euglenid bloom, which consisted of several species, was remarkable for its baywide occurrence, magnitude and persistence. This community previously was detected at Station 7 only sporadically in much lower numbers, and rarely in bloom concentrations (Smayda, unpublished). It is commonly considered to be an indicator of nutrient-enriched waters. Given this, its baywide occurrence, abundance and persistence are remarkable, and unique, and equally interesting and enigmatic as the "brown-tide" event.

The 1985 "brown-tide" in Narragansett Bay was clearly a multi-species event, and not a mono-specific bloom of Aureococcus anophagefferens. This "brown-tide" represented the blooms of both novel and normal species' occurrences. The Aureococcus bloom was "on top" of the normal summer blooms of species such as Skeletonema costatum, Thalassiosira cf. pseudonana, Prorocentrum redfieldii, P. triangulatum (= P. minimum) and P.

scutellum. Anomalous and/or unusual blooms were not restricted to Aureococcus, but included bloom occurrences of euglenids, Fibrocapsa japonica, and bloom outbreaks of several dinoflagellates seasonally displaced to the period following the demise of Aureococcus, and extending into November. This suggests that over the six month period from May - October 1985 anomalous phytoplankton growth conditions and/or niche diversification prevailed in Narragansett Bay, and that the Aureococcus anophagefferens bloom was but one manifestation of this.

Key, unresolved questions are whether multiple species blooms also characterized the Long Island and Barnegat "brown-tides"; characterize phytoplankton mass occurrences generally; or whether "red-tide" outbreaks are primarily mono-specific blooms. The factors regulating mono-specific blooms may differ from those stimulating coincident or successive, multiple species blooms. Investigators are encouraged to describe and to quantify in greater detail phytoplankton community structure during such blooms to facilitate their quantification.

The results also suggest that a multiple number of phytoplankton niches opened both synchronously and progressively within Narragansett Bay, and were involved in the series of unusual, anomalous and seasonally normal species' bloom and successional events which collectively made up the 1985 "brown-tide" event. Such diverse niche involvement was unexpected, given the meso-scale dimensions (Narragansett Bay, Long Island embayments, Barnegat Bay) of the Aureococcus outbreak. This may indicate that its bloom initiation was a two-step event. Regional climatologic and/or hydrographic bloom-triggers or, more likely, predisposing conditions may have activated potential bloom-species, notably Aureococcus. A series of additional environmental changes selectively favorable to certain niches then appears to have occurred within Narragansett Bay. Such niche selection, accompanied by continuous niche modification, succession and exploitation, is required to provide the diversified species' responses characterizing the unprecedented phytoplankton bloom observed from May - October 1985. The corollary of this is that a large number of species-specific factor-interactions regulated observed bloom dynamics. However, a similar outcome might be possible should a given factor, grazing for example, directly or indirectly favor the suite of bloom species. The potential significance of grazing as a regulator of the Aureococcus bloom in Narragansett Bay has been discussed by Smayda and Fofonoff (1989), and will be expanded upon in a later section.

The complexity of the 1985 "brown-tide" event and our field study focusing on descriptive field analyses preclude quantification of the regulatory factors. However, the "brown-tide" bloom dynamics put into sharper focus the extent to which the summer phytoplankton niche is open within Narragansett Bay; the possible linkage between long-term phytoplankton changes and bloom outbreaks in this bay; and the provocative evidence linking occupancy of the open niche to grazing structure.

Rainfall Hypothesis

There is a general view that the 1985 Aureococcus bloom was partly regulated by salinity (Cosper et al., 1987; Cosper et al., 1989a; Sieburth et al., 1988). For Narragansett Bay, Sieburth et al. speculated that the record deficit in rainfall during the 10-month period prior to May 1985 was a factor underlying the 1985 "brown-tide" outbreak. They reasoned that reduced runoff into and flushing of Narragansett Bay reduced wash-out of Aureococcus, leading to its bloom. Cosper et al. (1987) previously noted the coincidence of very low rainfall, lowered sea level and expected reduction in the flushing rates in Long

Island embayments where *Aureococcus* bloomed. Subsequently, Cosper et al. (1989a) noted that elevated salinities (~30 ^{o}/oo) generally accompanied *Aureococcus* blooms in 1985 and 1986, whereas blooms did not occur previously, or concurrently in these same embayments at salinities from about 22 to 25 ^{o}/oo. They also report a significant reduction in *Aureococcus* growth rate below 28 to 30 ^{o}/oo salinity in laboratory experiments. Exceptions to these field and laboratory results were evident from strong inverse, statistical correlations found between *Aureococcus* abundance and salinity (down to 26 ^{o}/oo) during certain field surveys.

There are at least three aspects to a possible linkage between initial blooming of *Aureococcus* and salinity: an osmotic effect; growth rate dependency; a flushing rate effect, for which salinity serves as a marker. The available data preclude rigorous assessment of the significance of the apparent coincidence between the 1985 *Aureococcus* outbreak and the reduced rainfall manifested, at least in the Long Island embayments, as elevated salinity. For Narragansett Bay, we determined the deviations for selected month segments during the period from 1959-1987 from the mean rainfall measured at Providence, R.I. during 1901 to 1987 (Fig. 8). The 1959-1981 period covers the interval over which continuous phytoplankton measurements were made at Station 7 (Fig. 1) at approximately weekly intervals. The winter-spring phytoplankton bloom normally occurs during December - April. Deviations from mean rainfall during this interval reveal four years of conspicuous deficit (-7.8" to -3.9", i.e. -19.8 cm to -9.9 cm): 1985 > 86 > 66 > 63. For the two-month period (March - April) prior to the May outbreak, seven conspicuously dry years (-3.6" to -2.1") are evident: 1966 > 65 > 81 > 85 > 86 > 78 > 76. Given the absence of *Aureococcus anophagefferens* blooms prior to 1985, we suggest that the purported linkage between significantly reduced rainfall and bloom stimulation of Aureococcus in Narragansett Bay is tenuous. Sieburth et al. (1988) based their reduced rainfall - runoff - flushing - Aureococcus bloom hypothesis partly on their view that this bloom began in upper Narragansett Bay, a view not supported by field observations (Smayda & Villareal, 1989). The reduced flushing hypothesis for Narragansett Bay is weakened by observations that growth rates of natural population of Aureococcus can exceed 2.0 divisions d^{-1} (Cosper et al., 1989a; Dzurica et al., 1989). Such growth rates exceed those required to compensate for wash-out at the tidal flushing characteristics of these embayments (Ketchum, 1954) and allow bloom development.

In contrast to the rainfall deficits during December-April and March-April 1985, during May-July 1985 when the Aureococcus bloom was most intense the precipitation level was about +2.5" (= +6.4 cm) above the long-term mean. This was the fifth wettest May-July period since 1959. While considerably greater positive rainfall anomalies (+4" (= 10.2 cm) to +8" (= 20.3 cm)) have occurred during this period in 1984, 1982 and 1972, the association between increased rainfall and runoff and the 1985 bloom event is notable. The frequent initiation of "red-tide" blooms after the spring-diatom bloom following a period of extensive rainfall/runoff is a well-known phenomenon.

Thus, we find no support for the Sieburth et al. hypothesis and draw attention to the above-normal rainfall over Narragansett Bay during the initial stages of the Aureococcus bloom. We restrict our interpretation to Narragansett Bay, acknowledging that different environmental conditions, including in salinity, characterize the shallower, more slowly flushed Long Island embayments. The extent to which the apparent salinity changes and associated flushing rate and osmotic effects are merely in parallel series with the actual cause-and-effect variables remains enigmatic.

"Brown-tide" Bloom and the Open-Niche

The "brown-tide" began in May (Fig. 2) following termination of the winter-spring diatom bloom. The May - June period is a major transitional interval in Narragansett Bay characterized by low nutrients; a period when nannophytoplankton become dominant; zooplankton biomass is high; Acartia tonsa replaces Acartia hudsonica, the dominant winter-spring copepod; and benthic filter feeding increases. These biotic changes are accompanied by increasing temperature, daylength, irradiance and persistent mixing (Pratt, 1966; Smayda, 1973; Durbin et al., 1975; Durbin & Durbin, 1981; Hale, 1975). An important phytoplankton successional change also takes place, the outcome of which (including subsequent summer bloom species) is highly variable and unpredictable, i.e., the transition to the open-niche period. This uncertainty contrasts sharply with our present ability to predict, with reasonable accuracy, community structure and dynamics during the winter-spring diatom bloom and the May-June transitional period. That is, the open phytoplankton niche which developes during May-June persists through the summer. The 1985 "brown-tide" event is a manifestation of both this open-niche and our limited ability to predict which species will fill it.

The 1959 - 1980 occurrences of four summer bloom species (Olisthodiscus luteus, Prorocentrum redfieldii, Prorocentrum triangulatum (= P. minimum) and Katodinium (= Massartia) rotundata) illustrate this open-niche (Fig. 9). Each species has produced "red-tide" blooms. The first three species usually have their annual appearance sometime between calendar weeks 20 - 22; Katodinium rotundata may be present throughout the year. Each species has exhibited inexplicable periods of absence; sometimes for prolonged periods, such as the virtual disappearance of Katodinium from 1964 - 1974. Olisthodiscus luteus exhibits a fairly consistent time of maximal abundance (usually between weeks 25 - 28) in contrast to the other species. Considerable inter-annual variability in abundance characterizes all species, and is particularly evident for Prorocentrum redfieldii and P. triangulatum (= P. minimum). Thus, the open-niche period is characterized by a sudden shift to seasonal predominance of flagellates and a period of potential "red-tide" blooms. The characteristics of the open-niche are: it is variously filled with species which exhibit considerable interannual and interspecific variability in occurrence; duration of occurrence; time, magnitude and duration of maximal abundance; and frequently exhibits "red-tide" blooms, the occurrence of which and responsible causative species are highly unpredictable. The 1985 "brown-tide" event involving the blooms of 15 different taxa, including autochthonous and newly recognized taxa, which collectively exhibited unusual, anomalous or normal bloom dynamics (Figs. 2-7) is a dramatic illustration of the summer open-niche in Narragansett Bay. The general occurrence of an open-niche in Temperate and Boreal coastal waters is suggested by the similarly unpredictable summer phytoplankton blooms well-known for those waters.

