ABSTRACT

Anthony B. Hall. TOTAL COMMUNITY METABOLISM MODIFICATION OF AN AQUATIC ECOSYSTEM BY 2,4-D APPLICATION. (Under the direction of Mark M. Brinson) Department of Biology, August 1976.

A macrophyte community composed primarily of Eurasian water-milfoil (Myriophyllum spicatum L.), located in Kitty Hawk Bay, North Carolina, was treated on 13 July 1974 with a 20% acid equivalent formulation of the butoxyethanol ester of 2,4-dichlorophenoxyacetic acid (2,4-D) attached to attaclay granules (100 lb/acre). This large-scale application of 2,4-D to an aquatic ecosystem provided a unique opportunity to determine the form or pathways of energy flow and nutrient cycling which replace those found in the ecosystem before the destruction of the Myriophyllum spicatum community. Prior to treatment, diurnals conducted in both treatment and control study areas were indicative of a relatively stable and very productive ecosystem with no extreme changes in oxygen production or consumption. Gross primary productivity (GPP) for the treatment study area (5.64 g $O_2/m^2 \cdot day$) and control study area (4.59 g $O_2/m^2 \cdot day$) were quite comparable. Following treatment with 2,4-D there was a tremendous die-back of the M. spicatum community concomitant with an increase in ammonium concentration in the water. Seventeen days following treatment with 2,4-D the lowest oxygen level of the entire study (4.09 mg O_2/ℓ) was obtained in the treatment study area. On 13 August 1974, however, a phytoplankton bloom dominated by two genera of the Cyanophyta (Aphanizomenon and Anacystis) occurred in the treatment area. The highest GPP value during the entire study

(12.66 g $O_2/m^2 \cdot day$) was obtained where no plankton activity was previously detectable.

One year following herbicide application the treatment study area appeared to be returning to a system dominated by macrophytes. Gross primary productivity for the treatment study area (4.25 g $O_2/m^2 \cdot day$) and control study area (5.50 g $O_2/m^2 \cdot day$) were quite similar. Minimum oxygen levels in the treatment study area were much higher than those after treatment in 1974 and were comparable to the control minimum levels. Plankton biomass and productivity had declined from the values recorded after treatment in 1974 but were still greater than pretreatment values.

TOTAL COMMUNITY METABOLISM MODIFICATION OF AN AQUATIC ECOSYSTEM BY 2,4-D APPLICATION

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TOTAL COMMUNITY

METABOLISM MODIFICATION OF AN

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INTRODUCTION

The Concept of Ecosystem Perturbation

Myriophyllum spicatum L., commonly known as Eurasian water-milfoil, is a submersed aquatic plant native to Europe and Asia which has been introduced into the United States and has grown to become a "nuisance" species in lower Currituck Sound and Kitty Hawk Bay, North Carolina. The plan for the control of *M. spicatum* was to apply the herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) over 304 hectares (750 acres) of Kitty Hawk Bay. The effects of 2,4-D on ecosystems are poorly understood and information on the effects of 2,4-D on aquatic systems is scarce (Odum, E. P., 1971). Obviously 2,4-D is capable of modifying plant communities, indirectly affecting herbivores, carnivores and detritivores and altering nutrient cycles and pathways of energy flow. This large-scale application of 2,4-D to an aquatic ecosystem provided a unique opportunity to determine the forms or pathways of energy flow and nutrient cycling which replace those found in the ecosystem before the destruction of the *M. spicatum* community.

Studies of terrestrial ecosystem perturbation from the Hubbard Brook Experimental Forest, New Hampshire (Likens et al., 1970; Bormann et al., 1974; Hobbie and Likens, 1973) have shown that when an ecosystem is disrupted on a large scale, the system temporarily loses its capacity for maintenance and repair. Noticeable effects of disruption were increased run-off due to reduced rates of evapo-transpiration accompanied by increased losses of nitrate, magnesium, calcium, phosphorus and fine particulate carbon. Examples of aquatic

ecosystem perturbation range from studies of the acceleration of lake eutrophication of the Great Lakes (Beeton, 1965) to controlled nutrient inputs to small experimental lakes (Schindler, 1974). Edmondson (1971) found that advanced stages of eutrophication can be reversed in lakes where the input of pollutants can be controlled. This was found to be true for Lake Washington near Seattle, Washington, which has recovered rapidly since 1968 when the amount of sewage released into the lake was decreased. This demonstrates the ability of natural systems to recover from perturbation if they are not disturbed too greatly.

The diversity of organisms within a natural system contribute to the stability of the system allowing it to accommodate stress. With the introduction of M. spicatum the diversity of Kitty Hawk Bay decreased as native species were displaced, based upon the data of Crowell et al. (1967) and Getsinger (1976).

The stability of an ecosystem can also be defined in terms of the ecosystem's response to an externally originated perturbation. A more stable system such as one dominated by several grasses, has a greater ability to reduce the effect of such perturbations than a less stable system such as the one dominated by M. spicatum. The ecosystem's stability can be characterized by three components: (1) the rapidity of the response to the external input, (2) the magnitude of the response, and (3) the time required for the response to decay back to the original, or some new ground state (McNaughton and Wolf, 1973). Information about these three components following 2,4-D treatment is crucial for evaluation of the total impact of herbicide application on the ecosystem.

Oxygen concentrations in the water reflect community metabolism and can give vital information on disruption of an ecosystem following herbicide application. Thus, the diurnal dissolved oxygen method (Odum, 1956) which measures changes in total oxygen concentration can yield valuable information about changes in community metabolism (both productivity and respiration) that take place following the application of 2,4-D and, therefore, the total impact of herbicide application. Information about changes in specific components of the system (plankton and benthos) would also be of value so that any alterations in energy flow detected for the entire community could be traced to a specific component of the system. A basic need of State and Federal Agencies is to characterize the habitat to which game fish and other valuable organisms must adapt following the impact of herbicide application.

Myriophyllum spicatum in North Carolina

History of Establishment

Myriophyllum spicatum was first reported in North Carolina in fresh water impoundments at the Pea Island National Wildlife Refuge and may have been introduced by waterfowl, carrying seeds in their feces or seeds clinging to mud on their feet. This community of M. spicatum was eradicated by an ocean overwash during the "Ash Wednesday" storm of March 1962 (Crowell et al., 1967). M. spicatum was released in the United States in the 1880's and spread southward from New Jersey. It was reported from the Potomac River in 1933 and by 1956-57 it had spread explosively throughout the more saline areas of the lower Poto-

mac and Chesapeake Bay (Fish, 1974). An intensive ecological study of aquatic vegetation of Back Bay, Virginia and Currituck Sound, North Carolina was conducted from 1958-1963 and M. spicatum was not found in any of the thousands of plant samples collected (Crowell et al., 1967). Myriophyllum spicatum was first reported in Currituck Sound in the summer of 1965, when interviews with commercial fishermen revealed that it had been seen occasionally during the summer of 1964 and that growth had reached infestation stage in 1965 (Crowell et al., 1967). By the summer of 1966, a heavy infestation of M. spicatum covered 8,000 acres (3,238 ha) of Currituck Sound with another 67,000 acres (27,114 ha) supporting more limited growth. Areas of infestation were observed in Back Bay, Albemarle Sound, Kitty Hawk Bay, Croatan Sound and North River during the fall of 1966 and the same areas remain infested today (Fish, 1974).

Growth of M. spicatum, like most recently introduced exotic species, seems to be explosive following introduction followed by stabilized growth at a relatively high incidence, and ultimately a gradual subsidence to a lower level in equilibrium with native vegetation. The M. spicatum infestation of Currituck Sound and adjacent waters apparently is in the stabilization stage for there has been no significant spread of the infestation since the late 1960's (Fish, 1974).

Problems Associated with M. spicatum

The rapid spread of M. spicatum in the United States warrants concern because this plant grows in extremely high densities and tends

to dominate the waters in which it occurs (Steenis et al., 1961). Heavy infestations of M. spicatum make most recreational uses of the waters difficult or impossible. An exception is large-mouth bass fishing which is enhanced by the rich cover provided. Boating, swimming and commercial fishing are severely hampered by heavy growths of M. spicatum. This plan t is not a significant component of waterfowl diet and it tends to replace native plants preferred by many species of waterfowl. Growths of M. spicatum do provide a food source for waterfowl by supporting macrobenthic food organisms as well as affording sanctuary from disturbance (Fish, 1976). Displacement of native vegetation by M. spicatum in Kitty Hawk Bay has been documented by a series of plant collections. A study in July 1963, prior to the appearance of M. spicatum, revealed that the aquatic plant community (reported as dense) was composed of 50% widgeongrass (Ruppia maritima), 45% sago pondweed (Potamogeton pectinatus), and 5% redhead grass (P. perfoliatus). In August 1966, aquatic plant growth was still reported as dense, but the composition had shifted to 90% R. maritima, 5% wild celery (Vallisneria americana), 1% P. perfoliatus and traces of southern naiad (Najas guadalupensis) and P. pectinatus. By 1968 M. spicatum comprised an estimated 20-25% of the plant composition of Kitty Hawk Bay. In April 1973 it represented approximately 75% of the aquatic vegetation of Kitty Hawk Bay while P. pectinatus and R. maritima were the only native species present (Fish, 1974). Hall et al. (1976) reported that M. spicatum comprised 58% of the total aquatic vegetation during the early summer of 1974 in Kitty Hawk Bay. Remaining densities were R. maritima,

23%, N. guadalupensis, 17%, and P. pectinatus, only 2%. Some observers have stated that dense M. spicatum mats enhance mosquito breeding by providing improved conditions for egg laying and hatching. Further opposition to M. spicatum focuses on the large mats of the decomposing plants that emit an unpleasant odor. On the positive side, root systems of M. spicatum stabilize loose organic sediments while the upright stems reduce wave action. The net effect is reduced turbidity. Some investigators have suggested that M. spicatum may play a role in inhibiting the growth of filamentous algae (Thompson and Hartwig, 1973).

Control of Myriophyllum spicatum

The types of control applicable to this sytem are: (1) biological control, (2) salinity manipulation (increasing the salinity of the bay), (3) mechanical control and (4) chemical control. Biological control, either intentional or inadvertent, of introduced species of aquatic plants has met with some success in several areas of the United States. In New Mexico a crayfish (Orconectes causeyi Jester) was used to control aquatic macrophyte vegetation, in California the slender spikerush (Eleocharis acicularis L.) out-competed less desirable macrophytes, in Arkansas the white amur (Ctenophyngodon idellus Val.) controlled the growth of M. spicatum (Thompson and Hartwig, 1973) and in the Chesapeake watershed two diseases (Northeast disease and Lake Venice disease) controlled M. spicatum (Bayley et al., 1968). However, unanticipated problems may result from the introduction of non-native species for the control of undesirable macrophytes. In New Mexico introduction of the crayfish resulted in a two-fold increase in tur-

bidity. Introduced species may attack desirable species in addition to undesirables, or the control organisms could themselves undergo a population explosion and become a nuisance.

Three types of activities utilizing salinity control have been proposed (Fish, 1976):

1. Creation of salt water overwash areas across the barrier island which would allow sea water into the sound during spring and fall high tides.

2. Creation of an inlet through the barrier island, resulting in the change of the sound from a fresh-water to salt-water environment.

3. Construction of a salt-water pumping facility to increase the salinity level in Currituck Sound.

The first of these actions would not provide enough salt-water to eradicate the M. spicatum throughout the entire area of infestation. Such limited introduction of salt-water might even stimulate its growth. Inlet construction would be very expensive and would require a great deal of land acquisition. Control by salt-water pumping stations is also unfeasible due to high construction and maintenance costs. Also, attempts to control M. spicatum by salt-water pumping stations located at Back Bay, Virginia, have not been very successful.

The most feasible method of mechanical control presently available appears to be mowing. Mowing and harvest machinery includes a mowing barge, either self-propelled or propelled by a tow boat, a harvester, a transporter and a conveyor. Also for the harvesting system, transport trucks and disposal areas are required. Disadvantages to this system are a high initial capital investment (approximately $60,000 according to Fish, 1974) and the slow rate of cutting. Thomp-

son and Hartwig (1973) found that in Dane County, Wisconsin, M. spicatum was controlled by mowing for a total cost of $21.38 per acre during the summer of 1971. They also state that harvesting is an economical method of control of M. spicatum.

Chemical herbicides traditionally have been considered the least expensive of available control methods. The butoxyethanol ester of 2,4 dichlorophenoxyacetic acid (2,4-D) attached to attaclay granules applied at 30 lbs. acid equivalent per acre (AE/A) exhibited no lethal effect on caged animals and did not kill native plants (Beavan et al., 1963:Rawls, 1971). In 1968 an experiment conducted on 200 acres (81 ha) in Currituck Sound using 20 lbs AE/A of the butoxyethanol ester of 2,4-D showed no acute adverse effects on fish or wildlife (Whitney et al, 1973). One of the concerns in treatment of large areas of M. spicatum with herbicides with subsequent die-off and decay of these plants is decreasing water quality as a result of large-scale decomposition. Subsequent decay of immense quantities of organic matter could initiate fish kills resulting from oxygen deficit or become a nuisance when decaying masses of dead plants drift inshore. Application of herbicides on such a large scale could damage game fish directly and would certainly threaten the food webs upon which the sport fishery is dependent (Thompson and Hartwig, 1973). Cost for herbicide application has been estimated at a minimum of $50.00 per acre (Fish, 1976).

Mode of Action of 2,4-D

A recent theory concerning the mode of 2,4-D action is based upon the broad effects of 2,4-D on many different plant metabolites.

