PLANKTON ASSEMBLAGES OF THE GAMBIA RIVER, WEST AFRICA 1983-1984

by

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INTRODUCTION

Background

Knowledge of aquatic ecosystems, especially in the tropics, is small relative to terrestrial ecosystems (Farnworth and Golley 1974). As a result, the seasonal dynamics of plankton in estuarine and freshwater environments in tropical and subtropical Africa have remained a somewhat unexplored subject. The construction of dams on the large rivers of Africa - the Nile, Zambezi, Volta, and Niger - has served to increase interest in the ecology of these major watercourses. Study of the bacterioplankton, phytoplankton, and zooplankton has focused on the role these organisms play in determining the quality of the impoundment water and the composition of the fish populations.

The majority of plankton research on dammed rivers has been performed after the dams were constructed. Much of the plankton work has focused on the Nile River and its tributaries. Brook and Rzoska (1954) studied the density and composition of the phytoplankton and zooplankton populations at several points upstream of the Gebel Aulyia Dam on the White Nile. A subsequent study by Rzoska et al. (1955) focused on the seasonal development of the phytoplankton and zooplankton populations in the White and Blue Nile above Khartoum. Prowse and Talling (1958) summarized previous research on algae in the White Nile below the Gebel Aulyia Dam and followed plankton development in relation to physical and chemical variables. Rzoska (1961) summarized the relationships between hydrology and plankton development for the Blue and White Nile. Talling and Rzoska (1967) focused on the development of the plankton in relation to the hydrological regime in the Blue Nile. Ecological studies of Volta Lake in Ghana have included the seasonal growth of the phytoplankton and their relation to physical-chemical variables (Biswas 1966a,

1966b, 1969). Lawson et al. (1969) described the physical, chemical, and biological changes that accompanied "lacustrinisation" of the Volta River. In the Eleiyele Reservoir near Ibadan, Nigeria, Imevbore (1967) followed the seasonal variation in the abundance of the phytoplankton and zooplankton populations after impoundment.

Pre-impoundment studies in Africa concentrated on the phytoplankton and zooplankton and were limited in scope and duration of sampling. Abdin (1948a, b) traced the seasonal distribution of phytoplankton on the lower Nile before the Aswan Dam was constructed. Primary production and quantitative phytoplankton and zooplankton studies were also carried out on the Blue Nile 3 years before the construction of the Roseires Dam (Hammerton 1972). Holden and Green (1960) studied the seasonal abundance of phytoplankton and zooplankton in the River Sokoto, a tributary of the Niger River, while Imevbore and Bakare (1974) compared bacterioplankton and phytoplankton densities in the swamp and river area that later became Lake Kainji. Before closing of the Asejire Dam on the River Oshun in Nigeria, Egborge (1974) studied the seasonal variation in the density and composition of the phytoplankton. Biswas (1968) briefly examined the hydrobiology of the Volta River and some of its tributaries before impoundment. The universities of Laurenço Marques in Mozambique and Rhodes in South Africa also performed unpublished work on the Zambezi River before the Cabora Bassa Dam was built (Beadle 1981).

The pre-impoundment plankton study of the Gambia River basin (Fig. 1) was unique in that it studied, over the course of 1 year, the abundance of bacterioplankton, phytoplankton, and zooplankton in relation to spatial and temporal variables: transect, station, depth, and tide/time-of-day. The rele-

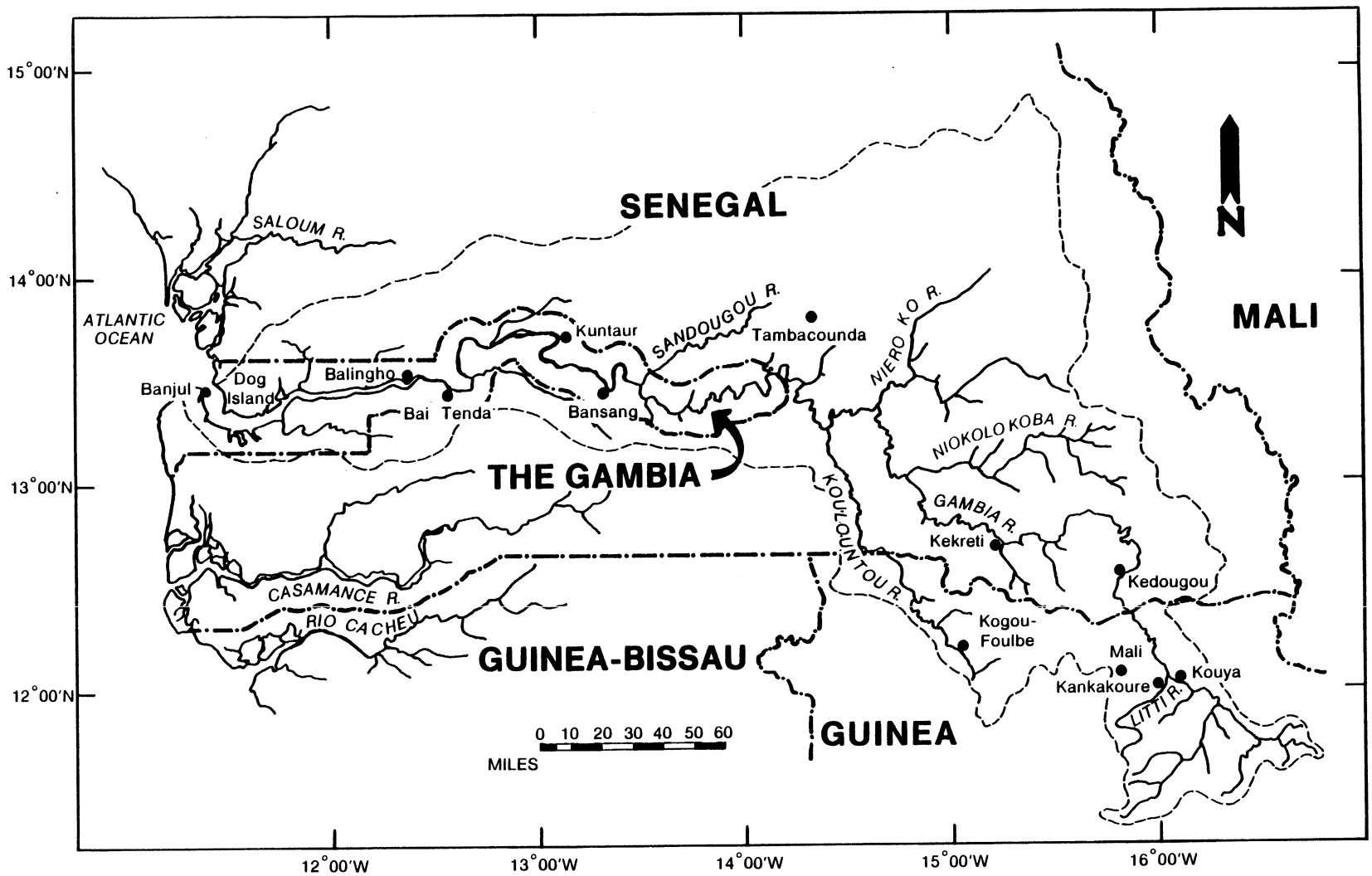

FIG. 1. Drainage basin of the Gambia River, within dashed line.

vance of the plankton to the entire ecological study and the environmental impact assessment as a whole is associated with the role that plankton will play in determining the quality of the water in the reservoirs projected for the Gambia River.

Objectives of the Plankton Studies

Four primary objectives were established for the plankton studies. The enumeration of the free and attached bacterioplankton was undertaken to evaluate the importance of heterotrophs to the ecosystem. Similarly, phytoplankton and zooplankton were identified and enumerated to assess the relative importance of the autotrophs and herbivores. The process studies, which focused on the measurement of the metabolic activity of autotrophs and heterotrophs, were undertaken in an effort to understand where and when photosynthesis or heterotrophy was important.

EXPERIMENTAL DESIGN

The two most important concepts used in defining the nature of the ecological survey of the Gambia River were a) collection of new data, and b) the need to sample a variety of habitats. Major factors considered in the research plan were spatial heterogeneity and temporal variation. Three sources of spatial heterogeneity were identified: longitudinal, latitudinal, and vertical. Temporal variation was associated with diel, tidal, and seasonal periodicity.

The integration of all parts of the study into a cohesive plan that satisfied the two most important concepts and major factors was accomplished by using a Greco-Latin Square experimental design. By using the Greco-Latin

Square design, spatial heterogeneity was addressed by taking samples in one of five predesignated river zones, at different transects within each zone to assess longitudinal variation (distance along the river), at different locations on each transect to assess latitudinal variation (distance across the river), and at different depths at each station to assess vertical variation. Temporal variation was addressed by collecting samples at different times of the day and at different phases of the tide.

Sampling for the ecological survey was conducted at two levels of effort: high frequency and low frequency. High frequency sampling consisted of collection of 16 samples (one four-sided Latin Square) during each of four time periods in each zone. The four time periods were: day flood, night flood, day ebb, and night ebb. This yielded a total of 1,280 samples. High frequency samples included all of the physical and chemical measurements. Low frequency sampling was reserved for biological samples such as the plankton, benthos, and fish. This sampling regimen called for the collection of four samples during each of the four tide/time-of-day periods in each zone. This yielded an overall sampling design with 4 zones x 16 samples x 4 seasons = 256 samples for each component of the plankton. The Greco-Latin Square sampling scheme defined the particular transect (longitudinal), station (latitudinal), depth (vertical), time-of-day, and tide of samples taken. The sampling regime was repeated at four different times of the year corresponding to rising, flood, declining, and low streamflows in the Gambia River. A major statistical assumption required that there was no interaction among any of the main blocking variables: transect, station, depth, tide/time-of-day (Winer 1971).

Use of the Greco-Latin Square design permitted testing of seven hypotheses for each component of the plankton. These seven hypotheses concerned the

presence/absence of statistical differences, as determined by Analysis of Variance (ANOVA) among zones, among transects within a zone, among stations within a zone, among different depths, between day and night, between ebb and flood tide, and between seasons. A more complete description of the Greco-Latin Square sampling design used for this study is presented by Berry et al. (1985).

The measurement of processes by phytoplankton and bacterioplankton did not follow the Greco-Latin Square sampling design because of sampling constraints. There was not sufficient time during the collection and analysis of routine samples to conduct the necessary process measurements. Furthermore, the measurements of primary productivity were conducted *in situ* and thus required sunlight; half of the sampling conducted during the ecological survey was carried out at night. As a compromise, the process studies were conducted during the same general time period as the ecological survey. But incubations used to estimate rates of photosynthesis and heterotrophic uptake were conducted during the 4-day period of the ecological survey; the incubations were conducted in between collection of samples.

BACTERIOPLANKTON

Methods

Bacterioplankton from the Gambia River and associated tributaries were collected on a low frequency basis according to a Greco-Latin Square sampling design. Samples were collected with a Kemmerer bottle, stored in 25-mL plastic vials, fixed with two drops of glutaraldehyde, and refrigerated until enumeration. An Acridine Orange staining method was used to enumerate the bacterioplankton by epifluorescence microscopy (Francisco et al. 1973).

Nuclepore filters (0.2-μm pore size, 25-mm diameter) were stained by immersing up to thirty filters for at least 2 days in a petri dish containing an Irgalan Black solution. The filtering apparatus and frit were rinsed with ethanol and then with sterile distilled water. A Gelman backing filter was then placed on the frit so that no air bubbles were trapped beneath the base of the filter. Suction was applied to secure the backing filter in place. A stained Nuclepore filter, which was rinsed twice in sterile distilled water, was placed over the backing filter while excluding air bubbles. The filter funnel was then secured in place.

A sterile Eppendorf pipette tip was used to extract 1 mL of gently mixed sample which was pipetted into a sterile scintillation vial. One mL of Acridine Orange stain was then put into the vial and the contents were mixed and left for 5 to 6 minutes. This mixture was poured into the filter funnel. Four to five mL of sterile distilled water were added to the vial and the contents were poured into the filter funnel and evacuated at approximately 8 to 14 psi. The scintillation vial was then rinsed with another 4 to 5 mL of sterile distilled water and the contents were again poured into the funnel and evacuated. This step was repeated once more. When 1 to 2 mL remained in the funnel, it was rinsed with approximately 5 mL of sterile distilled water and allowed to fully evacuate. After the fluid had been evacuated, the vacuum was kept on for an additional 10 seconds to ensure that the Nuclepore filter was as free from water as possible.

One drop of mineral oil was placed on a 50 x 75 mm glass slide as a mounting medium and the Nuclepore filter was carefully placed on top of the oil so as to exclude air bubbles. Two drops of mineral oil were placed on the filter and then a 43 x 50 mm glass cover slip was gently placed on top.

Moderate thumb pressure was applied to the cover slip which sat on top of the filter so as to further remove water and exclude air bubbles. Excess mineral oil was soaked up with a wadded Kimwipe.

Bacterioplankton were enumerated by counting the number of appropriately sized fluorescing points which represented the stained nucleic acids of the bacteria. Between six and ten fields were counted at 625 or 1,250x using epifluorescence microscopy. Bacterioplankton in the sterile distilled water were also enumerated weekly to determine the appropriate correction to be subtracted from the field samples.

The calculation of plankton densities per mL (no./mL) involved the following variables and constants.

C = the total sum of organisms counted

A_f = total area of the filter through which the sample was filtered

O_c = area of ocular at 625x or 1,250x

F = number of ocular fields counted

V = volume of sample filtered

$$\text{No.} = \frac{C \times A}{O \times F \times V}$$

Bacterioplankton were differentiated according to whether they were free or attached. For each sample, counts/mL, percentage composition, mean, standard deviation, and variance for both free and attached bacteria were calculated.

Results and Discussion

Bacterioplankton counts were made from samples collected in all five zones taken during three or four seasons. Samples were collected from the lower river (Bansang), upper estuary (Bai Tenda), and the lower estuary (Dog Island) during rising (July 1983), flood (October 1983), declining (December 1983), and low (March 1984) water seasons. Samples in the upper river zone (Kedougou) were taken during flood, declining, and low water. Samples from the headwaters zone (Guinea) were taken during the rising (June 1984), declining, and low water periods. In addition to the samples collected during the routine ecological survey, samples were collected from a mangrove bolon (small creek) during low water and at the Kekreti Dam site during declining water.

Mean free and attached counts, expressed as millions of cells per mL, were an average of four values taken from a particular transect, station, depth, or tide/time-of-day. Grand mean values were an average of sixteen values at one zone during a particular sampling period. Significant differences among stations, transects, depths, and tides were determined by ANOVA using the Greco-Latin Square design (Winer 1971) and are summarized in Table 1.

TABLE 1. Significant ($P < 0.05$) differences in free bacteria (FB) and attached bacteria (AB) concentrations in relation to spatial and temporal variables, Gambia River, 1983-1984.

	Rising	Flood	Low
Upper Estuary	AB; transect		FB; station, depth, tide
Lower River	AB; transect, tide	FB; station	
Upper River		FB; station	

Abundance in Relation to Transect, Station, Depth, and Tide

Free bacteria - Significant differences among stations in the concentrations of free bacteria were found at the upper and lower river zones during flood water. During low water in the upper estuary zone, significant differences among stations in the concentrations of free bacteria, depths, and tide/time-of-day were observed.

In the upper and lower river zones during flood water, the two stations located closest to the south bank of the river exhibited higher mean concentrations of free bacteria than stations located closer to the north bank. The highest mean free bacteria concentrations of all four stations were found closest to the south bank in both zones.

In the upper estuary zone during low water, higher mean free concentrations of bacteria were found at the middle two stations compared to the stations located closest to the river banks. Higher mean free concentrations of bacteria were observed in the upper half of the water column and during the night for both flood and ebb tides.

Four samples from a mangrove bolon near Bai Tenda were taken during ebb and flood tides at both the bolon mouth as well as at a distance of 1.7 km up the bolon. Free bacterioplankton counts were generally higher during ebb tide (3.15×10^6 cells/mL at the bolon mouth and 7.26×10^6 cells/mL in the bolon) than flood tide (1.95×10^6 cells/mL at the mouth and 3.9×10^6 cells/mL at the source). The concentration of free bacteria decreased during both tidal cycles at the mouth compared to the upstream sampling point.

Attached bacteria - Significant differences in the concentration of attached bacteria among transects and tide/time-of-day were found in the lower river

zone during rising water. The two upstream transects had higher mean attached bacteria concentrations compared to the two downstream transects. Higher mean concentrations of bacteria were noted during the night flood and ebb tides as compared to the day flood and ebb tides.

In the upper estuary zone during rising water, the highest mean attached bacteria concentrations were associated with the transect located farthest downstream.

Attached bacteria concentrations in the bolon during ebb tide were greater at the mouth (0.33×10^6 cells/mL) as compared to the upstream sampling point (0.03×10^6 cells/mL). This relationship was reversed during the flood tide when the attached bacteria counts were greater upstream (0.33×10^6 cells/mL) than at the bolon mouth (0.02×10^6 cells/mL).

Abundance in Relation to Physical and Chemical Variables

Free bacteria - The concentration of free bacteria was positively correlated with chlorophyll *a* and negatively correlated with phaeopigment, suspended solids, conductivity, and salinity (Table 2). Free bacteria abundance was also shown to be inversely proportional to pH, alkalinity, soluble reactive phosphorus, total phosphorus, and total nitrogen concentrations. Free bacteria abundance was also inversely proportional to dissolved oxygen, soluble reactive silica (SRS), and water temperature. The relationships not listed in Table 2 were thought to be spurious because free bacteria densities declined going downstream, probably because the bacteria were not halotolerant (Rheinheimer 1971).

TABLE 2. Correlation coefficients between free bacteria (FB), attached bacteria (AB) concentrations, and chlorophyll a (chlor a), phaeopigment (phaeo), suspended solids (SS), conductivity (cond), and salinity (sal).

	Chlor a	Phaeo	SS	Cond	Sal
FB	0.265[b] (238)	-0.211[b] (238)	-0.323[b] (236)	-0.298[b] (175)	-0.370[b] (116)
AB	--	0.257[b] (238)	0.150[a] (236)	0.170[a] (175)	--

[a] significance at P <0.05.
[b] significance at P <0.01.
Values in parentheses indicate the number of pairs of observations.

Attached bacteria - Attached bacteria concentrations were positively correlated with conductivity, phaeopigment, and suspended solids (Table 2). Spurious relationships may have included small positive correlations among alkalinity, soluble reactive phosphorus, total nitrogen, temperature, and attached bacteria.

River Zone Description

Headwaters (Guinea and Kekreti) - The headwaters region of the Gambia River in the Fouta Djallon mountains of Guinea is 1,000-1,500 m above sea level and approximately 965 km from Banjul, the capital of The Gambia. River width varies between 0 and 75 m. The Fouta Djallon mountains are composed of relatively hard and impermeable Precambrian rocks that are overlaid with a thin, highly leached lateritic layer. River bed slope is 0.1% in the lower reaches and 0.4% in the upper reaches.

At Kekreti, in Senegal Oriental, the Gambia River flows through more permeable strata that are overlaid with a heterogeneous mixture of silts,

sands, and clays. River width varies between 50 and 150 m and the slope is approximately 0.03% overall. Distance from Banjul is approximately 790 km.

Free and attached bacteria concentrations during declining (December) (2.2/.01 x 10^6 cells/mL) and low (March) (2.4/.01 x 10^6 cells/mL) water in Guinea were comparable. In early June 1984 (rising water), the Gambia River in Guinea had no streamflow and was pooled. The density of bacterioplankton in pools increased from 7.4 x 10^5 cells/mL at 1.0 m depth to 2.07 x 10^6 cells/mL at 2.5 m depth. During the June field trip, river level rose suddenly as a result of precipitation in the upper portion of the basin. Bacterioplankton densities became more uniform with depth as densities at 1.0 m depth increased to 1.49 x 10^6 cells/mL and at 2.5 m depth decreased to 1.87 x 10^6 cells/mL. Grand mean density increased slightly from 1.4 x 10^6 cells/mL when the river was pooled to 1.54 x 10^6 cells/mL when flow was restored. Attached bacteria were present only in the 2.5 m sample (0.06 x 10^6 cells/mL) when the river was pooled.

Upper river (Kedougou) - The upper river zone, located between 500 and 900 km upstream, was free of tidal fluctuations. River width varied between 25 and 150 m. Increases and decreases in streamflow were regulated by the annual flood.

