

**CLADOPHORA INTERNAL PHOSPHORUS MODELLING:
VERIFICATION**

by

D.Scott Painter¹ and Michael B. Jackson²

NWRI Contribution Series # 86-72

¹Aquatic Ecology Division
National Water Research Institute
Canada Centre for Inland Waters
Burlington, Ontario, Canada, L7R 4A6

²Aquatic Ecosystems Section
Ontario Ministry of the Environment
P.O. Box 213
Rexdale, Ontario, Canada M9W 5L1

MANAGEMENT PERSPECTIVE

Cladophora, a nuisance filamentous green alga, grows in the nearshore zone of the Great Lakes. Accumulations of decaying Cladophora cause aesthetically unpleasant shorelines and have been implicated in drinking water taste and odor events. Phosphorus control programs were initiated in the Great Lakes in the early 70's to control phytoplankton growth in the open lake and Cladophora growth in the nearshore zone. Since 1972, the Ontario Ministry of the Environment (MOE) has monitored Cladophora in the Great Lakes to determine the extent of problem accumulations and to assess the impact of phosphorus control measures on the alga's growth. In 1983, Environment Canada initiated a project to implement a Cladophora simulation model to serve as a predictive management tool for the Cladophora problem in the Great Lakes. This report presents a verification of Environment Canada's Cladophora model using data collected in large part by MOE.

The paper discusses several predictions of the model such as the effect of upwelling events and current surveillance methods used for trend analysis.

The report was prepared jointly with the Ontario Ministry of Environment.

Cladophora Internal Phosphorus Modelling: Verification

D. Scott Painter

Aquatic Ecology Division

National Water Research Institute

Canada Center for Inland Waters

Burlington, Ontario, L7R 4A6

and

Michael B. Jackson

Aquatic Ecosystems Section

Ontario Ministry of the Environment

P.O. Box 213 Rexdale, Ontario, M9W 5L1

ABSTRACT. A mathematical model, simulating Cladophora internal phosphorus, was verified using data sets obtained from Lakes Ontario, Erie, Huron and Simcoe. The model's response was evaluated over a broad range of environmental conditions likely to occur in the Great Lakes. The environmental conditions required for simulation of internal phosphorus were temperature, Secchi disc transparency and soluble reactive phosphorus. The model was used to determine the necessary reduction in soluble reactive phosphorus to decrease Cladophora growth rates at a eutrophic site in northwestern Lake Ontario by 50%.

Additional Index Words: Phosphorus, Nearshore zone, Great Lakes

INTRODUCTION

Canale and Auer (1982) and coworkers designed a Cladophora growth model which was described in a series of seven publications in a special issue of the Journal of Great Lakes Research (Vol 8(1), 1982) which dealt with filamentous algae in the Great Lakes. Canale and Auer's papers were a significant milestone in the understanding of Cladophora growth dynamics and the work reported in this paper relied heavily on their contribution. Since 1972, the Ontario Ministry of the Environment (MOE) has monitored Cladophora in the Great Lakes to determine the alga's distribution and growth potential and to assess the impact of phosphorus control measures on the alga's growth. In 1983, Environment Canada initiated a project to implement a Cladophora simulation model based on Canale and Auer's previous papers. This report presents a verification of Environment Canada's Cladophora model using data collected in large part by MOE.

METHODS

Environmental Data

The locations of the sites and the agency responsible for sample collection are illustrated in Figure 1. Water temperature and Secchi disc transparency were measured on site and water samples were field filtered and submitted in acid-washed glass bottles for soluble reactive phosphorus analysis according to MOE (1981) or Analytical Methods Manual (IWD, Environment Canada, 1979). Cladophora samples were collected for analysis of internal phosphorus and loss of ignition. Internal phosphorus was expressed on a dry weight (DW) and ash-free dry weight basis (AFDW).

Model Development

A computer model was developed from an interpretation of Canale and Auer's publications with several additions or alterations to ensure that the model's performance under standard environmental conditions was consistent with expected performance. For example, if the light compensation point and optimum light intensity for net photosynthesis at 19 C are known to be 25 and 300 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$, respectively, then the model was tested to ensure that the output was as expected.

The model was designed to simulate internal phosphorus. No attempt was made to predict biomass since actual biomass is dependent on storm induced sloughing events which require site specific relationships. Canale and Auer's model had growth rate modified by biomass quantity to incorporate a self-shading relationship. Sloughing of biomass was also dependent on the quantity of biomass and the wind speed and direction. Both these functions are absent from our model. The validity of the model's output is dependent on the assumption that biomass is sloughed frequently enough so that the self-shading is insignificant. The amount of information required from the specific site is reduced to water temperature, Secchi disc transparency, solar input and soluble reactive phosphorus(SRP). Therefore, data required to run a simulation are simple to collect and this expands the utility of the model, provided the model's response without self-shading and sloughing can be verified.

The model's solar input was based on an "average year" to further decrease the data requirements from the specific site. The solar input was determined from a data file on solar radiation at CCIW, Burlington, Ontario. The solar input database was constructed from

hourly irradiance information over the past 9 years.

The decisions to ignore self-shading and sloughing and to use an "average solar year" were a result of an attempt to make the model "generic", readily transportable from site to site, utilizing a minimum of site specific information and yet capable of predicting Cladophora's response under average conditions. Therefore, the model was designed to predict internal tissue phosphorus. Since growth rate is dependent on internal tissue phosphorus, the model can, however, be used to predict growth rate provided the simulated tissue phosphorus can be reasonably verified.

The Canale-Auer equation to calculate tissue phosphorus concentration for each time interval was :

$$Q_2 = Q_1 + (p - u \cdot Q_1) \cdot (t_2 - t_1) \quad (1)$$

where

Q_2 is internal phosphorus conc. (%P) for interval t_2 ;

Q_1 is internal phosphorus conc. (%P) for interval t_1 ;

p is P uptake during the interval (%P/interval);

and u is specific growth rate (interval⁻¹).

This equation has been derived from chemostat experiments as described by Turpin et al. (1981) and involves a term for dilution loss of cells out of the chemostat and the cellular phosphorus they take with them. When the internal phosphorus concentration (Q) is high relative to Q_{\min} (the minimum internal phosphorus concentration for growth), u approaches u_{\max} (the maximum specific growth rate) using the equation of Droop (1968)

$$u = u_{\max} \cdot (1 - Q_{\min}/Q); \quad (2)$$

and p approaches 0 using the equation of DiToro (1980)

$$P = P_{\max} * (P/(K_m + P)) * (K_q/(K_q + (Q - Q_{\min}))) \quad (3)$$

where

P is ambient phosphorus concentration (ppb)

K_m is the half-saturation constant for uptake as a function of ambient phosphorus (ppb)

and K_q is the constant relating uptake rate to internal phosphorus concentration (%P).

When the biomass doubles (ie $u=1$) and Q is high relative to Q_{\min} then Q_2 decreases by 100% to 0 using equation 1 but should in fact only approach 50% of Q_1 because dilution loss of cells and cell phosphorus do not apply to Cladophora. If the term for dilution loss of cells and cell phosphorus is removed from the equations described in Turpin et al. (1981), then the equation becomes:

$$Q_2 = dQ/dt + Q_1 \quad (4)$$

where $dQ/dt = (p * N_2 - ((N_2 - N_1)/(t_2 - t_1)) * Q_1)/N_2; \quad (5)$

N_2 and N_1 are cell numbers for time intervals

t_2 and t_1 .

Under the same conditions described above, where cell numbers double and uptake (p) is 0, and using equations 4 and 5, Q_2 is 50% of Q_1 which is more applicable to Cladophora. The equation used in the model is

$$Q_2 = Q_1 / (u * (t_2 - t_1) + 1) + p * (t_2 - t_1) \quad (6)$$

which gives the same results as equations 4 and 5.

The Canale-Auer equation for Cladophora respiration was derived from laboratory experiments conducted with an excess of phosphate (Graham et al., 1982) and under varying irradiance and temperatures. In other experiments, growth and respiration were determined on field-collected material containing various internal phosphorus concentrations and respiration was shown to be related to internal

phosphorus (Auer and Canale, 1982a). According to Canale and Auer's publications, their model did not have respiration modified by internal phosphorus. When Cladophora growth simulations were run with internal phosphorus close to Q_{\min} for net specific growth, using the Environment Canada model, the calculated net photosynthesis was zero or negative because the respiration value subtracted from gross photosynthesis was too high. When respiration was modified in the model by internal phosphorus concentration, net production then approached zero as expected when internal phosphorus approached Q_{\min} .

Dark respiration consumes carbon but not phosphorus, therefore, during dark periods a small increase in the internal phosphorus concentration relative to cell carbon could be expected. The model includes the following equation that would increase cell P relative to respiratory consumption of carbon:

$$Q_2 = Q_1 / (1 - R \cdot (t_2 - t_1)) \quad (7)$$

where R is the dark respiration rate (interval^{-1}).

Auer and Canale compared growth rates of laboratory cultured Cladophora with growth rates of field collected Cladophora under similar conditions (19°C and $300 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$). They determined that the laboratory photosynthesis and respiration polynomial response surfaces should be multiplied by 3.18 and 1.75, respectively, to convert them to field rates. We found, however, that since photosynthesis was magnified more than respiration, simulations run at low light intensities yielded positive net photosynthesis in the dark. The two correction factors used in the model were identical (3.18 was chosen) so that the calculations would be similar to the polynomial response surfaces observed by Graham et al. (1982). Net photosynthesis was no longer positive in the dark and light

compensation points were similar to observed values.

Auer and Canale(1982a) experimentally determined the Q_{min} for net specific growth to be $0.06\%P$ and the Q_{min} for respiration to be $0.04\%P$. They chose to use an average Q_{min} of $0.05\%P$ for their model. The model uses gross photosynthesis and light respiration to calculate net photosynthesis. If a Q_{min} of 0.05 for both gross photosynthesis and respiration was used, the predicted Q_{min} for net photosynthesis is greater than Auer and Canale's experimental results. Therefore, the model uses a Q_{min} for respiration of $0.04\%P$ and determined a Q_{min} for gross photosynthesis so that net photosynthesis would have a Q_{min} of $0.06\%P$ in accordance with Auer and Canale's findings. The Q_{min} for gross photosynthesis was determined to be $0.052\%P$.

The half-saturation constant for phosphorus uptake as a function of internal phosphorus concentration (K_p) was determined by Auer and Canale (1982b) to be $0.07\%P$. Their value was determined using uptake data corrected to remove the demand for growth and represent surge uptake only. The demand for growth is removed elsewhere in our model so the uptake data used to derive a K_q was the total uptake (uptake required for growth plus surge uptake). Therefore, the K_q used in our model was $0.095\%P$ which was determined from data presented in Auer and Canale (1982b).

The Canale-Auer model modified phosphorus uptake relative to temperature based on nitrate uptake of the planktonic algae Scenedesmus. Maximum uptake occurred at 15 C and decreased exponentially away from 15 C so that at 5 C intervals, the rate decreased by 50% (Rhee and Gotham, 1981). Gray (1984) examined the relationship between phosphorus uptake and temperature for Cladophora and found that the optimum temperature for uptake was in the vicinity

of 18 C. For a 10 degree decrease in temperature, the uptake rate decreased to 77% of the rate at 18 C and for a 10 degree rise in temperature, the uptake rate decreased to 59% of the rate at 18 C (Q_{10} 's of 1.3 and 1.7, respectively). The equations for temperature correction of phosphorus uptake were

$$e^{((t-18)/39)} \text{ for } T < 18 \text{ C} \quad (8)$$

and $e^{((18-t)/18.75)} \text{ for } T > 18 \text{ C.} \quad (9)$

Auer and Canale (1982b) reported laboratory-determined phosphate uptake rates on field collected Cladophora with internal phosphorus concentrations ranging from 0.05%P to 0.96%P. They observed that K_m , the half-saturation constant for uptake as a function of external SRP, varied inversely with internal phosphorus. Nevertheless, they elected to use an average value of 125 for K_m .

The value of K_m is very important for the model since the K_m represents the affinity or ability of Cladophora to absorb phosphate from the water column. When the K_m is high, the alga has a low affinity for phosphate and when the K_m is low, the alga has a high affinity for phosphate.

In an attempt to derive an operational K_m for the model, Cladophora internal phosphorus was simulated using K_m 's ranging from 30 to 250 for several data sets obtained by Environment Canada. A relationship between K_m and internal phosphorus was found to be necessary for the simulated and observed internal concentrations to be comparable over a broad range of environmental conditions.

Two sources of published field data (Canale and Auer, 1982b; Jackson and Hamdy, 1982) comparing Cladophora internal phosphorus and SRP were compared to the model's simulated internal phosphorus relative to SRP.

Model Description

The model uses the environmental inputs of solar irradiance, temperature, Secchi disc transparency and SRP. The solar irradiance input is obtained from a data file that contains the average solar irradiance for every hour of every day. The average values were calculated from the previous nine years data from CCIW records for a global irradiance sensor maintained on the CCIW roof. Temperature, Secchi disc transparency and SRP are specific to each site. The Secchi disc transparency is used to calculate an extinction coefficient from a relationship between Secchi disc and extinction coefficient derived by Auer and Canale for Lake Huron and confirmed for Lakes Ontario and Erie. The hourly light intensity at any depth is then calculated from the hourly solar input, a back reflection correction of 10% and the calculated extinction coefficient.

The light intensity and temperature are then used to calculate hourly gross photosynthesis and light respiration according to the polynomial response surface described by Graham et al. (1982). Gross photosynthesis and light respiration are modified by internal phosphorus concentration. Net photosynthesis is calculated from gross photosynthesis and light respiration. The growth demand for internal phosphorus is calculated from gross photosynthesis. Phosphorus uptake from the water is determined by a function dependent on SRP, internal phosphorus and temperature. The internal phosphorus for hour two is then determined from the previous internal phosphorus minus the growth demand plus uptake. Uptake is determined at the end of the hour based on the internal phosphorus concentration after the growth demand has been subtracted. If uptake was calculated at the beginning of the hour rather than at the end of the hour, the effect on internal

phosphorus was insignificant.

During the dark, only temperature is used to calculate dark respiration. The dark respiration rate is modified by internal phosphorus. Internal phosphorus is replenished due to consumption of carbon as well as from uptake of SRP. Daily net production is calculated from the sum of the hourly net photosynthesis rates minus the sum of the hourly dark respiration rates.

A schematic of the model is provided in Figure 2. Pool sizes and rates are provided for a typical hour using mid-day, mid-summer conditions for an oligotrophic site.

RESULTS AND DISCUSSION

The model was tested to ensure that the output was consistent with our present understanding of Cladophora physiology. For example, if internal phosphorus concentration was in excess and light intensity was optimum, the model predicted that net photosynthesis and net production would be highest at 14 C and net production would be positive from 4 C to 26 C. Net photosynthesis was predicted to be optimum at a light intensity of $400 \text{ uE.m}^{-2}.\text{sec}^{-1}$ at a temperature of 18 C, and at $300 \text{ uE.m}^{-2}.\text{sec}^{-1}$ at a temperature of 22 C. Light compensation points for net photosynthesis would be $22 \text{ uE.m}^{-2}.\text{sec}^{-1}$ and $30 \text{ uE.m}^{-2}.\text{sec}^{-1}$ at temperatures of 18 and 22 C, respectively.

Figures 3 and 4 illustrate the predicted response of net photosynthesis with light at three internal phosphorus concentrations and net photosynthesis with internal phosphorus at three different light intensities. Both curves conform to the classical understanding of photosynthetic reactions (Bidwell, 1979). At low light intensities, a higher internal phosphorus concentration is required to achieve a positive net photosynthesis (Fig 4), whereas the light

compensation point was not affected by the internal phosphorus concentration (Fig 3).

Predicted internal phosphorus concentration as a function of SRP, when light and temperature are optimum, is illustrated in Figure 5. Two reported field-observed relationships are also included on the graph (Jackson and Hamdy, 1982; Canale and Auer, 1982b). The model prediction agrees favourably with the field observations.

The simulated internal phosphorus concentration and actual internal phosphorus concentration for 27 sites are presented in Figures 6 through 38. The sites provided a range of initial internal phosphorus concentrations from 1.0%P to 0.1%P (AFDW) which represented Cladophora's response from hypereutrophic to oligotrophic conditions. Observe that the internal phosphorus concentration on a ash-free dry weight basis matched the simulated internal phosphorus concentration better than the internal P on a dry weight basis. The correction for ash content was a significant correction at the eutrophic sites but insignificant at the oligotrophic sites. The higher ash content in the eutrophic sites was probably due to the marl accumulation from photosynthetic processes.

The model's performance in simulating the internal phosphorus concentration from 33 different data sets from 27 different locations in four lakes was good (correlation coefficient $r=0.95$, $df=230$). The frequency of data collection was important to ensure that an event was not simulated too long or was missed. The best simulations came from sites which experienced reasonably uniform environmental conditions. The worst simulations came from sites such as river mouths or harbours which are obviously highly variable locations. For example, compare simulations from Jordan Harbour Mouth with Jordan Shore (Fig 9-12),

and Collingwood Harbour Mouth with Mary Ward Shoals (Fig 22-25). The correlation coefficient mentioned above was for the AFDW internal phosphorus and did not include the Jordan Harbour Mouth or Collingwood Harbour Mouth sites (ie 4 of the 33 data sets).

Observed Cladophora internal phosphorus concentrations responded more rapidly to increases in SRP than the predicted internal phosphorus concentration. Observed internal phosphorus concentrations during and after storm events indicated that internal phosphorus rapidly increased but also rapidly decreased once nutrient poor water returned to the site. For example, fluctuations in the observed internal phosphorus concentration at the Jordan Harbour mouth site occurred hourly during three storm events (fig 12).

During the three years of data collection at the Oakville site in northwestern L. Ontario, four hypolimnetic upwelling events were recorded (MOE unpublished data). The effect on Cladophora was examined using model simulations. Each upwelling event was characterized by an increase in water clarity and SRP and a decrease in water temperature. Typical temperatures during the upwelling events ranged from 7.2 to 11.5 C. SRP concentrations during the four events were 22, 18, 40, and 260 $\mu\text{g.l}^{-1}$. The SRP increases during the events were greater than what would be expected from simple displacement of epilimnetic water by hypolimnetic waters, suggesting local municipal contributions. Both observed and simulated internal phosphorus increased during the events but quickly returned to pre-event concentrations when epilimnetic water returned. Simulated production increased in three of the four events but also declined after the events were over. The decline in production in the fourth event was due to a lower light intensity at the plant depth compared

to the other events. From these observations and the known relationship between temperature and photosynthesis, it would appear that the net effect of an upwelling event would be an increase in production in shallow, clear water and a decrease in production in deeper waters, although the effect would only be apparent during the upwelling event. Once epilimnetic water returned, the Cladophora quickly equilibrated with the new ambient SRP concentration and no benefit in terms of continued increased production was apparent.

Various model simulations were conducted to evaluate the influence of seasonal variations in temperature and water clarity on predicted internal phosphorus. Predicted Cladophora internal phosphorus concentrations at three different temperatures and Secchi disc transparencies but identical SRP concentrations, for growing depths of 0.1 and 5.0 meters are presented in Table 1. Under clear conditions, water temperature had very little effect on internal phosphorus at the 5.0 m depth; however, if the water was turbid then water temperature became important. Internal phosphorus concentrations at the shallow depth were much less variable. Although year-to-year fluctuations in water temperature and water clarity in the nearshore zone have little to do with trends in eutrophication, Cladophora internal phosphorus concentrations at deeper depths are highly susceptible to both temperature and water clarity conditions prior to sampling.

An assessment of the model's predictions would suggest that monitoring programs designed to observe trends in eutrophication should concentrate on shoreline samples only. A spin-off benefit of collecting only shoreline samples is that divers are no longer necessary, thereby decreasing resource requirements and costs. The internal phosphorus concentration in the shore samples is dependent on

SRP and relatively independent of temperature and clarity, therefore, an analysis of historical trends in eutrophication using shore samples only would be more valid and less susceptible to year-to-year climatic or storm-induced factors.

Cladophora in Lake Ontario during the last decade has responded to the phosphorus control program through reductions in biomass and internal phosphorus concentration (Painter and Kamaitis, 1986). Importantly, the internal phosphorus concentrations in 1983 were growth-limiting, even at Oakville which has historically been a problem area. The model was used to determine the necessary reduction in SRP to further decrease production by 50% at the Oakville site. The model predicted that seasonal net production would be 50% of 1983 levels if the SRP was reduced by 12.5%. The production predictions of the model were not validated; however, since growth rate is a function of internal phosphorus concentration and the growth rate determines internal phosphorus depletion and prediction of internal phosphorus was good, the likelihood of the model being correct with regards to production is also good. The Ministry's data for the three years at Oakville indicate that year-to-year differences in production were significant as a result of differences in ambient SRP. Such a large potential decrease in production with a comparatively small decrease in SRP is encouraging and we should ensure that any changes in Cladophora growth as a result of further reductions in phosphorus loading are well documented. Year-to-year differences in Cladophora internal phosphorus, however, will continue to be significant as was observed at the Oakville and Rathfon Point sites (fig. 6-8, 14-16). Any proposed monitoring program would have to account for these yearly differences.

CONCLUSIONS

A computer model which simulates Cladophora internal phosphorus concentrations using the environmental inputs of Secchi disc transparency, temperature, and soluble reactive phosphorus was developed and tested on many different sites of varying nutrient status from four large lakes. The model simulations were acceptable and model predictions of Cladophora's response were physiologically correct.

Year-to-year differences in spring temperature and water clarity were predicted to have a significant effect on internal tissue phosphorus concentrations of Cladophora growing at 5.0m. Cladophora internal phosphorus concentrations from shoreline samples were much less affected by temperature and water clarity. Monitoring programs designed to observe trends in eutrophication should concentrate on shoreline samples only.

