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STRATIFICATION OF KINETIC ORIGIN AND ITS BIOLOGICAL CONSEQUENCES IN A NEOTROPICAL MAN-MADE LAKE*

ABSTRACT: A distinct thermal stratification and metalimnetic oxygen deficits were observed in the tropical dam Madden Lake throughout the year as a result of cool river influents. The role of the steep density gradient in metalimnion is discussed as a factor slowing down the rate of sinking of organic matter. As a result, the thermocline layer, which is in most cases immediately below the lowest extents of the euphotic layer, prevents a substantial part of the nutrients from falling out of the cycling in epilimnion and provides for the nonfluctuating and high standing crop and production of phytoplankton in the limnetic zone.

Contents

1. INTRODUCTION

Stratification of a lake is generally the result of the formation of vertical density gradients persisting due to stability of water mass. Currents, whether caused by climatic changes or concerned with inflow of river waters, usually have a weakening action on stratification. The

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*This work was carried out in 1969/1970 at Smithsonian Tropical Research Institute, Balboa, Canal Zone.

weakening effect of cold influents has been observed not only in lakes of the temperate zone (Strøm 1933, 1935, after Hutchinson 1957) but also in tropical lakes (Capart 1952, after Hutchinson 1957).

Opposite situations are to be observed however, particularly in man-made lakes with short renewal time and with small surface spillage but large leakage from the bottom layers. When influents are cooler than hypolimnetic waters stratification is intensified by constant cooling of the hypolimnion, with the consequence that the density gradient is steepened in the metalimnion. This phenomenon has been noted in man-made lakes both of the temperate zone (Olszewski 1946) and the subtropics (Anderson and Pritchard 1951, after Hutchinson 1957). It would appear, however, that this phenomenon is common only in the tropical zone, where it has been noted not only in reservoirs (Lake Kariba: Dr. D. S. Mitchell, pers. comm.), but also in natural lakes (Lake Edward: Worthington and Beadle 1932; Lake Bulera: Damas 1955; Lake Malawi: Eccles 1965 cited in Talling 1969). It is probable, that in the tropical conditions this process, together with the process of profile-bound density currents observed by Talling (1963) in Lake Albert, Africa, is not just a stratification steepening agent, but is in fact one of the basic mechanisms of its formation.

One may expect that density gradients formed in tropical lakes by way of this mechanism should be far steeper than in lakes stratified exclusively by climatic action. This seems to have a significant influence on the functioning of lake biocoenosis.

2. THE LAKE

Madden Lake, Panama, Canal Zone (Fig. 1, Table I) is a dam reservoir constructed for the purposes of the Panama Canal system. It was finally flooded in 1935 by completing a dam of 66 m height and 13 complementary short saddle dams. It is used to compensate for water losses

Table I. Morphometry, hydrology and light characteristics of Madden Lake

	Details	Min*	Max**
	Elevation (m above sea level)	71.1	75.7
S	Surface (km^2)	37	50
z_m	Maximal depth (m)	43	48
$\bar{z}$	Mean depth (m)	12.7	16.2
v	Volume (km^3)	0.47	0.81
L	Length of shoreline (km)	about 250	
$\frac{L}{2\sqrt{\Pi s}}$	Development of shoreline	about 10	
	Drainage area (km^2)	1,025	
	Total inflow (m^3 · 10^6 · day^{-1})	2.9	12.5
	Secchi disc reading (m)	2.0	2.8
	Vertical light extinction (ln unit · m^{-1})	0.511	0.657

*At the end of the dry season (March-May).

