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Seasonal niche strategy of the bloom-forming dinoflagellate *Heterocapsa triquetra*

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ABSTRACT: *Heterocapsa triquetra* is one of the most common bloom-forming dinoflagellates found in estuaries and near shore regions around the world. This work examined the environmental factors associated with 3 separate wintertime *H. triquetra* blooms in the shallow tidally mixed Newport River estuary, North Carolina, USA. During 2 of the blooms in 1982 and 1983, the estuary was sampled from a fixed, single location every hour for 14 d. During the third study, the estuary was sampled at 9 fixed locations over its entire length each week from late December 1997 through March 1998. This time period included the formation and decline of the *H. triquetra* bloom. Barometric pressure, precipitation, photosynthetically active radiation, salinity, temperature, nutrient concentrations, and chl *a* were measured in each study. During the 1997–1998 study, pigments were analyzed using HPLC to characterize the phytoplankton assemblages and the dominant dinoflagellates in each sample were counted. The prevailing environmental conditions associated with the wintertime blooms were largely the result of atmospheric forcing. Low pressure systems moved through the study area at 3 to 4 d intervals and were accompanied by low ambient air temperatures and regular rainfall. Runoff following the rainfall events supplied inorganic nutrients critical for bloom initiation and development. It also created a mesohaline frontal zone in the middle portion of the estuary with salinity and hydrodynamic conditions favorable for *H. triquetra* growth. Here, the *H. triquetra* bloom reached its maximal development with chl *a* levels >100 µg l^{-1} and cell densities between 1 and 6×10^6 l^{-1}. As the *H. triquetra* bloom developed, nutrient inputs from the river became insufficient to meet growth demand and *H. triquetra* began feeding mixotrophically, supplementing its nutritional requirements and reducing competition from co-occurring dinoflagellates. Cloud cover associated with the low pressure systems transiently limited *H. triquetra* growth as did low temperatures. More importantly though, low temperatures limited micro- and macrozooplankton populations to such an extent that grazing losses were minimal. Hence, in order to bloom, *H. triquetra* optimizes a suite of factors including low grazing pressure, increased nutrient inputs, alternative nutrient sources, and favorable salinity and hydrodynamic conditions, as well as the negative factors of temperature-limited growth, short day lengths, and periods of transient light limitation.

KEY WORDS: Dinoflagellate blooms · Seasonal niche strategy · HPLC · Meteorological forcing

INTRODUCTION

Heterocapsa (= *Peridinium*) *triquetra* (Ehrenberg) Stein is one of the most common bloom-forming dinoflagellates found in the coastal and estuarine waters of the world. Regular blooms have been observed in the North Sea, the north and south Atlantic, the Mediterranean, and in the eastern Pacific (Braarud & Pappas 1951, Braarud 1962, Marshall 1967a,b, 1980, Mulford 1972, Anderson et al. 1983, Yamochi & Joh 1986, Marshall & Alden 1990, Kim et al. 1990, Pierce & Turner 1994, Kononen et al. 1999). A large dinoflagellate bloom dom-

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inated by *H. triquetra* usually occurs sometime between January and March in North Carolina estuaries (Hobbie 1971, Hobbie et al. 1972, Campbell 1973, Kuenzler et al. 1979, Lapennas 1980, Lee et al. 1990, Rudek et al. 1991). These blooms generally begin as a mixture of different dinoflagellate species, but rapidly become dominated by *H. triquetra*. At the height of these blooms, *H. triquetra* chl *a* levels typically exceed 150 µg l^{-1} and can account for up to one-half of the annual phytoplankton carbon production in North Carolina estuaries (Paerl et al. 1998, Pinckney et al. 1998). The occurrence of these highly productive winter blooms is somewhat surprising because they develop when water temperatures are at, or near, the annual minimum and incident light fluxes are low compared with other times of the year (Litaker et al. 2002, this volume).

To better understand how *Heterocapsa triquetra* exploits the wintertime environment, we sampled the Newport River estuary, North Carolina (34° 45′ N, 76° 40′ W) during 3 different winter blooms. In the first 2 studies, the middle portion of the estuary was sampled time-intensively, every h for 2 wk, from a single station during February 1982 and February 1983. In the third study, samples were taken weekly from late December 1997 through the end of March 1998 at 9 stations along the length of the estuary. The physical, chemical, and biological factors associated with bloom formation were measured. Despite suboptimal temperatures and light levels, *H. triquetra* was able to utilize the prevailing nutrient and salinity conditions, and low grazing environment, to bloom during January and February.

MATERIALS AND METHODS

Time-intensive studies (1982 and 1983). The Newport River estuary, North Carolina, is a shallow (ca. 1 m depth), well-mixed estuary covering 27 km^2 (Litaker et al. 1987). During this study, a station located in the geographic middle of the estuary was monitored hourly from 11 to 25 February 1982 and from 30 January to 13 February 1983 (Stn 7 in Fig. 1). These 2 studies spanned the period when *Heterocapsa triquetra* blooms regularly occur in the Newport River estuary. Basin residence times for water near the sampling station ranged from 7 to 45 d, longer than for the narrower oligohaline upper estuary and the higher salinity, tidally flushed lower estuary (Hyle 1976).

Salinity (psu) as conductivity and water temperature were determined using an Industrial Instruments RS-5-2 salinometer. Photosynthetically active radiation (PAR, µE m^{-2} s^{-1}) was determined with a Li-Cor 192S sensor attached to a recording integrator. Secchi depth (SD) was measured using a 0.3 m Secchi disk attached to a calibrated pole. Attenuation coefficients (k) were calculated empirically from the simultaneous SD and light attenuation measurements. The relationship was found to be $k = 1.35/SD$. Cumulative daily PAR was determined by summing the average hourly water column fluxes (Riley 1957). Residual NO_3^-, NO^-_2, and PO^{-3}_4 were measured using a Technicon II autoanalyzer. NH_4^+ was measured using the phenol hypochlorite method (Koroleff 1970). Chl *a* (µg l^{-1}) was determined by fluorometric analysis (Turner Design III fluorometer) of particulate material collected by gentle suction onto glass fiber filters (Gelman A/E) and extracted into 90% acetone (Yentsch & Menzel 1963, Parsons et al. 1984).

Spatially intensive study (1997 to 1998). The Newport River estuary was sampled at 9 locations every week from 23 December 1997 through 27 March 1998 (Fig. 1). The 1982 and 1983 studies showed no significant vertical differences in temperature, salinity or pH. Hence, only surface samples were collected. Temperature was measured at each station with a thermometer.

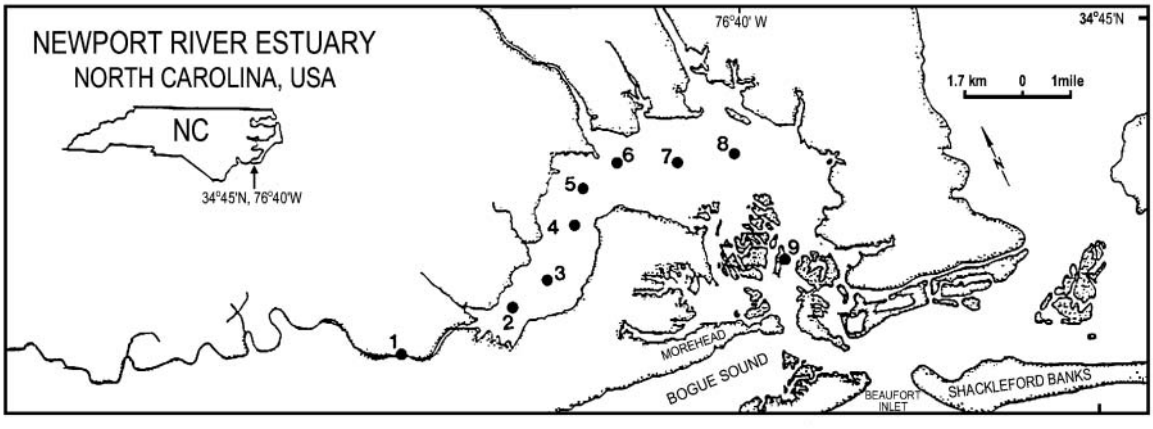

Fig. 1. Location of the Newport River estuary, North Carolina, and the various sampling sites. The fixed-point sampling station for the 1982 and 1983 studies is located at Stn 7. Stns 1 through 9 were sampled during the 23 December 1997 through 27 March 1998 study

Salinity was determined with a model 180 Orion conductivity meter. Chl *a* was determined as in the time-intensive studies. For nutrient analysis, 100 ml of water from each station was filtered through a Gelman GF/F glass fiber filter into an acid cleaned container. The filtrate was frozen immediately at −80°C. These nutrient samples were subsequently thawed and analyzed for NO_3^-+ NO^-_2, NH_4^+, and PO_4^{3-} using a Model QuikChem 8000 Lachat autoanalyzer system. Samples for HPLC pigment analyses were obtained by filtering 80 to 400 ml samples through a 45 mm Gelman GF/F glass fiber filter. Excess water was removed from the filters by blotting before freezing the samples at −80°C. The HPLC pigment profiles for each sample were determined using the methods described in Tester et al. (1995) and Pinckney et al. (1998).