John B. Hanson (as reported in Salisbury and Ross, 1969) found a rapid increase in RNA, DNA, protein and the number of mitochondria, ribosomes and several other cell constituents following treatment of young meristematic tissues with 2,4-D. This phenomenon is most readily observable in roots and stems and less so in leaves. Merrill Ross (also reported in Salisbury and Ross, 1969), found an increase in ATP level, respiration and incorporation of metabolites immediately following treatment with 2,4-D. After several days and as the plants approached death, however, these values dropped below those of controls.

The observations of Hanson, Ross and others suggest that 2,4-D is acting upon the DNA-RNA-protein system. The herbicide 2,4-D may activate at random many otherwise repressed genes, resulting in rapid synthesis of enzymes and a consequent increase in general metabolic turnover rates. Such an increase in metabolism can not be sustained with limited substrates and metabolic equilibria within the cell are upset, resulting in the death of the plant (Salisbury and Ross, 1969).

Presently there is no clear understanding as to the specificity of 2,4-D. The specificity of 2,4-D for broad leaf plants over grasses was first explained by the fact that the broad leaf varieties have more surface area to absorb the herbicide. However, 2,4-D was shown to penetrate grasses but it is inactivated rapidly within the plant. The current concept of 2,4-D specificity is based upon differential penetration, translocation and detoxification in susceptible and resistant species (Salisbury and Ross, 1969).

Kitty Hawk Bay Control Plan

Prior to making a decision on any action to cope with M. spicatum, the North Carolina Department of Natural and Economic Resources (NER) investigated the problem for approximately six months (August 1973 - January 1974). Upon completion of this study, a report was prepared and a public hearing was held at Kitty Hawk School in Dare County, North Carolina. The findings were presented and discussed and opinions of local citizens were solicited concerning alternative actions. The majority of the 120 persons present at the meeting favored a positive control or herbicide control alternative. No one favored a "no action" alternative and one person favored the mechanical mowing alternative (Fish, 1976).

The chemical control alternative was chosen. The herbicide selected was the butoxyethanol ester of 2,4-D attached to attaclay granules [8/15" (1.35 cm) mesh size] applied at a rate of 20 lbs AE/A. Application was carried out using Evergreen Helicopters, Inc. under the direction of the U.S. Army Corps of Engineers, Wilmington District. The total cost of this contract was $38,000 of which $25,000 was provided by the federal government, $9,120 by the state government and $2,280 by local government (Fish, 1976).

The treatment plan for M. spicatum in Kitty Hawk Bay included a provision by the NER to monitor the herbicide application activities and to document any adverse effects on water quality and/or flora and fauna in the vicinity of treatment. Certain basic changes in the ecosystem subsequent to 2,4-D application were expected to be expressed in altered rates of photosynthesis and respiration of organisms within

the ecosystem. Therefore, a method of study which measures changes in community metabolism (such as the diurnal dissolved oxygen method) would be a sensitive and meaningful way of monitoring any adverse effects which might take place in the treatment area.

Measurement of Community Metabolism

Free water techniques of measuring community metabolism were developed in order to eliminate certain problems associated with the light-dark bottle method. The light-dark bottle method, while adequate for measuring planktonic metabolic rates is seldom applicable in aquatic ecosystems where much of the community is composed of emergent or submersed macrophytes. Free water techniques should be superior to the light-dark bottle method since changes in the entire natural system are measured rather than changes that take place within a small sample of the total system isolated within a bottle.

Changes in either carbon dioxide or oxygen concentration can be used to estimate community metabolism. However measurements of carbon dioxide concentration is more difficult to make in the field than measurement of oxygen concentration. A sensitive pH meter must be used and frequent determination of the buffering capacity of the water is required. For this reason, oxygen measurements have had wider use than carbon dioxide measurements (Odum, 1956). Both oxygen and carbon dioxide levels in the water are affected by four main influences during the usual daily cycle: (1) release of oxygen into the water and removal of carbon dioxide from the water by primary producers; (2) uptake of oxygen and release of carbon dioxide due to the respiration of organ-

isms and chemical oxidation; (3) exchange of oxygen and carbon dioxide with the atmosphere (diffusion) and (4) influx of oxygen with accrual of ground water (usually negligible).

The diurnal dissolved oxygen method used in the study is based upon H. T. Odum's upstream-downstream method developed during his research in Silver Springs, Florida (Odum, 1956, 1957).

Odum used two stations in this study, one of which had a constant oxygen concentration of 2.5 mg/l where the water surfaced from the aquifer and another station downstream in which the oxygen concentration varied. The change in oxygen concentration at the downstream station relative to the constant value of the upstream station was determined. Diurnal change in oxygen concentration (mg O_2/l) was used to indicate the metabolic rates per unit area by calculating the depth, velocity of discharge and water surface between the two stations.

In this study, as in most studies using the diurnal dissolved oxygen method, only one station in each study area was established. In using the single station method, one assumes that the water within each study area is homogeneous. Odum and Hoskin (1958) outlined techniques for using a single station to get diurnal oxygen curves. This technique was the one followed in this study with a few modifications to better suit it to Kitty Hawk Bay.

DESCRIPTION OF STUDY AREA

Kitty Hawk Bay is a shallow protected body of water located at the confluence of Currituck, Albemarle and Roanoke Sounds in Dare County, North Carolina (Fig. 1). It is separated from the Atlantic Ocean by Bodie Island which extends from southeastern Virginia to Oregon Inlet, 25 miles (40 km) south of Kitty Hawk Bay. Oregon Inlet is relatively shallow with a low exchange volume and is the nearest connection between the ocean and Kitty Hawk Bay. Kitty Hawk Bay has an irregular shoreline and is dotted with numerous marsh islands. Bodie Island makes up the northern and eastern boundaries of Kitty Hawk Bay, Colington Island the southern boundary, and to the west, Kitty Hawk Bay opens into Albemarle Sound.

Due to the distance from Kitty Hawk Bay to Oregon Inlet and the large input of fresh water from the various sounds, Kitty Hawk Bay is usually considered to be freshwater (less than 1°/$_{oo}$salinity). However, the salinity can increase temporarily with infrequent ocean overwash during storms. Kitty Hawk Bay is only slightly affected by lunar tides because of its isolation from the ocean. However, wind tides affect the entire area causing water level to fluctuate greatly depending upon direction, force and duration of the wind.

The 750 acres (340 ha) of Kitty Hawk Bay treated with 2,4-D supported a dense community of aquatic macrophytes being dominated by M. spicatum at the time of treatment. Ruppia maritima, Potamogeton pectinatus and Najas guadalupensis were the native species present. These aquatic macrophytes effectively reduced water turbidity and wave

Fig. 1. Study Areas in Kitty Hawk Bay, North Carolina

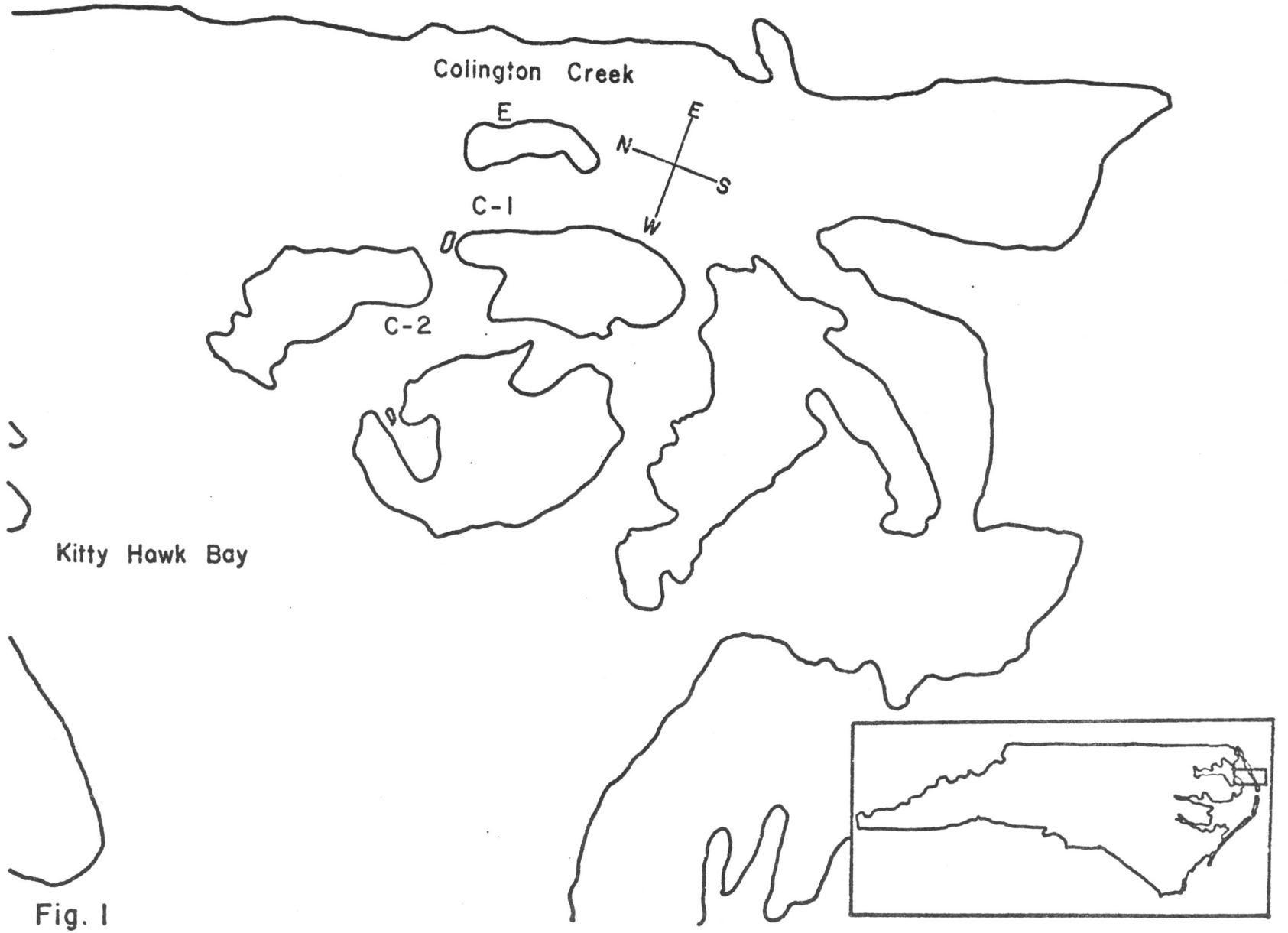

Fig. 1

action. The study area was approximately 1.2 m deep and the bottom was clearly visible at most times. Sediments in Kitty Hawk Bay consisted of a sandy-mud mixture which was fairly firm in most areas of the bay but became softer and more organic in the cove areas.

On 30 May 1974, two study stations were established in Kitty Hawk Bay. One served as the experimental station (E) located in the area to be treated with 2,4-D and the other a control (C-1) being located well outside the area to be treated (Fig. 1). Both stations were approximately 1.2 m deep and had similar substrates. On 20 July 1974, it became necessary to establish a second control station (C-2) because of the death of M. spicatum in the original control area.

MATERIALS AND METHODS

Community Metabolism

Total community metabolism estimates were made by the diurnal dissolved oxygen method described by Odum and Hoskin (1958). During the diurnals, water samples were collected every 3 hr over a 24-hr period using a van Dorn horizontal water sampler (2.2 l). Duplicate samples were taken at 0.3 m, 0.9 m, 1.2 m depths, the temperature was recorded, samples were drained into 300 ml BOD bottles and immediately fixed with 2.5 ml of $MnSO_4$ solution, and 2.5 ml of alkaline iodide-azide solution according to the Winkler method (Golterman, 1969). Fixed samples were titrated within 2 hr of collection with 0.01 N $Na_2S_2O_3$ using 2 ml of 1% starch solution as an indicator. Three pretreatment diurnals were conducted to establish base-line conditions of 31 May, 7 June and 19 June 1974. Treatment with 2,4-D took place on 13 July 1974 in the Kitty Hawk Bay area and during that week (8 July - 15 July 1974), dawn and dusk determinations of oxygen concentrations were made in the two study areas.

Five post-treatment diurnals were conducted over the remainder of the 1974 study period: 16 July, 20 July, 30 July, 13 August and 26 August 1974. Four one-year post-treatment diurnals were conducted during the 1975 study period: 17 July, 24 July, 31 July and 7 August 1975. Gross primary productivity (GPP) and total respiration (R) were determined graphically for the diurnals following techniques outlined by Odum and Hoskin (1958). Net primary productivity (NPP) was determined by subtracting R values from GPP values.

The oxygen concentration values for the entire water column obtained by Winkler's determination were plotted against time for each diurnal. The resulting curve for the first diurnal (pretreatment 31 May 1974) in the treatment area can be seen in Fig. 2a. Rates of change between points on this curve were determined and plotted against time (Fig. 2b, uncorrected line). Losses or gains of oxygen due to diffusion between the atmosphere and the water tend to modify dissolved oxygen values attributable to plant metabolism. Thus it is necessary to correct this curve for this source of error. This was accomplished by plotting oxygen concentration values of the surface sample (0.3 m) for the diurnal against time (Fig. 3a), determining the rate of change between the points of the curve and then plotting the rate of change values against time (Fig. 3b). Using oxygen concentration values for the surface samples, temperature of the surface samples, and a standard table of oxygen saturation values, the percent saturation of surface samples was determined and these values were then plotted against time (Fig. 3c). A diffusion constant K was then calculated (following the example of Odum and Hoskin (1958)) using the equation:

$$k = 100\ (q_m - q_e / S_m - S_e)$$

in which k is the diffusion constant expressed on a volume basis, q_m and q_e are the predawn (0500 hrs) and postdusk (2000 hrs) values from the surface rate of change curve respectively (Fig. 3b) and S_m and S_e are the predawn and postdusk oxygen deficit values from the surface oxygen saturation curve respectively (Fig. 3c). In this instance:

Fig. 2. Graphs of the first diurnal (31 May 1974) in the treatment area. a. Oxygen concentrations on an area basis (g O_2/m^2) versus time of day. b. Rate of change curves (both corrected for diffusion and uncorrected) of oxygen concentration (g $O_2/m^2 \cdot hr$) versus time of day.