Regulation of Open-Niche Occupancy

The growth dynamics of the diatom Skeletonema costatum is an important determinant of which non-diatomaceous species will occupy the summer open-niche. Skeletonema was an important component of the 1985 "brown-tide" (Figs. 3, 7); its maximal abundance ranked third among the 15 bloom taxa, and it was the most persistent species during this event. Thus, since Skeletonema is a viable competitor for available summer niches, the success of competing species to achieve summer dominance is partly dependent upon growth regulation of this diatom. One mechanism is allelochemic control. There is a remarkable allelochemic competition (Pratt,

1966) between Skeletonema costatum and Olisthodiscus luteus during May-June in Narragansett Bay (Fig. 10). Co-dominance does not occur; dominance of the successful species is accompanied by the virtual exclusion of the other. However, there is no evidence for a similar allelopathic regulation of phytoplankton during the 1985 "brown-tide" event, notably by Aureococcus anophagefferens, based on species' abundance patterns. Although the numerical abundances of Skeletonema and Aureococcus were inversely correlated during late August, an allelopathic explanation can not be invoked without experimental demonstration. Cosper et al. (1989), however, were unable to demonstrate allelopathic inhibition of Minutocellus polymorphus and Prorocentrum triangulatum (= P. minimum) cultured in nutrient-enriched filtrate from Aureococcus-conditioned medium. These two species were bloom-species during the 1985 "brown-tide" (Figs. 3, 4). Thus, while allelochemic regulation of species competiting to fill the summer open-niche occurs (see also Iwasaki, 1979), it does not appear to have been a significant determinant of the 1985 Aureococcus outbreak.

Grazing structure also influences occupancy of the summer open-niche, the evidence again being clearest for Skeletonema. Summer blooms of Skeletonema are inversely related to abundance of the herbivorous copepod Acartia tonsa (Fig. 11; Deason & Smayda, 1982). Copepod predation regulates whether Skeletonema, dinoflagellates or other taxa will predominate. Acartia abundance, in turn, is regulated by its carnivorous predator, the ctenophore Mnemiopsis leidyi (Fig. 11). Consequently, a direct correlation exists between Skeletonema abundance and ctenophore abundance (Fig. 12). These concomitant grazing interactions at the carnivorous (Mnemiopsis - Acartia) and herbivorous (Acartia - Skeletonema) levels mediate the competition between Skeletonema and other phytoplankton taxa competing to fill the summer bloom niche. When the latter out-compete Skeletonema, grazing further defines which species within this group will predominate.

A very notable feature of the 1985 "brown-tide" is the antagonistic effect on herbivorous grazers, an effect primarily attributable to Aureococcus anophagefferens. The numerical abundance of the predominant copepod Acartia tonsa was inversely correlated (r = -0.91) with Aureococcus abundance. That this has a physiological basis is evident from Durbin and Durbin's (1989) experiments. Adult female Acartia fed Aureococcus had lower rates of feeding, egg production, body growth and weight, and were in poor physiological condition. The ecological effect of this was reduced grazing pressure on the phytoplankton bloom species by the primary summer herbivore.

Failure of the cladoceran community to develop was the most remarkable zooplankton modification accompanying the brown-tide outbreak (Fig. 13). Evadne nordmanni and Podon sp. normally exceed 10,000 animals m^{-3} during June-August, but failed to appear in 1985. Based on the six-year interannual comparisons at Station 7, the mean 1985 May-August cladoceran abundance of only 80 animals m^{-3} was 10- to 75-fold lower than the means for comparison years. The strong cladoceran recovery in Narragansett Bay during 1986, when a "brown-tide" did not develope, is notable. Thus, the virtual elimination of the cladoceran community in 1985 further decreased zooplankton predation pressure on the "brown-tide" species.

Mero-zooplankton abundance was also reduced during the "brown-tide" (Smayda & Fofonoff, 1989). Benthic larval abundance and Aureococcus abundance were inversely correlated (r = -0.58). Mean larval abundance at Station 7 during 1985 was the lowest observed for available comparison years (1981-1986). Mean abundances of polychaete larvae and bivalve veligers were 1.5- and 3.6-fold lower, respectively, than the previous minima.

The reduced abundance, feeding rates and fecundity of three major herbivorous zooplankton components (copepods, cladocerans, benthic larvae) represent a major aspect of the 1985 "brown-tide" in Narragansett Bay, and one which influenced the outcome of the competition for occupancy of the summer phytoplankton niche.

Strong benthic-pelagic coupling characterizes the relatively shallow 9 m), well-mixed Narragansett Bay. The clam Mercenaria mercenaria and the mussel Mytilus edulis are important filter feeders. Field studies during the 1985 "brown-tide" revealed reproductive failure and massive bay-wide mortality (up to 100%) of the mussels (Tracey, 1988). Tracey's laboratory experiments suggest drastically reduced mussel filtration rates occurred at Aureococcus concentrations between 250 to 500 x 10^6 cells L^{-1}, even when provided in combination with the highly palatible Isochrysis galbana. The filtration threshold of 250 x 10^9 cells m^{-3} indicated on the Aureococcus abundance cycle shown in Fig. 2 suggests that marked feeding inhibition of Mytilus edulis on Aureococcus occurred from May-August. This suggests that, as for herbivorous zooplankton, reduced benthic grazing also occurred during the 1985 "brown-tide". This also probably influenced the outcome of the competition for occupancy of the summer niche.

An inimical effect at the nekton level was also found. Mean egg abundance of the bay anchovy, Anchoa mitchilli, a major component of the Narragansett Bay nekton (Herman, 1963) was only 10% of mean levels during the 1973 and 1981-1986 comparison years (Fig. 14). Egg abundance strongly rebounded in 1986 when the "brown-tide" failed to develope, a response similar to that for cladocerans (Fig. 13). The actual mechanisms causing the reduced anchovy fecundity are unknown. The picoplanktonic (~2 μm) Aureococcus is significantly below the minimal particle size ingested by Anchoa mitchilli

(Detwyler & Houde, 1970; Houde & Lovdal, 1984). Reproductive failure of Anchoa would therefore not appear to be linked to the food quality of Aureococcus. Moreover, Detwyler, Houde and Lovdal's work shows that Anchoa larvae appear to feed predominantly on copepods (including developmental stages), gastropod and bivalve larvae, and tintinnids, with some ingestion of dinoflagellates and diatoms. The expected ecological consequences of this inimical impact on Anchoa recruitment would be a reduction in Anchoa's grazing pressure on herbivorous zooplankton, benthic larval stages and microzooplankton (= tintinnids). This reduced predation should have favored greater herbivorous grazing pressure on the phytoplankton.

Collectively, these observations suggest that seriously altered and/or impaired grazing pressure by major components within the zooplankton, benthos and nekton trophic levels accompanied the 1985 "brown-tide". This altered grazing is expected to have had major impacts on phytoplankton community structure, niche competition, and bloom development.

There is evidence that heterotrophic flagellates also regulated the Aureococcus bloom and influenced competition for the open-niche. Following maximal abundance on 25 July, Aureococcus declined baywide in the pattern depicted at Station 7 (Fig. 2). Phagotrophic flagellate abundance surged significantly bay-wide in mid-August, and persisted through September; maximal abundance ranged from 20 to 44 x 10^9 cells m^{-3}. Regression of the mean heterotrophic flagellate abundance against mean Aureococcus abundance during the "brown-tide" period (Fig. 15) yields a statistically significant direct correlation ($r = +0.66$).

Following its disappearance in October 1985 (Fig. 2), Aureococcus reappeared in great numbers during the survey of 14 May 1986. Surface populations ranged from 53 to 180 x 10^6 cells L^{-1}; bottom populations (10^6 to

254×10^6 cells L^{-1}) were 18% to 236% more abundant. The phytoplankton community was otherwise depauperate, dominated by Skeletonema costatum (< 0.5×10^6 cells L^{-1}) and, secondarily, by Chaetoceros socialis. A survey on 18 June 1986 revealed the continued presence of Aureococcus. At Stations 1-5 (Fig. 1), abundance was considerably reduced; at Stations 6-7, it increased considerably. The diatom community remained depauperate, dominated by Thalassiosira cf. pseudonana (3 to 4×10^6 cells L^{-1}), whereas Skeletonema declined since May. The principal floristic features were a modest bloom of the "red-tide" species Olisthodiscus, which did not appear until October in 1985 (Figs. 6, 7), and more vigorous growth of the "red-tide" species Prorocentrum redfieldii. The latter persisted in abundance during the 1985 "brown-tide" (Figs. 4, 7). Prorocentrum triangulatum (= P. minimum) and Prorocentrum scutellum co-occurred in lesser abundance, as in 1985 (Figs. 4, 7). A modest euglenid bloom also occurred, particularly at Station 2 (Fig. 1) where 360×10^5 cells L^{-1} were present. (Euglenid blooms did not develope before August in 1985 (Fig. 6).) Thus, by mid-June 1986 Aureococcus anophagefferens co-occurred with several red-tide Prorocentrum species, as in 1985. Skeletonema was then insignificant, whereas Olisthodiscus luteus was abundant (up to 1.4×10^6 cells L^{-1}), i.e., the reverse of the 1985 situation. Olisthodiscus outcompeted Skeletonema for the May-June open-niche, presumably aided by its allelochemic ability (Pratt, 1966).

The most significant difference from 1985 at this stage of the 1986 Aureococcus bloom, however, was the large population (up to 0.5 million cells L^{-1}) of heterotrophic dinoflagellates (Gymnodiniaceans). These holozoic species, capable of feeding on particles in the size range (~2 μm) of Aureococcus were insignificant during the initial bloom stages in 1985, and relatively unimportant during the "brown-tide" (Figs. 5, 7). In 1986, Aureococcus failed to bloom thereafter, following the "bloom of holozoic dinoflagellates, and disappeared from the community. A red-tide outbreak then developed, consisting primarily of Olisthodiscus luteus and, secondarily, of the dinoflagellates Prorocentrum redfieldii, P triangulatum = P. minimum) and Heterocapsa triquetra. Heterotrophic dinoflagellates remained abundant. These observations, which suggest that grazing of Aureococcus by the holozoic gymnodiniaceans and other heterotrophic flagellates (Fig. 15) influenced its bloom dynamics, are consistent with the experimental evidence of Caron et al. (1989) that heterotrophic flagellates and certain heterotrophic microflagellates avidly graze Aureococcus.

Grazing Hypothesis

The field associations between Aureococcus and microbial grazers, zooplankton and benthic filter feeders suggest some specific examples of the general paradigm that the grazing process influences the competition between phytoplankton species for the open-niche. A progressive failure of the grazing process at several trophic levels appears to have driven the 1985 "brown-tide" outbreak. Failure of the heterotrophic flagellates during growth inception of Aureococcus was the first break-down. In 1985, when these grazers were sparse, Aureococcus continued to increase following its appearance (triggered by unknown factors). In 1986, these grazers were abundant and grazed down Aureococcus following its growth inception. Failure of the heterotrophic flagellate community to develope during 1985 was followed by zooplankton grazing failure. Continued Aureococcus growth was then facilitated by the reduced grazing, fecundity and associated population growth of Acartia tonsa. Elimination of the cladoceran component further facilitated this bloom. Failure of the herbivorous zooplankton component was followed by the third grazing failure after Aureococcus reached an apparent threshold density off 250×10^6 cells L^{-1} (Fig. 2): the reduction in, and cessation of benthic (= mussel) filter feeding. Aureococcus was, thus, essentially an ungrazed species, reaching very high numerical abundance which gave it a competitive advantage over other phytoplankton species. Moreover, this general reduction in grazing pressure on the phytoplankton appears to have stimulated the remarkable, anomalous series of both successional and coincident bloom-episodes of the other species during 1985 (Fig. 7).