Surface water samples (~125 ml) were taken at each station, preserved with Utermöhl solution (Guillard 1973), and kept tightly capped in dark bottles. A total of 103 samples was counted for the presence of the dinoflagellate *Heterocapsa triquetra* and the ciliate *Mesodinium rubrum* (= *Myronecta rubra*, *Cyclotrichium meunieri*, *Halteria rubra*) at either 100× or 200× using an inverted Wild microscope (Lund et al. 1958). The volumes of the sample chambers were between 2.07 and 3.03 ml. Normally half of the chamber was counted. When samples were too concentrated to allow accurate counts (>500 cells per half chamber), an aliquot was diluted 1:3 or 1:10 prior to counting. *Prorocentrum minimum* was also abundant from 23 January through 13 February 1998, and counts were recorded for all samples where there were >100 cells ml^{-1}. At no time during this winter bloom was any other dinoflagellate species more abundant than this.

Laboratory studies have shown that *Heterocapsa triquetra* increases in size by approximately 60% when it switches from autotrophic growth to feeding mixotrophically on other phytoplankton species (Legrand et al. 1998). To determine if a similar size shift occurred in the field, the width and length of 100 cells were measured from the station with the highest *H. triquetra* concentrations on 16 January, 6 February, and 20 February 1998. These sampling periods were selected as representative of the pre-bloom, bloom, and bloom decline. A calibrated eyepiece micrometer was used to determine if the dimensions and volume of *H. triquetra* cells changed during the course of the bloom, indicating a switch to mixotrophic feeding. Cell volume was calculated as described in Hillebrand et al. (1999).

Net tows for zooplankton were made at the surface with a 333 µm mesh (0.5 m diameter) net on 13 and 20 February 1998 to assess the abundance of macrozooplankton grazers. Three to 5 min tows were made at speeds between 0.5 to 1 m s^{-1}. The filtered volume was calculated using a General Oceanics, Inc. flow meter (Model 2030). On 13 February 1998, the zooplankton from 16.6 and 25.8 m^3 tows was almost entirely (>95%) *Acartia tonsa*. *A. tonsa* strongly dominated the zooplankton again on 20 February with ca. 10% of the material in the tow composed of resuspended particulate material. Zooplankton abundances (excluding gelatinous plankton) were estimated by settling the filtered plankton in volumetric cylinders. The displacement volumes of the tows were 1.0 (13 February) and 1.3 ml (20 February). Final copepod abundance estimates were calculated using a displacement volume to dry weight conversion (Wiebe 1988) and a mean dry weight of 6.44 µg adult $female^{-1}$ *A. tonsa* (Ambler 1982).

The grazing rate of *Acartia tonsa* on a *Heterocapsa triquetra* bloom population was determined as follows. Copepods were returned to the laboratory in insulated coolers and sorted within 1 to 2 h of collection. They were allowed to acclimate to laboratory conditions for 24 h before the start of the grazing experiments. All experimental copepods were robust and actively swimming *A. tonsa*. Twenty adult female *A. tonsa* were placed in each of 5 replicate containers with 370 to 390 ml of Newport River water with ambient concentrations of *H. triquetra* (~5550 to 6800 cells ml^{-1}). Copepods were allowed to graze in the dark for 26.18 to 26.25 h at 18 to 19°C. An initial sample was fixed at $t = 0$ and a control sample without copepods was maintained under the same conditions as the grazing samples to account for the growth of phytoplankton during the experiment. At the end of each experiment, the grazing containers were visually inspected to ensure that all copepods were actively swimming and then fixed in Utermöhl's solution. Aliquots of at least 2 ml of the *H. triquetra* cells from the grazing experiments were settled in an Utermöhl chamber and counted using a Wild inverted microscope. Filtration (clearance) rates were calculated using the equations of Frost (1972).

Microzooplankton abundances were estimated by settling 25 ml of Utermöhl preserved material and counting the number of ciliates at 100× for all 9 stations on 30 January, 13 February, and 27 February 1998. These dates represent the beginning, middle and end of the *Heterocapsa triquetra* bloom during the spatially intensive study.

Analysis of historical data to establish annual patterns of runoff, temperature, copepod abundance, and chl *a*. The monthly runoff for the major coastal North Carolina rivers and streams was estimated by averaging the mean monthly flow rates for the Neuse River measured at the US Geological Survey station (02089500), Kinston, NC (35° 15′ N, 77° 35′ W), from 1930 to 1998 (Fig. 2). The Neuse River was chosen because it has a drainage basin of 6972 km^2 and is representative of the major rivers and streams entering North Carolina estuaries.

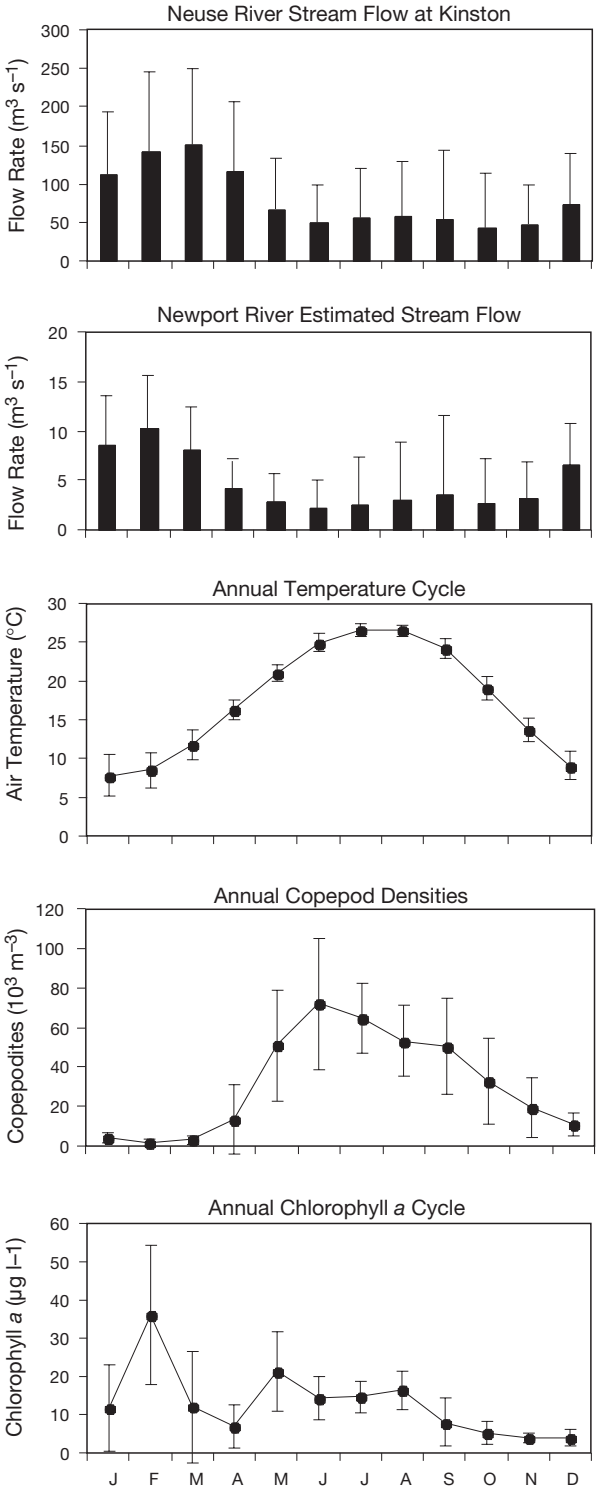

Fig. 2. The mean monthly values ± SD for stream flow (m^{-3} s^{-1}) for the Neuse River at Kinston, North Carolina, from 1930 to 1998, estimated mean monthly flow of the Newport River, air temperature from 1930 to 1998, copepod densities from data in Fulton (1982), and chl *a* concentrations from studies of the middle portion of the Newport River estuary (Thayer 1971, Pfaender & Paerl 1984, Litaker et al. 1987, 1993, and present study)

Unfortunately, no flow rate monitoring stations are located on the Newport River, which supplies the major freshwater input into the Newport River estuary. Monthly runoff values were therefore estimated using a program written by Albrecht (Stone et al. 1971) and based on work by Thornthwaite & Mather (1955, 1957). Both mean monthly rainfall and temperatures are required inputs for this model, and those data were available from 1946 to 1998 for Cherry Point and Morehead City, NC. These 2 locations are on opposite sides of the Newport River drainage basin. Flow rates calculated for each of the 2 sites were averaged to estimate the runoff over the entire drainage basin (Fig. 2). The Newport River estuary is representative of the smaller sub-estuaries located along the coast and sounds of North Carolina that receive input from small localized watersheds. The average monthly runoff pattern in these smaller watersheds can vary slightly from those of the major river basins due to a greater influence of localized differences in rainfall.