Figure 2 shows the changes in bacterioplankton concentrations among seasons at four of the five intensively studied river zones. Free bacteria concentrations in the upper river zone were lowest during flood water (October) (1.2 x10^6 cells/mL), rose to a maximum during declining water (December) (2.5 x 10^6 cells/mL), and declined slightly during low water (March) (2.2 x 10^6 cells/mL). Attached bacteria values were two orders of

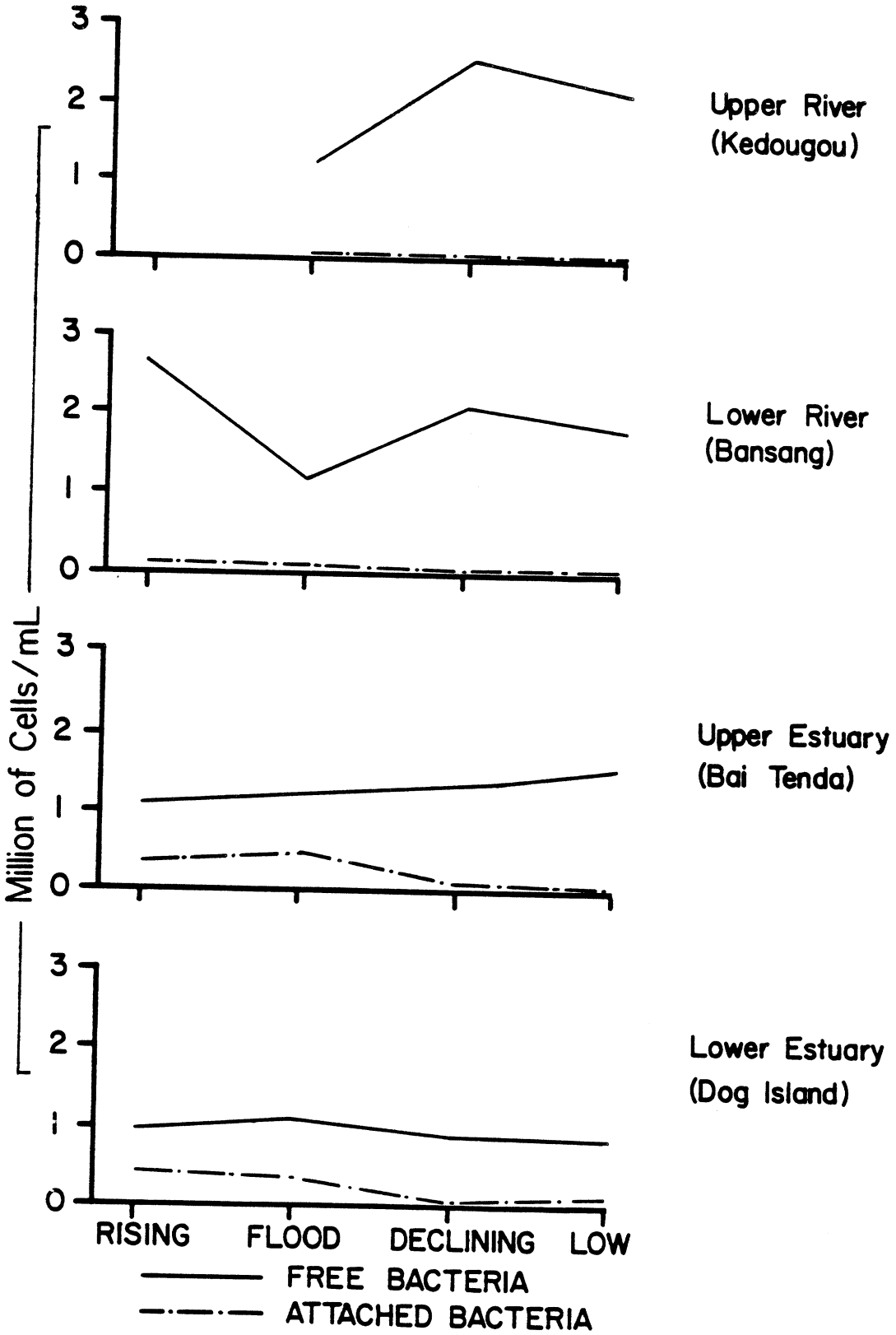

FIG. 2. Concentration of free bacteria (FB) and attached bacteria (AB) in relation to flood stage at four intensively studied river zones on the Gambia River, 1983-1984.

magnitude lower than the free bacteria counts. Concentrations of attached bacteria were similar during flood and declining water (0.05 x 10^6 cells/mL) and one order of magnitude smaller during low water (0.006 x 10^6 cells/mL).

The low free bacteria counts in the upper river zone during flood water were related to the timing of the annual flood which exhibited the greatest flows during September and October (Fig. 3). The increase in volume most likely reduced the concentration of free bacteria by dilution. As the flood receded, bacteria from inundated areas were probably entrained. *In situ* growth may also have taken place. This may have accounted for the rise in free bacteria concentrations during declining and low water. The low attached counts during the flood water period suggested that only small amounts of organic matter were incorporated into the river as compared to downstream zones.

A significant difference (0.05 probability limit) in free bacteria concentrations among stations of the upper river zone was shown during flood water. Because flooding of surrounding land appeared greater on one side of the river (right bank) than on the other, bacterial concentrations in this zone were not homogeneous.

Lower river (Bansang) - Bansang is located approximately 310 km upstream of Banjul. The Gambia River is about 180 m wide at this location. The river water exhibited freshwater characteristics throughout the year despite the fact that this zone is subject to tidal fluctuations.

Figure 2 shows that free bacteria counts were highest during rising water (July) (2.6 x 10^6 cells/mL), declined during flood water (October) (1.2 x 10^6 cells/mL), rose again during declining water (December) (2.1 x 10^6 cells/mL), and slightly decreased during low water (March) (1.8 x 10^6 cells/mL).

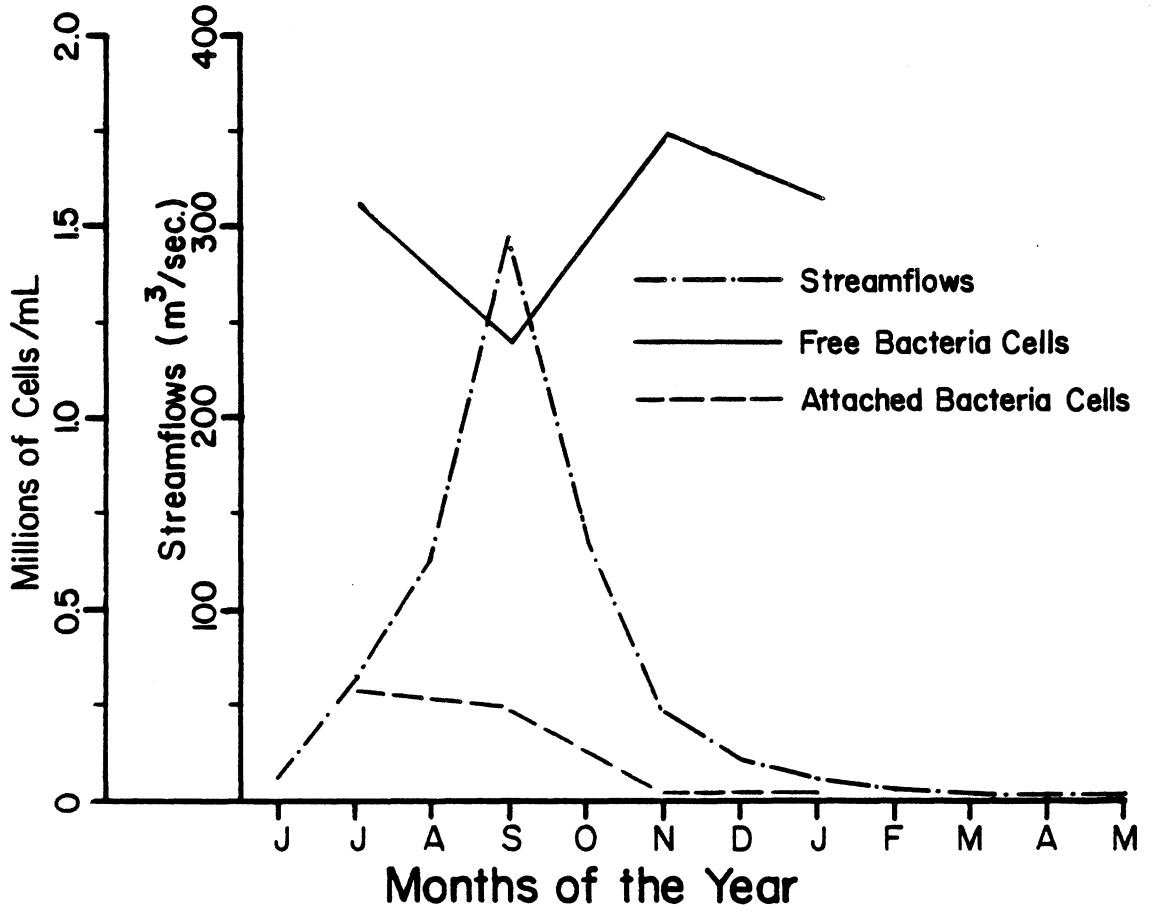

FIG. 3. The relationship between flow, free bacteria (FB), and attached bacteria (AB) concentrations on the Gambia River, 1983-1984.

Attached bacteria values were one order of magnitude lower than free bacteria counts during rising water (.13 x 10^6 cells/mL) and two orders of magnitude lower during flood (.09 x 10^6 cells/mL), declining (.02 x 10^6 cells/mL), and low water (.02 x 10^6 cells/mL).

Free bacteria concentrations were greatest during July when the river level was at or near its lowest level and the phytoplankton density (10,122 cells/mL) in this zone was at its peak. The decrease in both free and attached bacteria concentrations during flood water was attributed in part to dilution. Flood waters probably had lower indigenous concentrations of bacteria and thus served to dilute the standing crops. As the flood receded during declining water the free bacteria concentration most likely increased as a result of bacteria entrainment into the river from the floodplains.

Attached bacteria concentrations were significantly different among transects and tides/times-of-day during the rising water field trip. These differences showed that the sampling area was not homogeneous and that there were greater abundances of attached bacteria during the night. The heterogeneous character of the sampling site was possibly related to differences in topography, vegetation, and land use patterns. The significant difference for free bacteria concentrations among stations during annual flood also suggested that the river had a more heterogeneous character in this zone during this time of year.

Upper estuary (Bai Tenda) - Bai Tenda is located on the upstream from Banjul. The river in this zone is about 500 m wide and is influenced by the tides all year.

Figure 2 illustrates the gradual increase in the concentration of free bacteria during rising (1.1 x 10^6 cells/mL), flood (1.2 x 10^6 cells/mL), declining (1.3 x 10^6 cells/mL), and low water (1.5 x 10^6 cells/mL). Attached bacteria values were one order of magnitude lower than free bacteria counts during rising (.31 x 10^6 cells/mL) and flood (.46 x 10^6 cells/mL) water, and two orders of magnitude lower during declining (.09 x 10^6 cells/mL) and low water (.06 x 10^6 cells/mL). Attached bacteria were a significant fraction of the total bacteria population during rising and flood water. Free bacteria counts only gradually increased between the rising and flood water field trips. Bacteria attached to detritus appeared to constitute a major portion of the total counts in this zone. Levels of particulate matter entrained into the river were extremely high during the flood (Berry et al. 1985). Mean suspended solids values were greatest during the flood (116 mg/L) and declining (112 mg/L) water field trips in this zone.

A significant effect (0.05 probability limit) due to transects was observed in attached bacteria concentrations during the rising water field trip. Significant differences in free bacteria concentrations among stations, depths, and tide/time-of-day were observed during low water. Differences in bacteria concentrations and transect and station reflect the non-homogeneous character of this zone when freshwater flow was at or near its lowest point (between March and July). The greatest concentration of free bacteria was located in the middle portion of the water column and during the night tides in the low water sampling period.

Lower estuary (Dog Island) - Dog Island is located on a wide segment of the Gambia River (about 8 km) approximately 12 km upstream of the mouth. This zone

exhibited marine characteristics all year and was strongly influenced by the tides.

Free bacteria concentrations remained fairly uniform during rising (.94 x 10^6 cells/mL), flood (1.09 x 10^6 cells/mL), declining (.90 x 10^6 cells/mL), and low water (.83 x 10^6 cells/mL) (Fig. 2). Attached bacteria counts were one order of magnitude lower than free counts during rising (.40 x 10^6 cells/mL) and flood (.36 x 10^6 cells/mL) waters and two orders of magnitude lower during declining (.03 x 10^6 cells/mL) and low water (.05 x 10^6 cells/mL).

Free bacteria counts were relatively constant during the course of the four sampling periods, except for a small increase during flood water. Attached bacteria contributed significantly to the total bacteria counts in this zone during rising and flood water, possibly because more particulate matter was incorporated into the river from the mangrove forests and because of tidal scouring of soft bottom muds.

The decrease in attached bacteria during declining and low water was attributed to the loss of substrate from sedimentation. Significant differences were not found among free or attached bacteria concentrations due to the effects of transect, station, depth, and tide/time-of-day. This indicated that the estuary was well-mixed from tidal currents. No clear relationships were observed between chemical variables and free and attached bacteria populations.

Interzone Comparisons

The distance between Dog Island and the source of the Gambia River in Guinea is more than 1,100 kilometers. Over this distance the differences in

riparian vegetation, floodplain width, and water quality characteristics are large. The magnitude and composition of the bacterioplankton population should reflect these changes in river character.

In Guinea, the mean total bacteria concentration was 1.90 x 10^6 cells/mL with a mean free concentration of 1.88 x 10^6 cells/mL. At Kekreti, the mean total was 2.92 x 10^6 cells/mL and the mean free concentration was 2.74 x 10^6 cells/mL. Of all the sites studied, the few samples from the mangrove bolon exhibited the highest concentration of bacteria. The mean total was 4.23 x 10^6 cells/mL and the mean free concentration was 4.06 x 10^6 cells/mL.

The lower freshwater river zone (Bansang) had the greatest grand mean of the five zones (average of the grand means for the four sampling periods) for total (2.03 x 10^6 cells/mL) and free (1.98 x 10^6 cells/mL) bacterioplankton populations over the course of the four sampling periods. Kedougou had mean total (2.02 x 10^6 cells/mL) and free (1.98 x 10^6 cells/mL) bacteria concentrations only slightly lower than Bansang. Bai Tenda had a mean total of 1.51 x 10^6 cells/mL and mean free bacteria concentration of 1.28 x 10^6 cells/mL. At Dog Island the mean total was 1.15 x 10^6 cells/mL and the mean free bacteria concentration was 0.94 x 10^6 cells/mL.

Bai Tenda exhibited the highest grand mean of attached bacteria concentrations over the course of the four sampling periods (.23 x 10^6 cells/mL). This was followed by Dog Island (.21 x 10^6 cells/mL), Bansang (.05 x 10^6 cells/mL), and Kedougou (.04 x 10^6 cells/mL) in terms of mean attached bacteria concentrations.

Free bacteria were numerically more important at Bansang and Kedougou; both had smaller attached bacteria populations than Bai Tenda and Dog Island. The converse was true for attached bacteria as averaged over the course of the

four sampling periods. Bansang and Kedougou are located in the freshwater reaches of the river, while Bai Tenda and Dog Island are located in the estuarine portion of the river. Free bacteria were numerically more important in the freshwater reaches of the river apparently because they were more likely to survive and reproduce in the freshwater environment than in the estuary or sea. Attached bacteria appeared to be more important in the estuarine regions because of the presence of extensive mangrove swamps which produced litterfall throughout the year.

Figure 2 shows a drop in free bacteria concentrations during flood water at Kedougou and Bansang. Free bacteria concentrations did not fall during this same period at Bai Tenda and Dog Island. River channel widths at Kedougou (25-100 m) and Bansang (100 m) were much less than at Bai Tenda (500 m) and Dog Island (8 km). This indicated that the river channel was much narrower and that the river banks were much more confining in the upper and lower river zones as compared to the two estuarine zones. It is probable that when flood waters reached Kedougou and Bansang the concentration of free bacteria was diluted because less floodplain was inundated than at Bai Tenda and Dog Island.

Figure 4 shows the relationships between free and attached bacteria and different zones sampled over the course of four sampling periods. This figure shows the high concentrations of free bacteria at upstream sampling points that decrease markedly approaching Bai Tenda and Dog Island. At the same time, it shows the unimportance of attached bacteria in upriver zones where extensive mangrove swamps, rich in organic matter, are not present as they are in the estuary.

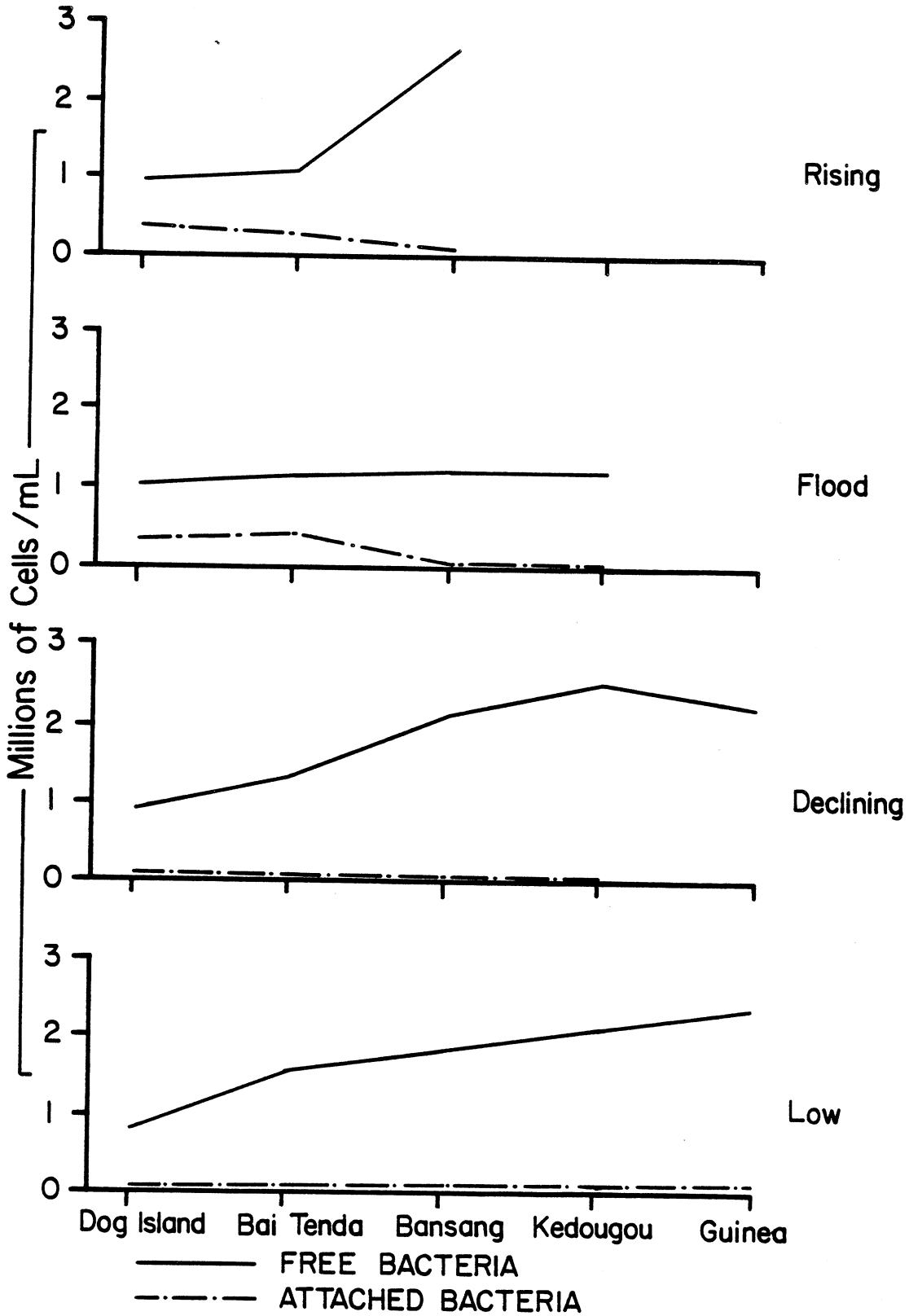

FIG. 4. The relationship between concentration of free bacteria (FB), attached bacteria (AB), and flood stage at different sampling locations on the Gambia River, 1983-1984.

Previous studies by Imevbore and Bakare (1974) of bacterioplankton in the swamps submerged by the Kainji reservoir demonstrated the preference of bacteria for particulate matter. These investigators reported concentrations of 5.1 x10^{11} cells/mL in swamp mud, 1.3 x 10^{11} cells/mL in river mud, 6.3 x 10^7 cells/mL in swamp water, and 3.5 x 10^4 cells/mL in river water. Visser (1973) also investigated pre-impoundment bacterioplankton concentrations on the Niger near Kainji. Bacterioplankton concentrations for river mud were similar (8.4 x 10^{11} cells/mL), while concentrations in the river at the surface (7.3 x 10^5 cells/mL) and in the first 3 meters (4.4 x 10^6 cells/mL) were markedly higher. Schmidt (1970) found concentrations of 2.3 x 10^5 cells/mL for the Rio Negro River and 5.0 x 10^5 cells/mL for the Solimoes River in the Amazon basin. These values do not differ significantly from Mucha (1967) who worked on the Danube River (1.5 x 10^6 - 2.6 x 10^6 cells/mL).

Seasonal Comparisons

Seasonal comparisons involving bacterioplankton in the Gambia River naturally focus on the advent, duration, and intensity of rainfall, the resultant flood and floodplain inundation, and the intervening period when there is no rainfall. Figure 4 follows the changes in the bacterioplankton population over the course of a flood cycle.

Figure 3 is a hydrograph of mean monthly flows at Gouloumbou which also traces mean free and attached bacteria concentrations (mean of grand means) over the course of the 1983-84 flood cycle. Total bacteria concentrations decreased during the transition from rising (1.84 x 10^6 cells/mL) to flood (1.44 x 10^6 cells/mL) water. During declining water the population of total bacteria increased to 1.78 x 10^6 cells/mL and then dropped to 1.61 x 10^6

cells/mL during the low water period. Attached bacteria formed a greater part of the total bacterioplankton population during rising (15.2%) and flood (16.7%) water; the attached forms dropped precipitously during declining (2.1%) and low water (1.9%).

In the interval between rising and flood waters, total bacterioplankton numbers decreased while the relative proportion of attached forms remained static. This reflected probable dilution of the total bacteria concentration and recruitment of attached forms from floodplain sediment. An increase in the total bacterioplankton population and precipitous drop in the attached bacteria population occurred during the declining water period. Active recruitment of bacteria and probable *in situ* bacterioplankton growth can account for the rise in free bacteria concentrations. The decline in attached bacteria may be attributed to sedimentation of particulate matter which served as a suitable substrate for these bacteria.

During low water the free bacteria population (1.58×10^6 cells/mL) decreased to levels close to that encountered during rising water (1.56×10^6 cells/mL). This suggests that there was a true holoplanktonic bacteria population that existed during the dry season. Attached forms during low and declining water were significantly below rising and flood water levels. This indicated that entrainment of attached forms occurred primarily during rising and flood water. Attached bacteria division on particulate matter may also have occurred during the period between rising and flood water because the attached population remained static at a time when the total bacteria population was decreasing.

PHYTOPLANKTON

Methods

Phytoplankton samples were collected on a low frequency basis according to the Greco-Latin Square sampling design. A Kemmerer bottle was used to collect samples which were immediately placed into 1-L, dark plastic bottles to which 1.5 mL of Lugol's Preservative (Prescott 1970) was added. Upon return to the laboratory, 1-L samples were allowed to settle for from 24 to 36 hours. The top 900 mL was gently siphoned off and discarded. The remaining 100 mL was stored in a 250-mL plastic bottle and used for identification and enumeration purposes. Each mL of sedimented sample therefore represented 10 mL of raw sample.