In 1986, successful heterotrophic flagellate predation on Aureococcus prevented its bloom, and the ensuing grazing failure of the herbivorous zooplankton and benthic filter feeders associated with its 1985 bloom occurrence did not occur. However, the Olisthodiscus luteus red-tide event in 1986 caused at least partial grazing failure. This species is widely lethal to zooplankton, causing mortality of Acartia tonsa (Tomas & Deason, 1981) and protozoan grazers (Verity & Stoecker, 1982), two major components of the summer zooplankton community in Narragansett Bay. Nonetheless, the 1986 summer phytoplankton bloom dynamics were within the range of "normal" interannual variations associated with the open-niche variability.

These events in Narragansett Bay suggest not only that an open-niche occurs during summer, but that grazers are important in regulating the competition for, and occupancy of this niche. Viewed collectively with the numerous published descriptions of "red-tides", nuisance blooms and other mass occurrences of phytoplankton in the sea, they suggest strongly that such bloom-events fundamentally reflect the failure of the normal grazing process (for any of several reasons), rather than are primarily in consequence of augmented or altered nutrient conditions. This will be considered in greater detail elsewhere.

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FIGURE LEGENDS

Figure 1. Station locations in Narragansett Bay.

Figure 2. Surface abundance of Aureococcus anophagefferens (= brown tide cells) at Station 7 from May-June 1985. Filtration threshold represents Aureococcus abundance at which filtration of the mussel (Mytilus edulis) reported to cease (see text). GLORIA identifies occurrence of hurricane.

Figure 3. Surface abundance of three diatom species at Station 4 during 1985 "brown tide".

Figure 4. Surface abundance of three dinoflagellate species belonging to Prorocentrum at Station 4 during and following the 1985 "brown-tide".

Figure 5. Surface abundance of the autotrophic dinoflagellates Scrippsiella trochoidea and Massartia (= Katodinium) rotundatum and the heterotrophic gymnodinioid assemblage at Station 4 during and following the 1985 "brown-tide".

Figure 6. Surface abundance of various autotrophic phytoflagellates at Station 4 during and following the 1985 "brown-tide".

Figure 7. Time and magnitude of maximal abundance of the major bloom species at Station 4 present during the 1985 "brown-tide".

Figure 8. The deviations (Δ) from mean precipitation levels (1901-1987) at Providence, R.I.) during various month segments fro the years 1958-1987.

Figure 9 The interannual variation (1959-1980) in periods of occurrence (blackened area) and annual maxima (X) of four red-tide species at Station 7. The whitened area indicates absence; the striped histogram represents no observations. Graphs in the right panel represent the mean annual abundance.

Figure 10. Annual patterns of co-occurrence of the red-tide flagellate Olisthodiscus luteus and the diatom Skeletonema costatum at Station 7 during 1959 - 1964 (from Pratt, 1966).

Figure 11. Abundance patterns of total phytoplankton, Skeletonema costatum, zooplankton dry weight and numerical abundance of the ctenophore Mnemiopsis leidyi at Station 7 illustrating representative abundance correlation between these trophic levels (from Deason and Smayda, 1982).

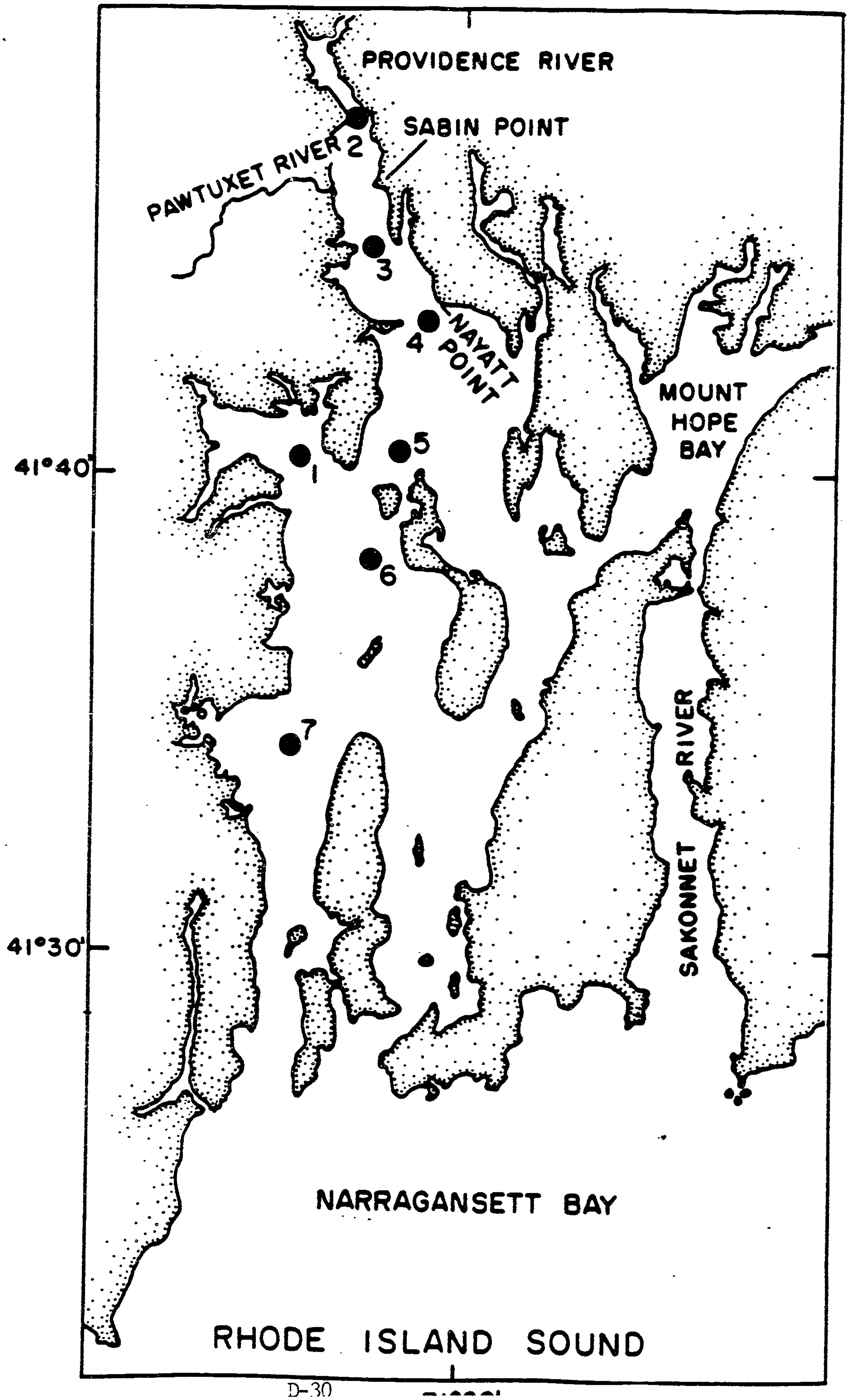
Figure 12. Relationship between mean abundances of Skeletonema costatum and ctenophores at Station 7 during 1972-1977.

Figure 13. Mean annual numerical abundance of cladocerans at Station 7 during 1981-1986.

Figure 14. Mean annual numerical abundance of bay anchovy, Anchoa mitchilli, eggs at Station 7.

Figure 15. Relationship between mean surface abundances of heterotrophic flagellates and Aureococcus anophagefferens during the 1985 brown-tide event. Numbers identify the sampling stations.

Figure 1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SABIN POINT
PAWTUXET RIVER
2
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NAYATT POINT
MOUNT HOPE BAY
5
1
41°40'
6
7
SAKONNET RIVER
41°30'
NARRAGANSETT BAY
RHODE ISLAND SOUND

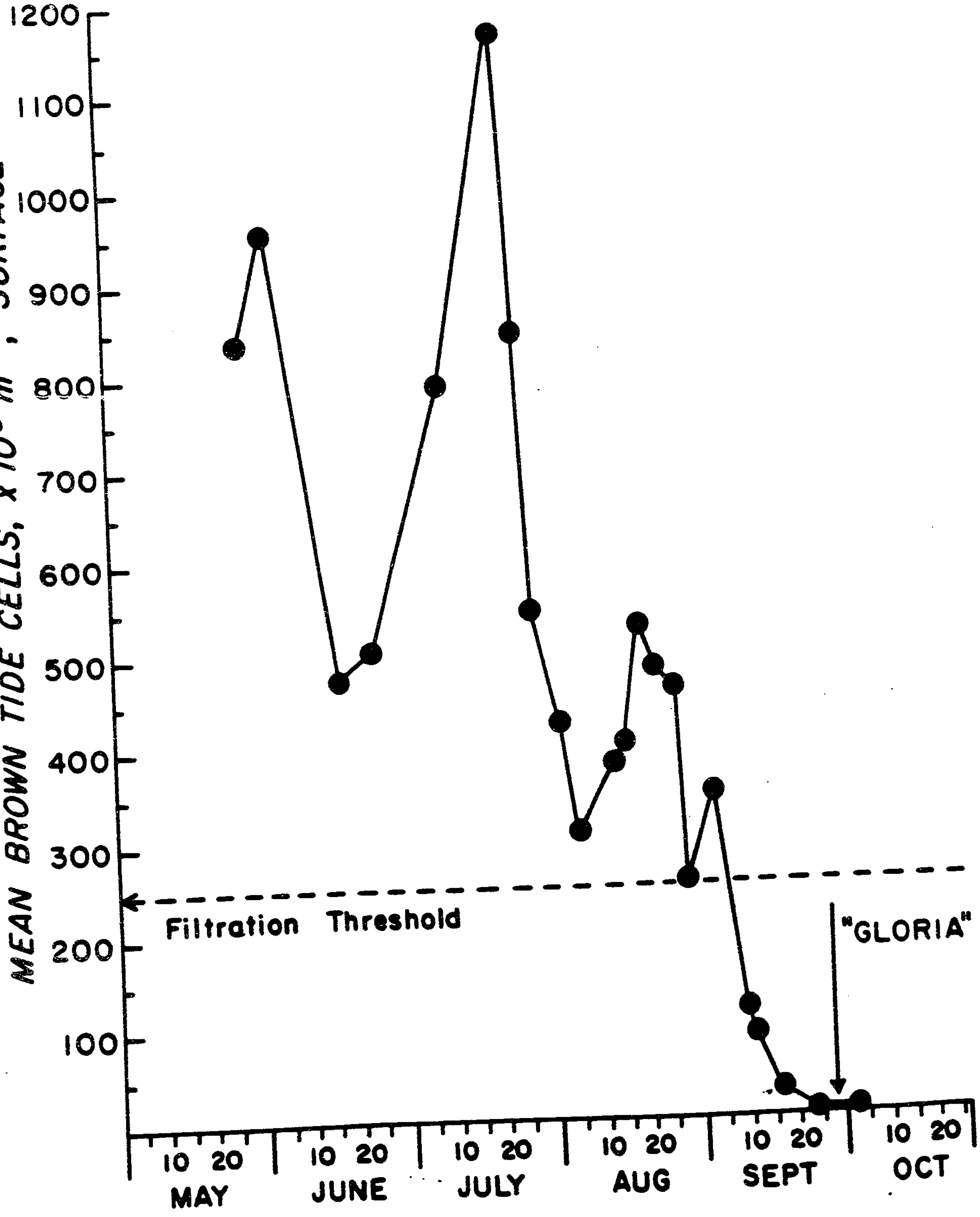

MEAN BROWN TIDE CELLS, x 10^9 m^{-3}, SURFACE
1200
1100
1000
900
800
700
600
500
400
300
200
100
Filtration Threshold
"GLORIA"
10 20
MAY
10 20
JUNE
10 20
JULY
10 20
AUG
10 20
SEPT
10 20
OCT