The model was used to determine the necessary reduction in soluble reactive phosphorus at Oakville to realize a 50% reduction in seasonal net production. Encouragingly, from a lake management perspective, the required reduction was only 12.5%. While significant year-to-year variation in Cladophora growth can be expected, the phosphorus control program will become increasingly effective at reducing growth-related problems in the future.

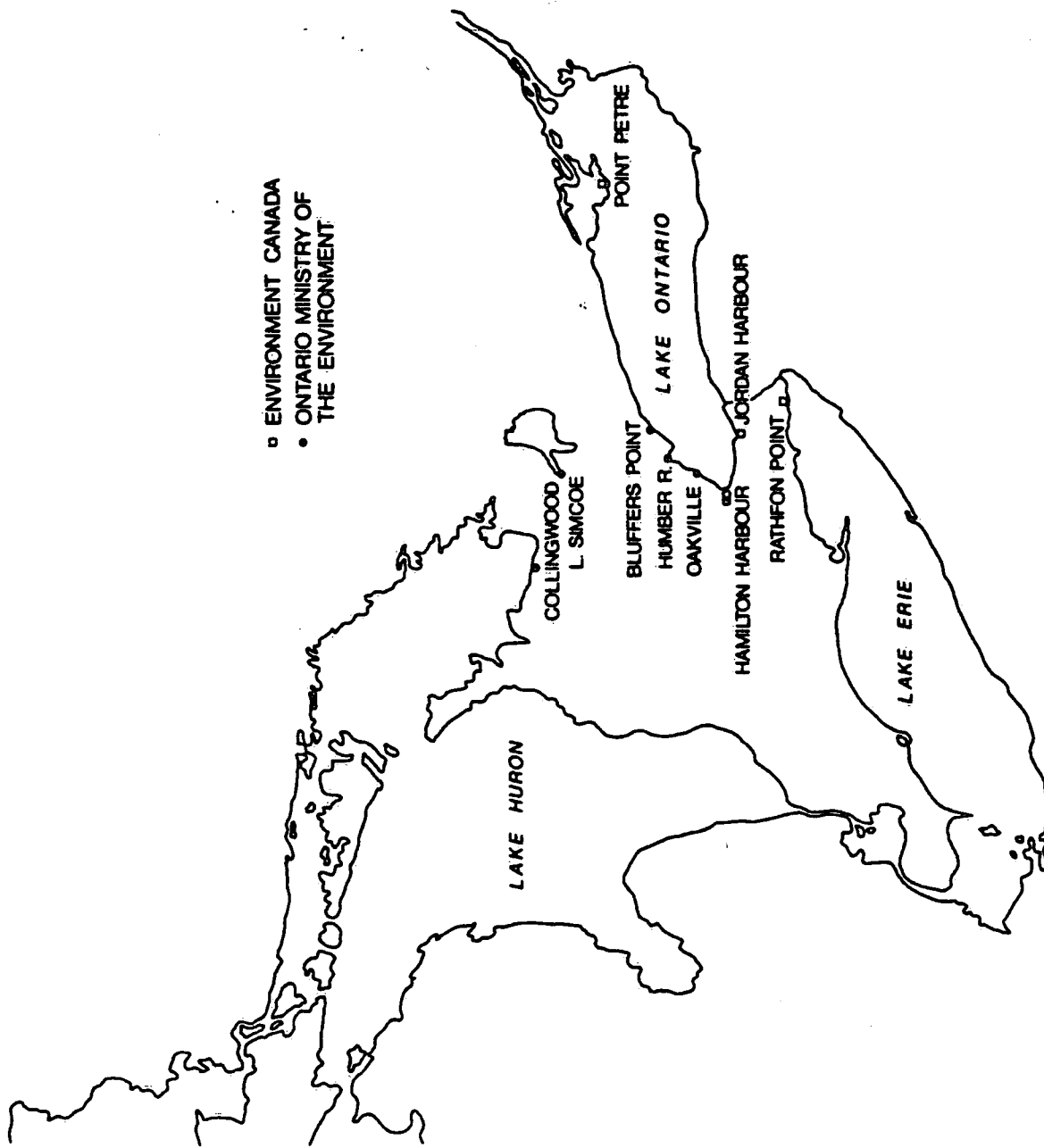
REFERENCES

- Auer, M.T., and Canale, R.P. 1982a. Ecological studies and mathematical modeling of Cladophora in Lake Huron:3. The dependence of growth rates on internal phosphorus pool size. J.Great Lakes Res. 8(1):93-99.
- Auer, M.T., and Canale, R.P. 1982b. Ecological studies and mathematical modeling of Cladophora in Lake Huron:2. Phosphorus uptake kinetics. J. Great Lakes Res. 8(1):84-92.
- Bidwell, R.G.S. 1979. Plant Physiology. MacMillan Pub. Co., New York, NY.
- Canale, R.P., and Auer, M.T. 1982. Ecological studies and mathematical modeling of Cladophora in Lake Huron:5. Model development and calibration. J.Great Lakes Res. 8(1):112-125.
- DiToro, D.M. 1980. Applicability of cellular equilibrium and Monod theory to phytoplankton growth kinetics. Ecological Modelling 8:201-218.
- Droop, M.R. 1968. Vitamin B₁₂ and marine ecology. IV. The kinetics of uptake, growth and inhibition in Monochrysis lutheri. J. Mar. Biol. Assoc. U.K. 48:689-733.
- Graham, J.M., Auer, M.T., Canale, R.P., and Hoffmann, J.P. 1982. Ecological studies and mathematical modeling of Cladophora in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res. 8(1):100-111.
- Gray, I.M. 1984. Study of Cladophora dynamics in Lake Ontario Contract Rept. N.W.R.I. CCIW, Burlington, Ontario, Canada.
- IWD. 1979. Analytical Methods Manual. Environment Canada, Inland Waters Directorate, CCIW, Burlington, Ontario, Canada.
- Jackson, M.B., and Hamdy, Y.S. 1982. Projected Cladophora growth in southern Georgian Bay in response to proposed municipal sewage treatment plant discharges to the Mary Ward Shoals. J. Great Lakes Res. 8(1): 153-163.
- MOE Unpublished Data. Aquatic Ecosystems Sec., Water Res. Br. Rexdale Ont.
- Ontario Ministry of Environment. 1981. Outlines of analytical methods: a guide to the occurrence, significance, sampling and analysis of chemical and microbiological parameters in water, sediment, soil, vegetation and air. Coordinated by the Water Quality Section, Laboratory Services Branch, Toronto, Ontario.
- Painter, D.S., and Kamaitis, G. in press. Reduction of Cladophora Biomass and tissue phosphorus in Lake Ontario 1972-1983. Can. J. Fish. Aquat. Sci. 42:000-000.
- Rhee, G-Y., and Gotham, I.J. 1981. The effect of environmental factors on phytoplankton growth: Temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26(4): 635-648.
- Turpin, H.D., Parslow, J.S., and Harrison, P.J. 1981. On limiting nutrient

patchiness and phytoplankton growth: a conceptual approach. J. Plankton
Res. 3:421-431.

FIGURE LEGENDS

- Figure 1. Location of the study sites of Environment Canada and Ontario Ministry of Environment
- Figure 2. Schematic illustration of one hour's calculations by the model
- Figure 3. Relationship between relative net photosynthesis and light intensity at three different internal phosphorus concentrations
- Figure 4. Relationship between relative net photosynthesis and internal phosphorus concentration at three different light intensities
- Figure 5. Observed and model-predicted relationship between internal phosphorus concentration and soluble reactive phosphorus concentration
- Figures 6-38. Observed and model-predicted internal phosphorus concentrations versus time at 27 sites



- ENVIRONMENT CANADA
- ONTARIO MINISTRY OF THE ENVIRONMENT

LAKE HURON

POINT PETRE

LAKE ONTARIO

COLLINGWOOD
L. SIMCOE

BLUFFERS POINT

HUMBER R.

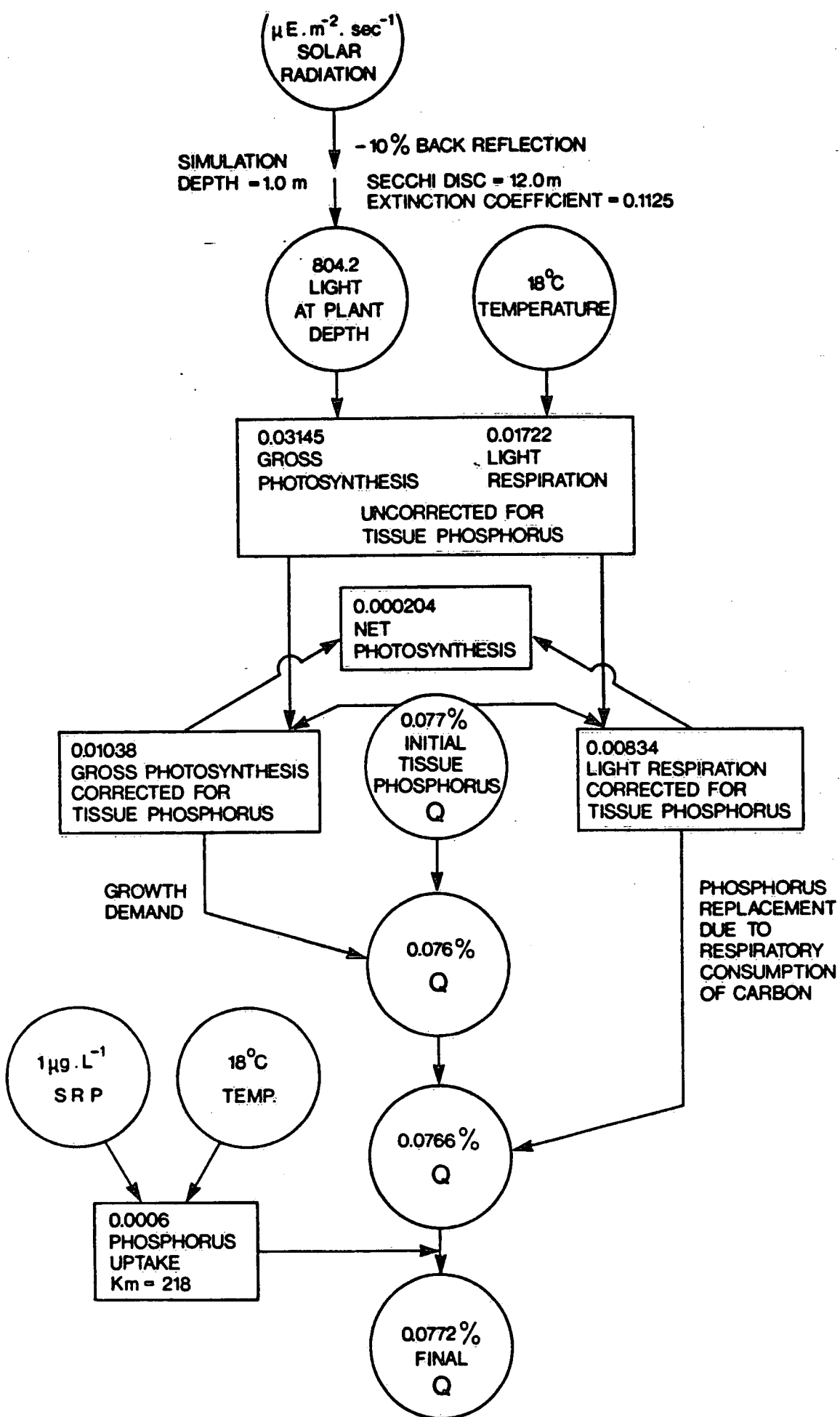
OAKVILLE

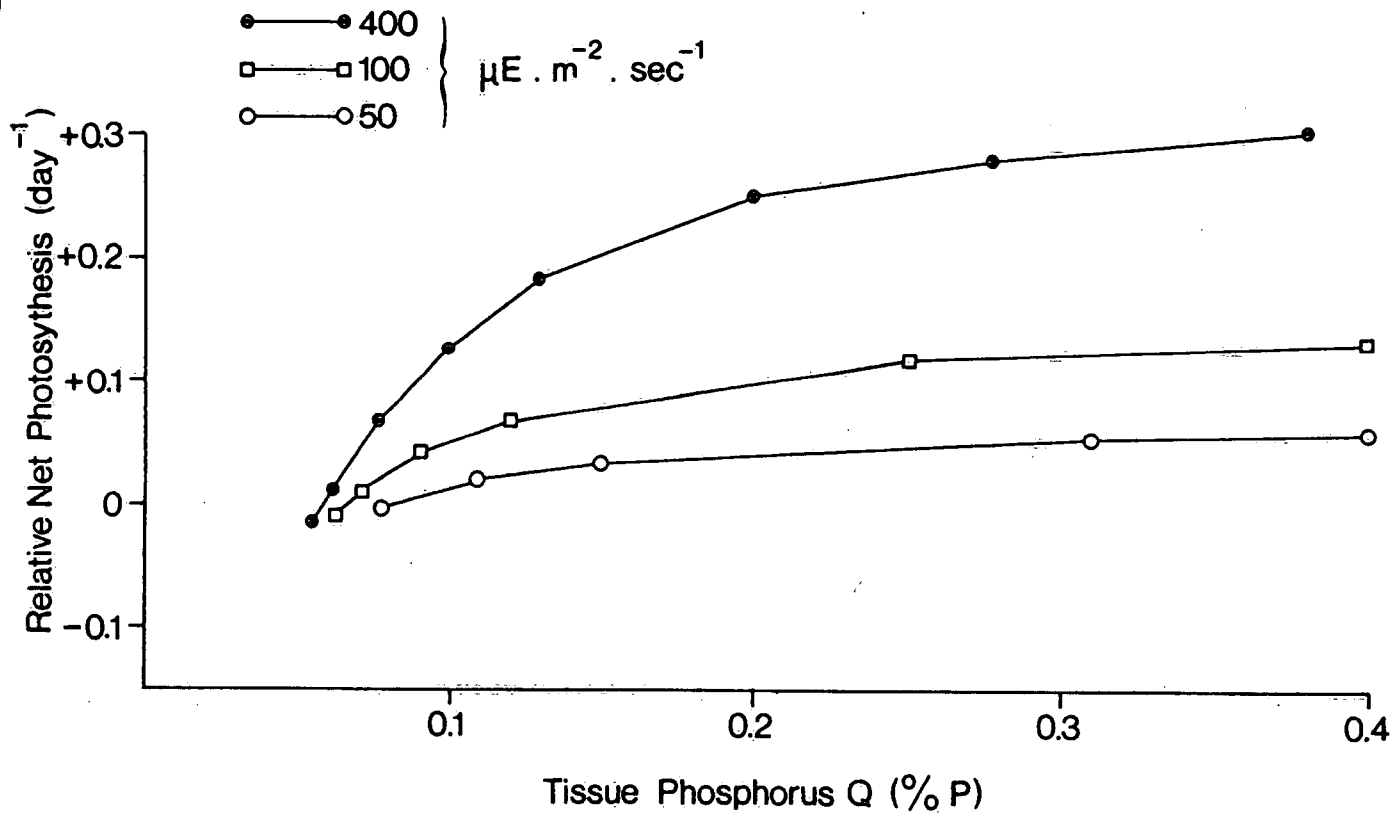
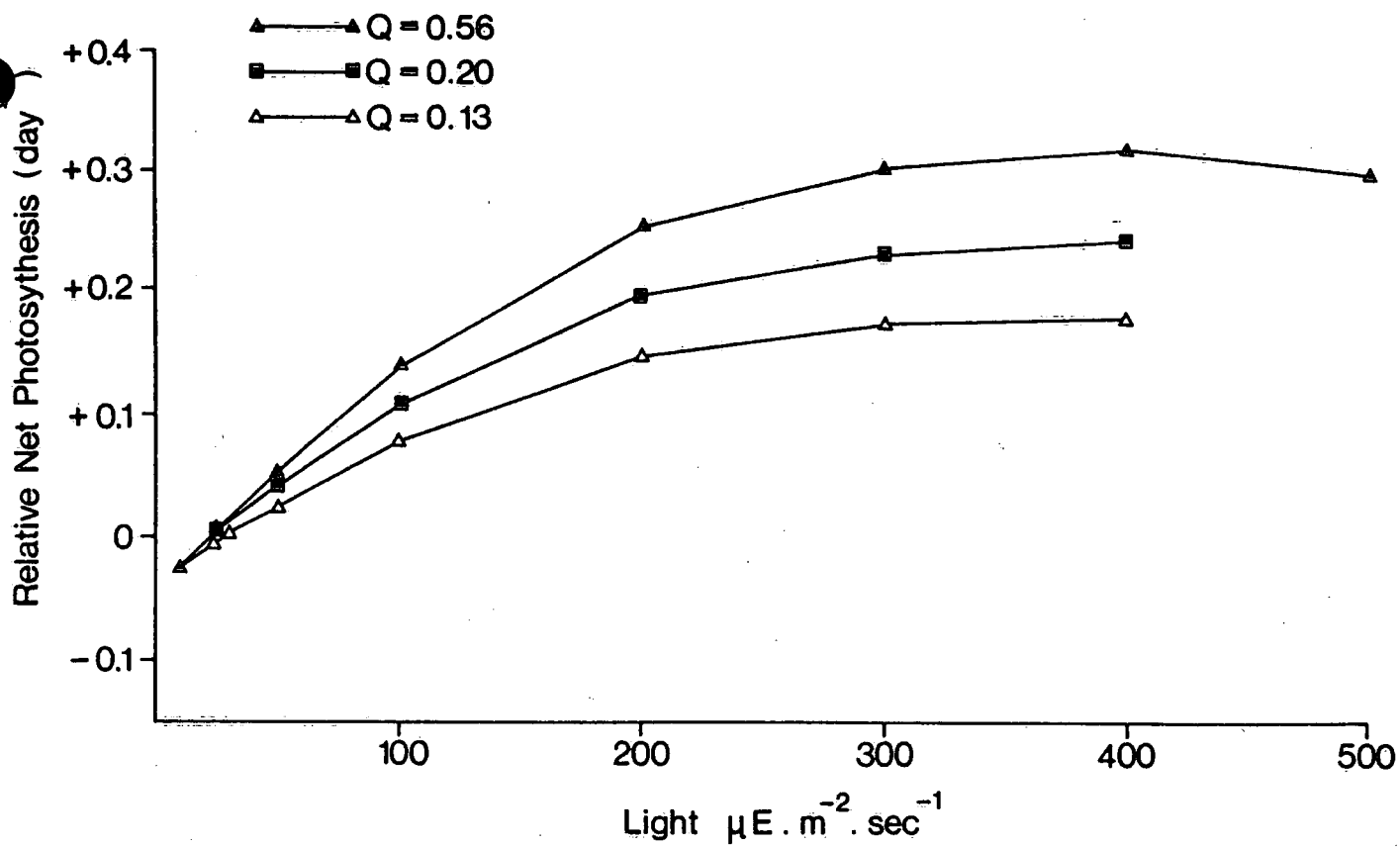
HAMILTON HARBOUR