**At the end of the rainy season (November-January).

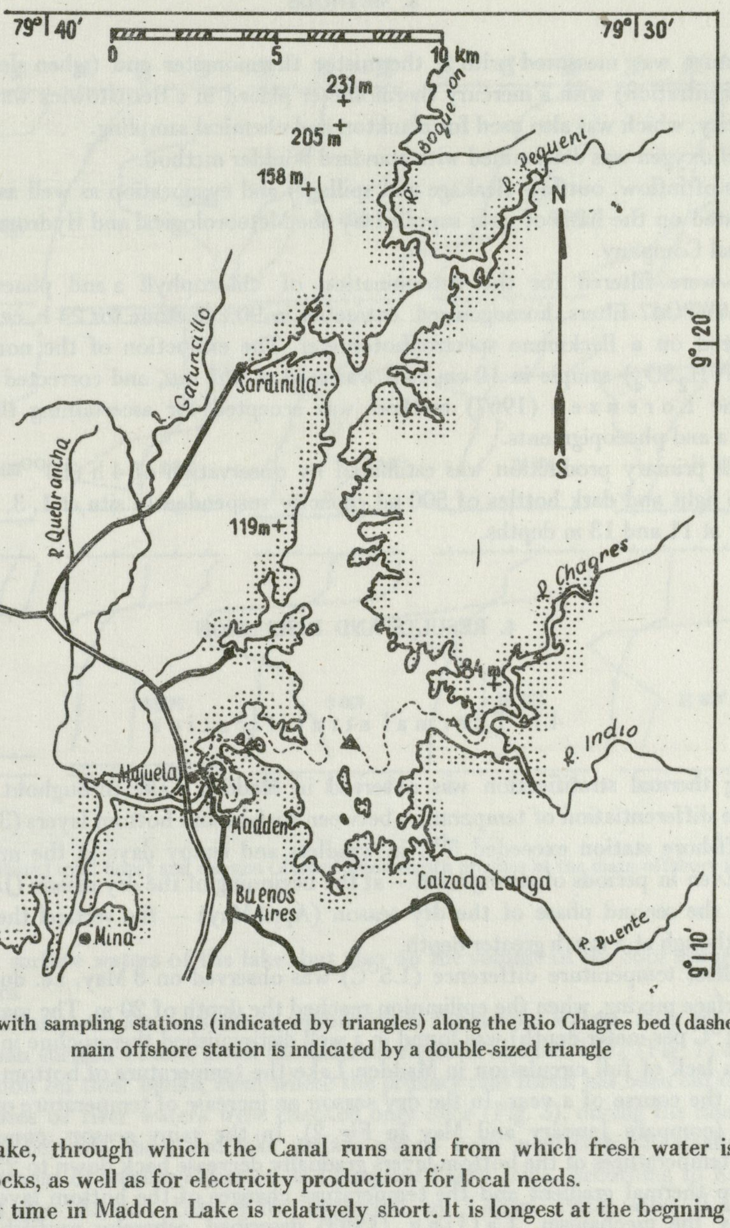

Fig. 1. The lake with sampling stations (indicated by triangles) along the Rio Chagres bed (dashed line). The main offshore station is indicated by a double-sized triangle

from Gatun Lake, through which the Canal runs and from which fresh water is used for operating the locks, as well as for electricity production for local needs.

The renewal time in Madden Lake is relatively short. It is longest at the begining of the dry season (February-March) when it is over 120 days and shortest (about 60 days) towards the end of the rainy season (October-January) and during the secondary, short rainy season (April-May), which divides the dry season into two periods. The volume of leakage from the bottom layers of the lake is relatively constant, whereas the volume of spillage from the surface fluctuates (Fig. 4).

The type of exploitation of Madden Lake determines its water balance. conditions its hydrological phenomena, and, in consequence, determines its biological nature.

3. METHODS

Temperature was measured with a thermistor thermometer and (when determining the oxygen concentration) with a mercury thermometer placed in a Bernatowicz water sampler of 5 liter capacity, which was also used for plankton and chemical sampling.

Dissolved oxygen was determined with standard Winkler method.

Volumes of inflow, outflow (leakage and spillage) and evaporation as well as renewal time were calculated on the basis of data supplied by the Meteorological and Hydrographic Branch, Panama Canal Company.