Within each set of sixteen samples at each zone per cruise, two to three samples were chosen at random and used to determine the appropriate volume of sedimented sample required to give sufficient counts. The criteria employed to determine sufficient counts were somewhat subjective. A balance was achieved between filtering as large a volume of sedimented sample as possible, counting enough fields to ensure approximately 40 counts, and completing the analysis of all samples in a timely fashion. After determining the appropriate sedimented sample volume, a qualitative scan of a few samples from each zone was performed to familiarize the investigator with the different taxa present.

A Gelman 0.45-μm backing filter was placed on the filter frit, wetted with 50% ethanol, and then a vacuum was applied so as to secure the filter. A Nuclepore 0.2-μm filter was placed on top of the Gelman filter in such a manner that no air bubbles or wrinkles were present beneath or on the filter. The filter funnel was secured in place and a known volume of sedimented sample

was transferred to the filter apparatus after the sample had been thoroughly shaken. Fifty percent ethanol was added to the sample in the filter apparatus in an effort to dry the filter as much as possible, and a vacuum was then applied. When 1 to 2 mL of sample remained in the filtering apparatus, the walls of the filter funnel were washed with 50% ethanol and the entire contents of the funnel were drawn through the filter. The vacuum was left on for an additional 10 seconds to ensure that most of the water had been removed from the filter surface.

The Nuclepore filter was removed and placed on a few drops of immersion oil which rested on a glass slide. Immersion oil was added to the top of the filter, a cover slip was put on top, and a wadded Kimwipe was used to press the cover slip on the filter and remove air bubbles and excess oil. A sample identification label was then attached to the slide. A variable number of fields on the slide were then quantitatively examined.

The identification of phytoplankton was undertaken using the keys of Bourrelly (1966, 1968, 1970) as the primary references. Additional keys in Prescott (1970) and Edmondson (1959) were employed occasionally. The unit of cells in the phytoplankton abundance measurement (cells/mL) referred to single cells (e.g., *Chlamydomonas* sp.), each distinct member of a colony (e.g., *Pediastrum* sp.), and each cell in a filament (e.g., *Anabaena* sp.). In cases where it was not possible to view septation (e.g., *Aphanizomenon* sp.), counts were made of filaments. In Tables 4-9 and in the text, most algae have been identified to the species level. Identifications of algae to the generic level was assumed correct, while species identifications were uncertain in a few cases.

Calculation of phytoplankton densities involved the following variables and constants:

N = total sum of cells counted

Af = total area of filter through which the sample was filtered

Oc = total area of ocular at 625x

F = number of ocular fields counted

C = mL of concentrated sample filtered

Ct = total mL of concentrated sample

D = total mL of original sample

$$\frac{\text{Cells}}{\text{mL}} = \frac{N}{F} \times \frac{Af}{Oc} \times \frac{1}{C} \times \frac{Ct}{D}$$

Diversity was calculated according to the formula developed by Shannon (1948).

H = species diversity index

pi = proportion of the total in the i-th category

E = the sum of

$$H = - E\ pi\ \log pi$$

Results and Discussion

The abundance and diversity of the phytoplankton in relation to transect, station, depth, and tide/time-of-day was investigated over the course of four field trips representing different hydrologic seasons: rising (July 1983), flood (October 1983), declining (December 1983), and low (March 1984) water in the lower estuary (Dog Island), upper estuary (Bai Tenda), and lower river

(Bansang) zones. Phytoplankton samples from the upper river and headwaters zone (Kedougou) were taken during flood, declining, and low water. The Kekreti dam site was sampled during declining water, while a mangrove bolon near Bai Tenda was sampled during rising and low water. Analysis of variance (ANOVA) was used to detect significant differences between the main blocking variables and phytoplankton abundance within each intensively studied zone. Phytoplankton abundance and diversity were related to chemical and physical variables within each zone and bolon studied.

Abundance and Diversity in Relation to Transect, Station, Depth, and Tide/Time-of-Day

The ANOVAs indicated that no significant differences between abundance of phytoplankton and the main blocking variables were evident during the four sampling periods at each of the four intensively studied zones: upper river, lower river, upper estuary, and lower estuary. ANOVAs comparing diversity to the main blocking variables were not performed. Summary data for diversity have indicated that there were no significant differences between phytoplankton diversity and the main blocking variables.

Abundance and Diversity in Relation to Physical and Chemical Variables

Figure 5 and Table 3 show an inverse relationship between salinity and phytoplankton abundance. At Dog Island the salinity was typically very close to that of the ocean, and the abundance of phytoplankton was low compared to the other zones. At Bai Tenda, higher cell densities were associated with lower salinities. Bansang exhibited typical freshwater conditions and consistently had higher cell densities compared to the other zones. Table 3

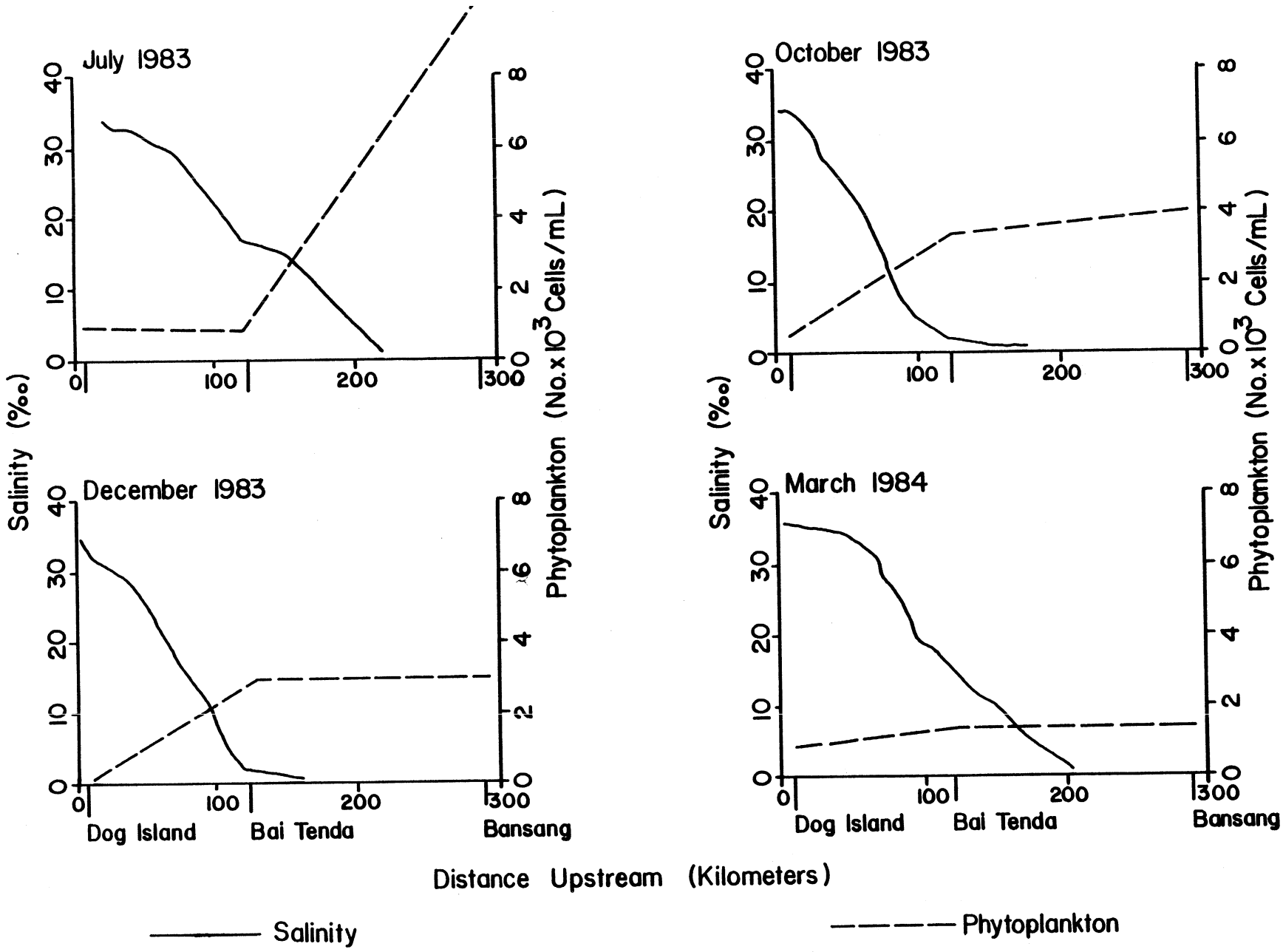

FIG. 5. Phytoplankton abundance in relation to salinity and distance upstream during different flood stages on the Gambia River, 1983-1984.

TABLE 3. Correlation coefficients between phytoplankton abundance (cells mL^{-1}) and biological and chemical variables. All coefficients are statistically significant at the P <.001 probability level except conductivity which is significant at the P <.01 level.

Variable	Correlation
Water temperature	.398 (239)
Conductivity	-.220 (175)
Salinity	-.415 (115)
pH	-.384 (239)
Alkalinity	-.284 (239)
Soluble reactive phosphorus	-.323 (219)
Nitrate-nitrogen	.241 (223)
Chlorophyll	.533 (237)
Free bacteria	.237 (239)

Values in parentheses indicate the number of pairs of observations.

shows an inverse relationship among a suite of variables associated with salt water in the Gambia River.

As was expected, phytoplankton abundances paralleled changes in chlorophyll concentrations over time and space. In the lower river zone, chlorophyll a values decreased substantially between rising (12.69 μg/L) and flood (2.34 μg/L) water. A corresponding decrease in algal density (10,122 cells/mL to 4,005 cells/mL) was also noted. Between flood (2.34 μg/L) and declining (2.41 μg/L) water, chlorophyll a values increased slightly, while density decreased from 4,005 cells/mL to 2,949 cells/mL during the same period. Between declining (2.41 μg/L) and low (2.01 μg/L) water, chlorophyll a and phytoplankton density (2,949 cells/mL to 1,291 cells/mL) decreased.

In the lower estuary zone a decrease in chlorophyll a values (3.89 μg/L to 1.96 μg/L during the period between rising and flood water was paralleled by a decrease in phytoplankton density (954 cells/mL to 506 cells/mL). Between declining (1.94 μg/L) and low water (3.11 μg/L) chlorophyll a values

increased in conjunction with phytoplankton density (171 cells/mL to 841 cells/mL).

In the upper river zone phaeopigment decreased from flood (0.68 μg/L) to declining (0.49 μg/L) to low (0.17 μg/L) water. A corresponding decrease in phytoplankton densities from 1,857 cells/mL to 901 cells/mL to 233 cells/mL during the same time periods was also noted. In the lower river zone phaeopigment decreased progressively from rising (1.52 μg/L) to flood (1.14 μg/L) to declining (0.86 μg/L) to low (0.50 μg/L) water. Parallel decreases in algal density from 10,122 cells/mL to 4,005 cells/mL and from 2,949 cells/mL to 1,291 cells/mL during the same time periods were noted. The upper estuary exhibited increases in phaeopigment and density between rising (1.77 μg/L and 920 cells/mL) and flood (2.31 μg/L and 3,132 cells/mL) water. Between flood and declining (1.88 μg/L and 2,859 cells/mL) water both phaeopigment and density dropped. This was also true for the period between declining and low (1.32 μg/L and 1,320 cells/mL) water. In the lower estuary phaeopigment decreased from 1.44 μg/L (rising) to 0.79 μg/L (flood) to 0.68 μg/L (declining). Phaeopigment concentration increased to 2.13 μg/L during low water. Phytoplankton density also decreased from 954 cells/mL (rising) to 506 cells/mL (flood) to 171 cells/mL (declining). Density increased during low water to 841 cells/mL.

River Zone Description

Headwaters (Guinea and Kekreti) - The sampling period for rising water in Guinea was June 1984. Initial sampling was carried out in pools. Streamflows increased from 0 to over 40 m^3/s during the course of the field trip due to precipitation upstream of the sampling site, so a comparison between pooled and

flowing water samples was possible. Pooled samples during rising water had a greater density and diversity (1,715 cells/mL, 1.29) at the 1.0-m depth as compared with the 2.5-m depth (1,049 cells/mL, 1.00). Flowing river water appeared well mixed and samples exhibited comparable density and diversity values at 1.0-m depth (684 cells/mL, 2.24) and at the surface (731 cells/mL, 2.19). The mean density of pooled (1,382 cells/mL) water samples was almost double what was found in the flowing water samples (708 cells/mL). Mean diversity was lower during the period of pooling (1.14) than during the period when flow was restored (2.22). The total mean density and diversity (mean of all means for that sampling period) in Guinea (1,045 cells/mL, 1.68) was comparable to what was found at Bai Tenda and Dog Island (Figs. 6 and 7) during the rising water sampling period in July 1983. A diatom, Melosira granulata, was the dominant alga found in the headwaters region during this time period.

The headwaters region was not sampled during the period immediately following the rainy season. The declining water sampling was undertaken in December 1983. Gambia River streamflows at the sampling site exceeded 50 m^3/s. Phytoplankton density was greater near the banks (278 cells/mL) than in midstream (188 cells/mL), while diversity was the same (1.86). The grand mean (mean of all means for that zone) density was 242 cells/mL, a value similar to what was recorded at Dog Island (171 cells/mL) during the same sampling period. No phytoplankton species were dominant.

During low water in Guinea, phytoplankton density in pools (498 cells/mL) was greater than in midstream (312 cells/mL). Diversity was greater in midstream (2.30) than in pools (2.02). The total mean density (405 cells/mL) and diversity (2.16) were similar to what was found at Kedougou during the same sampling period. No dominant members of the phytoplankton assemblage were found.

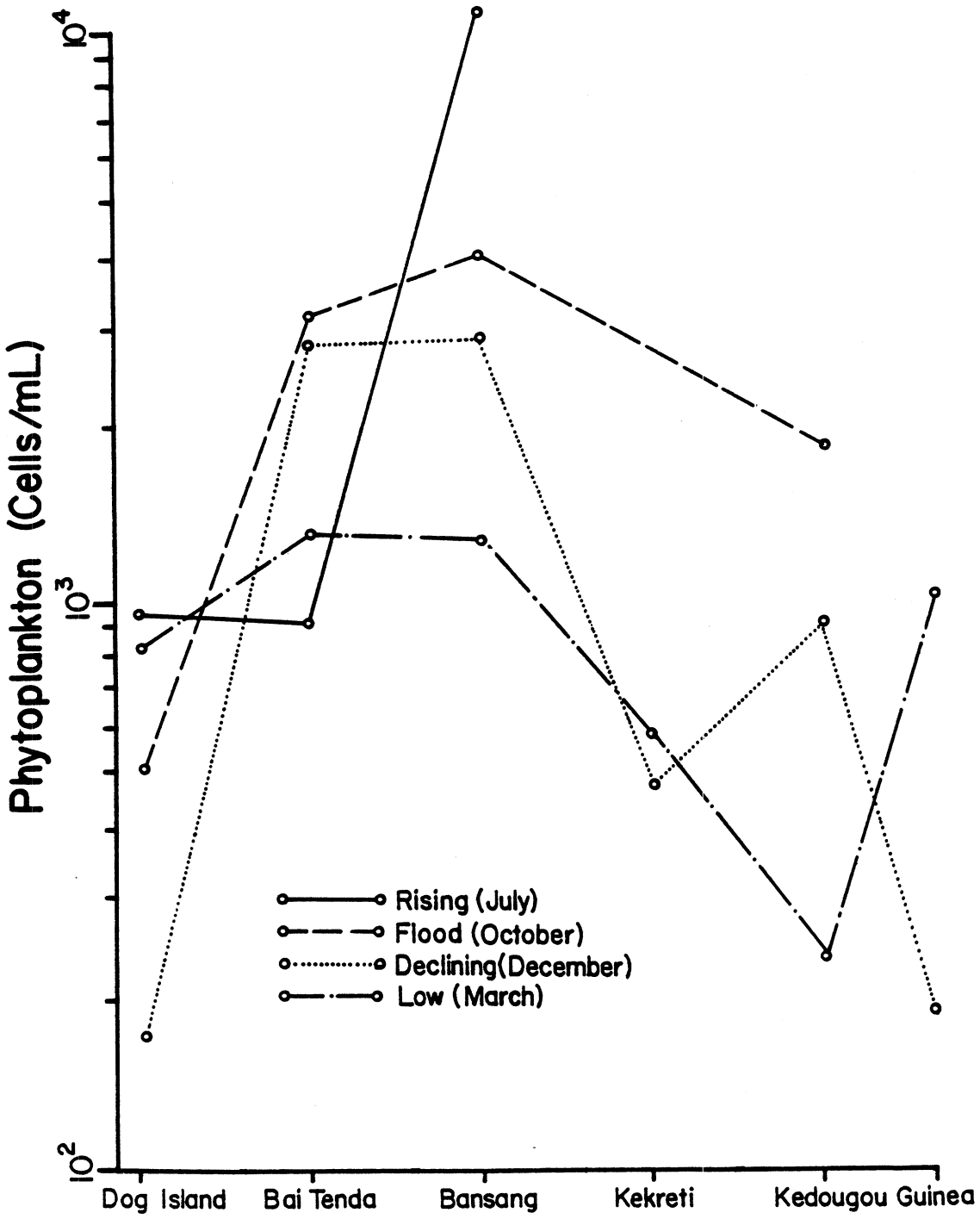

FIG. 6. Phytoplankton abundance in relation to flood stage at different sampling locations in the Gambia River, 1983-1984.

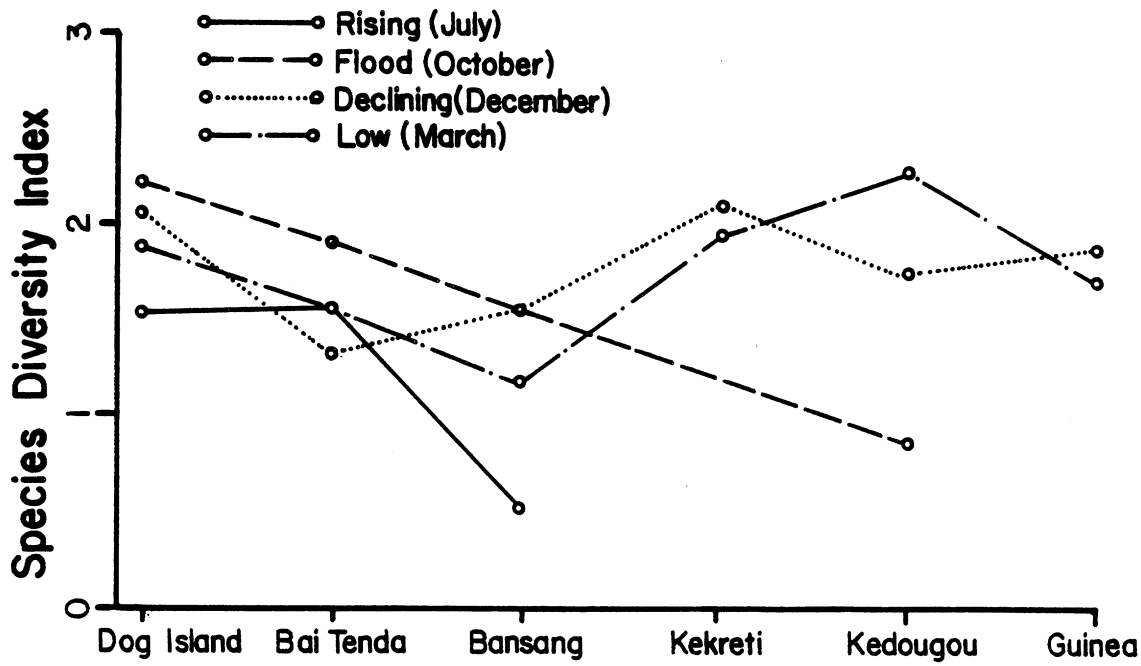

FIG. 7. Phytoplankton species diversity in relation to flood stage at different sampling locations in the Gambia River, 1983-1984.

The Kekreti dam site was sampled during declining water (December). Phytoplankton density was greater nearshore than in midstream. Diversity was similar in both environments. The total mean density (485 cells/mL) was low and comparable to what was found in Guinea and at Dog Island during the same sampling period. Mean diversity (2.12) was also similar to what was found in Guinea and Dog Island during declining water. No one species of phytoplankton was found to be dominant.

The headwaters region of the Gambia River appeared less dominated by diatoms than other regions within the basin. An average of twenty-two species were found over the course of all the sampling periods; approximately 54% of the species identified were diatoms. Three different species were found in Guinea and Kekreti during every sampling period: Achnanthes lanceolata (a diatom), Chlamydomonas sp. (a green alga), and Hapalosiphon fontinalis (a blue-green alga). Table 4 lists all the species encountered in this region.

The density and diversity of the phytoplankton in pools were greater at intermediate depths (1.0 m) than near the bottom (2.5 m). Under flowing water conditions, density and diversity were similar at both depths. Mean phytoplankton density in pools was almost twice as great as in flowing waters. Pools act like small lakes and generally have a higher phytoplankton density than flowing water. Diversity was greater in flowing water than in pools, which suggested that turbulence resuspended settled algal species and incorporated epiphytic algae from surrounding vegetation.

Upper river (Kedougou) - No significant differences between blocking variables and the abundance of phytoplankton were found during the periods of flood, declining, and low water. As indicated by the summary of species diversity,

TABLE 4. Algal species encountered in the headwaters zone (Guinea) of the Gambia River.

Perennial species:

Achnanthes lanceolata
Chlamydomonas sp.
Hapalosiphon fontinalis

Other species encountered:

Division Chrysophycophyta
Class Bacillariophyceae

Cocconeis diminuta
Cymbella ventricosa
Eunotia veneris
Gomphonema angustatum
Melosira granulata
Melosira herzogii
Melosira islandica (helical)
Melosira islandica (straight)
Navicula sp. I
Navicula confervacea
Navicula crucicula
Navicula cryptocephala
Navicula placentula
Navicula pupula
Neidium pygmea
Nitzschia acicularis
Nitzschia amphibia
Nitzschia dissipata
Nitzschia linearis
Nitzschia palea
Nitzschia paradoxa
Pinnularia acrosphaeria
Rhoicosphenia curvata
Rhopaplodia gibba
Surirella sp.
Surirella ovata
Synedra ulna I
Synedra ulna II
Tabellaria flocculosa

Division Chlorophycophyta
Class Chlorophyceae

Ankistrodesmus convolutus
Chlorococcum wimmeri
Chodatella quadriseta
Cosmarium sp.
Crucigenia tetrapedia
Dispora crucigenoides
Kirchneriella obesa
Pediastrum tetras
Pediastrum clathratum
Pleurotaenium minutum
Poloidon didymos
Scenedesmus crassus
Scenedesmus flexulossa
Scenedesmus protruberens
Staurastrum sp.
Staurastrum sebaldi
Teilingia granulata
Tetrallantos lagerheimii

Division Cyanochloronta
Class Cyanophyceae

Dermocarpa sp.
Microcystis sp.

no significant differences between diversity and the blocking variables were noted. These results suggested that algal abundance and diversity were homogeneous in relation to transect, station, depth, and time-of-day.

