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Biomass and Primary Production of Microphytes and Macrophytes in Periphyton Habitats of the Everglades



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Southern Everglades

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in
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PREFACE

This report is the second of four reports covering research performed by the Rosenstiel School of Marine and Atmospheric Science, University of Miami for the National Park Service under Contract CX-528081904. The primary research objectives are covered in Part I.

Part I is concerned with the taxonomic composition of the periphyton, factors affecting composition, and ramifications of compositional variation on aquatic animals that feed on periphyton. Part II discusses biomass and primary production of periphyton and associated macrophytes. In Part III, details of the methodology used to quantify taxonomic composition are presented. Part IV presents details of the aspect of the study relating periphyton taxonomic composition to aquatic animals. Participants in each part of the study are included as authors for each part. These parts are:

- Part I: Perspective on the Ecological Causes and Effects of the Variable Algal Composition of Southern Everglades Periphyton
- Part II: Biomass and Primary Production of Microphytes and Macrophytes in Periphyton Habitats of the Southern Everglades.
- Part III: Methodology Development of Quantitative Analysis of Taxonomic Composition of Everglades Periphyton
- Part IV: Comparisons of Laboratory Growth of Hyla squirella Tadpoles Fed Three Different Types of Periphyton

INTRODUCTION

This report covers aspects of the quantity, chemical composition, and primary productivity of periphyton and the quantity and rate of production of associated macrophytes. It includes:

- 1) seasonal biomass of periphyton and associated macrophytes
- 2) temporal and spatial variation in percent organic content of periphyton
- 3) carbon:nitrogen ratios in periphyton
- 4) estimated annual production of macrophytes
- 5) aquatic community primary productivity

The parameters that are covered in this report were selected for examination because they each relate in some way to the availability of food for aquatic organisms in periphyton habitats. Determining biomass and primary production rates are first steps to take in the evaluation of food availability. Because of the relatively large volume of calcium carbonate (CaCO_3) occurring within the periphyton structure it is essential to differentiate between organic and inorganic material in periphyton communities of south Florida. The CaCO_3 associated with periphyton not only has no food value but actually may influence food quality by affecting digestion rates, since it is ingested by organisms grazing on the periphyton and would tend to neutralize digestive acids in animal stomachs. Other studies have shown that the quantity of nitrogen relative to organic carbon in plant material can be more important than biomass to the reproduction and growth of animals such as snails (McMahon et al., 1974); therefore we measured carbon:nitrogen ratios in periphyton harvested from several different habitats.

Although the word periphyton means around plants, in this report we refer to "stem" periphyton and "mat" periphyton rather than to "periphyton" and "epibenthos" so as not to obscure the fact that we are talking about the same material, found both surrounding plants and covering the bottom surface. The mat periphyton in our samples includes the material covering submerged macrophytes. We use periphyton as a synonym for "aufwuchs."

METHODS

Schedule

Periphyton samples were collected quarterly. Four sampling visits were made to the park sites: February-March, May-June, August-September, and November-December, 1978. Four sampling visits were made to the County-208 sites: July, September, and December, 1978; and March, 1979. Exact dates are given in Appendix A (Table A-1).

Sampling Stations

The sampling stations are listed with brief descriptions of their macrophytic vegetation in Table 1. Twelve stations were in Everglades

National Park and five were in the Dade County 208-East Everglades area. Ten of the park stations were located in Taylor Slough. Two park stations were in Shark Slough. One County-208 station was in the C-111 area of the southeast coastal plain. Three County-208 stations were immediately east of Levee 67 in eastern Shark Slough. Another County-208 station was immediately southwest of Chekika Hammock.

Biomass

A one meter-square sample was harvested at each station on each sampling date for biomass determinations. The meter-square area was harvested in two stages. First all standing material (live and dead) was clipped at ground level and placed in a bag. The periphyton surrounding the lower stems was included with this material. Then the algal mat, including dead, prostrate macrophytic material and live submergent plants, was placed in a separate bag. The stem and mat samples were handled differently in laboratory drying and weighing procedures.

Separation of live and dead macrophytes and periphyton in these samples posed a formidable problem. Handling time was much greater than anticipated and probably was considerably greater than that experienced in harvesting experiments in other wetland systems. Following are the procedures we developed for handling the two types of samples.

Mat Samples

The collected mat was poured into a wide, shallow container and a timed 10-min interval was spent removing the largest macrophytic material from the mat. This macrophytic material was separated into live and dead, then dried and weighed.

Fifteen 50-ml aliquots were removed from the mat. Five were dried and weighed, then ashed and weighed, as in a gravimetric procedure that will be described later. Ten were treated with 1-N phosphoric acid and washed to separate the periphyton from the macrophytes. The periphyton material was not retained. A rough estimate was made of the percent live and dead in this small macrophytic material. The macrophytic material from each aliquot was then dried and weighed and ashed and weighed separately. The remaining mat was dried and weighed as a unit. This procedure yields the type of data shown in matrix form in Table 2. Standard deviations as well as means are reported for several samples in Table 3 to give an indication of the precision of the estimates developed by this method.

We assumed that the first five aliquots are representative of the entire sample (minus the large macrophytes) and that the weight of small macrophytes in aliquots 6 through 15 was representative of the small macrophytes in aliquots 1 through 5. Average values of dry weights and ash weights from the two sets of samples were used to compute the dry weights of (a) macrophytes, (b) organic periphyton, and (c) inorganic periphyton covering the substrate of a square meter area.

Definitions and equations are in Appendix A.

Stem Samples

Separate estimates of standing biomass and stem periphyton were obtained by the following procedure.

- Step 1. Cut macrophytes into two parts just above the periphyton so that one part contains periphyton and macrophytes and other part contains only macrophytes.
- Step 2. Separate both groups into live and dead macrophytes.
- Step 3. Dry the four groups and weigh separately.
- Step 4. Place the two groups of macrophytes (live and dead) with stem periphyton, into 1-N HCl bath for several minutes. Rinse thoroughly to remove loosened periphyton.
- Step 5. Dry the two rinsed samples.
- Step 6. Reweigh separately.

Total stem periphyton is assumed to be the difference in dry weight of the macrophyte samples before and after the acid bath and rinsing. Percentages from the mat analysis or the gravimetric analysis were used to estimate the weight of the organic component of the stem periphyton.

Organic Content of Mat (Gravimetric Analysis)

The principal inorganic component of periphyton is CaCO_3 , which can represent more than 90% of the weight of periphyton at some southern everglades locations. CaCO_3 is precipitated under conditions of high pH, such as are formed in the photosynthesis process. Silica (SiO_2) is a minor chemical component of periphyton, despite the fact that the frustules of diatoms, a major component of periphyton at some everglades stations, are composed of SiO_2 . Other inorganic compounds are found in everglades periphyton in only miniscule quantities.

Organic weight was taken as the difference between dry weight and ash weight. Samples were dried for approximately 24 hrs in a drying oven set at 70°C . Samples were ashed by placing them in a muffle furnace set at 500°C for 4 hrs. Water was added to ashed samples to replace hygroscopic water lost in ashing, and samples were redried before obtaining ash weights (Paine, 1964). This analysis was performed on stem periphyton samples collected in triplicate at each site on each sampling date.

Carbon:Nitrogen Ratios

Carbon:nitrogen ratios were determined on a Perkin-Elmer elemental analyzer. Samples were corrected for inorganic carbon by separating each sample into two subsamples and ashing one prior to the CHN

analyses. Organic carbon was assumed to be the difference in carbon content of the two subsamples. The C:N ratios were obtained on 12 samples from the third quarter collections. Samples for the CHN analysis were taken from one jar for each station. All were stem periphyton.

Annual Production of Macrophytes

Annual primary production of macrophytes was estimated from the quarterly biomass data by a technique similar to that described by Wiegert and Evans (1964). Steps taken in the calculation were as follows:

- 1) Differences were determined between sequential quarterly values. For this calculation, Quarter 1 was assumed to follow Quarter 4 so that four seasonal differences were obtained for each station.
- 2) Positive differences were summed to estimate net production between measurement dates.
- 3) Negative differences were summed.
- 4) The number of days in each period of negative differences was counted.
- 5) The sum of the negative differences was divided by the number of days over which they occurred to obtain an estimate of average daily rate of loss of material through decomposition.
- 6) The estimated daily loss rate was multiplied by 365 to account for total loss to decomposition over the 1-year period.
- 7) Estimated total material loss was added to positive differences to yield an estimate of annual production per square meter.

This method of estimating daily loss rate is less than ideal because material that was alive at the beginning of a period may have died and been added to the pool of dead material, which would have reduced the difference in dead material over the period measured. This occurrence would cause underestimates of daily loss rates. Annual primary production would be underestimated also. Wiegert and Evans avoided this problem by clipping and removing live material at the beginning of the measurement period from sites used to measure decomposition losses. This was not possible within the scope of our study because it would have doubled the number of biomass samples we would have had to handle. Our annual primary production estimates should be considered very crude approximations of reality. Because some decomposition was taken into account, our estimate probably is better than those from studies in which only positive differences were used to estimate production (Turner, 1976).

Aquatic Primary Productivity

Most methods of measuring aquatic community metabolism are based on consumption and production of oxygen. In flowing waters, various techniques based on diurnal changes of ambient dissolved oxygen concentration have been employed (Odum, 1956). These methods have advantages due to simplicity of application, but their major disadvantage is that oxygen escapes from the water column by diffusion, particularly under supersaturated conditions. Correction for diffusion is possible, but may be subject to error due to the influence of air and water movements on diffusion rate. In order to overcome the disadvantages inherent in methods based on diurnal changes, monitoring changes in dissolved oxygen concentrations of the water enclosed over a parcel of the community in in situ chambers or bell jars has been widely employed (Odum, 1957; Pamatmat, 1968; Edwards, 1973). A chamber designed and built by R. Edwards was used in the present study to analyze the energetics of the periphyton community.

A large plexiglass chamber confined an area of $.25 \text{ m}^2$. Supporting apparatus circulated water through the chamber and past oxygen and temperature probes. The probes were connected to their respective meters and meter output was recorded on Rustrak DC recorders (Figure 1) for at least 24 hrs. In the July and August samples, ambient pH was monitored in place of temperature, since the oxygen meter can measure instantaneous temperature by switching the meter mode. (Temperature is only important in determining the saturation concentration for dissolved oxygen.)

Saturation was prevented by a system of timers operating solenoids that supply compressed air to a set of 3 valves to allow the system to circulate chamber water or exhaust chamber water and replace it with deoxygenated ambient water. Replacement water was taken from an area covered with black, plastic tarps, which inhibited photosynthesis. The water was filtered through a combination cotton and 1-mm plastic screen mesh to avoid introduction of extraneous microorganisms. The cycle was timed to circulate for about 2 hrs, then replace water for 15 min, and then circulate again for another 2 hrs.

The system was designed to monitor the rate of oxygen production and consumption in a closed system under field conditions. The final output of the meters reflected the rate of oxygen production and consumption under field conditions. A mechanical pyranograph was used to record solar radiation during the sampling cycle.