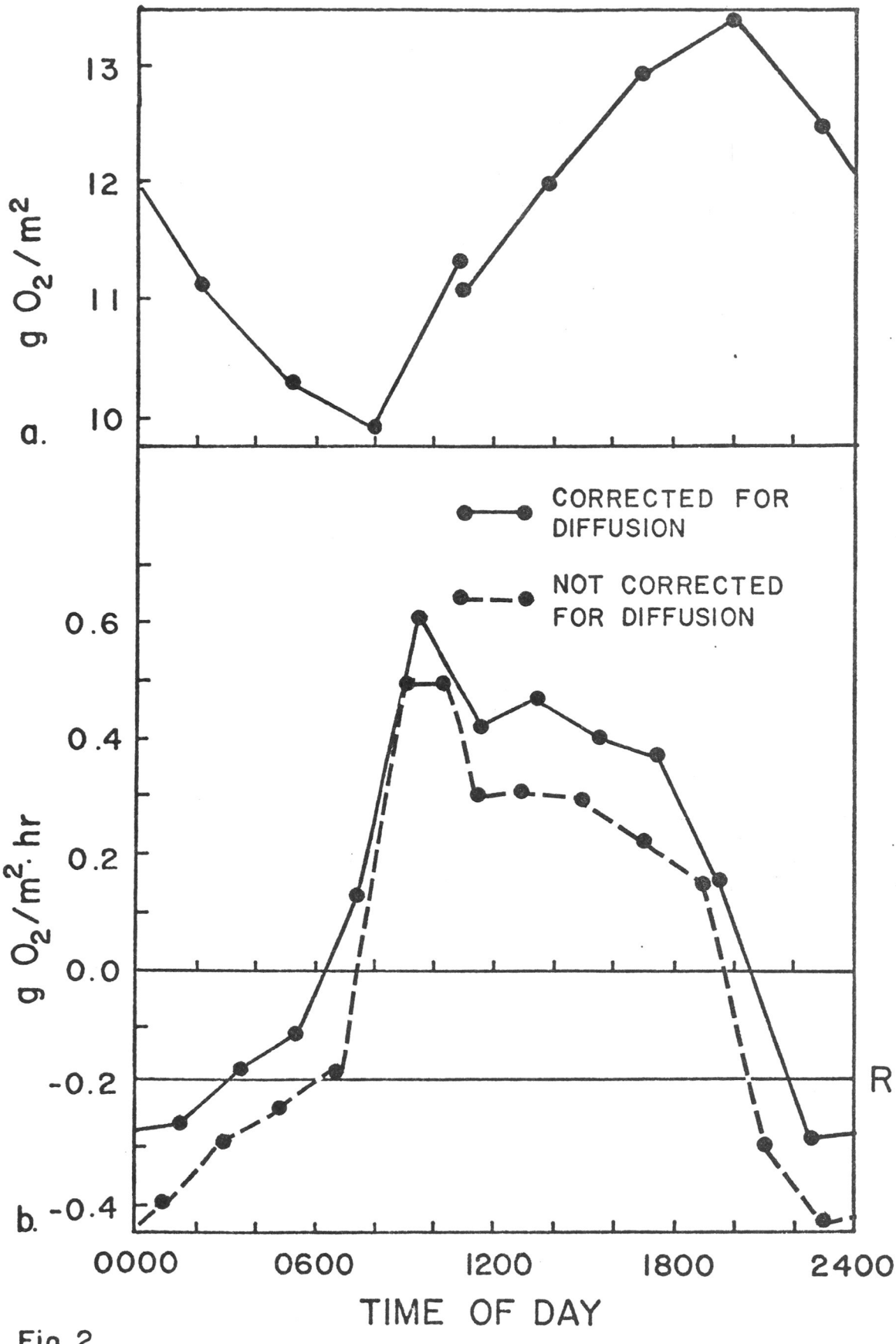
a.
13
12
11
10
g O2 / m2
CORRECTED FOR DIFFUSION
NOT CORRECTED FOR DIFFUSION
0.6
0.4
0.2
0.0
-0.2
-0.4
b.
g O2/m2. hr
R
0000
0600
1200
1800
2400
TIME OF DAY

Fig. 2

Fig. 3 Graphs of the surface water sample (0.3 m depth) of the first diurnal (31 May 1974) in the treatment study area. a. Oxygen concentrations (mg O_2/l) versus time of day. b. Rate of change curve of oxygen concentrations (mg O_2/l·hr) versus time of day. c. Percent oxygen saturation versus time of day.

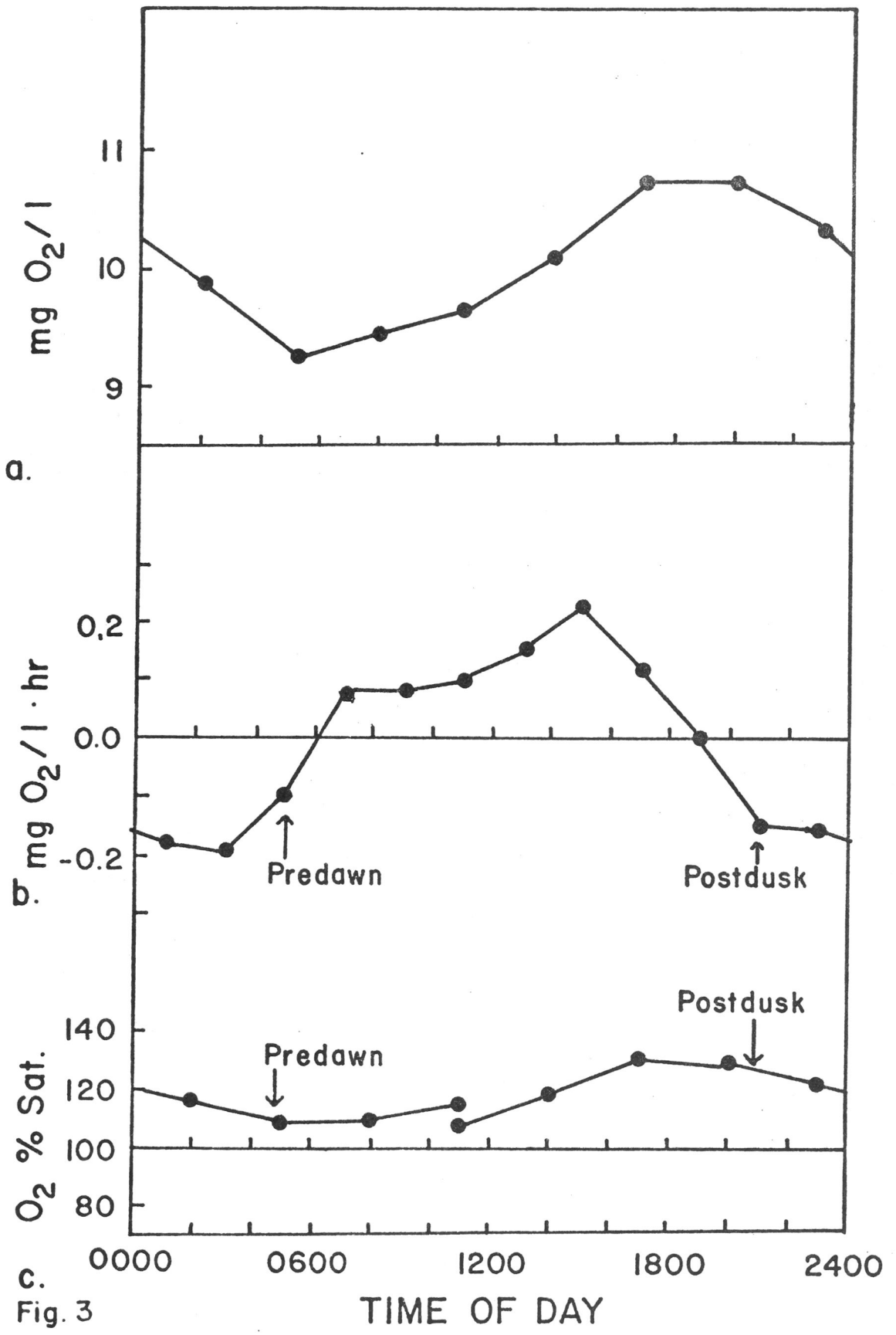
11
10
9
mg O2/l
a.
0.2
0.0
-0.2
mg O2/l · hr
b.
Predawn
Postdusk
140
120
100
80
O2 % Sat.
Predawn
Postdusk
c.
0000
0600
1200
1800
2400
TIME OF DAY

Fig. 3

$$k = 100\ (-0.10 + 0.14/-9 + 28)$$

$$k = 0.21\ g\ O_2/m^3 \cdot hr$$

The area based diffusion constant (K) may be obtained by multiplying the volume based diffusion constant (k) by the depth of the water column sampled (0.6 m) so that:

$$K = (0.6\ m)\ (0.21\ g\ O_2/m^3 \cdot hr)$$

$$K = 0.13\ g\ O_2/m^2 \cdot hr$$

Odum and Hoskin (1958) report that K in g $O_2/m^2 \cdot hr$ has been found to be 0.1 to 1 in quiet waters such as Kitty Hawk Bay. This agrees favorably with the value calculated above. The diffusion constant (K) is multiplied by the percentage of saturation for each point on the rate of change curve for the entire water column (Fig. 2b, uncorrected curve) and the product is either added to or subtracted from the rate of change curve graphically so as to replace oxygen which diffused out or to retract the oxygen which diffused in. The corrected curve can be seen above the original curve in Fig. 2b.

Community respiration is estimated by averaging the nighttime respiration rates and then extrapolating this value (0.195 g $O_2/m^2 \cdot hr$) across the daytime period ("R" - Fig. 2b). The average respiration value multiplied by 24 hours yields the community respiration rate (R = 4.68 g $O_2/m^2 \cdot day$).

The area below the corrected curve and above the respiration line (R) in Fig. 2b is equivalent to the gross primary productivity (GPP = 8.01 g $O_2/m^2 \cdot day$). The final diffusion corrected graph for the control area during the first diurnal can be seen in Fig. 4 (GPP = 7.17

Fig. 4 Rate of change curve of oxygen concentrations (g $O_2/m^2 \cdot$ hr) for the first diurnal (31 May 1974) for the control study area versus time of day.

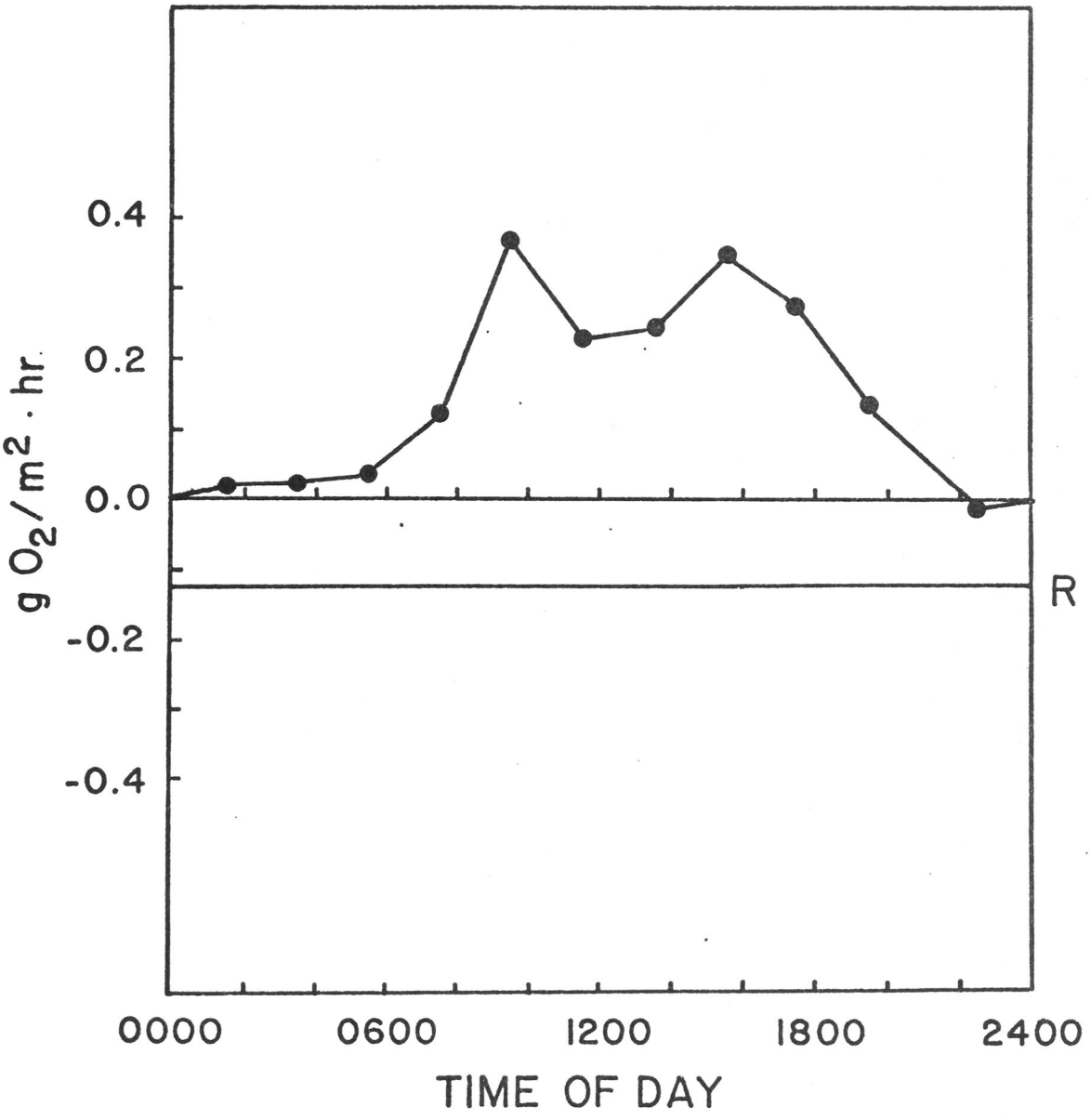

Fig. 4

g $O_2/m^2 \cdot day$, R = 3.00 g $O_2/m^2 \cdot day$).