The annual temperature cycle was determined by averaging mean monthly temperature from 1950 to 1998 (Fig. 2). The mean monthly abundances of copepods in the Newport River estuary were calculated by averaging data for a 3 yr period presented in Fulton (1982) and expressed as copepodites $\times 10^3$ m^{-3} (Fig. 2). The annual pattern of chl *a* in the middle to upper estuary was determined by averaging the chl *a* data for each month taken from Thayer (1971), Pfaender & Paerl (1984), and Litaker et al. (1987, 1993), as well as the values measured in these studies.

RESULTS

Prevailing air temperatures were at, or near, the annual low during each of the 3 studies (Figs. 2, 3 & 4). These cold temperatures reduced evapotranspiration rates to the lowest point of the year. Strong, well-organized frontal systems moved through the study area at regular 3 to 4 d intervals as evidenced by low pressure waves accompanied by precipitation (Fig. 3). As a consequence, runoff following the rainfall events was higher than at other times of the year (Fig. 2) and provided maximal loading of inorganic NO_2^-, NO_3^-, NH_4^+, and PO_4^{3-} into the Newport River estuary during January and February. In the time-intensive studies (1982 and 1983), sampling was done from a fixed point. Increased runoff was indicated by a drop in mean salinity through time, and an increase in nutrients as the lower salinity, higher nutrient water moved past the sampling site (Fig. 4). Nutrients were taken up rapidly upon entering the estuary (Figs. 3 & 4). The only exception to this was observed during the spatially intensive study for one period in early March when the NO_3^-

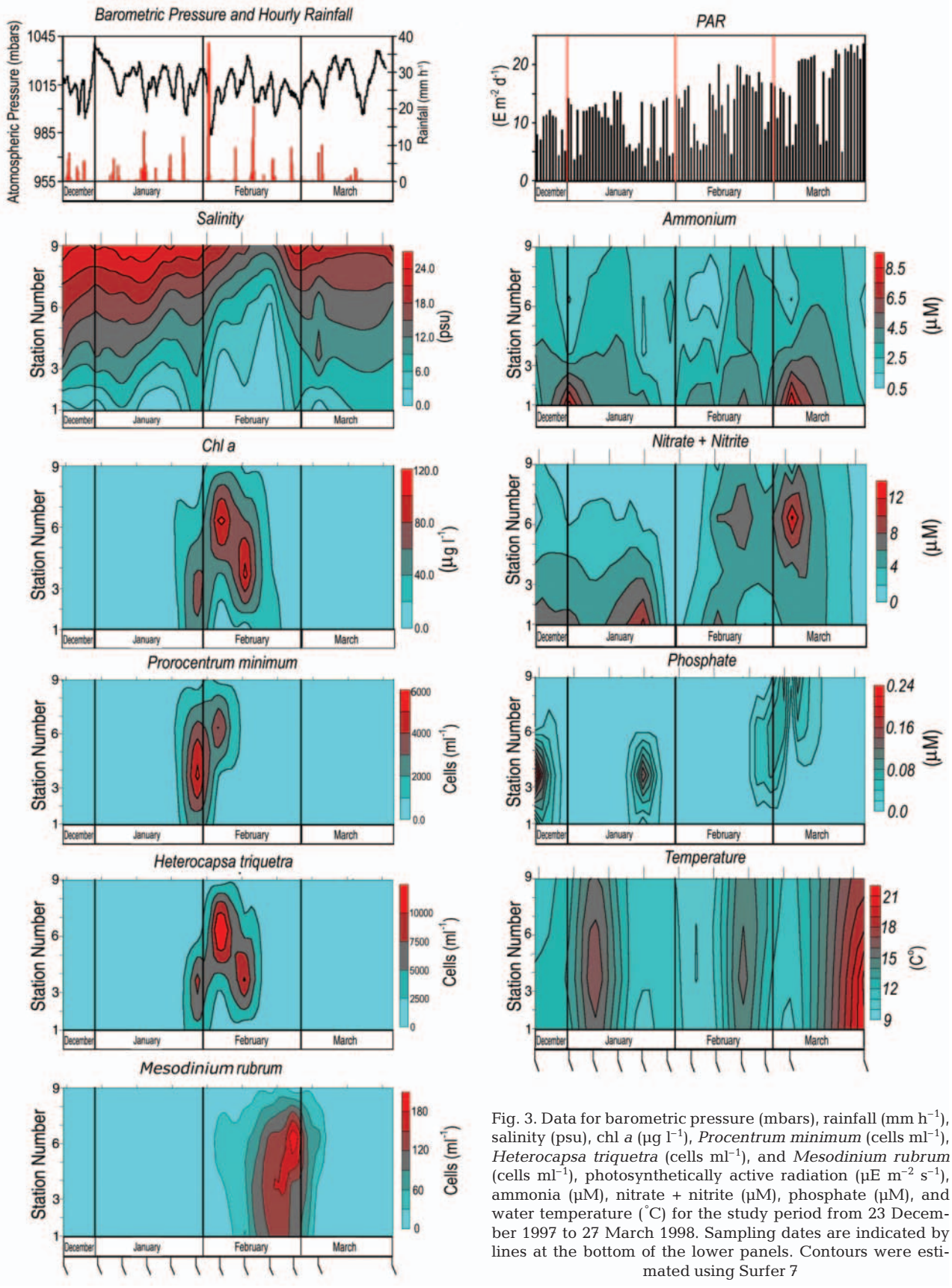

Fig. 3. Data for barometric pressure (mbars), rainfall (mm h^{-1}), salinity (psu), chl *a* (µg l^{-1}), *Procentrum minimum* (cells ml^{-1}), *Heterocapsa triquetra* (cells ml^{-1}), and *Mesodinium rubrum* (cells ml^{-1}), photosynthetically active radiation (µE m^{-2} s^{-1}), ammonia (µM), nitrate + nitrite (µM), phosphate (µM), and water temperature (°C) for the study period from 23 December 1997 to 27 March 1998. Sampling dates are indicated by lines at the bottom of the lower panels. Contours were estimated using Surfer 7