At the end of the sampling period, the meters were checked and recalibrated to detect any drift in the measurements. After the instrument check, 25 ml of saturated-MgCl₂ solution was injected into the circulating system and allowed to circulate for 15 min. A sample of ambient water was taken and another sample of water containing the

diluted MgCl_2 solution was also taken in order to estimate the volume of the chamber.² Details of the lab procedure are as follows:

A standard chloride titration was carried out with $\text{K}_2(\text{CrO}_4)$ (Hellige Testing Outfit #650-2) to find the concentration of chloride in the ambient and chamber water.

Calculations:

To determine ppm Cl^- added and subsequently diluted, ambient Cl^- was subtracted from the Cl^- concentration found in the chamber after mixing.

$$\text{ppm (chamber)} - \text{ppm (ambient)} = \text{ppm (diluted)}$$

By empirical titration, we found that a saturated solution of MgCl_2 contains 8875 ppm Cl^- /25 ml of saturated solution, which agrees well with published values of MgCl_2 solubility (Lang's Handbook of Chemistry). Since the volume of MgCl_2 solution added to the chamber was very small in relation to the volume of water in the chamber, it can be assumed that it did not change the volume in the chamber. Therefore, we could consider the concentration of MgCl_2 in the chamber to be equal to 8875 ppm divided by the volume of water in the chamber. Volume in the chamber could therefore be calculated as follows:

$$\frac{8875}{\text{ppm (diluted)}} = \text{Volume in chamber in liters.}$$

After the water samples were taken, the system was disassembled and the biomass contained by the plexiglass chamber was harvested to obtain dry weight and ash weight.

Production and consumption of O_2 were calculated by measuring the slope of the continuous output of the O_2 recorder on strip chart paper. Values of O_2 production or consumption were measured for each hourly interval of recording. The values from the chart gave units of ml O_2 /l of water/hr. These values were converted to mg O_2 /hr by multiplying by 1.42857, and converted to mg $\text{O}_2/\text{m}^2 \cdot \text{hr}$ by multiplying by 3.8917 (the inverse of the area of the chamber, 70.2569 m^2).

A daytime net primary production (NPP_D) was determined by summing the positive values of change in oxygen per hour. A nighttime respiration (R_N) was determined by summing the negative values of change in oxygen per hour. Average hourly rate of respiration (R_H) was determined by dividing R_N by the number of hours when oxygen change was negative. Daytime respiration (R_D) was estimated by multiplying R_H by the number of hours of positive oxygen change. Total respiration for the 24 hr period (R_{24}) was estimated by multiplying R_H by 24. The following calculations could then be made:

$$\text{GPP}_{24} = \text{NPP}_D + R_D$$

$$NPP_{24} = GPP_{24} - R_{24}$$

$$P/R = GPP_{24}/R_{24}$$

The gross primary productivity in the aquatic systems we measured can be attributed almost entirely to periphyton, as we selected sites where submergent macrophytes were not present and emergent vegetation was minimal.

RESULTS

Biomass

The measured above-ground organic biomass varied from a low of 7 g/m² (dry weight organic matter) (d.w.o.m.) at Station XIII fifth quarter to a high of 1,738 g/m² at Station III third quarter. In general, the biomass of macrophytes was greater than the organic biomass of periphyton, even though our sampling areas were selected for their relative abundance of periphyton. Macrophyte biomass varied from a low of 6 g/m² at Station XIII in Quarter 5 to a high of 1,405 g/m² at Station III in Quarter 3. Organic periphyton biomass varied from a low of 1 g/m² at Station XIII in Quarter 5 to a high of 526 g/m² at Station X in Quarter 2. Maximum measured biomass did not occur during the same quarter at all stations. Periphyton biomass peaked most frequently during Quarter 4. Peaks in above-ground macrophyte biomass at the various stations were distributed over all quarters. Measured biomass values at each station for each quarter are given in Table 4. Low periphyton values at Station XIII fifth quarter (March, 1979) were due to the fact that the standing crop of periphyton in that area had become detached and floated in high water early the previous winter.

The stem periphyton appeared to be more closely associated with dead standing macrophytes than with living standing macrophytes. A quantitative comparison of the distribution of periphyton between living and dead standing material is given for a few stations in Table 5. A breakdown of the values is given in Appendix B.

Percent Organic in Periphyton

The organic component of periphyton biomass represented approximately one-third of the total periphyton biomass. Total periphyton (including inorganic component) varied from 1 g/m² at Station II first quarter to 2,682 g/m² at Station X second quarter (Table 6). Organic periphyton is also shown in Table 6.

The mean percent organic in periphyton from the three small stem samples collected at each station each quarter are shown in Table 7. Percentages varied from a low of 18.75 at Station XVII fifth quarter (see under first quarter) to a high of 51.57 at Station XII fourth quarter. Station means for all quarters varied from a low of 21.38

percent at Station XVII to a high of 48.37 percent at Station II. The variation between quarters, which is reflected in station standard deviations, varied between stations but was relatively low, averaging 5.6 percent of the mean.

Carbon:Nitrogen Ratios

Measured periphyton values, corrected for inorganic carbon, ranged from 4.84:1 to 8:1 (Table 8). The C:N ratio with total carbon considered was much higher (19.00-30.42), but the organic C:N ratio probably is the more functionally relevant figure.

The sites can be grouped as follows on the basis of Quarter 3 C:N ratios:

4.80 - 4.99:1	III, VII, VIII, X, XIII, XVI
5.00 - 5.99:1	IV, VI, IX, XVII
6.00 - 6.99:1	XI
7.00 - 7.99:1	
8.00 - 8.99:1	XIV

Annual Production of Macrophytes

The quantity of living and dead macrophytic material at each station for each quarter is shown in Table 9. In general, living biomass peaked during the last half of the year (Quarters 3 and 4) and dead biomass peaked during the first half of the year (Quarters 1 and 2). The lowest measured living biomass (3 g/m^2) occurred at Station XI third quarter and Station XIII Quarter 5. The highest living biomass (583 g/m^2) was encountered at Station VI fourth quarter. The lowest measured dead biomass was 3 g/m^2 at Station XIII fifth quarter. The highest measured dead biomass was $1,095 \text{ g/m}^2$ at Station II second quarter.

Calculated differences in living biomass between successive quarters and calculated differences in dead biomass between successive quarters are shown in Table 10. Days between sampling at each station are given in Table 11. These sets of information provided input to the calculations of annual primary production in Table 12.

Sufficient information was available to calculate annual production of macrophytes at only nine stations. Estimated annual production ranged from a low of 419 g/m^2 at Station XIII to a high of 1744 g/m^2 at Station VI. Ranked in order from lowest to highest estimated annual primary production, the stations were: XIII, XIV, IX, I, V, XI, VII, VIII, XVI, X, II, VI.

Aquatic Primary Productivity

The Edwards respirometer was employed at four stations: IV, VIII, XI, and XV. Both a winter measurement and a summer measurement were taken at Stations VIII and XV, which allows comparison of productivity under two different sets of conditions. In this particular year water levels

were low during both measurement periods, whereas water levels would ordinarily be high in the summer and low in the winter. Solar radiation, as expected, was consistently higher when summer measurements were made than when winter estimates were made. Plots of oxygen changes for each 24 hr period monitored are given in Figures 2-7.

Gross primary productivity (GPP_{24}) was higher at all stations during the summer than during the winter. GPP_{24} at Station VIII was $4.49 \text{ g O}_2/\text{m}^2\cdot\text{day}$ on July 11-12, 1979 and $2.00 \text{ g O}_2/\text{m}^2\cdot\text{day}$ on January 9-10, 1979. Summer (July 23-24, 1979) and winter (January 19-20, 1979) values of gross primary productivity at Station XV were 1.41 and $1.16 \text{ g O}_2/\text{m}^2\cdot\text{day}$, respectively. Station IV had a gross primary productivity of $2.65 \text{ mg O}_2/\text{m}^2\cdot\text{day}$ in summer (August 13-14, 1979). Station XI had a gross primary productivity of $1.46 \text{ mg O}_2/\text{m}^2\cdot\text{day}$ in winter (December 22-23, 1979). No net primary productivity (NPP_{24}) occurred at any of the three stations during winter. This was reflected in P/R ratios of less than one. NPP_{24} was $2.01 \text{ g O}_2/\text{m}^2\cdot\text{day}$ at Station VIII and $1.08 \text{ g O}_2/\text{m}^2\cdot\text{day}$ at Station IV during summer measurements. Station XV did not have any NPP_{24} during the summer measurement. Values relating to primary productivity are summarized in Table 13. The conversion from grams of O_2 production to grams of organic matter (d.w.) produced is approximately one to one.

Winter and summer values for GPP_{24} and NPP_{24} at Stations VIII and XV were used to obtain a rough estimate of annual GPP and NPP at the two sites by assuming that the winter value approximated an average for one half of the year and the summer value approximated an average for the other half of the year. At Station VIII, annual GPP was $1,186 \text{ g/m}^2$ and annual NPP was 366 g/m^2 . At Station XV, annual GPP was 469 g/m^2 and annual NPP was zero.

It is impossible for R_{24} to exceed GPP_{24} continuously in a given community unless there is an outside source of organic material to the community. In the case of aquatic communities we measured in the southern everglades, the most likely "outside source" would be (1) the emergent macrophytes growing on or near the sites, or (2) organic soils, which might oxidize under flooded conditions, when bottom oxygen levels are high. Winter R_{24} at Station XV was lower than at the other two sites and summer R_{24} was lower than that at Site VIII. NPP_{24} was very low at Station XV and resulted in the low GPP_{24} and low P/R. If GPP_{24} can be considered the "pulse" of a community, then the "health" of the Station XV aquatic community was very poor.

DISCUSSION

Seasonal maximum above-ground biomasses (d.w.o.m.) of emergent macrophytes in a review of Westlake (1963) were $4,200 \text{ g/m}^2$ for Spartina alterniflora in Georgia, $10,000 \text{ g/m}^2$ for Scirpus lacustris in Germany and $4,600 \text{ g/m}^2$ for a Typha hybrid in Minnesota. Maximum macrophyte biomass in the present study was $1,405 \text{ g/m}^2$, which was low by comparison. Our biomass values also were low in comparison to the

average above-ground biomass for sawgrass reported by Stewart and Ornis (1975) for Conservation Area 3B. In that study, average live biomass was $1,100 \text{ g/m}^2$, average dead biomass was $1,200 \text{ g/m}^2$, and average total biomass was $3,200 \text{ g/m}^2$.^a Our values were an order of magnitude higher than the seasonal peak biomass value of 161.4 g/m^2 reported by Porter (1967) for a wet prairie dominated by hairgrass, sawgrass and beardgrass (*Andropogon rhizomatus*). Both hairgrass and sawgrass were dominant macrophytes at several of our sites. Macrophyte biomass at our sites probably was lower than that of surrounding areas because we deliberately selected sites where periphyton was well developed. In sites such as these, the density of macrophytes appeared lower than in areas where periphyton was poorly developed or absent.

Total biomass at our sites did not reach the $2,000 \text{ g/m}^2$ for "living organic matter" frequently exceeded by southern everglades communities studied by Wood and Maynard (1974) from 1964 through 1967. Results of our study differed from those of the Wood and Maynard study in another respect; in their study, organic periphyton biomass usually greatly exceeded the biomass of macrophytes, whereas in our study the macrophyte biomass usually was the greater.