Samples were filtered for the determination of chlorophyll a and phaeopigments on Millipore AAWPO47 filters, homogenized, extracted in 90% acetone for 24 h, centrifuged, and then measured on a Beckmann spectrophotometer. The extinction of the nonacidified and acidified (4N H_2SO_4) sample in 10 cm cells was read at 665 mμ, and corrected by reading at 750 mμ. The Lorenzen (1967) method was accepted for ascertaining the amount of chlorophyll a and phaeopigments.

The gross primary production was estimated by observation of 4 h (10^{00}–14^{00}) oxygen evolution in light and dark bottles of 500 ml capacity suspended in situ at 1, 3, 5, 7, 9 m, and occasionally at 11 and 13 m depths.

4. RESULTS AND DISCUSSION

4.1. Thermal stratification

A strong thermal stratification was observed in Madden Lake throughout a whole year (Fig. 2). The differentiation of temperature between surface and bottom layers (30 m depth) at the main offshore station exceeded 5°C in windless and sunny days in the mid dry season (8 March). Even in periods of strong wind – at the beginning of the dry season (January-February) and of the second phase of the dry season (April-May) – the vertical thermal gradient persisted, although at a much greater depth.

The smallest temperature difference (1.5°C) was observed on 8 May, i.e. during the most intensive surface mixing, when the epilimnion reached the depth of 20 m. The maximal thermal gradient (1.1°C per meter depth) was found in a well distinguished thermocline in June.

Despite a lack of full circulation in Madden Lake the temperature of bottom layers change gradually in the course of a year. In the dry season an increase of temperature of about 3.5°C takes place (compare January and May in Fig. 2). In the rainy season, commencing with August, the temperatures of the bottom layers gradually decrease back down to 25.0°C.

The steep thermal gradient and the temperature changes of the bottom layers can not be explained by the mechanism Talling (1963) described, whereby profilebound density currents of water cooled in the shallows of a lake sink down the slopes to the deeper layers. It would appear that such a mechanism can be at the root of only small temperature gradients, not greater than 1°C, observed by Talling in Lake Albert, but of course this depends on diurnal fluctuations of air temperature.

It seems obvious that the steep thermal gradient and the changes of the bottom layer temperatures in Madden Lake can only be caused by the effect of cool river waters flowing into the lake. The extent of this effect depends not only on the temperature difference between the

