PLANKTONIC TROPHIC TRANSFER IN AN ESTUARY: SEASONAL, DIEL, AND COMMUNITY STRUCTURE EFFECTS[1]

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Abstract. The high tertiary production of estuaries is largely supported by phytoplankton primary production. An important question thus concerns how much phytoplankton production enters the food web through planktonic grazing and what physical, chemical, or biological factors influence this trophic transfer. We conducted a 2-yr, diel investigation of planktonic trophic transfer and the factors influencing it in the Neuse River Estuary, North Carolina.

Zooplankton community grazing rates were generally lowest in winter and highest spring through late summer, ranging from 0.1 to 310 mL·L⁻¹·h⁻¹. There were few significant diel differences in community grazing rates. The overall daytime mean (± 1 SE) rate was 3.30 ± 0.62 mL·L⁻¹·h⁻¹ while the night mean rate was 3.07 ± 0.60 mL·L⁻¹·h⁻¹. Post-naupliar copepods were usually more abundant at night than day, but tintinnids were often more abundant by day, while total zooplankton, copepod nauplii, and rotifers displayed no significant diel abundance differences.

Community grazing was positively correlated with primary productivity and the abundance of total phytoplankton, centric diatoms, dinoflagellates, and the small centric diatom *Thalassiosira.* Community grazing was also positively correlated with upstream river flow and negatively correlated with salinity. However, there were no significant correlations with water temperature, nutrient concentrations, or grazer abundance variables.

On an annual basis, the zooplankton community grazed ≈38–45% of daily phytoplankton production. Planktonic trophic transfer was coincidentally greatest in late spring through summer, during the period when anadromous fish larvae migrating from the open ocean reach their estuarine primary nursery areas. The fish arrive when planktonic trophic coupling is strongest and depart in fall, when planktonic trophic transfer, zooplankton abundance, and phytoplankton productivity all decrease.

Key words: community; diel; estuary; food webs; grazing; phytoplankton; southeastern United States; trophic transfer; zooplankton.

INTRODUCTION

Areas of high fishery productivity are generally characterized by a combination of high primary productivity and short, efficient food chains. Examples of this are coastal upwelling zones, where large phytoplankton are often consumed directly by fish (Ryther 1969, Sheldon et al. 1977), and coral reefs, where many reef fish graze directly on macroalgae (Choate 1991, Russ 1991). Estuaries, while highly variable geologically and physically, are likewise areas of high biological productivity. They are of considerable value both ecologically (as primary nursery areas and breeding grounds for fish) and economically (as fin- and shellfishing areas). Phytoplankton primary production generates a flow of en-

ergy that moves up the food chain, and is a major source of food energy supporting tertiary production of estuarine systems (Day et al. 1989). Because of the ecological and economic value of estuaries, it is important to understand what factors control or alter the biological pathways along which the system's energy flows. Thus, an important question concerns how much of the phytoplankton production is consumed by the zooplankton, as opposed to what is removed by current, sedimentation, or grazing by benthic organisms. Depending on the system in question, a certain amount of the primary production can be rerouted through the microbial community (the microbial loop). However, in mesotrophic and eutrophic systems, a large proportion of the system's energy moves along the classical food chain of phytoplankton–zooplankton–fish (Fenchel 1988). Many studies assume the food web importance of phytoplankton–zooplankton trophic relations in estuarine systems, but rarely has this been directly measured at the community level.

One way of assessing the magnitude of planktonic

trophic transfer is to determine zooplankton grazing rates, preferably over a long-term, seasonal basis. In assessing grazing rates, it is important to obtain both day- and nighttime rates. One reason for this is the well-known phenomenon of diurnal vertical migration (in fresh, estuarine, and marine waters), in which certain zooplankton species or stages will remain at the bottom during either the day or night and move into the surface waters during the other period (Haney 1988). A lesser known phenomenon is periodicity in grazing by different life stages. For instance, adult stages of certain copepods will only feed in darkness or dim light (Paffenhofer 1971, Stearns 1986), whereas the naupliar stages may only feed during the light (Paffenhofer 1988). It is, therefore, important to obtain both day and night rates to determine more realistic daily grazing effects.

Most copepod grazing studies have been performed on adult females of a single species of interest. The likely reasons for this include ease of identification and manipulation and reduction of interference from non-target zooplankton taxa in the rest of the community. However, adult single-species studies ignore the effect of grazing by young stages of that organism, as well as other species in lower abundance, and small organisms such as rotifers and protozoans. In this investigation a goal was to examine the dynamics of grazing by the zooplankton community as a whole and utilize grazing rates to obtain a trophic level energy transfer perspective. Planktonic trophic level energy transfer experiments have rarely been performed in the field; generally, they have been conducted under semicontrolled mesocosm conditions (Mullin and Evans 1974, Roman et al. 1988), or estimated by other means (Ryther 1969). Community-level grazing studies have dealt primarily with microzooplankton, mainly protozoans (Heinbokel 1978, Capriulo and Carpenter 1980, Burkhill et al. 1987, Verity 1987, Gifford 1988, Gallegos 1989). Most of these analyses have involved zooplankton assemblages that have passed through a mesh of certain dimensions. These studies have generally not determined the grazing impact of larger species or larger life stages of the zooplankton community. In the present study the grazing impact of the zooplankton community associated with the classical planktonic food chain, organisms between 60 and 2500 μm in size, was considered to be the community of interest.

Phytoplankton community structure is important to higher trophic levels because it influences the efficiency of energy transfer between trophic levels. Phytoplankton that are easily grazed and assimilated by zooplankton enhance trophic efficiency (Porter 1977). Noxious, toxic, large, or otherwise inedible algae lead to inefficient zooplankton grazing and decreased trophic efficiency. In a planktonic system dominated by easily grazed and assimilated phytoplankton species, trophic efficiency should be high, which should contribute to greater secondary and tertiary production (Ryther 1969).

The objectives of this study were to measure zooplankton grazing rates in the lower Neuse River Estuary, over an extended period (2 yr) and relate its temporal variability to plankton community composition and physical–chemical characteristics of the water. Utilizing grazing rate data, carbon content of the phytoplankton community, and primary production rates, we assessed planktonic trophic transfer as the amount of daily primary production grazed by the zooplankton community. Finally, by defining the biotic, chemical, and physical factors affecting this trophic pathway, we hoped to provide information as to how future changes or disruptions of these factors will ultimately affect energy flow in this estuarine system.

Site description

The Neuse River Estuary is the major southern tributary of North Carolina's Pamlico Sound (Fig. 1). It drains a watershed of $\approx 16\,000$ km^2 and is the recipient of considerable nutrient loading from a variety of sources including agricultural runoff, industrial discharge, and municipal wastewater treatment plants (Paerl 1987, Christian et al. 1991). The lower estuary can be considered a mesohaline, mesotrophic system that becomes eutrophic at times, depending upon meteorologic conditions. Years when rainfall is high exhibit increased nutrient loading into the system, leading to increased phytoplankton productivity (Mallin et al. 1993). Mean phytoplankton carbon production from three stations during a moderate flow year (1990) was 290 g/m^2 while in a high flow year (1989) it was 340 g/m^2 (Paerl et al. 1990, Mallin et al. 1991). This is a comparatively high amount of phytoplankton production among estuaries (Nixon 1986, Day et al. 1989, Mallin et al. 1991).