Westlake (1965) gives $100\text{--}500 \text{ g d.w./m}^2$ as the minimum and maximum biomass for periphyton on fertile sites. Minimum and maximum values for organic periphyton in the southern everglades were 1 and 526 g/m^2 . Minimum and maximum values for total periphyton biomass (ash weight included) were 2 and $2,682 \text{ g/m}^2$. It is difficult to compare our values to the literature values used by Westlake because at least some of his values were not ash-free (Odum, 1957).

Our values for organic periphyton biomass were very low compared to those of Wood and Maynard (1974), which were as high as $2,550 \text{ g d.w./m}^2$, ash-free, and frequently were above $1,000 \text{ g/m}^2$, ash-free. In the Wood and Maynard study, total periphyton biomass was as high as $6,000 \text{ g/m}^2$. Wood and Maynard apparently did not separate detritus from the algal mat, and this might account for some, although probably not all, of the differences between results of the two studies. The two studies were conducted in the same general areas. Comparison of results of the two studies suggest that the quantity of periphyton in the southern everglades may have declined from 1967 to 1978. On the other hand, Gleason and Spackman (1973) reported periphyton biomass values ranging from $45.7 \text{ g d.w.o.m./m}^2$ to 447 g/m^2 . Their ash-free periphyton values were considerably smaller than ours. Most of their work was done in Conservation Area 1, although one site was in the Paurotis Palm area of Everglades National Park.

^a "Live" and "dead" do not equal "total" in the Stewart and Ornis (1975) study.

In a study of southern everglades periphyton by Van Meter-Kasanof (1973), organic content of periphyton ranged from 90 percent in "young" samples to 27 percent in the heaviest and oldest samples. Gleason and Spackman (1974) reported organic periphyton values of less than 70 percent to more than 88 percent in Conservation Area 1. Percent organic in periphyton in the present study ranged from 18.75 to 51.57 percent and averaged approximately 33 percent. The average was about the same all quarters.

According to Westlake (1974), the annual NPP of freshwater emergent macrophytes on fertile sites can be 3,000-8,500 g/m². Our values were low by these standards, ranging from 419 to 1,744 g/m². Our annual NPP values were higher, however, than the 200 g/m² in NPP estimated by Porter (1967) for wet prairie sites in the Big Cypress dominated by hairgrass, sawgrass, and beardgrass.

The 43 and 57 g O₂/m².day measured by Talling et al. (1973) in two Ethiopian lakes are near the theoretical upper limit of phytoplankton GPP₂ (Lieth and Whittaker, 1975). Lieth and Whittaker considered 1,500 g C/m².year (3,984 g d.w.o.m./m².year) to be an average annual value for freshwater swamps and marshes. Using ¹⁴C uptake, Allen (1971) found that daily NPP for periphyton in Lawrence Lake, a temperate lake, averaged 2.2 g d.w.o.m./m² on Scirpus and 21.3 g o.m./m² on submergent vegetation. In our southern everglades habitats, maximum measured daily GPP₂ was 4.49 g d.w.o.m./m².day. Highest estimated annual GPP was 1,186 g/m². Our highest daily NPP was 2.0 g/m². Calculated annual NPP was 366 g/m².

Van Meter-Kasanof (1973) measured an average net periphyton production rate of 2.68 g d.w.o.m./m².day. (An annual NPP of 978 g/m².year results from multiplying this figure by 365.) Her NPP figure appears to include CaCO₃. If the annual value estimated from the Van Meter-Kasanof figure were multiplied by 0.33 to estimate ash-free NPP, then our annual NPP figures would be similar. Hers was an average, however, whereas ours was the highest of three measured.

Our periphyton C:N ratios of 4.84:1 to 8:1 are within the range (3.7:1-10.1:1) found in the study by McMahon et al. (1974). The average C:N ratio of pure protein is 3.25:1. A maximum of 17:1 is required in animal diets. The lower the ratio, the more favorable the ration, with regard to protein content.

CONCLUSIONS

Southern everglades periphyton communities are moderately productive but are not as productive as some lake phytoplankton systems and freshwater emergent plant systems. Total above-ground biomass of periphyton systems in the southern everglades may have declined in the past decade. Southern everglades periphyton is good animal ration with respect to protein content, as indicated by its C:N ratio, if the inorganic carbon content can be disregarded.

REFERENCES CITED

- Allen, H.L. 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecol. Monogr.* 41: 97-127.
- Boyd, C.E. 1967. Some aspects of aquatic plant ecology, p. 114-129. In Symposium on reservoir fishery resources. Univ. of Georgia Press. Athens.
- Edwards, R.R.C. 1973. Production ecology of two Caribbean marine ecosystems II. Metabolism and energy flow. *Est. Coastl. Mar. Sci.* 1: 319-333.
- Gleason, P.J. and W. Spackman, Jr. 1974. Calcareous periphyton and water chemistry in the Everglades, p. 146-181. In P.J. Gleason (ed.), *Environments of South Florida: Present and Past*. Miami Geological Society Memoir 2.
- Likens, G.E. 1975. Primary production in inland aquatic systems, p. 185-202. In H. Leith and R.H. Whittaker (eds.), *Primary Productivity of the Biosphere*. Springer-Verlag, New York.
- McMahon, R.F., R.D. Hunter and W.D. Russel-Hunter. 1974. Variation in aufwuchs at six freshwater habitats in terms of carbon biomass and of carbon:nitrogen ratio. *Hydrobiol.* 45: 391-404.
- Odum, H.T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecology* 27: 55-112.
- Paine, R.T. 1964. Ash and caloric determinations of sponge and opisthobranch tissues. *Ecology* 45: 384-387.
- Pamatmat, M.M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. *Int. Rev. Gesamten Hydrobiol.* 53: 211-298.
- Porter, C.L., Jr. 1967. Composition and productivity of a subtropical prairie. *Ecology* 48: 937-942.
- Snedecor, G.W. and W.G. Cochran. 1967. *Statistical Methods* (Sixth Edition), Iowa State University Press. Ames. 593 p.
- Steward, K.K. and W.H. Ornis. 1975. The autecology of sawgrass in the Florida Everglades. *Ecology* 56: 162-171.
- Talling, J.F., R.B. Wood, M.V. Proper and R.M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian lakes. *Freshwater Biol.* 3: 53-76.
- Turner, R.E. 1976. Geographic variations in salt marsh macrophyte production: a reievew. *Mar. Sci.* 20: 47-68.

- Van Meter-Kasanof, N. 1973. Ecology of the micro-algae of the Florida Everglades. Part I - Environment and some aspects of freshwater periphyton, 1959 to 1963. *Nova Hedwigia* 24: 619-664.
- Westlake, D.F. 1963. Comparisons of plant productivity. *Bio. Rev.* 38: 385-425.
- Westlake, D.F. 1965. Some basic data for investigations of the productivity of aquatic macrophytes, p. 313-322. In C.R. Goldman (ed.), *Primary Productivity in Aquatic Environments*. Mem. Ist. Ita. Idrobiol. 18 Suppl. University of California Press. Berkeley.
- Wiegart, R.G. and F.C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. *Ecology* 45: 49-63.

Table 1. Estimated species composition (percentage volume) at each sampling station.

Park Taylor Slough Sites

- I. Muhlenbergia (90), Centella (5), Cladium (2), Other (3).
- II. Muhlenbergia (90), Centella (5), Cladium (2), Other (3).
- III. Cladium (55), Muhlenbergia (20), Centella (8), Eleocharis (6), Panicum (2), Misc. (9).
- IV. Eleocharis (30), Rhynchospora (30), Bacopa (30), Centella (5), Utricularia (4), Cladium (1)
- V. Muhlenbergia (95), Cladium (2), Utricularia (3).
- VI. Cladium (95), Utricularia (5).
- VII. Cladium (99), Centella (1).
- VIII. Eleocharis (90), Panicum (5), Utricularia (5).
- IX. Eleocharis (90), Bacopa (5), Rhynchospora (3), Misc. (2).
- X. Cladium (99), Misc. (1).

Park Shark Slough Sites

- XI. Eleocharis (98), Cladium (1), Bacopa (1).
- XII. Eleocharis (50), Utricularia (50).

East Everglades Shark Slough Sites

- XIII. Eleocharis (50), Utricularia (40), Cladium (10).
- XIV. Eleocharis (30), Rhynchospora (30), Utricularia (30), Centella (5), Bacopa (5).

XV. Eleocharis (90), Utricularia (10).

East Everglades Chekika Site

XVI. Muhlenbergia (75), Eleocharis (20), Utricularia (5).

East Everglades Canal III Site

XVII. Cladium (45), Utricularia (35), Eleocharis (20).

Plants are referred to above by generic name only because of limited space. Species names and common names are given below:

Bacopa sp., water hyssop
Centella asiatica, coinwort
Cladium jamaicensis, sawgrass
Eleocharis cellulosa, spikerush
Muhlenbergia filipes, hairgrass
Panicum hemitomon, maidencane
Rhynchospora tracyi, beakrush
Utricularia sp., bladderwort

Table 2. Matrix of measurements taken in mat biomass analysis.

		Dry Wt.	Dry Wt. Ground	Ash Wt.	Estimated % Dead
A ₁₋₅	Aliquots 1 through 5, total	X	X	X	
A ₆₋₁₅	Aliquots 6 through 15, macrophytes only	X		X	X
P	Remaining mat	X			
N	Large dead macrophytes	X			
L	Large living macrophytes	X			

Table 3. Means and standard deviations on sample aliquots used to obtain separate weight estimates for Quarter 2 mat periphyton and associated macrophytes at several stations.

Station	Wet Vol. n	A ₁₋₅		B ₁₋₅		C ₁₋₅		A ₆₋₁₅		C ₆₋₁₅		
		\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	
I	50 5	14.23	0.414	14.3465	0.4082	10.0011	0.2638	10	0.2306	0.0410	0.0124	0.0054
II	30 5	7.83	0.273	7.8485	0.2983	4.0381	0.1886	8	0.5665	0.0827	0.0264	0.0093
III	50 5	18.45	0.942	11.3154	0.7210	8.1903	0.5032	10	0.8022	0.1152	0.1149	0.0642
V	50 5	11.81	0.4505	11.925	0.4411	6.8589	0.2686	10	0.6851	0.0901	0.0245	0.0052
VI	50 5	10.83	0.3618	10.7214	0.3543	6.8888	0.2463	10	1.1773	0.1975	0.2751	0.0763
VII	50 5	14.05	0.6211	13.7674	0.5046	9.2731	0.4121	10	0.9137	0.1918	0.0618	0.0465
VIII	50 5	26.94	0.8736	1.8509	0.2146	1.3886	0.1617	11	0.0088 ^a 0.0831 ^b	0.0073 0.0288	0.0160	0.0091

A₁₋₅ average total dry weight of complete aliquots (1-5)

B₁₋₅ average dry weight of complete aliquot after grinding (1-5)

C₁₋₅ average ash weight of ground complete aliquot (1-5)

A₆₋₁₅ average dry weight of macrophytes from separated aliquots (6-15)

C₆₋₁₅ average ash weight of macrophytes from separable aliquots (6-15)

a live

b dead

Table 4. Biomass of macrophytes^a and a organic biomass of periphyton (g/m² dry wt) at sampling stations.