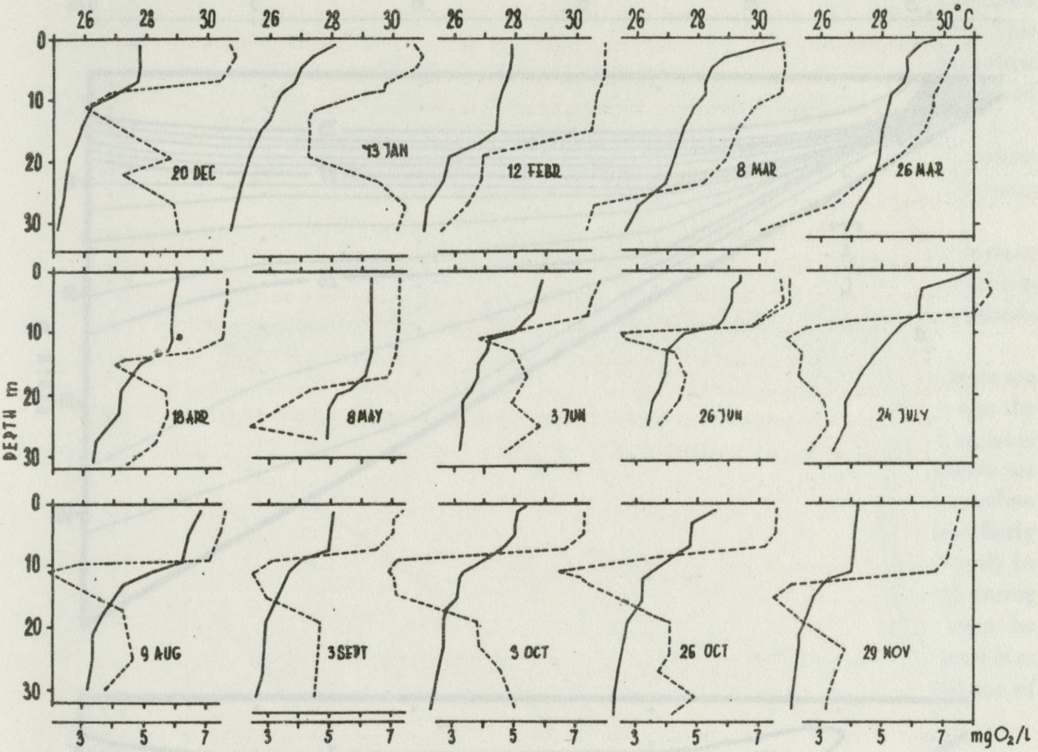

Fig. 2. Temperature (solid lines) and oxygen (dashed lines) depth profiles at the main offshore station

river waters and surface waters of the lake, but also on the volume of the cool influents filling the bottom layers.

Although the influents are sometimes warmer than the deeper waters, they are, however, always cooler than surface waters, as all the influent rivers of Madden Lake (Fig. 1) are shaded by thick vegetation on their banks, even where the primary rain forest has been cut down. The lower temperatures of river waters were checked only once (Fig. 3), during the rainy season, when differences between them and lake surface waters were most certainly smaller than in other periods because of weaker radiation and frequent heavy rains. According to Kufferath's observations on the African Lake Kivu (reported by Capart 1952, after Hutchinson 1957) this can significantly lower the temperature of surface waters.

Both the steepness and the depth of the temperature gradient depend on the strength of wind action as well as on temperature and volume of river influents. The most distinct division of the lake into epilimnion and hypolimnion occurs towards the end of the rainy season (August-December, Fig. 4), a period of weakest winds and intensive river inflow. During this period there is a marked thermocline at about 10 m (Fig. 2). In the dry season (February-March), a period of strong winds and smaller river inflows, thermal stratification is much less distinct and spread over the whole water column (Fig. 4).