As stated previously, application of 2,4-D occurred on 13 July 1974 in the treatment area of Kitty Hawk Bay. During the week of treatment (8 July - 15 July), dawn and dusk readings in oxygen concentration, representing minimum and maximum values respictively, were made in the two study areas. Following the example of Welch (1968) and McConnell (1962), values for GPP, R and NPP were calculated using these dawn and dusk oxygen concentration values. A least squares analysis was conducted between the difference in the values in oxygen concentration at dawn and at dusk for each of the diurnals of the 1974 study and GPP and R values obtained for each diurnal in both the control and treatment areas. This was done so that a correlation might be obtained which could be used to estimate the values of GPP, R and NPP from the dawn and dusk readings of the week of treatment. Correlations in the treat- area were significant with the correlation coefficient between GPP and the difference in dawn and dusk readings being 0.79. The correlation coefficient between R and the difference in dawn and dusk readings was even higher at 0.84. For the control area the correlation between R and the difference in dawn and dusk readings was quite high ($r = 0.89$) and the correlation between GPP and the difference in dawn and dusk readings in the control area was much lower ($r = 0.57$). Since significant correlations were found in all cases, the dawn and dusk oxygen readings for the week of treatment could be used to estimate GPP, R and NPP.

Total insolation was monitored constantly with a recording pyroheliometer. This information was then used to calculate the efficiency of community fixation of available energy. The efficiency

of energy fixation by the ecosystem was determined as the percentage that total photosynthesis (GPP) comprised of the total available energy (total insolation).

Plankton Community Metabolism

The light and dark bottle technique was used in the study areas described previously to measure planktonic metabolism. Respiration rates were measured in 300 ml BOD bottles covered with black electrical tape and wrapped with aluminum foil to reduce temperature increases relative to the clear bottles. From each of three depths (surface, 0.3 m and 0.9 m) water samples were taken with a van Dorn sampler and distributed among three bottles, one of which was fixed for the initial dissolved oxygen concentration. A clear and a dark bottle were suspended at each depth of sampling for a 3 hr incubation period. At the end of the incubation period, the bottles were collected, fixed and the oxygen concentrations were determined in the laboratory by the Winkler method. The oxygen values for the surface 0.3 m and 0.9 m depths in mg O_2/l were then converted to oxygen in g O_2/m^2 by multiplying each value by 0.2, 0.4 and 0.6 m respectively -- the depths of the water volumn that they represented. NPP was calculated from the oxygen concentration increase in the light bottle relative to the initial value. The change in the dark bottle relative to the initial value was measure of respiration rate. GPP was then derived by summing the rates of NPP and R.

Three pretreatment plankton metabolism determinations were conducted (31 May, 7 June, and 19 June 1974), six runs were conducted

following treatment (16, 18, 22, 24, 26, and 26 August 1974) during the 1974 study period, and four one year post-treatment studies were conducted (17 July, 24 July, 31 July and 7 August 1975) during the 1975 study period. All runs were conducted from 1000 to 1300 EDT.

Plankton abundance determinations were made with hand dip samples of 200 mℓ and by passing 200 ℓ of water through a #20 mesh plankton net. A compound binocular microscope and a Palmer counting cell of 0.10 mℓ volume were used for plankton enumeration. Three subsamples of 0.10 mℓ were taken from each sample and five microscope field counts were made on each subsample. Plankton biomass estimates were made for both the hand dip and net samples. Samples were filtered through preweighed dried (76° C for 4 hr) 0.45 μ Millipore filters using a vacuum filtering apparatus. Filters containing plankton organisms were dried for 8 hr at 76° C, cooled and then weighed on an analytical balance.

Benthic Metabolism

Benthic respiration was estimated by measuring dissolved oxygen uptake in darkened plastic bucket enclosures placed upside down in the sediments of both study areas. The volume of the bucket was 14 ℓ and enclosed a mud surface area of 0.56 m^2. Tygon tubing, suspended above the bottom by a small stake within the bucket, was used to draw water samples from the bucket to the surface where duplicate samples were obtained. Samples were taken every 2 hr for a 6 hr period. After placing the apparatus in the muds, the disturbed sediments were allowed to settle for 0.5 hr before the initial water samples were taken.

Water samples were fixed and titrated for dissolved oxygen as described previously. Three benthic studies were conducted during the 1974 study period: 19, 22, and 26 August 1974. Two one-year post-treatment benthic studies were conducted during the 1975 study period: 31 July and 7 August 1975. Oxygen concentrations obtained in mg O_2/l by the Winkler method were converted to values in g O_2/m^2 by multiplying the values in mg O_2/l by a factor derived from the volume of the bucket and the surface area covered by the bucket so that:

$$g\ O_2/m^2 = (mg\ O_2/l)\ (0.014\ m^3/0.56\ m^2).$$

RESULTS

Community Metabolism

The diffusion corrected rate of change graphs for the treatment (Fig. 2b) and control (Fig. 4) areas for the first diurnal (30 May 1974) are representative of all pretreatment diurnals. Both treatment and control areas exhibited the same basic pattern with both reaching maximum productivity rates at approximately 0930 EDT. In both areas respiration did not exceed photosynthesis until after sunset (2030 EDT - treatment; 2200 EDT - control). Both graphs are indicative of a relatively stable ecosystem with no sudden changes in oxygen production or consumption, but rather a smooth response over the length of the day.

Figure 5 shows the rate of change curves for the treatment and control plots 17 days following treatment with 2,4-D (13 July 1974). The control area followed the same basic pattern as that seen for this area before treatment except that high photosynthetic rates did not persist as long during the daytime period. In the treatment area graph, however, there were substantial changes in oxygen dynamics. Photosynthesis attained a higher maximum rate early in the day with a precipitous drop beginning at about 1100 EDT. Community respiration exceeded photosynthesis by 1400 EDT. In contrast to this, respiration in the control area did not exceed photosynthesis until 1900 EDT. At the end of this diurnal (30 July 1974) there was visual evidence of decomposing M. spicatum in the treatment area. This is reflected in the rate of change curve that shows respiration exceeding photosynthesis early in the afternoon. It was during this diurnal that the lowest oxygen con-

Fig. 5. Rate of change curves of oxygen concentrations (g $O_2/m^2 \cdot$ hr) for the sixth diurnal (30 July 1974) for both the treatment and control study areas versus time of day.

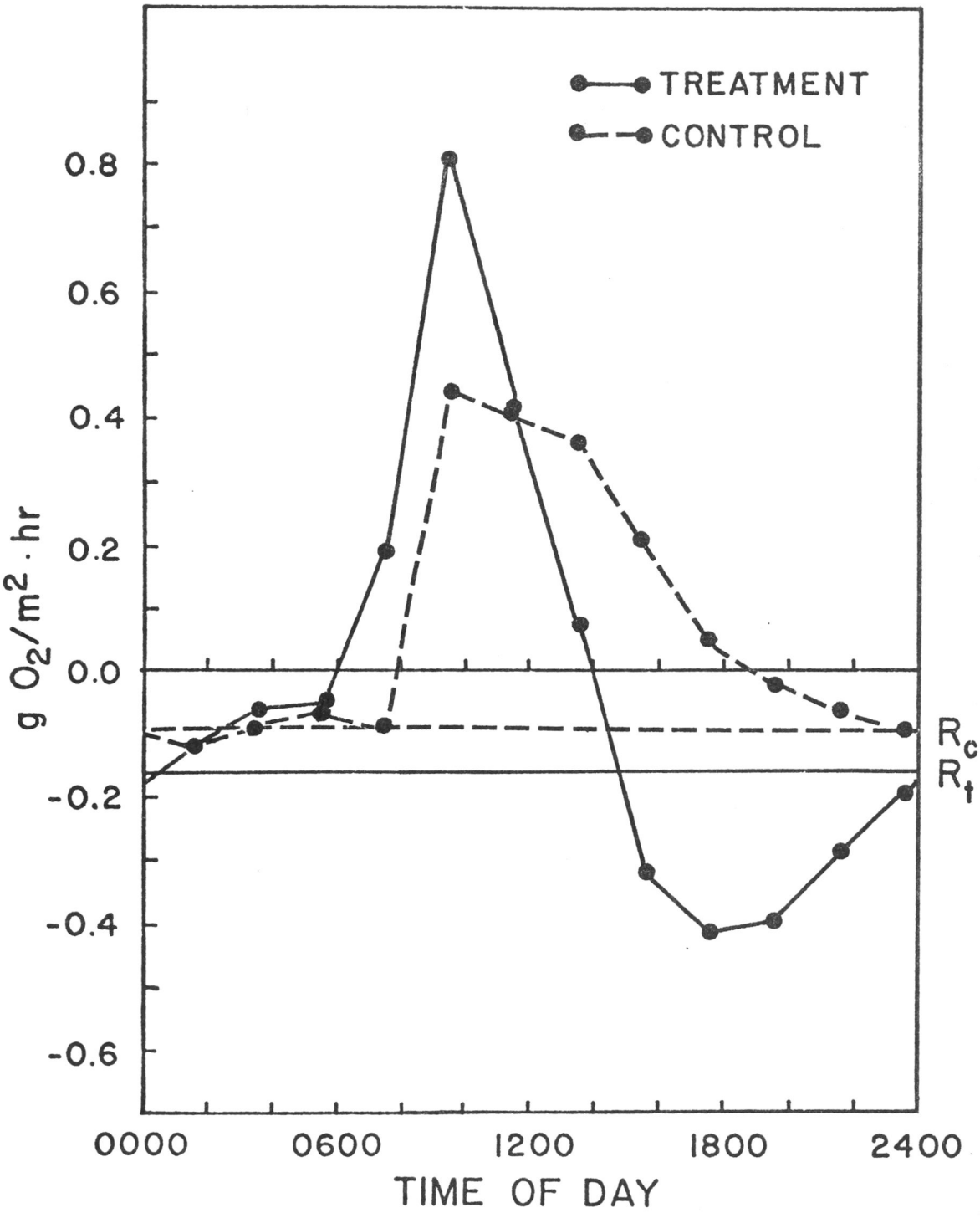
TREATMENT
CONTROL
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
g O2/m2 · hr
Rc
Rt
0000
0600
1200
1800
2400
TIME OF DAY

Fig. 5

centration reading of the season were obtained (4.09 mg/l).

When the next diurnal was conducted on 13 August 1974, the water in the treatment area exhibited an uncharacteristic green color due to high densities of phytoplankton. The composition of the plankton bloom will be discussed in a later section. The control area did not exhibit the same green color as the treatment area and the rate of change curve for the control area (Fig. 6) followed the same basic shape as those before. However, a greater rate of respiration was measured and upon observation, M. spicatum located in the control area appeared to be deteriorating. A "die-off" of M. spicatum followed within the next few weeks. Figure 6 also shows the rate of change curve for the treatment area for the 13 August 1974 diurnal made during the dense bloom of phytoplankton. This bloom is reflected in the rate of change curve which showed a very rapid increase after sunrise, peaking at 1200 EDT and then rapidly decreased in the afternoon. This early peak is probably attributable to the fact that phytoplankton were utilizing a large pool of available nutrients generated by nighttime respiration. Because of such high rates of photosynthesis, it is likely that the available nutrients became depleted during the day. Similarly, rates of planktonic respiration may have increased in the afternoon as pools of labile organic carbon accumulated from the rapid primary productivity.

Figure 7 shows the rate of change curves for both treatment and control study areas for the diurnal conducted on 24 July 1975, one year and eleven days following treatment with 2,4-D. Both graphs again follow the same shape as those seen prior to treatment. M. spicatum was rarer in the control area than it had been preceding treatment and was

Fig. 6. Rate of change curves of oxygen concentrations (g $O_2/m^2 \cdot$ hr) for the seventh diurnal (13 August 1974) for both the treatment and control study areas versus time of day.