The most abundant algal form found during flood water was the blue-green alga Hapalosiphon fontinalis which consisted of decaying cells and budding fragments. During declining water the two most prevalent forms were Hapalosiphon fontinalis and a filamentous fungus tentatively identified as belonging to the Fungi Imperfecti. Three species of blue-green algae were frequently encountered during low water, but no dominant alga was evident. These algae were Hapalosiphon fontinalis, Synechococcus sp., and Anabaena sp. Figures 6, 7, and 8 outline changes in phytoplankton abundance and diversity over the course of the three sampling periods. The total mean cell counts and diversity values were 1,857 cells/mL and 0.86 during flood water, 901 cells/mL and 1.73 during declining water, and 233 cells/mL and 2.23 during low water.

An average of thirty-one species of algae were encountered over the course of the three sampling periods. Approximately 65% of the identifiable species were diatoms. Nine perennial species were found in this zone: Synedra ulna, Nitzschia amphibia, Navicula cryptocephala, Navicula confervacea, Rhoicosphenia curvata, Synedra rumpens, Achnanthes lanceolata, Chlamydomonas sp. and Hapalosiphon fontinalis. The first seven species listed are diatoms. Table 5 lists all the species encountered in this zone.

The decrease in phytoplankton abundance over the course of the first three sampling periods at Kedougou was related to the timing of the annual flood which exhibited the greatest flows during September and October (Fig. 9). Although the total quantity of algal cells in the river may have remained the same, dilution by runoff from the annual flood most likely

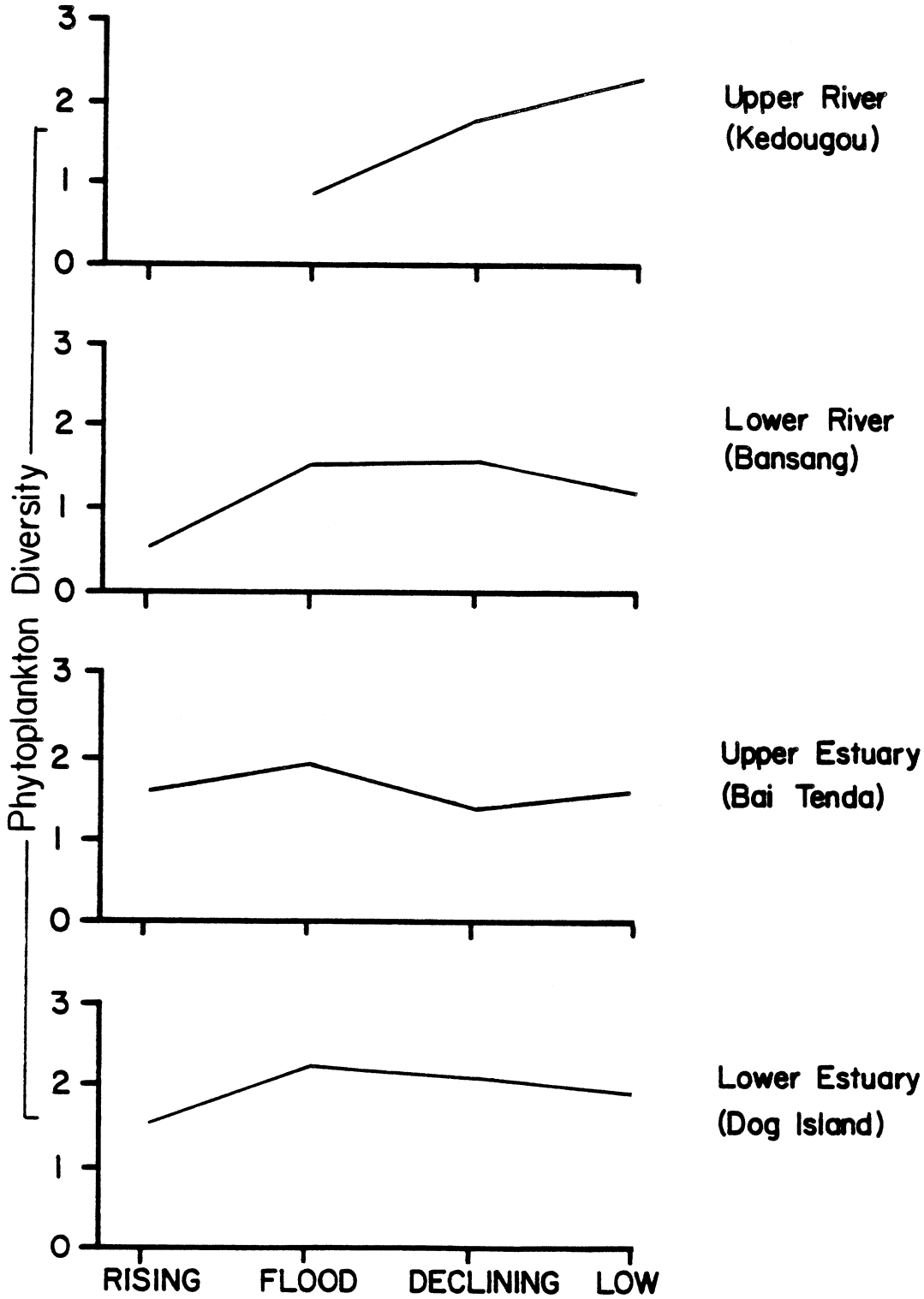

FIG. 8. Phytoplankton species diversity in relation to flood stage at four intensively studied river zones on the Gambia River, 1983-1984.

TABLE 5. Algal species encountered in the upper river zone (Kedougou) of the Gambia River.

Perennial species:

Achnanthes lanceolata
Chlamydomonas sp.
Hapalosiphon fontinalis
Navicula confervacea
Navicula cryptocephala
Nitzschia amphibia
Rhoicosphenia curvata
Synedra rumpens
Synedra ulna I

Other species encountered:

Division Chrysophycophyta
Class Bacillariophyceae

Cymbella sp.
Cymbella ventricosa
Eunotia faba
Fragillaria virescens
Gomphonema angustatum
Melosira arenaria
Melosira binderana
Melosira distans
Melosira herzogii
Melosira islandica (helical)
Melosira islandica (straight)
Melosira italica
Navicula crucicula
Navicula gibbula
Navicula placentula
Navicula pupula
Neidium iris
Nitzschia acicularis
Nitzschia dissipata
Nitzschia linearis
Nitzschia obtusa
Nitzschia palea
Nitzschia paradoxa
Nitzschia tryblionella
Pinnularia undulata
Surirella sp.
Synedra actinastroides
Synedra capitata
Synedra ulna II
Synedra ulna III
Tabellaria flocculosa

Class Chrysophyceae
Lagynion sp.

Division Chlorophycophyta
Class Chlorophyceae

Ankistrodesmus convolutus
Chlorococcum wimmeri
Chodatella quadriseta
Cosmarium sp.
Crucigenia tetrapedia
Euastrum sp.
Euastrum pectinatum
Pseudotetraspora gainii
Scenedesmus crassus
Scenedesmus flexulossa
Scenedesmus incrassatus
Scenedesmus protruberens
Staurastrum sp.
Staurastrum sebaldi
Tetrallantos lagerheimii
Treubaria triappendiculata

Division Pyrrophycophyta
Class Dinophyceae

Peridinium sp.

Division Cyanochloronta
Class Cyanophyceae

Anabena sp.
Lyngbya sp.
Synechococcus sp.

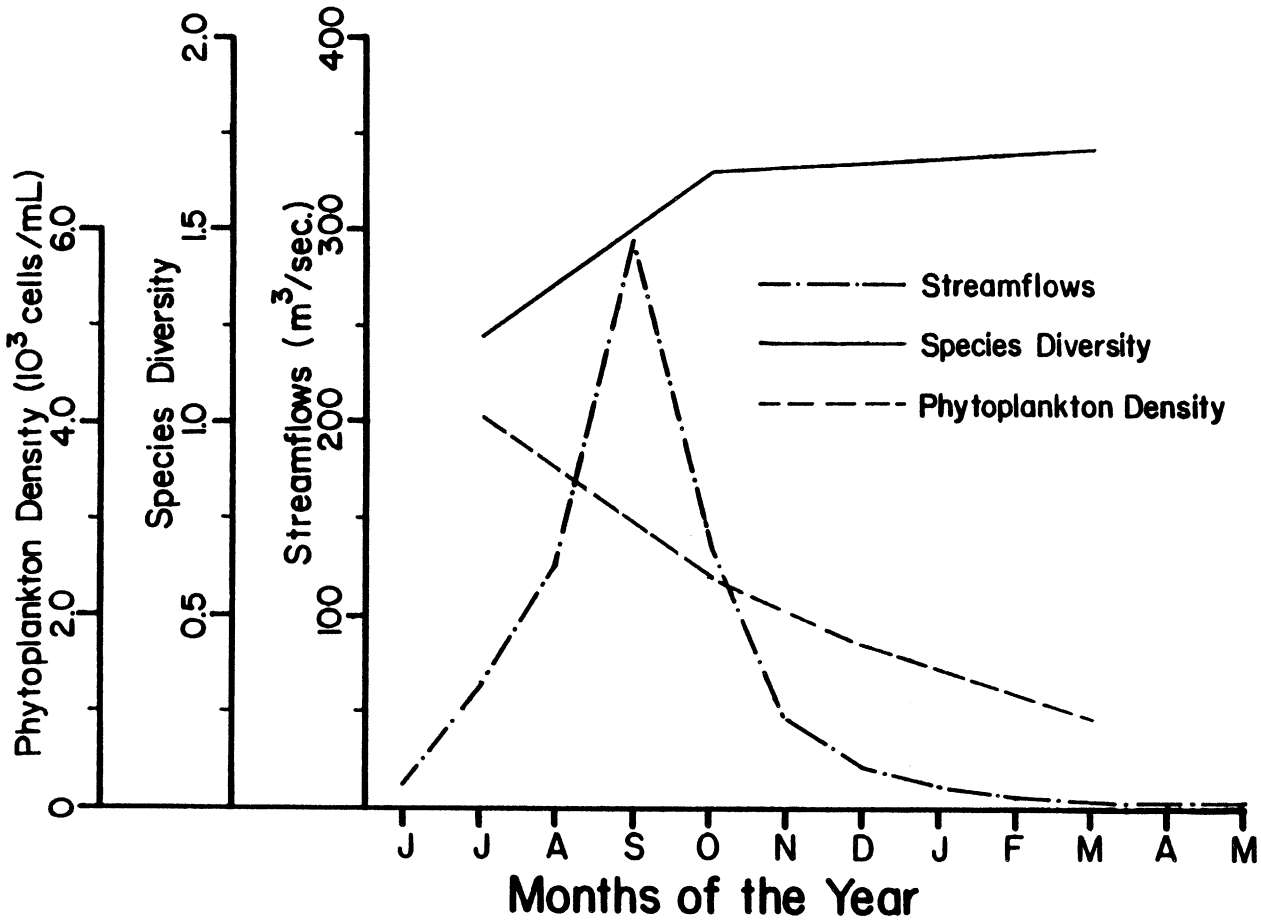

FIG. 9. The relationship between streamflow, phytoplankton, abundance, and diversity in the Gambia River at Kedougou, 1983-1984.

reduced the concentration of algae. Increased turbulence caused by the flood appears to have brought about an increase in diversity through resuspension of settled algae and spores and the introduction of algal material from adjacent floodplains. Resuspension has been shown to be important for the growth of Melosira spp. in various English lakes (Lund 1954, 1955) and in Lake Victoria (Fish 1956, Talling 1957) near the headwaters of the Nile River.

The upper river zone exhibited correlations between chlorophyll a and free bacteria, phaeopigment and attached bacteria, and phaeopigment and phytoplankton. These correlations have pointed to a possible close relationship between bacterioplankton and phytoplankton abundance.

Lower river (Bansang) - During the four sampling periods algal abundances were homogeneous and unaffected by any of the four blocking variables. ANOVA was not performed for species diversity. Summary data have indicated that diversity was homogeneous in relation to transect, station, depth, and tide/time-of-day.

During the rising water field trip the most abundant alga was a helical form of Melosira islandica, a diatom. The same helically shaped alga, along with other members of the genus, was most abundant during flood water. Occasionally, a fungus belonging to the Fungi Imperfecti and Hapalosiphon fontinalis, a blue-green alga, were the dominant algae during flood water. The two most abundant declining water forms were the helical form of Melosira islandica along with Melosira distans. The low water period was again dominated by the helical form of Melosira islandica. The grand mean (the mean of the sixteen samples taken during each sampling period) cell counts decreased from 10,122 cells/mL to 4,005 cells/mL between rising and flood water, while

species diversity increased from 0.53 to 1.59. Between flood and declining water, the density decreased to 2,949 cells/mL while the diversity remained constant at 1.57. During low water, density decreased to 1,291 cells/mL and the diversity decreased to 1.17.

On the average, twenty-nine species were encountered in this zone over the course of the four sampling periods. Seventy percent of the identifiable forms were diatoms. Eight perennial species were found in this zone: *Melosira islandica* (helical), *Melosira islandica* (straight), *Melosira granulata* (small), *Melosira distans*, *Melosira herzogii*, *Nitzschia acicularis*, *Achnanthes lanceolata*, and *Hapalosiphon fontinalis*. The first seven species listed are diatoms. Table 6 lists the species encountered in this zone.

The decrease in phytoplankton abundance and the concomitant increase in diversity also appear to have been related to the timing of the annual flood. Density was greatest in this zone when streamflow was reduced; diversity was at its peak when flow was greatest. The apparent inverse relationship between phytoplankton abundance and river discharge has been alluded to by van Oye (1926) who worked on the Congo River, Holden and Green (1960) who studied phytoplankton and zooplankton abundance on the River Sokoto, and Talling and Rzoska (1967) who studied the development of the phytoplankton populations on the Blue Nile in relation to the hydrological regime.

Bansang was similar to Kedougou in that many correlations existed between chemical variables and the abundance of the biota: phaeopigment and attached bacteria, suspended solids and attached bacteria, chlorophyll *a* and phytoplankton, and phaeopigment and phytoplankton. These correlations have also pointed to a possible association between bacterioplankton and phytoplankton populations.

TABLE 6. Algal species encountered in the lower river zone (Bansang) of the Gambia River.

Perennial species:

Achnanthes lanceolata
Hapalosiphon fontinalis
Melosira distans
Melosira granulata
Melosira herzogii
Melosira islandica (helical)
Melosira islandica (straight)
Nitzschia acicularis
Nitzschia obtusa
Nitzschia palea
Nitzschia tryblionella
Pinnularia undulata
Stauroneis crucicula
Stephanodiscus invisitus
Surirella sp.
Surirella angustata
Surirella ovata
Synedra ulna
Synedra ulna II
Synedra ulna III

Other species encountered:

Division Chrysophycophyta
Class Bacillariophyceae

Achnanthes sp.
Amphora ovalis
Attheya zacharasi
Cocconeis diminuta
Coscinodiscus denarius
Cyclotella meneghiniana I
Cyclotella meneghiniana II
Cymatopleura solea
Cymbella ventricosa
Diploneis elliptica
Diploneis smithii
Gomphonema herculeana
Melosira granulata (large)
Melosira italica
Navicula sp. I
Navicula sp. II
Navicula confervacea
Navicula cryptocephala
Navicula placentula
Navicula pupula
Navicula subtilissima
Nitzschia sp.
Nitzschia amphibia
Nitzschia dissipata
Nitzschia hungarica
Nitzschia linearis

Division Chlorophycophyta
Class Chlorophyceae

Ankyra judai
Chlamydomonas sp.
Chlorococcum wimmeri
Closterium sp.
Closterium nematodes
Cosmarium sp.
Crucigenia tetrapedia
Pediastrum clathratum
Pediastrum tetras
Scenedesmus sp.
Scenedesmus brasiliensis
Scenedesmus crassus
Scenedesmus protruberens
Scenedesmus smithii
Stichococcus sp.
Tetrastrum heterocanthum

Division Cyanochloronta
Class Cyanophyceae

Anabaena sp.
Aphanizomenon holsetica
Merismopedia sp.
Microcystis sp.

Upper estuary (Bai Tenda) - During the periods of rising and flood water, no significant differences in the abundance of the phytoplankton were caused by blocking variables. ANOVA was not performed for species diversity. Summary data for species diversity have shown that no significant differences in diversity values were caused by blocking variables. Algal abundance and species diversity appeared to be homogeneous throughout this zone. The most abundant alga found during rising water was the centric diatom, *Cyclotella meneghiniana*, while during flood water the two most abundant algae were *Hapalosiphon fontinalis* and the helical form of *Melosira islandica*. During the declining water field trip, the most abundant alga found was *Stichococcus* sp., a filamentous green alga, which was previously encountered in this zone during rising water. The low water period was dominated by another filamentous green alga, *Geminella* sp. The abundance of the phytoplankton increased from 920 cells/mL to 3,132 cells/mL between rising and flood water. Diversity values also increased from 1.54 to 1.89 during the same time period. Between the flood and declining water field trips, phytoplankton density remained somewhat static at approximately 2,900 cells/mL, while diversity decreased to 1.31. Low water phytoplankton densities decreased to 1,320 cells/mL, while diversity increased to 1.57. These relationships are shown in Figures 6 and 8.

The density of the phytoplankton increased between the rising and flood water field trips in this zone, most likely as a result of the introduction of phytoplankton from upstream. *Melosira islandica* (helical) had previously only been dominant in the lower river zone. With the onset of the flood, its dominance expanded into the upper estuary zone. The variety and abundance of other *Melosira* spp. also increased.

An average of thirty species were identified in this zone throughout the year. Seventy-one percent of the identifiable algae were diatoms. Seven perennial species were found: Melosira islandica (helical), Coscinodiscus excentricus, Coscinodiscus denarius, Coscinodiscus rothii, Cyclotella meneghiniana, Cyclotella comta, and Hapalosiphon fontinalis. The first six species listed are diatoms. Table 7 lists all the species encountered in this zone throughout the year.

Bolon (near Bai Tenda) - During the rising water field trip the bolon exhibited a mean algal density (886 cells/mL) and diversity (1.23) comparable to Bai Tenda (920 cells/mL, 1.54) and Dog Island (954 cells/mL, 1.55) at the same period. The greatest densities were exhibited at stations between the mouth and the source of the bolon. Day ebb densities and diversities (1,065 cells/mL, 1.36) were generally greater than the day flood (707 cells/mL, 1.10) densities and diversities. Two centric diatoms, Cyclotella meneghiniana and Coscinodiscus rothii, and a green alga, Stichococcus sp., were dominant during the first sampling period.

The bolon was not sampled for phytoplankton during the flood and declining water stages. Bolon phytoplankton density (580 cells/mL) during the low water period was greater than that found at Kedougou (233 cells/mL) but less than that at Bansang (1,291 cells/mL), Bai Tenda (1,320 cells/mL), and Dog Island (841). The diversity in the bolon (2.05) was similar to what was found in the upper river (2.23) and lower estuary (1.88) zones during the same sampling period. At the bolon mouth during the low water sampling period, phytoplankton density (744 cells/mL) was greater than at the source (416 cells/mL); diversity was only slightly higher at the source. Day ebb density

TABLE 7. Algal species encountered in the upper estuary zone (Bai Tenda) of the Gambia River.

Perennial species:

Coscinodiscus denarius
Coscinodiscus excentricus
Coscinodiscus rothii
Cyclotella comta
Cyclotella meneghiniana I
Hapalosiphon fontinalis
Melosira islandica (helical)

Other species encountered:

Division Chrysophycophyta
Class Bacillariophyceae

Achnanthes lanceolata
Caloneis sp.
Chaetoceros subtilis
Cocconeis diminuta
Cocconeis placentula
Coscinodiscus concinnus
Coscinodiscus nitidus
Cyclotella meneghiniana
Cymatople solea
Cymbella sp.
Cymbella affinis
Cymbella ventricosa
Diploneis elliptica
Eunotia faba
Fragillaria virescens
Melosira distans
Melosira granulata
Melosira granulata (large)
Melosira herzogii
Melosira islandica (straight)
Melosira italica
Navicula sp. I
Navicula confervacea
Navicula cryptocephala
Navicula gastrum
Navicula pupula
Nitzschia acicularis
Nitzschia amphibia
Nitzschia dissipata
Nitzschia linearis
Nitzschia littoralis
Nitzschia obtusa
Nitzschia tryblionella
Pinnularia gibbera
Rhaphoneis amphiceros
Rhoicosphenia curvata
Stenoptero intermedia
Stephanodiscus sp.
Surirella angustata
Synedra actinastroides
Synedra ulna I
Synedra ulna II

Class Xanthophyceae
Tribonema sp.

Class Chrysophyceae
Lagynion sp.

Division Pyrrophycophyta
Class Dinophyceae

Peridinium sp.

Division Euglenophycophyta
Class Euglenophyceae

Trachelomonas sp.

Division Chlorophycophyta
Class Chlorophyceae

Actinastrum rhapidoides
Ankistrodesmus convolutus
Ankyra judai
Chlamydomonas sp.
Chlorococcum wimmeri
Closterium venus
Cosmarium sp.
Geminella sp.
Nephrochlamys subsolitaria
Palmella miniata
Pleurotaenium minuta
Scenedesmus brasiliensis
Scenedesmus crassus
Scenedesmus smithii
Schroderia setigera
Stichococcus sp.
Tetrallantos lagerheimii

Division Cyanochloronta
Class Cyanophyceae

Anabaena sp.
Microcystis sp.
Pleurocapsa sp.