Community composition of the lower Neuse Estuary phytoplankton varies both with season and salinity. Centric diatoms often predominate in spring and early summer, blue-green algae and dinoflagellates in late summer and early fall, cryptomonads in late fall and spring, and chlorophytes and dinoflagellates in winter (Mallin et al. 1991). Periods of extensive rainfall load the system with nutrients and lead to pulse blooms of cryptomonads in fall or spring, and dinoflagellates in late winter–early spring (Mallin et al. 1991, Rudek et al. 1991). Sampling and field experiments were conducted in the lower estuary at Channel Marker 6, located near the mouth of the estuary where it joins Pamlico Sound (Fig. 1). During the study the mean water depth at this station was 3.3 m, the mean light attenuation coefficient k was ≈ 1.1 m^{-1}, and salinity ranged between 9 and 22 g/kg. The water column was usually well mixed by current and wind at this location (Mallin and Paerl 1992). Water quality at this station is representative (chemically and physically) of a large area of the lower Neuse Estuary and southwest Pamlico Sound.
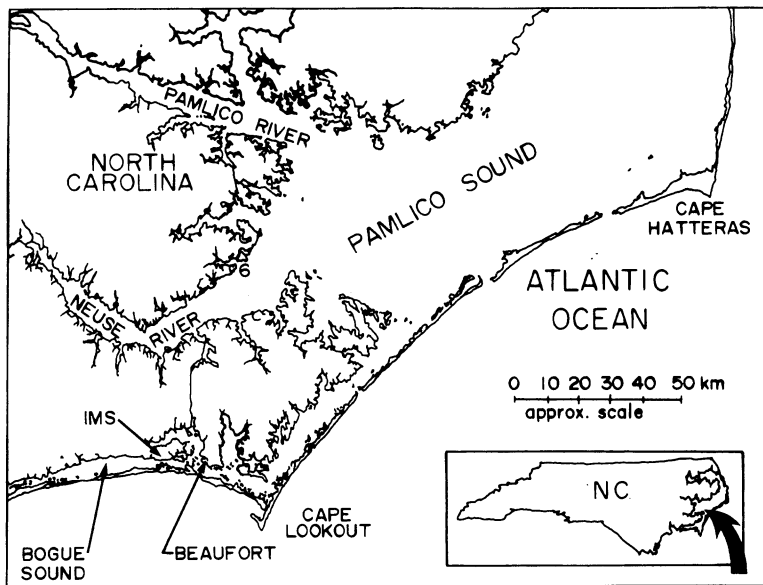
FIG. 1. Map of the Pamlico Sound area showing the sampling site (Channel Marker 6) in the lower Neuse River Estuary.

MATERIALS AND METHODS

Physical–chemical, primary productivity, and biomass data

Vertical profiles (0.5-m intervals) of dissolved oxygen, water temperature, and salinity were taken on station using a YSI Model 54A oxygen meter and a YSI Model 33 salinometer. Neuse River flow data were acquired at the nearest river flow gauging station (Kinston, North Carolina), 120 km upstream from the sample site. The river flow parameter showing best fit relative to estuarine primary productivity and nutrient concentrations was mean daily flow for the 14-d period preceding each experiment (Mallin et al. 1993). Nutrients (nitrate, ammonia, phosphate) were analyzed from surface samples according to the methods detailed in Mallin et al. (1991) and Rudek et al. (1991).

Water was collected just below the surface in large (25-L) polypropylene carboys and returned to the Institute of Marine Sciences for phytoplankton productivity determinations. A novel system, which we termed a light-field simulator (LFS), was designed to estimate phytoplankton productivity, accounting for the continual and rapid changes in irradiance that vertical mixing causes phytoplankton to experience in the shallow, windswept Neuse River Estuary. The LFS is a large, horizontally rotating wheel consisting of increasing and decreasing layers of neutral density screening providing a variable natural sunlight regime from 100% to $\approx 5\%$ surface irradiance (I_0). The LFS is positioned outdoors in a 1.0 m deep flow-through seawater pond. The design, testing, and operation of the LFS has been detailed in Mallin et al. (1991) and Mallin and Paerl (1992).

Triplicate light bottles and one dark bottle of water

from each station were injected with 0.5 mL ^{14}C bicarbonate (258 Bq/mL) and allowed to incubate while hung on racks just beneath the water surface under the LFS. Incubations of 3.5–4.0 h centered around 1200 were used (Wetzel and Likens 1979). Upon termination of the incubations, 50 mL of sample were filtered, air dried, and fumed with HCl for 30 min to remove nonbiologically precipitated ^{14}C labelled carbon. The filters were then placed in vials with a scintillation cocktail, and activity determined using a Beckman LS 5000TD liquid scintillation counter. Dissolved inorganic carbon content of the sample water was determined using a Beckman Model 864 infrared analyzer. Primary productivity over the incubation period was calculated following the formulae in Wetzel and Likens (1979). Surface irradiance flux readings (PAR: 400–700 nm) were recorded throughout the day at 10-min intervals with a LI-COR Model LI-550B printing integrating photometer/radiometer equipped with a LI-COR 2 pi quantum sensor. Productivity during the incubations was divided by a daylight factor (irradiance during the incubation/total daily irradiance) to convert to daily productivity.

Chlorophyll a was determined from surface samples. These samples were kept in darkness and on ice and returned to the laboratory, where 300–500 mL were filtered on 4.25 cm Whatman 934 AH glass fiber filters with $MgCO_3$ added to prevent organic acid degradation of chlorophyll. Pigments were subsequently extracted with $MgCO_3$-buffered 90% acetone and determined by spectrophotometer using the trichromatic method (Strickland and Parsons 1972). From April 1990 to December 1991, three zooplankton samples and three samples of water filtered through 60-μm mesh sieving were also collected, filtered through GFC filters, and

stored frozen in the dark for later elemental carbon and nitrogen analysis (performed using a Model 440 Elemental Analyzer, Control Equipment Corporation).

Plankton community analysis

During the incubations, samples were collected to determine phytoplankton and zooplankton community structure. Three replicate zooplankton samples were collected in the same manner as the zooplankton for the grazing tests and field preserved with formalin to 2% of total volume. In the laboratory, the samples were counted at 50× using a Wild M5 dissecting microscope, and identifications confirmed using a Wild M20 compound microscope. The entire sample was counted in all cases. Counts were expanded volumetrically to number per cubic metre and areally to number per square metre. Biomass of zooplankton (as dry mass) was estimated by applying literature values to the count data. Sources used included Durbin and Durbin (1981) for *Acartia tonsa* nauplii and copepodites, and Dumont et al. (1975), Lonsdale and Coull (1977), and Pauli (1989) for the remaining taxa.

Two replicate phytoplankton surface samples were collected monthly on station and field preserved with Meyer's Modified Media, a Lugol's iodine–formalin solution (Meyer 1971). A 10–15 mL subsample was filtered through a 2.5-cm Gelman membrane filter (0.45 μm porosity) and cleared following the procedure outlined by Crumpton (1987). The preparations were examined using phase contrast at 400× under a Zeiss type B compound light microscope and either sufficient random fields to count 400 cells or all cells in 35 random fields were counted, whichever occurred first.

Zooplankton grazing analysis

A useful method of measuring zooplankton grazing rates is to follow radiotracer uptake (i.e., ^{14}C, ^{3}H, ^{32}P, and ^{33}P) through the different trophic levels. This method has the advantage of speed, as a grazing test can successfully be completed in a matter of minutes. Grazing rate tests of the ^{14}C method vs. Coulter counter and chlorophyll uptake methods have shown good agreement between these methods (Hargis 1977, Daro 1978).

A method used for the study of community grazing rates is the Haney chamber (Haney 1971), an in situ radioisotope method using short-term incubations. Variations of this method have been used in both freshwater (Haney 1971, Hart and Christmas 1984, Gawler and Chapuis 1987, Havens 1991), and marine systems (Daro 1978, Roman and Rublee 1981, Napp and Long 1989, Garcia-Pamanes et al. 1991). With this method either a prelabelled algal species is added to the chamber or the natural phytoplankton community is radiolabelled and resident zooplankton are allowed to graze the algae within the chamber. There are some disadvantages to this method. If one adds a prelabelled alga or bacterium to the chamber, grazing rates are computed from a food source that may not be representative of the natural community. Labelling of natural phytoplankton communities provides the grazers with a more realistic food source than monocultures; a potential drawback is uneven distribution of label among phytoplankton species. Some workers have labelled the natural communities in situ and allowed the grazing tests to extend from 1 to 2 h (Daro 1978, Roman and Rublee 1981, Napp and Long 1989). However, gut passage times of zooplankton may be less than the length of the test, causing label to be defecated and/or excreted and recycled into the system and causing error in the uptake rate assessment (Conover and Francis 1973). Additionally, natural phytoplankton communities cannot be labelled at night with ^{14}C, although ^{32}P or ^{33}P can be used as tracer in the dark (Napp and Long 1989). Phosphorus can be taken up by bacteria and inert particles, which may or may not be food items for the zooplankton community.