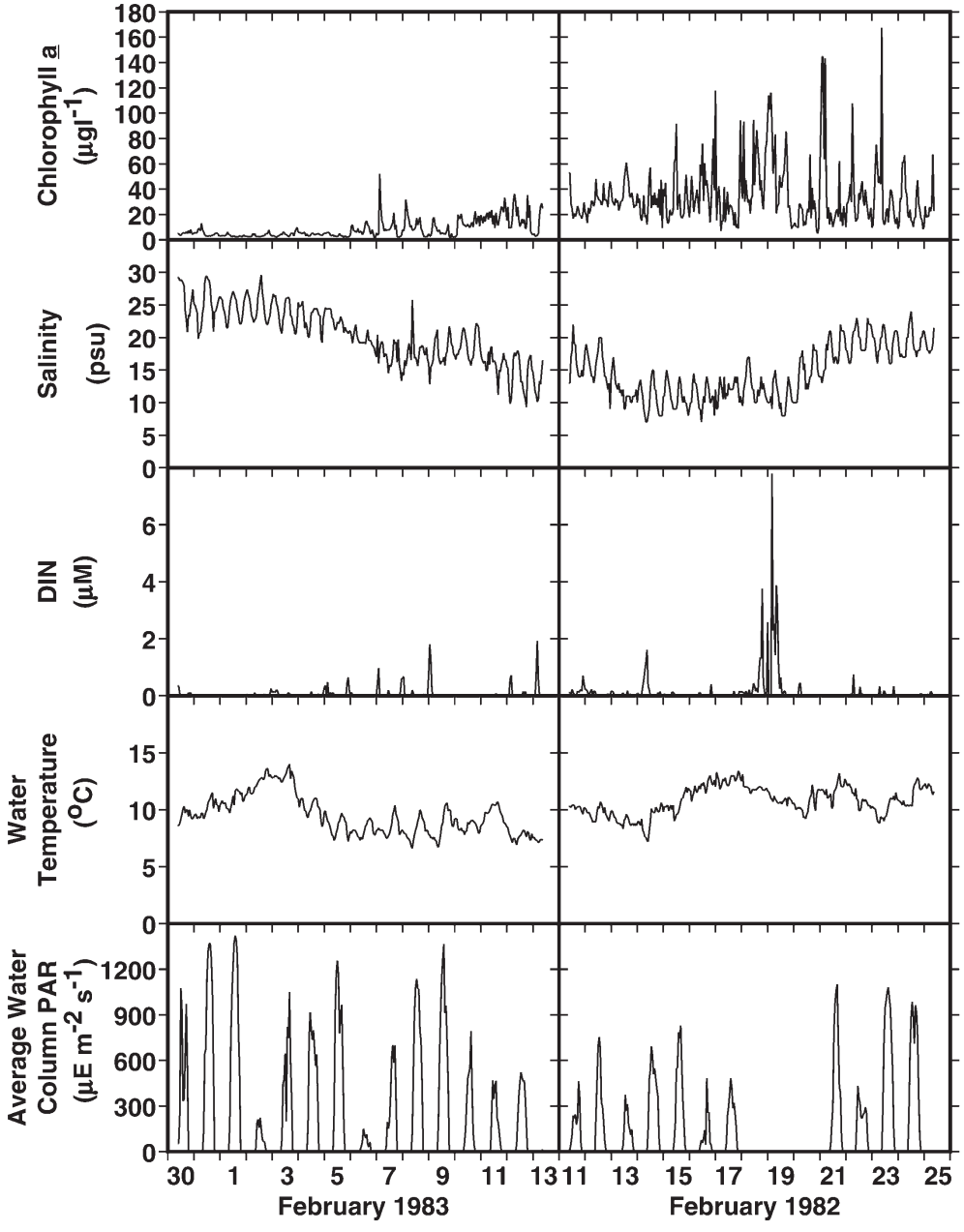

Fig. 4. High-resolution time series measured every hour for 2 wk at Stn 7 for the following variables: chl *a* (µg l^{-1}), salinity (psu), dissolved inorganic nitrogen (NO_3^- + NO_2^- + NH_4^+) µM, water temperature (°C), and average water column photosynthetically active radiation (PAR, µE m^{-2} s^{-1}). Sampling dates were from 11 February to 25 February 1982 and 30 January to 13 February 1983. The environmental conditions were very similar during late January and February of 1982 and 1983. To show the bloom progression more clearly, the data from the first 2 weeks in February 1983 were plotted before the data from the last 2 weeks in 1982

+ NO_2^- levels were elevated at Stns 6 and 7, which are opposite some of the larger creeks entering the estuary (Figs. 1 & 3). A small salinity anomaly during that same time period indicates the increased NO_3^- + NO_2^- inputs originated in one or more of the local creeks. Inorganic phosphate concentrations were generally below detection (<0.2 µM) during all 3 studies due to a net uptake of PO_4^{3-} by the sediments during winter in North Carolina estuaries (Kuenzler et al. 1977).

In each study, the winter dinoflagellate bloom started in mid-January and was initially dominated by a mixture of *Heterocapsa triquetra* and *Prorocentrum minimum*. By early February, the bloom was essentially monospecific for *H. triquetra* (Fig. 3). On average, the *H. triquetra* blooms required approximately 2 to 3 wk to develop. All 3 blooms were preceded by a drop in the average salinity and an increase in inorganic nutrient input (Figs. 3 & 4). During each study period, the highest chl *a* concentrations were located in the intermediate salinity section of the estuary. The steep salinity gradient in this mesohaline region represents a frontal zone, where dispersion rates are lower than in the upper and lower

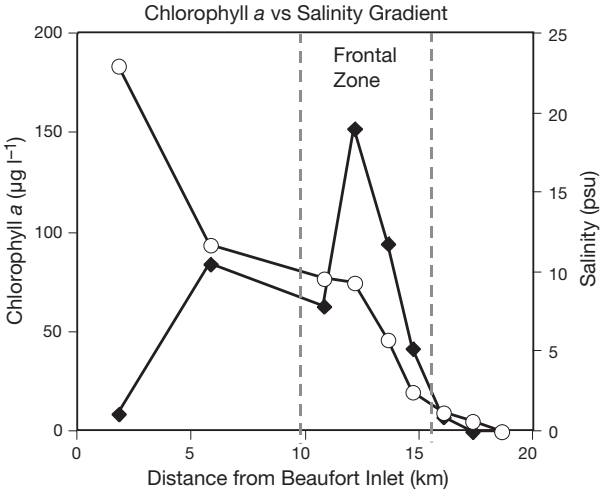

Fig. 5. Chl *a* (µg l^{-1}) and salinity (psu) gradients plotted at each station (Fig. 1) for the transect of the estuary made on 6 February 1998 when the *Heterocapsa triquetra* bloom was maximally developed. ◆ = chl *a*, ○ = psu. The frontal zone is bracketed by the 2 vertical lines

portions of the estuary (Figs. 1 & 5). The relationship between chl *a* concentrations and the mesohaline structure was evident during all of the 1982 fixed point time-intensive series and in the later part of the 1983 series (Fig. 4). During these periods, chl *a* levels varied dramatically over a tidal cycle as the chl *a* maximum moved back and forth past the study site (Figs. 4 & 5). In each study, the overall bloom progression can be seen as changes in the mean chl *a* levels with time. Maximal chl *a* concentrations at the height of the February 1982 bloom were in excess of 100 µg l^{-1} and occurred when salinities were between 7 and 20 psu and at temperatures between 7 and 14°C. The samples taken during February 1983 represented the pre-bloom and bloom initiation periods and were generally far less than 35 µg l^{-1}. During the spatially intensive study (1997 to 1998), chl *a* concentrations at the height of the *H. triquetra* bloom again exceeded 100 µg chl *a* l^{-1} and were located in a mesohaline patch that ranged from 6 to 18 psu (Fig. 3). Chl *a* levels during the *H. triquetra* bloom typically exceeded those at any other time of the year (Fig. 2).

Macrozooplankton and microzooplankton abundances were estimated during the 1997 to 1998 study. The dominant macrozooplankton species capable of consuming *Heterocapsa triquetra* was the copepod *Acartia tonsa*. *A. tonsa* densities were estimated to be 642 to 832 individuals m^{-3} and agree with the wintertime copepod densities of <1000 m^{-3} determined previously for the Newport River estuary (Fig. 2; Fulton 1984a,b) and other nearby estuaries (Mallin & Paerl 1994). Adult female *A. tonsa* isolated at the peak of the *H. triquetra* bloom were used for grazing experiments with ambient concentrations of *H. triquetra* (5 to 7 × 10^6 cells l^{-1}). Ingestion rates ranged from 605 to 1400 *H. triquetra* cells copepod^{-1} h^{-1} and corresponded to filtration rates of 0.09 to 0.24 ml copepod^{-1} h^{-1} (Fig. 6). Using these grazing estimates and a copepod abundance of ~1 copepod l^{-1}, *A. tonsa* could graze approximately 1% of the *H. triquetra* cells d^{-1} during the bloom. Decreasing filtration rates with increasing food concentrations indicated the copepods were food-saturated and unlikely to feed continuously at the maximal rate.

The dominant microzooplankton grazers were primarily tintinnids (average 94.3 ± 6.6 µm in length) and oligotrichs (average 38.1 ± 12.8 µm in length). Rotifers were rare. Combined tintinnid and oligotrich densities ranged from ~200 to 3500 individuals l^{-1} (Table 1). Tininnids made up >90% of the microzooplankton assemblage in most of the samples, though there were a few stations where oligotrichs constituted as much as 80% of the population. Tintinnid grazing rates on *Heterocapsa triquetra* can be as high as 15 cells h^{-1}, but are more typically in the range of 0.7 to 3 cells h^{-1} (Stoecker & Evans 1985). Using the observed densities, and assuming a relatively high ingestion rate of 3 cells h^{-1}, microzooplankton would only be capable of removing between 0.04 and 4% of the *H. triquetra* bloom population per day.

During the 1997–1998 field study, *Heterocapsa triquetra* was observed engulfing whole *Prorocentrum minimum* through an opening in the sulcul region. This ingestion was accompanied by an increase in width and length of the *H. triquetra* cells. The average cell volume changed from 2168 ± 1192 µm^3 on 16 January 1998 when the *H. triquetra* bloom was just beginning, to 3432 ± 1253 µm^3 on 6 February 1998 at the height of the *H. triquetra* bloom, to 3197 ± 1262 µm^3 on 20 February 1998 when few *P. minimum* cells remained. This increase in volume of *H. triquetra* cells was accompanied by a significant increase in the % of the population with lengths and widths exceeding 25 µm

Table 1. Microzooplankton abundances (tintinnids and oligotrich ciliates) (l^{-1}) measured at 9 sampling stations in the Newport River estuary, North Carolina, on 30 January, 13 February and 27 February 1998

Stn	30 Jan	13 Feb	27 Feb
1	1300	400	2160
2	380	200	720
3	1480	800	600
4	640	480	520
5	400	600	280
6	800	1480	1120
7	1840	2760	440
8	1160	3040	680
9	1480	3360	1600

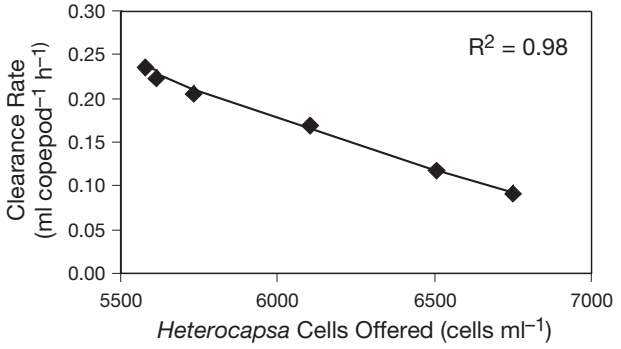

Fig. 6. Clearance rates (ml copepod^{-1} h^{-1}) of the dominant copepod *Acartia tonsa* feeding on ambient concentrations of *Heterocapsa triquetra* from February 1998 in the Newport River estuary, NC

(Fig. 7). The average cell volume increased by 58% from the pre-bloom to bloom period.