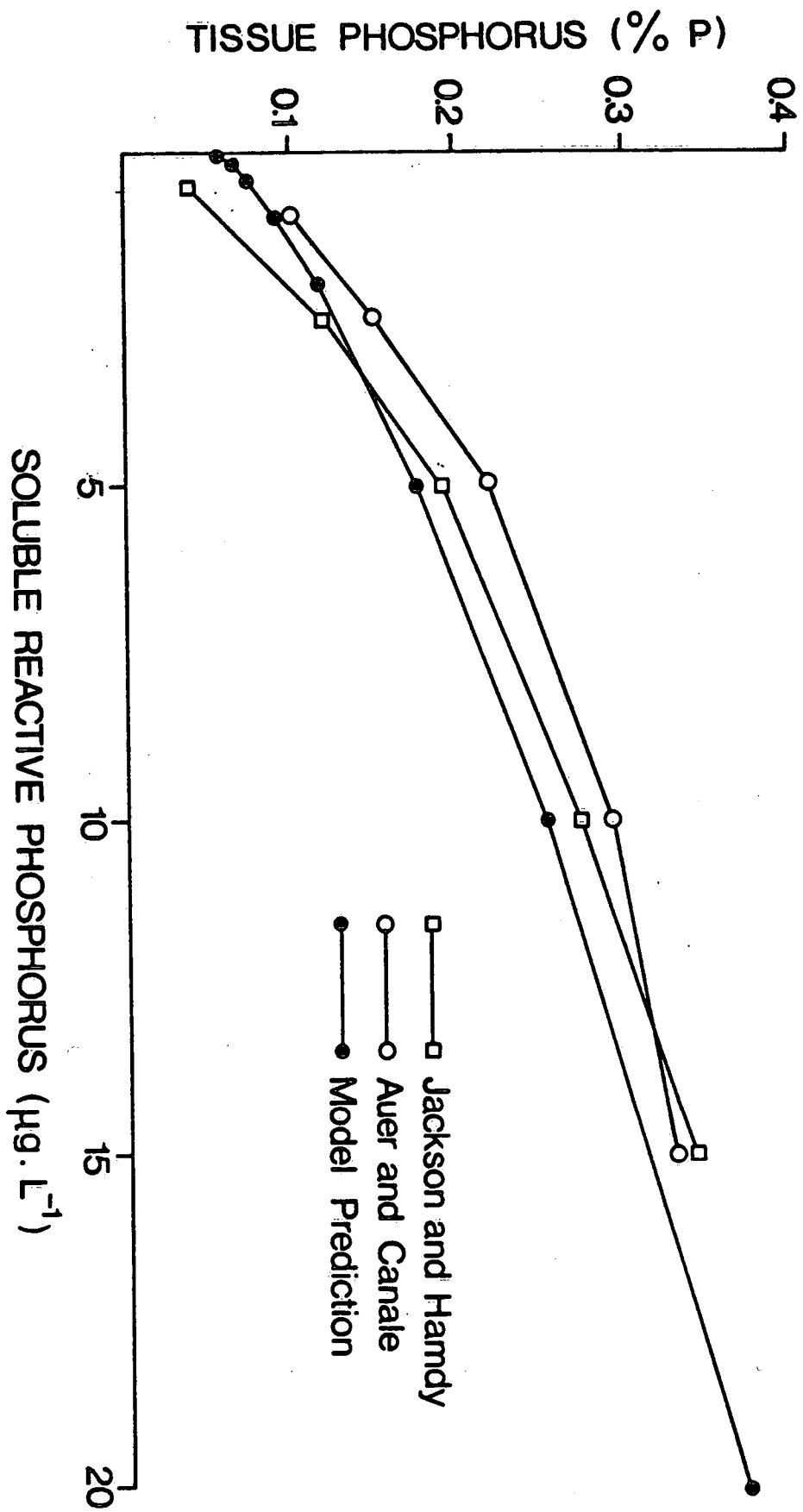
RATHFON POINT

JORDAN HARBOUR

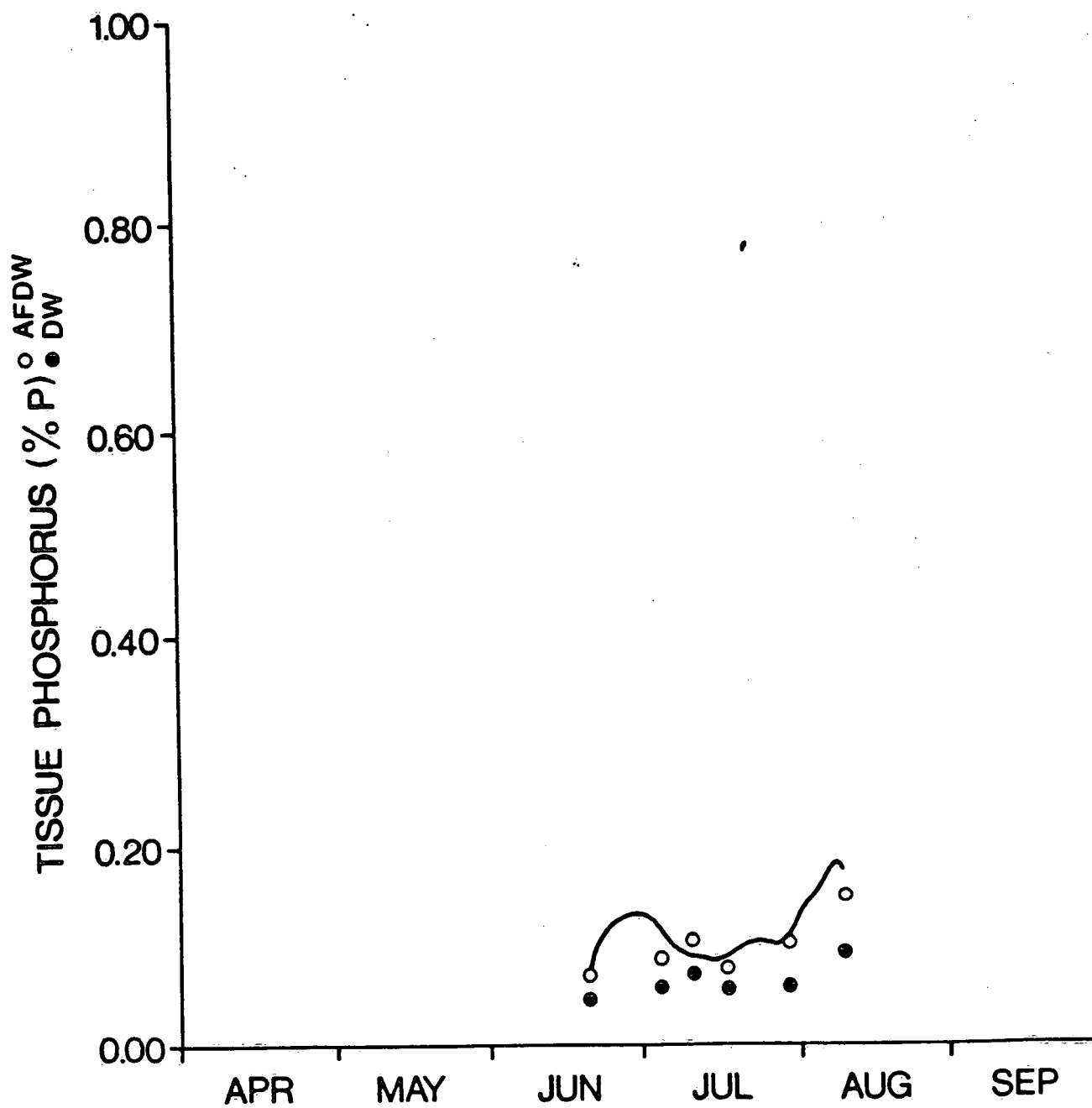
LAKE ERIE



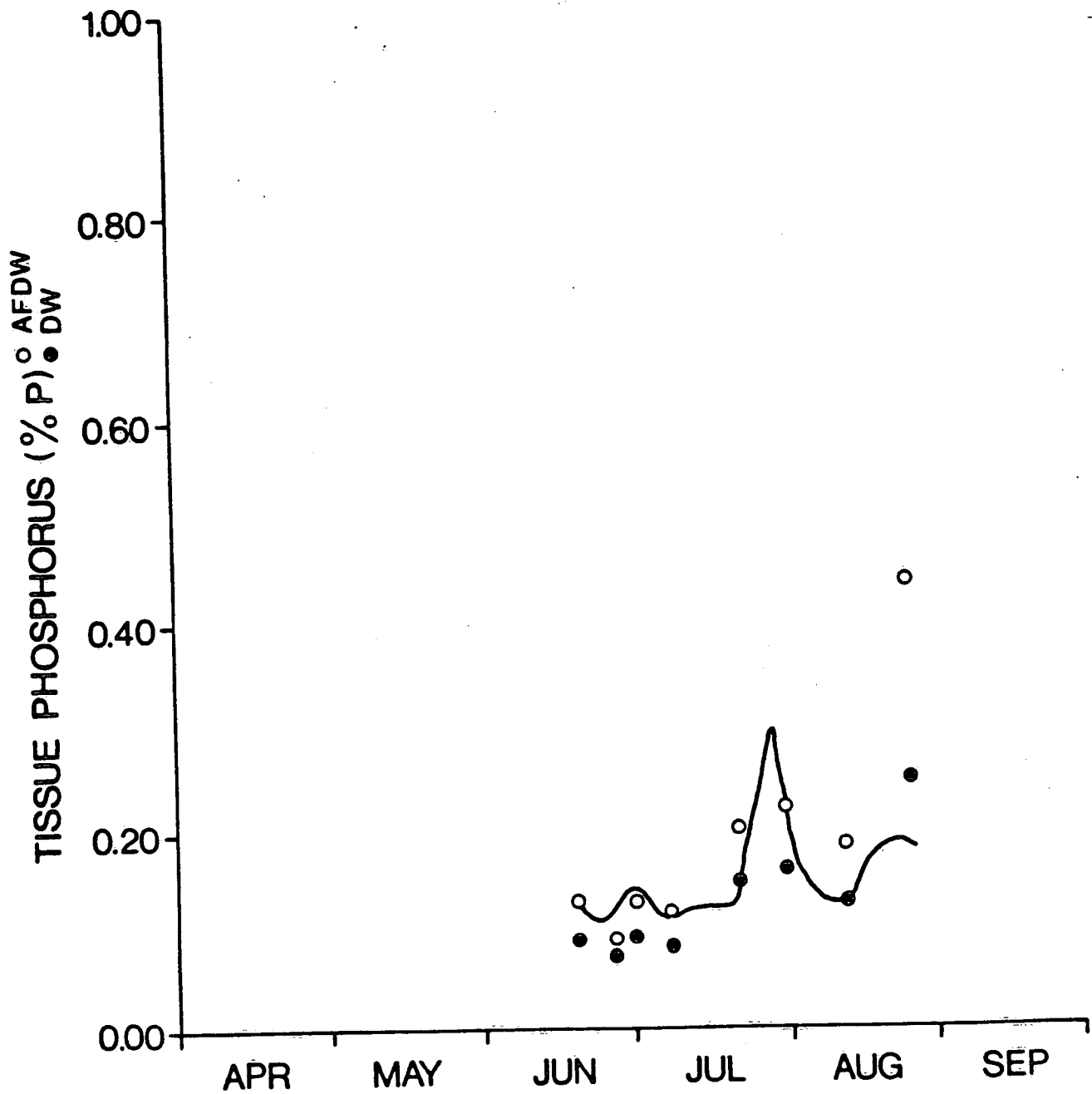




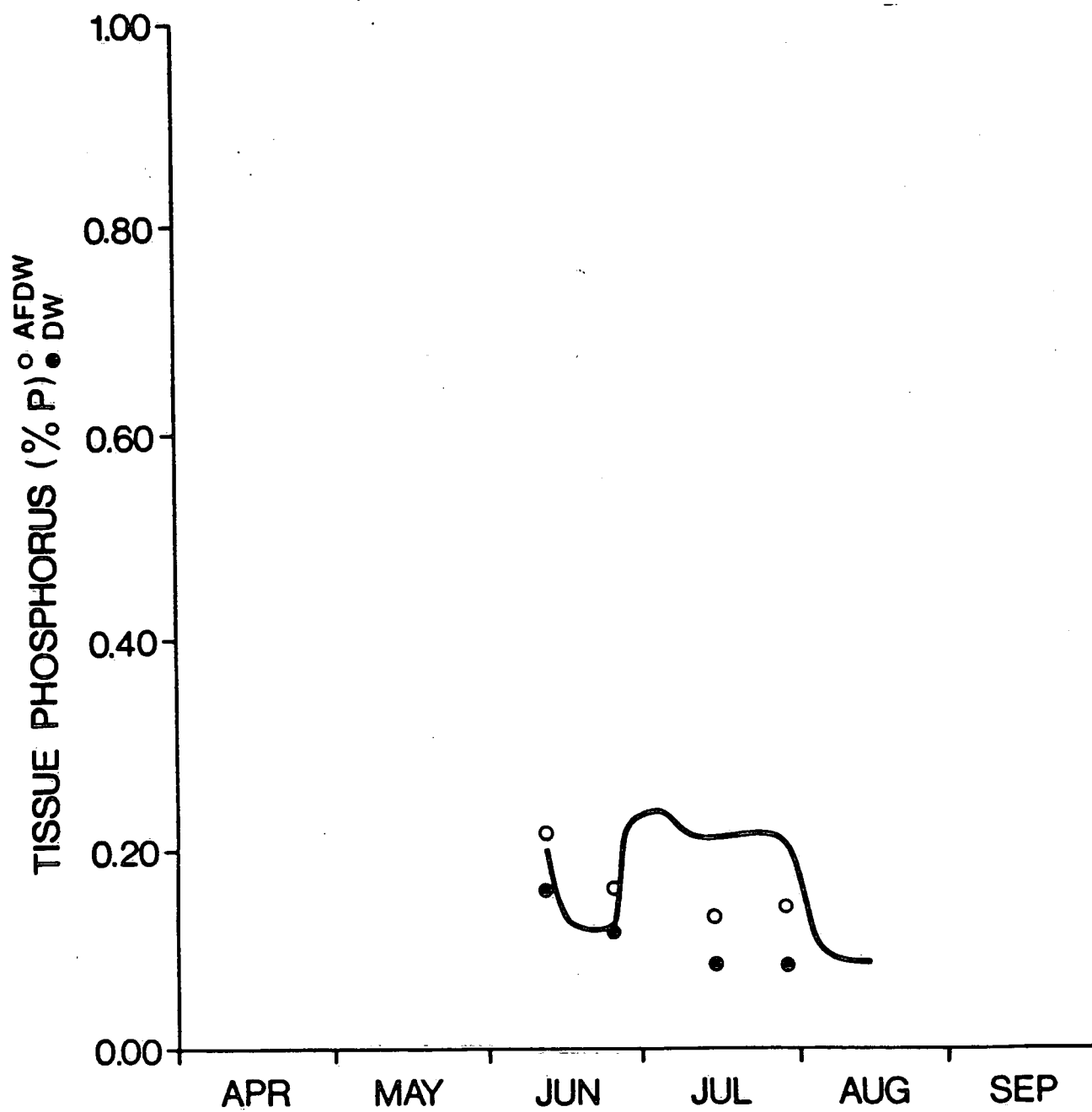
RATHFON 1.0m 1979



RATHFON 1980 1.0m



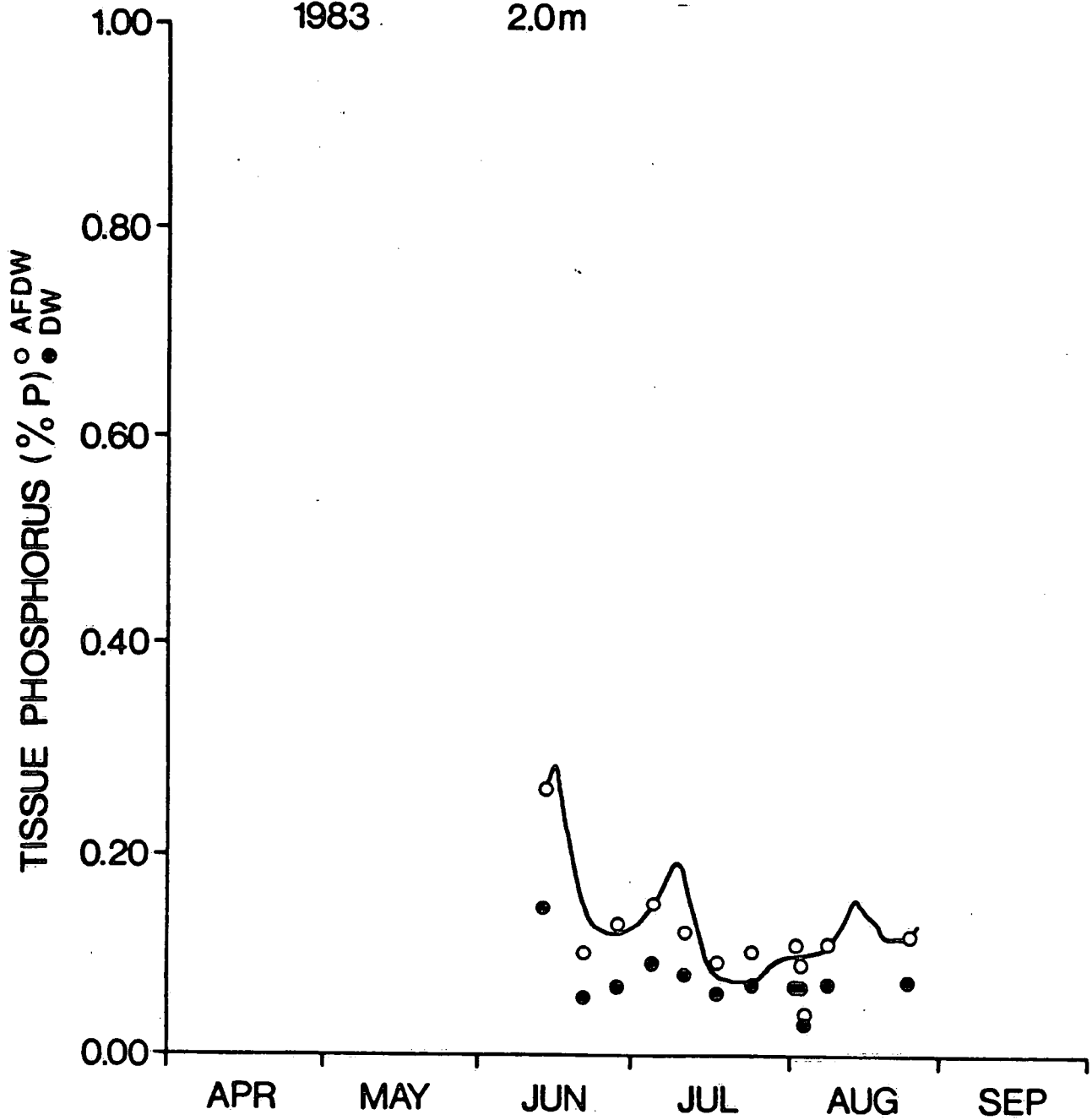
LAKE ERIE 1985 Rathfon



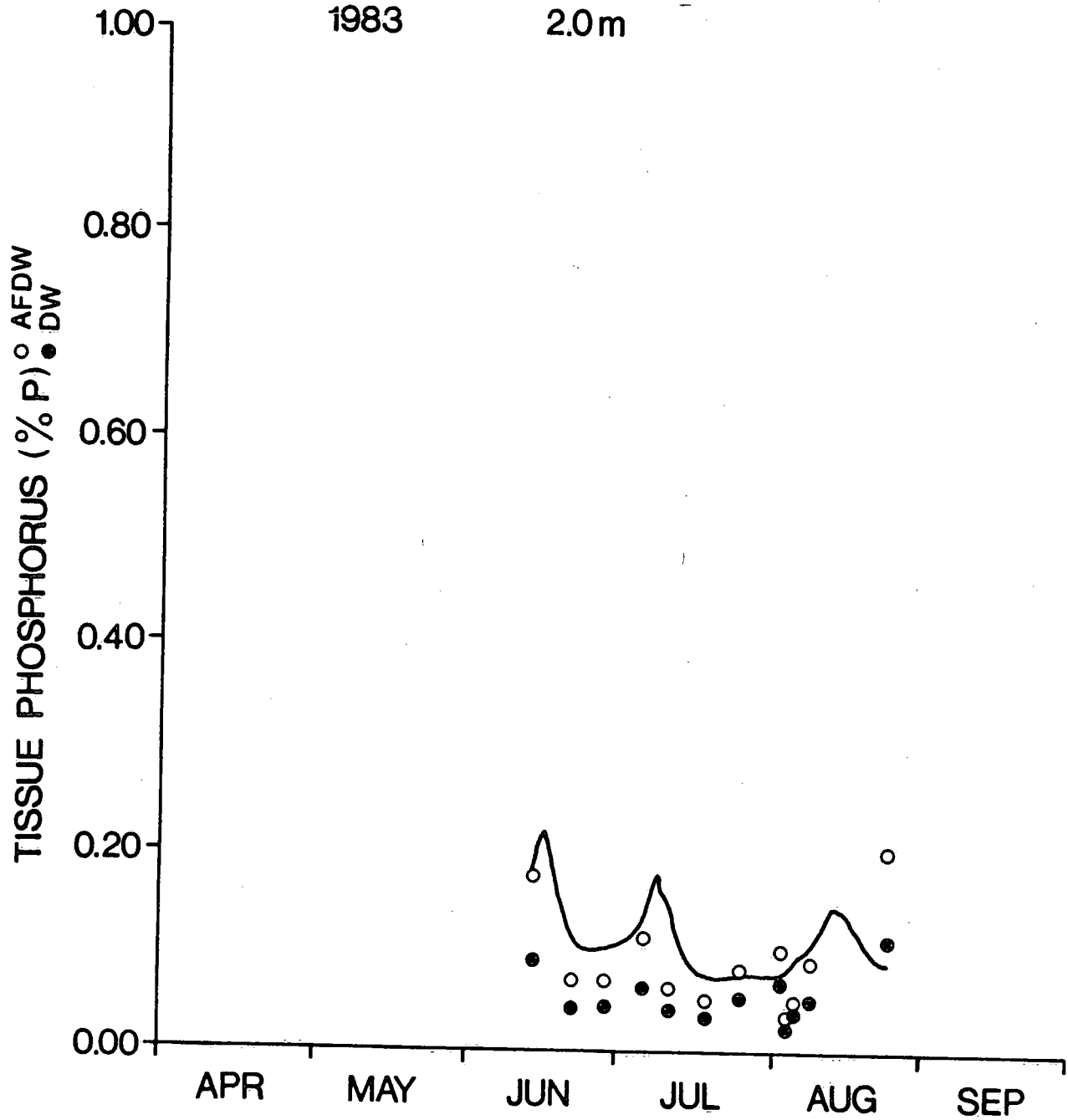
JORDAN SHORE No. 1

1983

2.0m

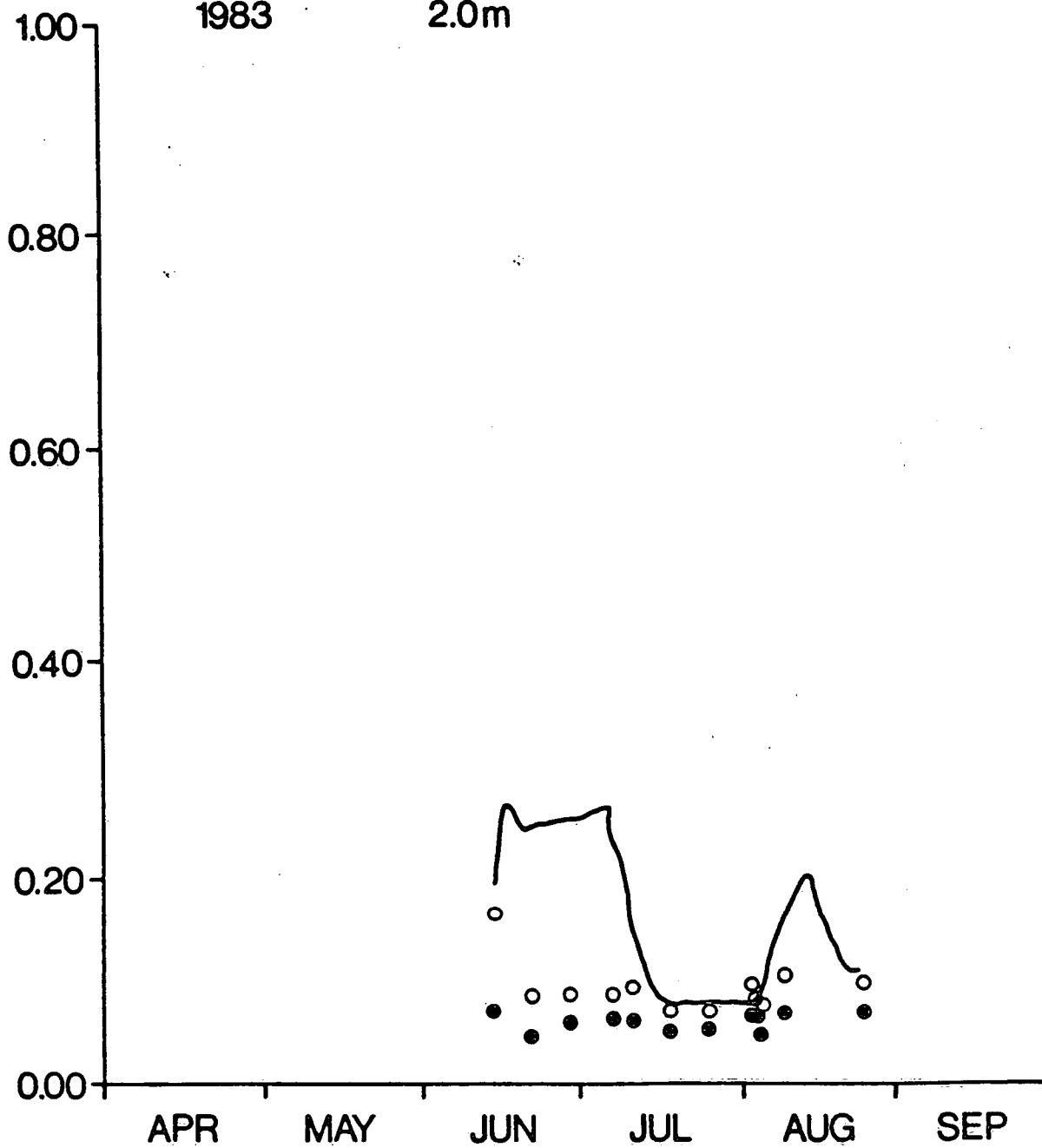


JORDAN SHORE No. 2
1983 2.0m



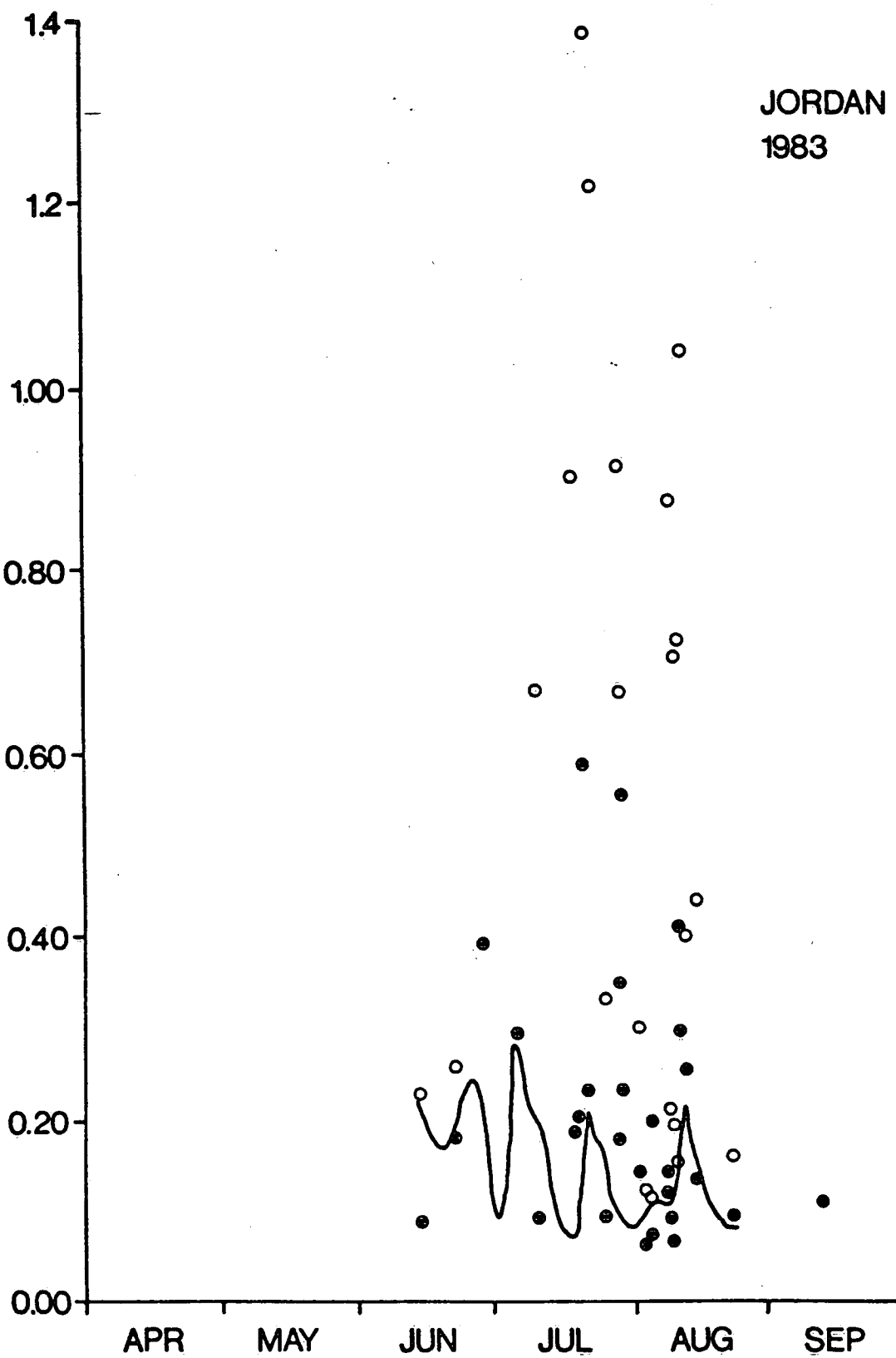
1983

TISSUE PHOSPHORUS (% P) • AFDW • DW