In view of these concerns, we utilized a pulse-labelling method to radiolabel natural phytoplankton assemblages with ^{14}C-bicarbonate to permit short-term shipboard assessments of community grazing rates at night. We chose a grazing period of 15 min, a period shorter than the gut passage time of the dominant local fauna (Peters 1984: Table 9.1, Stearns 1986). This is a measure of ingestion of phytoplankton rather than incorporation of material into zooplankton tissue.

Zooplankton community grazing rates were measured on a monthly basis from March 1990 through December 1991. The zooplankton community was defined as the fraction that passed through a 2500-μm mesh net, but was retained by a 60-μm mesh net. This size was chosen because it included the great majority of the crustacean zooplankton community, and it should have retained most nauplii of the local copepod fauna (Conover 1956, Grice 1969, Lawson and Grice 1973). Also, the dominant rotifer fauna consisted of large *Synchaeta* species, many of which were retained by this mesh. The organisms retained by a 60-μm mesh sieve are those most available as prey to larval and juvenile fish, the next trophic level (Thayer et al. 1974, Kjelson et al. 1975). Sieving with a 60-μm mesh unavoidably causes retention of some large phytoplankton and permits passage of some small zooplankton (protozoans). Live whole-water samples were concentrated and examined for protozoans after each trip; microscopic examination indicated that protozoans passing the sieve were a minor portion of the total zooplankton in this system; however, some protozoans may have served as a food source for the larger zooplankton.

The experiments were performed aboard the 15-m (50 ft) RV Capricorn. Both day and night grazing rates were measured, except for April 1990, April 1991, and August 1991 when rough weather forced cancellation of night experiments. The tests were run in duplicate

from March through June 1990 and in triplicate in July 1990 and thereafter.

The tests were conducted as follows. A surface bucket haul was taken and gently filtered through a 60-μm mesh sieve to remove the grazer community. A sample of 4-L filtrate was retained in a 8-L clear plastic container, injected with $^{14}CO_2$-NaHCO$_3$ (specific activity 2.15 $\times$ 10^6 Bq/mmol; ICN Radiochemicals, Irvine, California, USA), stirred occasionally, and allowed to incubate in full sunlight for $\approx$1 h. Preliminary tests showed that sufficient label was taken up during this time period to obtain easily measured results in grazing experiments. About 15 min before the test was to begin another 4-L water sample (surface bucket haul) was collected, gently poured through a 2.5-mm mesh sieve to remove jellyfish and ctenophores, and sieved with and retained in a 250-mL size cup with 60-μm mesh netting on the sides. The cup was hung in a bucket of seawater to permit passage of water and phytoplankton through the netting to the captive zooplankton. Storage time in the cups was minimized ($<$15 min) to reduce the chances of predation loss within the cup from raptorially feeding zooplankton. This method of zooplankton collection was used to minimize physical trauma to the zooplankton, which might occur using other, larger volume collection techniques (i.e., pumps, towed nets).

Upon cessation of the ^{14}C incubation, two 50-mL aliquots of the labelled water were withdrawn and filtered through 2.5 cm Whatman GFC filters; the filters were stored in scintillation vials for later HCl fuming and subsequent assessment of radiolabel uptake by phytoplankton (CPMpo). The zooplankton in the cup were then gently released into the chamber of labelled phytoplankton, mixed, and allowed to graze for 15 min away from direct sunlight. The contents were then filtered through a 60-μm mesh Nitex sieve, rinsed with soda water brought to estuarine salinity, and immediately placed in a 7-mL polyethylene scintillation vial for later assessment of radiolabel uptake by grazers (CPMz). Two 50-mL filtrate samples were then assayed for ^{14}C content (CPMpt).

The entire process outlined above was repeated $\approx$1 h after sundown at the same location. Instead of using sunlight for photosynthetic incubations an incubation chamber was devised, consisting of a battery of three cool-white fluorescent lights and one Gro-lux light. The outer edge of the chamber was lined with aluminum foil for reflective purposes, thus providing, measured as photon flux density, $\approx$230 μmol·m^{-2}·s^{-1} to the incubating phytoplankton. Cool white fluorescent light provides a spectrum similar to that of natural sunlight (Lobban et al. 1985). The apparatus was tested by incubating water from the same carboy in sunlight during late afternoon and using the lights after dark, with grazing tests as above conducted under laboratory lighting ($\approx$50 μmol·m^{-2}·s^{-1}). Grazing rates obtained using both incubation methods were similar, with a daytime mean

($\pm$ 1 SE) of 21.1 $\pm$ 0.3 mL·L^{-1}·h^{-1} and nighttime mean of 19.5 $\pm$ 3.2 mL·L^{-1}·h^{-1}. The monthly night shipboard grazing experiments were conducted in darkness.

In the laboratory the scintillation vials were opened, allowed to dry, and fumed with concentrated HCl vapors for 30 min to removed nonbiologically precipitated labelled carbon. Vials used for phytoplankton filters were injected with 4 mL of Ecolume (ICN Radiochemicals) scintillation cocktail. Vials containing labelled zooplankton were first treated with 1 mL of Scintigest (Fisher Scientific) tissue-solubilizing agent, stored overnight in a 50°C oven, and subsequently injected with 4 mL of Scintiverse (Fisher Scientific) scintillation cocktail. Experiments showed that zooplankton samples required storage for at least 72 h in Scintiverse for counts per minute to stabilize. This period both allows for complete extraction of radionuclide and reduction of random counts generated from chemoluminescence resulting from the mixing of tissue solubilizer and scintillation cocktail. Sample activity was determined using a Beckman LS 5000TD liquid scintillation counter. Community grazing rates were then determined by using the data in the following formula (after Lampert and Taylor 1985):

$$CGR = \frac{CPMz - Cz}{(CPMp - Cp)/v} \cdot \frac{60}{V \cdot t},$$

where community grazing rate (CGR) is in millilitres of labelled phytoplankton suspension grazed per litre per hour, CPMz is counts per minute for zooplankton samples, Cz is zooplankton control (background activity of an unlabelled zooplankton sample), CPMp is counts per minute for phytoplankton samples, Cp is phytoplankton control (background activity of an unlabelled phytoplankton sample), v is volume of the phytoplankton activity sample in millilitres (usually 50 mL), 60 is minutes per hour, V is volume of grazing chamber in litres (4 L in these experiments), and t is grazing time in minutes (15 min for these experiments).

Phytoplankton controls were activity of a 50-mL unlabelled filtered phytoplankton sample. CPMp is obtained by using the average activity of the two phytoplankton samples taken at the beginning (CPMpo) and the two samples taken at the end (CPMpt) of the 15-min grazing period (Baars and Oosterhuis 1984). The grazing rate is thus the volume of water (in millilitres) cleared of phytoplankton by the zooplankton found in a litre of water per hour. Grazing test controls were obtained by running a grazing test on labelled phytoplankton as outlined above, except that the zooplankton added to the labelled phytoplankton chamber were previously heat killed by holding them in boiling water for 2 min. The killed zooplankton controls were used to account for possible retention of labelled phytoplankton on the sieves and also adherence of labelled material to zooplankton bodies. Grazing rates computed from controls were subtracted from rates ob-

tained from the tests using live zooplankton. Daily grazing rates were estimated by multiplying daytime hourly grazing rate by number of daylight hours and nighttime hourly grazing rates by number of hours of darkness. Trophic transfer was defined as the percent of daily phytoplankton production grazed by the zooplankton community. Community grazing rate was transformed from millilitres per litre per day to milligrams of carbon per cubic metre per day by multiplying elemental carbon content of the phytoplankton fraction (milligrams of carbon per millilitre) by the number of millilitres filtered, and multiplying the number of litres times 1000. Converted grazing rates (milligrams of carbon per cubic metre per day) were then divided by daily primary productivity (milligrams of carbon per cubic metre per day) to obtain the trophic transfer estimate.