Stations	Total Macrophytes Quarter				Organic Periphyton Quarter				Total Organic Biomass Quarter			
	1	2	3	4	1	2	3	4	1	2	3	4
I	659	1,039	738	591	302	127	187	542	961	1,166	925	1,133
II	817	1,265	1,405	589	T	60	66	86	817	1,325	1,471	675
III	-	267	1,305	332	-	232	433	337	-	499	1,738	669
IV	-	62	138	94	-	293	257	173	-	355	395	267
V	478	441	602	379	74	219	45	243	552	660	647	622
VI	786	540	1,177	1,205	249	150	127	-	1,035	690	1,304	-
VII	749	538	279	523	329	392	433	474	1,078	930	712	997
VIII	532	249	551	425	-	87	149	176	-	336	700	601
IX	167	82	178	209	175	263	226	309	342	345	404	518
X	546	552	152	341	388	526	441	359	934	1,078	593	700
XI	213	220	221	88	185	244	419	262	398	464	640	350
XII	618	435	-	414	94	256	-	61	712	691	-	475
XIII	6 ^b	174	63	127	1 ^b	157	116	71	7 ^b	331	179	198
XIV	345 ^b	366	192	262	183 ^b	72	22	33	528 ^b	438	214	295

Table 4. Continued.

Stations	Total Macrophytes Quarter				Organic Periphyton Quarter				Total Organic Biomass Quarter			
	1	2	3	4	1	2	3	4	1	2	3	4
XIV	345 ^b	366	192	262	183 ^b	72	22	33	528 ^b	438	214	295
XV	88 ^b	95	-	46	63 ^b	244	-	158	151 ^b	339	-	204
XVI	932 ^b	63	197	212	319 ^b	485	176	242	1,251 ^b	548	373	454
XVII	1,214 ^b	599	452	416	159 ^b	122	98	-	1,373 ^b	721	550	-

^a above-ground biomass only

^b March 1979 (Quarter 5)

Table 5. Dry weights of different components of standing macrophytes and associated periphyton in some Quarter 1 samples.

	Condition of Macrophyte	Stem Dry Weight g/m ²	Total ^a Periphyton Dry Weight g/m ²
I	Live	170	5
	Dead	<u>860</u>	<u>37</u>
	TOTAL	1,030	42
II	Live	169	0
	Dead	<u>1,621</u>	<u>43</u>
	TOTAL	1,790	43
V	Live	145	-
	Dead	<u>267</u>	<u>236</u>
	TOTAL	411	236
VII	Live	104	-
	Dead	<u>313</u>	<u>204</u>
	TOTAL	417	204

^a includes inorganic component

Table 6. Total and organic periphyton biomass (g/m^2 dry wt) at sampling stations each quarter.

	Total Periphyton Quarter				Organic Periphyton Quarter			
	1	2	3	4	1	2	3	4
I	1,047	434	489	773	302	127	187	542
II	1	133	155	206	T	60	66	86
III	-	925	1,358	1,408	-	232	433	337
IV	-	1,492	942	797	-	293	257	173
V	203	538	134	885	74	219	45	243
VI	918	486	321	-	249	150	127	-
VII	1,534	1,363	1,530	1,531	329	392	433	474
VIII	231	325	398	690	-	87	149	176
IX	1,152	1,059	595	1,035	175	263	226	309
X	2,030	2,682	1,770	1,269	388	526	441	359
XI	724	876	1,430	1,049	185	244	419	262
XII	236	562	-	160	94	256	-	61
XIII	2 ^a	651	271	216	1 ^a	157	116	71
XIV	516 ^a	242	78	93	183 ^a	72	22	33
XV	136 ^a	1,171	-	718	63 ^a	244	-	158
XVI	1,224 ^a	1,509	383	794	319 ^a	485	176	242
XVII	1,080 ^a	607	482	-	159 ^a	122	98	-

^a March, 1979 (Quarter 5)

Table 7. Summary of mean^a percent organic in stem periphyton for four sampling quarters.

	Mean Percent Organic				Station Mean	Station S.D.
	First Quarter	Second Quarter	Third Quarter	Fourth Quarter		
I	40.56 ^b	34.55 ^b	37.56 ^c	33.94	36.65	2.64
II	49.34 ^b	44.51 ^a	49.16 ^c	50.46	48.37	2.28
III	30.07	29.24	30.37	26.47	29.04	1.54
IV	27.33	28.13	24.25	25.51	26.31	1.52
V	44.96	42.43	37.82	34.48	39.92	4.05
VI	37.38	39.03	39.68	31.82	36.98	3.09
VII	32.11	30.36	30.46	28.32	30.31	1.34
VIII	28.25	29.52	25.66	25.13	27.14	1.81
IX	26.74	32.33	27.30	28.82	28.80	2.18
X	30.05	29.89	28.73	32.37	30.26	1.32
Quarter ^e Mean	34.68	34.00	32.10	31.73		
S.D. ^g	(7.96)	(5.93)	(7.47)	(7.41)		
XI		30.21	27.08	27.70		
XII		42.59	47.38	51.57		
XIII	30.86 ^d	27.66	31.41	51.47	35.35	9.42
XIV	27.55 ^d	32.76	27.52	36.03	30.97	3.62
XV	19.39 ^d	24.09	29.15	25.82	24.61	3.52
XVI	31.07 ^d	45.22	32.61	31.43	35.08	5.88
XVII	18.75 ^d	20.72	20.64	25.40	21.38	2.45
Quarter ^f Mean		33.13	31.58	35.63		
S.D. ^g		(7.22)	(7.57)	(11.45)		

^a Mean of three jar samples collected at each station each quarter.

^b Based on three samples pooled for one dry and ash weight.

^c Mean based on two samples only.

^d Collected in March, 1979 ("fifth" quarter).

^e Mean of 10 stations.

^f Mean of 17 stations.

^g Numbers in parentheses represent standard deviations

Table 8. Carbon:nitrogen ratios and other results (percent dry weight) of CHN analysis of some stem periphyton samples from third quarter collections.

Sample	Total C	Total N	Total H	Organic C	Total Total C:N	Organic Total C:N
III-2	21.28	0.91	1.94	4.41	23.38	4.85
IV-2	19.64	0.82	1.71	4.29	24.25	5.23
VI-2	22.54	1.17	2.29	6.45	19.26	5.51
VII-2	21.23	0.91	1.95	4.50	23.32	4.95
VIII-3	20.14	1.06	1.91	5.15	19.00	4.86
IX-3	20.66	0.86	1.70	4.92	24.02	5.72
X-3	21.20	0.91	1.91	4.47	23.30	4.91
XI-3	20.96	0.87	2.01	5.22	24.09	6.00
XIII-3	21.48	1.09	2.20	5.28	19.71	4.84
XIV-3	20.08	0.66	1.87	5.28	30.42	8.00
XVI-3	21.97	1.08	2.31	5.28	20.34	4.89
XVII-3	17.76	0.72	1.34	3.66	24.67	5.08

Table 9. Estimated living and dead macrophyte biomass (g/m^2 dry wt) at each sampling station each quarter.

	Live Macrophytes Quarter				Dead Macrophytes Quarter			
	1	2	3	4	1	2	3	4
I	143	170	135	32	516	869	625	612
II	67	170	360	177	750	1,095	1,052	443
III	-	105	41	225	-	162	241	228
IV	-	30	60	56	-	32	90	88
V	10	146	200	165	468	295	404	275
VI	90	284	418	583	696	382	963	653
VII	137	112	64	191	612	426	257	510
VIII	98	143	284	248	434	106	324	256
IX	38	40	90	141	129	42	114	115
X	89	78	28	88	457	474	193	314
XI	72	77	3	45	141	143	278	97
XII	237	283	-	134	381	592	-	375
XIII	3 ^a	80	35	72	3 ^a	94	56	138
XIV	180 ^a	217	88	66	96 ^a	149	105	207
XV	56 ^a	39	-	44	32 ^a	56	34	89
XVI	713 ^a	30	137	96	219 ^a	77	141	133
XVII	805 ^a	141	193	108	409 ^a	458	343	312

^a March 1979 (Quarter 5)

Table 10. Differences in macrophyte biomass (g/m² dry wt) of each type, living and dead, between successive quarters.^a

	Living Biomass					Dead Biomass				
	Quarters				Sum of Positive Differences	Quarters				Sum of Positive Differences
	1-2	2-3	3-4	4-1		1-2	2-3	3-4	4-1	
I	+ 27	- 37	-101	+111	138	+353	-264	- 38	- 51	353
II	+103	+189	-182	+110	292	345	- 49	-628	+332	677
V	+136	+ 54	- 35	-155	190	-173	+107	-174	+240	347
VI	+194	+134	+165	-493	473	-314	+528	-192	+ 59	587
VII	- 25	- 48	+127	- 54	127	-186	-169	+253	+102	355
VIII	+ 45	+141	- 36	-150	186	-328	+218	- 68	+178	396
IX	+ 2	+ 50	+ 51	- 10	103	- 87	+ 72	+ 1	+ 14	87
X	- 11	- 50	+ 60	- 1	60	+ 17	-281	+121	+143	281
XI	+ 5	- 74	+ 42	+ 27	74	+ 2	+135	-181	+ 44	181
XIII	+ 77 ^a	- 45	+ 37	- 69 ^b	114	+ 91 ^a	- 38	+ 82	-135 ^b	173
XIV	+ 37 ^a	-129	- 22	+114 ^b	151	+ 53 ^a	- 44	+102	-111 ^b	155
XVI	-683 ^a	+107	- 41	+617 ^b	724	-142 ^a	+ 64	- 8	+86 ^b	150
XVII	-664 ^a	+ 52	- 85	+697 ^b	749	+ 49 ^a	-115	- 31	+ 97 ^b	146

^a Quarters 5-2

^b Quarters 4-5

Table 11. Days between sampling at each station.

	Number of Days			
	1-2	2-3	3-4	4-1
I	98	86	84	97
II	98	86	84	97
III	97	85	84	99
IV	97	85	84	99
V	98	86	84	97
VI	98	86	84	97
VII	98	86	84	97
VIII	99	87	84	95
IX	98	86	84	97
X	98	86	84	97
XI	90	91	90	94
XII	90	91	90	94
XIII	106 ^a	56	102	101 ^b
XIV	106 ^a	56	102	101 ^b
XV	106 ^a	56	102	101 ^b
XVI	107 ^a	56	103	100 ^b
XVII	107 ^a	56	102	100 ^b

^a Quarters 5-2

^b Quarters 4-5

Table 12. Calculation of annual production ^{a,b} of macrophytes.

1.	2.	3.	4.	5.	6.
Sum of quarterly positive changes in living biomass g/m ²	Sum of quarterly negative changes in dead biomass g/m ²	Number of days of negative changes in dead biomass total days	Estimated min. average daily decomposition rate g/m ² day	Estimated annual loss to decomposition g/m ² yr	Estimated annual production ^c g/m ²
I	138	267	1.32	482	620
II	292	170	3.84	1,400	1,692
V	190	182	1.66	606	796
VI	493	182	3.43	1,251	1,744
VII	127	184	1.92	704	831
VIII	186	183	2.16	790	976
IX	103	98	0.89	324	427
X	60	86	3.27	1,193	1,253
XI	74	90	2.01	734	808
XIII	114	207	0.836	305	419
XIV	151	207	0.749	273	424
XVI	724	208	0.721	263	987
XVII	749	158	0.924	337	1,086

^a Method is that described by Wiegert and Evans (1964), except that live organic material was not removed from plots to be used to estimate loss of dead organic matter by decomposition. Calculated decomposition rates should therefore be considered minimum estimates.