Figure 2

Figure 3

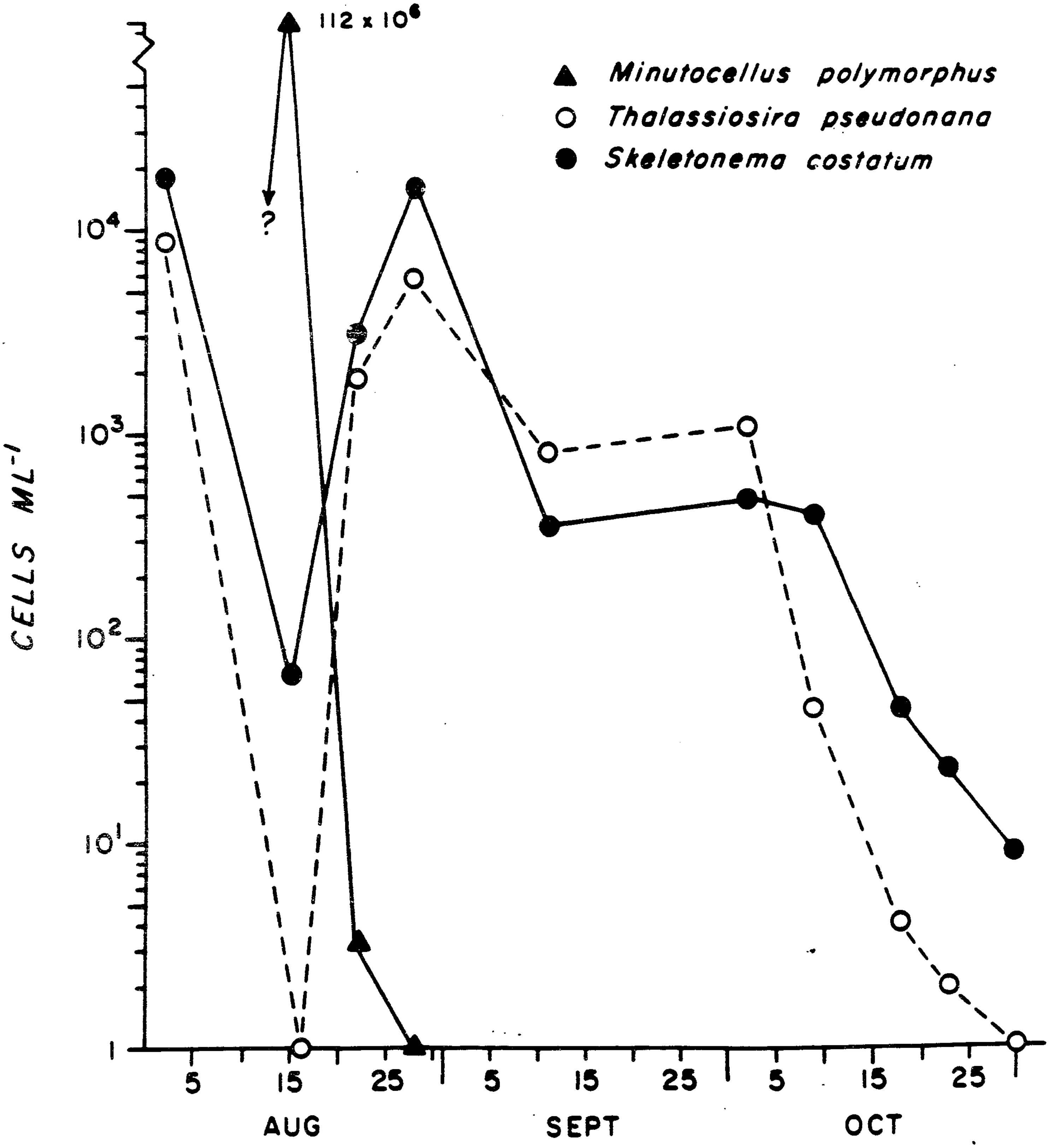
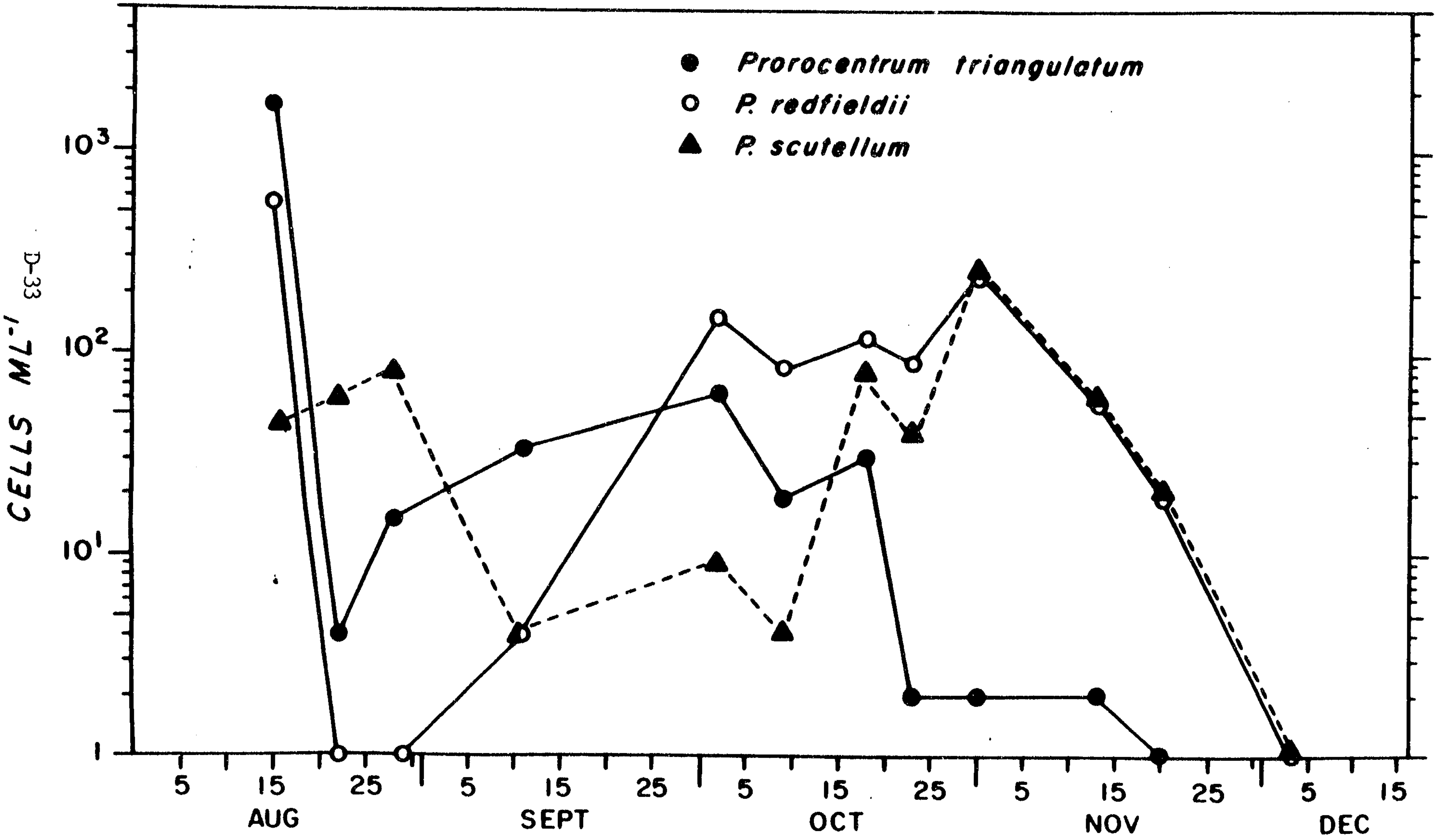

112 x 10^6
?
▲ Minutocellus polymorphus
○ Thalassiosira pseudonana
● Skeletonema costatum
CELLS ML^-1
10^4
10^3
10^2
10^1
1
5
15
25
5
15
25
5
15
25
AUG
SEPT
OCT

Figure 4


Prorocentrum triangulatum
P. redfieldii
P. scutellum
CELLS ML^{-1}
10^3
10^2
10^1
1
5
15
25
5
15
25
5
15
25
5
15
25
5
15
AUG
SEPT
OCT
NOV
DEC