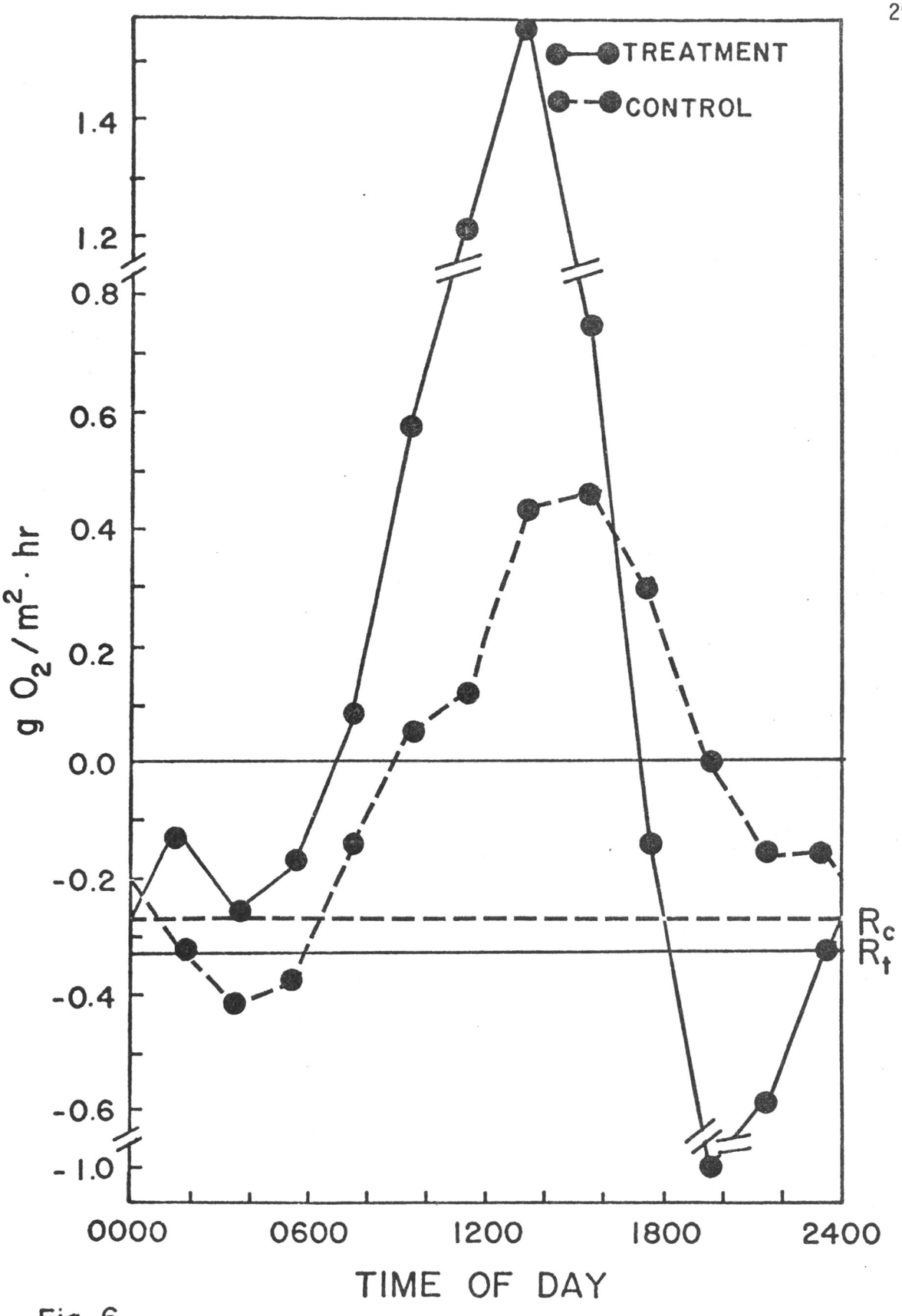
TREATMENT
CONTROL
1.4
1.2
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-1.0
g O2 / m2 · hr
Rc
Rt
0000
0600
1200
1800
2400
TIME OF DAY

Fig. 6

Fig. 7 Rate of change curves of oxygen concentrations (g $O_2/m^2 \cdot$ hr) for the tenth diurnal (24 July 1975) for both the treatment and control study areas versus time of day.

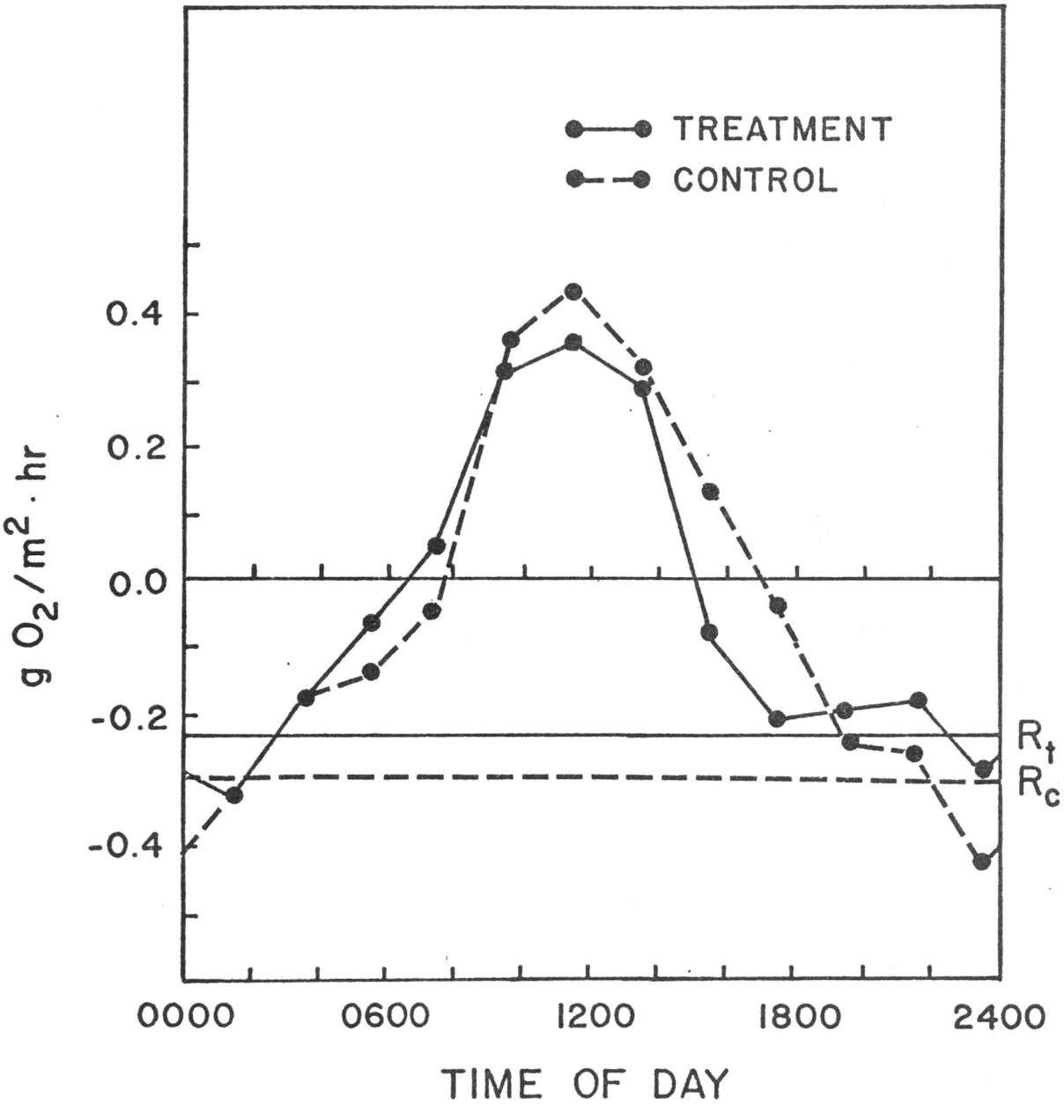
TREATMENT
CONTROL
0.4
0.2
0.0
-0.2
-0.4
g O2/m2 · hr
Rt
Rc
0000
0600
1200
1800
2400
TIME OF DAY

Fig. 7

absent from the treatment area (Getsinger, 1976). Native grasses (primarily Ruppia maritima and Najas guadalupensis) were abundant in the control area but were not as abundant in the treatment area. Another dominant species in the treatment area was the macrophytic alga Nitella hyalina. Regardless of the differences in vegetation type and abundance, similar productivity values were observed (GPP = 4.91 g $O_2/m^2 \cdot day$ - treatment; GPP = 6.41 g $O_2/m^2 \cdot day$ - control). Treatment and control area rate of change curves followed the same pattern depicted here throughout the rest of the study period of 1975 with approximately the same values for gross primary productivity and respiration. This figure indicates that the ecosystem was recovering from the perturbation imposed by 2,4-D application, which was exemplified in Fig. 6. The drastic oscillations in production seen after treatment with 2,4-D are no longer evident. The diurnal curves have once again returned to the same smooth changes seen prior to treatment indicating again the recovery of the system.

Figure 8 and Table 1 show general trends in the gross primary productivity values for both the treatment and control study areas through the study period. Community metabolism values for both treatment and control areas obtained from dawn-dusk oxygen concentrations for the week of treatment (8 - 15 July 1974) can be seen in Table 2. Prior to the application of 2,4-D, both areas follow the same basic pattern of increases and decreases in production. Following treatment, however, the pattern of productivity evident in the control area was not mimicked by the treatment area. This is particularly noticeable from 20 July until 13 August 1974. The slight change in GPP values seen in

Fig. 8 Gross primary productivity (GPP) values (g $O_2/m^2 \cdot day$) for both treatment and control study areas over the entire study period.

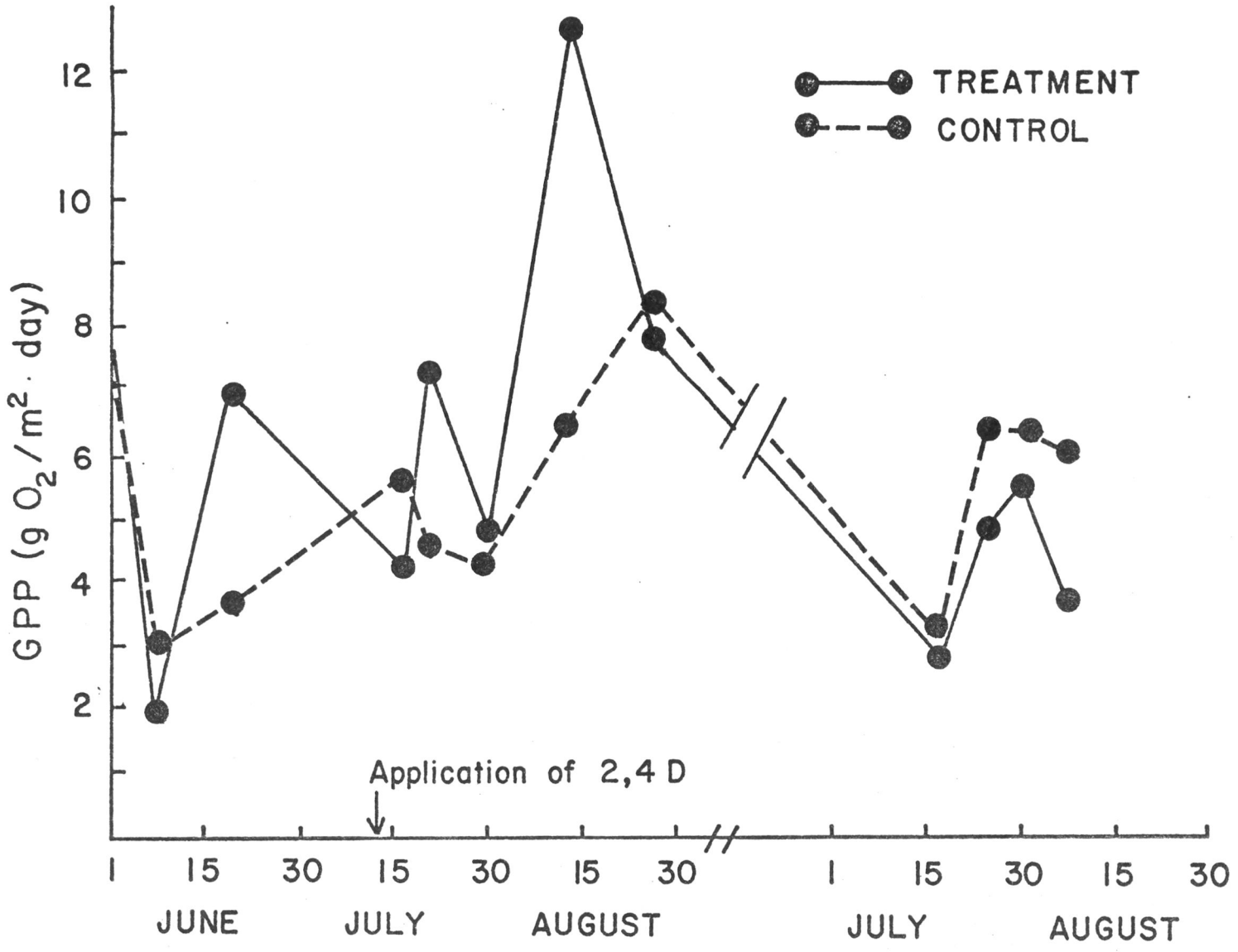
TREATMENT
CONTROL
GPP (g O_2 / m^2 · day)
12
10
8
6
4
2
Application of 2,4 D
1
15
30
15
30
15
30
1
15
30
15
30
JUNE
JULY
AUGUST
JULY
AUGUST
1974
1975

Fig. 8

Table 1. Community metabolism values (g $O_2/m^2 \cdot day$) and P:R ratios obtained from the dissolved oxygen method prior to and following treatment with 2,4-D and one year following treatment, 1975.

Date 1974	Treatment GPP	R	P:R	Control GPP	R	P:R
31 May	8.01	4.68	1.71	7.17	3.00	2.39
7 June	1.95	1.44	1.35	2.92	3.22	0.91
19 June	6.95	8.16	0.85	3.67	1.99	1.84
Mean	5.64	4.76	1.30	4.59	2.74	1.71
13 July			Application of 2,4-D			
16 July	4.21	0.91	4.63	5.64	3.36	1.68
20 July	7.37	8.16	0.90	4.52	3.90	1.16
30 July[a]	4.74	3.95	1.20	4.20	2.28	1.84
13 August[b]	12.66	7.94	1.59	6.41	6.50	0.99
26 August	7.84	5.01	1.56	8.42	8.57	0.98
Mean	7.36	5.19	1.98	5.84	4.92	1.33

Table 1 (cont'd.)

	GPP	R	P:R	GPP	R	P:R
1975						
17 July	2.83	1.30	2.18	3.14	0.34	9.24
24 July	4.91	5.73	0.86	6.41	6.98	0.92
31 July	5.54	5.09	1.09	6.35	4.72	1.34
7 August	3.73	5.22	0.71	6.08	7.04	0.86
Mean	4.25	4.34	1.21	5.50	4.77	3.09

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[a] The lowest oxygen concentration encountered was recorded during this diurnal.