(706 cells/mL) was greater than day flood density (454 cells/mL). Diversity index values during day ebb (2.02) and day flood (2.07) tidal cycles were similar. During the low water sampling period no dominant algae were found near the bolon source. Near the mouth Geminella sp. and Stichococcus sp. were frequently encountered.

An average of nineteen species of algae were found in the bolon during rising and low water. Approximately 68% of the identifiable species were diatoms. Eight species were found during both sampling periods: Melosira islandica (helical), Navicula cryptocephala, Synedra ulna, Cyclotella meneghiniana, Cyclotella comta, Coscinodiscus rothii, Cosmarium sp., and Stichococcus sp. The first six species are diatoms. Table 8 lists all the species encountered in this zone.

Day ebb densities were greater than day flood densities during both rising and low water field trips. Diversity values were similar. During the rising water field trip phytoplankton density appeared to be greater at the two stations farthest upstream when compared with the stations nearest the mouth. Diversity values were comparable. During low water the density was greater at the mouth than at the source; diversity values were similar.

Lower estuary (Dog Island) - The lack of significant differences caused by blocking variables in the abundance and diversity of the phytoplankton during the four sampling periods was also observed in the lower estuary zone. As with the other zones, this indicated that algal abundance and diversity were homogeneous in relation to the main blocking variables.

TABLE 8. Algal species encountered in the mangrove bolons of the Gambia River.

Perennial species:

Coscinodiscus rothii
Cosmarium sp.
Cyclotella comta
Cyclotella meneghiniana
Melosira islandica (helical)
Navicula cryptocephala
Stichococcus sp.
Synedra ulna I

Other species encountered:

Division Chrysophycophyta
Class Bacillariophyceae

Achnanthes lanceolata
Chaetoceros subtilis
Coscinodiscus denarius
Coscinodiscus excentricus
Coscinodiscus nitidus
Cyclotella meneghiniana II
Gyrosigma sp.
Gyrosigma attenuatum
Navicula sp. I
Navicula crucicula
Nitzschia amphibia
Stephanodiscus sp.
Synedra actinastroides
Synedra ulna II

Class Chrysophyceae
Lagynion sp.

Division Euglenophycophyta
Class Euglenophyceae

Trachelomonas sp.

Division Pyrrophycophyta
Class Dinophyceae

Peridinium sp.

Division Cyanochloronta
Class Cyanophyceae

Hapalosiphon fontinalis

Division Chlorophycophyta
Class Chlorophyceae

Chlamydomonas sp.
Closterium sp.
Geminella sp.
Pleurotaenium minutum

While the centric diatoms, Cyclotella meneghiniana and Coscinodiscus rothii, appeared in this zone throughout the four field trips, true dominants were not evident. Hapalosiphon fontinalis was also frequently encountered. The abundance of the phytoplankton decreased from 954 cells/mL to 506 cells/mL between rising and flood water, while the species diversity index values increased from 1.55 to 2.21. Phytoplankton density decreased to 171 cells/mL during declining water, while the diversity remained somewhat static at 2.06. During low water the phytoplankton density had increased to 841 cells/mL, while the diversity decreased to 1.88. Figures 6 and 7 outline these relationships.

An average of twenty-six species were encountered in this zone throughout the year. Seventy-nine percent of the identifiable forms were diatoms. Six species were found in this zone perennially: Cyclotella meneghiniana, Cyclotella comta, Coscinodiscus rothii, Coscinodiscus denarius, Gyrosigma sp., and Hapalosiphon fontinalis. The first five forms listed are diatoms. Table 9 lists every species encountered in this zone.

In this zone a relationship between chlorophyll a and phytoplankton density was observed. Between the rising and flood water field trips chlorophyll a values and phytoplankton density decreased. The period between declining and low water was characterized by an increase in phytoplankton abundance and chlorophyll a concentration. The concentration of phaeopigment also paralleled increases and decreases in algal density (Table 3).

Figure 6 shows a decline in phytoplankton abundance during the flood and declining water field trips that appears to have been associated with the annual flood. Diversity appears to have increased during flood water due to the introduction of freshwater algal forms from upstream (Fig. 8).

TABLE 9. Algal species encountered in the lower estuary zone (Dog Island) of the Gambia River.

Perennial species:

Coscinodiscus denarius
Coscinodiscus rothii
Cyclotella comta
Cyclotella meneghiniana I
Gyrosigma sp.
Hapalosiphon fontinalis

Other species encountered:

Achnanthes lanceolata
Amphora ovalis
Asterionella formosa
Attheya zachariasi
Chaetoceros subtilis
Coscinodiscus excentricus
Coscinodiscus nitidus
Cyclotella meneghiniana II
Cymbella affinis
Diatoma vulgare
Diploneis interrupta
Diploneis maulerii
Diploneis smithii
Fragillaria virescens
Gyrosigma sp.
Gyrosigma acuminatum
Melosira islandica (helical)
Navicula sp. I
Navicula sp. II
Navicula confervacea
Navicula crucicula
Navicula cryptocephala
Navicula gastrum
Nitzschia amphibia
Nitzschia dissipata
Nitzschia filiformis
Nitzschia holsatica
Nitzschia lineais
Ornithoceros sp.
Pinnularia gibbera
Rhaphoneis amphiceros
Rhizosolenia sp.
Stephanodiscus sp.
Surirella sp.
Surirella angustata
Surirella biseriata
Surirella delicatissima
Synedra actinastroides
Synedra ulna I
Synedra ulna II
Triceratium favus
Triceratium patagonicum

Class Chrysophyceae
Lagynion sp.

Division Euglenophycophyta
Class Euglenophyceae

Trachelomonas sp.

Division Chlorophycophyta
Class Chlorophyceae

Actinastrum rhapidoides
Chlamydomonas sp.
Closterium venus
Closterium sp.
Cosmarium sp.
Nephrochlamys subsolitaria
Schroderia setigera
Staurastrum sp.
Stichococcus sp.

Division Cyanochloronta
Class Cyanophyceae

Anabena sp.
Merismopedia sp.
Microcystis sp.

Division Pyrrophycophyta
Class Dinophyceae

Ceratium furca
Glenodinium trochoiderum
Peridinium sp.

Interzone Comparisons

During the rising water field trip, the total mean phytoplankton density (sixteen values) was greatest in the lower river (10,122 cells/mL) and was more than one order of magnitude greater than what was exhibited in the upper estuary (920 cells/mL) and lower estuary (954 cells/mL) zones. The phytoplankton abundance was highest in the lower river zone (4,005 cells/mL) and decreased at the upper estuary (3,132 cells/mL) and lower estuary (506 cells/mL) zones during the flood water field trip. The upper river zone during flood water exhibited a density of algae (1,857 cells/mL) greater than the lower estuary but less than the other two zones.

The lower river zone exhibited the highest phytoplankton density (2,949 cells/mL) during the declining water field trip. The upper estuary had a comparable density of 2,859 cells/mL, while the upper river zone exhibited a density of 901 cells/mL during the same sampling period. The lower estuary zone again had the lowest density (171 cells/mL). During the low water sampling period the lower river (1,291 cells/mL) and the upper estuary (1,320 cells/mL) zones exhibited comparable densities. The lower estuary had a density of 841 cells/mL, while the upper river zone exhibited the lowest density (233 cells/mL). These relationships are outlined in Figure 6.

Visser (1973), in a pre-impoundment study of the Kainji Lake area in Nigeria, found markedly higher phytoplankton densities: 6.6×10^4 cells/mL in surface water, 4.2×10^4 cells/mL in the first three meters, and 7.1×10^6 cells/mL in the mud. In a study of Amazonian waters, Schmidt (1970) found peaks in algal densities that were similar to those found in this study: 1.5×10^4 cells/mL in the Solimoes River and 1.0×10^4 cells/mL in the River Negro.

During the rising water field trip, the lower river exhibited a low total mean species diversity index value (0.53), while in the upper and lower estuary zones diversity index values were much higher (1.54 and 1.55 respectively). The diversity of the phytoplankton during the flood water field trip increased progressively from the upper river (0.86), to the lower river (1.59), to the upper estuary (1.89), to the lower estuary (2.21). During the declining water field trip, species diversity decreased progressively from Kedougou (1.73), to Bansang (1.57), to Bai Tenda (1.31). Dog Island samples again exhibited the highest diversity (2.06). Conditions changed considerably between the declining and low water field trips. During the latter, the upper river zone exhibited a diversity (2.23) greater than the lower estuary zone (1.88). The upper estuary zone showed an increase in diversity (1.57), while the lower river zone diversity (1.17) decreased from the declining water sampling period. These relationships are shown in Figure 8.

The grand mean (mean of all means for all four sampling periods in each zone) phytoplankton density was greatest in the lower river zone (4,592 cells/mL), followed by the upper estuary (1,276 cells/mL), the upper river (997 cells/mL), the bolon (733 cells/mL), the lower estuary (618 cells/mL), and the headwaters zone in Guinea (544 cells/mL). The grand mean species diversity values for each zone appeared to be inversely related to phytoplankton density. The headwaters zone, which had the lowest density, exhibited the greatest diversity (1.96), followed by the lower estuary (1.92), the bolon (1.64), the upper river (1.60), the upper estuary (1.58), and the lower river (1.22). The inverse relationship between density and diversity reflects the characteristics of Shannon's species diversity index, which measures richness and evenness. Richness refers to the quantity of indi-

viduals within each taxa. Evenness refers to the spread or partition of individuals within each taxa. The lower river zone, which exhibited a low diversity value, was "rich" in numbers of individual cells that were not spread evenly through different taxa. Conversely, the headwaters region had a number of different taxa each with approximately the same number of individuals.

The headwaters region was characterized by having no dominant algae (except for Melosira granulata during rising water) for most of the year. The upper river zone was dominated by Hapalosiphon fontinalis and occasionally other blue-green algae throughout the year. The lower river zone was dominated by the genus Melosira throughout the year. One species, Melosira islandica (helical), was dominant, but as many as five other members of the same genus were present in lower densities at the same time. The upper estuary zone was dominated by different algae during each sampling period, as was the mangrove bolon during each of the two sampling periods. The lower estuary zone was primarily dominated by the centric diatoms belonging to the genera Cyclotella and Coscinodiscus and Hapalosiphon fontinalis, a blue-green alga, throughout the year.

In the lower Nile River before impoundment, Abdin (1948b) found that the diatoms Melosira granulata and Melosira varians were most abundant. Occasionally blue-green algae such as Microcystis sp. and Anabaena sp. were nearly as abundant as Melosira sp. Egborge (1974) showed that the River Oshun in Nigeria before impoundment was also dominated by diatoms. Blue-green algae were never dominant and their density was frequently less than that of the green algae.

The prevalence of diatoms increased going downstream. The headwaters region had an average of 55% diatoms, the upper river (65%), the lower river (70%), the upper estuary (71%), the bolon (68%), and the lower estuary (79%). Algae found in one zone throughout the course of the year were frequently encountered in adjacent zones. Achnanthes lanceolata, a diatom, was found in the headwaters, upper river, and lower river regions perennially. Chlamydomonas sp., a unicellular green alga, was found in the headwaters and upper river zones throughout the year. These two algae appeared restricted to the freshwater portions of the river.

The blue-green alga Hapalosiphon fontinalis exhibited a perennial and pan-basinal character unmatched by any other alga. The greatest densities were exhibited in the freshwater portions of the river, but this alga could be found in all zones throughout the year (the only exception being the bolon during rising water). Melosira islandica (helical) exhibited a range throughout the year from the lower river to the bolon and upper estuary zones. Both algae appeared to be halotolerant, primarily freshwater species. Primarily saltwater algal species such as Cyclotella meneghiniana, Cyclotella comta, and Coscinodiscus rothii were found throughout the year in the bolon and upper and lower estuary zones.

One hundred and fifty-four different species of planktonic algae were identified in the course of this study. Diatoms (97 species), green algae (41 species), and blue-green algae (10) were the most important groups of phytoplankton. Brook (1954) listed 160 species of plankton algae from the White Nile and Blue Nile. According to Brook and Rzoska (1954), Rzoska et al. (1955), Prowse and Talling (1958), and Talling and Rzoska (1967), who studied post-impoundment plankton assemblages, very few of the 160 listed species were

important in quantitative terms. Melosira granulata and its variety angustissima, Anabaena flos-aquae f. spiroides, and Lyngbya limnetica were dominant in the Blue Nile and White Nile. Noted in the Blue Nile after construction of the Roseires Dam were Microcystis flos-aquae and a member of the epiplankton Phormidium mucicola (Hammerton 1972). In the Gambia River, before impoundment, approximately three species belonging to the genus Melosira, one specie of fungus, and one species of blue-green algae (Hapalosiphon fontinalis) were quantitatively important. It remains to be seen whether more blue-green algae will assume a greater quantitative importance in the river after the construction of one or more dams.

Seasonal Comparisons

The headwaters zone exhibited the greatest grand mean algal densities during the rising water period (June) (1,045 cells/mL). Declining water (December), in contrast, was characterized by markedly lower densities (242 cells/mL in Guinea and 485 cells/mL in Kekreti) which increased slightly (405 cells/mL) at low water. Figure 6 shows the changes in phytoplankton densities over time at each of the intensively studied zones. Phytoplankton densities decreased from rising to flood water at the lower river and lower estuary zones.

The decrease in phytoplankton density in the lower river and lower estuary zones during the period between the rising and flood water field trips appeared to be attributable to dilution. Phytoplankton abundance increased in the upper estuary zone during this period. This appeared to have been the result of the introduction of phytoplankton from upstream freshwater regions where they were more abundant. Between the flood and declining water field trips phytoplankton abundances decreased in all zones, while between the declining and low water

field trips phytoplankton density decreased in all zones except the lower estuary. Dilution and increased turbidity after the flood most likely served to cause the general decrease in abundance in all zones.

Figure 7 depicts the changes in phytoplankton species diversity over the course of the four sampling periods. Between the rising and flood water field trips, the lower river, upper estuary, and lower estuary zones exhibited increases in species diversity. Between the flood and declining water field trips, species diversity decreased slightly in both the lower river and lower estuary zones. At the upper estuary zone species diversity declined to its lowest level, while at the upper river zone diversity increased during the same time period. Between the declining and low water field trips diversity decreased at the lower river and lower estuary zones. Species diversity increased slightly at the upper estuary zone and to a greater degree at the upper river zone during the same time period.

Figure 9 shows the changes in phytoplankton density and diversity in relation to streamflows over the course of the four sampling periods. Phytoplankton abundance and diversity values represent averages of the values from each of the zones during one particular sampling period. As streamflows increased, phytoplankton density decreased and species diversity increased. The increase in diversity was apparently a result of the introduction of freshwater forms downstream, the incorporation of soil algae, and the resuspension of viable cells that had previously settled.

During the rising water field trip *Hapalosiphon fontinalis* was the only alga to be found throughout the entire basin. The flood water period had five algae, three of which were diatoms, that were found throughout the basin: *Hapalosiphon fontinalis*, *Chlamydomonas* sp., *Nitzschia amphibia*, *Navicula*

confervacea, and Achnanthes lanceolata. Achnanthes lanceolata and Chlamydomonas sp. were previously only found in the headwaters and upper river zones. They appear to have been washed downstream by the flood. The number of pan-basinal species decreased during declining water. Only Hapalosiphon fontinalis and Navicula cryptocephala were found in each zone. This was equally true during the low water period which was characterized by the presence of Hapalosiphon fontinalis and Nitzschia amphibia throughout the basin. These observations have indicated the importance of the flood in distributing phytoplankton throughout the length of the river.

In the lower river zone, chlorophyll a values decreased between the rising and flood water field trips and were accompanied by a corresponding decrease in phytoplankton density. The same was true for the lower estuary zone, where a decrease in chlorophyll a values was paralleled by a decrease in phytoplankton density between rising and flood water. Phaeopigment concentrations decreased in the lower river and lower estuary zones between the rising and flood water field trips as well. An increase in phaeopigment concentrations between the rising and flood water field trips at the upper estuary was matched by a corresponding increase in algal density. Decreases in phaeopigment concentrations at all zones between flood and declining water were paralleled by decreases in algal density.

PROCESS STUDIES

Methods

Uptake of glucose was considered an indication of the metabolic activity of the bacteria community. The method used in this study was based on the principle of adding a trace amount of carrier-free radioactive glucose to

natural bacteria populations and measuring the rate at which the glucose is consumed by that population (Azam and Holm-Hansen 1973). Uptake rates were interpreted as gross uptake of the added substrate (Wright and Burnison 1979).

The experimental procedure was as follows. A sample of river water was collected with either a 5-L Niskin bottle or a 3.5-L Kemmerer bottle. Fifteen mL of sample were immediately placed into a sterile 25-mL screw-top test tube. The test tube was sterilized in an autoclave at approximately 2 atmospheres pressure and 127°C (260°F) for 20 min. Sterile tubes were kept tightly stoppered until used in the field. Sample water was placed into the tubes with a 5-mL macro-pipette (three 5-mL injections). Incubations were conducted in triplicate (three tubes) for each water sample. Usually from three to six water samples were collected from each sampling location, with each sample from a different depth. Two to four sets of incubations were conducted during each field trip in each zone for a total of 6 to 24 incubations conducted in triplicate.

Each test tube with 15 mL of sample was injected with 2 μCi of ^{3}H glucose as soon as all the incubation test tubes were filled. The glucose had a specific activity of 30 Ci/mmole and was carrier-free. The weight of the injected glucose was 12 ng which when diluted in 15 mL of sample yielded a final concentration of 4.44 nM. Injection of the radionuclide was conducted in subdued light and the samples were incubated in the dark at a temperature within 2C° of the original water temperature. The 2 μCi of radioactive glucose was contained in 0.2 mL of sterile water which was slightly acidic with an approximate pH of 4.0. The glucose was prepared from sterile stock purchased in the United States and diluted to the correct working concentration. Five mL of glucose solution were sealed into glass ampoules and autoclaved before shipment to Africa. One 5-mL ampoule was opened immediately

prior to each set of incubations and the unused portion discarded. Extreme care was taken not to contaminate samples in the tropical environment which had an abundance of aerosol bacteria.

Samples were incubated for 2 hours, after which they were immediately filtered through a 4.5-cm diameter filter with a pore size of 0.2 microns (μm). Samples were filtered with the aid of a slight vacuum (about one half atmos.). Damp filters were removed from the filtering apparatus and placed in a scintillation vial containing 10 mL of a water-dispersing scintillation cocktail. Vials were assayed for radioactivity on a Phillips Scintillation Counter at the Centre des Recherches Oceanographiques de Dakar-Thiaroye. Uptake of glucose was calculated by the use of an external standard and corrected for quench and time-zero uptake by the following formula:

$$\text{Uptake in ng/L/h} = \frac{[\text{cpm uptake} - \text{time zero uptake}]}{[\text{cpm added} \times \text{time of incubation}]} \times \text{quench ratio} \times 800$$

where the factor 800 is used to convert the concentration of glucose in the test tube (4.44 nM) to weight in ng of glucose.

Primary productivity was estimated using the ^{14}C uptake method as described in Hall and Moll (1975). The basic procedure followed standard techniques for the *in situ* incubation of phytoplankton. That procedure was as follows. Stocks of ^{14}C bicarbonate were purchased in the United States and cut to working strength with a slightly basic (pH 8.0) solution of distilled-deionized water. The pH of this solution was adjusted using trace amounts of carbonate and .01N HCl. One-mCi lots of ^{14}C were diluted to 1 L to yield a final concentration of 1 μCi/mL. Two mL of the diluted ^{14}C solution were pipetted into 2-mL soft glass ampoules and the ampoules were sealed with a

torch. The ampoules were autoclaved to check for leaks as well as to make the ^{14}C bicarbonate solution sterile, and then packed for shipment to Africa.

The incubations were conducted at the same time as the glucose uptake incubations were carried out. In as many cases as possible, heterotrophic uptake and primary productivity incubations were carried out on the same water samples. Generally, primary production incubations were conducted on samples collected from one, two, and three meters below the surface. In about one third of the experiments, a sample collected either above one meter or below three meters was also incubated.

Samples were collected with either a 3.5-L Kemmerer or a 5-L Niskin bottle. The incubations were conducted as a set of two clear or light bottles and one opaque or dark bottle. The bottles were hard glass 250-mL reagent bottles. Sample water was transferred into the incubation bottles under subdued light. After all bottles were filled, the contents of one ampoule containing 2 μCi of ^{14}C bicarbonate in 2 mL of solution were transferred into each of the incubation bottles. The bottles were then tightly stoppered and attached to a chain and float for incubation in the river at the same depth from which they were collected. Incubation periods were kept to four hours or less, with a target of four hours.

At the termination of the incubation, the bottles were removed from the river and stored in the dark until the contents were filtered. The radioactivity accumulated by the algae over the course of the incubation was assayed by liquid scintillation counting using the same equipment for the glucose uptake experiments. Each primary productivity bottle was filtered through a 0.45-μm pore size Millipore filter which was 4.5 m^3/s in diameter. Care was taken to keep the sample in the dark during the filtration process;

small hoods were placed over the filtration funnels during filtration. After the sample was completely filtered, damp filters were placed into empty scintillation vials and 1 mL of .1 N HCl was added to the vial. The acid soak removed carbonate build-up on the filter which was known to be a problem in the estuarine segment of the Gambia River. Filters were allowed to soak for 2 hours and then 10 mL of water-dispersing scintillation cocktail was added to each vial.

External standards were prepared for each 1 mCi lot of ^{14}C used overseas. Those external standards were counted at the same time as the samples and used to determine the activity of radioactivity added to each incubation bottle. Water samples for alkalinity determinations were collected and analyzed immediately after incubation samples were placed in the river. In most cases, sufficient sample water existed to use for alkalinity determinations from the same sample as well as for the primary productivity incubations. The uptake of carbon by algae was computed with the following formula:

$$\text{C uptake in } \mu\text{g C/L/h} = \frac{[\text{light uptake-dark uptake}] \times W \times 1.06}{[\text{activity added} \times \text{duration of incubation}]}$$

where W = the weight of carbon in the original sample water as computed from the alkalinity and salinity, and 1.06 = a factor to correct for the discrimination against the uptake of ^{14}C versus ^{12}C.

Results from the primary productivity and glucose uptake experiments were entered into the University of Michigan computing system for more extensive data analyses. The MIDAS (Fox and Guire 1976) software package was used to compute descriptive statistics as well as correlations among uptake values and selected physical, chemical, and biological variables.