Statistical analysis

Correlation analyses and multiple regression models between grazing rate and a variety of physical, chemical, and biological variables were performed using SAS (1985a, b). Analyses were performed using both untransformed data and data transformed as log(value + 1); where both yielded similar results values reported within are from untransformed data. Results using transformed data are noted as such. For individual months, diel differences in grazing rate and zooplankton abundance were compared using Student's t test (P < 0.05). Diel grazing rate differences for the entire study were assessed using ANOVA on transformed data (SAS 1985a, b). Bonferroni's technique was used to adjust alpha values for multiple correlations (Rice 1989).

RESULTS

Physical–chemical parameters

Water temperature at the study site ranged from 8.2°C in February 1990 to 29.0°C in July 1991, and salinity ranged from 9.2 g/kg in April 1990 to 22.2 g/kg in August 1991. No temperature stratification and only occasional slight salinity stratification were observed during the study period. Dissolved oxygen concentrations were always greater than 4.0 mg/L, even at the bottom.

Surface nitrate concentration was greatest in January 1990 (83.5 μg/L), following heavy December rains. Concentrations fell to 0.6 μg/L by March, and remained below 3.5 μg/L for the remainder of the study except for a brief pulse up to 8.8 μg/L in May 1990. Mean ($\pm$ 1 SE) nitrate concentration 1990–1991 was 7.3 $\pm$ 3.7 μg/L, median 2.6 μg/L. Ammonium concentrations displayed no clear pattern, with levels below 50 μg/L with the exception of an increase to 114.5 μg/L in May 1990. Mean ammonium was 17.4 $\pm$ 5.3 μg/L, median was 8.0 μg/L. Phosphate displayed a pattern of high levels in summer (up to 165 μg/L) and low

levels during the cooler months, with the exception of high levels (145 μg/L) in January 1990. Mean phosphate concentration was 42.2 $\pm$ 9.9 μg/L, median 27.0 μg/L. Phosphate was positively correlated with water temperature (r = 0.58, P = 0.008); high summer phosphate concentrations are common in the Neuse (Rudek et al. 1991).

Phytoplankton community characteristics

Phytoplankton productivity, measured as carbon, ranged from 40.0 mg·m^{-3}·d^{-1} in March 1991 to 1010.0 mg·m^{-3}·d^{-1} in January 1990 (Table 1). Mean annual carbon production for the sampling area was $\approx$95 g/m^3 in 1990 and 61 g/m^3 in 1991. Annual production in this system has been linked to temporal variations in hydrological loading of inorganic nitrogen to the lower estuary (Mallin et al. 1993).

Chlorophyll a concentrations ranged from 1.6 mg/m^3 in November 1990 to 64.8 mg/m^3 in January 1990 (Table 1), with no seasonal pattern. Mean annual chlorophyll a concentrations were 17 mg/m^3 in 1990 and 10 mg/m^3 in 1991.

Phytoplankton cell counts ranged from 560 cells/mL in May 1991 to 4400 cells/mL in March 1990, with no evident seasonal pattern (Table 1). Mean annual cell counts were 2310 cells/mL in 1990 and 1130 cells/mL in 1991. As in previous years (Mallin et al. 1991), the phytoplankton community was dominated by small flagellates and centric diatoms (Table 2, Fig. 2). The most conspicuous phytoplankton community event was a major bloom of the dinoflagellate Heterocapsa triquetra in January and February 1990.

Zooplankton community characteristics

Zooplankton taxa richness was generally low in the mesohaline Neuse River Estuary. The most abundant copepod was Acartia tonsa, with other taxa present in much lower abundance (Table 3). Cladocerans were also found only in low abundance during the study. Rotifers were periodically abundant with members of the genus Synchaeta dominating (Table 3). Tintinnids were occasionally abundant and the large (75 μm) myxotrophic dinoflagellate Polykrikos hartmanni appeared in high densities a few times (Tables 3 and 4). This genus is believed to ingest algae and small zooplankton (Kofoid and Swezy 1921), and this particular species possessed chromatophores as well (Campbell 1973).

Mean total zooplankton abundances for the entire study were 141 500 organisms/m^3 (day) and 132 800 organisms/m^3 (night); total copepod densities were 54 800 organisms/m^3 (day) and 64 900 organisms/m^3 (night); postnaupliar copepod densities were 5800 organisms/m^3 (day) and 17 400 organisms/m^3 (night). Nauplii comprised 90% of the day total copepod abundance and 75% of the night abundance. Mean rotifer abundance was 47 900 organisms/m^3 (day) and 48 900 organisms/m^3 (night), and mean tintinnids were 16 000

TABLE 1. Phytoplankton monthly productivity, cell counts, and biomass as chlorophyll *a*, and day and night zooplankton biomass as dry mass at Station 6, January 1990–December 1991. Chlorophyll data are from single chlorophyll samples. NA = not available.

Year	Date	Volumetric carbon prod. ($mg \cdot m^{-3} \cdot d^{-1}$)		Counts (no./mL)		Chlor. *a* (mg/m^3)	Day (mg/L)		Night (mg/L)	
		Mean	SE	Mean	SE		Mean	SE	Mean	SE
1990	23 Jan	1013	11	3600	340	64.8	NA		NA	
	6 Feb	402	11	4200	530	37.7	NA		NA	
	9 Mar	391	4	4400	620	19.7	34.1	2.4	65.7	2.6
	17 Apr	97	3	2680	160	10.5	3.5	0.8	NA	
	7 May	427	15	1500	230	6.2	18.2	0.9	1.8	2.1
	5 Jun	131	5	800	13	14.4	18.9	3.9	15.4	1.4
	17 Jul	128	3	2210	200	9.2	57.8	23.0	33.1	4.2
	13 Aug	216	8	2500	4	15.4	24.5	5.7	28.1	3.1
	10 Sep	91	6	820	200	11.4	89.3	4.5	84.8	8.3
	22 Oct	114	3	1470	40	9.8	8.4	1.2	25.4	3.7
	27 Nov	55	3	1760	420	1.6	2.4	1.1	6.1	0.4
1991	14 Jan	102	3	1290	150	10.6	3.0	0.7	2.9	0.8
	18 Feb	144	1	1180	210	6.9	42.0	9.0	39.7	0.6
	11 Mar	40	3	1340	60	8.8	10.2	2.1	15.8	2.9
	9 Apr	302	2	560	90	6.9	20.4	4.0	NA	
	21 May	258	18	1600	460	25.1	72.8	7.8	84.8	10.2
	20 Jun	68	2	1200	185	8.7	29.3	1.0	43.6	5.4
	17 Jul	242	4	700	250	13.6	56.9	3.5	86.5	5.3
	13 Aug	188	2	720	4	12.9	27.2	1.3	NA	
	10 Sep	454	21	1240	90	10.1	126.6	8.2	170.0	13.2
	21 Oct	112	3	1260	80	6.5	13.2	2.2	28.8	3.2
	10 Dec	44	8	1360	35	3.5	10.0	0	5.4	0

organisms/m³ (day) and 24 000 organisms/m³ (night). On average, postnaupliar copepods comprised only 4% of total zooplankton abundance in day samples and 13% in night samples. The surface bucket haul collec-

tion method did not either over- or underestimate postnaupliar copepod abundance when compared with the entire water column pump sampling conducted in 1988–1989 (Mallin 1991: Table 1). Bucket hauls did yield
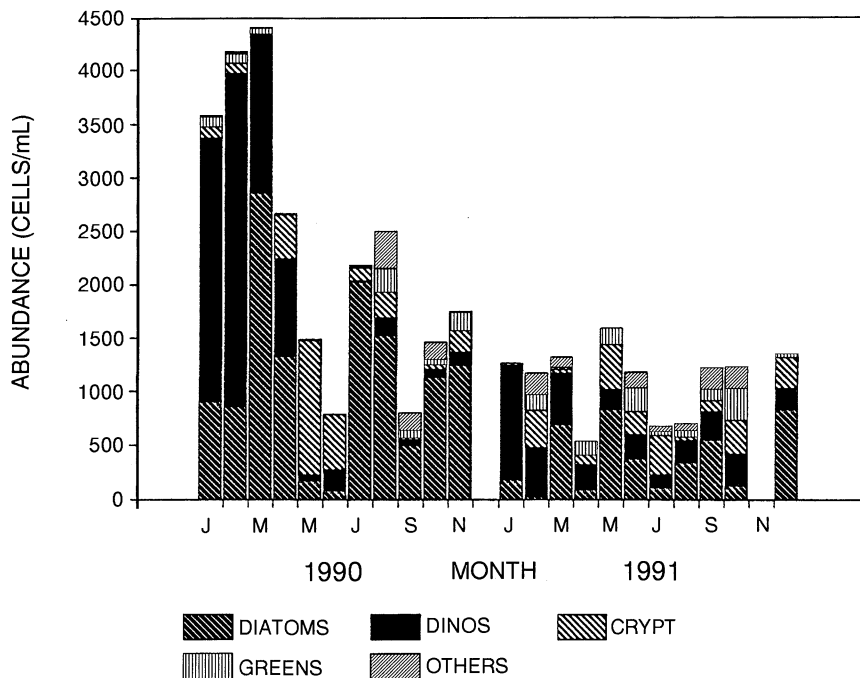