[b] A phytoplankton bloom was evident during this diurnal in the treatment area, resulting in the highest GPP value found during the study period.

Table 2. Community metabolism values (g $O_2/m^2 \cdot day$) obtained from dawn-dusk oxygen concentrations prior to and following treatment with 2,4-D.

	Treatment		Control	
Date	GPP	R	GPP	R
8 July	11.86	5.04	5.37	2.22
9 July	7.11	6.17	5.39	3.16
10 July	5.68	3.14	5.02	3.75
11 July	3.89	5.37	3.59	3.82
12 July	9.29	4.39	6.45	4.12
13 July[a]	9.78	8.09	5.39	2.82
14 July	9.26	6.08	5.89	5.35
15 July	4.45	4.35	5.21	4.80

[a] Application of 2,4-D

the control area were greatly overshadowed by the drastic oscillations in production in the treatment area. Gross primary productivity of the treatment area on 13 August 1974 (12.66 g $O_2/m^2 \cdot day$) was the highest found during the entire study period. By 26 August 1974, however, GPP had dropped to 7.84 g $O_2/m^2 \cdot day$, perhaps indicating a stabilization of the phytoplankton community. GPP in the control area increased slightly toward the latter part of the 1974 study period, possibly due to the die-back of M. spicatum, the release of nutrients and subsequent recycling of nutrients by a phytoplankton community resulting in higher productivity values. The similarlity in GPP for the treatment (7.84 g $O_2/m^2 \cdot day$) and control (8.42 g $O_2/m^2 \cdot day$) areas for the last diurnal of the 1974 study period might indicate that the recovery of the ecosystem in terms of productivity was taking place quite soon (approximately six weeks) following treatment with 2,4-D. However, M. spicatum was still absent from this area at this time.

In the 1974 study period both treatment and control (C-2) areas had sediments of similarly high organic content. By 1975, however, the treatment area had lost most of its organic layer resulting in a much firmer substrate than the substrate found in the control area. This loss of organic sediment can probably be attributed to resuspension of the particulate matter due to increased wave action, made possible by the absence of a dense community of M. spicatum. During 1975 the consistently higher turbidity in the treatment study area compared to the control study area confirmed this. Increased turbidity would be expected to result in a decreased productivity. The treatment study

area, with the consistently higher turbidity was found to have lower GPP values than those found in the control area during the 1975 study period (Table 1). The mean GPP value for the control area (5.50 g $O_2/m^2 \cdot$ day) was approximately 1.3 times as large as that for the treatment study area (4.25 g $O_2/m^2 \cdot$day), whereas mean respiration was approximately equal in the two areas (4.34 g $O_2/m^2 \cdot$day - treatment; 4.77 g $O_2/m^2 \cdot$day - control) for the 1975 study period. The treatment area had a mean P:R ratio of 1.21 whereas the control area had a mean P:R ratio of 3.09. This can be interpreted to mean that the control area was accumulating more biomass and structure relative to the treatment area one year following treatment.

The one year post-treatment (1975) mean GPP value in the treatment area (4.25 g $O_2/m^2 \cdot$day) was substantially less than the mean GPP value for the pretreatment period (5.64 g $O_2/m^2 \cdot$day) of the treatment area. It was also substantially less than the post-treatment (1974) mean GPP value for the area (7.36 g $O_2/m^2 \cdot$day). One reason for the lower mean GPP treatment area value for the 1975 post-treatment period is that phytoplankton density was less than for the 1974 post-treatment period in the treatment area. Following treatment in 1974, a plankton bloom in the treatment area resulted in one very high GPP value (12.66 g $O_2/m^2 \cdot$day) which caused the mean 1974 post-treatment GPP value to be higher. In the control area, the 1975 mean GPP value (5.50 g $O_2/m^2 \cdot$day) is comparable to the mean GPP for the area during the entire 1974 study period (5.37 g $O_2/m^2 \cdot$day).

Mean respiration in both treatment and control areas for the 1975 study did not differ substantially from that before treatment or

for the post-treatment (1974) period (Table 1.)

Perhaps of greater importance for the heterotrophic organisms such as fish and shellfish in the Kitty Hawk Bay area is the occurrence of minimum or lowest oxygen values measured (Table 3). Minimum oxygen levels were relatively constant throughout the 1974 study period (range 10.22 to 7.62 mg O_2/ℓ) until the die-off period (26 August 1974) when a minimum value of 5.31 mg O_2/ℓ was obtained. The values for the treatment area decreased following treatment (13 July 1974) to a level far below any found in the control area. The values increased from a low of 4.09 mg O_2/ℓ on 30 July to a high during the phytoplankton bloom of 13 August 1974 of 9.69 mg O_2/ℓ. Minimum oxygen concentrations in the one year post-treatment (1975) study in the treatment study area remained relatively high during the entire study. The lowest value for the 1975 study in the treatment study area (7.66 mg O_2/ℓ) was well above the lowest value found soon after treatment in 1974 (4.09 mg O_2/ℓ). In the control area the 1975 mean minimum oxygen level (8.25 mg O_2/ℓ) was slightly lower than the mean minimum oxygen level for the entire 1974 study (8.94 mg O_2/ℓ).

Photosynthetic efficiency of the community (Table 4) calculated using the insolation values from the pyroheliometer and gross primary productivity (GPP) showed no substantial difference between treatment and control study areas with one exception. The efficiency in the treatment area on 13 August 1974 (1.66%) was nearly twice that found for the control area (0.84%). This coincided with a plankton bloom in the treatment area which was not evident in the control area. The plankton

Table 3. Maximum and minimum dissolved oxygen concentrations (mg O_2/ℓ) found before treatment (1974), after treatment (1974), and one year after treatment (1975) for both treatment and control areas in Kitty Hawk Bay.

Date	Treatment		Control	
1974	Maximum	Minimum	Maximum	Minimum
31 May	13.39	9.29	12.81	9.39
7 June	11.48	9.56	11.46	9.84
19 June	13.05	8.50	12.30	10.22
Mean	12.64	9.12	12.19	9.82
13 July		Application of 2,4-D		
16 July	11.80	8.35	11.60	9.17
20 July	11.64	7.45	11.79	9.08
30 July	7.76	4.09	11.91	9.15
13 August[a]	17.98	9.69	10.95	7.62
26 August[b]	13.58	8.33	9.54	5.31
Mean	12.55	7.58	11.16	8.07

Table 3 (cont'd.)

1975	Maximum	Minimum	Maximum	Minimum
17 July	10.40	8.92	11.42	9.77
24 July	10.66	7.66	11.42	8.03
31 July	11.36	8.46	11.90	8.47
7 August	9.58	7.77	10.17	6.73
Mean	10.50	8.20	11.23	8.25

[a] A phytoplankton bloom was evident in the treatment area during this diurnal.

[b] A die-back of M. spicatum was occurring in the control area at this time.

Table 4. Efficiency (%) of community fixation (GPP = Kcal/m^2·day) of available energy (Kcal/m^2·day) for both treatment and control areas prior to and following treatment (1974-1975).

Date	Insolation	Treatment		Control	
		GPP	%	GPP	%
1974					
31 May	4429	32.04	0.72	28.68	0.65
7 June	3221	7.80	0.24	11.68	0.36
19 June	5288	27.80	0.52	14.68	0.28
Mean	4313	22.55	0.49	18.35	0.43
13 July		Application of 2,4-D			
16 July	4378	16.84	0.38	22.56	0.52
20 July	4913	29.48	0.60	18.08	0.37
30 July	4396	18.96	0.43	16.80	0.38
13 August[a]	3050	50.64	1.66	25.64	0.84
26 August	4340	31.36	0.72	33.68	0.78
Mean	4215	29.46	0.76	23.35	0.58
1975					
17 July	3714	11.32	0.30	12.56	0.34
24 July	5342	19.64	0.37	25.64	0.48
31 July	4616	22.16	0.48	25.40	0.55
7 August	4948	14.92	0.30	24.32	0.49
Mean	4655	17.01	0.36	21.98	0.46

[a] A phytoplankton bloom was evident in the treatment area at this time and persisted throughout the 1974 study period.

apparently were more efficient in the utilization of sunlight than the community of macrophytes in the control area.

Phytoplankton Community Metabolism and Abundance

Prior to the treatment date (13 July 1974), three plankton community studies were conducted (31 May, 7 June and 19 June 1974). Gross primary productivity on these three dates (Table 5) reflected low values of phytoplankton productivity in both treatment ($\bar{x}$GPP = 0.041 g $O_2/m^2 \cdot hr$) and control ($\bar{x}$GPP = 0.042 g $O_2/m^2 \cdot hr$) study areas. Plankton counts (Table 6) and plankton biomass estimates (Table 7) failed to show the presence of any planktonic organisms in either area during this pretreatment period.

Following treatment, plankton studies were conducted when the bloom in the treatment area was noted. Average GPP in the treatment area following 2,4-D application was 20 times greater than the average pretreatment rate. This increase in productivity was verified by counts of the plankton present during this time (Table 6). An unconcentrated sample (200 ml) revealed the presence of three genera representing the phylum Cyanophyta: Aphanizomenon, Anacystis and Anabaena with Aphanizomenon and Anacystis being codominant phytoplankton during this post-treatment (1974) period. There were also 3 genera of rotifers and 3 genera of copepods observed. Plankton biomass (Table 7) was detectable during this time in the treatment area with unconcentrated samples having a mean weight of 37.5 mg dry wt./ℓ.

In the control area during the 1974 post-treatment period, a mean GPP value of 0.360 g $O_2/m^2 \cdot hr$ was obtained which was approximately a nine-fold increase over the pretreatment mean GPP value. Phytoplankton counts revealed the same genera in the control area as in the treat-

Table 5. Community metabolism values (g $O_2/m^2 \cdot hr$) and P:R ratios obtained by the light-dark bottle method for the plankton community prior to and following treatment with 2,4-D (1974-1975).

Date	Treatment			Control		
	GPP	R	P:R	GPP	R	P:R
1974						
31 May	0.027	0.029	0.93	0.054	0.030	1.80
7 June	0.036	0.066	0.54	0.042	0.008	5.25
19 June	0.060	0.080	0.75	0.030	0.060	0.50
Mean	0.041	0.058	0.74	0.042	0.033	2.52
13 July	Application of 2,4-D					
16 August[a]	0.840	0.470	1.79	0.690	0.380	1.82
18 August	0.730	0.700	1.04	0.160	0.250	0.64
22 August	0.470	0.360	1.30	0.080	0.130	0.62
24 August	0.860	0.420	2.05	0.390	0.220	1.77
26 August	0.830	0.310	2.68	0.310	0.150	2.07
26 August	1.170	0.300	3.90	0.550	0.240	2.29
Mean	0.820	0.430	2.13	0.360	0.230	1.54
1975						
17 July	0.047	0.017	2.76	0.143	0.047	3.04
24 July	0.106	0.120	0.88	0.131	0.074	1.77
31 July	0.228	0.114	2.00	0.188	0.157	1.20
7 August	0.170	0.137	1.24	0.117	0.083	1.41
Mean	0.138	0.097	1.72	0.145	0.090	1.86

[a] A phytoplankton bloom was evident at this time in the treatment area and persisted through the end of the study period.

Table 6. Plankton counts (cells/ml) from unconcentrated samples for the treatment and control study areas prior to and following 2,4-D treatment (1974-1975).

Date	Aphanizomenon	Anacystis	Anabaena	Merismopedia	Total phytoplankton
TREATMENT AREA					
1974					
31 May[a]					
13 July		Application of 2,4-D			
18 August	875	250	125	0	1250
24 August	584	458	166	0	1208
1975					
31 July	667	417	83	0	1167
CONTROL AREA					
1974					
31 May[a]					
13 July		Application of 2,4-D			
18 August	458	417	0	42	917
24 August	354	375	0	0	729
1975					
31 July	667	958	83	42	1750

[a] Informal counts were made and only negligible amounts of plankton were found.

Table 7. Plankton biomass estimates (mg dry wt./ℓ for both treatment and control study areas prior to and following 2,4-D treatment (1974-1975)[a].

Date	Treatment		Control	
	Unconcen. Sample	Net Plankton Sample	Unconcen. Sample	Net plankton Sample
1974				
31 May[b]				
13 July	Application of 2,4-D			
18 August	25.00	0.10	30.00	0.14
24 August	50.00	0.16	20.00	0.09
1975				
31 August	5.00	0.03	0.00	0.05

[a] Weights actually represent seston, which includes all suspended particulate matter.

[b] Informal samples were taken on this date and only negligible amounts of plankton were found.

ment area, but at lower densities. Another member of the Cyanophyta, Merismopedia, was found in low numbers in the control area but not in the treatment area following treatment. Plankton biomass (Table 7) was detectable from unconcentrated samples yielding a mean value of 25.00 mg dry wt./ℓ for the 1974 post-treatment study period in the control area.

During the 1975 post-treatment study period, the treatment area had a mean GPP of 0.138 g $O_2/m^2 \cdot hr$ which was higher than the pre-treatment 1974 value of 0.041 g $O_2/m^2 \cdot hr$ yet considerably lower than the 1974 post-treatment value of 0.820 g $O_2/m^2 \cdot hr$. However, plankton counts of unconcentrated samples yielded numbers comparable to the 1974 post-treatment values (Table 6). Plankton biomass (Table 7) was 5.00 mg dry wt./ℓ at this time in the treatment area.