The succession of dominant phytoplankton groups during the winter was estimated by HPLC pigment analysis of samples taken during the 1997–1998 study (Fig. 8). The assemblage was initially dominated by cryptophytes (as indicated by alloxanthin), cyanobacteria (zeaxanthin), and diatoms (fucoxanthin). Starting in late January, a bloom of *Prorocentrum minimum* and *Heterocapsa triquetra* began. This dinoflagellate bloom (seen as peridinin in Fig. 8) was initially dominated by *P. minimum*, but by the first week in February, *H. triquetra* was the most abundant species (Fig. 3). The *H. triquetra* bloom declined in mid- to late February and was followed by a bloom of the ciliate *Mesodinium rubrum*. The *M. rubrum* bloom (alloxanthin from endosymbiotic cryptophytes) was followed in mid- to late March by a sudden increase in the diatom population (as indicated by fucoxanthin) as water temperatures began to rise (Figs. 3 & 8).

DISCUSSION

Atmospheric forcing in the form of low temperatures and strong frontal systems moving through coastal regions at 3 to 4 d intervals creates a seasonal niche favorable to *Heterocapsa triquetra* blooms during winter in temperate estuaries. *H. triquetra* exploits these conditions and out-competes co-occurring species, even though some of the prevailing conditions, such as temperature and light, are suboptimal for phytoplankton growth (Hobbie 1971, Hobbie et al. 1972, Campbell 1973, Kuenzler et al. 1979, Lapennas 1980, Palumbo 1982, Pfaender & Paerl 1984, Stanley & Daniel 1985, Litaker et al. 1993, Mallin et al. 1991, Tester et al. 1995). How *H. triquetra* exploits and responds to the various environmental conditions is discussed below.

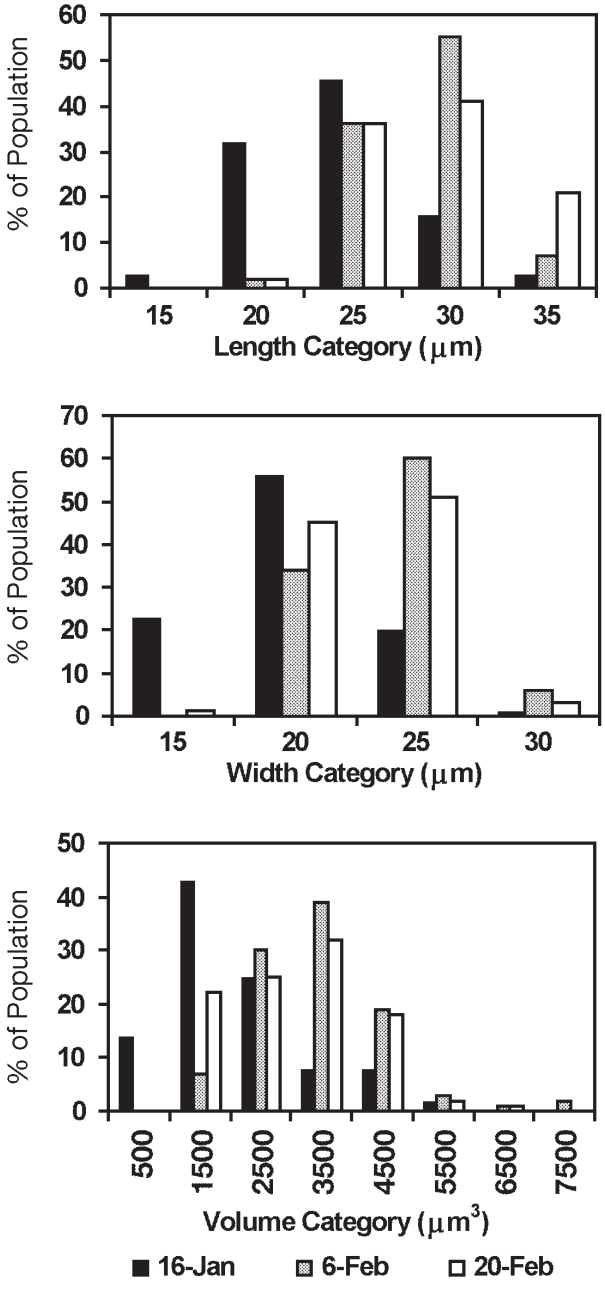

Fig. 7. *Heterocapsa triquetra* size (length and width) and volume changes during the course of the 1997 to 1998 bloom reflect the shift from phototrophy to mixotrophy. The percentage of the cells in the *H. triquetra* population that were in various width, length, or volume size classes change from 16 January - ■ (early bloom), 6 February - ■ (full bloom development), and 20 February 1998 - □ (declining bloom)

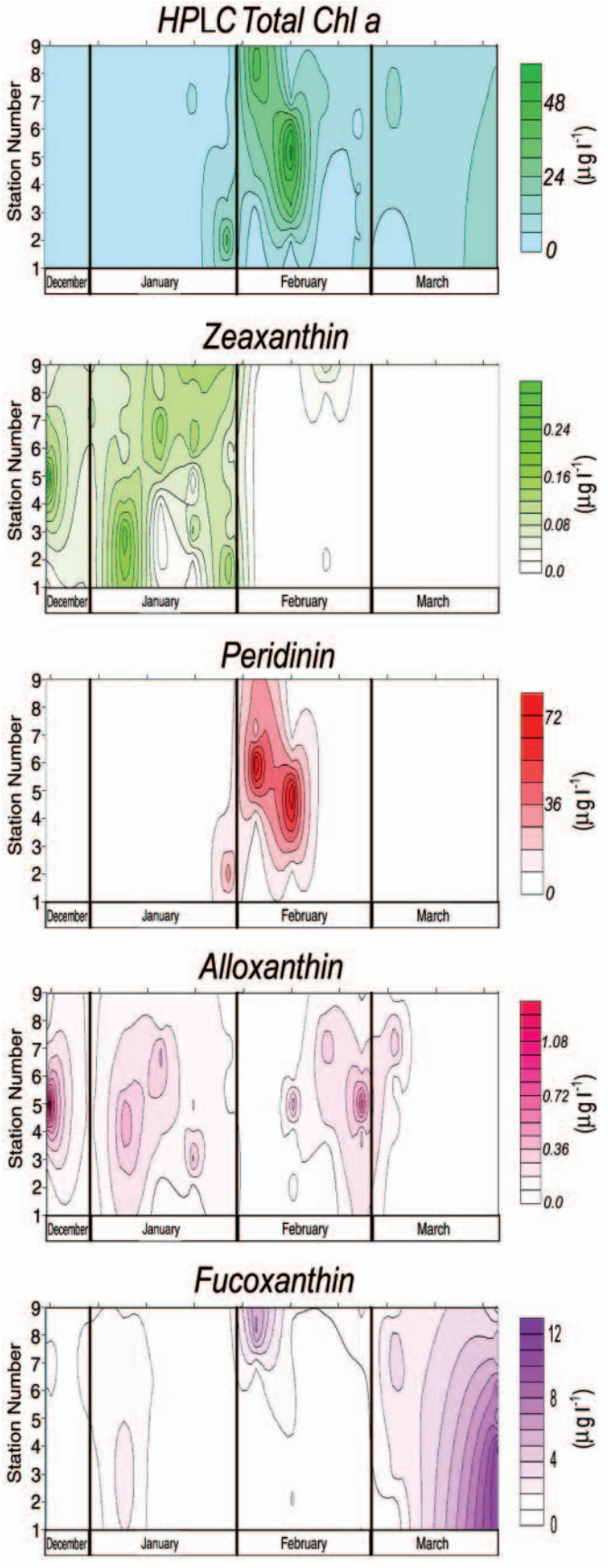

Fig. 8. Succession of dominant phytoplankton groups as determined by HPLC pigment analysis. A total of 109 samples from all the 1997 to 1998 sampling stations were analyzed. The diagnostic pigments included zeaxanthin (cyanobacteria and rhodophytes), peridinin (dinoflagellates), alloxanthin (cryptophytes), and fucoxanthin (contributed by diatoms in this season). The chl *a* measured by HPLC does not include chlorophyllide or chl c_1, c_2 or c_3 as does the fluorescence technique used to determine chl *a* in Fig. 3. This accounts for the difference in the amount of chl *a* reported (Figs. 3 & 8). However, the patterns of abundance are the same. Pigment concentrations are reported in µg l^{-1}. Contours were estimated using Surfer 7

Abiotic factors associated with atmospheric forcing and frontal systems (rainfall, light, nutrient inputs, salinity regime, and a runoff-induced frontal zone)

The passage of strong wintertime low pressure systems affects a suite of abiotic factors, including rainfall, nutrient loading, and the prevailing light and salinity regimes. Specifically, as low pressure systems move through the area at 3 to 4 d intervals, they are associated with regular rainfall events that frequently exceed 50 mm d^{-1} (Fig. 3). These rainfall events coincide with the coldest part of the year (<12°C), when evapotransporation rates are suppressed (Fig. 2). Even though rain falls equally in the winter and summer, significantly greater runoff occurs in the December to March period than at any other time of the year, excluding hurricane runoff events (Thornwaithe & Mather 1957, Kuenzler et al. 1977; Fig. 2). Higher runoff elevates nutrient inputs into the system and produces mesohaline conditions throughout much of the estuary (Figs. 3 & 4).