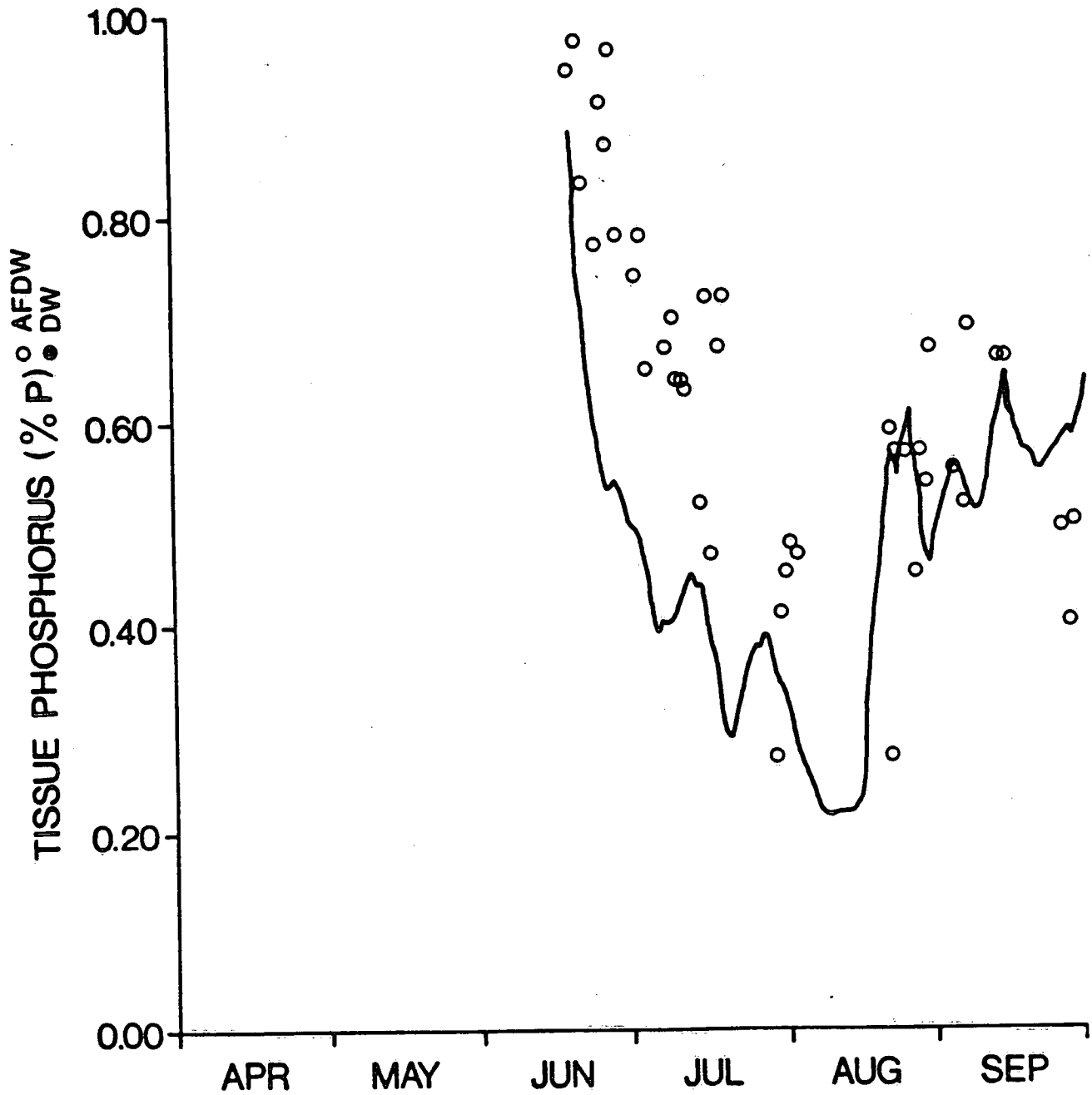


TISSUE PHOSPHORUS JS (% P) \circ AFDW \bullet DW

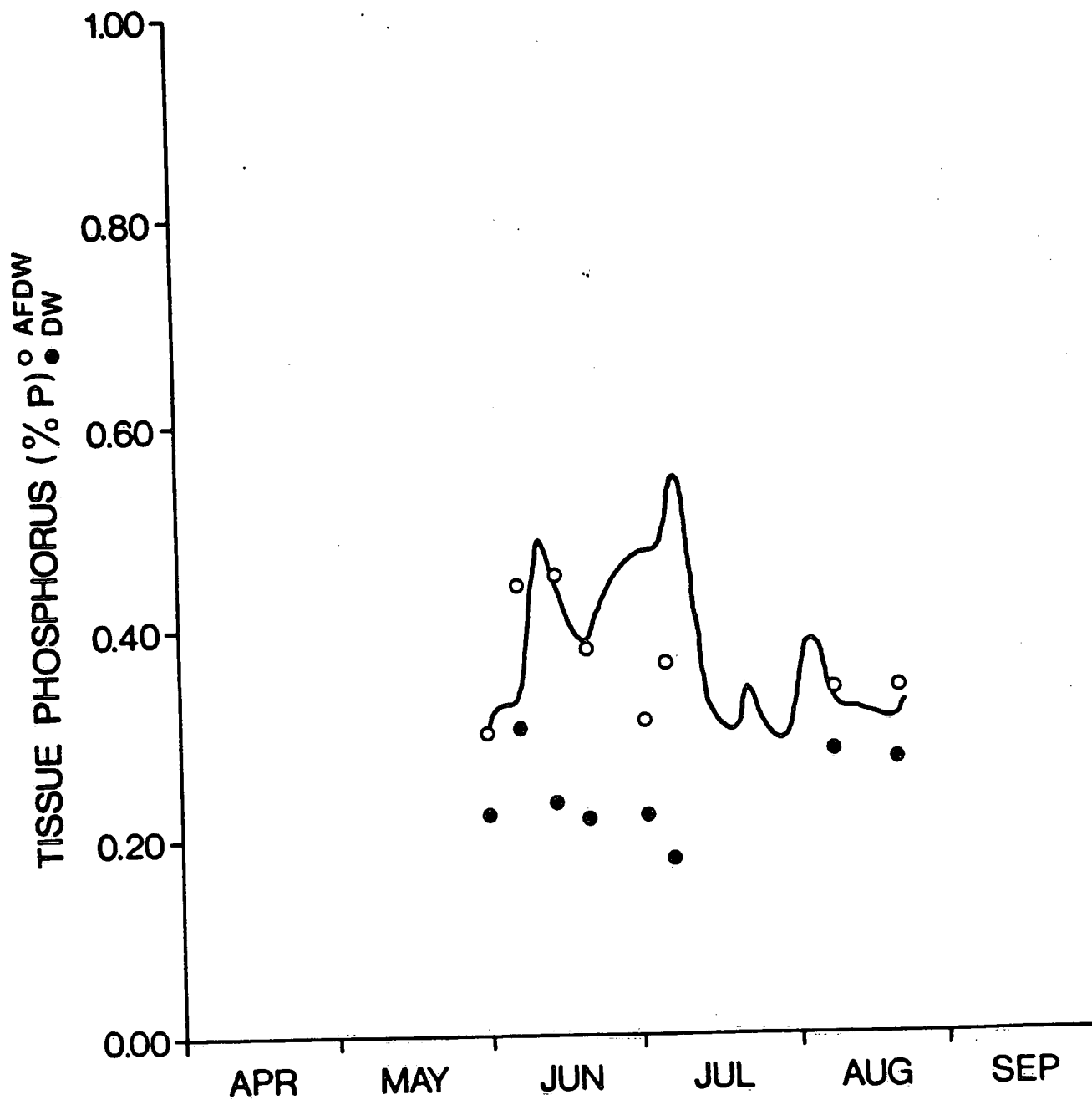
JORDAN HARBOUR MOUTH
1983 0.25m



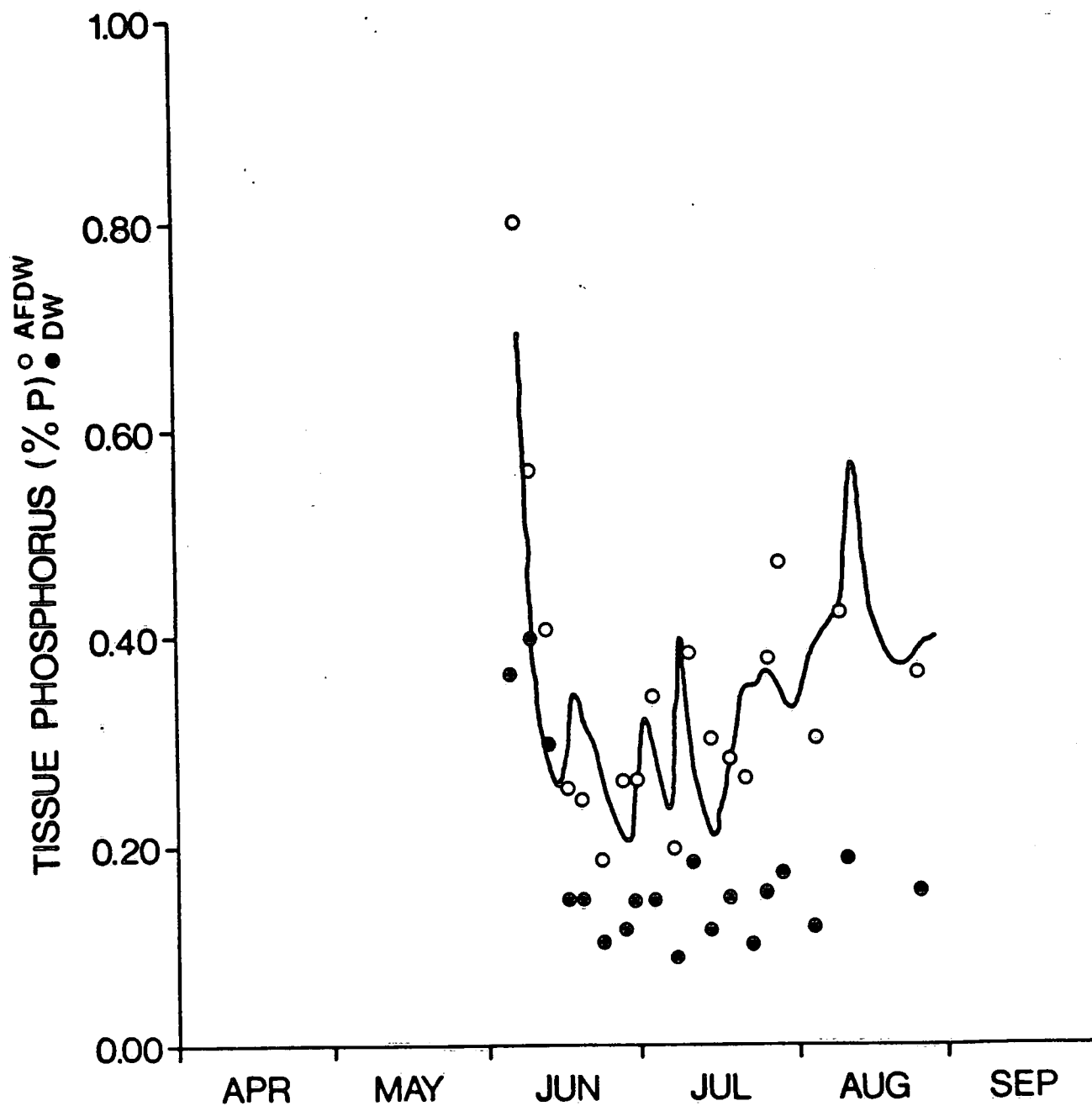
HAMILTON HARBOUR
0.0m



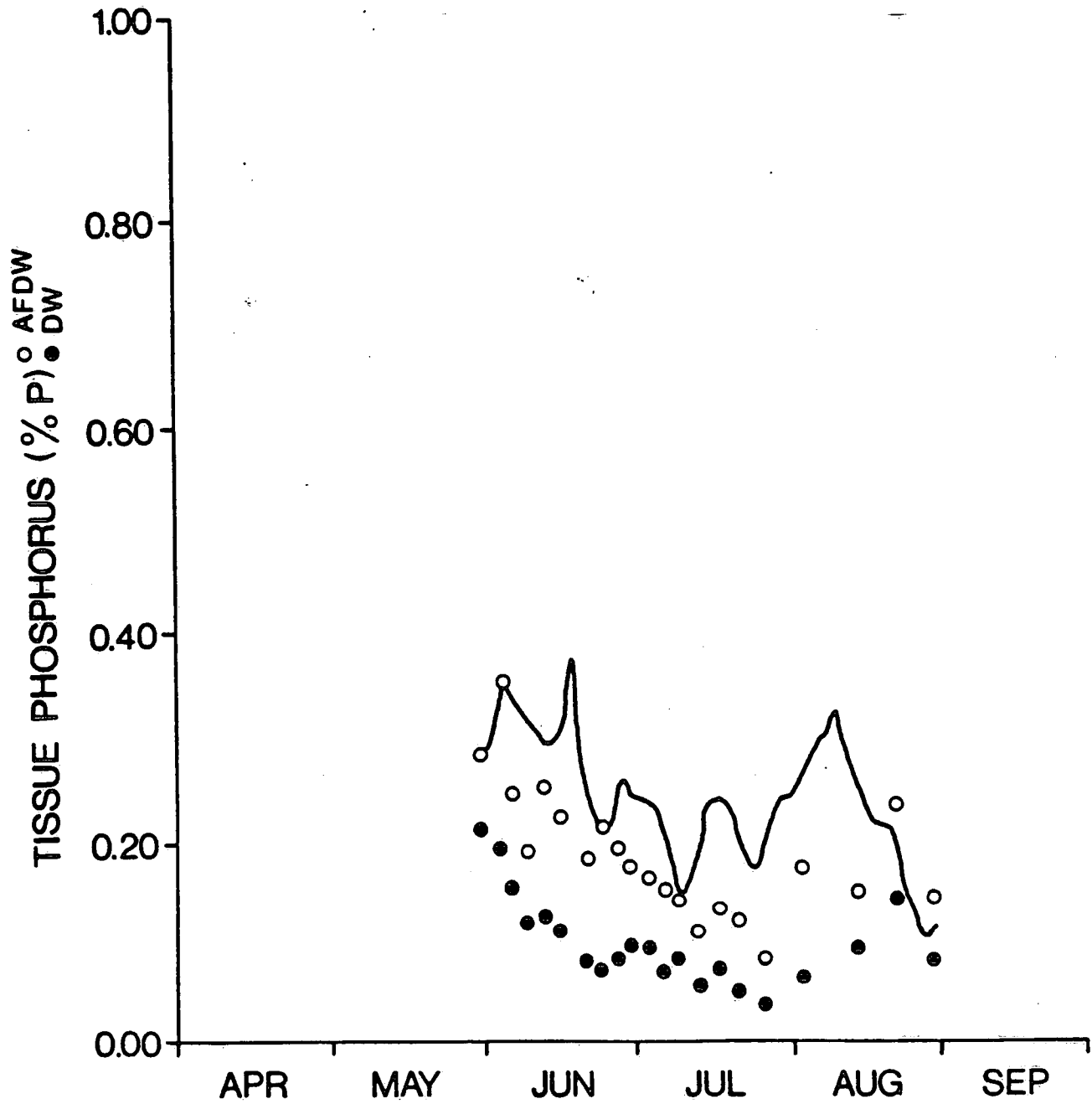
OAKVILLE 1981 0.5m



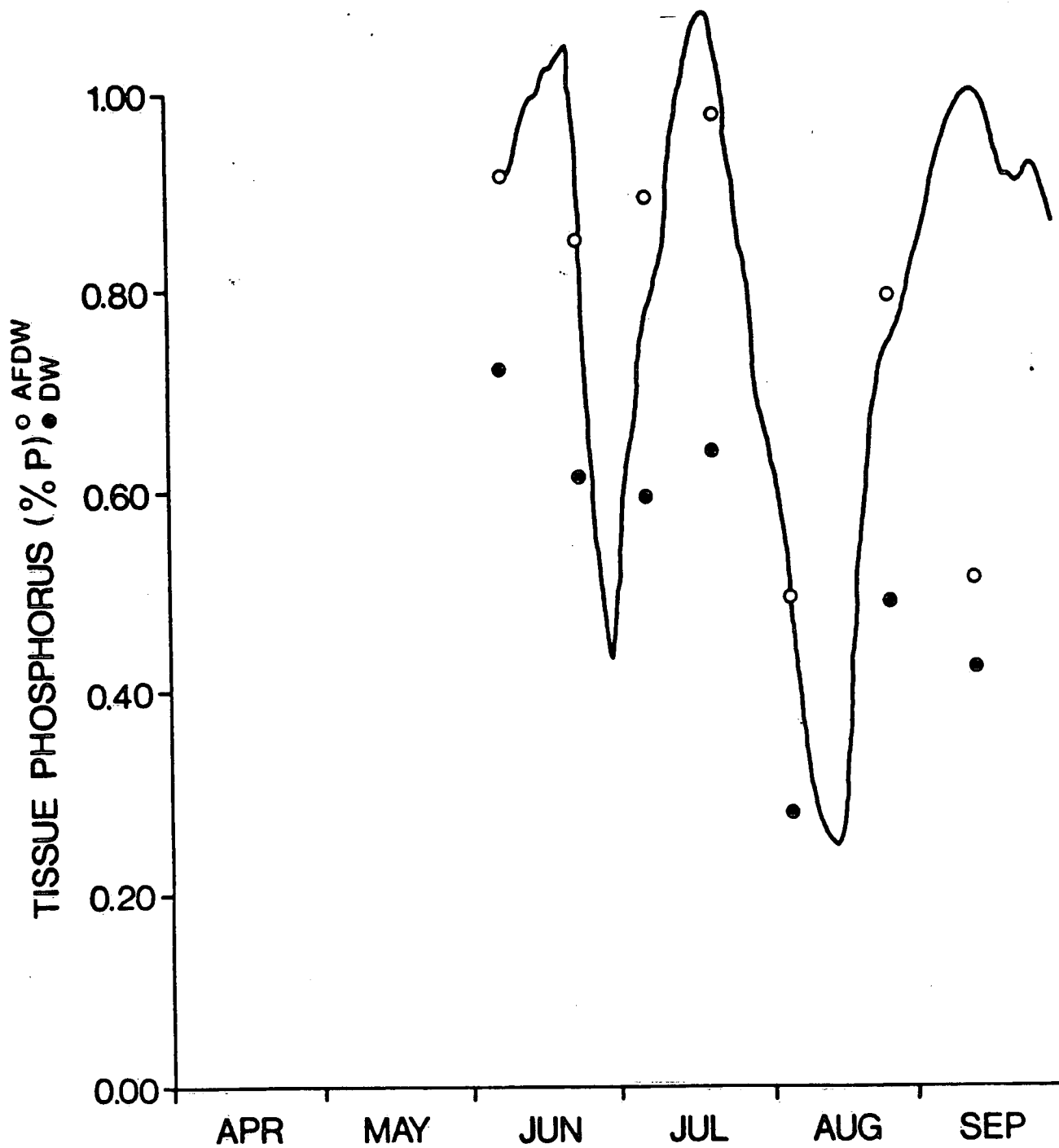
OAKVILLE 1982 0.5m



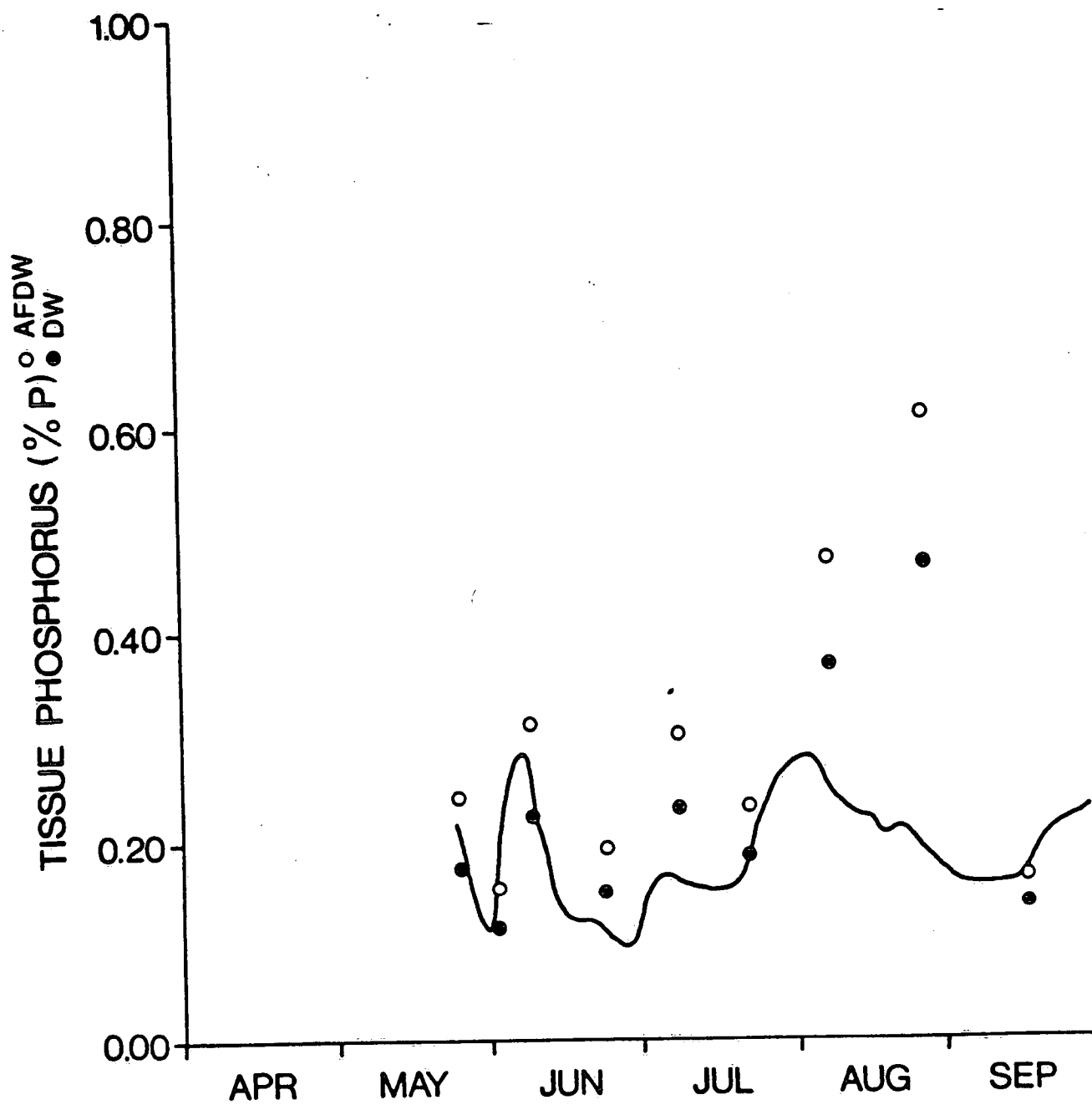
OAKVILLE 1983 0.5 m



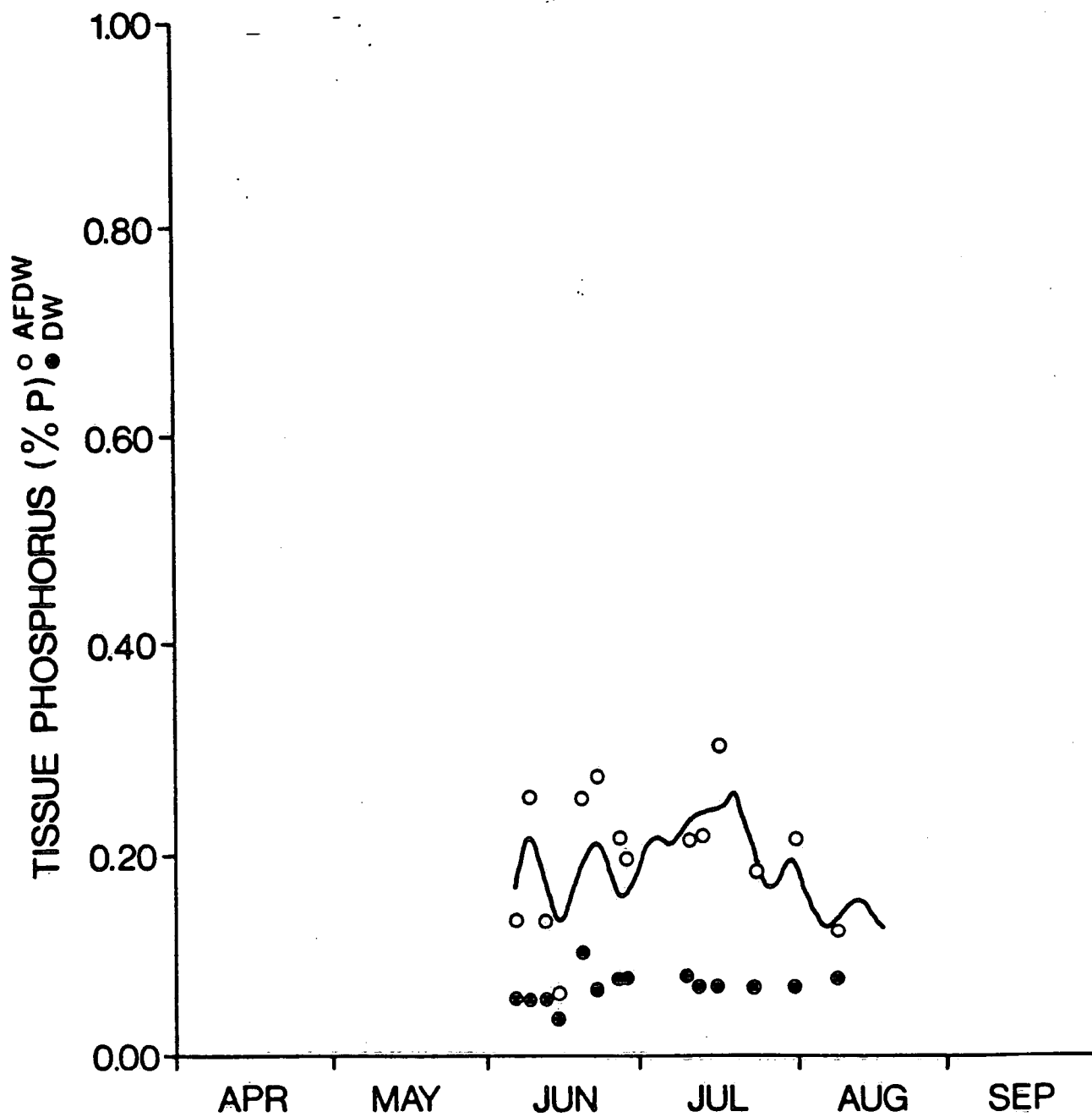
HUMBER RIVER 1980 0.5 m



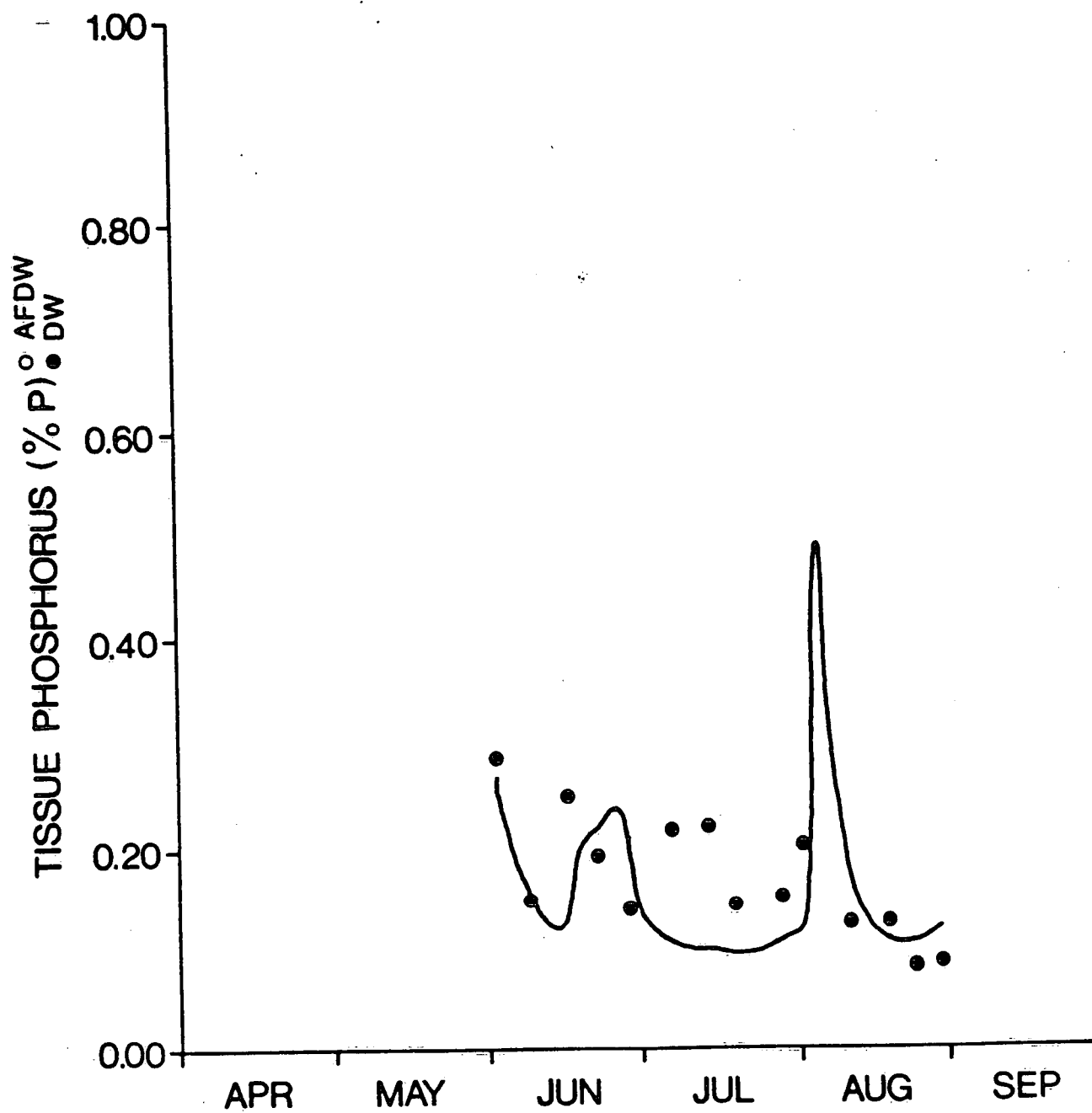
BLUFFERS PARK 1980 0.2 m



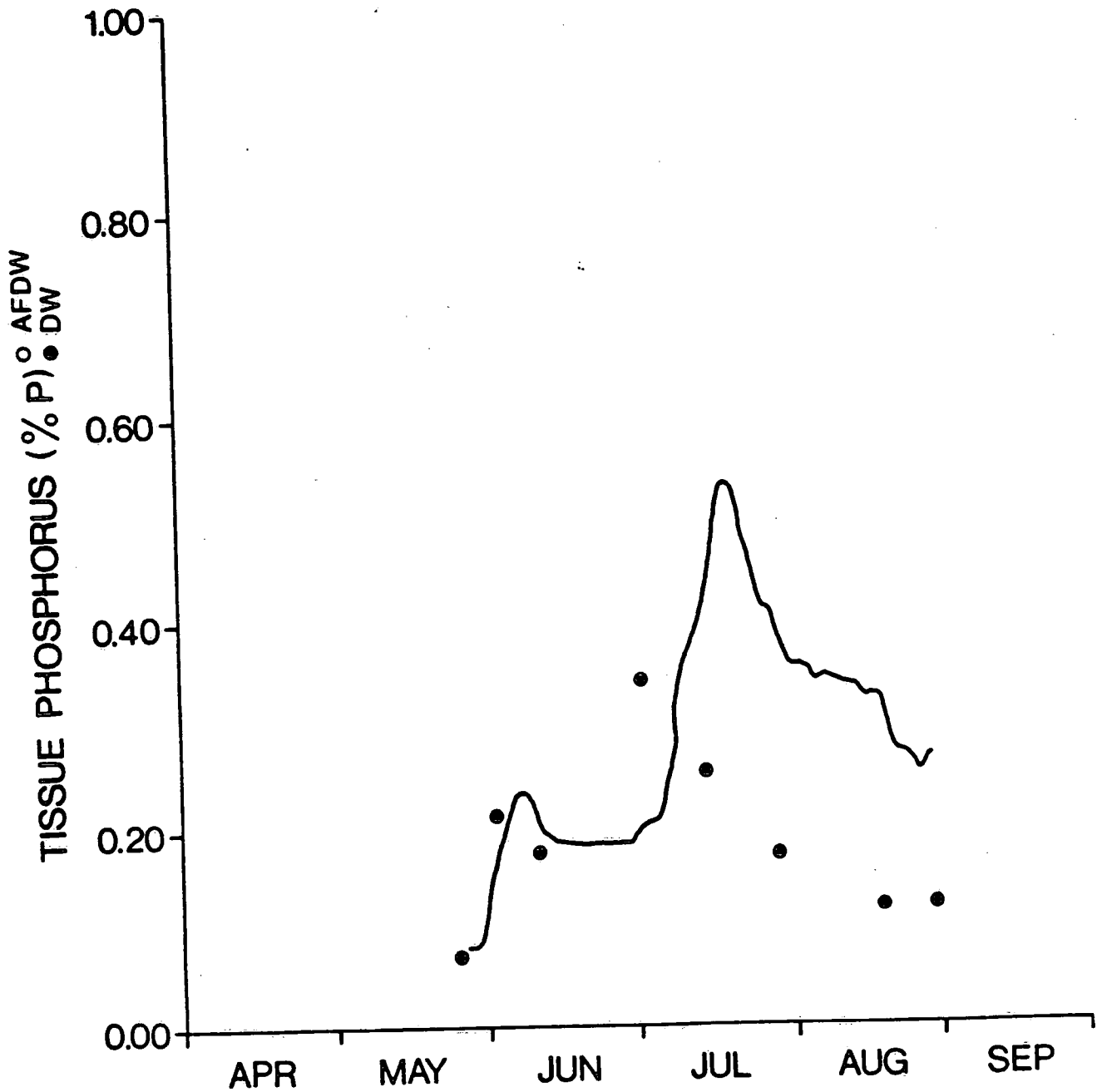