In the control study area during the 1975 study the mean GPP (0.145 g $O_2/m^2 \cdot hr$) was slightly higher than for the treatment area (0.138 g $O_2/m^2 \cdot hr$) for the same time period. This agrees with plankton count data (Table 6) which shows the control area with a greater number of phytoplankton than the treatment area. Plankton biomass was undetectable in unconcentrated samples. During the 1975 post-treatment study period, both study areas had established plankton communities of similar densities and productivities in areas where plankton were quite rare prior to treatment.

Water samples collected in Kitty Hawk Bay during the study (1974-1975) and were analyzed for nitrite, nitrate, ammonium, total nitrogen (Kjeldahl), ortho phosphorus, total phorphorus and for selected cations. These data are reported in Getsinger (1976). Following treatment with 2,4-D (13 July 1974), ammonium concentration showed a clear

trend of increasing in concentration shortly after treatment and then decreasing on 5 August 1974 and afterwards. The increases in concentration following treatment might be attributed to the release of bound nutrients from the decomposing M. spicatum. The decline in ammonium concentration on 5 August 1974 and afterwards coincided with the measured increase in plankton biomass and productivity. Thus it might be attributed to uptake by the plankton community. Daniel (1972) has also found that the herbicide treatment of rooted aquatic plants can lead to increased levels of nitrogen and phosphorus in the water column which favors phytoplankton blooms.

Benthic Metabolism Studies

Three benthic metabolism runs were conducted following the treatment of the area with 2,4-D (19, 25, and 26 August 1974). During this time, the treatment area had a mean benthic respiration rate of 0.013 g $O_2/m^2 \cdot hr$ (0.304 g $O_2/m^2 \cdot day$) (Table 8), while the control area had a mean benthic respiration rate of 0.006 g $O_2/m^2 \cdot hr$ (0.136 g $O_2/m^2 \cdot day$). Benthic respiration rates in the treatment area during this time represented 4.13% of the total community respiration while the benthic respiration in the control area represented 2.33% of the total.

For the two benthic metabolism runs conducted during the 1975 study period, the treatment area had a mean benthic respiration rate of 0.004 g $O_2/m^2 \cdot hr$ (0.084 g $O_2/m^2 \cdot day$) and the control area for this same period had a mean benthic respiration rate of 0.008 g $O_2/m^2 \cdot hr$ (0.204 g $O_2/m^2 \cdot day$). The value for the treatment area represented 1.98% of the total community respiration for the treatment area during this period, while the control area value represented 3.71% of total community respiration in that area.

During the 1974 post-treatment study period the treatment area had higher benthic respiration rate than the control area, probably because of the greater quantities of decomposing M. spicatum present in the former. During the 1975 study period the higher value for the benthic respiration rate in the control area may be attributable to the more highly organic sediments found in that area. Resuspension of sedi-

Table 8. Respiration rates of the benthic community in the treatment and control study areas following treatment with 2,4-D (1974-1975).

Date	Benthic Respiration			
	Treatment		Control	
	g $O_2/m^2 \cdot hr$	g $O_2/m^2 \cdot day$	g $O_2/m^2 \cdot hr$	g $O_2/m^2 \cdot day$
1974				
19 August	0.020	0.480	0.013	0.312
25 August	0.008	0.192	0.002	0.048
26 August	0.010	0.240	0.002	0.048
Mean	0.013	0.304	0.006	0.136
1975				
31 July	0.006	0.144	0.009	0.216
7 August	0.001	0.024	0.008	0.192
Mean	0.004	0.084	0.008	0.204

ments in the treatment area may have resulted in export of organic particulate matter as a result of the destruction of the M. spicatum population.

Limitations of the Methods Employed

The diurnal dissolved oxygen method using one station assumes that the water in the area is homogeneous. This might not be true in some cases. It is imperative that the investigator utilizing this method be reasonably sure that the station is representative of the entire area. This method also assumes that the oxygen released and measured in the water is equivalent to productivity. Some of the oxygen produced by photosynthesis could be bound in special air chambers (lacunae) so that the total productivity of the plants would not be reflected in the oxygen increase in the surrounding water. Hartman and Brown (1967) showed that Myriophyllum exalbescens had a very large air storage system so it is probable that accumulation of oxygen resulted in an underestimation of the total productivity of a submersed vascular plant community such as the community found in Kitty Hawk Bay. This method also assumes that respiration is constant throughout the day. This is questionable and has yet to be documented. The problem of determining the amount of oxygen that is lost or gained by a natural aquatic community through diffusion also exists. Field techniques have not been developed which will adequately measure molecular diffusion rates between the atmosphere and an aquatic medium, so it still seems best to utilize the equation proposed by Odum (1956) to calculate diffusion rates (Lyford and Phinney, 1968). Estimates of total photosynthesis and respiration by this method are also susceptible to changes in cloud cover (available light), wind (diffusion rates), water temperature, salinity and other environmental and biological factors

which are not completely understood.

Vollenweider (1969) and Pratt and Berkson (1959) mention several sources of error in using the light and dark bottle technique for measuring plankton metabolism. Within enclosures such as the bottles used in this method, the available nutrients may be depleted and limit plankton productivity. The glass substrate of the bottles is preferred by diatoms and bacteria so that completely different populations of organisms might replace those present initially in the bottles. By enclosing the water in a container, the amount of mixing which normally occurs is eliminated. Bottles placed near the surface could be exposed to high levels of sunlight resulting in photoinhibition of the plankton present. Finally by restricting diffusion, oxygen concentration could become so great that the plankton might photorespire, thus altering "true" rates of metabolism.

The darkened enclosures used for estimating benthic respiration are subject to limitations similar to those in the light and dark bottle method. The enclosure limits mixing, provides a new substrate which favors perhaps one population or organisms over another, and nutrients could become limiting within such an enclosure. These problems were minimized by conducting these studies over short time periods - 3 hr incubations for plankton metabolism studies and 6 hr for benthic studies.

DISCUSSION AND CONCLUSIONS

Within an aquatic ecosystem, nutrients may occur on or exchange between three general compartments: (1) available nutrients, (2) organic matter and (3) primary and secondary minerals (Likens, 1972). Available nutrients are those dissolved in the water or on exchange surfaces of pelagic particulate matter or bottom sediments. Nutrients incorporated in living and dead organic matter, both in the pelagic region or in sediments comprise the organic matter compartment. Nutrients incorporated in rocks, as primary and secondary minerals in the sediments or suspended in the water constitute the primary and secondary mineral compartments. Available nutrients are released from organic matter by excretion, exudation, leaching, respiration and decomposition. Rooted macrophytes can obtain and utilize nutrients directly from the sediments as well as from the surrounding water (Bristowe and Whitcombe, 1971).

The macrophyte community in Kitty Hawk Bay prior to 2,4-D treatment was very dense, indicating that most of the nutrients were bound in the organic matter compartment. Application of 2,4-D to the water of Kitty Hawk Bay killed most of the macrophytes and shifted the nutrient pool from the organic matter compartment to the available nutrient compartment, with the mineral compartment remaining approximately the same. By shifting the nutrients from the organic matter compartment to the available nutrient compartment, these nutrients were made available to those organisms most capable of utilizing them -- in this case the bloom-forming blue green algae.

In addition to the nutrients Kitty Hawk Bay receives from the sources listed above, it also receives additional nutrients from agricultural runoff which occurs upstream and from septic tank leakage from cottages which line the shore of the bay. These additional nutrients enabled the macrophyte community of Kitty Hawk Bay to reach relatively high density prior to the application of 2,4-D. Models of the Kitty Hawk Bay ecosystem prior to treatment, following treatment and at one year following treatment with 2,4-D can be seen in Figs. 9, 10 and 11.

The symbol and modelling scheme seen in these figures follows those of H. T. Odum (1971). Total community metabolism values (GPP and R) determined by the diurnal dissolved oxygen method in g $O_2/m^2 \cdot day$ (Table 1) were converted to $Kcal/m^2 \cdot day$ assuming that one (1) gram of oxygen was equivalent to 4 Kcal. Phytoplankton hourly respiration rates (Table 5) and benthic hourly respiration rates (Table 8) were multiplied by 24 to obtain daily respiration rates. These values were then converted to Kcal by multiplying by 4. Phytoplankton GPP hourly rates (Table 5) were multiplied by 10 to determine daily phytoplankton GPP and then by 4 to convert the values to Kcal. Phytoplankton and benthic rates, where measured, were subtracted from total community metabolism to determine the macrophyte contribution.

The macrophyte community of Kitty Hawk Bay was a very productive one prior to treatment with 2,4-D (Fig. 9) both in terms of biomass (1034 $Kcal/m^2$) and in terms of GPP (20.92 $Kcal/m^2 \cdot day$). The plankton community biomass was undetectable and the daytime GPP value for that component was very low (1.64 $Kcal/m^2 \cdot day$). The model pre-

Fig. 9. Model of energy flow through the Kitty Hawk Bay ecosystem prior to treatment with 2,4-D. (Values are the means of all pretreatment values 31 May - 19 June 1974). Symbols follow the convention of Odum, H.T. (1971). Values inside the symbols are biomass (Kcal/m^2) and values on the lines are energy flow rates (Kcal/m^2·day).

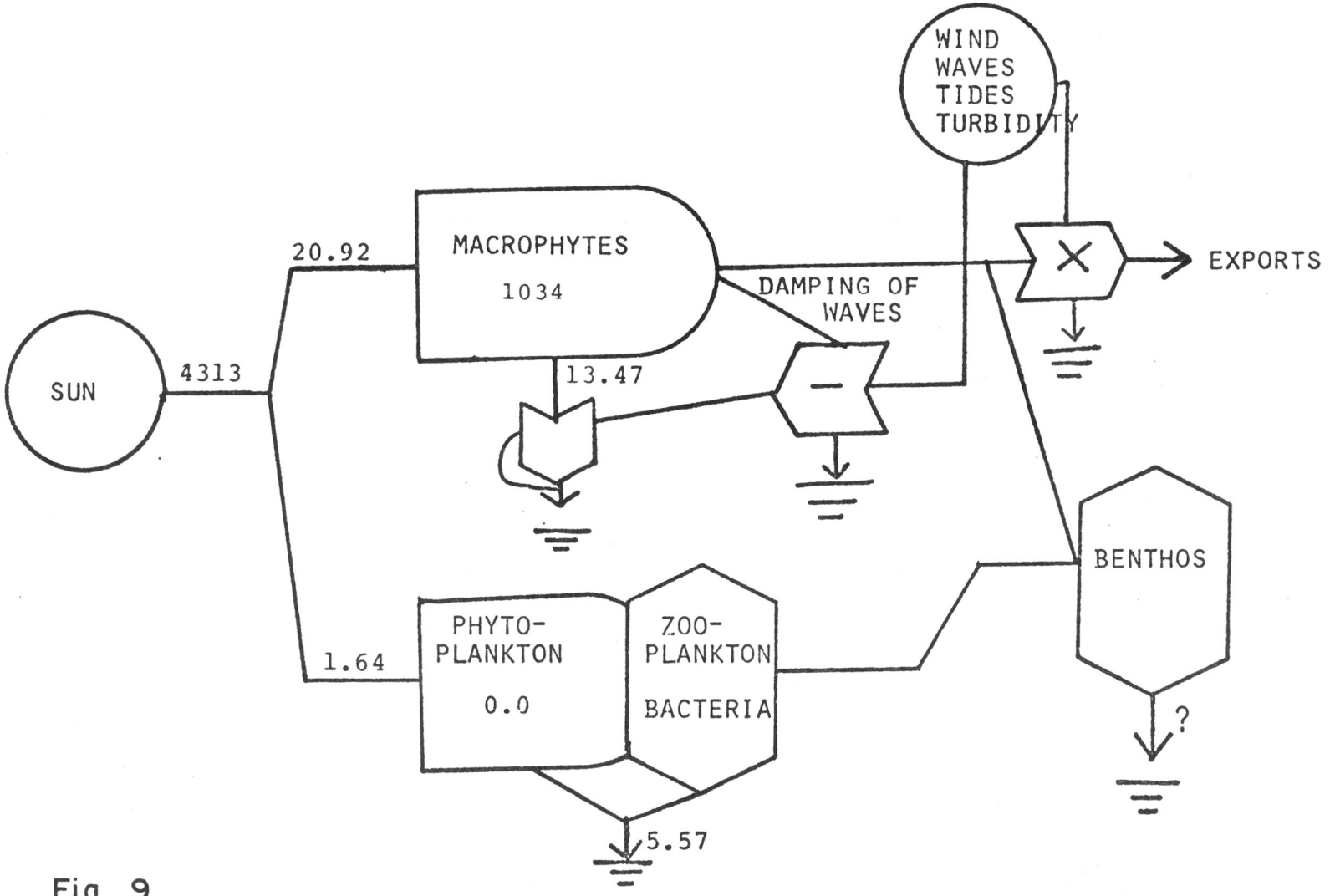
WIND
WAVES
TIDES
TURBIDITY
MACROPHYTES
1034
20.92
SUN
4313
13.47
DAMPING OF
WAVES
EXPORTS
BENTHOS
PHYTO-
PLANKTON
0.0
ZOO-
PLANKTON
BACTERIA
1.64
5.57
?

Fig. 9

sented in Fig. 10 shows the marked decline in macrophyte importance. Biomass has dropped to 14.0 Kcal/m^2 and GPP and R have become negligible. This model also shows the increased importance of the phytoplankton. Biomass increased to 0.12 Kcal/m^2, GPP to 32.80 Kcal/m^2•day and R to 41.28 Kcal/m^2•day. This clearly shows the shift in importance of the components from macrophyte to phytoplankton following 2,4-D treatment.