The passage of low pressure systems is also associated with the increased cloud cover that transiently reduces PAR relative to other times of the year (Litaker et al. this volume). Low PAR in combination with an average 9 h day length versus a 16 h day length in midsummer produces the lowest incident light levels of the year. *In situ* growth rate studies conducted during the 1983 time-intensive study indicate that *Heterocapsa triquetra* blooms undergo transient day to day light limitation due to increased cloud cover (Litaker et al. 2002). The transient light limitation, however, does not affect bloom formation, indicating that *H. triquetra* is well adapted to low light conditions.

Inputs of nitrate, and to a lesser extent ammonium, appear to be crucial for *Heterocapsa triquetra* bloom formation (Hobbie et al. 1972, Harrison & Hobbie 1974, Hobbie & Smith 1975, Kuenzler et al. 1977, 1979, Lapennas 1980, Stanley & Daniel 1985, Marshall & Alden 1990, Mallin et al. 1991). Major runoff events are most frequent from November to March in the North Carolina coastal plain, with maximal runoff and inorganic nutrient inputs occurring in late January to early

March (Hobbie 1970, Kuenzler et al. 1977; Fig. 2). The *H. triquetra* blooms tend to occur during the January to early March period. There are, however, occasional years when the winter conditions are unusually warm and dry, and mean daily air temperatures seldom drop below 14°C. Under these conditions, nutrient inputs are severely curtailed, and the *H. triquetra* bloom either fails to develop or is significantly reduced relative to years when normal runoff occurs (Mallin et al.1991).

Heterocapsa triquetra is physiologically well suited to take advantage of episodic nutrient inputs. It possesses a high NO_3^- uptake and assimilation capacity and readily takes up NH_4^+ (Harrison 1973). Uptake rates of NO_3^- are nearly the same in the dark as in the light, even when the cells are nutrient replete (Paasche et al. 1984). *H. triquetra* is also capable of producing high levels of the extracellular enzyme alkaline phosphatase, allowing it to escape P limitation, which transiently occurs in late winter or early spring in North Carolina estuaries (Thayer 1971, Kuenzler et al. 1979, Rudek et al. 1991).

Heterocapsa triquetra's ability to respond to episodic N inputs was best documented by the work of Lapennas (1980). She studied the demographic characteristics of over 30 phytoplankton species in the South River estuary, North Carolina (34° 58′ N, 76° 35′ W), over a 2 yr period. *H. triquetra* was the most consistent bloomer of any species studied relative to the number of cell divisions needed to reach bloom concentration. It was observed to be the dominant or co-dominant bloom species on 22 occasions during the course of the study. These blooms all occurred in the winter or early spring and were associated with episodic N inputs following runoff events. On average, 2 to 3 wk and 7 cell divisions were required for *H. triquetra* to reach bloom concentrations, defined as >50 µg C l^{-1}. A 2 to 3 wk estimate for bloom formation is consistent with the development period observed in this study (Figs. 3 & 4).

The input of NO_3^--rich water, though essential for *Heterocapsa triquetra* bloom development, is not always sufficient to trigger bloom formation. For example, Harrison (1973) found that salinities decreased and nutrient inputs increased more than a month before *H. triquetra* began to bloom in the Pamlico River estuary. Indeed, NO_3^- and NH_4^+ inputs are often abundant in November, yet most of the blooms in the Pamlico River (Harrison 1973), South River (Lapennas 1980), and Newport River estuaries are restricted to the early January to March period.

A secondary benefit of the increased runoff is the production of a large mesohaline region in the estuary favorable to growth. Ecologically, *Heterocapsa triquetra* is often classified as a mesohaline species (Marshall & Alden 1990), even though it is functionally euryhaline. In culture, *H. triquetra* grows at salinities ranging from <5 to >45 psu (Braarud 1961). *H. triquetra*'s tolerance for a broad range of salinities is further supported by blooms reported from waters with salinities as low as 3 to 4 psu (Hobbie 1971, Hobbie et al. 1972, Kuenzler et al. 1979) and as high as 35 psu (Pieterse & Van der Post 1967). Under optimal nutrient and light conditions, *H. triquetra* can achieve >80% of maximal growth over a salinity range of 10 to 30 psu, with maximal growth occurring between 15 to 20 psu (Braarud & Pappas 1951). The salinity regimes during this study were generally between 5 to 25 psu and were often within the range reported for optimal growth (Figs. 3 & 4).

The mesohaline region also represents a frontal zone, where dispersion is reduced relative to the river flushed uppermost portions of the estuary and the tidally flushed lower estuary (Hyle 1976; Figs. 1, 3 & 6). It was in this region where the *Heterocapsa triquetra* blooms were found to reach their fullest development (Figs. 3, 4 & 6). Accumulation of cells in excess of maximal measured growth rates during the 1997–1998 study indicate that *H. triquetra* was physically concentrated in this zone (Litaker et al. this volume). *Prorocentrum minimum* (= *P. mariae-lebouriae*) and *Mesodinium rubrum*, species that were prominent in the mesohaline frontal region before and after the *H. triquetra* bloom, are also known to concentrate along frontal zones with sharp nutriclines or salinity gradients (Tyler & Seliger 1978, Lindholm & Mork 1990). In Chesapeake Bay, the accumulation of *H. triquetra* along frontal zones is so pronounced that these blooms are visible on satellite images (Tyler & Stumpf 1989).

Frontal zones, functionally analogous to those in the Newport River estuary, are also found during the winter in the lateral sub-estuaries of the nearby Albemarle-Pamlico estuary, NC (35° 21′ N, 76° 32′ W), the largest lagoonal estuary in the US. Blooms in the sub-estuarine systems form as follows. *Heterocapsa triquetra* begins to bloom in late January in the uppermost portions of the river systems as winter runoff increases. This runoff generally continues to increase through February and into March. As a consequence, the bloom is pushed into the middle portions of the estuary, where the water entering the main channel of the estuary is relatively fresh and carries large inputs of nutrients (Hobbie 1971, Kuenzler et al. 1979). This nutrient-rich water moves laterally into the peripheral sub-estuaries forcing a limited 2 layer flow circulation with sharply defined salinity gradients (Lapennas 1980, Ustach et al. 1986). *H. triquetra* is positively phototactic and can migrate in such a way as to exploit these flow regimes to maintain higher than expected population densities (Braruud & Pappas 1951, Pietrese & Van der Post 1967, Anderson & Stolzenbach 1985, Lindholm & Nummelin 1999). As a result, *H. triquetra* densities commonly exceed 1×10^8 cells l^{-1} (chl *a* con-

centrations >250 µg l^{-1}) in these sub-estuaries. Higher dilution rates in the main channel of the estuary during the same bloom periods limit the corresponding *H. triquetra* cell densities to ~1 to 5×10^6 l^{-1} (Hobbie 1971).

Heterocapsa triquetra blooms also can develop as aggregations at stable thermohaline boundaries. These boundaries represent a rich source of inorganic nutrients and have stability properties favorable to *H. triquetra* accumulation. Kononen et al. (2000) for example observed intense blooms of *H. triquetra* localized in 0.2 to 5 m thick layers 20 to 40 m below the surface of the water at the entrance to the Gulf of Finland in July 1998. Horizontal patch sizes were generally in the order of 1 km. In every case, the densest concentrations of *H. triquetra* were located at the sharpest part of the nitrocline. Given the strong swimming ability of *H. triquetra*, it was presumed that these bloom concentrations simply represented *H. triquetra* behaviorally aggregating in order to take up nutrients before migrating higher in the water column, where they began active photosynthesis upon exposure to surface illumination.

Low temperatures impose growth limitation on *Heterocapsa triquetra* and potential grazers (copepods, cilitates, juvenile fish, ctenophores, and benthic filter feeders)

The primary negative effect imposed on *Heterocapsa triquetra* by low temperatures is severe growth limitation. *H. triquetra* has a broad temperature growth optimum, with rates >0.45 d^{-1} observed from 15 to 26°C, and maximal rates of between 0.55 and 0.69 d^{-1} occurring at 19 to 20°C (Braarud & Pappas 1951, Yamochi 1984, Chang & Carpenter 1988). However, below 15°C, maximal *H. triquetra* growth rates decline rapidly from 0.4 d^{-1} at 15°C, to 0.1 d^{-1} at 10°C. Cell division ceases altogether at 4 to 5°C. The significantly lower growth rate below 15°C is also supported by field data. Minimal daily *in situ* growth rates for *H. triquetra* estimated during the 1983 study varied from 0.02 to 0.14 d^{-1} over a 7.6 to 12.0°C temperature range (Litaker et al. 2002). Each of the observed *H. triquetra* blooms occurred when average daily water temperatures were generally <12°C, and often <10°C. Despite the severe growth limitations imposed by these low temperatures, blooms were still able to develop over a 2 to 3 wk period (Figs. 2, 3 & 4).