FIG. 2. Composition of the phytoplankton community by major taxonomic group, January 1990–December 1991. Height of bars represents total phytoplankton cell abundance by month.

TABLE 2. Dominant phytoplankton taxa at Marker 6, Neuse River Estuary, January 1990–December 1991.

Taxa	% of total community by number
Dinophyceae	
Prorocentrum minimum	8.3
Gymnodinium spp.	0.5
Heterocapsa triquetra	19.0
Gyrodinium estuariale	0.5
Katodinium rotundatum	1.7
Bacillariophyceae	
Thalassiosira spp.	25.6
Cyclotella meneghiniana	3.7
Skeletonema costatum	3.9
Nitzschia closterium	5.9
Thalassionema nitzschoides	1.0
Cryptophyceae	
Cryptomonas testaceae	3.2
Chroomonas spp.	10.6
(C. minuta and C. amphioxiae)	
Chlorophyceae	
Chlamydomonas spp.	0.6
Prasinophyceae	
Pyramimonas micron	0.8
Pyramimonas spp.	2.6
Cyanophyceae	
Phormidium spp.	2.3

higher day and night naupliar abundances than the pump method, however.

There was a general pattern of greatest zooplankton abundance in the warmer months, although blooms of rotifers in cooler months at times disrupted this pattern (Table 4). Copepods were generally most abundant in warm months with the exception of high densities in March 1990, following the Heterocapsa triquetra bloom (Table 5).

Total copepod abundance (both day and night) showed significant positive correlation with water temperature in the estuary ($P < 0.05$). Neither salinity nor nutrient concentrations were correlated with abundance of any zooplankton taxa. Abundance of Acartia tonsa was positively correlated with primary productivity ($P = 0.01$).

There were few significant diel differences in total zooplankton abundance (Tables 4 and 6). Copepods often displayed greater abundance during the night than the day; this was mainly caused by postnaupliar copepods, particularly Acartia tonsa (Tables 5 and 6). There were no consistent diel differences in copepod nauplii abundance (Tables 5 and 6). Rotifers likewise displayed a lack of diel differences (Tables 4 and 6), but tintinnids tended toward greater daytime abundance (Tables 4 and 6).

Estimated mean daytime total zooplankton biomass was 33.4 μg/L (as dry mass); night biomass was 44.0 μg/L (Table 1). Postnaupliar copepod biomass was 9.7 μg/L (day) and 20.9 μg/L (night); copepod naupliar

biomass was 9.8 μg/L (day) and 10.4 μg/L (night); and rotifer biomass was 7.8 μg/L (day) and 6.4 μg/L (night). Zooplankton biomass (dry mass) was positively correlated ($P = 0.001$) with abundance of total zooplankton, total copepods, A. tonsa, nauplii, and also with elemental C and N concentration of seston >60 μm. Zooplankton biomass was also positively correlated (day: $r = 0.47$, $P = 0.04$; night: $r = 0.59$, $P = 0.01$) with primary productivity.

Zooplankton community grazing

Community grazing displayed a general tendency of low rates in winter 1990–1991 and moderate to high rates late spring through early fall of 1990 and midsummer of 1991 (Fig. 3). There were notable exceptions to this pattern; the highest rates obtained during the study were from March 1990, coincident with high grazer abundance, primary productivity, and phytoplankton cell counts (Tables 1, 4, and 5). Another anomaly occurred in August 1991, when there were unusually low grazing rates (Fig. 3). There were concurrent reductions in both grazer densities and primary production between July and August 1991.

Community grazing rates ranged broadly from 310 mL·L^{-1}·h^{-1} in March 1990 to lows of ≈0.1 mL·L^{-1}·h^{-1}. For all sample dates the mean (± 1 SE) day grazing rate was 19.3 ± 39.6 mL·L^{-1}·h^{-1} and night rate was 12.3 ± 20.0 mL·L^{-1}·h^{-1}. However, on a few occasions unusually high grazing rates were obtained, causing considerable variability (Fig. 3). Grazing rates were thus transformed as log (grazing rate + 1), and means

TABLE 3. Zooplankton grazer community from Marker 6, Neuse River Estuary, March 1990–December 1991.

Taxa	% of total community by number[*]
Copepods	
Acartia tonsa	3.4
Paracalanus crassirostris	0.4
Oithona colcarva	2.1
Microsetella norvegica	0.3
Other harpacticoids	0.5
Copepod nauplii	34.5
Cladocerans	
Podon polyphemoides	0.1
Evadne nordmanni	2.6
Rotifers	
Synchaeta monopus	10.1
Synchaeta bicornis	1.1
Synchaeta spp.	18.0
Others	
Polykrikos hartmanni (dinoflagellate)	6.3
Mixed tintinnids	13.8
Polychaete larvae	1.3
Barnacle nauplii	0.1
Ciliates	5.4

[*] Percent of total community includes both day and night samples.

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TABLE 4. Day–night comparisons of group densities of selected zooplankton taxa (no./m³), rounded to ± 50 organisms/ m³. D = day density, N = night density, densities are means of three replicates, December 1991 data from single samples only.

Date	Statistic	Total zoop.		Rotifers		Tintinnids		*Polykrikos*	
		D	N	D	N	D	N	D	N
				1990					
Mar	$\bar{X}$	96 500	159 000*	15 200	38 300	3600*	1200	0	0
	SE	13 900	10 700	6200	6100	700	200	...	...
Apr	$\bar{X}$	17 800	nt†	2000	nt	600	nt	0	nt
	SE	2000	...	400	...	300	...	...	...
May	$\bar{X}$	82 200**	23 700	77 800**	16 000	800*	0	0	0
	SE	3800	4300	3500	3800	140	...	...	...
Jun	$\bar{X}$	78 300	53 000	58 200	46 400	1300	1400	0	0
	SE	7200	5500	7600	3800	200	800	...	...
Jul	$\bar{X}$	60 200	77 900	5500	1300	7300	7400	0	0
	SE	18 300	2800	1100	200	2500	1900	...	...
Aug	$\bar{X}$	148 200	102 600	7400	2800	14 100*	4400	100 500	50 200
	SE	20 000	18 300	2400	1400	700	800	19 600	9700
Sep	$\bar{X}$	377 500**	133 500	6900	5100	2300	4300*	148 600*	5400
	SE	17 800	3900	1000	2800	500	200	37 200	1500
Oct	$\bar{X}$	38 200	41 800	14 500	8500	0	0	0	0
	SE	9600	4400	6800	2000	...	...	...	...
Nov	$\bar{X}$	13 400	23 800	11 400	20 400	1800	900	0	0
	SE	5400	4400	4800	3900	500	300	...	...
				1991					
Jan	$\bar{X}$	7900	2300	5900	300	0	100	0	0
	SE	3100	200	2900	200	...	100	...	...
Feb	$\bar{X}$	374 800	435 300	189 800	123 400	145 000	297 100**	0	0
	SE	58 700	39 800	36 400	30 500	22 100	10 200	...	...
Mar	$\bar{X}$	51 900	67 400	47 400	61 500	2500	1900	0	0
	SE	13 100	14 100	12 200	14 100	1200	700	...	...
Apr	$\bar{X}$	104 600	nt	98 800	nt	1700	nt	0	nt
	SE	22 000	...	22 500	...	200	...	...	...
May	$\bar{X}$	391 750**	215 167	224 300**	48 600	34 800	32 200	0	0
	SE	34 500	11 700	22 100	2700	1000	2000	...	...
Jun	$\bar{X}$	132 200	146 900	41 300	31 500	21 200**	9500	0	0
	SE	900	6000	4300	100	900	800	...	...
Jul	$\bar{X}$	155 200	200 000	5100	8800	4000*	1300	0	0
	SE	27 600	8600	2100	1200	900	80	...	...
Aug	$\bar{X}$	75 200	nt	2900	nt	11 300	nt	0	nt
	SE	5000	...	700	...	1100	...	...	...
Sep	$\bar{X}$	519 200	496 500	66 500	164 000*	66 800	50 800	0	0
	SE	24 900	62 000	10 300	14 600	6100	9600	...	...
Oct	$\bar{X}$	58 000	58 600	31 800	17 200	0	0	15 500	12 100
	SE	1800	8900	1900	3600	...	...	6100	2100
Dec	$\bar{X}$	48 000	19 800	45 800	18 500	500	0	0	0