^b Weights are dry weights of organic material.

^c Values in column 6 are sum of values in columns 1 and 5.

Table 13. Estimated gross primary productivity (GPP_{24}) and net primary productivity (NPP_{24}) of periphyton, with P/R ratios and GPP_{24} /gram organic biomass.

	Periphyton ^b					
	GPP_{24} ^a g/m ² .day	NPP_{24} ^a g/m ² .day	P/R	No. daylight hrs	organic biomass g/m ²	GPP_{24} / g biomass
VIII Winter (Jan 9-10, 1979)	2.0	-.042	0.979	10	82	.024
XI Winter (Jan 19-20, 1979)	1.46	-.376	0.795	10	207	.007
XV Winter (Dec 22-23, 1979)	1.16	-.015	0.988	10	192	.006
VIII Summer (Jul 11-12, 1979)	4.49	2.01	1.808	13	157	.029
IV Summer (Aug 13-14, 1979)	2.65	1.08	1.691	13	123	.022
XV Summer (Jul 23-24, 1979)	1.41	-.649	0.684	13	220	.006

^a Units are grams oxygen, which is approximately the same as grams organic matter.

^b Units are grams organic matter.

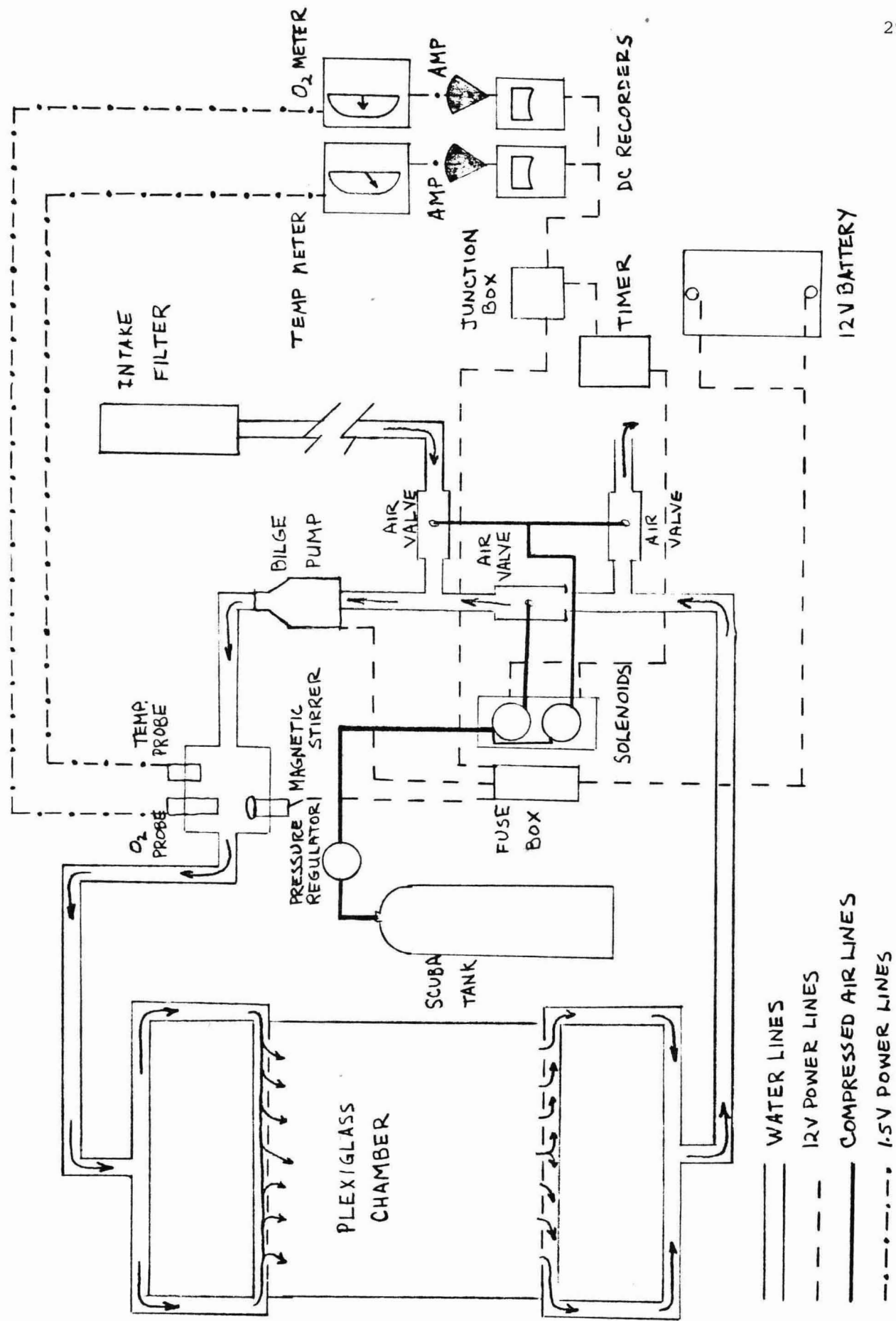


Figure 1. Schematic for field installation of Edwards respirometer.

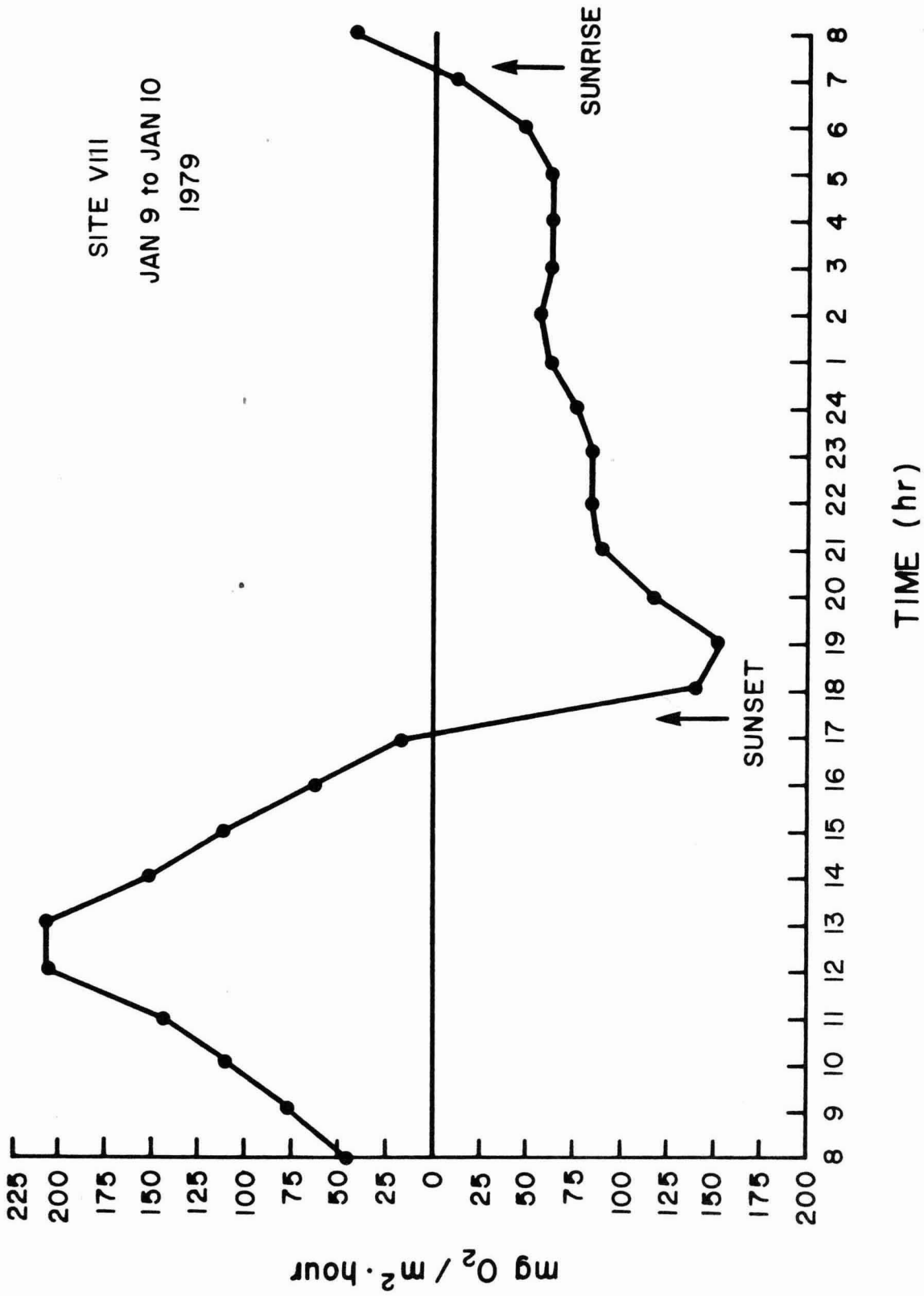


Figure 2. Change in oxygen per hour for 24 hr period, Station VIII, winter (January 9-10, 1979).