POINT PETRE 1983 1.5m



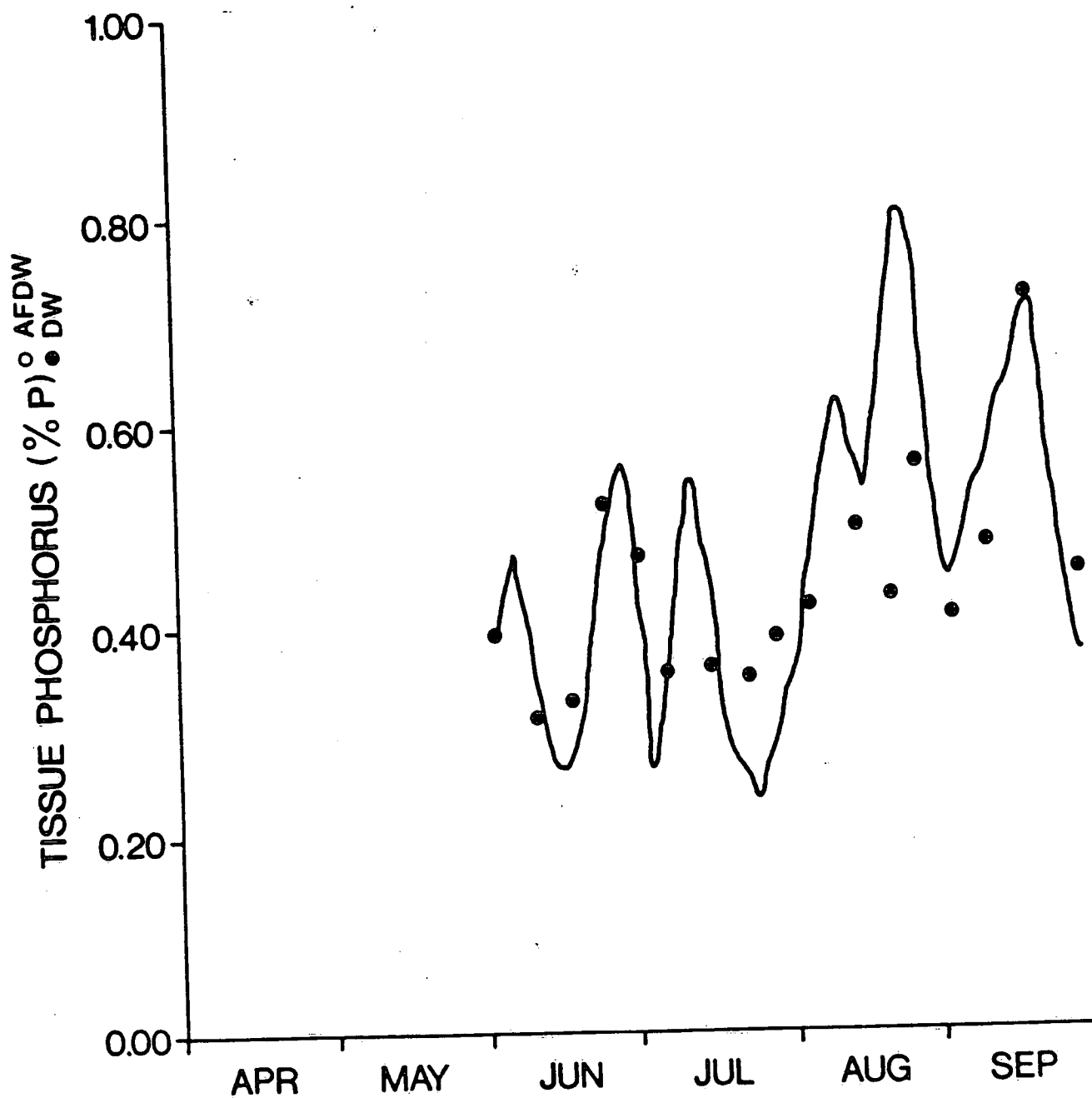
LAKE SIMCOE 1976 0.5m



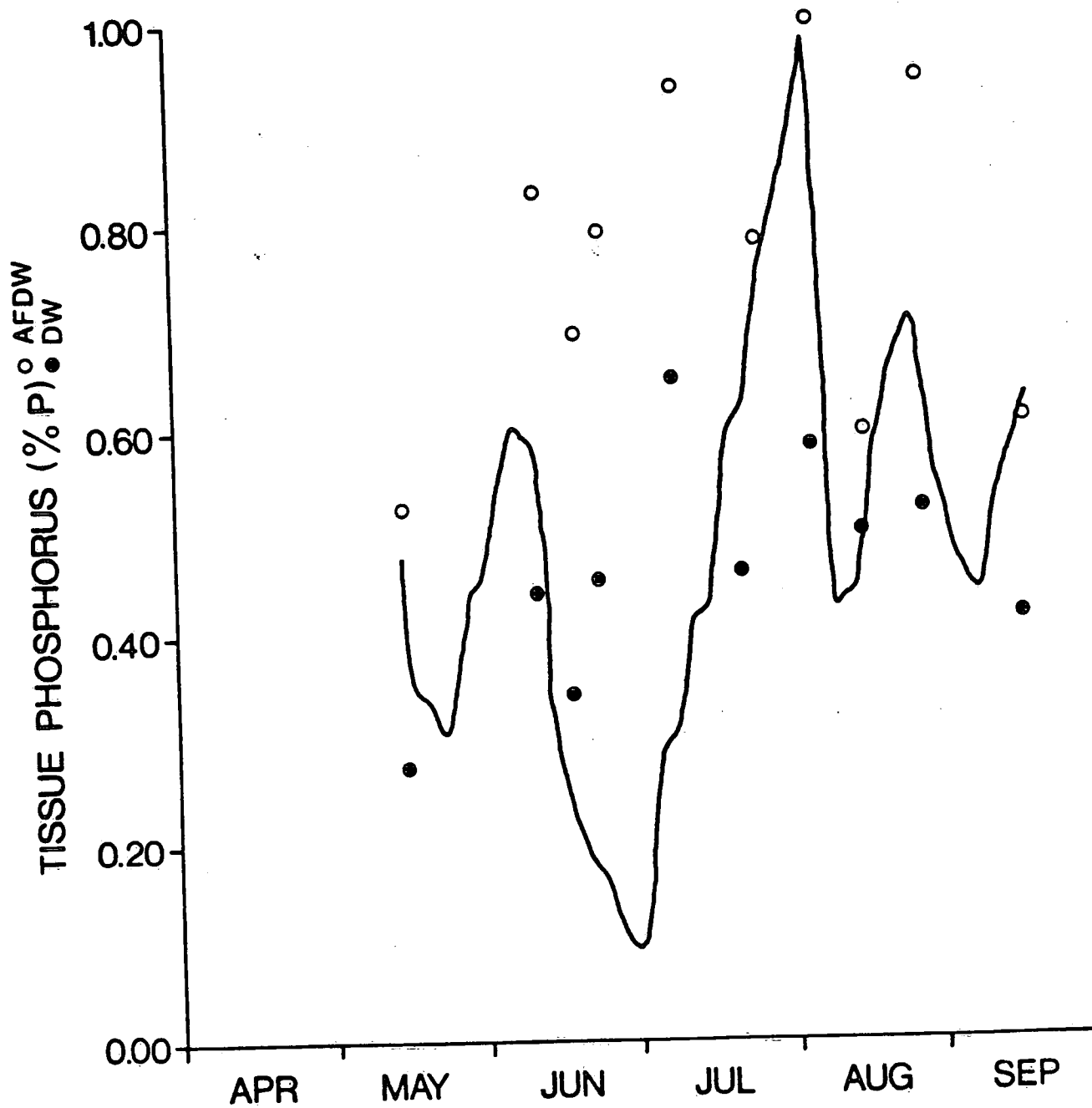
LAKE SIMCOE 1980 0.5 m



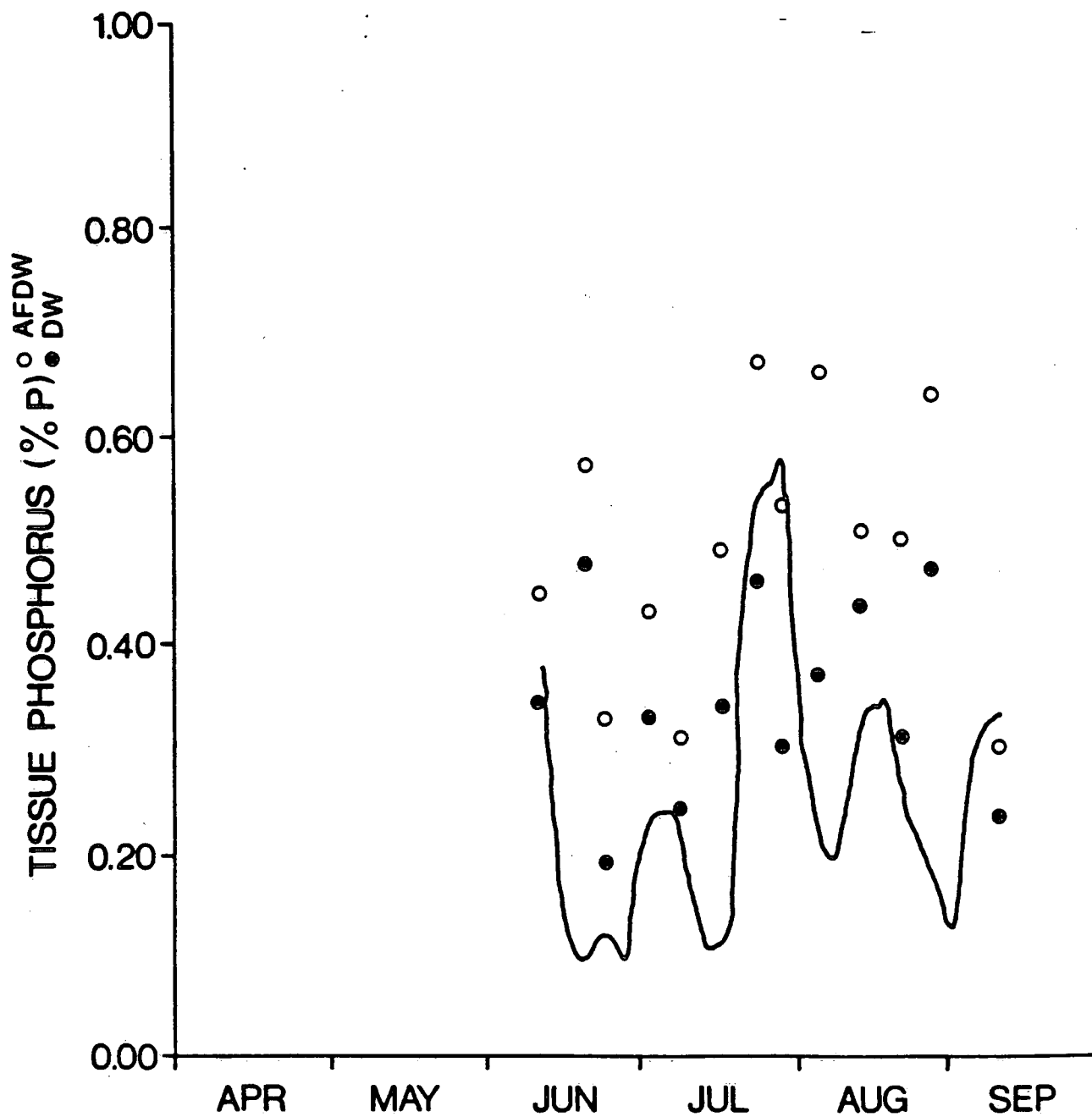
COLLINGWOOD HARBOUR CTB 1979



COLLINGWOOD HARBOUR CTB 1980

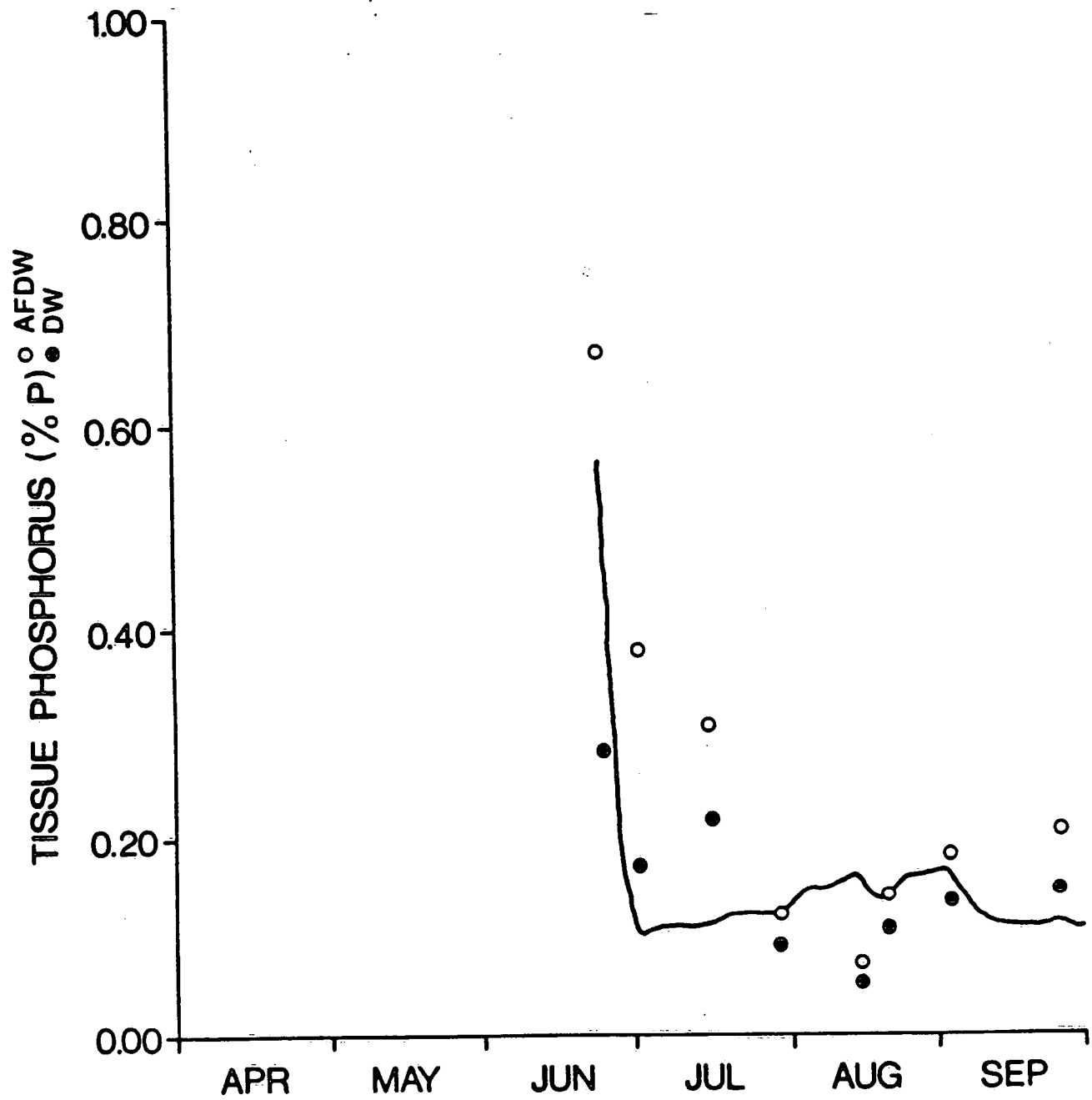


COLLINGWOOD MOUTH CTI 1980 DEPTH 0.2m

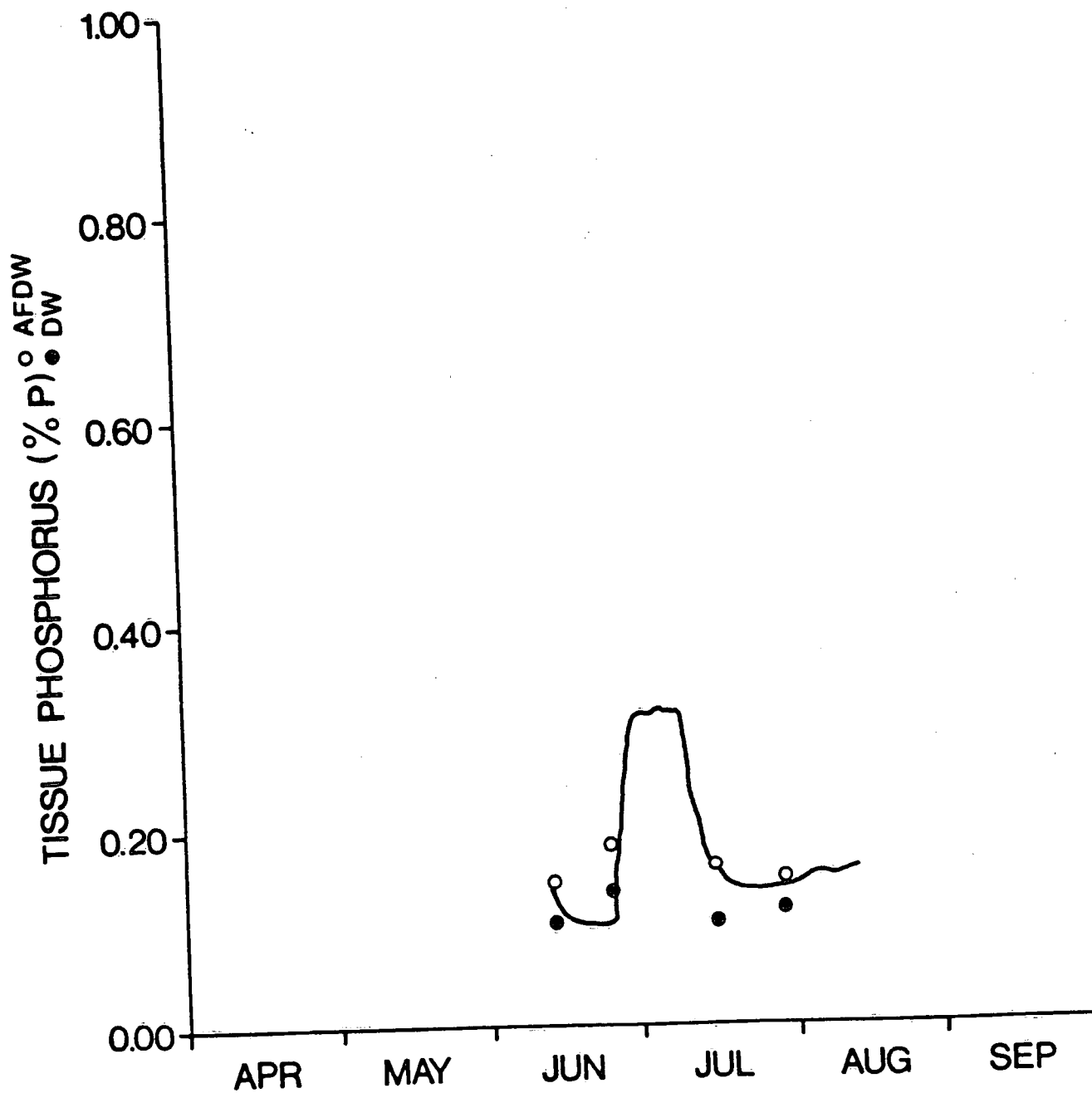


COLLINGWOOD SHOALS 1980

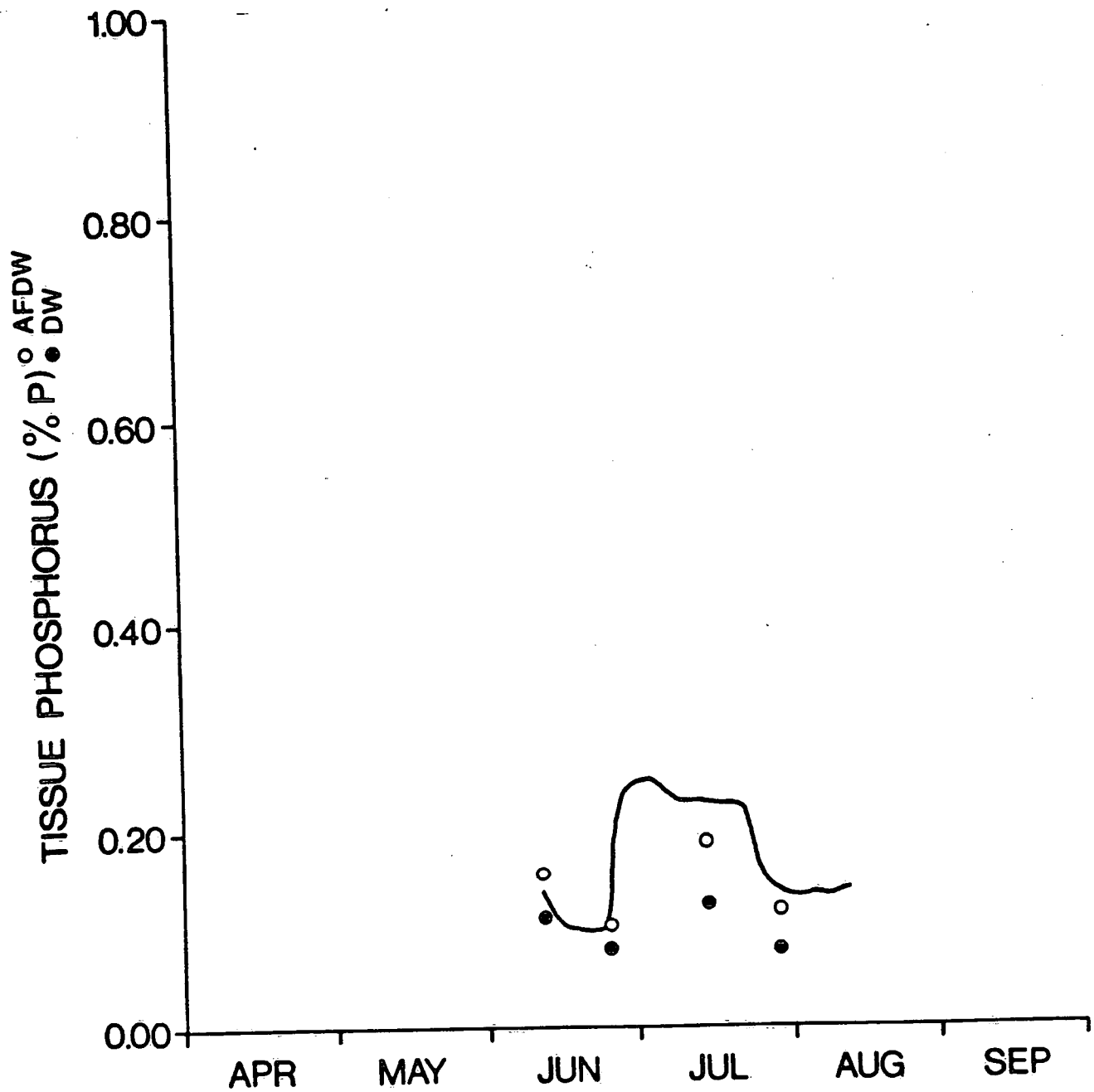
0.2m



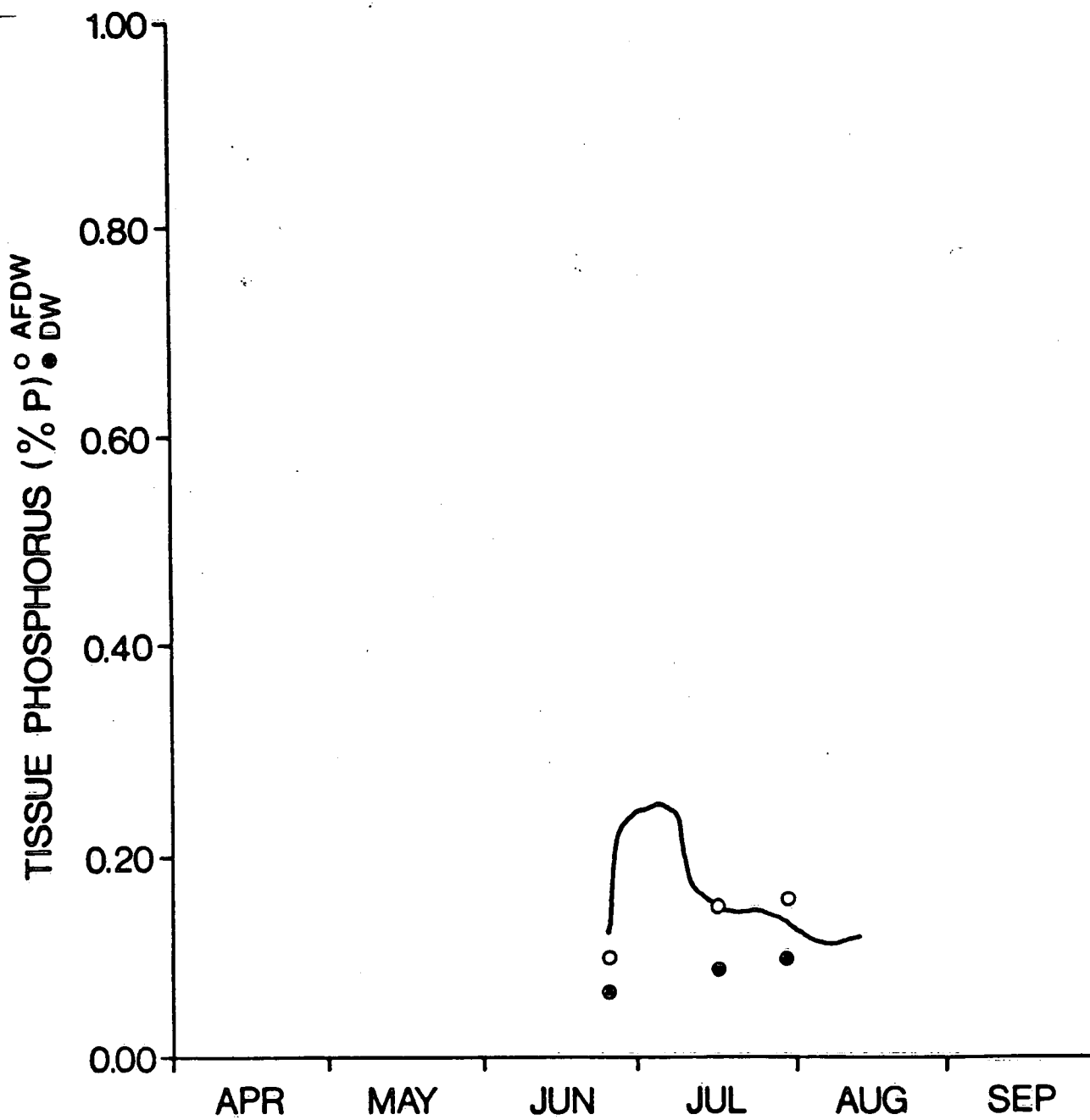
LAKE ERIE 1985 FEATHERSTONE