Kitty Hawk Bay was dominated by phytoplankton following 2,4-D treatment. Therefore, total community metabolism estimates made by the diurnal dissolved oxygen method should be comparable to phytoplankton community metabolism estimates made by the light and dark bottle method. Phytoplankton 1974 post-treatment GPP estimated by the light and dark bottle method was 32.80 Kcal/m^2•day and total community GPP was 29.44 Kcal/m^2•day. These values are quite comparable indicating that both methods are adequate for measuring phytoplankton productivity. Respiration values are not quite so comparable. The light and dark bottle method yielded a respiration value of 41.28 Kcal/m^2•day and the diurnal dissolved oxygen method yielded one of 20.76 Kcal/m^2•day. The higher value for the light and dark bottle method could be due to an overestimation caused by extrapolating the hourly respiration rate to the entire day. Bacteria enclosed within the dark bottle could also cause an overestimation of phytoplankton respiration.

The model presented in Fig. 11 shows that macrophyte biomass has increased one year following treatment to a value of 91.2 Kcal/m^2 and the GPP value increased to 11.48 Kcal/m^2•day. The phytoplankton

Fig. 10 Model of energy flow through the Kitty Hawk Bay ecosystem following treatment with 2,4-D (Values are the means of all 1974 post-treatment values -- 16 July - 28 August 1974). Symbols follow the convention of Odum, H.T. (1971). Values inside the symbols are biomass ($Kcal/m^2$) and values on the lines are energy flow rates ($Kcal/m^2 \cdot day$).

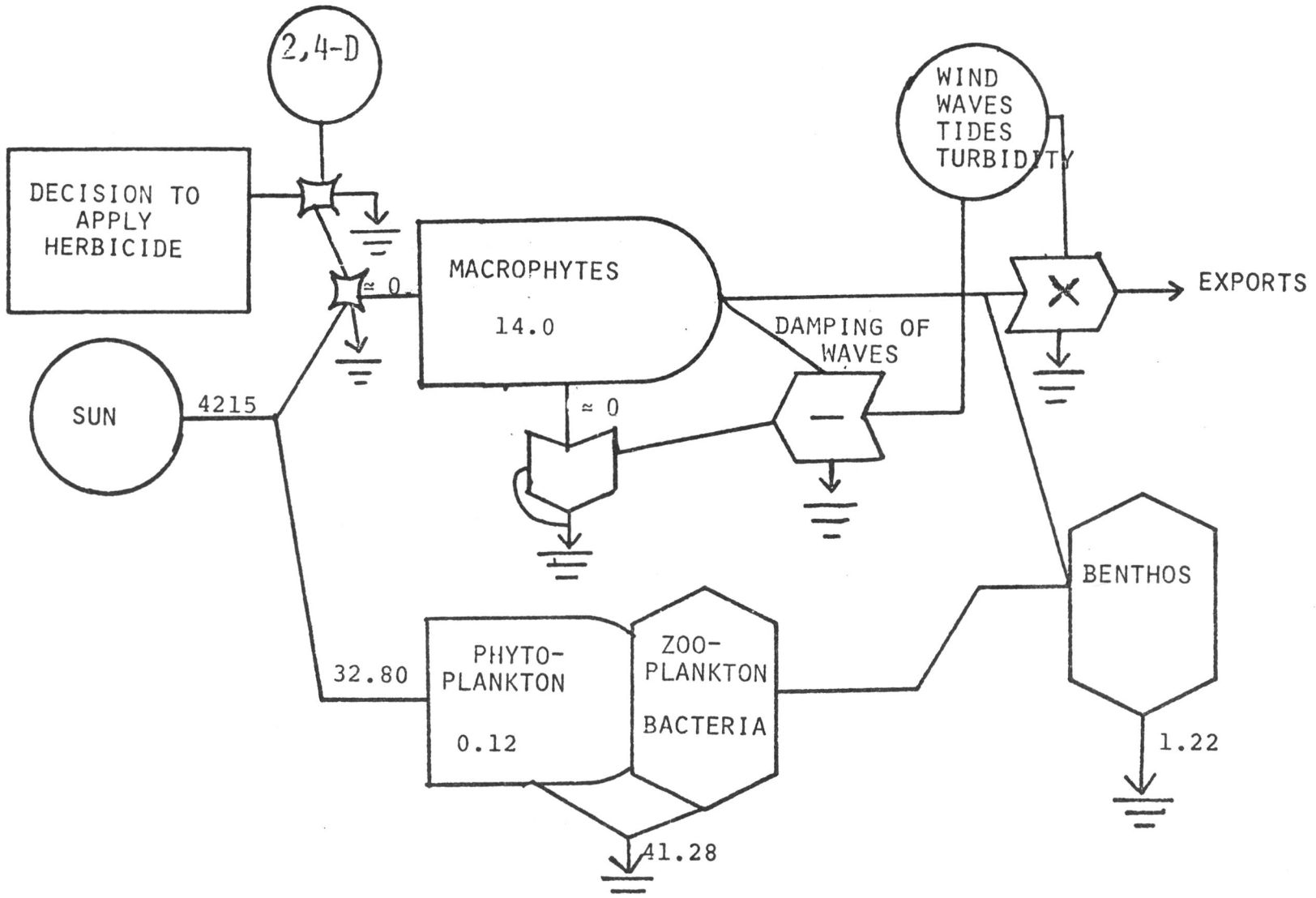
2,4-D
DECISION TO APPLY HERBICIDE
≈ 0
MACROPHYTES
14.0
WIND
WAVES
TIDES
TURBIDITY
EXPORTS
DAMPING OF WAVES
SUN
4215
≈ 0
BENTHOS
32.80
PHYTO-PLANKTON
0.12
ZOO-PLANKTON
BACTERIA
1.22
41.28

Fig. 10

Fig. 11. Model of energy flow through the Kitty Hawk Bay ecosystem one year following treatment with 2,4-D (values are the means of all 1975 post-treatment values -- 17 July - 7 August 1975). Symbols follow the convention of Odum, H.T. (1971). Values inside the symbols are biomass ($Kcal/m^2$) and values on the lines are energy flow rates ($Kcal/m^2 \cdot day$).

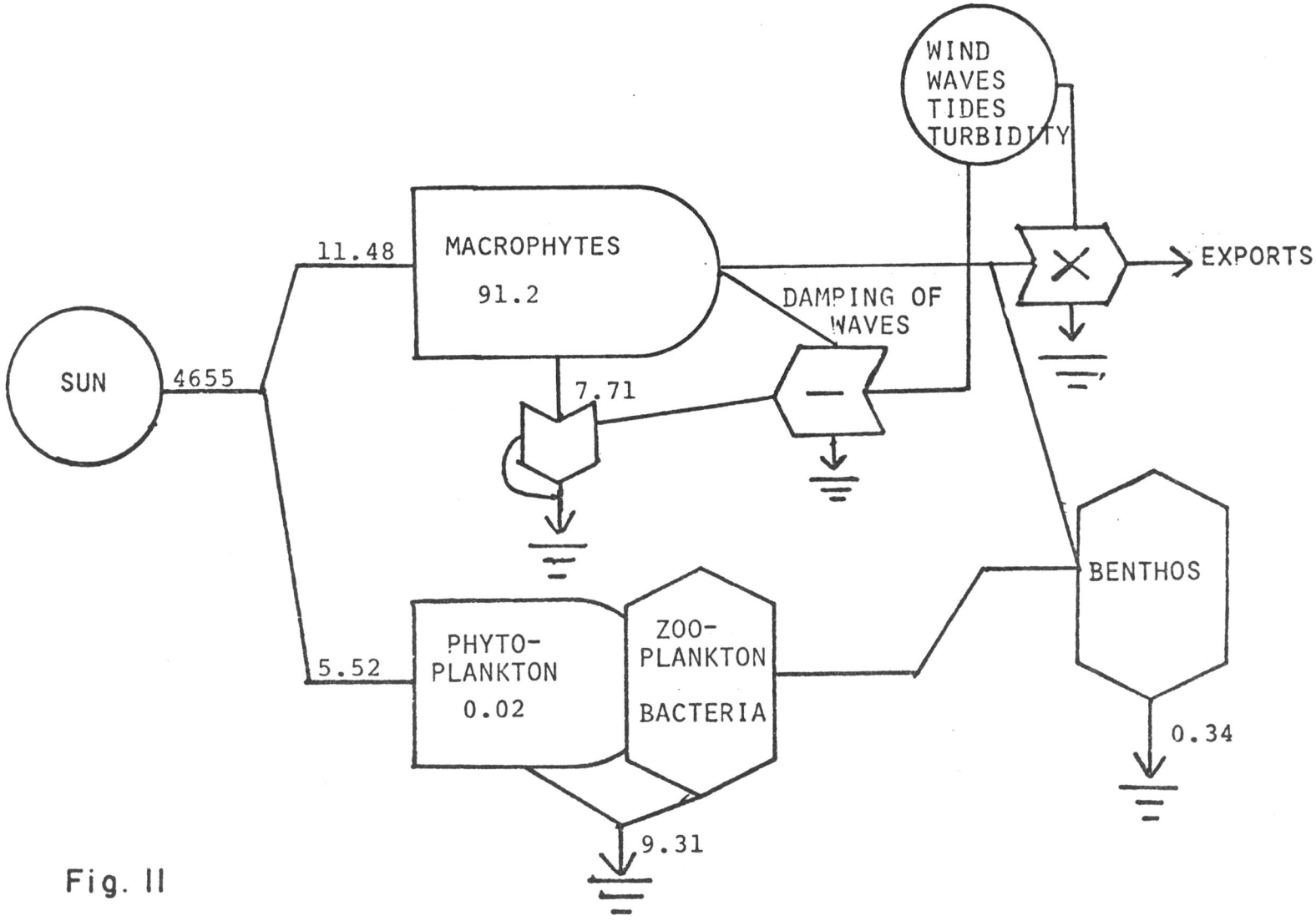
WIND
WAVES
TIDES
TURBIDITY
11.48
MACROPHYTES
91.2
EXPORTS
DAMPING OF
WAVES
SUN
4655
7.71
BENTHOS
5.52
PHYTO-
PLANKTON
0.02
ZOO-
PLANKTON
BACTERIA
0.34
9.31

Fig. II

biomass declined to 0.02 Kcal/m^2 as did the daytime GPP value (5.52 Kcal/m^2·day). This appears to indicate that the ecosystem was recovering to dominance by macrophytes since it was returning to a system with productivity dominated by macrophytes.

The application of 2,4-D did result in the total destruction of M. spicatum within the treated area as well as the additional destruction of M. spicatum in surrounding areas. Other species of macrophytes declined after the application of 2,4-D as a result of: (1) being trapped and pulled to the bottom by the sinking mats of M. spicatum, (2) increased turbidity caused by the suspension of sediment particulate matter as a result of the loss of the extensive root system of M. spicatum, or (3) toxic conditions present in the water as a result of the rapid decomposition of large amounts of M. spicatum. These conditions kept dissolved oxygen levels below pretreatment values in the treatment area for approximately one month following the application of 2,4-D. At the end of this time a plankton bloom was witnessed which resulted in higher dissolved oxygen readings than those found before treatment. The plankton bloom was composed of species of blue-green algae which are usually indicative of high nutrient levels in the water (Anacystis and Aphanizomenon). Therefore, it is possible to speculate that as a direct result of 2,4-D application, the community of M. spicatum was destroyed along with the partial destruction of other species of macrophytes which released nutrients which were bound in the cellular material of the macrophytic species. Those nutrients were then available to other species, in this case, the bloom-forming blue-green algae. The extremely turbid

conditions abetted by suspended sediments and the plankton bloom further decreased the probability of submersed macrophyte survival. One year following treatment with 2,4-D the macrophyte component of the ecosystem showed a remarkable recovery, once again demonstrating the capacity of a natural system for recovery from extensive human perturbation.

Water quality in Kitty Hawk Bay has declined in recent years to the point that shell fishing has been forbidden in those waters due to high coliform bacteria levels. A likely source of those substances which are responsible for the decline in water quality (coliform bacteria and high levels of nutrients) is leakage from septic tank sorption fields of the cottages which surround the bay. As the number of people occupying recreational homes increases along Kitty Hawk Bay, larger quantities of nutrients will become available resulting in increased biomass of those organisms which are most capable of utilizing the nutrients -- in this case, M. spicatum. Thus the M. spicatum community of Kitty Hawk Bay is operating as a form of advanced wastewater treatment by transferring the nutrients available from septic tank leakage from the available nutrient compartment to the organic matter compartment. Kitty Hawk Bay is also serving as a sink for those nutrients, preventing their movement into the surrounding waters of Albemarle and Currituck Sounds.

Since the spread of M. spicatum has been attributed to decreasing water quality (Fish, 1976) and the bloom-forming blue-green algae are also known to be indicative of poor water quality, it appears that the main problem in the control of M. spicatum is the availability of nutrients. As long as there are great amounts of nutrients available in Kitty Hawk

Bay there will be some form of plant growth utilizing those nutrients and the available solar energy source. In Kitty Hawk Bay available energy in the form of solar radiation is abundant during the summer months, temperatures are mild, the water is shallow and disturbance is minimal. These are ideal conditions to support a large community of macrophytes. Prior to the introduction of M. spicatum, native species of macrophytes abounded in the waters of Kitty Hawk Bay. With the introduction of M. spicatum and the increasing levels of nutrients to the bay, M. spicatum was able to displace the native species in this environment. The application of 2,4-D caused the destruction of M. spicatum along with members of the native species releasing vast amounts of nutrients which only compounded the water quality problem instead of alleviating it. After the destruction of the M. spicatum plants, the bay did not return to one being composed purely of native species. Since destruction was not widespread, fragments of M. spicatum allowed the re-establishment of that species. Under present conditions herbicide application alone will never eradicate M. spicatum from an open system such as Kitty Hawk Bay. There will always be a source of plant material or seed which will allow the re-establishment of the species. The most important aspect of long-range control of M. spicatum should focus on improvement of water quality to reduce the abundance of nutrients in the water, possibly giving an advantage to the native species once again.

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