Results and Discussion

Heterotrophic Uptake

The uptake of glucose was used as an indication of the overall level of dark heterotrophy in the river water. Because the experiments were conducted in the dark, uptake was interpreted as dark heterotrophy as contrasted to light or photoheterotrophy (Vincent and Goldman 1980). Furthermore, the natural concentration of glucose dissolved in the water was not measured, thus the observed uptake of glucose was considered as net uptake of added substrate (Azam and Holm-Hansen 1973). Despite these qualifications of the experiments, the uptake of glucose in the dark has been accepted as one of the routine estimates of ecosystem water column heterotrophy (Wright and Burnison 1979).

The uptake of simple sugars such as glucose in the dark is generally attributed to the activity of bacteria, particularly bacterioplankton (Wright and Burnison 1979). However, there is a growing body of evidence that suggests that under certain conditions algae may take up a significant fraction of the sugar (Moll 1984). As a result, allocating all of the uptake to the bacteria population is not always a safe assumption. But, for the most part, bacteria are considered the primary pathway of incorporation of organic materials into the food web. Comparing the overall flux of organic material into the food web either by bacterial heterotrophy or algal photosynthesis is not possible with a database such as the Gambia River basin study. But, the relative magnitudes of heterotrophy and autotrophy can be compared by such factors as the size of the algal and bacterial populations, their relative metabolic activity (process studies), and the structure of the higher levels of the food web.

All indications were that the Gambia River was dominated by heterotrophic activity. The levels of carbon fixation by photosynthesis were very low (see Primary Productivity section below), and the euphotic zone was extremely small. The results concurred in that only a small portion of the water column (upper one to one and a half meter) supported meager levels of primary productivity. There were exceptions to these results which are discussed in detail below. But, the relative importance of heterotrophic activity cannot be overstated in the Gambia River. For these reasons, the trends in heterotrophic activity, although imperfectly estimated by glucose uptake, are of great importance in biological activity of the river.

Figure 10 and Table 10 show some spatial and temporal trends in glucose uptake. Based on the results from 141 incubations conducted in triplicate, a pronounced seasonal and spatial pattern was observed. Seasonally, glucose uptake increased monotonically from the first field trip in August (rising water) to the last trip in March (low water). Average uptake values were approximately three times higher in March than August (Table 10), increasing from approximately 7 ng glucose/L/hr to over 21 ng glucose/L/hr. The spatial trend among zones was even more pronounced. The lowest uptake rates were consistently observed in the lower estuary zone, followed by the lower river, the upper estuary, and the upper river (Table 10). The uptake averages increased from slightly below 5 ng glucose/L/hr to over 39 ng glucose/L/hr, almost an 8-fold increase (Table 10).

The trends in glucose uptake are much more apparent when observed as a plot of uptake versus season by zone (Fig. 10). The difference between the lower estuary zone and the other three zones is large both in terms of magnitude of uptake as well as seasonal patterns. The lower estuary zone had

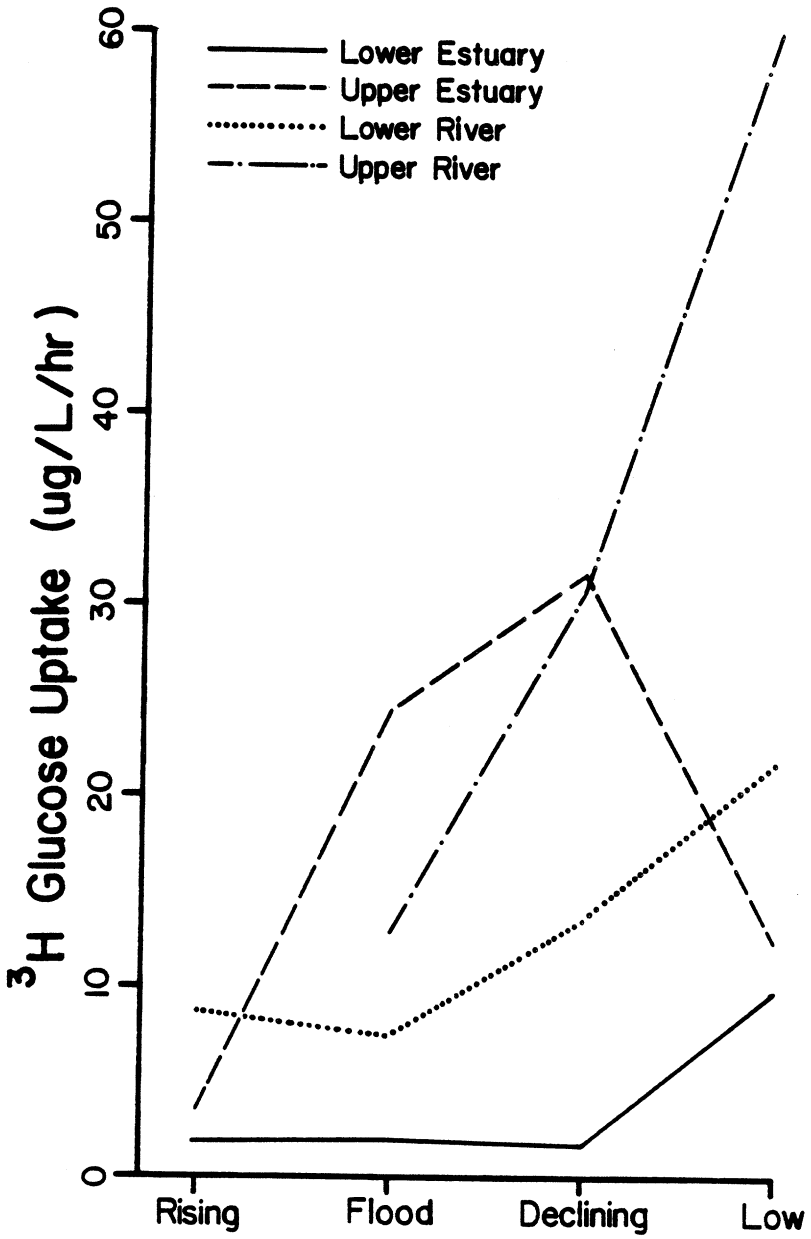

FIG. 10. Uptake of ^{3}H glucose in relation to flood stage at four intensively studied river zones on the Gambia River, 1983-1984.

TABLE 10. Glucose uptake for different strata of The Gambia River. Values reported in ng glucose/L/hr are means ± standard errors.

SEASON			
Rising	Flood	Declining	Low
6.95 ± 1.37	8.91 ± 1.88	18.23 ± 3.40	21.01 ± 3.05
(33)	(32)	(35)	(41)

ZONE			
Lower Estuary	Upper Estuary	Lower River	Upper River
4.75 ± 0.98	16.52 ± 2.86	12.97 ± 2.14	39.52 ± 8.57
(35)	(37)	(46)	(9)

TIDE	
Flood	Ebb
5.32 ± 1.56	4.32 ± 1.27
(15)	(20)

Values in parentheses are number of incubations conducted in triplicate.

uniformly low uptake rates except for a slight increase between the declining (December) and low (March) waters field trips. The other three zones displayed trends that were similar to one another with relatively low uptake rates in August (rising waters), increasing to an annual maximum in December (declining waters), and remaining high through March. The inference from these results is that the lower estuary does not act in concert with the rest of the river; this result is compatible with findings for many other physical, chemical, and biological variables (Berry et al. 1985). The lower estuary zone evidently derives its characteristics from the nearshore marine environment rather than the river as do the other three zones. In the other three zones, the onset of the annual flood appeared to stimulate a large increase in heterotrophic activity, possibly from an influx of allochthonous materials carried into the river by runoff.

The analysis of physical and chemical variables showed that tide/time-of-day was an important factor in determining the status of almost every variable (Berry et al. 1985). The overall conclusion was that the shifts in the direction of the currents associated with the change of the tides brought about a significant change in the physical, chemical and biological regime. The same was true for glucose uptake in the upper estuary and lower river zones (Table 11). In those zones uptake differed by a factor of 2 to 3 between the ebb and flood tides (Table 10). However, the direction of the change was not consistent; uptake increased on ebb tides in the upper estuary zone, but decreased in the lower river zone. There was little difference in rates of glucose uptake between tides in the lower estuary zone.

Glucose uptake is strongly controlled by the size of the bacteria population (Jones 1971). Thus, comparing magnitudes of uptake is difficult unless the extent of the bacteria population is also known. Enumeration of the bacteria population was a routine part of the Gambia River Basin Study (see BACTERIOPLANKTON section). While every sample used for a glucose uptake experiment did not have a matching bacteria count, samples were collected from the same location as uptake samples less than 6 hours before or after the incubation samples. These data allow comparison of means of uptake and bacterial abundances from the same zone and/or same field trip. Table 11 is a summarization of bacterial abundances over four field trips and four zones. The results are presented as free-living bacteria (bacterioplankton), bacteria attached to detritus, and the ratio of free to attached. Table 12 presents biomass adjusted glucose uptake as ng glucose/L/hr/million cells/mL (uptake divided by biomass).

TABLE 11. Bacteria abundance for different strata of the Gambia River. Values are in millions of cells per mL ± standard errors with number of observations.

FREE			
Season			
R	F	D	L
1.56 ± 0.14 (48)	1.20 ± 0.07 (64)	1.73 ± 0.10 (64)	1.58 ± 0.08 (64)
Zone			
LE	UE	LR	UR
.939 ± 0.05 (64)	1.29 ± 0.06 (64)	1.98 ± 0.09 (64)	1.99 ± 0.13 (48)
ATTACHED			
Season			
R	F	D	L
.283 ± 0.04 (48)	.240 ± 0.05 (64)	.0485 ± 0.009 (64)	.0320 ± .008 (64)
Zone			
LE	UE	LR	UR
.211 ± 0.03 (64)	.229 ± 0.05 (64)	.0638 ± 0.01 (64)	.0396 ± 0.008 (48)
FREE BACTERIA/ATTACHED BACTERIA			
Season			
R	F	D	L
5.51	5.00	35.67	49.38
Zone			
LE	UE	LR	UR
4.45	5.63	31.23	50.25

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River, UR = Upper River.

TABLE 12. Glucose uptake adjusted for bacteria biomass. Values are ng glucose/L/L/million cells/mL.

Season			
R	F	D	L
3.77	6.19	10.25	13.03
Zone			
LE	UE	LR	UR
4.13	10.88	6.35	19.47

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River, UR = Upper River.

The distribution of bacteria has been discussed in detail above, but briefly summarized in Table 11 as follows. Free bacterioplankton concentrations remained relatively constant among seasons, but increased significantly with distance up the river. Free bacteria concentrations were over two times higher in the upper river zone compared to the lower estuary. Attached bacteria concentrations declined significantly among seasons, beginning at 0.283 million cells/mL in August (rising waters) and falling to 0.032 million cells/mL by March (low water). Spatially, attached bacteria concentrations were the opposite of free bacteria, and were lowest in the upper river and highest in the lower estuary. Presented as a ratio of free to attached bacteria, the results are very dramatic. Ratios increased from about 5 in the rising waters to almost 50 in the low waters. Spatially, ratios increased from slightly below 5 in the lower estuary to over 50 in the upper river zone.

The results of uptake and biomass determinations are compared in Table 12 as glucose uptake adjusted for counts. Considered among seasons, there was an increase in activity from 3.77 to 13.03 ng glucose/L/hr/million cells/mL.

Although this is a somewhat large range, it is not highly variable considering the diversity of habitats and seasons included in those ratios. The ratios considered among zones range from 4.13 to 19.47, about the same magnitude as among seasons. Again, this is not an extremely large range. The ecological inference from these results is that while bacteria appeared somewhat more metabolically active in the low water season and the upper river zone, glucose uptake was greatly controlled by the size of the population present. The size of the population was determined by a variety of ecological factors as discussed above.

Comparison of glucose uptake results to physical, chemical, and biological variables clearly showed the inverse relationship between uptake and the presence of salt water. Table 13 shows the significant correlations among uptake and physical-chemical variables. The suite of variables associated with salt water, which included salinity, dissolved oxygen, pH, and alkalinity, was negatively correlated with glucose uptake. Correlations among glucose uptake and soluble nutrients followed a seasonal trend. Uptake and nutrients both tended to increase during the low water season. Higher glucose uptake was observed from samples collected closer to the bottom of the river. This correlation appears to arise from slightly higher bacterial biomass promoting higher rates of uptake.

Primary Productivity

The estimation of autotrophy by algae is somewhat more straight-forward than estimates of heterotrophy. The ^{14}C uptake technique, while fraught with numerous errors, is a relatively standard part of aquatic science research (Hall and Moll 1975). Within certain limits, results can be compared from one

TABLE 13. Correlation coefficients between ^{3}H glucose uptake and biological and chemical variables. Correlations between uptake and pH, suspended solids, total nitrogen, and attached bacteria are significant at the $P < .05$ level. Correlations between soluble reactive phosphorus and uptake are significant at the $P < .01$ level. All other correlations are significant at the $P < .001$ level.

Variable	Correlation
Depth of sample	.333 (119)
Salinity	-.541 (73)
Dissolved oxygen	-.368 (119)
pH	-.227 (119)
Alkalinity	-.301 (119)
Suspended solids	.233 (119)
Soluble silica	.415 (119)
Soluble reactive phosphorus	-.261 (119)
Nitrate-nitrogen	.324 (119)
Total nitrogen	-.207 (119)
Attached bacteria	-.195 (119)

Values in parentheses indicate the number of pairs of observations.

study to another or from one location to another. For these reasons, the results from the ^{14}C incubations in the Gambia River have a slightly broader interpretation. The experimental design of the process studies called for ^{14}C incubations at the same time, location, and depth as the glucose uptake incubations. Thus the same trends and patterns can be evaluated as above.

Table 14 and Figure 11 present the results of the primary productivity measurements in units of μg C fixed/L/hr. A total of 143 sets of three bottles (2 light, 1 dark with light uptake adjusted for dark uptake) were incubated over the course of the study. Considered among seasons, ^{14}C uptake was low during the flood and declining waters (October and December) and over two times higher during the rising and low waters (August and March). On a spatial basis, ^{14}C uptake was uniform among zones except for the lower river zone which had an average of less than one half of the other three zones (Table 14).

TABLE 14. Productivity, chlorophyll, and assimilation ratios for different strata of the Gambia River. Chlorophyll values are in µg/L, uptake are µg C/L/hr, and assimilation ratios are uptake/chlorophyll. Values are means ± standard errors with number of observations.

^{14}C UPTAKE			
Season			
R	F	D	L
2.76 ± 0.06 (23)	1.04 ± 0.34 (33)	1.09 ± 0.21 (41)	2.85 ± 0.57 (46)
Zone			
LE	UE	LR	UR
1.96 ± 0.38 (34)	2.26 ± 0.77 (32)	0.958 ± 0.34 (42)	2.27 ± 0.57 (11)
CHLOROPHYLL			
Season			
R	F	D	L
7.36 ± 0.38 (174)	1.50 ± 0.06 (264)	1.74 ± 0.05 (270)	2.87 ± 0.09 (260)
Zone			
LE	UE	LR	UR
2.53 ± 0.08 (270)	2.37 ± 0.10 (305)	4.62 ± 0.27 (309)	0.749 ± 0.04 (84)
ASSIMILATION RATIO			
Season			
R	F	D	L
0.38	0.69	0.63	0.99
Zone			
LE	UE	LR	UR
0.77	0.95	0.21	3.03

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River, UR = Upper River.

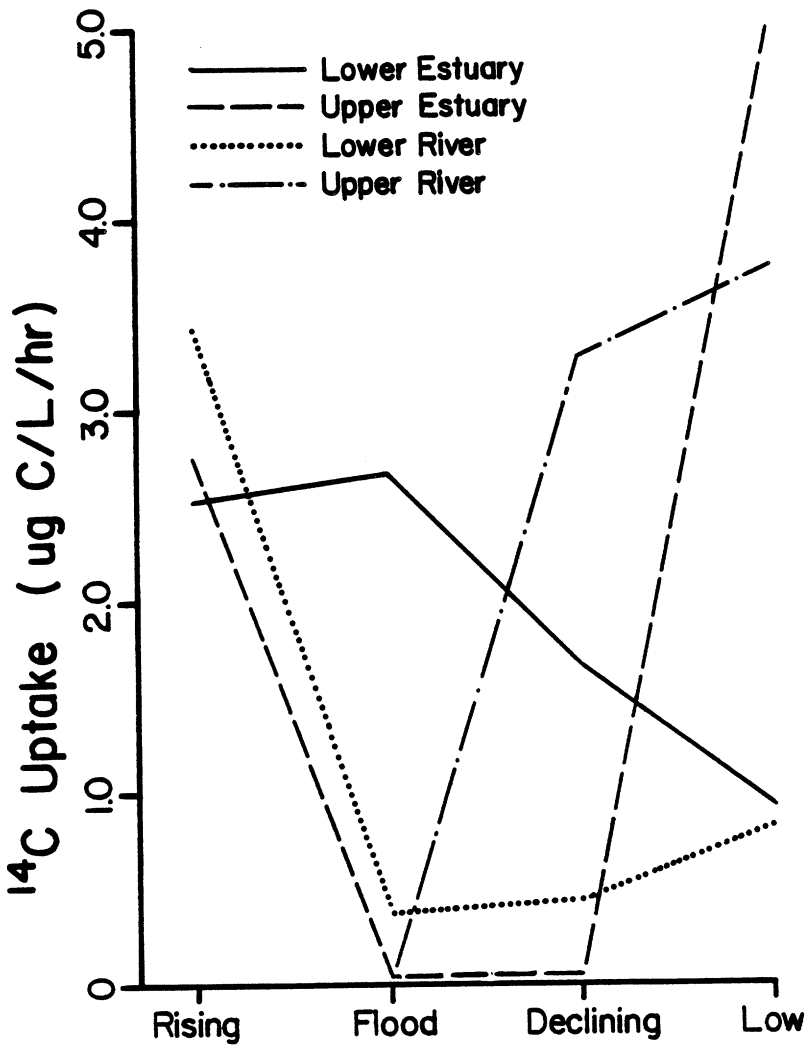

FIG. 11. ^{14}C uptake in relation to flood stage at four intensively studied river zones on the Gambia River, 1983-1984.

Primary productivity showed a high level of interaction when viewed on a zone by cruise basis (Fig. 11). Uptake rates in all zones were high during rising waters. Similar to glucose uptake, the lower estuary zone displayed a trend that differed from the other zones. Uptake rates remained high in the lower estuary through the flood and began to drop to an annual low during March (low water). In contrast, the other three zones had extremely low uptake rates during the flood and recovered at differing rates throughout the year. The upper river rates returned to pre-flood levels by the declining waters field trip (December), while the lower river zone had not recovered by the low water filed trip (March).

Tide changes in the estuary and lower river brought about significant changes in chlorophyll concentrations (Berry et al. 1985). However, the same tide changes did not significantly alter rates of ^{14}C uptake. As explained below, many factors contribute to primary production rates. The synergism of physical-chemical shifts with the tides served to suppress changes in ^{14}C uptake.

Similar to the analysis of the glucose uptake data, the ^{14}C uptake results can be presented as a ratio of uptake to biomass. These ratios were determined by using averages from each field trip and each zone. The ratios computed were assimilation ratios generated by dividing ^{14}C uptake by chlorophyll biomass. The chlorophyll biomass and assimilation ratios in Table 14 show several trends. Chlorophyll concentrations were very high during the rising waters field trip, declined to an annual low during the flood, and increased through the remaining two field trips (Table 14). Considered on a spatial basis, chlorophyll concentrations in the two estuarine zones were similar, high in the lower river, and very low in the upper river (Table 14).

The assimilation ratios showed that productivity per unit of biomass was fairly uniform among seasons, but very different among zones. The ratio varied from 0.38 to 0.99 among the four seasons (Table 14), which indicated little seasonality in primary productivity. But, the ratio varied from 0.21 in the lower river zone to 3.03 in the upper river zone; the ratios in the two estuarine zones were almost the same at 0.77 and 0.95 for the lower and upper estuary zones, respectively. With the exception of the value of 3.03, these ratios were low compared to other environments (Wetzel 1983). This large variance in the ratio among zones could be attributed to the diversity of the physical and chemical environment, particularly the nutrient regime. Large shifts in dissolved nutrient concentrations and suspended solids loads were invoked by the annual flood. As a result the amount of potential productivity was vastly changed by a shift in the nutrient base and the size of the euphotic zone.

The numbers of factors which control primary productivity are large and often require a comprehensive model to yield useful predictions (Talling and Rzoska 1967). Many of the variables needed for such a model were measured as part of the Gambia River Basin Study including nutrient status, water temperature, solar insolation, and plankton biomass as chlorophyll. The major data deficiency for estimating primary production was underwater light intensity which was estimated coarsely with Secchi depths. This deficiency proved to be crucial because the conclusion regarding the primary productivity was that light was by far the most important factor. Table 15 shows that over the course of the study very few variables were highly correlated with primary productivity. In particular, the absence of correlations among soluble nutrients and primary productivity suggests a rather loose association between

TABLE 15. Correlation coefficients between ^{14}C uptake and biological and chemical variables. All correlations are significant at the P <.001 level. Values in parentheses indicate the number of pairs of observations.

Variable	Correlation
Depth of sample	-.332 (108)
Conductivity	.381 (74)
Chlorophyll	.334 (108)

nutrient status and productivity. Considered on a cruise-by-cruise basis or by each zone, soluble silica and nitrate showed occasional significant negative correlations with productivity. These correlations were generally significant during the flood and declining water season in the upper estuary and lower river zones. However, they were probably spurious because productivity fell in the turbid flood water; during the flood season nitrate and silica concentrations greatly increased from runoff (Berry et al. 1985). The only indication of a direct tie between productivity and nutrient status was a large drop in soluble silica concentrations in the lower river zone during the low flow season (Berry et al. 1985). This drop was matched by a marked increase in algal biomass and productivity. The dominant algae were Melosira spp. which require silica for growth. However, for the majority of samples, primary productivity was low and river waters highly turbid.