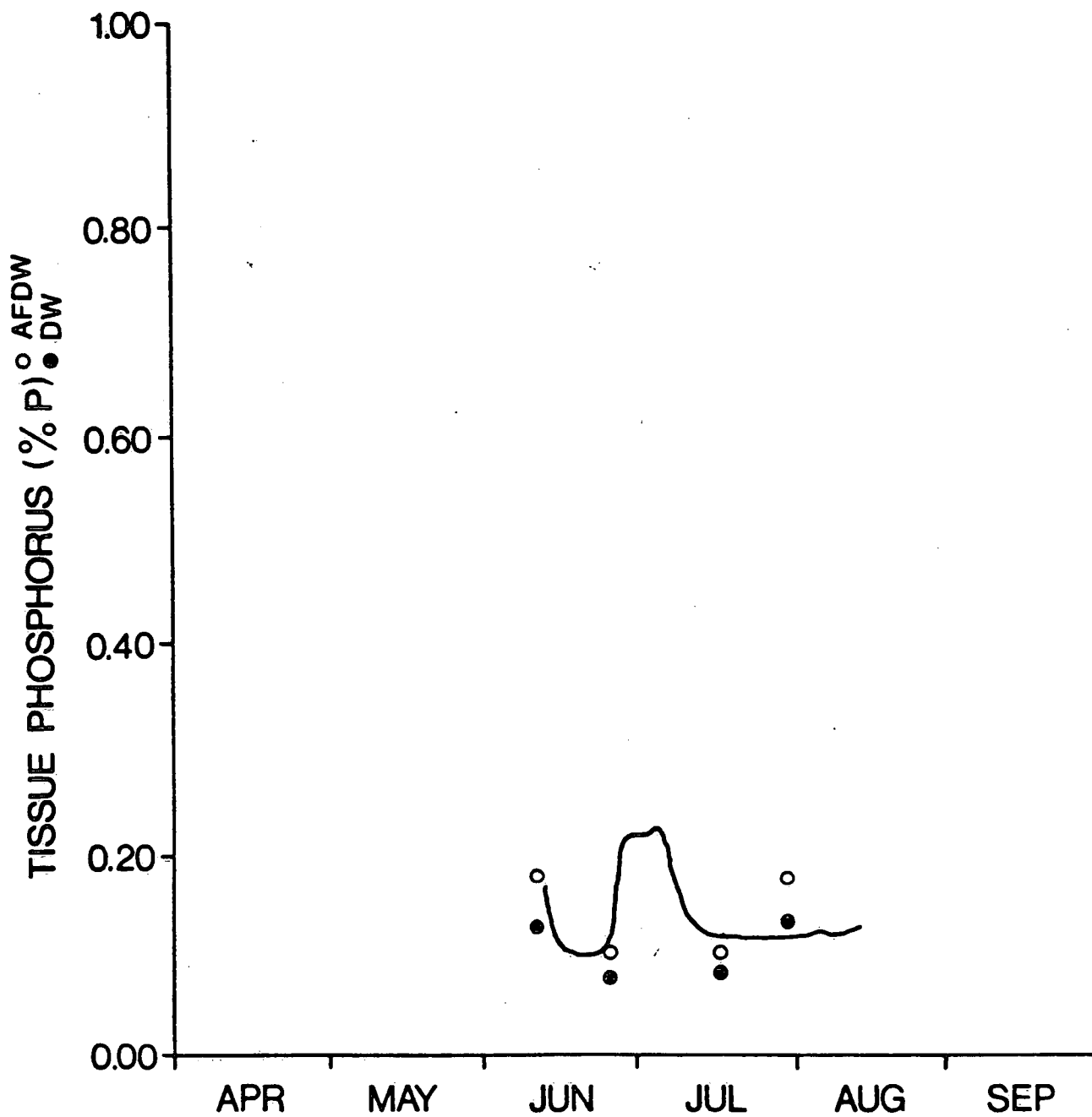
LAKE ERIE 1985 EVANS



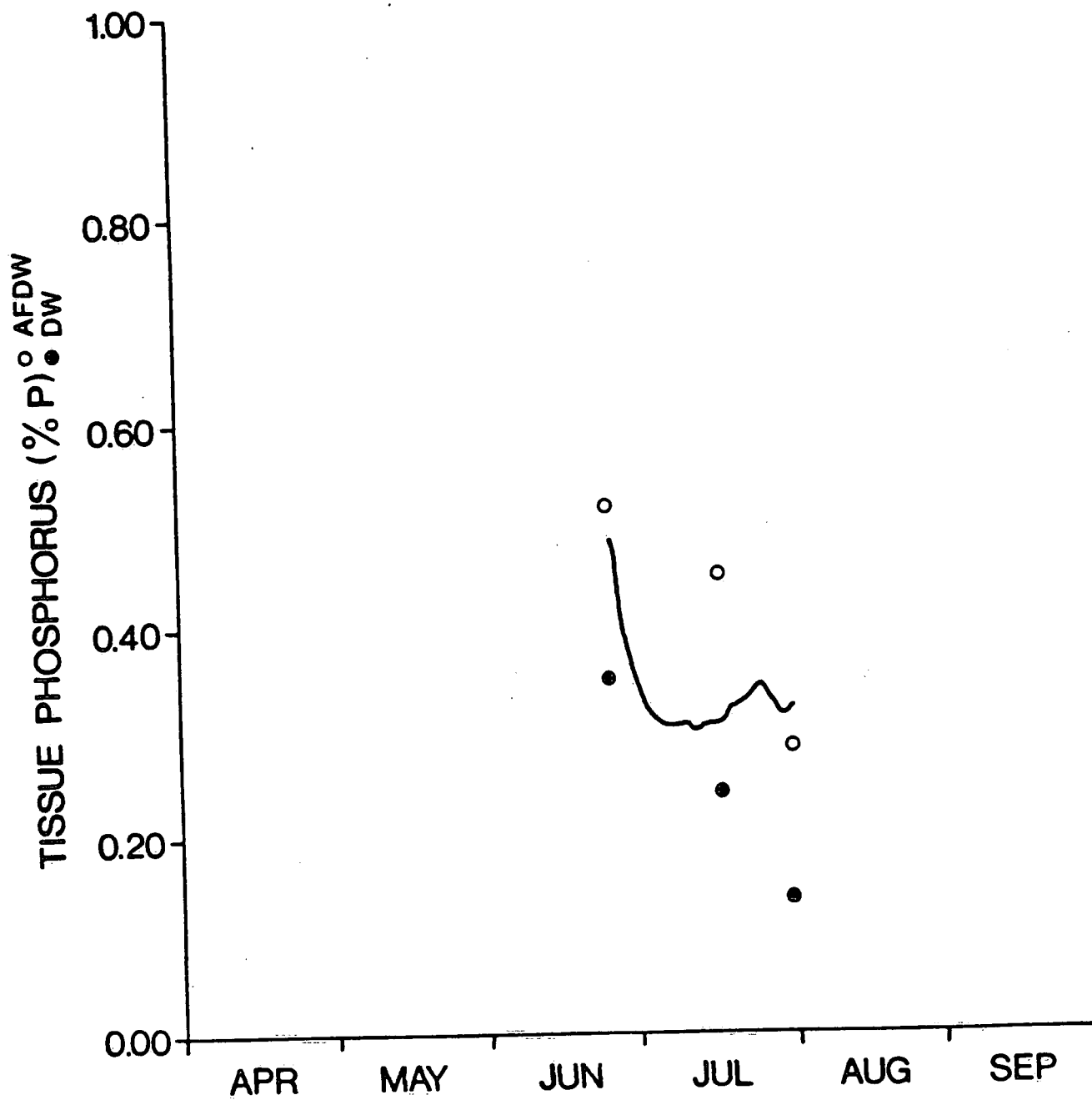
LAKE ERIE LOW 1985



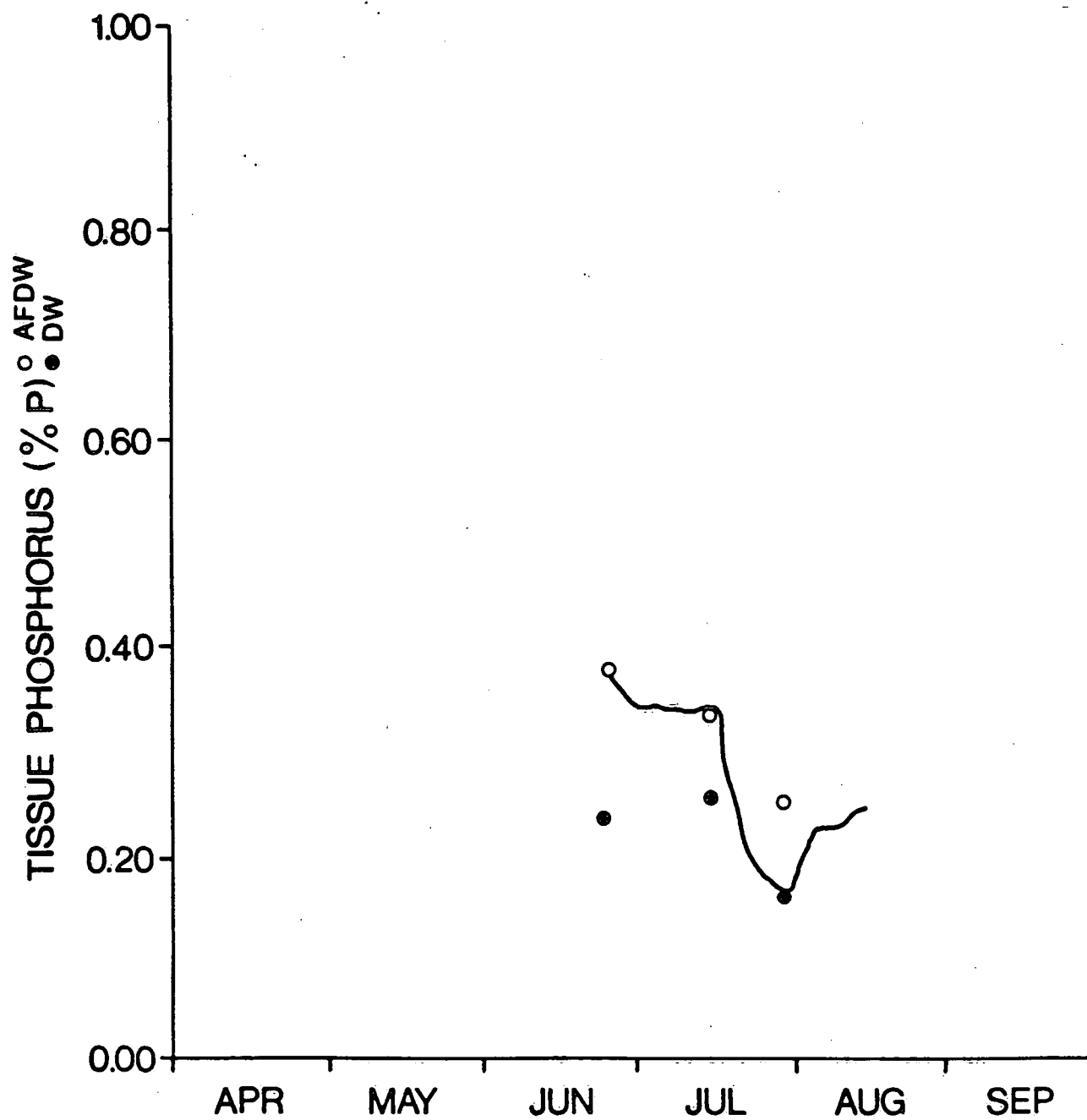
LAKE ERIE 1985 GRANT



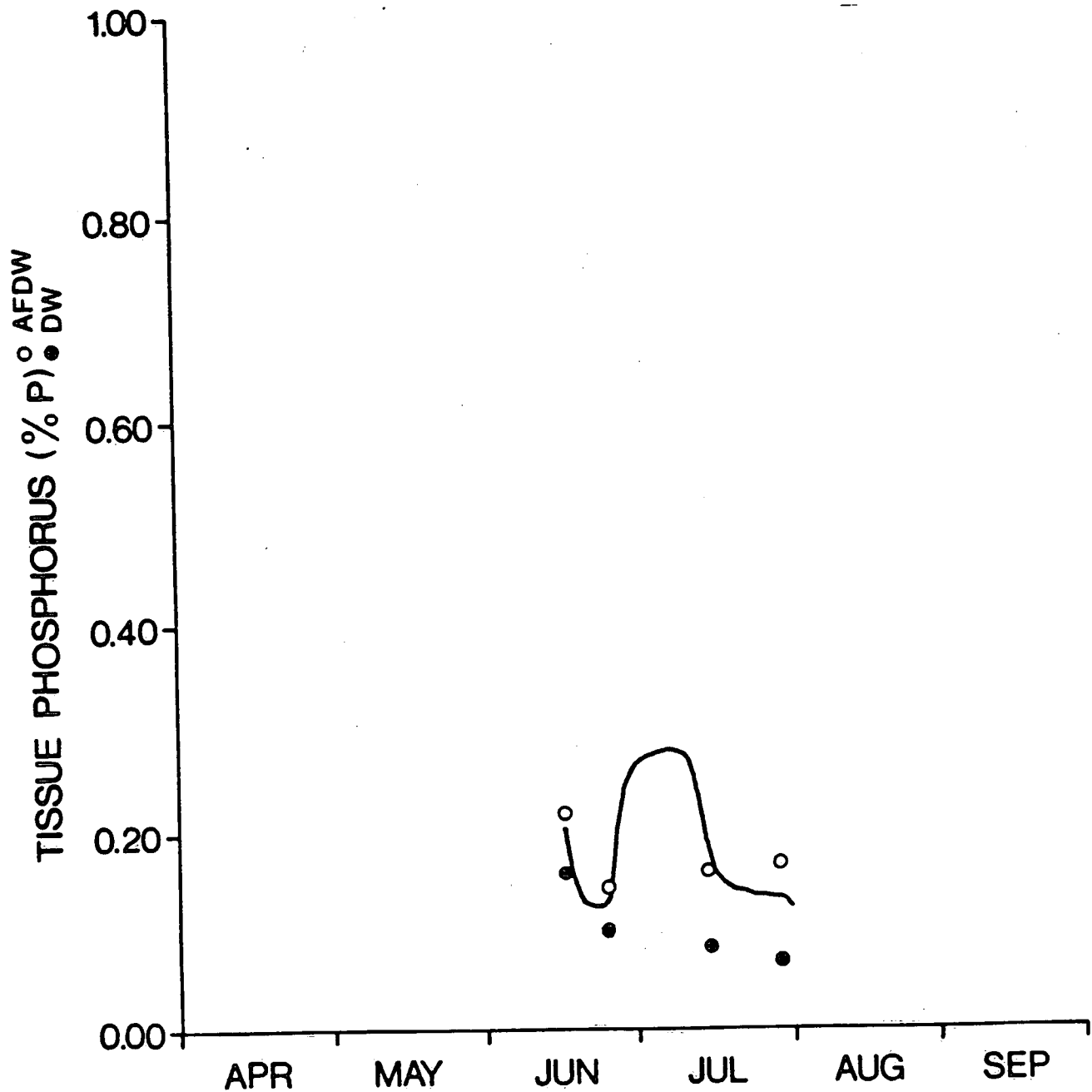
LAKE ERIE 1985 GRAND RIVER



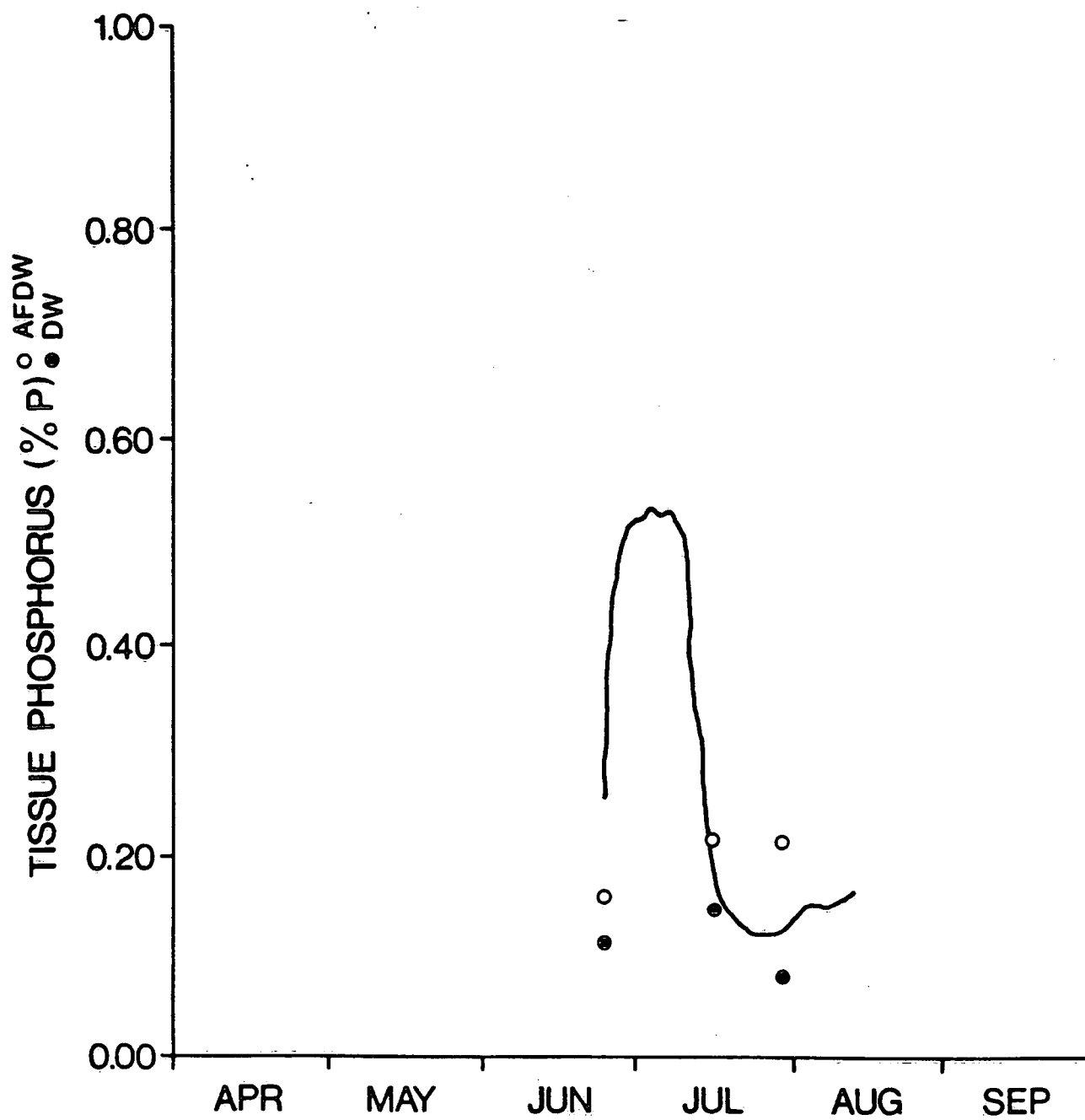
LAKE ERIE 1985 ROCK No. 2



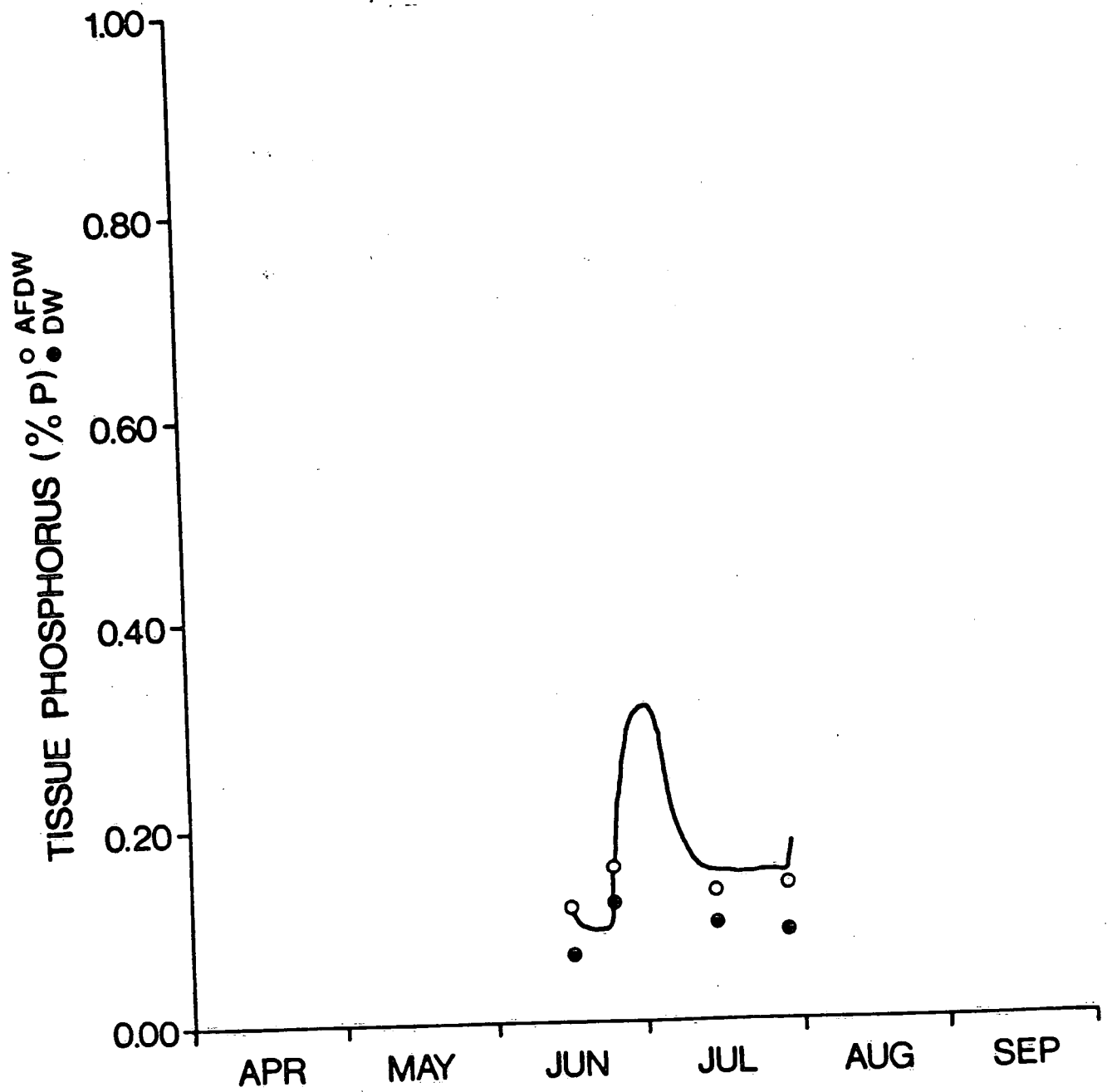
LAKE ERIE 1985 ROCK No.1



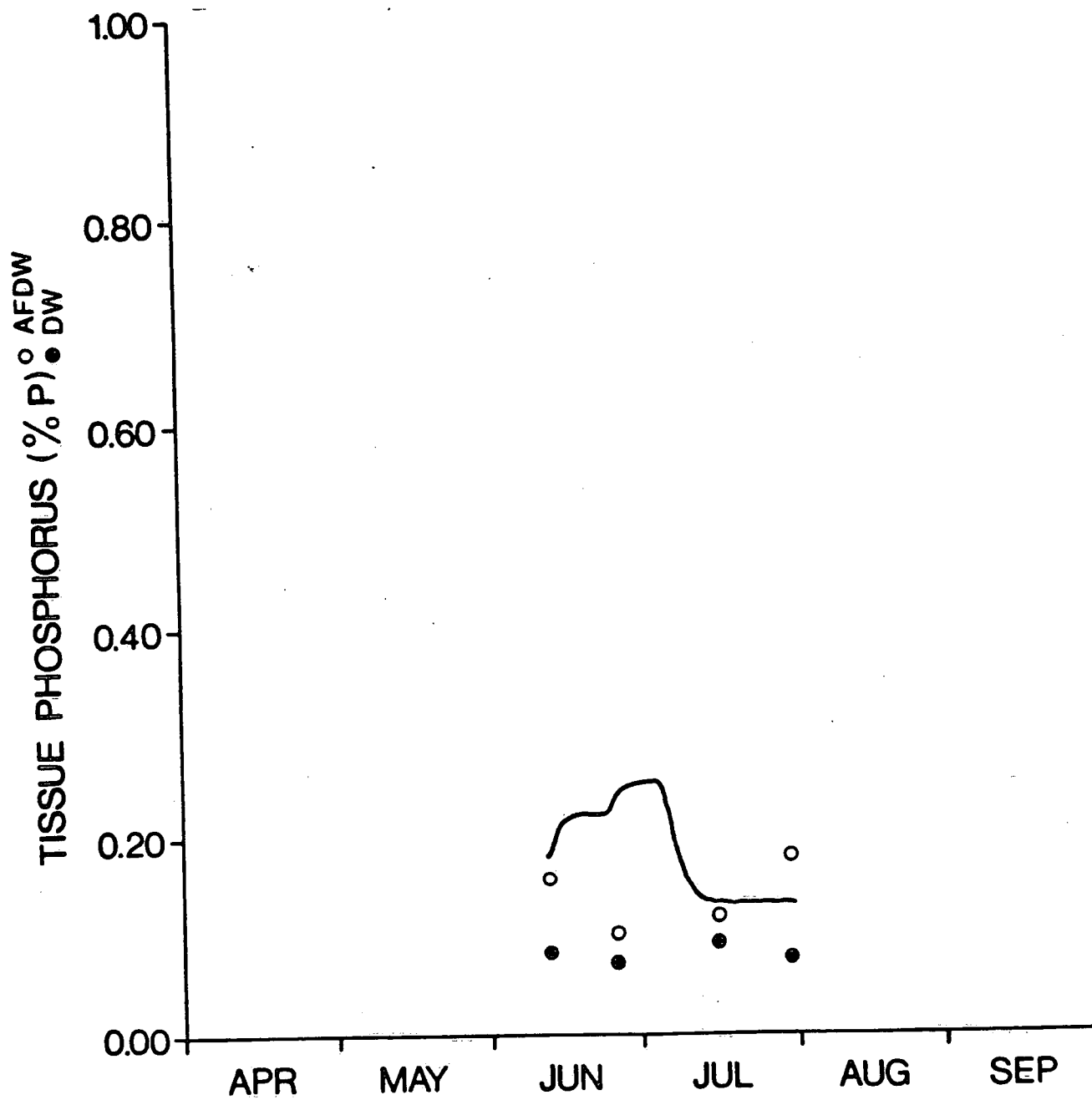
LAKE ERIE MOHAWK ISLAND 1985



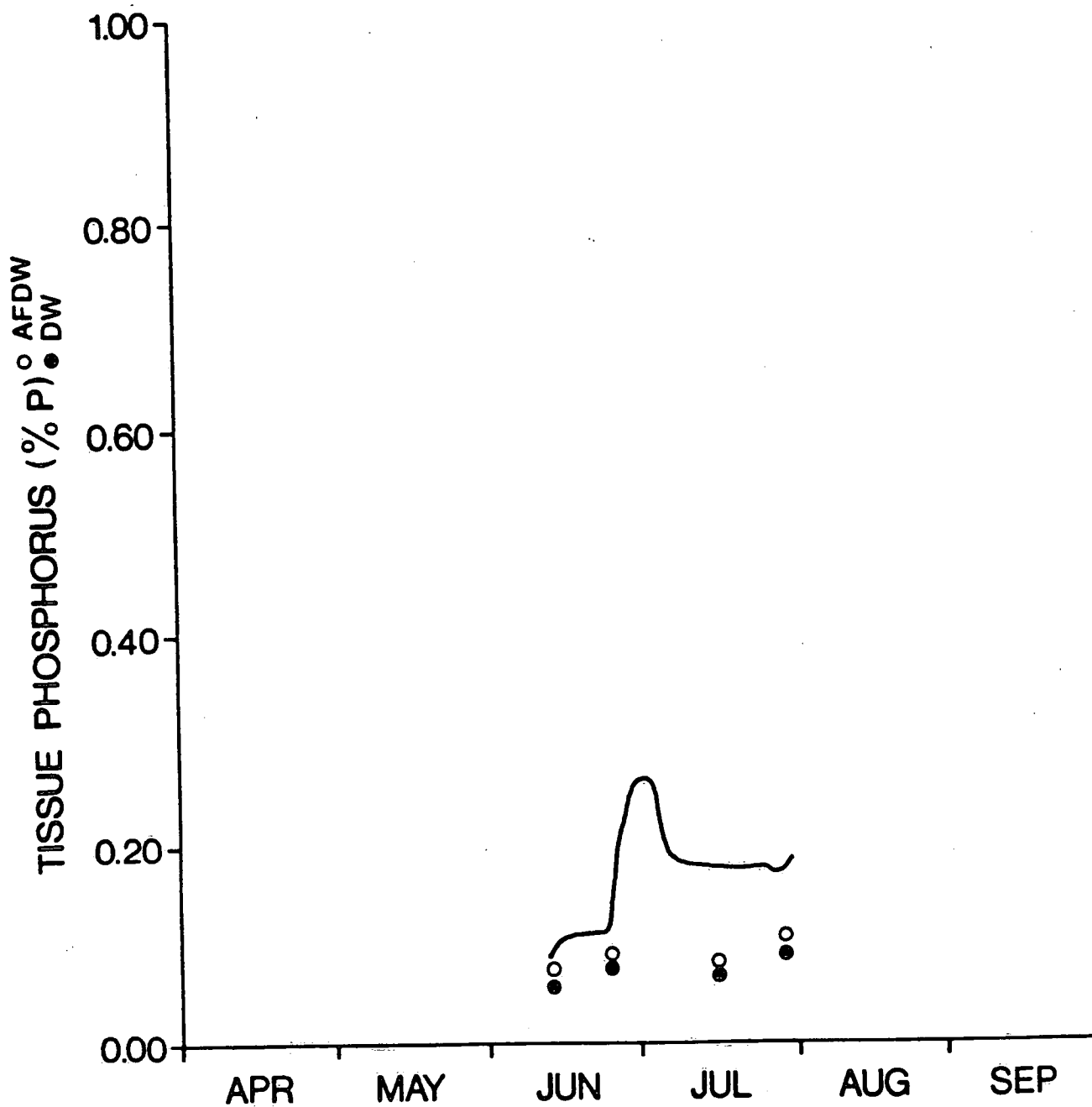
LAKE ERIE MOHAWK 1985



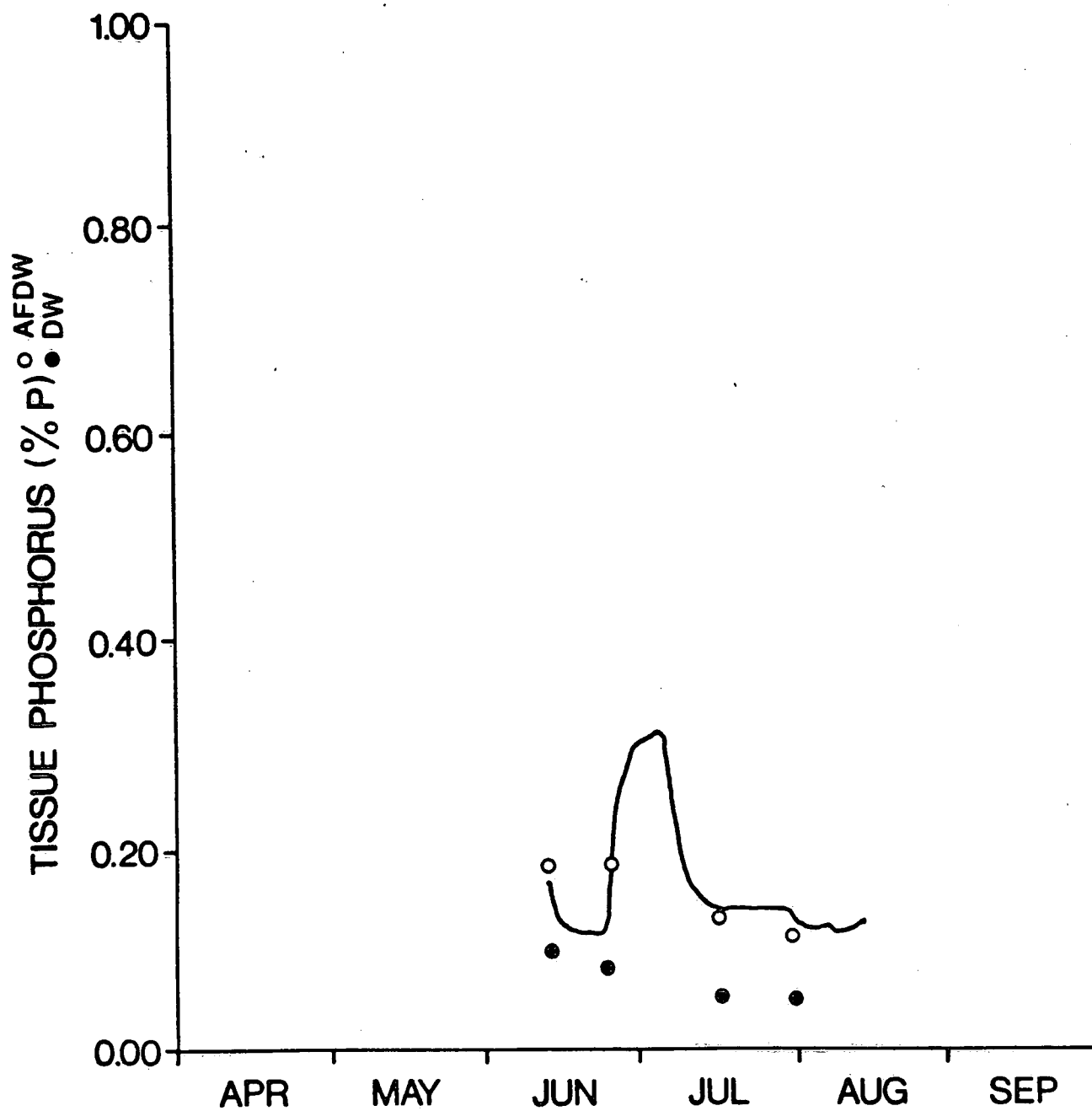