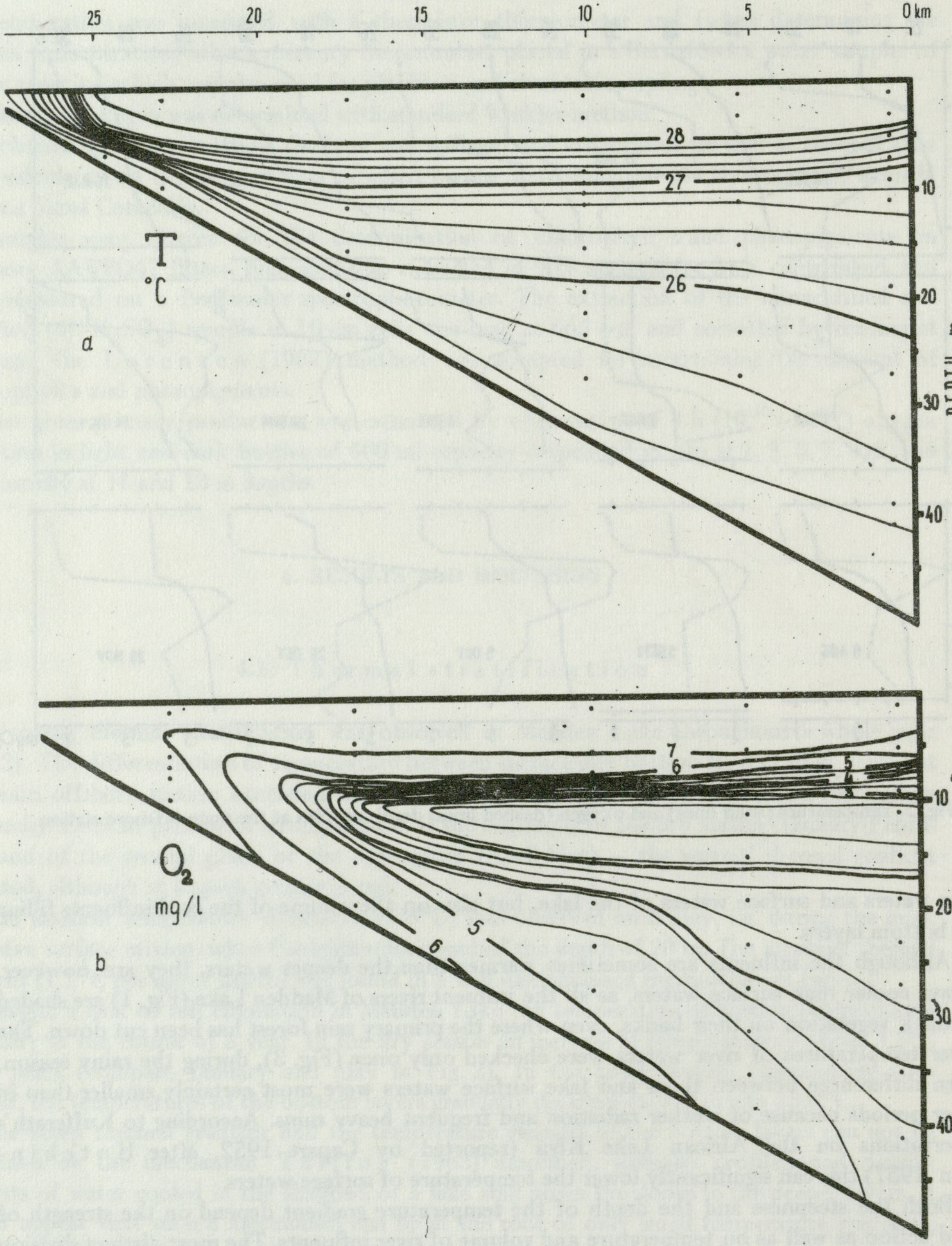

Fig. 3. Temperature (*a*) and oxygen (*b*) stratification in the lake, 3 September 1970 (section along the Rio Chagres bed, distances from the dam in kms along this bed are indicated at the top)