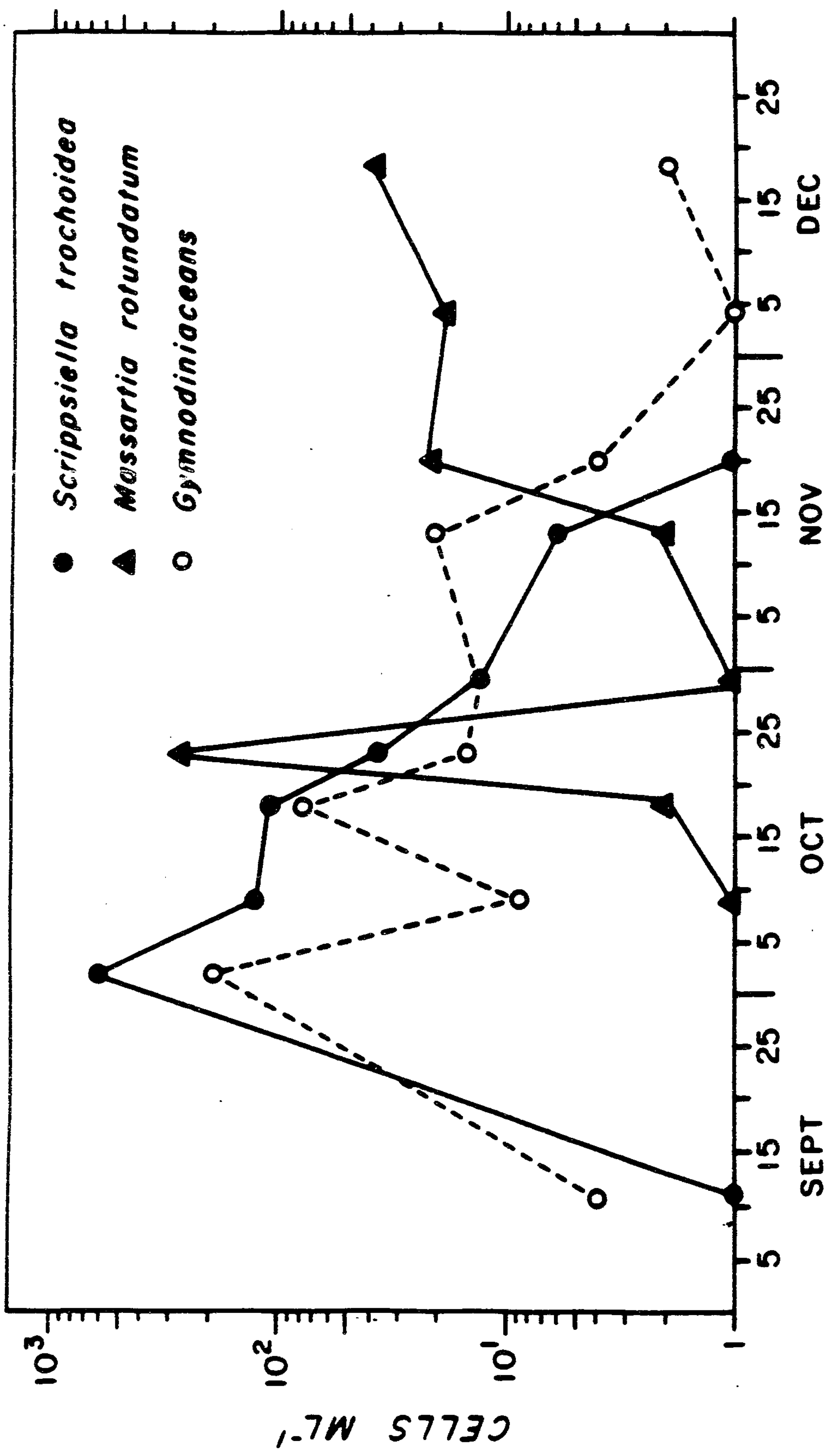
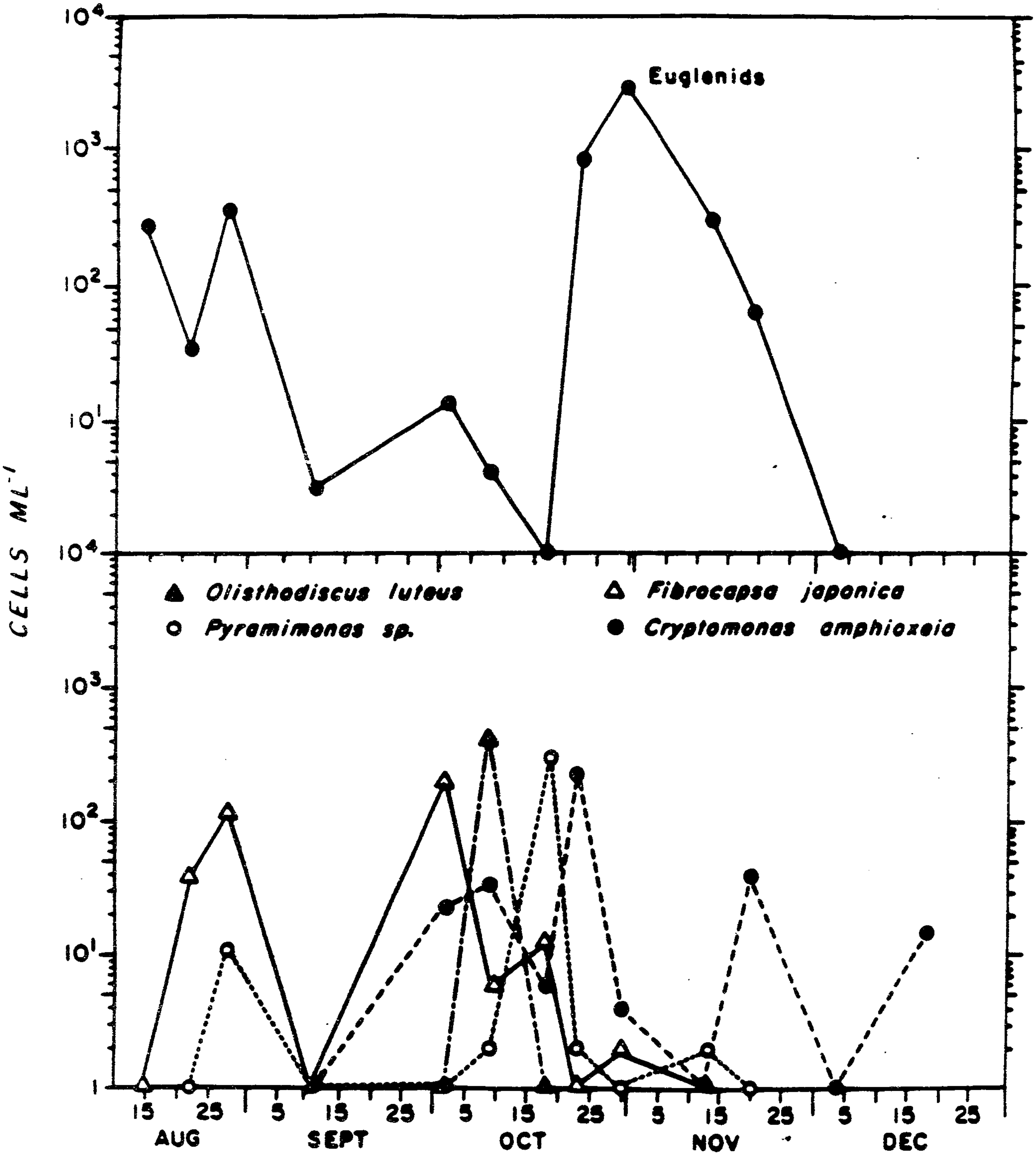

CELLS ML⁻¹
10³
10²
10¹
1
Scrippsiella trochoidea
Massartia rotundatum
Gymnodiniaceans
5
15
25
5
15
25
5
15
25
5
15
25
SEPT
OCT
NOV
DEC

Figure 5



10⁴
10³
10²
10¹
10⁴
10³
10²
10¹
1
CELLS ML⁻¹
Euglenids
▲ Olisthodiscus luteus
△ Fibrocapsa japonica
○ Pyramimonas sp.
● Cryptomonas amphioxeia
15
25
5
15
25
5
15
25
5
15
25
5
15
25
AUG
SEPT
OCT
NOV
DEC

Figure 6

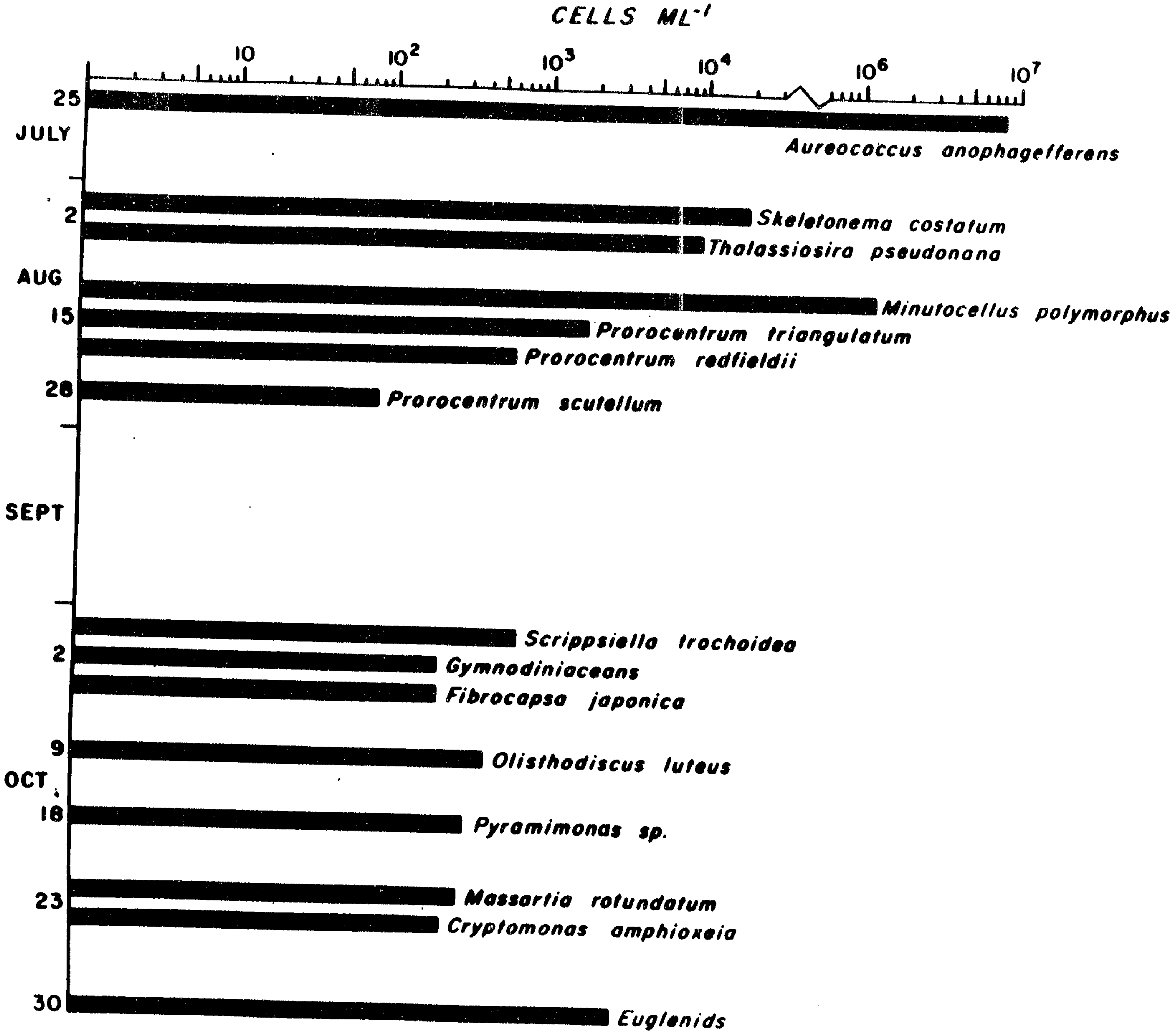

CELLS ML⁻¹
10
10²
10³
10⁴
10⁶
10⁷
25
JULY
2
AUG
15
28
SEPT
2
9
OCT
18
23
30
Aureococcus anophagefferens
Skeletonema costatum
Thalassiosira pseudonana
Minutocellus polymorphus
Prorocentrum triangulatum
Prorocentrum redfieldii
Prorocentrum scutellum
Scrippsiella trochoidea
Gymnodiniaceans
Fibrocapsa japonica
Olisthodiscus luteus
Pyramimonas sp.
Massartia rotundatum
Cryptomonas amphioxeia
Euglenids