In contrast to the negative effects on *Heterocapsa triquetra* growth, low ambient water temperatures limited macro- and microzooplankton abundance, thereby reducing grazing losses. Both *H. triquetra*'s size (~17 × 26 µm) and palatability make it an excellent food source for copepods (Uye & Takamatsu 1990) and many common ciliate species (Gifford 1985). Copepod population densities estimated in the 1997–1998 study were 1000-fold lower than in the summer, when copepods can remove up to 25% of the phytoplankton biomass as chl *a* day^{-1} (Stearns et al. 1987). Approximately 1% of the *H. triquetra* cells d^{-1} were grazed by *Acartia tonsa*, the dominant macrozooplankter present during this study.

There is a parallel argument for reduced microzooplankton grazing during these winter blooms. Microzooplankton grazing rates often exceed those of macrozooplankters, particularly when water temperatures are elevated and the average cell size is <10 µm (Burkhill et al. 1987, Litaker et al. 1988). In contrast, during winter in temperate estuaries, microzooplankton concentrations are generally too low to graze significant numbers of phytoplankton cells, although there are exceptions to this general trend (Verity 1986, Sanders 1987, Baird & Ulanowicz 1989, Mallin 1991, Kamiyama 1994, 1997, Gallegos & Jordon 1997). The microzooplankton assemblage measured during the spatially intensive study (1997 to 1998) was dominated by tintinnids and oligotrichs. The tintinnid/oligotrich cell concentrations ranged from ~200 to 3500 individuals l^{-1} (Table 1). These population densities, like those of the macrozooplankton grazers, were too low to cause significant gazing losses in the Newport River estuary. Similarly, low grazing losses during dinoflagellate blooms have been reported by Sellner & Brownlee (1990) in the Chesapeake Bay.

Juvenile Atlantic menhaden *Brevortia tyrannus* are the only major species of planktivorous fish present in the estuary between December and March, but they are not capable of reducing *Heterocapsa triquetra* numbers substantially. Menhaden have an unusual life history in that the early larvae feed only on zooplankton, but during metamorphosis increase their capacity to retain smaller phytoplankters. The adults are plantivores and their distribution is positively correlated with the abundance of microflagellates, diatoms, and to a limited extent, dinoflagellates (Friedland et al. 1989). The switch from feeding on zooplankton to becoming filter feeders occurs as the larvae increase in size from about 30 to 45 mm fork length (FL) (June & Carlson 1971, Govoni et al. 1983). The average size of menhaden that migrate into the Newport River estuary from offshore between December and early March, however, is between 23 to 30 mm FL (Warlen 1994). Hence, most of the larval menhaden are too small to be effective filter feeders during the period when the *H. triquetra* bloom occurs. Furthermore, the abundances of menhaden larvae in the Newport River estuary between December and early March is in the order of 7 to 8 per 100 m^3 (Warlen 1994), far too low to significantly impact phytoplankton standing stocks.

Ctenophores were also observed during the study, and were particularly abundant during several weeks of the bloom. However, they, like the juvenile menhaden, are not capable of grazing particles the size of *Heterocapsa triquetra* either (Stoecker et al. 1987). If anything, grazing by ctenophores on zooplankton would further reduce grazing pressure on *H. triquetra* (Robertson 1983). The only other members of the estuarine community with the potential to remove significant amounts of phytoplankton are benthic filter feeders. However, water temperatures <12°C can severely limit filtration and growth rates, rendering them incapable of removing significant quantities of phytoplankton (Grizzle et al. 2001).

Success strategies: cysts and mixotrophic nutrition

Resting cysts, keyed to the annual temperature cycle, may be important in controlling the timing of *Heterocapsa triquetra* bloom formation. Yamochi & Joh (1986) studied the effects of temperature on the excystment of 7 species of red tide algae found in the sediments of Osaka Bay, including *H. triquetra*. They examined the hypothesis of Anderson & Wall (1978) that a close correlation exists between germination of benthic cysts and initiation of certain dinoflagellate blooms. At incubation temperatures <10°C, *H. triquetra* germinated in 56 to 94% of the sediment samples. Very few of the samples incubated >20°C contained *H. triquetra*, and none of the samples incubated >23°C produced vegetative cultures. The appearance of *H. triquetra* was attributed to the germination of benthic cysts and not the growth of vegetative cells sequestered in the sediments. During the same period, *H. triquetra* was abundant in the water column only at temperatures <15°C as is commonly the case in the Newport River estuary. Whether a similar excystment occurs in the Newport River estuary is unknown because cyst densities there were not measured. However, *H. triquetra* hypnocysts have been reported for the nearby South River (Lapennas 1980) and Gales Creek estuaries (Campbell 1973). Evolution of cyst germination timed to the annual temperature minimum, or slightly higher, would allow *H. triquetra* to take advantage of the recurrent wintertime conditions formed by atmospheric forcing in many temperate estuaries. Temperature regulated excystment could also account for the fact that blooms often lag the initial input of nutrients into the estuary by more than a month.

Laboratory studies have shown that *Heterocapsa triquetra* grew phototrophically when sufficient inorganic nutrients were available, but fed mixotrophically when nutrients became limiting (Legrand et al. 1998). The switch to mixotrophy was characterized by a 61 to 64% increase in average cell volume. In contrast, nutrient-starved cells in the absence of available phytoplankton prey actually decreased in size. Mixotrophic feeding provided a means for nutrient-depleted cells to meet their N and P demands. In the 1997–1998 study, *H. triquetra* began consuming *Prorocentrum minimum* cells once the bloom became established. The switch to mixotrophy was accompanied by a 58% increase in cell volume. Nutrient depleted *H. triquetra* cells ingest 0.2 to 0.4 algal cells d^{-1} in laboratory studies, implying grazing rates in the field were significant when *H. triquetra* cell numbers exceeded 2000 cells ml^{-1}. Interestingly, laboratory studies of *P. minimum*, the primary food source available to *H. triquetra* during the bloom, showed that this species also switched to mixotrophic consumption of co-occurring phytoplankton when nutrients became limiting (Stoecker et al. 1997). The consumption of dinoflagellate blooms by other dinoflagellates may therefore be relatively common in estuarine and near shore regions (Jeong 1999, Jeong et al. 1999). An ancillary benefit of mixotrophy is the reduction of co-occurring species that compete for similar resources (Thingstad et al. 1996).

Changes in the phytoplankton community structure reported during other *Heterocapsa triquetra* blooms also suggested that this species frequently resorted to mixotrophy. At the start of these blooms, *H. triquetra* almost always co-occurred with 1 or more of the following dinoflagellate species: *Alexandrium tamarense*, *Ceratium fusus*, *Gonyaulax spinifera*, *Gonyaulax* sp., *Karoldinium micrum* (= *Gymnodinium galatheanum*), *Gyrodinium aureolum*, *Katodinium rotundatum*, *Prorocentrum micans*, *Prorocentrum minimum*, *Protoperidinium* sp., or *Scrippsiella trochoidea* (Marshall 1967, Pieterse & Van Der Post 1967, Anderson et al. 1983, Stoecker et al. 1983, Anderson & Stolzenbach 1985, Lee & Yoo 1990, Marshall & Alden 1990, Mallin 1994, Akselman 1996). The association between *H. triquetra* and *P. minimum* was particularly strong. As these blooms progressed, however, the community often changed with *H. triquetra* becoming numerically dominant.

Fate of the *Heterocapsa triquetra* bloom?

The decline of a phytoplankton bloom can be caused by either single or concomitant factors including dilution, grazing or disease. The only data in this study from a bloom decline comes from the 1997 to 1998 period. In this instance, washout appeared to be the major factor responsible for the bloom decline. A large drop in salinity, associated with a significant runoff event, coincided with a sharp decline in *Heterocapsa*

triquetra cell numbers (Fig. 3). Besides reducing *H. triquetra* cell numbers, the runoff event supplied new nutrients to the system. *H. triquetra*, however, did not respond with renewed growth (Figs. 3 & 8). One possibility for *H. triquetra*'s lack of response is that the cells were already senescing after a period of nutrient depletion indicated by the switch to mixotrophy.