* Significant difference at $P < 0.05$ level; ** significant difference at $P < 0.01$ level.

† nt denotes sample not taken.

and medians were computed using antilog values. This yielded a mean (± 1 SE) day grazing rate of 3.30 ± 0.62 mL·L⁻¹·h⁻¹, and a mean night grazing rate of 3.07 ± 0.60 mL·L⁻¹·h⁻¹. Median values were 3.2 mL·L⁻¹·h⁻¹ (day) and 1.9 mL·L⁻¹·h⁻¹ (night). Day and night grazing rates generally displayed the same seasonal pattern (Fig. 3). For the entire data set there was no significant difference in grazing rates between day and night; for individual dates there were only a few differences (Table 6).

Grazing rate was significantly correlated with a variety of phytoplankton taxa group abundances (Table 7). The correlation with total phytoplankton is largely a result of centric diatoms; this group comprised 83% of the diatom community, and *Thalassiosira* spp. comprised 71% of the centric diatoms over the course of the study. Abundance of cryptomonads, green algae, pennate diatoms, and blue-green algae were not significantly correlated ($P < 0.05$) with grazing, nor were water temperature or nutrient concentrations. Log-

TABLE 5. Day–night comparisons of group densities of selected copepod taxa (no./m³), rounded to ± 50 organisms/m³. D = day density, N = night density, densities are means of three replicates, December 1991 data from single samples only.

Date	Statistic	Total cope. D	Total cope. N	Postnaupliar D	Postnaupliar N	Nauplii D	Nauplii N	A. tonsa D	A. tonsa N
					1990				
Mar	$\bar{X}$	73 600	113 700**	6000	19 300**	67 600	94 400	5900	15 500**
	SE	9700	5700	600	1100	9600	5800	700	1600
Apr	$\bar{X}$	14 900	nt†	0	nt	14 900	nt	0	nt
	SE	1700	⋯	⋯	⋯	1700	⋯	⋯	⋯
May	$\bar{X}$	3000	7100**	100	4200*	2900	2200	0	300
	SE	500	800	100	600	400	600	⋯	100
Jun	$\bar{X}$	17 300	4100	200	100	17 100	2700	200	100
	SE	10 300	1400	100	600	10 200	900	100	100
Jul	$\bar{X}$	47 300	68 200	1900	11 700	45 400	56 500	900	8400*
	SE	17 900	4700	500	2200	17 500	3600	100	2200
Aug	$\bar{X}$	25 900	44 900*	8800	10 300	17 400	34 900	8200	6300
	SE	3900	6500	3900	1700	3100	6900	3600	800
Sep	$\bar{X}$	218 300*	117 900	23 300	39 200	195 100*	78 800	5300	26 900*
	SE	24 800	2700	1100	6300	22 300	4100	900	5700
Oct	$\bar{X}$	22 800	30 700	600	9200*	22 200	21 600	400	8100*
	SE	3900	3000	100	2000	4000	1700	100	2200
Nov	$\bar{X}$	100	1800**	0	600*	100	1200**	0	100
	SE	100	200	⋯	200	200	100	⋯	100
					1991				
Jan	$\bar{X}$	1300	1000	300	600	900	400	300	300
	SE	300	100	100	200	300	200	100	100
Feb	$\bar{X}$	600	2100*	0	500	600	1600**	0	500
	SE	200	300	⋯	200	100	300	⋯	200
Mar	$\bar{X}$	100	400*	100	300	0	200	0	0
	SE	100	100	100	100	⋯	100	⋯	⋯
Apr	$\bar{X}$	800	nt	200	nt	600	nt	0	nt
	SE	300	⋯	100	⋯	200	⋯	⋯	⋯
May	$\bar{X}$	117 300	123 300	10 900	30 400	106 500	92 800	7300	20 000*
	SE	19 969	11 558	3600	9900	17 900	7200	3000	3400
Jun	$\bar{X}$	63 800	87 400*	5200	11 400*	58 600	76 000	1300	5600**
	SE	2600	7800	600	1500	2200	6300	400	800
Jul	$\bar{X}$	126 600	173 800	12 000	31 700**	106 900	142 100	7800	20 300**
	SE	20 600	8300	100	3200	20 600	9000	900	2300
Aug	$\bar{X}$	56 800	nt	8900	nt	47 900	nt	1300	nt
	SE	6200	⋯	300	⋯	6500	⋯	400	⋯
Sep	$\bar{X}$	294 700	244 400	27 800	35 000	266 800	209 400	10 800	12 800
	SE	21 400	30 000	2200	3400	19 100	26 800	2200	1900
Oct	$\bar{X}$	8800	23 100	1500	6800*	8400	16 300	600	3400
	SE	2500	3500	700	0	3000	3500	300	700
Dec	$\bar{X}$	1300	500	300	500	1000	0	0	0

* Significant difference at $P < 0.05$ level; ** significant difference at $P < 0.01$ level.
† nt denotes sample not taken.

transformed grazing rate was positively correlated with primary productivity ($r = 0.52$, $P = 0.017$). Zooplankton abundance, biomass, and elemental C and N concentrations from both seston size fractions were not correlated with grazing rate, although log-transformed grazing rate was weakly correlated with log-transformed zooplankton biomass ($r = 0.47$, $P = 0.038$). Salinity displayed a significant inverse relationship with night grazing rate (Table 7). River flow was significantly correlated with night grazing rate, and near-significantly correlated with day grazing rate (Table 7). Mul-

tiple regression analysis showed the most appropriate model explaining variation in zooplankton grazing rates was: grazing rate = 0.19 (primary productivity) + 0.06 (centric diatom abundance) − 3.35 (water temperature) + 18.4, $r^2 = 0.68$, $P = 0.0003$.

Trophic transfer

An estimate of trophic transfer was obtained by determining the percent of the daily primary production grazed by the zooplankton community. This is not a measure of the phytoplankton material incorporated

TABLE 6. Summary of significant diel grazing rate and zooplankton taxa group density differences (t test, P < 0.05, df = 4, comparisons for 17 mo). D = day density, N = night density.