LAKE ERIE 1985 MORGANS



LAKE ERIE 1985 MILLER



LAKE ERIE WHITEMANS POINT 1985



LAKE ERIE ABINO 1985

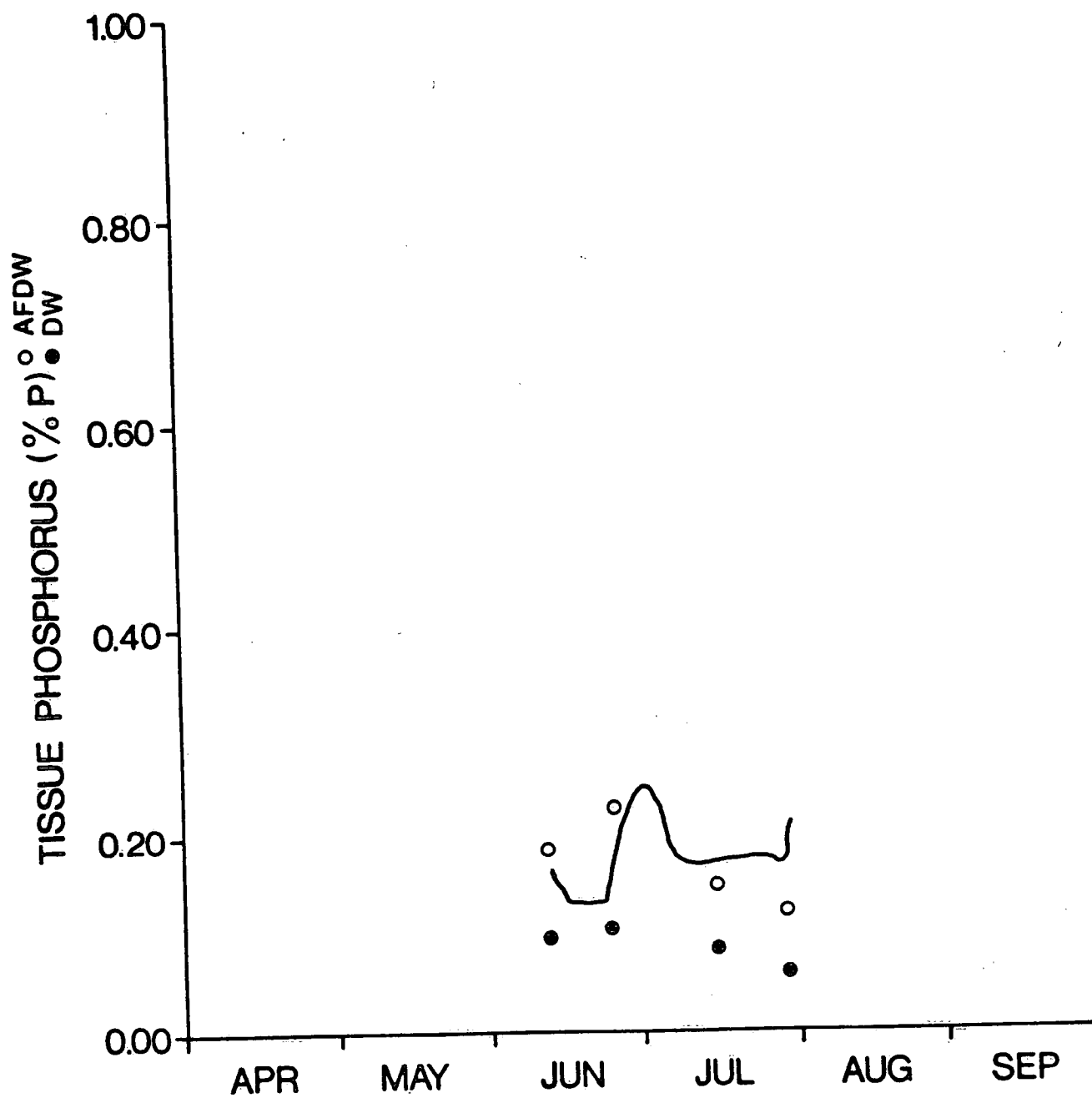


TABLE LEGENDS

Table 1. The influence of temperature and water clarity on internal phosphorus concentrations (%P) when soluble reactive phosphorus concentration remains constant

CLADOPHORA TISSUE PHOSPHORUS (% P)

SRP IDENTICAL ($20\mu\text{g} \cdot \text{L}^{-1}$)

SIMULATION DEPTH 0.1m				
SECCHI DISC TRANSPARENCY				
TEMP.	1.0m	3.0m	5.0m	
14 C	.32	.31	.31	
18 C	.37	.36	.37	
22 C	.40	.40	.40	
TEMP.	SIMULATION DEPTH 5.0m			
14 C	2.28	.56	.37	
18 C	2.90	.68	.40	
22 C	3.26	.62	.38	

TABLE LEGENDS

Table 1. The influence of temperature and water clarity on internal phosphorus concentrations (μP) when soluble reactive phosphorus concentration remains constant

CLADOPHORA TISSUE PHOSPHORUS (% P)

SRP IDENTICAL ($20\mu\text{g} \cdot \text{L}^{-1}$)

SIMULATION DEPTH 0.1m

TEMP.	SECCHI DISC TRANSPARENCY			
	1.0m	3.0m	5.0m	
14 C	.32	.31	.31	
18 C	.37	.36	.37	
22 C	.40	.40	.40	
TEMP.	SIMULATION DEPTH 5.0m			
	1.0m	3.0m	5.0m	
14 C	2.28	.56	.37	
18 C	2.90	.68	.40	
22 C	3.26	.62	.38	