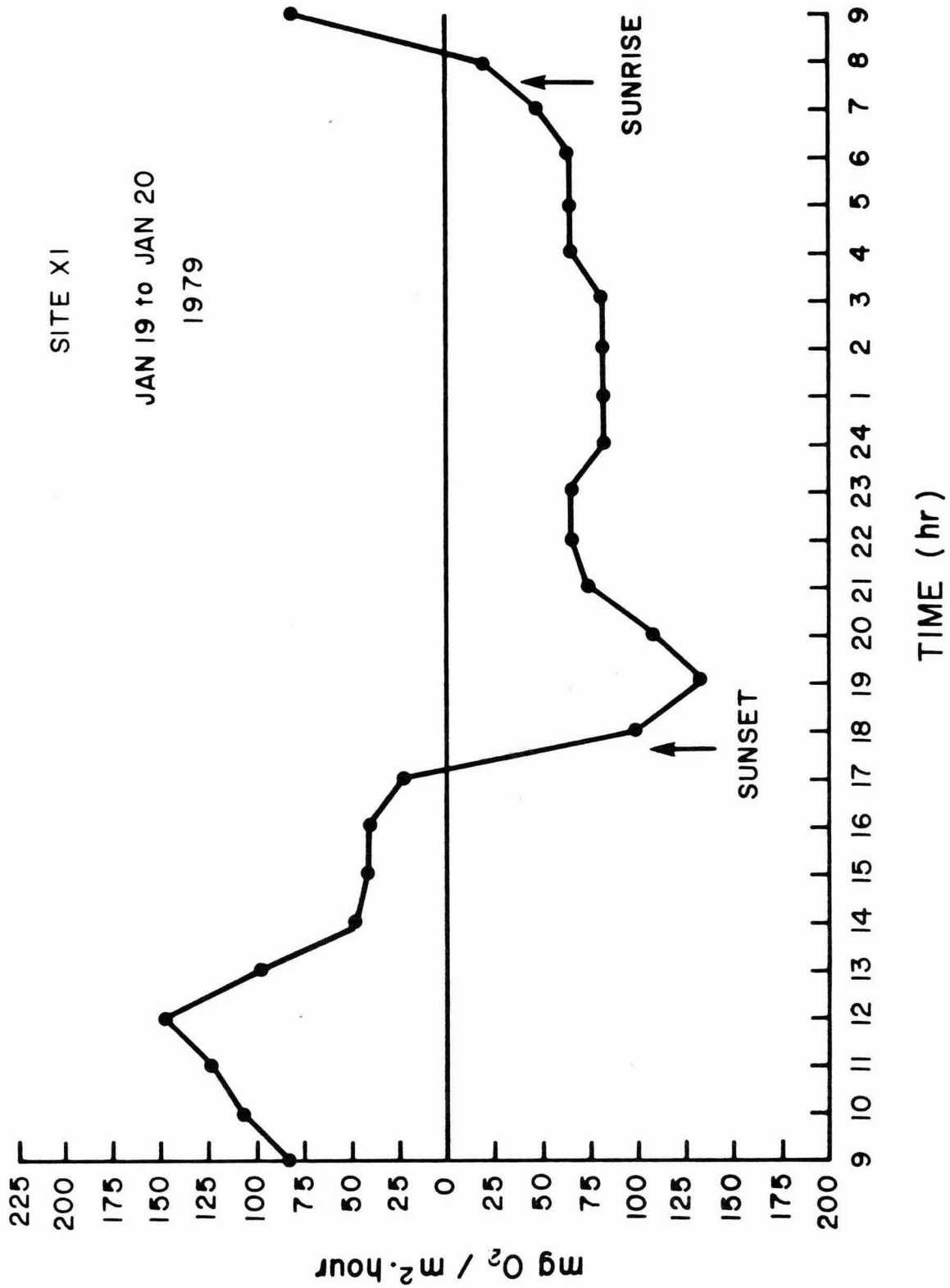


Figure 3. Change in oxygen per hour for 24 hr period, Station XI, winter (January 19-20, 1979).

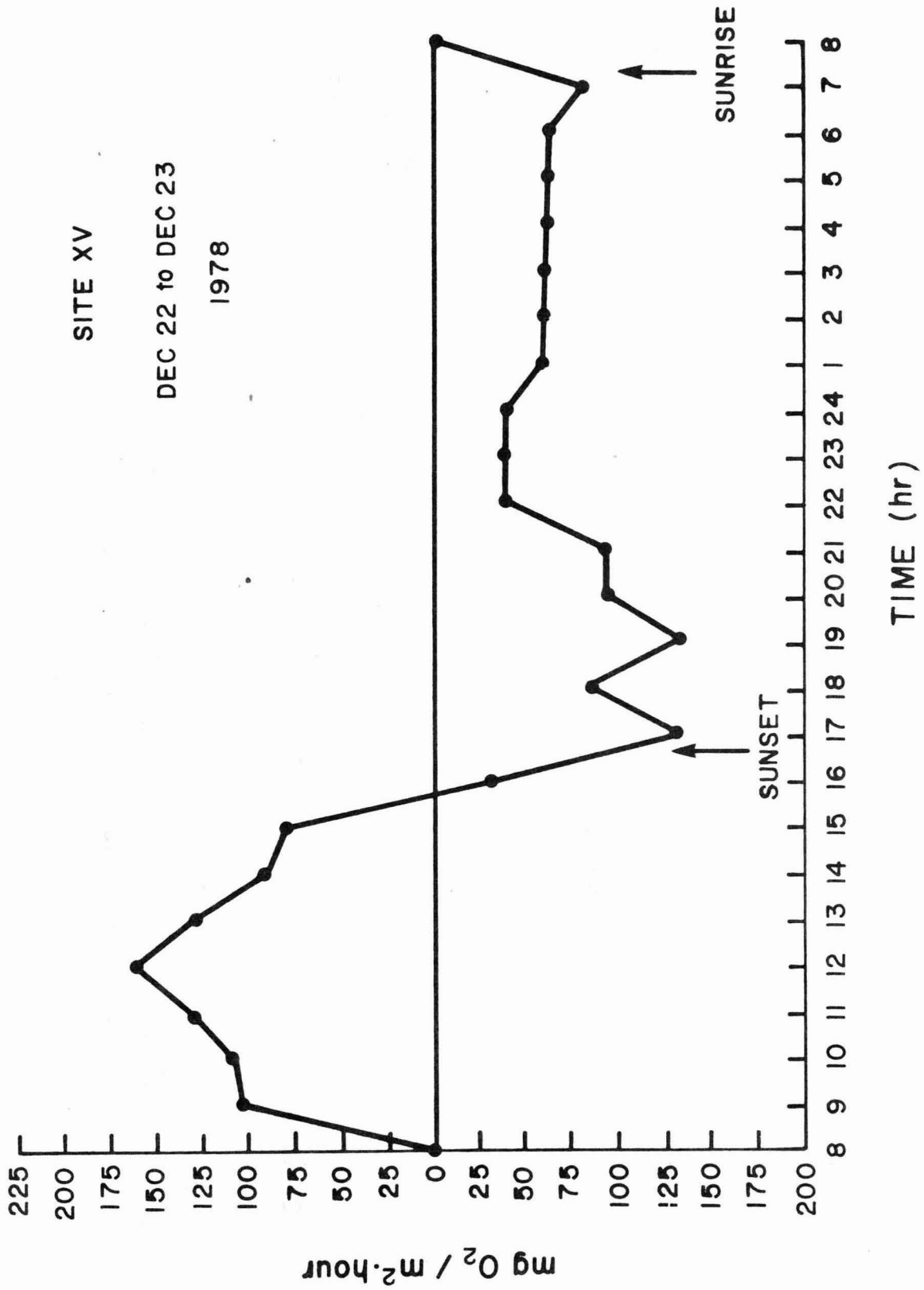


Figure 4. Change in oxygen per hour for 24 hr period, Station XV, winter (December 22-23, 1978).

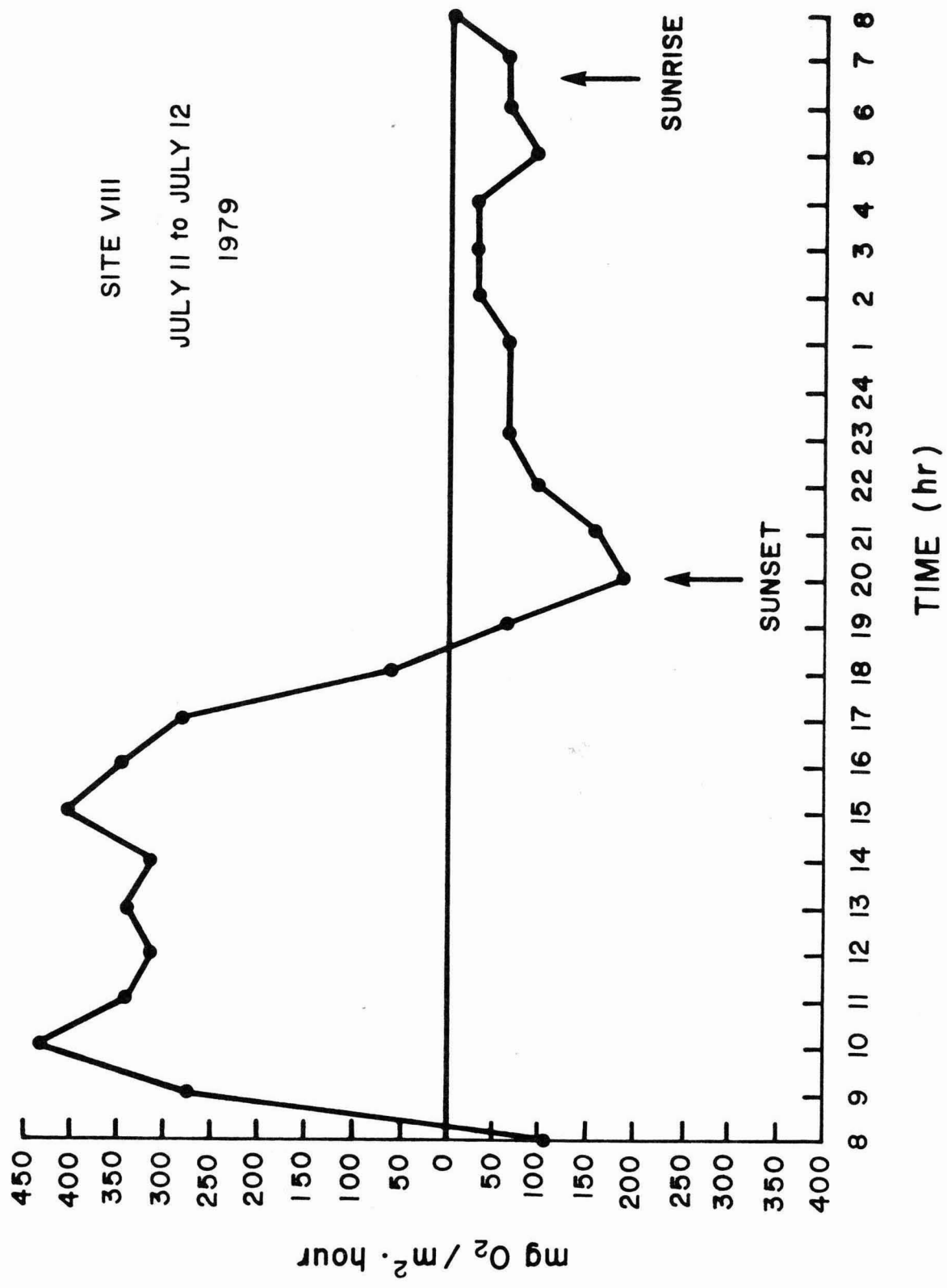


Figure 5. Change in oxygen per hour for 24 hr period, Station VIII, summer (July 11-12, 1979).