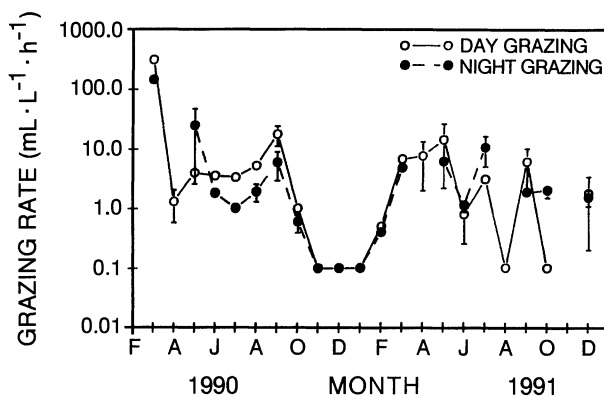| Parameter	D > N	N > D	D = N
Grazing rate	3	1	13
Total copepods	1	7	9
Postnaupliar copepods	0	8	9
Copepod nauplii	1	2	14
Acartia tonsa	0	7	10
Total rotifers	3	1	13
Total tintinnids	5	2	10
Total zooplankton	3	1	13
Zooplankton biomass	1	6	10

FIG. 3. Diel zooplankton community grazing rates, March 1990–December 1991. Results presented are means of three replicates; error bars represent standard error of the mean.

or assimilated into the zooplankton; rather it is a measure of what is eaten. Respiration, excretion, and defecation will release some amount of this material back into the water column. Percent primary production grazed ranged from 2 to 107% of daily production, with two outlying values of 340% in September 1990 and 550% in March 1991. After log transformation, analysis, and subsequent back transformation the study mean (± 1 SE) was 38 ± 3.0%, median 45%. There was a strong seasonal component evident from early 1990 through midsummer 1991, with generally low values in winter 1990–1991 and moderate to high values during spring through summer of both years (Fig. 4). More variability occurred in late 1991, when a very low value occurred in August and a high value in December.

DISCUSSION

As noted previously, there was a significant correlation between primary productivity and both zooplankton biomass and A. tonsa abundance. All of these parameters tend to be elevated during summer and were unusually high in March 1990. Herbivore biomass in general tends to be positively correlated with primary productivity, both in aquatic systems (Cyr and Pace 1993) and terrestrial systems (McNaughton et al. 1989). The correlation between copepod abundance and water temperature is evidently a common regional pattern, noted previously (1988–1989) in the Neuse (Mallin 1991), the Pamlico River Estuary (Peters 1968),

and the Beaufort area estuaries (Fulton 1984). Thus, under normal circumstances, copepod abundance is strongly seasonal, and winter or spring algal blooms may not be affected by copepod grazing. However, there is some evidence that a prolonged algal bloom may stimulate copepod production in the cooler seasons. The January–February *Heterocapsa* bloom maintained high biomass for an extended period (Table 1, Fig. 2), providing an abundance of food for the zooplankton community. *Heterocapsa* is considered a good quality food for copepods (Uye and Takamatsu 1990) and apparently stimulated copepod production in late winter 1990 in the Neuse, compared with 1988–1989 (Mallin 1991) and 1991 (Table 5). By March there were unseasonably high abundances of both copepods and rotifers (Tables 4 and 5). High centric diatom densities coincided with the decline of the *Heterocapsa* bloom (Fig. 2), perhaps as a result of nutrient recycling and increasing water temperature. The combination of high zooplankton abundance and high centric diatom abundance coincided with the highest grazing rates noted during the study.

The only estimate of grazing within the *Heterocapsa* bloom itself was an unreplicated test run in February 1990 (not shown in Fig. 3), when a moderate grazing rate of 2.65 $mL \cdot L^{-1} \cdot h^{-1}$ was measured. Low to moderate grazing rates in such a bloom may not be unusual,

TABLE 7. Correlations among community grazing rate and associated biological and physical variables. Pearson correlation coefficient (r)/probability (p). Adjusted alpha value = 0.008. GRAZ = zooplankton community grazing rate, PPROD = phytoplankton productivity, TPHYT = total phytoplankton abundance, CDIAT = centric diatom abundance, THAL = *Thalassiosira* spp. abundance, DINOS = total dinoflagellate abundance, SAL = salinity, FLOW = upstream river flow.

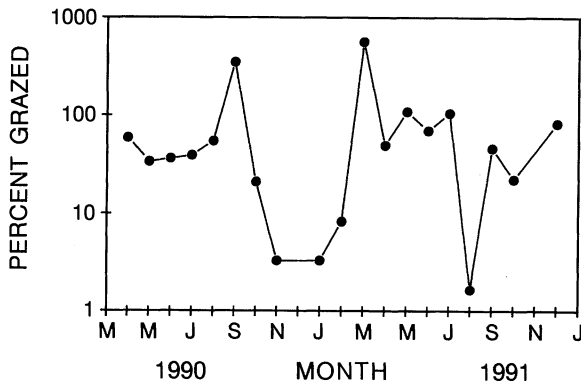|	PPROD	TPHYT	CDIAT	THAL	DINOS	SAL	FLOW
			Day samples (n = 20)				
GRAZ	0.402	0.754	0.693	0.766	0.685	−0.411	0.395
	0.079	0.001	0.001	0.001	0.001	0.072	0.084
			Night samples (n = 17)				
GRAZ	0.498	0.920	0.684	0.790	0.728	−0.619	0.779
	0.042	0.001	0.003	0.001	0.001	0.008	0.001

FIG. 4. Percent of daily phytoplankton production grazed by the zooplankton community, April 1990–December 1991.

however. In Chesapeake Bay, Sellner and Olsen (1985) noted low grazing rates for the copepod *Eurytemora affinis* on a *Heterocapsa* bloom. They stated that the algal biomass was rich enough so that the zooplankton were able to obtain 30% of their daily carbon requirement within a 1-h grazing period.

Diel abundance patterns in surface waters for the larger copepods were not surprising. Later stage copepodites and adult copepods generally migrate into the upper water column at night and downward in the morning (Fulton 1984, Stearns 1986). In the Neuse Estuary copepod nauplii did not demonstrate significant diel migration patterns (Table 5). Because of the larger individual biomass of adult copepods and their tendency to eat more at night (Stearns 1986, Durbin et al. 1990), it would seem reasonable to assume that overall community grazing pressure would be greatest at night. The situation is more complex, however. Whereas zooplankton biomass and postnaupliar copepod abundance were often significantly more abundant at night, postnaupliar copepod biomass overall was only ≈40% of total zooplankton biomass in the Neuse; copepod nauplii was 27%, rotifers 18%, and the remaining 15% consisted of cladocerans, invertebrate larvae, tintinnids, ciliates, and phagotrophic dinoflagellates (Table 4). Also, in some copepods grazing and ingestion rates per unit body mass decrease with increasing body mass (Paffenhofer 1971). Thus, while grazing by larger stage copepods is undoubtedly very important, their presence did not mean significantly greater night grazing rates for the whole zooplankton community. This illustrates the important role micrograzers such as nauplii, rotifers, and protozoans can play in planktonic grazing dynamics, a situation recognized previously by other researchers (Paffenhofer 1971, Capriulo and Carpenter 1980, Landry and Hassett 1982, Verity 1987, Gifford 1988, McManus and Ederington-Cantrell 1992).

The positive correlation between community grazing rate and phytoplankton cell counts is probably the result of a combination of factors. Zooplankton grazing

rates often increase with increasing phytoplankton abundance, to some eventual maximal rate (Frost 1972, Reeve and Walter 1977). Also, the majority of the phytoplankton in the Neuse Estuary were of a size easily grazed by the dominant zooplankton taxa groups. For example, tintinnids graze particles 2–20 μm in diameter (Conover 1982). *Acartia tonsa* grazes a wide range of particles, depending on growth stage, from a minimum of 2 to a maximum of 250 μm. However, the preferred sizes are ≈7 μm for stages NII-NIV, 14 μm for NV-CIII, and 14–70 μm for CIII-adult (Berggreen et al. 1988). Finally, another possible contributer to the correlation is that, in some circumstances, herbivore grazing has been found to cause increases in plant productivity, possibly due to regeneration of nutrients. This has been noted for limnetic systems (Porter 1977, Bergquist and Carpenter 1986), littoral systems (Flint and Goldman 1975), coral reefs (Carpenter 1986), and terrestrial grasslands (McNaughton 1985). The correlations between grazing rate and primary productivity tended toward a positive relationship (Table 7), and log-transformed grazing rate showed an even better relationship ($P = 0.017$) with primary productivity.