Heterotrophy Versus Autotrophy in the Gambia River

As mentioned above, the comparison of the two processes, algal photosynthesis and bacterial heterotrophy, is difficult in that the measures of these processes are not equivalent. But, general knowledge of aquatic biology and some simple conversions allows the development of ecological inferences. These inferences strongly suggest that the Gambia River is dominated by

heterotrophic processes throughout its entire length with a few exceptions. Algal biomass as measured both by chlorophyll and cell counts was low by most all limnological standards (Wetzel 1983). While chlorophyll values of 1 - 2 μg/L and cell counts of 1,000 - 2,000/mL are higher than those of oligotrophic waters, these are relatively low biomass estimates. The rates of ^{14}C uptake were very low, even compared to large, clear lakes. These low rates of production were probably caused by the turbid and turbulent waters of the river and estuary. Assimilation coefficients (Table 14) were extremely low except in the calm, non-flowing pools of the upper river zone during the end of the dry season. As a consequence, the overall contribution of algal photosynthesis toward the carbon budget of Gambia River was trivial.

The conclusion from the heterotrophic uptake data was very much the opposite from the photosynthesis results. Heterotrophic activity was high in all zones except the lower estuary on a year-round basis. Furthermore, bacteria biomass (as estimated by AODC) was also high, consistently exceeding 1,000,000 cells/mL. Converting the bacteria counts and chlorophyll measurements to carbon allows comparison of the two trophic levels with common units. The results (Table 16) show that for much of the year and at most locations phytoplankton biomass was about three to four times bacteria biomass. Given the high metabolic activity of the bacteria, the dominance of heterotrophy over autotrophy emerges. Results of free-water oxygen measurements for estimating productivity by diel changes support this finding (A. P. DeGeorges, Gambia River Basin Development Organization, personal communication).

The ecological structure in the Gambia River appears to be one of strong reliance on heterotrophic activity with occasional large but brief inputs of primary productivity. The lower estuary zone was the exception in that

TABLE 16. Phytoplankton carbon:bacteria carbon ratios for different flood stages and locations in the Gambia River, 1983-1984. Estimates of carbon were derived by converting chlorophyll concentrations and bacteria cell counts according to Rublee (1982).

SEASON			
R	F	D	L
8.65	2.56	2.83	4.54
ZONE			
LE	UE	LR	UR
6.22	3.90	5.46	1.07

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River, UR = Upper River.

bacteria populations were generally smaller than in the rest of the river, while algal populations were comparable. Therefore, autotrophy may play a more important role in this segment of the river. The composition of the aquatic fauna in the river supports the concept of heterotrophy as the base of the food web. The vast majority of invertebrates and fish collected in the river were detritivores (Van Maren 1985; J. Dorr, University of Michigan, Great Lakes and Marine Waters Center, personal communication). Most of these organisms were collected from the bottom or near-bottom waters where they were apparently scavenging food from the sediments. Gut contents of many of the fish showed a diet composed of rich organic matter with little in the way or herbivory or carnivory. Again, the exception was in the lower estuary zone where a more complex food web existed but had its fair share of detritivores.

The source of organic material to drive the high rates of heterotrophy is not difficult to find. Large amounts of grasses, shrubs, and trees line the banks of the river. These plants grow most of the year in the absence of dis-

tinct seasonality, although many have dormant periods during the late dry season. Thus a relatively constant source of organic matter enters the river as allochthonous carbon inputs. The water of the river remains relatively warm on a year-round basis, supporting high rates of metabolic activity. Twilley (1985) estimated that in the estuarine segments of the Gambia River inputs from mangrove forests exceed algal photosynthesis by almost one order of magnitude. Thus, the river system has adopted a very heterotrophic nature.

ZOOPLANKTON

Methods

Zooplankton samples were collected from the appropriate depth and location as determined by the Greco-Latin Square sample design for each sampling period in each zone. In general, samples were collected with a 0.5-m diameter net of 76-μm aperture mesh in all zones except the headwaters where a 0.3-m diameter net was used. For the rising water period in the upper estuary and lower river zones, samples were taken with a 156-μm net and supplemental samples with a 76-μm net.

Samples were collected either by vertical haul or oblique tow. Occasionally, in the headwaters, the net was held stationary and the water allowed to flow through it. The method used depended on water depth and river conditions. A calibrated flowmeter (General Oceanics model 2030) was mounted in the mouth of all nets to measure the volume of water filtered through the net. Samples were preserved with a sugar and formalin solution (Haney and Hall 1973).

In the laboratory, samples were split with a Folsom plankton splitter to obtain a subsample of 300 to 600 organisms. The subsample was then placed in

a circular counting chamber and examined under a Wild M8 Stereozoom microscope at magnifications of 12 to 100x. Two equal fractions of a sample were counted to check splitting and counting methods.

Organisms were identified to the lowest practical taxonomic level. Cladocerans and adult copepods were identified to genus and, where possible, to species. Taxonomic keys used included Brooks (1959), Wilson and Yeatman (1959), and Dussart (1967). Several identifications of marine copepods were made by C. Seret (personal communication, Centre de Recherches Oceanographique de Dakar-Thiaroye). Immature copepods and other planktonic invertebrates were grouped according to subclass or order.

Samples were enumerated from the lower and upper estuaries and lower river zones for each of the four sampling periods (rising, flood, declining, and low water). Upper river samples were examined only qualitatively because cursory examination revealed very few, if any, zooplankters among large amounts of debris. A standard subset of the samples collected was examined. This subset included samples from one transect (Transect 1) covering all stations, depths, and tides. Occasionally, other samples were also examined.

After enumeration, information from each zooplankton sample was coded, and species abundance, percentage composition, and diversity were calculated. The Shannon-Weiner index ($H' = - \Sigma$ pi log pi) was used to calculate diversity. This information was matched with physical and chemical data collected at the same time as the sample. Means and correlations with physical and chemical data were calculated using the statistical package Michigan Interactive Data Analysis System (MIDAS) (Fox and Guire 1976).

Results and Discussion

River Zone Description

Headwaters (Guinea)

The headwaters of the Gambia River were sampled three times: declining water (December 1983), low water (March 1984), and rising water (June 1984) periods. Samples were taken from fast and slow flowing parts of the river or from pools when the river was not flowing. These samples were examined qualitatively. Table 17 shows the species identified and when they were found.

In the declining water samples (December), there were almost no zooplankton found in the fast running water. Copepod nauplii were quite numerous in a slow running water sample. Cladocerans (*Bosminopsis deitersi* and *Alona* spp.) and immature cyclopoids were also found.

The low water samples (March) were almost devoid of zooplankton in the fast and slow flowing water. Copepod nauplii and cladocerans (*Moina* sp., *Chydorus* sp., and *Alona* sp.) were occasionally observed.

On the first day of sampling during the rising water field trip, the river was not flowing and consisted of unconnected pools. The river began to flow the next day. Samples were taken from both the pools and the flowing water. Preliminary examination of these samples revealed a large zooplankton population. Cladocerans (especially *Bosminopsis deitersi*) dominated the samples. Immature and adult cyclopoids, copepod nauplii, and *Asplanchna* sp. were also numerous.

Upper River (Kedougou)

Samples taken from the upper river zone were only examined qualitatively because they contained large amounts of sand and debris but very few

TABLE 17. Zooplankton species found in the Gambia River in relation to flood stage at five different locations.

	LE				UE				LR				UR				HW			
	R	F	D	L	R	F	D	L	R	F	D	L	R	F	D	L	R	F	D	L
Crustacean nauplii	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cyclopoid C_1-C_5 (immature)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cyclopoid C_6 (adult)																				
Corycaecus sp.				x																
Halicyclops sp.						x	x			x	x	x								
Mesocyclops sp.						x	x		x	x	x	x	x							
Oithona nana	x	x	x	x	x			x												
Oithona simplex		x	x	x				x												
Tropocyclops sp.												x								
Calanoid C_1-C_5 (immature)	x	x	x	x	x	x	x	x			x									
Calanoid C_6 (adult)																				
Acartia clausi		x	x	x		x	x	x												
Arctodiaptomus sp.									x		x									
Clausocalanus spp.	x	x	x	x	x															
Eucalanus sp.			x	x																
Labidocera scotti			x																	
Pseudodiaptomus serricaudatus		x	x	x	x															
Temora tuchinata		x		x																
Thermodiaptomus sp.						x	x													
Harpacticoid C_1-C_5 (immature)		x	x		x	x	x	x						x						
Harpacticoid C_6 (adult)						x	x			x						x				
Euterpina sp.		x	x					x												
Euterpina acutifrons		x	x	x																
Cladocerans																				
Alona spp.								x			x		x			x			x	
Bosmina longirostris									x	x	x	x								
Bosminopsis deitersi																	x		x	
Chydorus sp.													x	x						x
Diaphanosoma excisum						x	x		x	x	x	x	x				x			
Macrothrix sp.										x										
Moina dubia						x			x	x	x	x		x		x	x			x
Tlyocryptus spinifer										x						x				
Larvae																				
Insect																				
Chaeoborus sp.						x	x		x	x	x	x								
Bivalve	x	x	x	x		x	x			x										
Crab		x	x	x	x	x	x	x		x										
Echinoderm	x	x	x	x																
Gastropod		x	x	x	x	x	x	x		x	x	x								
Shrimp		x			x	x	x	x		x										
Marine invertebrates																				
Medusa	x	x	x	x	x			x												
Chaetognath (*Sagitta* sp.)	x	x	x	x	x			x												
Ctenophore	x	x	x	x	x			x												
Tunicate (appendicularian)	x	x	x	x	x			x												
Mysid				x			x	x		x										
Protozoa - Tintinnids	x	x	x		x															
Rotifer *Asplanchna* sp.									x	x	x	x					x			

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River, UR = Upper River.

zooplankters. The species which were identified and the time period in which they were found are presented in Table 17.

The rising (July) water samples contained cladocerans (Diaphanosoma excisum, Alona spp., and Chydorus sp.), copepod nauplii, and immature and adult cyclopoids (Mesocyclops sp.). The flood (October) water contained immature cyclopoids, cladocerans (Moina sp. and Chydorus sp.), and benthic harpacticoids. In the declining water samples, only copepod nauplii and immature cyclopoids were observed. Samples from the low water period appeared to have less debris and more organisms than those from other sampling periods. Copepod nauplii and immature cyclopoids were the most numerous zooplankters. Cladocerans (Ilyocryptus spinifer, Moina sp., and Alona spp.) and adult cyclopoids were also found.

Lower River (Bansang)

Zooplankton abundance and composition - Seasonal patterns in total zooplankton abundance for the lower river zone paralleled those observed in the adjacent upper estuary zone (Fig. 12). Lowest abundances were observed during the flood field trip (October) when there were less than 2,000 animals/m^3. Highest densities were found during the following field trip (December) when approximately 130,000/m^3 were found. This range yielded a statistically significant difference among seasons as confirmed by one-way ANOVA.

Total zooplankton densities in the rising water (July) period averaged 32,568/m^3 (Fig. 12). The zooplankton population was dominated by cladocerans (especially Diaphanosoma excisum) which comprised an average of 82% of the samples. Immature cyclopoids were also important. Samples taken during rising waters were collected with a larger mesh net (156 μm) than all other

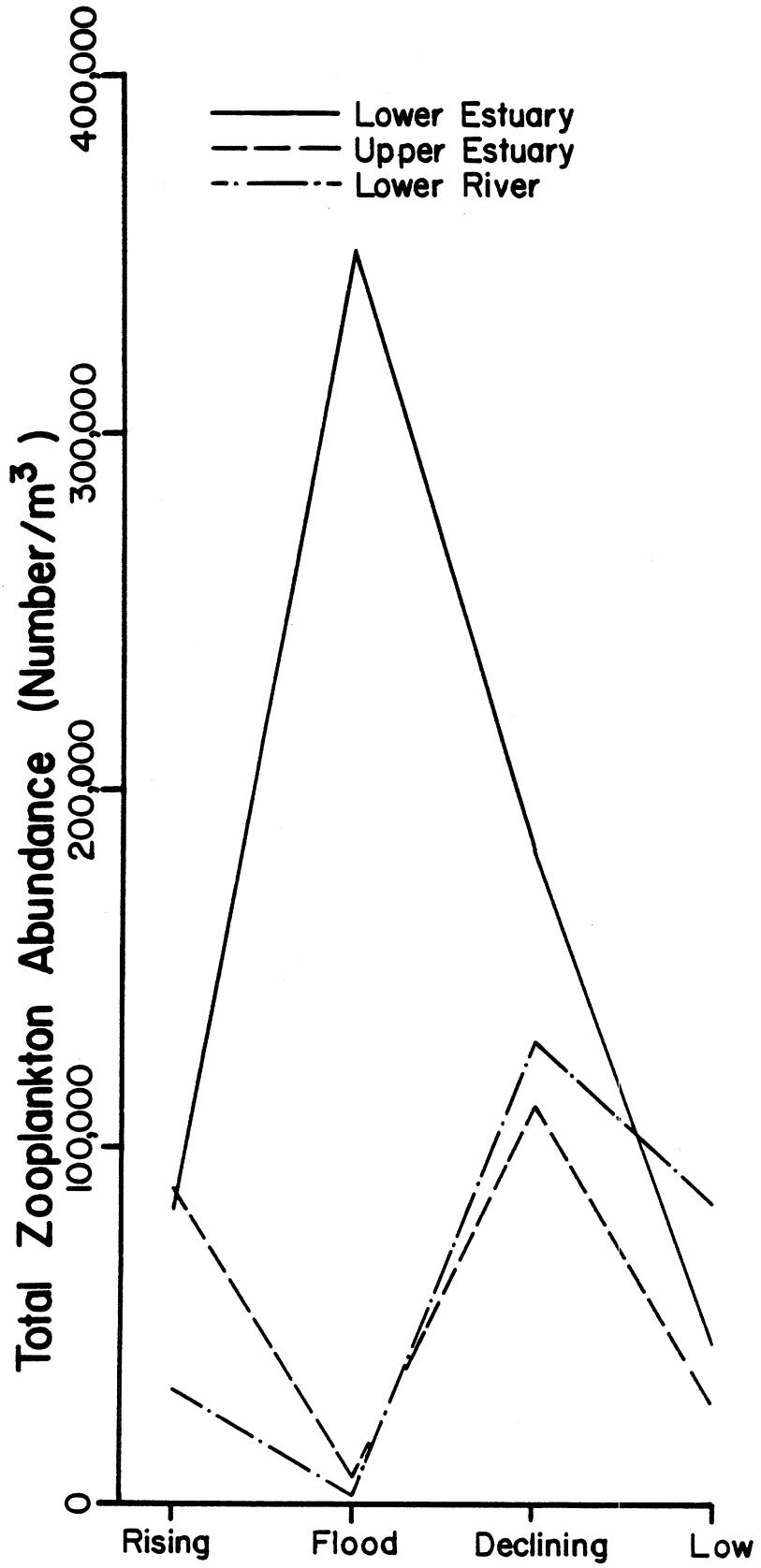

FIG. 12. Average zooplankton abundance in relation to flood stage at different sampling locations in the Gambia River, 1983-1984.

samples (76 μm) so small animals, such as copepod nauplii, may not have been adequately sampled.

Total zooplankton concentrations for the flood water field trip were much lower than the rising water field trip, averaging 1,676/m^3 (Fig. 12). Copepod nauplii were the major component of the population, comprising 55% of the samples. Immature and adult cyclopoids (mainly Halicyclops sp.) and the planktonic insect larvae, Chaoborus sp., were also important. Cladocerans made up a much smaller fraction of the zooplankton population than they did in the rising water period.

In the declining water period, mean zooplankton abundance increased to 129,880/m^3 (Fig. 12). The zooplankton community was mainly composed of cladocerans (primarily Bosmina longirostris) which made up 54% of the population. Copepod nauplii and immature cyclopoids were the next most abundant taxa.

Total zooplankton concentrations in the low water period were lower than those in the declining waters, averaging 83,580/m^3 (Fig. 12). The zooplankton population was dominated by cladocerans (mostly Bosmina longirostris and Diaphanosoma excisum) which comprised 72% of the samples. Immature cyclopoids and copepod nauplii were also important.

Comparisons of abundance with tide and station - Average total zooplankton abundance during all the field trips was not statistically different among tidal cycles. Highest zooplankton densities were generally found in the day flood tides and lowest in the night floods.

Within individual cruises some differences between abundance and tide were apparent. In the rising waters, average abundance was much higher during

the ebb tide samples (43,862/m^3) than flood tides (6,927/m^3). During the flood water period, when overall densities were low, abundances were higher in the flood tides (1,993/m^3) than ebb tides (566/m^3). There were no consistent differences in abundance between tides in the declining or low waters periods.

Overall, station density data demonstrated that zooplankton abundances were highest at the sides of the river (Stations 1 and 4), although this was mainly due to a few samples with high concentrations. Within individual cruises, no obvious trends in abundance with station were apparent and station was not a significant factor in zooplankton abundance.

Comparison of abundance with physical-chemical variables - In the lower river zone, total zooplankton abundance and physical-chemical data from all the cruises yielded negative correlations with nitrate and temperature. Additional high correlations were evident when the data were examined by cruise. In the rising waters, total zooplankton abundance was negatively correlated with nitrate. Abundance was positively correlated with silica, conductivity, alkalinity, and chlorophyll, and negatively correlated with nitrate in the flood waters. Total phosphorus, total nitrogen, nitrate, and silica were positive correlates with abundance, and conductivity was a strong negative correlate in the declining waters. In the low water period, silica was positively correlated and alkalinity and conductivity were negatively correlated with abundance.

Diversity - Diversity in the lower river zone was lowest in the rising waters and fairly uniform for the other cruises (Table 18). There were no large differences in diversity over the tide cycle. Values were slightly

TABLE 18. Zooplankton species diversity in relation to flood stage at different sampling locations in the Gambia River, 1983-1984.

	SEASON			
	R	F	D	L
LE	.69041	.78695	.63670	.82094
UE	.77795	.63202	.39130	.68547
LR	.46795	.63101	.59050	.60595

Key: Season - R = Rising, F = Flood, D = Declining, L = Low; Zone - LE = Lower Estuary, UE = Upper Estuary, LR = Lower River.

higher in night samples. Diversity among stations also showed little variation. Diversity was positively correlated with silica and negatively correlated with conductivity, alkalinity, and chlorophyll.

Upper Estuary (Bai Tenda)

Zooplankton abundance and composition - The highly seasonal composition of the aquatic flora and fauna of the upper estuary zone was reflected in the zooplankton as well. Abundances ranged from over 110,000 animals/m^3 to less than 7,000/m^3 (Fig. 12). The differences in abundances across seasons were statistically significant as determined by one-way ANOVA.

Total zooplankton density during the rising water field trip averaged 82,600/m^3 (Fig. 12). The dominant zooplankton taxa were immature cyclopoids, calanoids, and copepod nauplii, which accounted for 65% of the population. Adult cyclopoids (mainly *Oithona nana*) and calanoids (especially *Clausocalanus* sp.), appendicularians, and tintinnids were also important. Chaetognaths and shrimp and crab larvae were present in low concentrations.

Average total zooplankton concentrations during the flood water field trip dropped to 6,740/m^3 (Fig. 12). The samples were mainly composed of

copepod nauplii (40.9%) and immature cyclopoids (30.3%). Adult calanoids (primarily Thermodiaptomus sp.) and cyclopoids (mainly Halicyclops sp.) and immature calanoids were also important. Cladocerans and the larvae of shrimp, crabs, and insects (Chaoborus sp.) generally made up a small portion of the samples.

During the declining water field trip, average total zooplankton density increased to 112,800/m^3 (Fig. 12). Copepod nauplii dominated the zooplankton community, comprising 72% of the samples. Adult calanoids (primarily Acartia clausi) and immature calanoids accounted for most of the rest of the population. As in the flood water, there were small concentrations of cladocerans and larvae (Chaoborus sp., shrimp, crabs, etc.).

The total concentration of zooplankton averaged 27,890/m^3 (Fig. 12) in the low water sampling period. Copepod nauplii and immature calanoids were the main components of the zooplankton community. Larvae (primarily gastropod veligers), adult calanoids (mainly Acartia clausi), and immature and adult cyclopoids (primarily Oithona nana) were also important. Marine plankton, such as chaetognaths, appendicularians, and medusa, were present in small concentrations.

Comparisons of abundance with tide and station - There were no significant differences, as confirmed by ANOVA, in total zooplankton abundance over the tide cycle for all of the cruises. Although day flood and night ebb tides appeared to have higher abundances overall, this was not consistent within individual cruises.

During the rising water field trip, abundance was highest for night ebb samples. Densities were uniformly low (5,000 to 9,000/m^3) for all tides

during the flood water period. The day flood tide in the declining water period had a much higher abundance than the other tides. Abundances in the low water period showed the greatest variation with tide. Average zooplankton densities were much higher for day tides (48,077/m^3) than night tides (7,702/m^3). This was primarily the result of greater numbers of copepod nauplii present in the day samples. Nauplii concentrations averaged 32,254/m^3 in the day samples and 695/m^3 in the night tides. The densities of immature calanoids, which dominated the night zooplankton, were more consistent, averaging 5,253/m^3 in the day and 3,148/m^3 in the night.

Analysis of zooplankton densities for all cruises did not reveal significant differences in abundance among stations. Within individual cruises, high abundances in individual samples were found at Station 1 (declining water), Station 2 (low water), and Station 3 (rising water), but were probably not related to station location.

Comparison of abundance with physical-chemical variables - The physical-chemical and total zooplankton abundance data for all cruises in the upper estuary revealed a positive correlation between abundance and salinity for the composite database. Additional high correlations were found when the data were examined by cruise. During rising waters, total phosphorus, conductivity, chlorophyll, and salinity were positively correlated with abundance while silica was negatively correlated. Total phosphorus, total nitrogen, conductivity, and salinity were positive correlates during the flood waters, while silica and chlorophyll were negative. In the declining waters, temperature and silica were strongly correlated with abundance in contrast to total phosphorus, nitrate, conductivity, and alkalinity which were negatively

correlated. Abundance was positively correlated with chlorophyll, temperature, and nitrate in the low waters and negatively correlated with salinity and conductivity.

Diversity - Species diversity in the lower estuary zone was much lower in the declining waters than other river stages. Highest diversity was found in the rising waters. Over the tide cycle, diversity was lowest for day flood samples and fairly uniform for other tides. There were no obvious differences in diversity with station. Diversity was positively correlated with conductivity and negatively correlated with silica and nitrate.