Studies of other *Heterocapsa triquetra* blooms from different North Carolina estuaries indicated that these blooms all declined abruptly. Often this decline occurred by mid- to late February, with blooms seldom lasting beyond mid-March or the first week in April as water temperatures reached 17 to 19°C (Hobbie 1971, Hobbie et al. 1972, Carpenter 1973, Kuenzler et al. 1979, Tester et al. 1995). Though the general period when the blooms declined was fairly similar, the causes appeared variable. Sometimes the bloom decline was directly correlated with decreased inorganic N input. This typically occurred when runoff declined as evapotranspiration rates accelerated with warming air temperatures. Indeed, in extremely dry years, when the nutrient input dropped below a critical threshold, the *H. triquetra* blooms failed to materialize (Mallin 1994).

Other studies, however, have documented the demise of *Heterocapsa triquetra* blooms while nutrient and temperature conditions were apparently still conducive to growth (Mallin et al. 1991, Rudek et al. 1991). Since these declines are not likely due to grazing as discussed above, there must be other reasons for *H. triquetra* bloom termination. Typically the decline of a dinoflagellate bloom, when environmental conditions are favorable for growth, is generally attributed to either cyst formation (Anderson et al. 1983) or disease (Wommack & Colwell 2000). There is evidence that *H. triquetra* has cysts that germinate at low temperatures, which may help initiate bloom formation. However, whether *H. triquetra* is capable of forming cysts when conditions are still favorable for growth is not known.

The role of viruses or bacteria in limiting *Heterocapsa triquetra* blooms is similarly unknown. However, there is mounting evidence suggesting that common viral and bacterial diseases can quickly spread through a phytoplankton population causing rapid cell death (Wommack & Colwell 2000). To the extent that this is true, these pathogens will play a critical role in the overall structuring and functioning of marine food webs (Proctor 1997, Guixa-Boixereu et al. 1999).

Fate of the carbon fixed by the *Heterocapsa triquetra* bloom?

The *Heterocapsa triquetra* bloom represents large quantities of highly utilizable carbon. Up to 50% of the annual C fixation in North Carolina estuaries can be attributed to the winter dinoflagellate blooms dominated by *H. triquetra* (Paerl et al. 1998, Pinckney et al. 1998). Studies in the Chesapeake Bay indicate that most of the C from *H. triquetra* and other dinoflagellate blooms was metabolized before reaching the sediments (Sellner et al. 1991, 1993). Given that macro- and microzooplankton grazing was negligible during the bloom, it was unlikely that the large amount of C contained in the winter dinoflagellate bloom was transferred directly to higher trophic levels. Instead C, N, and P were probably being cycled indirectly to higher trophic levels through the microbial loop (Riemann et al. 2000).

Heterocapsa triquetra in the context of seasonal succession

The succession of the winter phytoplankton community was evident from HPLC pigment analyses (Fig. 8). The assemblage was dominated by cryptophytes and picoplanktonic cyanobacteria from late December to late January, when chl *a* levels were <10 µg l^{-1}. Salinities were generally declining during this period, indicating increased nutrient inputs. Cryptophytes in particular increased during mid-January. Similar increases in cryptophyte abundance in response to runoff events have also been documented for the nearby Neuse River estuary (Mallin et al. 1991). The cryptophyte community was then succeeded by a dinoflagellate community dominated by *Prorocentrum minimum* and to a lesser extent *Heterocapsa triquetra* in late January (Figs. 3 & 8). Recent studies have shown that *P. minimum* feeds mixotrophically, and has a preference for cryptophyte species (Stoecker et al. 1997). This raises the possibility that some of the decline in the cryptophyte assemblage was due to mixotrophic consumption as the *P. minimum* bloom developed.

An even more intense *Heterocapsa triquetra* bloom succeeded the *Prorocentrum minimum* bloom. This combined *H. triquetra*-*P. minimum* bloom is representative of the common wintertime dinoflagellate-dominated blooms that occur sometime between January and March. These blooms are a persistent feature of North Carolina estuaries (Pinckney et al. 1998). Evidence suggests that the decline in *P. minimum* numbers was due to the mixotrophic consumption by *H. triquetra*. The decline in *H. triquetra* abundance, in turn, was attributed to washout caused by a major runoff event (Fig. 3).

The next plankton species to dominate was the ciliate *Mesodinium rubrum*. This organism has an unusual nutritional ecology. It ingests cryptophytes and utilizes their chloroplasts to achieve extraordinarily

high rates of photosynthesis (Barber et al. 1969, Smith & Barber 1979, Gustafson et al. 2000). Presumably an assemblage of free-living cryptophytes benefited from the nutrient input during the washout event and began to grow (Figs. 3 & 8). Otherwise the increasing *M. rubrum* population would not have been able to acquire its requisite cryptophytes. The close correspondence between the cryptophyte pigment alloxanthin and the cell counts of *M. rubrum* indicated that a majority of the cryptophyte pigment was contained within *M. rubrum*.

In mid-March, the wintertime cryptophyte and dinoflagellate assemblages were succeeded by the spring diatom bloom, indicated by fucoxanthin (Fig. 8). This increase in diatom biomass was associated with the rapid increase in water temperatures that occurred in late March and appears to be a regular occurrence in North Carolina estuaries (Tester et al. 1995, Pinckney et al. 1998). The beginning of the annual increase in copepod abundances also coincides with this rapid increase in ambient temperatures (Fig. 2).

Heterocapsa triquetra: a dynamic model for harmful algal blooms (HABs)

While *Heterocapsa triquetra* is not a toxic algal species, many of the seasonal and environmental factors that allow it to form dense ($>10^6$ l^{-1}), nearly monospecific blooms in estuaries and coastal regions throughout the world (Kim 1997, Kononen et al. 1999, Lindholm & Nummelin 1999) are important to most harmful species as well. *H. triquetra* blooms are nutrient-driven and are identified with seasonal coastal dynamics similar to those proposed to promote the formation of *Alexandrium tamaranse* blooms in NE US waters (Keafer & Anderson 1993). Further, there is mounting evidence that nutrient inputs are required to sustain the extraordinarily high cell densities found during *Karenia brevis* (= *Gymnodinium breve*) blooms in the near shore waters of the eastern Gulf of Mexico (Vargo et al. 2000). *K. brevis*, like *H. triquetra*, is a superior nutrient competitor, capable of taking up both inorganic and organic nutrients (Steidinger et al. 1998). Like *H. triquetra*, *K. brevis* effectively adapts to low light conditions, so neither low ambient light conditions nor self-shading during a bloom significantly affects its growth. The *H. triquetra* bloom is driven by meteorological forcing events that alter the physical environment of the estuary in a manner favorable for bloom formation. Similar environmental forcing or circulation patterns are associated with the development of other HAB blooms including *Pseudo-nitzschia* spp. (Hickey 2000), *A. tamaranse* (Anderson et al. 2000) and *K. brevis* (Steidinger et al. 1993, Tester & Steidinger 1997). Finally, *H. triquetra* exploits seasonal niches to avoid grazing losses that would inhibit bloom formation. Other HAB species accomplish this by mucus production or being unpalatable (Turner & Tester 1997). Understanding the common conditions conducive to harmful algal bloom formation, as well as how individual harmful species in a successional series respond to a recurrent suite of biotic and abiotic factors, will provide greater predictive power as to when and where blooms are likely to occur.

SUMMARY

Late winter blooms of *Heterocapsa triquetra* in temperate estuaries are usually associated with low ambient water temperatures and atmospheric forcing events that produce extensive runoff. This runoff delivers inorganic nutrients to the estuary, reduces salinities, and creates frontal zones in the mesohaline portions of the estuary. Low pressure waves associated with the rain events that occur every 3 to 4 days also bring increased cloud cover that transiently light-limits *H. triquetra* growth. The low ambient water temperatures also suppress the growth of both macro- and microzooplankton grazers whose populations are at an annual low when *H. triquetra* blooms. *H. triquetra* effectively utilizes the nutrient inputs, mesohaline conditions, low grazing pressure, and favorable hydrodynamic conditions to bloom, despite suboptimal temperature and light conditions. As nutrients become depleted, *H. triquetra* switches to a mixotrophic feeding mode and begins to consume co-occurring algae to meet its nutritional needs. Mixotrophy has the added benefit of reducing competing algae.

Despite low levels of *Heterocapsa triquetra* being found throughout most of the year, there are several studies that indicate that *H. triquetra* has evolved a cyst that excysts at temperatures <10°C. Low temperature excystment would provide a seed population at exactly the right time to exploit the late winter conditions. A number of factors including dilution from high runoff, senescence, encystment, and viral diseases could be responsible for the decline of *H. triquetra* blooms. Evidence suggests that of all these possibilities, washout from a high runoff event in mid-February was primarily responsible for the 1997 to 1998 bloom decline (Fig. 3). The wintertime microzooplankton and macrozooplankton grazing rates were insufficient to significantly influence the succession of phytoplankton species. Hence, mixotrophic feeding relationships between the various phytoplankton groups, particularly dinoflagellates, may greatly influence species composition and the succession of various phytoplankton species during winter in temperate

region estuaries. The dynamics of *H. triquetra* blooms serve as a general model for dinoflagellate bloom development including harmful or toxic species.

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