The strong correlation between grazing rate and centric diatom abundance is not surprising. The dominant taxa from this group were mostly of a size and shape easily grazed by zooplankton, including *Thalassiosira* spp. (5–15 μm diameter), *Cyclotella meneghiniana* (5–25 μm), and *Skeletonema costatum* (8–16 μm). A number of researchers have concluded that centric diatoms provide a preferred food source for zooplankton (Porter 1977, Ryther and Sanders 1980, Crumpton and Wetzel 1982, Willen 1991), although one study in the Celtic Sea concluded that diatoms were avoided by zooplankton (Burkhill et al. 1987). In addition, *Skeletonema costatum* has long been regarded as a heavily grazed phytoplankter in marine waters (Martin 1965, Ryther and Sanders 1980). Many of the dominant dinoflagellate taxa were likewise small enough to be easily grazed by zooplankton, such as *Heterocapsa triquetra* (19–30 μm in length), *Katodinium rotundatum* (7–18 μm), and *Gyrodimium estuariale* (8–18 μm). There is literature noting the food value of and zooplankton grazing preference toward various dinoflagellates (Burkhill et al. 1987, Uye and Takamatsu 1990, Sellner et al. 1991). The strength of this correlation may be misleading in this study, however. During some periods of high community grazing, large mixotrophic dinoflagellates were numerous in the grazer community (Table 5). These dinoflagellates can ingest other phytoplankton, thus perhaps contributing toward elevated grazing rates as both grazers and zooplankton prey. Cryptomonads have also been cited as good food items for zooplankton (Knisely and Geller 1986, Burkhill et al. 1987, Kerfoot et al. 1988, Klaveness 1988, Xu and Burns 1991). In this study their abundance was not correlated with grazing rates, likely because crypto-

TABLE 8. Effect of zooplankton grazing on primary production from various marine and estuarine systems worldwide. EXP = experimentally derived, EST = estimated by other means. Percent grazed given as mean and range, if available.

System (study)	Taxon group	Period	Method	Prim. prod. grazed (%) Mean	Range
Long Island Sound (Riley 1956)	Community all sizes	Annual	EST	69	···
Peru Coast (Beers et al. 1971)	Community all sizes	June	EST	···	5–25
S. California Bight (Heinbokel and Beers 1979)	Tintinnids	Annual	EST	4	0–20
Solent Estuary, UK (Burkhill 1982)	Tintinnids	Annual	EST	70	···
Long Island Sound (Capriulo and Carpenter 1983)	Tintinnids Copepods	Annual	EST	27 44	··· ···
Gunpowder River, Maryland (Sellner 1983)	Community	Annual	EST	17	1–>100
Beaufort Estuary, North Carolina (Fulton 1984)	Copepods	Annual	EST	45	0–>100
Celtic Sea, UK (Burkhill et al. 1987)	Community <200 μm	Annual	EXP	···	30–65
Jones Sound, Canada Baffin Bay, Canada (Paranjape 1987)	Community <160 μm	Summer	EXP	66 61	40–114 36–88
Narragansett Bay, Rhode Island (Verity 1987)	Tintinnids	Annual	EST	26	···
Halifax Harbor, Nova Scotia (Gifford 1988)	Commuity <102 μm	Annual	EXP	49	0–100
Chesapeake Bay (White & Roman 1992)	Community >64 μm	Mar–Oct	EXP	51	15–112
Neuse Estuary, North Carolina (this study)	Community 60–2500 μm	Annual	EXP	38	2–>100

monads were often dominant in spring and fall periods when zooplankton abundance was low (Fig. 2). Green algae were likewise most abundant in fall and winter (Fig. 2).

The positive correlation between grazing rate and river flow, and negative correlation between grazing rate and salinity may be an indirect result of the relationship between flow and phytoplankton productivity. Elevated river flow increases nutrient availability downstream, thus stimulating primary productivity (Christian et al. 1991, Mallin et al. 1991, 1993, Rudek et al. 1991). Dinoflagellate abundance was positively correlated ($P = 0.002$) with river flow and negatively correlated with water temperature ($P = 0.005$); dinoflagellate blooms are common during high-flow winter/spring periods in the Neuse (Mallin et al. 1993).

It is difficult to compare trophic transfer or grazing impact among studies, mainly because of the differing size fractions used by the researchers. Most studies involving larger sized copepods have used a variety of nonexperimental means of estimating community grazing impact (Riley 1956, Beers et al. 1971, Sellner 1983, Fulton 1984). Researchers have most often determined grazing impacts of the microzooplankton (<200 μm) community (Table 8). It is evident from previous studies that the microzooplankton component can graze a substantial portion of the annual phytoplankton production (Table 8). In this study, micro-

zooplankton (60–200 μm) were often very abundant (Tables 4 and 5) and likely accounted for a considerable portion of the community grazing rate. There is a component of the microzooplankton community <60 μm (mainly protozoans and dinoflagellates) that was not considered here. These organisms may serve as grazers, prey, or both in the microzooplankton community.

This study was designed to consider the trophic transfer activity of a zooplankton group within a size range (60–2500 μm) readily utilized by the next trophic level, larval and juvenile fish. During the 2-yr study, an average of ≈38–45% of the daily phytoplankton production was grazed by this community. The amount was greater in the warmer seasons and considerably less in winter (Figure 4). The portion of the phytoplankton not grazed by the zooplankton was either lost through natural mortality, sedimentation, flushing, or grazed by benthos and planktonic organisms <60 μm.

The amount of annual phytoplankton production grazed by the zooplankton in this study and other planktonic systems is substantial, but moderate compared with other ecosystems (Table 8; see also Valiela 1984: Table 8-1). The most heavily grazed systems may be coral reefs, where fish and invertebrates typically graze 50 to >100% of the daily algal production (Carpenter 1986, Russ 1987, Klumpp and Polunin 1989). Tropical grasslands are also heavily grazed ecosystems; in the Serengeti, grazing by ungulates removes

an average of 66% of annual aboveground primary production (McNaughton 1985). Examples of the other extreme are temperate and tropical seagrass beds, where the grazing community (primarily waterfowl, invertebrates, and a few fish) remove only 3–10% of annual aboveground production (Nienhuis and Van Ierland 1978, Zieman et al. 1979, Thayer et al. 1984). Herbivory as a whole in pelagic systems may be considerably greater than estimated from zooplankton grazing alone. In shallow areas shellfish may graze a substantial amount of the phytoplankton crop (Carlson et al. 1984, Peterson and Black 1991), and mobile consumers such as larval or juvenile stages of selected fish species will also graze on larger phytoplankton cells (Lasker 1975, Peters and Kjelson 1975).

This study only considered surface samples; while the system is shallow and well mixed, there will undoubtedly be variability in grazing in the vertical plane. The diel component of this study showed that, for the community as a whole, there was little difference in grazing rates between day and night. By extending this study for 2 yr we were able to show strong seasonal variations, both in community grazing rates and the percent of daily phytoplankton primary production grazed. These factors allowed for a clearer picture of the dynamics of the predation process, not only biologically and physically, but seasonally as well.

The seasonal pattern of the magnitudes of trophic transfer in the Neuse is intriguing. Transfer rates were usually lowest in winter, when biological activity is normally lowest in temperate estuaries (Day et al. 1989). Trophic transfer rates increased in early spring and in general maintained moderate to high rates through fall. These results may help explain a possible evolutionary strategy concerning temporal patterns of fish migrations into estuarine habitats. During early spring, larval stages of anadromous fish begin entering Pamlico Sound, and by late spring are either transported by prevailing currents or actively migrate to their primary nursery areas in sheltered regions of western Pamlico Sound and the Neuse and Pamlico River Estuaries (Currin et al. 1984, Epperly and Ross 1986, Pietrafesa et al. 1986). Coincident with fish arrival, planktonic trophic transfer is greatest and remains that way until juvenile fish depart the nursery areas in fall to move out into the ocean. In addition, crustacean zooplankton abundance is normally greatest in late summer, and the most abundant copepod, *Acartia tonsa,* is a major food item for young fish (Thayer et al. 1974, Kjelson et al. 1975). During this critical period in fish development the planktonic food chain is shortest and most direct, therefore best able to supply zooplankton prey items to support tertiary production (Ryther 1969, Fenchel 1988).

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