Bolons (Near Bai Tenda)

To estimate the contribution of the mangrove bolons to the river zooplankton community, two bolons in the vicinity of the upper estuary sampling site were sampled. During rising water, a bolon near the main sampling site was sampled at three locations: in the mouth of the bolon (Station 1), about halfway up the bolon (approximately 750 m from the mouth: Station 2), and at the end of the bolon (as far as was navigable by small boat, approximately 1.6 km from the mouth: Station 3). Another bolon, near Bai Tenda, about 4 km downstream from the upper estuary sampling site, was sampled during the flood (3 stations) and low water (2 stations) periods. There were no bolon samples taken during the declining water period.

Rising water - The zooplankton population at the mouth of the bolon (Station 1) during rising water was similar in composition and concentration to that in the main river channel (Fig. 13). Total zooplankton density was

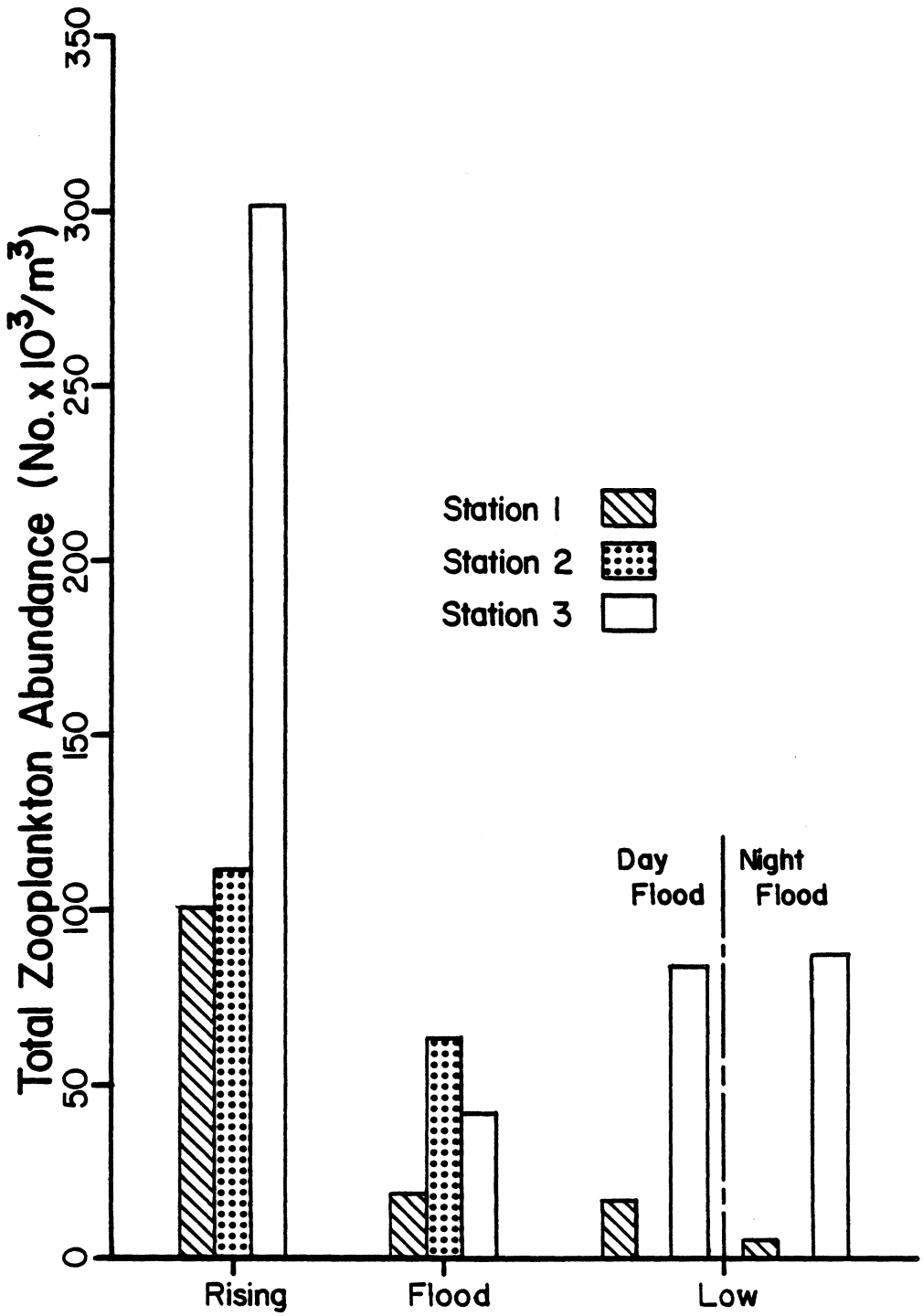

FIG. 13. Average zooplankton abundance observed in a mangrove bolon (tidal creek) in the upper estuary zone during three flood stages. Samples collected at the bolon mouth, 750 m upstream, and 1,600 m upstream were reported as stations 1, 2, and 3, respectively.

101,000/m^3 compared to 82,600/m^3 for the river channel. Immature cyclopoids were the numerically dominant group, followed by copepod nauplii and adult cyclopoids (primarily Oithona nana). Gastropod veligers and polychaete larvae, which made up a small portion of the zooplankton population in the main channel (4.1%), were more important in the mouth of the bolon (12.8%).

Total zooplankton density increased to 128,000/m^3 in the mid-bolon area (Station 2, Fig. 13). Gastropod veligers became the most abundant group, composing 32.7% of the population. Copepod nauplii (27.9%) and immature cyclopoids (25.9%) were also important.

In the station farthest upstream (Station 3), the total zooplankton concentration reached 303,000/m^3 (Fig. 13). Gastropod veligers composed 57% of the zooplankton population. The next most abundant taxa were copepod nauplii and immature cyclopoids.

Flood water - During the flood water period, samples were taken from the Bai Tenda bolon. Zooplankton density in the mouth of the bolon was 18,000/m^3 (Fig. 13), while the concentrations in the main channel averaged 6,759/m^3. The zooplankton population was dominated by copepod nauplii which comprised 79% of the sample. Adult calanoids (primarily Acartia clausi) made up most of the rest of the sample. Immature cyclopoids, which were the second most abundant group in the main channel, composed only a small portion of the bolon sample (2.2%). The channel population of adult calanoids was small and consisted mainly of Thermodiaptomus sp.

The total zooplankton density in the mid-bolon area, which was near a small floodplain, increased to 63,000/m^3. Copepod nauplii again dominated the zooplankton, accounting for 82% of the population. Adult calanoids (Acartia clausi) were the next most abundant group.

The upstream area of the bolon had a slightly lower concentration of zooplankton (42,000/m^3) than the area off the floodplain. The community was almost entirely composed of copepod nauplii (91%). Adult calanoids (Acartia clausi) were present in small concentrations.

Low water - In the low water period, the Bai Tenda bolon was sampled twice (day and night flood tides). Samples were taken at the mouth and the end of the bolon. Total zooplankton abundance at the mouth of the bolon was higher during the day (16,500/m^3) than at night (5,400/m^3) (Fig. 13). This day-night difference was also observed in the main river channel where it was more pronounced. Zooplankton composition in the day sample from the mouth of the bolon was similar to the day flood sample in the main river channel. Copepod nauplii composed 78% of the zooplankton population. Immature calanoids and larvae (mainly gastropod veligers) were other important groups.

The zooplankton composition of the night sample from the mouth of the bolon was different than that of the night flood sample from the main river channel in which immature calanoids were the most abundant group. Copepod nauplii dominated the zooplankton at the mouth of the bolon (although less than the day sample) and immature calanoids and appendicularians were the other major groups. Immature cyclopoids and gastropod veligers were also important.

Zooplankton abundances at the upstream station of the Bai Tenda bolon were much higher than in the mouth (Fig. 13), with densities of 84,000/m^3 (day) and 137,000/m^3 (night). The zooplankton community in the day flood was almost entirely made up of copepod nauplii (90%). Immature cyclopoids and calanoids were the next most abundant groups. In the night sample, copepod nauplii again dominated, but to a lesser extent (49%), while immature calanoids became very important. Other major groups were adult calanoids and gastropod veligers.

Lower Estuary (Dog Island)

Abundance and species composition - The mean total zooplankton density for the lower estuary zone in the rising water samples was 77,600/m^3 (Fig. 12). The major components of the zooplankton were copepod nauplii (38.6%) and immature calanoids (24.6%). Immature and adult cyclopoids (especially *Oithona nana*) were the next most abundant groups. Adult calanoids (mainly *Clausocalanus* sp.) were also numerous.

During the flood water sampling period, total zooplankton concentration was 354,260/m^3 (Fig. 12). The zooplankton community was dominated by copepod nauplii and immature calanoids and cyclopoids which, when combined, composed between 70 and 80% of the samples. Also important were adult cyclopoids (*Oithona nana* and *O. simplex*) and calanoids (mainly *Clausocalanus* sp. and *Pseudodiaptomus serricaudatus*).

The total mean zooplankton concentration for the declining water samples was 185,000/m^3 (Fig. 12). The zooplankton community was dominated by copepod nauplii, which comprised 58.2% of the samples. The next most abundant groups were immature calanoids and cyclopoids. Adult cyclopoids (mostly *Oithona nana*) and calanoids (primarily *Clausocalanus* sp.), appendicularians, and chaetognaths were also numerous.

The concentration of zooplankton during the low water period declined to 46,800/m^3 (Fig. 12). Copepod nauplii, immature and adult calanoids, and immature cyclopoids accounted for 83% of the zooplankton population. Chaetognaths and immature and adult harpacticoids (*Euterpina* spp.) were also numerically important. Although a considerable range existed in total zooplankton abundance among the four field trips, Analysis of Variance (ANOVA) showed that the differences were not statistically significant.

Comparison of abundance with tide and station - There were no obvious differences in total abundance over the tide cycle. ANOVA confirmed that total abundances were not statistically different among the four stages of the tide cycle, day flood (DF), night flood (NF), day ebb (DE), and night ebb (NE). Although highest mean abundance was found for the day ebb tides, this was largely due to one sample with very high density (>2,444,000/m^3). Excluding this sample, the mean abundance for the day ebb samples was 119,000/m^3. Day flood and night ebb tides had the next highest densities.

Station density data show much higher zooplankton abundances for Station 1, even when density data from the sample with very high abundance (>2,444,000/m^3) were excluded. This among-station variation was statistically significant as determined by one-way ANOVA. Station 1 was located on a shallow (<5 m) shelf which extends about 2 km out from the south bank of the river. This was evident during the annual flood when consistently higher concentrations were observed at Station 1 for all transects and tides. High densities were also observed at Station 1 during the declining water period (December).

Comparisons of abundance with physical-chemical variables - Overall, there were no large correlations between total zooplankton abundance and physical-chemical variables in the lower estuary zone. When the data were examined by individual cruises, some high correlations were apparent for these more limited data sets.

For the rising water period (August), salinity, chlorophyll, and nitrate were positively correlated with zooplankton abundance while silica, total phosphorus, and total nitrogen were negatively correlated. Nitrate was

negatively correlated with abundance in the flood water period (December). In the declining water period, temperature and salinity were strong positive correlates with abundance while chlorophyll, alkalinity, silica, and nitrate were negatively correlated. Abundance was positively correlated with temperature, chlorophyll, and silica in the low water period (March) and negatively correlated with salinity, nitrate, and total phosphorus.

Diversity - Diversity was highest in the low water period and lowest in the declining water period. Diversity was fairly consistent over the tide cycle and stations in the main channel (Stations 2 and 3) had the highest diversities. There were no strong correlations between diversity and any of the physical-chemical variables.

Interzone and Interseasonal Comparisons

When viewed on a basin-wide basis, the Gambia River displayed some salient features with regard to its zooplankton fauna. Similar to most of the physical-chemical characteristics, the river showed distinct seasonality both in terms of total zooplankton abundance and composition of the community. This seasonality was evident throughout the length of the river, although least prominent in the lower estuary zone and most dramatic in the lower river and headwaters zones. The seasonal change in average total zooplankton abundance was very large in the lower river zone, approaching two orders of magnitude.

Abundances and species shifts were clearly tied to three variables: water temperature, salinity, and streamflow. In many respects, these three variables are tied together and represent a basis for characterizing the hydrologic cycle. The onset of the annual flood appears to have "swept" the

river clean of most forms of zooplankton. The rapid-flowing, turbid waters of the flood present a poor habitat for zooplankton; these same flood waters chase the marine zooplankton farther downstream, thus vastly reducing abundances in the lower river and upper estuary zones. The year-round presence of salt water in the lower estuary zone provides a more stable environment than found upstream, thus reducing seasonal variability.

In comparison to the estuary, the upper river and headwaters zones provide more or less the opposite set of seasonal circumstances for zooplankton survival. Those portions of the river are generally unsuitable for zooplankton for over one half of the year because of the rapidly flowing water. Abundances were very low throughout the rising, flood, and declining water field trips. The calm water of the low flow season allowed the development of small communities, especially in pools. Zooplankton abundances were highest in the upper river and headwaters zones during the late dry season (March-June) when the Gambia River had no net flow and was dried to a string of discontinuous pools.

Similar to the bacterioplankton and phytoplankton populations, zooplankton were generally uniformly distributed across small spatial scales in the river. As a result, there were no significant differences in total abundances either across the river or along short stretches. The strong currents of the river evidently kept the plankton communities well mixed throughout in the river. The one exception was the occasional large difference in abundances found among stations of the lower estuary zone. These large differences were usually caused by samples with extremely high zooplankton abundances collected near the mangroves along the river bank.

The composition of the zooplankton community was highly affected by the presence of salinity. The saline or brackish reaches of the river had a typical marine fauna dominated by calanoids, while the freshwater reaches had mostly cladocerans. These results were not surprising in that marine forms usually dominated those areas of the river where the freshwater forms cannot survive. This biological-physical relationship was particularly interesting in the upper estuary zone where salinities at one location can range from almost 15 ppt to 0 ppt depending on the time of the year. As a result, not only does the size of the community change dramatically over the course of the year, but the species composition also changes.

The mangrove bolons along the Gambia River stand in contrast to the main river channel in terms of the aquatic fauna. The total zooplankton abundance of the bolons was much higher than the adjacent river channel. In addition, abundances increased with distance from the river channel in the bolons. The bolons also demonstrated their role as nursery areas for the zooplankton in that juvenile and larval forms were by the far the major component of the bolon zooplankton community.

The interaction of tidal mixing and the zooplankton community within the mangrove bolons produced some interesting phenomena. As tidal waves surged into the bolons, they carried the abundant communities deep into the mangrove forests. During the ebb tides, those same zooplankton were carried back toward the river and occasionally into the main river channel; this physical process evidently was responsible for the occasional high abundances found at stations adjacent to the river bank in the lower estuary zone. Within these mangrove bolons was the only location in the Gambia River system where tidal mixing appeared to have an important effect on zooplankton abundances.

SUMMARY

The ANOVA analyses indicated that bacterioplankton and zooplankton abundances were not consistently homogeneous with respect to transect, station, depth, and tide/time-of-day during the four sampling periods. The occasional localized spatial and temporal differences were probably due to variables such as increased substrate concentration and/or gross changes in habitat, e.g., the presence of a sand bar adjacent to a deep channel. Phytoplankton abundances were homogeneous in relation to the spatial and temporal variables as were species diversities for both the phytoplankton and zooplankton.

Free bacteria concentrations were negatively correlated with phaeopigment, suspended solids, conductivity, and salinity and positively correlated with chlorophyll a concentrations. Attached bacteria concentrations were positive correlates with phaeopigment concentrations and with suspended solids and conductivity. Phytoplankton density was positively correlated with chlorophyll a and negatively correlated with phaeopigment and salinity. For the zooplankters, chlorophyll a and salinity were positively correlated with total plankton most of the time, although occasionally both parameters were negative correlates with zooplankton abundance. There were no correlates between phytoplankton diversity and physical or chemical variables. In the lower river zone, chlorophyll a concentrations were negatively correlated with zooplankton diversity. The correlations between physical, chemical, or biological variables and the abundances of the plankton assemblages suggest that there was a constant and dynamic interplay among the different trophic levels that was primarily influenced by gross changes in the physical and chemical environment caused by the advent and retreat of the annual flood.

The range for the grand means of the total bacterial concentrations was 1.15-2.04 x 10^6 cells/mL. For the free bacteria the range of concentrations was from a low of 0.58 x 10^6 cells/mL at the lower estuary zone to a high of 7.26 x 10^6 cells/mL found in the mangrove bolon (tidal creek) near the upper estuary zone. The range for the attached bacteria concentrations was from a low of 0.01 x 10^6 cells/mL found in Guinea to a high of 0.90 x 10^6 cells/mL found in the upper estuary zone. The range for free bacteria concentrations found in this study was similar to what was found by other researchers on the Niger (Imevbore and Bakare 1974, Visser 1973), Rio Negro, and Solimoes (Schmidt 1970) Rivers. The consistency among these rivers suggests that a steady state mechanism(s), such as predation by microheterotrophs or the constant maintenance of low levels of substrate by a holoplanktonic community, may serve to limit the range of free bacteria concentrations in different river systems.

Mean glucose uptake rates were lowest in the lower estuary, two-fold higher in the lower river, three-fold higher in the upper estuary, and more than eight times greater in the upper river zone. Because glucose uptake is controlled by population size, which is itself controlled by a variety of ecological factors such as substrate concentration, predation, and physical-chemical variables, it is not surprising that it is higher going upstream, where higher total bacteria concentrations were found. The free bacteria to attached bacteria ratio was approximately five in the two estuarine zones, thirty in the lower river, and fifty in the upper river zone. The specific activity index (glucose uptake divided by bacteria abundance), which is a measure of metabolic activity, ranged from a low of 4.13 in the lower estuary to a higher of 19.47 in the upper river zone.

Total bacteria concentrations exhibited a small range (1.44 to 1.84 x 10^6 cells/mL) seasonally. Free bacteria concentrations were remarkably constant among different seasons, while attached bacterial concentrations decreased monotonically from the rising to the low water sampling periods. Glucose uptake increased monotonically from a low of 7 ng/L/hr to a high of 21 ng/L/hr from the rising through the low water sampling periods. The free to attached bacteria ratio was approximately 5 during rising and flood water, but increased to 35 and 50 during the declining and low water periods, respectively. The specific activity index also increased monotonically from 3.77 during the rising water period to 13.03 during the flood water period.

The abundance of phytoplankton ranged from a low of 171 cells/mL in the lower estuary zone to a high of 10,122 cells/mL in the lower river zone. Visser (1973) found concentrations of algae on the order of 10^4 cells/mL at the surface to 3 meters depth. Interestingly, the same investigator found the highest concentrations (on the order of 10^6 cells/mL) of algae in the mud.

Phytoplankton diversity was lowest in the lower river zone (0.53) and highest in the headwaters zone (2.30). Density and diversity were inversely related throughout the course of the study. The percentage of diatom species increased monotonically (with one exception, the bolon) from the headwaters zone to the lower estuary zone.

Of the 154 total species of algae identified, over 97 species were diatoms, 41 species were green algae, and 10 species were blue-green algae. In the upper river zone, Hapalosiphon fontinalis and occasionally other blue-green algae were dominant throughout the year. The lower river zone was dominated by Melosira islandica (helical) throughout the year. Five other species of the same genus were found in this zone. In the upper river and the

bolon, dominants changed each season, while in the lower estuary, centric diatoms belonging to the genera Coscinodiscus and Cyclotella were dominant. Occasionally, Hapalosiphon fontinalis was dominant in the lower estuary zone. In the Niger River near Kainji before the closure of the dam, Visser (1974) found that blue-green algae and the diatom Melosira sp. and Nitzschia sp. were dominant.

The uptake of ^{14}C was uniform in all zones except for the lower river zone, which exhibited an average less than one-half of the other three intensively studied zones. The lower river zone average was 0.96 μg C/L/hr and the upper river zone average was 2.27 μg C/L/hr. The assimilation ratio, which presents uptake on a per unit biomass basis, was similar for the two estuarine zones (0.71 and 0.95), much lower for the lower river zone (0.21), and much higher for the upper river zone (3.03).

Phytoplankton density decreased regularly from the rising to the low water sampling periods, while species diversity increased regularly at the four intensively studied zones. The uptake of ^{14}C paralleled the chlorophyll a measurements and was greatest during the rising and low water sampling periods when stream flow was at or near its annual low and transparency was high. The assimilation ratio increased fairly uniformly from the rising through the low water sampling periods (0.38 to 0.99).

Strictly freshwater phytoplankton species, Achnanthes lanceolata and Chlamydomonas sp., were present perennially in the headwaters and upper river zones. A halotolerant primarily freshwater species, Hapalosiphon fontinalis, exhibited its greatest densities in fresh water. This species was found perennially in at least one of the five zones and exhibited the most pan-basinal character of all the algae. Melosira islandica (helical) was found

perennially in the lower river, bolon, and upper estuary zones. Salt water species that were found in the bolon, upper estuary, and lower estuary zones were Cyclotella meneghiniana, Cyclotella comta, and Coscinodiscus rothii.

A total of 41 different species of zooplankton were identified: seven species were cyclopoids, nine species were colonoids, four species were harpacticoids, and eight species were cladocerans. Other species included the larvae of echinoderms, gastropods, bivalve mollusks, shrimp, and crabs. Calanoid copepods tended to dominate in the estuarine zones, while cladocerans were the dominant forms in the freshwater zones. Thomas (1965) found in the Niger River near Karaji prior to impoundment that cladocerans accounted for close to 73 percent and that cyclops species accounted for over 25 percent of the species identified.

The grand mean densities of the zooplankton were similar in the lower river and upper estuary zones (61,926 and 57,509 indiv./m^3, respectively) and considerably higher in the lower estuary zone (165,918 indiv./m^3). Diversity exhibited a small spatial range. The mangrove bolons exhibited higher densities than the main river channel and appeared to be important nursery areas for the juvenile and larval zooplankton forms.

Zooplankton grand mean densities were lowest during the low water sampling period (52,746 indiv./m^3) and increased regularly from the rising (64,270) through the flood (120,898) and declining (142,557) water periods. The densities of the zooplankton populations were out of phase with the phytoplankton populations and increased after the phytoplankton populations had peaked and were on a decline. The species diversity of the zooplankton community exhibited a small annual range (0.54 to 0.70).

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