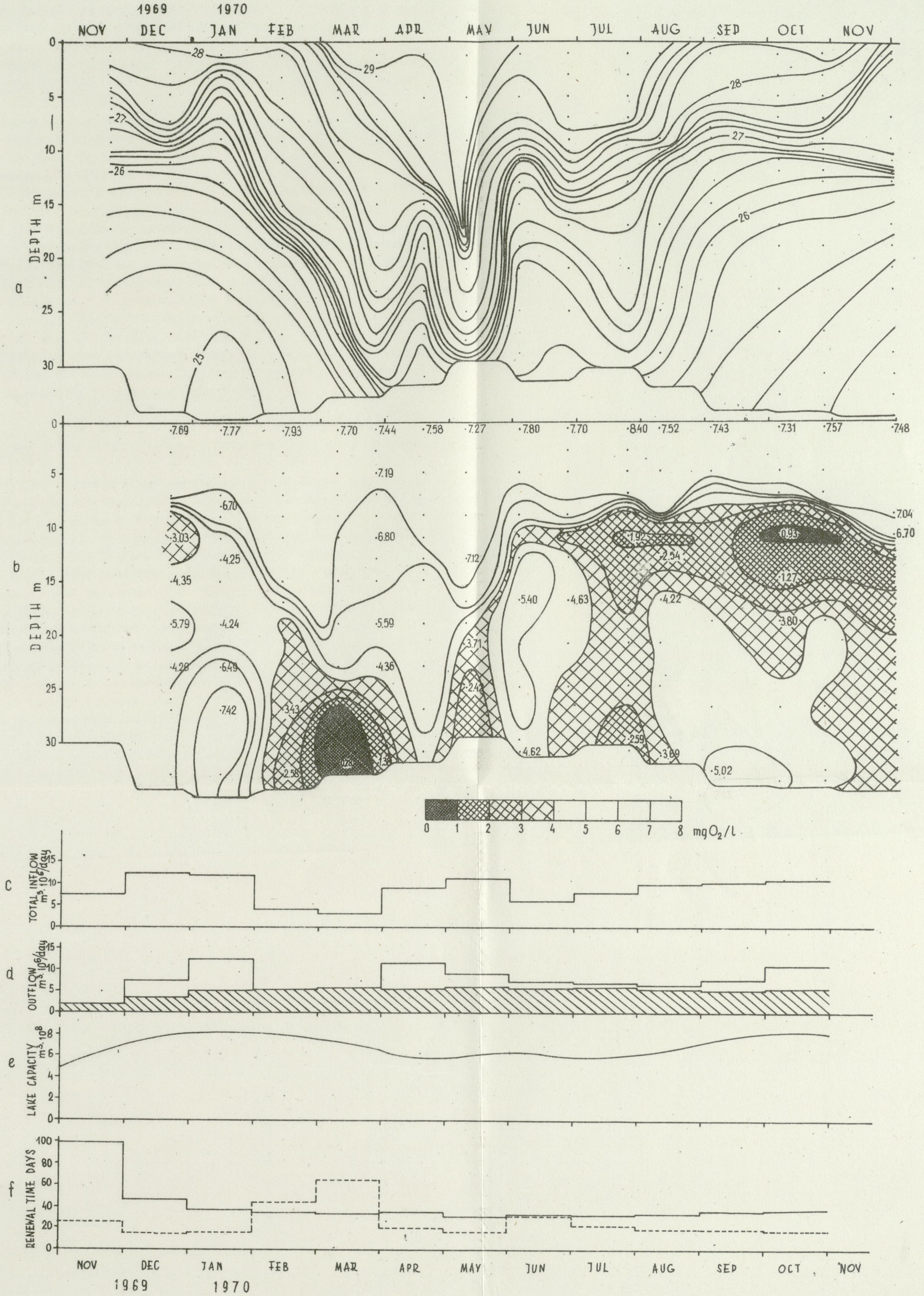

Fig. 4. Depth-time diagrams showing changing levels of isotherms (*a*) and oxygen isopleths (*b*) throughout the year at the main offshore station; monthly averages of the total inflow (*c*), and (*d*) of the total outflow (unshaded – dam spillage from the lake surface, shaded – the sum of hydroelectric plant throughflow and dam leakage from the hypolimnion); total lake capacity (*e*), and monthly averages of renewal time of the constant volume bottom part of the lake below the level of 60 m above sea level (*f*), i.e. the level situated immediately below the thermocline, calculated as the ratio of the volume of the bottom part to total inflow (dashed line) and as the ratio of the same volume to the sum of outflows from the hypolimnion (solid line)

4.2. Oxygen depth distribution

Madden Lake has a fairly high phytoplankton standing crop and primary production (Gliwicz in press) and therefore has a strong tendency toward oxygen deficiency. This tendency, however, seems to be kept in check by oxygen saturated river waters moving below the upper layers of the lake. A negative heterograde oxygen curve is in most cases thus observed (Figs. 2, 4).

The depth at which a steep oxygen decline begins is determined by the depth of surface mixing (Fig. 4). These can be seen particularly on 12 February, 18 April, 8 May, 26 June, 9 August and 29 November 1970 (Fig. 2).

So high is the oxygen consumption in Madden Lake, that in the absence of strong surface mixing, an oxygen content of about 1 mg/liter is found at a depth of 8 m (26 October), which is reached by 1% of the light available for photosynthesis (significant values of photosynthesis were ascertained at the depth of 7 m that day – Fig. 5).