Figure 7

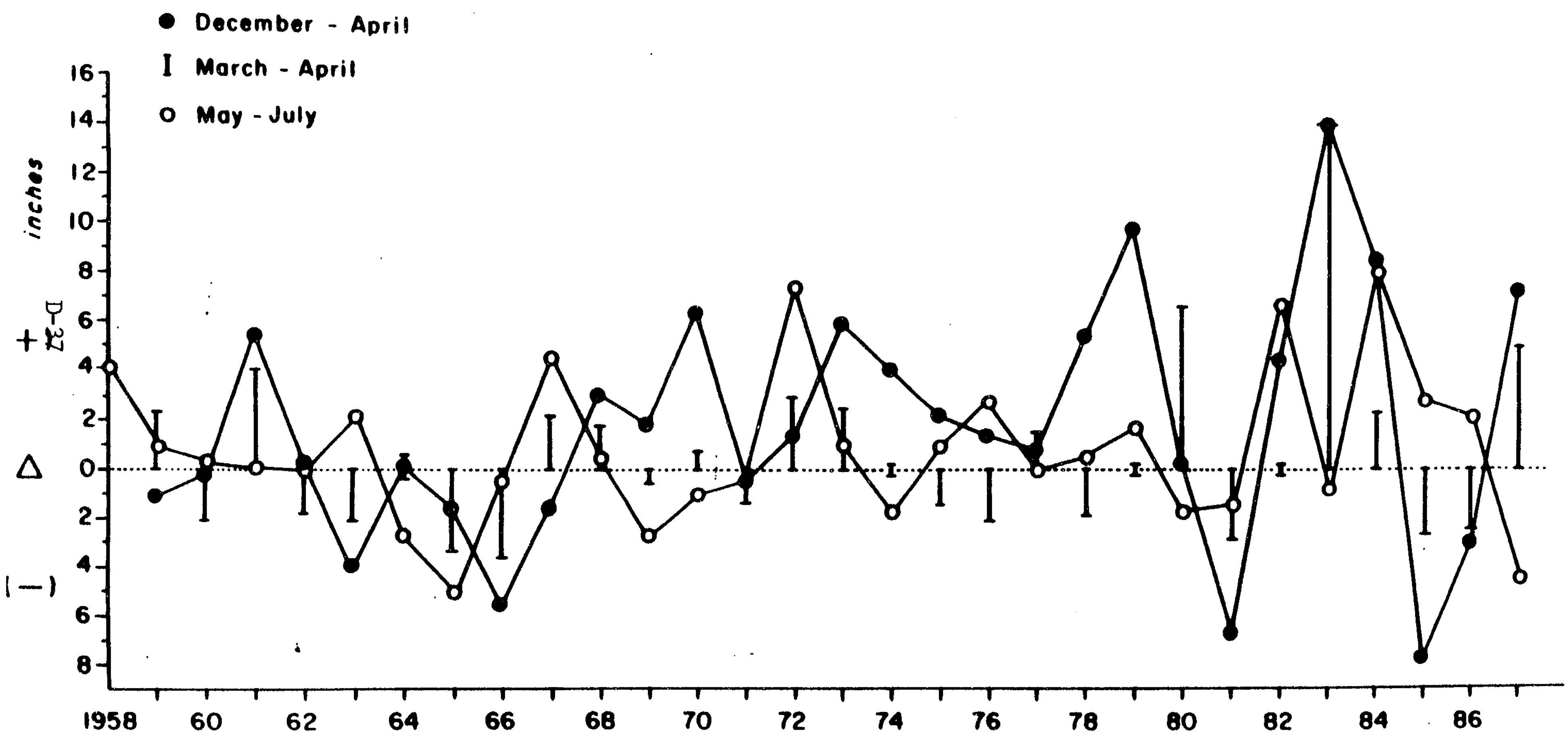

● December - April
I March - April
O May - July
inches
+
Δ
(−)
16
14
12
10
8
6
4
2
0
2
4
6
8
1958
60
62
64
66
68
70
72
74
76
78
80
82
84
86

Figure 8

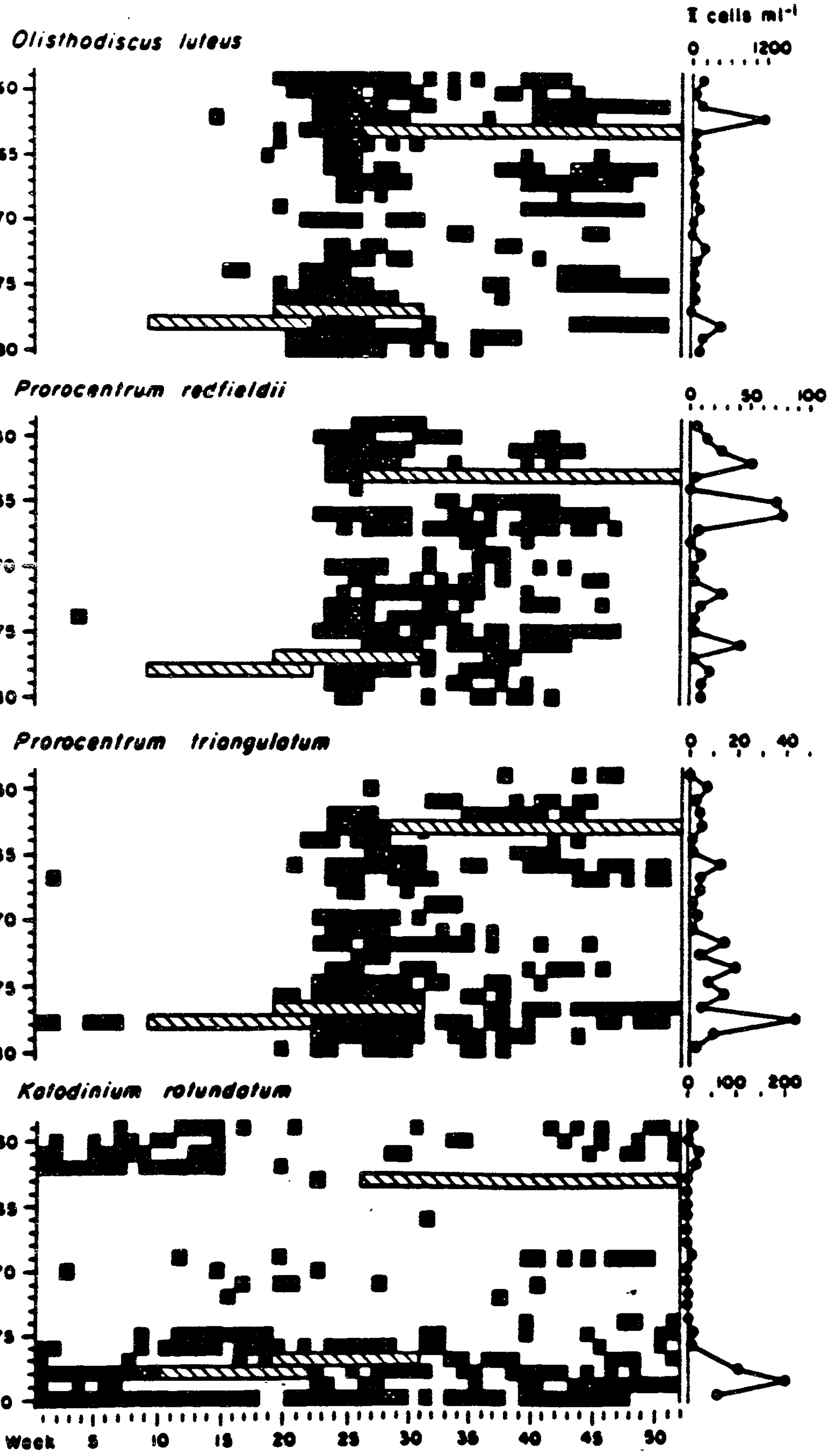

Olisthodiscus luteus
x̄ cells ml⁻¹
0
1200
1960
1965
1970
1975
1980
Prorocentrum redfieldii
0
50
100
Prorocentrum triangulatum
0
20
40
Katodinium rotundatum
0
100
200
Week
5
10
15
20
25
30
35
40
45
50