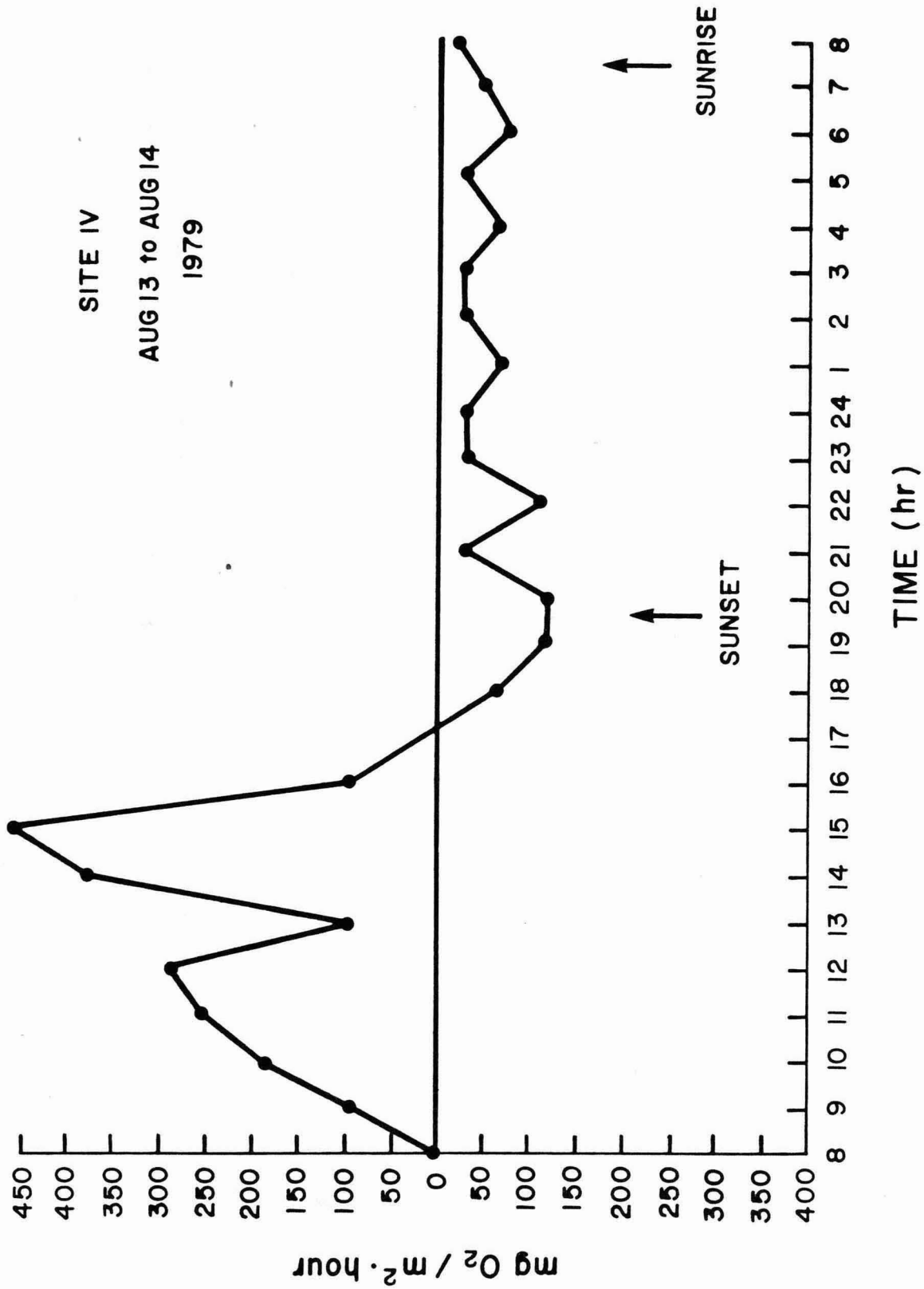


Figure 6. Change in oxygen per hour for 24 hr period, Station IV, summer (August 13-14, 1979).

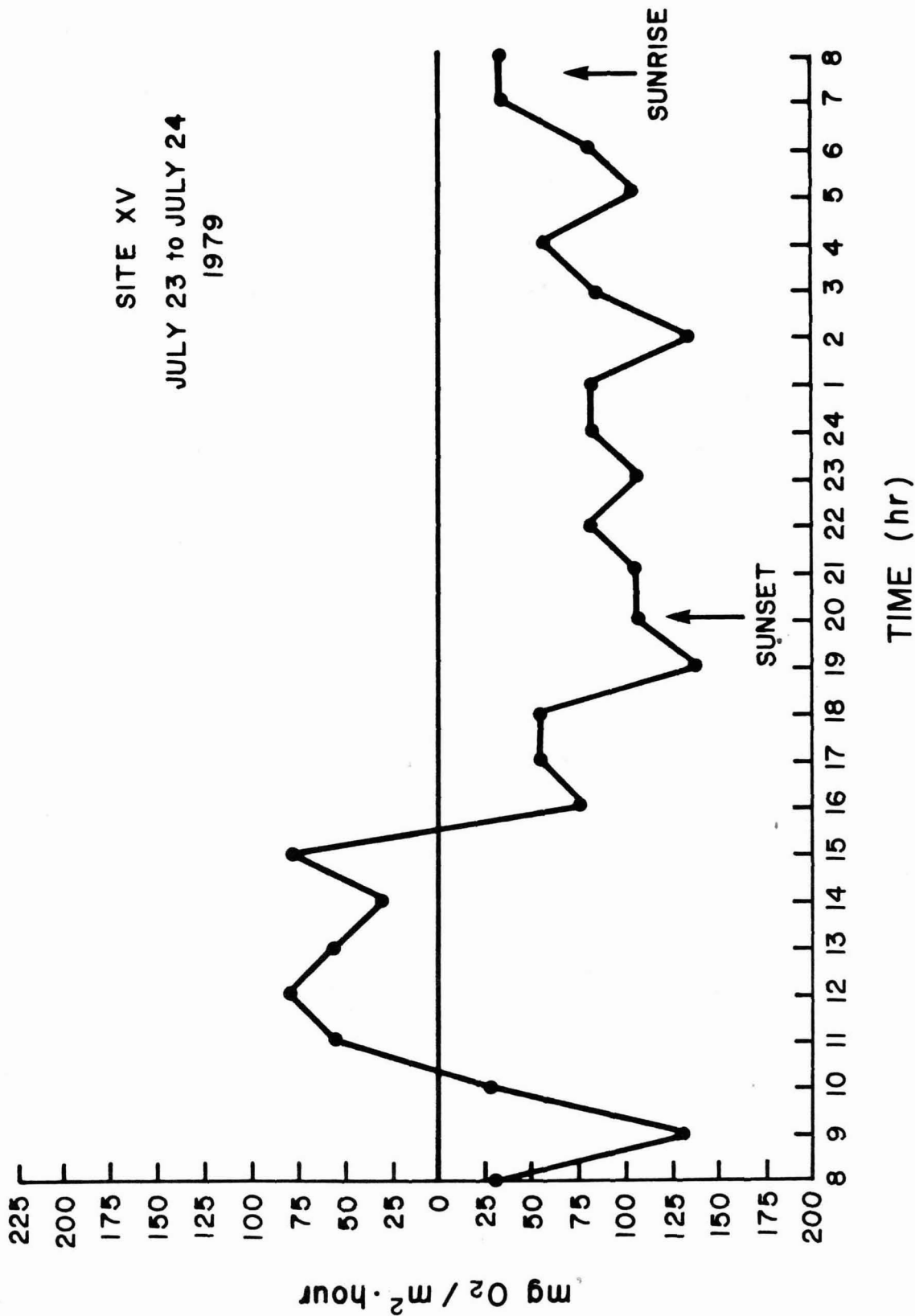


Figure 7. Change in oxygen per hour for 24 hr period, Station XV, summer (July 23-24, 1979).

Appendix Table A-1. Biomass sampling days and dates.

	<u>Biomass Sampling Dates</u>				
	Sample Quarter				
	1	2	3	4	5
I	2/23/78	6/1/78	8/26/78	11/18/78	
II	2/23/78	6/1/78	8/26/78	11/18/78	
III	2/24/78	6/1/78	8/26/78	11/18/78	
IV	2/24/78	6/1/78	8/26/78	11/18/78	
V	2/24/78	6/2/78	8/27/78	11/19/78	
VI	2/23/78	6/1/78	8/26/78	11/18/78	
VII	2/23/78	6/1/78	8/26/78	11/18/78	
VIII	2/23/78	6/2/78	8/27/78	11/19/78	
IX	2/24/78	6/2/78	8/27/78	11/19/78	
X	2/24/78	6/2/78	8/27/78	11/19/78	
XI	2/15/78	5/16/78	8/15/78	11/13/78	
XII	2/15/78	5/16/78	8/15/78	11/13/78	
XIII		7/8/78	9/2/78	12/13/78	3/24/79
XIV		7/8/78	9/2/78	12/13/78	3/24/79
XV		7/8/78	9/2/78	12/13/78	3/24/79
XVI		7/9/78	9/2/78	12/14/78	3/24/79
XVII		7/9/78	9/3/78	12/14/78	3/24/79

Appendix Table A-2. Definitions and equations for estimating macrophytic, algal, and inorganic components of "mat" biomass samples.

Average dry wt. 50 ml aliquot	$= \bar{A}_{1-5} = (\Sigma A_{1-5})/5$
Average dry wt. 50 ml aliquot after grinding	$= \bar{B}_{1-5} = (\Sigma B_{1-5})/5$
Average ash wt. ground sample	$= \bar{C}_{1-5} = (\Sigma C_{1-5})/5$
Average ash wt. 50 ml sample	$= D_{1-5} = (\bar{C}_{1-5}/\bar{B}_{1-5}) \bar{A}_{1-5}$
Average organic wt. 50 ml sample	$= E_{1-5} = \bar{A}_{1-5} - D_{1-5}$
Average organic wt. periphyton only 50 ml sample	$= F = E_{1-5} - E_{6-15}$
Average dry wt. small macro in 50 ml aliquots	$= \bar{A}_{6-15} = (\Sigma A_{6-15})/10$
Average ash wt. small macro in 50 aliquots	$= \bar{C}_{6-15} = (\Sigma C_{6-15})/10$
Average organic wt. small macro in 50 ml aliquots	$= E_{6-15} = \bar{A}_{6-15} - \bar{C}_{6-15}$
Dry weight of entire sample minus 15 aliquots and large macros	$= P$
Total weight of mat sample	$= T = P + (15 * \bar{A}_{1-5})$
Dry wt. total periphyton in mat	$= X = T (1 - \bar{A}_{6-15}/\bar{A}_{1-5})$
Dry wt. organic periphyton in mat	$= O = T (F/\bar{A}_{1-5})$
Dry wt. small macros in mat	$= M = T (\bar{A}_{6-15}/\bar{A}_{1-5})$
Large dead macros in mat	$= N$
Large live macros in mat	$= L$

Appendix Table B-1. First quarter (February) biomass (g/m² dry wt) at sampling sites I through XII.

	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
	Periphyton	Periphyton					
I	Floating Mat	0			172.4		
	Standing	1,046.8			343.7		
	Total	1,046.8	301.5	142.7	516.1		658.8
II	Floating Mat	0			141.6		
	Standing	0.5			608.0		
	Total	0.5	trace	67.2	749.6		816.8
III	No data						
IV	No data						
V	Floating Mat	0			156.2		
	Standing	202.6			312.1		
	Total	202.6	74.4	9.5	468.3		477.8
VI	Floating Mat	0			642.2		
	Standing	872.1			53.7		
	Total	918.4	249.4	90.3	695.9		786.2
VII	Floating Mat	0			260.9		
	Standing	1,240.8			350.5		
	Total	293.5	328.8	137.1	611.4		748.5

Table B-1 continued.

	Total Periphyton	Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
VIII	Floating	0				
	Mat	0		222.5		
	Standing	231.2		211.3		
	Total	231.2	98.3	433.8		532.1
IX	Floating	279.0				
	Mat	736.6		72.1		
	Standing	136.0		55.0		
	Total	1,151.6	37.7	127.1		164.8
X	Floating	0				
	Mat	1,730.5		137.2		
	Standing	299.7		320.3		
	Total	2,030.2	89.2	457.5		546.7
XI	Floating	0				
	Mat	637.5		2.7		
	Standing	86.5		137.8		
	Total	724.0	71.7	140.5		212.2
XII	Floating	184.2				
	Mat	0		146.5		
	Standing	51.3		234.9		
	Total	235.5	237.4	381.4		618.8

^a minus ash

Appendix Table B-2. Second quarter biomass (g/m² dry wt) at sampling sites (May and June, Stations I-XII; July, Stations XIII-XVII).