In the dry season, a period of little through-flow of river waters, bottom oxygen deficits are also to be found. They are particularly marked in February and March (Fig. 2 and 4), when the renewal time is significantly longer than in other months, both in ratio to the entire variable volume of the lake and also in ratio to the constant volume below the level of 60 m above sea level (Fig. 4). This level has been chosen as it is situated immediately below the thermocline separating it from the hypolimnion, which is in fact river water moving through the lake fairly fast. It corresponds through most of the year (except for the period of February-April) to about 15 m depth. The tendency for bottom oxygen deficits to arrise is also to be found during periods of large through-flows, but they are not readily apparent, and may even be indistinguishable, when renewal time of lake water below the level of 60 m above sea level is as low as 15 days (December-January, Fig. 4). The eradication of bottom deficits when volume of inflow increases (Fig. 4) can be seen quite clearly in Figure 4.

4.3. Effect of thermocline on rate of decomposition

The slight decrease in oxygen concentration in the deeper water layers, in the presence of the strong tendency towards oxygen deficiency, is less than expected, even assuming that river inflows have an intensive oxygenating role. In this situation the tendency toward oxygen deficiency is likely to be more characteristic of the metalimnion than of the hypolimnion. In this case there should be some mechanism preventing sedimentation of organic matter below a certain depth. These conditions could be fulfilled by a steep temperature gradient created immediately below the extent of the euphotic layer, which is a very rare phenomenon in the tropics. Equally steep temperature gradients have been observed only in small water bodies immediately below the surface as short lasting phenomena, arising daily in windless, sunny weather at noon (Vaas and Sachlan 1955; Rakusa-Suszczewski 1964). This steep thermal gradient may be additionally superimposed on a gradient of electrolyte content resulting from higher concentrations in river than in lake water although in other tropical man-made lakes the contrary is often true (e.g. Rhodesian lakes; D. S. Mitchell, pers. comm.). There is no data available for Madden Lake, but this kind of situation was observed in winter in Lake Mead, Nevada (Anderson and Pritchard 1951, after Hutchinson 1957). Such a steep density gradient in the thermocline layer would ensure that sinking organic particulate material from the euphotic zone is stopped and held within this gradient layer where it decomposes to a large degree. This phenomenon has been known for quite a long time to occur in deep, well-stratified temperate lakes of America (Birge and Juday 1911) and Europe (Lityński 1926) and to be characteristic of late summer, a period when algal blooms disappear from the euphotic zone. Also known for some time (Whitney 1938), and confirmed for many lakes by contemporary observations (Synowiec unpubl.), is the pheno-