Figure 9

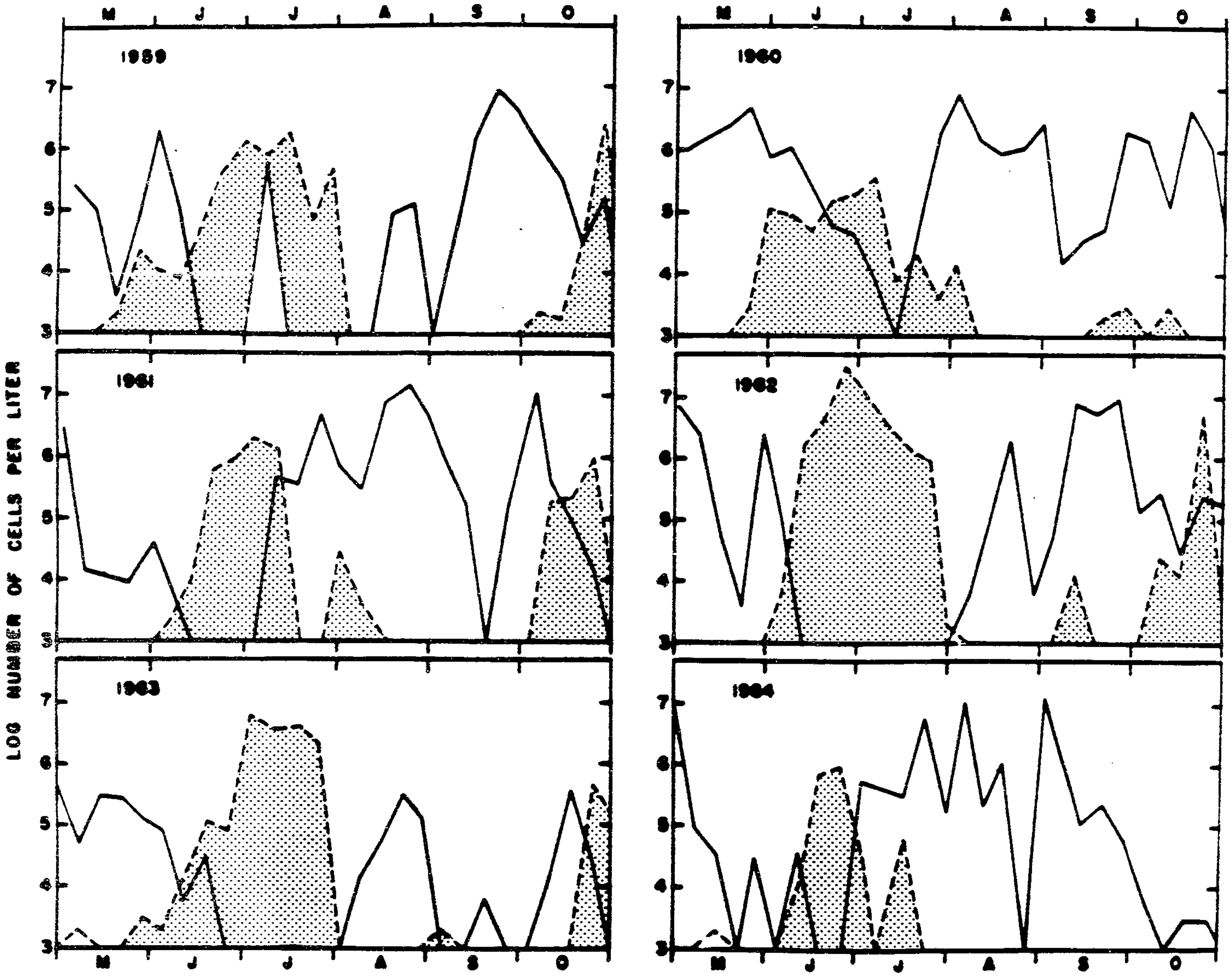

LOG NUMBER OF CELLS PER LITER
M
J
J
A
S
O
1959
1960
1961
1962
1963
1964
3
4
5
6
7

Figure 10

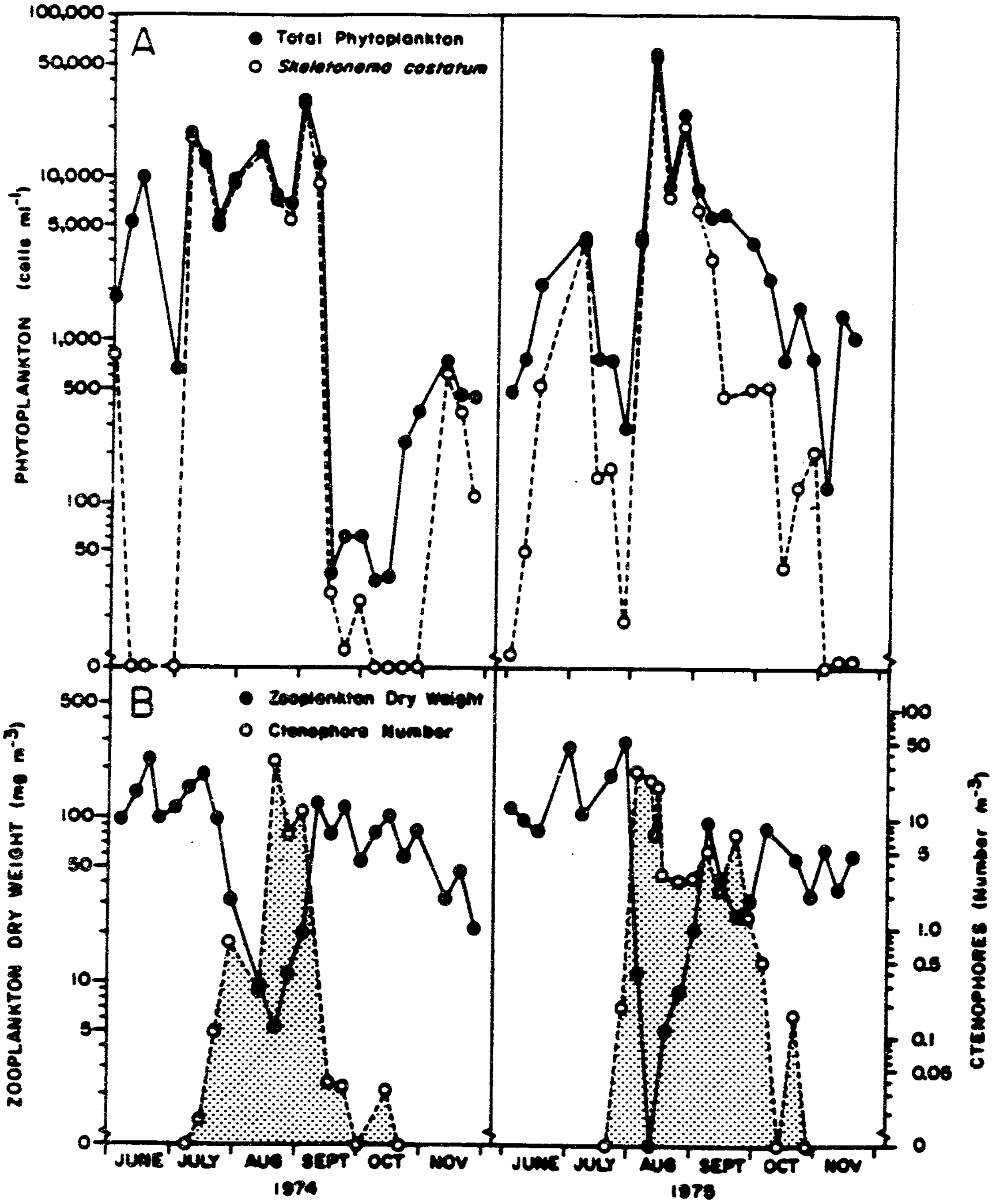
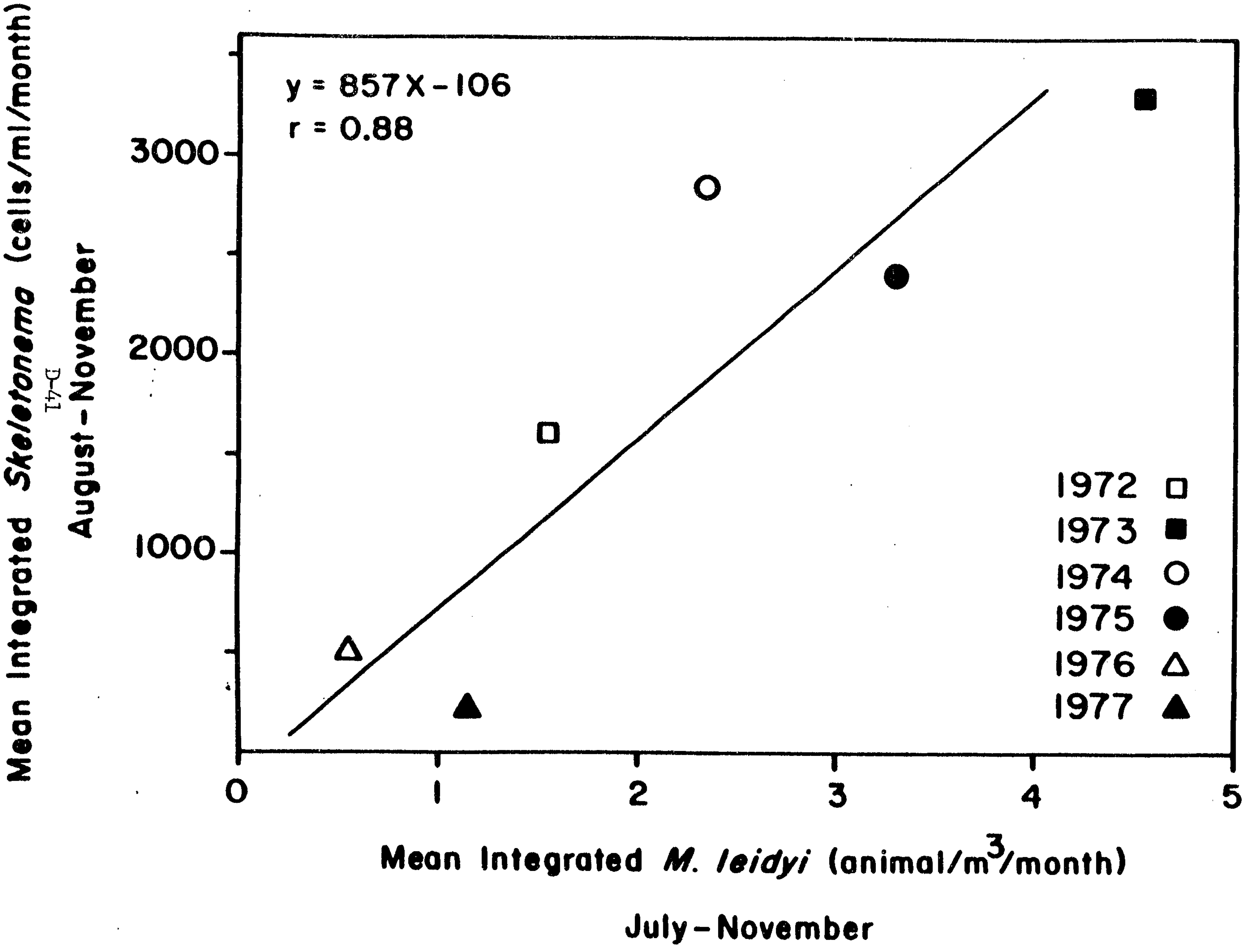

A
● Total Phytoplankton
○ Skeletonema costatum
PHYTOPLANKTON (cells ml⁻¹)
100,000
50,000
10,000
5,000
1,000
500
100
50
0
B
● Zooplankton Dry Weight
○ Ctenophore Number
ZOOPLANKTON DRY WEIGHT (mg m⁻³)
500
100
50
10
5
0
CTENOPHORES (Number m⁻³)
100
50
10
5
1.0
0.5
0.1
0.06
0
JUNE
JULY
AUG
SEPT
OCT
NOV
1974
JUNE
JULY
AUG
SEPT
OCT
NOV
1975

Figure 11

Figure 12


y = 857X - 106
r = 0.88
1972 □
1973 ■
1974 ○
1975 ●
1976 △
1977 ▲
3000
2000
1000
0
1
2
3
4
5
Mean Integrated *Skeletonema* (cells/ml/month)
August - November
Mean Integrated *M. leidyi* (animal/m3/month)
July - November