	Total Periphyton	Organic Periphyton	Live Macrophytes	Dead ^a Macrophytes	Undetermined Macrophytes	Total Macrophytes
I						
Mat	391.93	112.66	0.53	9.10		9.63
Standing	41.60	14.37	169.83	860.33		1,030.16
Total	433.53	127.03	170.36	869.43		1,039.79
II						
Mat	90.64	40.65	0.47	9.78		10.25
Standing	42.50	18.92	169.30	1,084.90		1,254.20
Total	133.14	59.57	169.77	1,094.68		1,264.45
III						
Mat	903.00	225.65	3.41	47.97		51.38
Standing	21.66	6.33	101.19	113.58		214.77
Total	924.66	231.98	104.60	161.55		266.15
IV						
Mat	1,471.51	287.09	5.69	18.29		23.98
Standing	20.84	5.86	24.14	13.95		38.09
Total	1,492.35	292.95	29.83	32.24		62.07
V						
Mat	302.41	118.42	1.05	27.91		28.96
Standing	235.81	100.07	144.59	266.67		411.26
Total	538.22	218.49	145.64	294.58		440.22
VI						
Mat	278.00	86.00 ^b	0	49.00	34.00	83.00
Standing	208.30	64.00	238.90	251.60	92.10	582.60 ^c
Total	486.30	150.00	238.90	300.60	126.10	665.60
VII						
Mat	1,159.00	330.02	8.06	113.13		121.19
Standing	203.67	61.84	103.54	313.06		416.60
Total	1,362.67	391.86	11.60	426.19		537.79

Table B-2 continued.

	Total Periphyton	Organic Periphyton	Live Macrophytes	Dead ^a Macrophytes	Undetermined Macrophytes	Total Macrophytes
VIII						
Mat	318.23	84.72	0	23.62		23.62
Standing	6.32	1.87	142.64	82.40		225.04
Total	324.55	86.59	142.64	106.02		248.66
IX						
Mat	1,051.94	260.55	1.91	22.42		24.33
Standing	6.70	2.40	38.57	19.99		58.56
Total	1,058.64	262.72	40.48	42.41		82.89
X						
Mat	2,578.44	494.80	40.75	76.58		117.33
Standing	103.42	30.91	37.49	397.22		434.71
Total	2,681.86	525.71	78.24	473.80		552.04
XI						
Mat	716.80	198.05	22.40	44.80		67.20
Standing	159.09	45.53	54.92	98.48		153.40
Total	875.89	243.58	77.32	143.28		220.60
XII						
Mat	277.51	138.23	7.56	53.76		61.32
Standing	39.99	21.55	267.81	488.79		756.60
Floating	244.77	96.41	7.46	49.73		57.19
Total	562.27	256.19	282.83	152.28		875.11
XIII						
Mat	636.08	152.47	35.02	47.21		82.23
Standing	15.10	4.17	44.50	46.70		91.20
Total	651.18	156.64	79.52	93.91		173.43
XIV						
Mat	234.53	69.05	45.04	56.08		101.12
Standing	7.66	2.87	171.98	92.46		264.44
Total	242.19	71.92	217.02	148.54		365.56

Table B-2 continued.

		Total Periphyton	Organic Periphyton	Live Macrophytes	Dead ^a Macrophytes	Undetermined Macrophytes	Total Macrophytes
XV	Mat	1,165.68	242.46	28.29	31.69		59.98
	Standing	4.96	1.48	10.80	24.00		34.80
	Total	1,170.64	243.94	39.09	55.69		94.78
XVI	Mat	1,456.24	461.05	0.00	44.18		44.18
	Standing	53.68	23.60	30.33	33.28		63.61
	Total	1,509.92	484.65	30.33	77.46		107.79
XVII	Mat	508.43	99.75	1.31	69.91		71.22
	Standing	98.47	22.00	139.71	387.68		527.39
	Total	606.90	121.75	141.02	457.59		598.61

^a excluding stem periphyton

^b estimate of organic component is based on calculated percent in mat sample

Appendix Table B-3. Third quarter (Aug.-Sept.) biomass (g/m² dry weight) at sampling sites I through XVII.

Station	Sample	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
		Periphyton	Periphyton					
I	Mat	489	187	3	25	22		50
	Standing	0	0	130	580			710
	Total	489	187	133	605	22		760
II	Mat	155	66	2	11	7		20
	Standing	0	0	357	1035			1392
	Total	155	66	359	1046	7		1412
III	Mat	1341	428	4	34	127		164
	Standing	17	5	24	93			116
	Total	1358	433	28	127	127		280
IV	Mat	854	236	2	26	12		40
	Standing	88	21	57	53			110
	Total	942	257	59	79	12		150
V	Mat	134	45	0	24	2		26
	Standing	0	0	200	378			578
	Total	134	45	200	402	2		604
VI	Mat	137	54	23	202			225
	Standing	184	73	325	627	204		1156
	Total	321	127	348	829	204		1381
VII	Mat	1519	430	6	41	42		89
	Standing	11	3	53	179			233
	Total	1530	433	59	220	42		322
VIII	Mat	367	141	19	42	57		119
	Standing	31	8	247	243			489
	Total	398	149	266	285	57		608

Table B-3 continued.

Station	Sample	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
		Periphyton	Periphyton					
IX	Mat	582	222	6	13	26	45	
	Standing	13	4	76	83	159		
	Total	595	226	82	96	204		
X	Mat	1702	421	1	15	69	85	
	Standing	68	20	23	113	136		
	Total	1770	441	24	128	221		
XI	Mat	1372	403	0	31	60	91	
	Standing	58	16	3	187	190		
	Total	1430	419	3	218	281		
XII	Mat	220	118	0	29	39	68	
	Standing	ND	ND	ND	ND	ND	ND	
	Total							
XIII	Mat	245	108	0	2	28	30	
	Standing	26	8	35	26	61		
	Total	271	116	35	28	91		
XIV	Mat	53	15	6	6	12		
	Standing	25	7	82	98	182		
	Total	78	22	88	104	194		
XV	Mat	522	128	0	1	33	34	
	Standing	ND	ND	ND	ND	ND	ND	
	Total	ND	ND	ND	ND	ND		
XVI	Mat	267	138	0	23	81	104	
	Standing	116	38	137	37	174		
	Total	383	176	137	60	278		

Table B-3 continued.

Station	Sample	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
		Periphyton	Periphyton ^a					
XVII	Mat	402	82	7	4	20	31	
	Standing	80	16	151	290	64	505	
	Total	482	98	158	294	84	536	

^aOrganic periphyton in standing samples calculated from percent organic in jar stem periphyton samples.

Appendix Table B-4. Fourth quarter (Nov.- Dec.) biomass (g/m² dry weight) at sampling sites I through VIII.

Station	Sample	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undetermined Macrophytes	Total Macrophytes
		Periphyton	Periphyton					
I	Mat	739	530	1	15	20		36
	Standing	34	12	23	552	33		608
	Total	773	542	24	567	53		644
II	Mat	186	76	4	33	18		55
	Standing	20	10	167	385	13		565
	Total	206	86	171	418	31		620
III	Mat	1269	301	4	16	118		138
	Standing	136	36	195	117	3		315
	Total	1408	337	199	133	121		453
IV	Mat	738	158	20	35	48		103
	Standing	59	15	18	21	2		41
	Total	797	173	38	56	50		144
V	Mat	853	232	3	25	38		66
	Standing	32	11	148	203	23		374
	Total	885	243	151	228	61		440
VI	Mat	ND	ND	ND	ND	ND		ND
	Standing	270	86	568	637	31		1236
	Total	ND	ND	ND	ND	ND		ND
VII	Mat	1420	443	1	43	168		212
	Standing	111	31	182	297	10		489
	Total	1531	474	183	340	178		701
VIII	Mat	674	172	4	11	72		87
	Standing	16	4	221	189	7		417
	Total	690	176	225	200	79		504

Table B-4 continued.

Station	Sample	Total		Organic		Live		Dead		Undetermined		Total
		Periphyton	Periphyton ^a	Periphyton	Macrophytes	Macrophytes	Macrophytes	Macrophytes	Macrophytes	Macrophytes	Macrophytes	
IX	Mat	720	218	4	6	36	46					
	Standing	315	91	117	82	11	210					
	Total	1035	309	121	88	47	256					
X	Mat	1219	343	0	14	59	73					
	Standing	50	16	88	239	2	329					
	Total	1269	359	88	253	61	402					
XI	Mat	919	226	1	6	53	60					
	Standing	130	36	36	45	1	82					
	Total	1049	262	37	51	54	142					
XII	Mat	133	47	0	23	81	104					
	Standing	27	14	129	262	14	405					
	Total	160	61	129	285	95	509					
XIII	Mat	188	57	0	18	68	86					
	Standing	28	14	63	46	15	124					
	Total	216	71	63	64	83	210					
XIV	Mat	56	20 ^b	3	18	6	27					
	Standing	37	13	61	180	5	246					
	Total	93	33	64	198	11	273					
XV	Mat	711	156	1	3	45	49					
	Standing	7	2	16	26	42	84					
	Total	718	158	17	29	87	133					
XVI	Mat	728	221	3	8	16	27					
	Standing	66	21	89	112	1	202					
	Total	794	242	92	120	17	229					

Table B-4 continued.

Station	Sample	Total		Organic Periphyton ^a	Live Macrophytes	Dead Macrophytes	Undertermined		Total
		Periphyton	Periphyton ^a				Macrophytes	Macrophytes	
XVII	Mat	ND	ND	ND	ND	ND	ND	ND	ND
	Standing Total	61	108	308	5	421	ND	ND	

^a Organic periphyton in standing samples calculated from percent organic in jar stem periphyton samples.

^b Calculated from percent organic in jar stem periphyton samples.

Appendix Table B-5. Fifth quarter (March) biomass (g/m² dry weight) at sampling sites XIII through XVII.

Station	Sample	Total		Organic Periphyton	Live		Dead		Undetermined		Total
		Periphyton	Periphyton		Macrophytes	Macrophytes	Macrophytes	Macrophytes	Macrophytes		
15-XIII	Mat	0	0	0	0	0	0	0	0	0	0
	Standing	2	1	3	3	3	3	3	0	0	6
	Total	2	1	3	3	3	3	3	0	0	6
15-XIV	Mat	477	169	100	100	34	0	0	0	0	134
	Standing	39	14	69	69	53	20	20	20	20	211
	Total	516	183	169	169	87	20	20	20	20	345
15-XV	Mat	135	63	50	50	28	0	0	0	0	78
	Standing	1	0	6	6	4	0	0	0	0	10
	Total	136	63	56	56	32	0	0	0	0	88
15-XVI	Mat	1,180	308	710	710	158	0	0	0	0	868
	Standing	44	11	3	3	53	8	8	8	8	64
	Total	1,224	319	713	713	211	8	8	8	8	932
15-XVII	Mat	1,021	150	647	647	78	0	0	0	0	725
	Standing	59	9	123	123	258	108	108	108	108	489
	Total	1,080	159	770	770	336	108	108	108	108	1,214