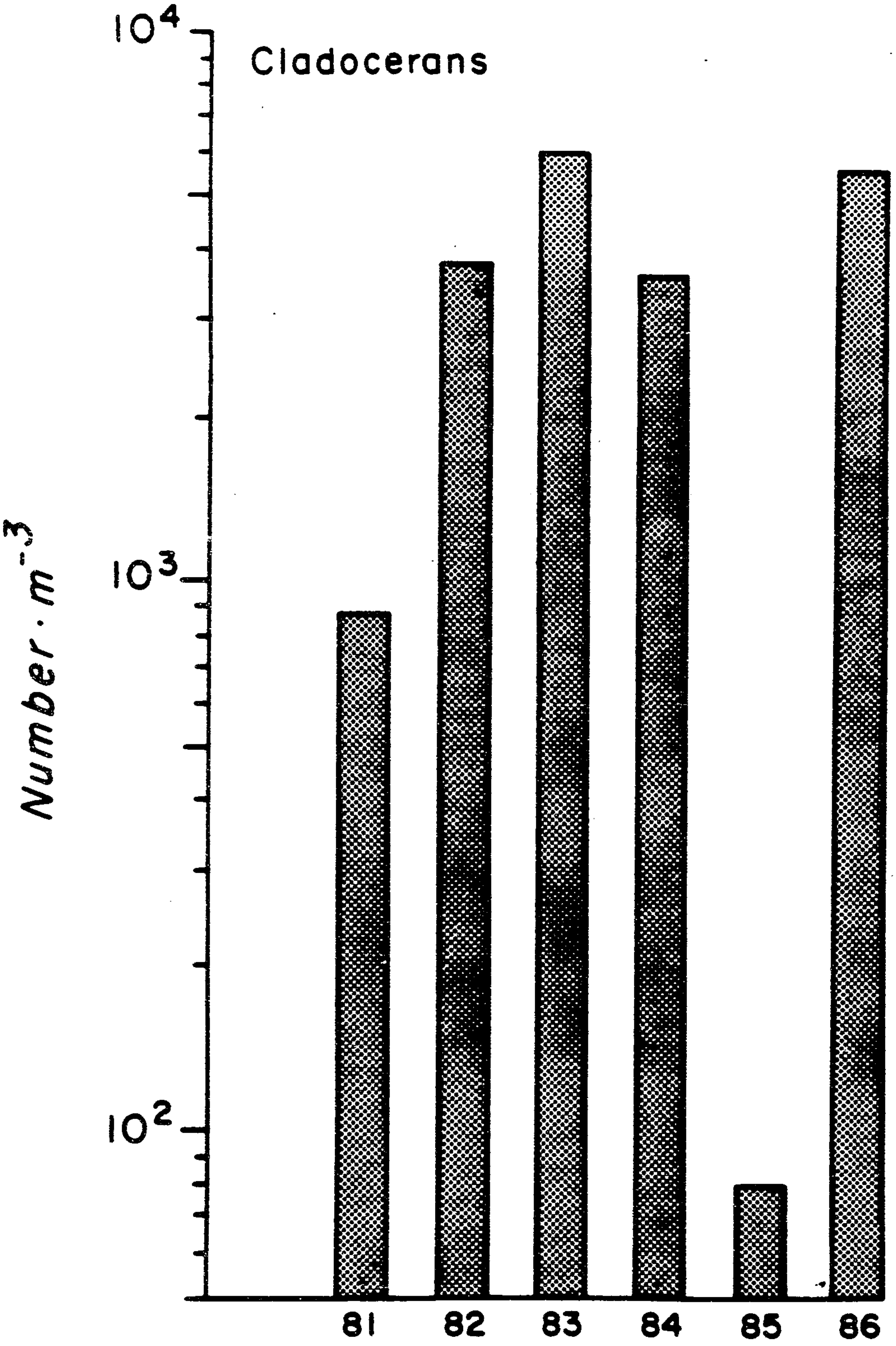


Figure 13

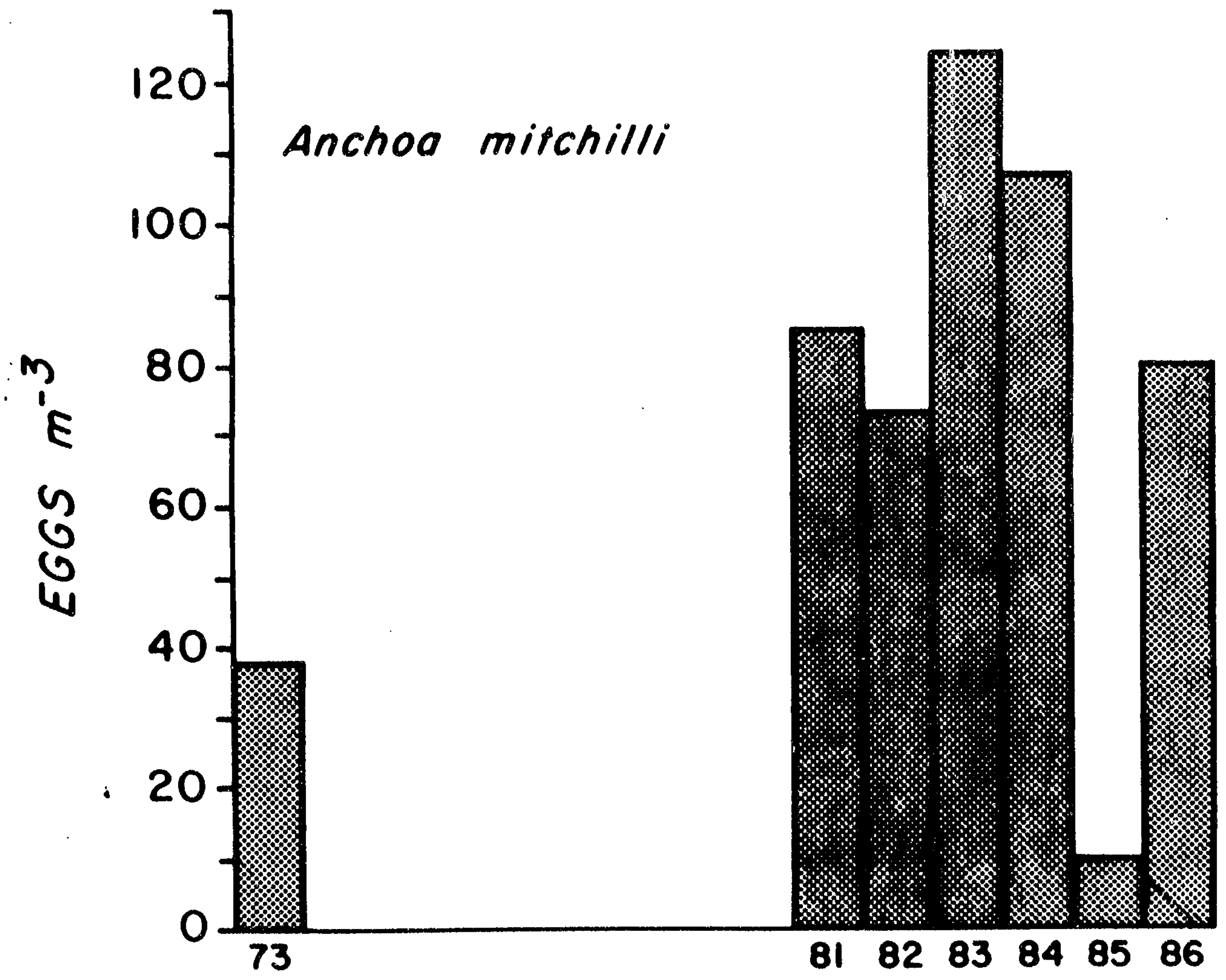

Anchoa mitchilli
EGGS m^{-3}
0
20
40
60
80
100
120
73
81
82
83
84
85
86

Figure 14

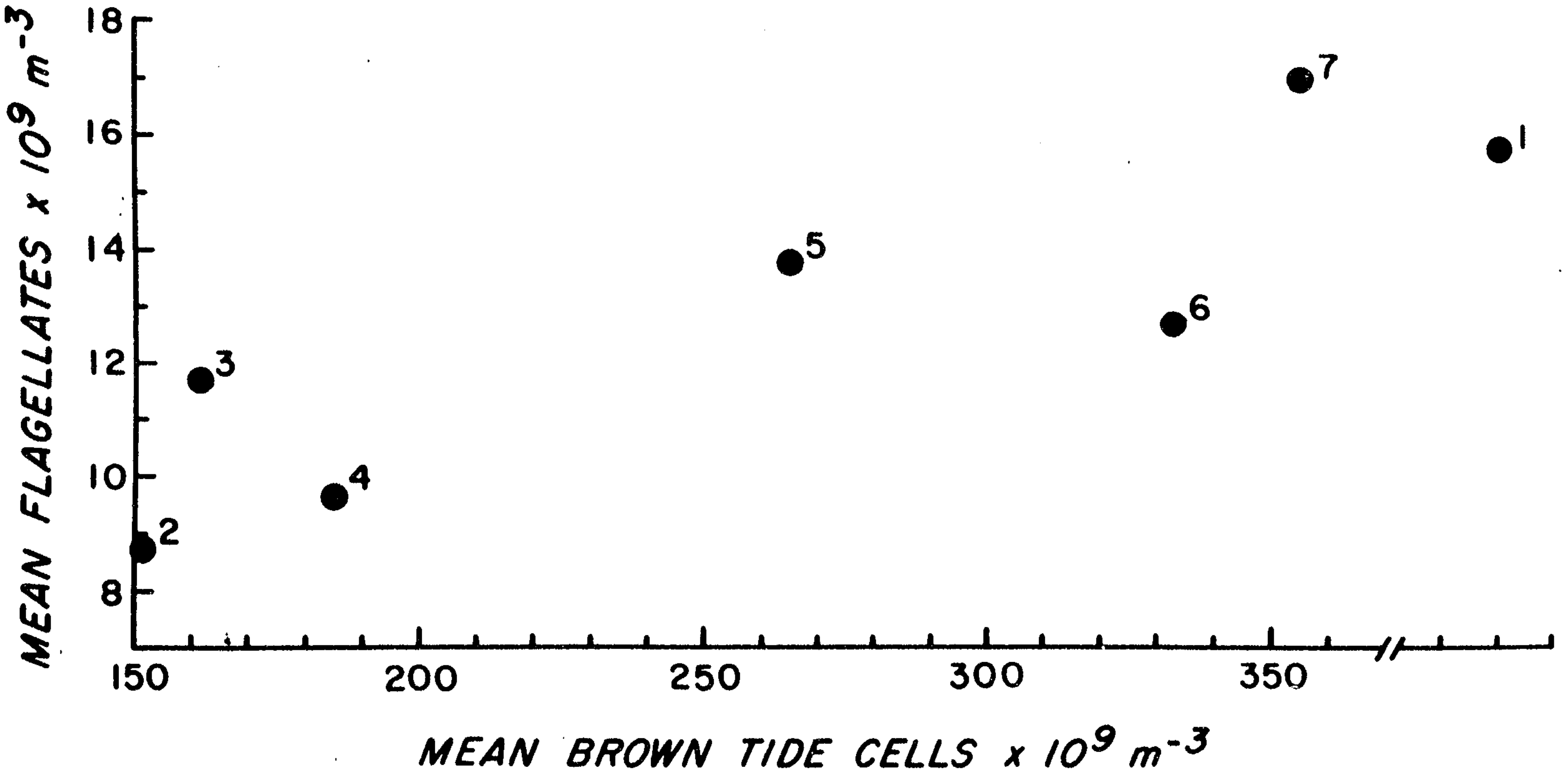

MEAN FLAGELLATES x 10^9 m^{-3}
18
16
14
12
10
8
MEAN BROWN TIDE CELLS x 10^9 m^{-3}
150
200
250
300
350
1
2
3
4
5
6
7

Figure 15