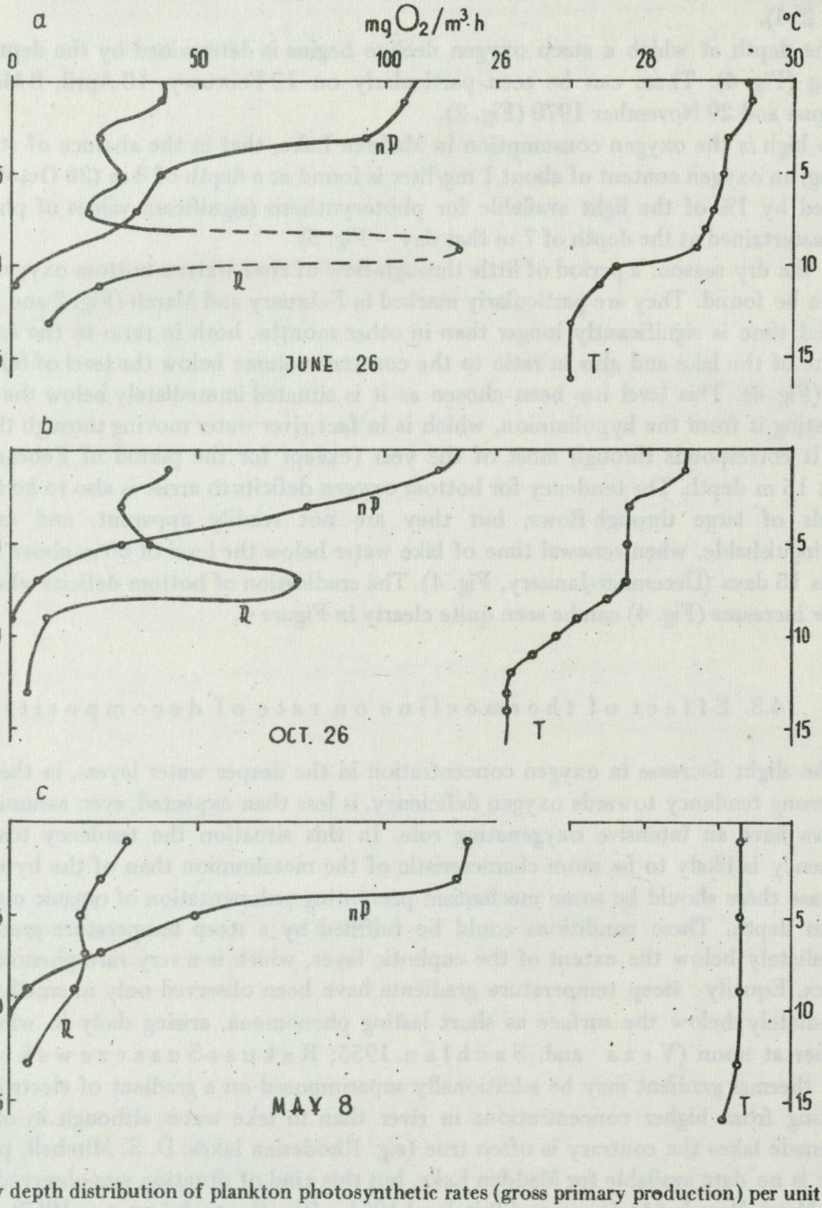

Fig. 5. Midday depth distribution of plankton photosynthetic rates (gross primary production) per unit water volume (*nP*), of the entire plankton community respiration rates per unit water volume (*R*), and thermal stratification (*T*) at the main off-shore station, when the thermal gradient is present (*a* and *b*) and absent (*c*)

menon of cumulation of particulate material in the upper part of metalimnion. This is demonstrated both by a light extinction measured in horizontal beam (maxima immediately below the epilimnion), as well as by direct determinations of organic seston at various depths (Ławacz unpubl.).

The assumption that sinking particulate organic matter is slowed down by the density gradient layer in Madden Lake is substantiated by the depth profiles of midday respiration intensity (*R*) of the entire plankton community on 26 June and 26 October (Fig. 5), which are quite different from the *R* depth profile of 8 May (Fig. 5), when there is no thermal gradient above the depth of 13 m. It is worth noting, that the maximum values of *R* are greater on 26 June than 26 October, when on the former date the steeper thermal gradient acts more efficiently in slowing down sinking organic matter (although the *R* values for the depth of 9 m were estimated less precisely on 26 June because of the steep oxygen concentration gradient, the error however does not exceed 30%, so these values are significantly greater).

It is also noteworthy that on 8 May the midday value of ΣR for the layer of 0–13 m is a third of midday ΣnP, while on 26 June and 26 October the midday value of ΣR for this layer is well above half of midday ΣnP. From this it can be concluded that on 26 June and 26 October the diurnal values of gross primary production (ΣnP) and of the entire plankton community respiration (ΣR) mutually balance each other in the surface layer (no photosynthesis during 12 night hours), and so, assuming that the standing crop of organic matter in this layer is invariable from day to day, one may expect that there is no sedimentation of organic matter from this layer to deeper waters.

That only small amounts of decomposing organic matter are present in the deeper layers of the lake is borne out by the spatial situation of 3 September (Fig. 3). It can be seen that oxygen saturated river water flowing below the metalimnion through the lake along the former Rio Chagres bed undergoes only slight deoxygenation when it covers the distance from the 20th km to the lower dam apertures (at this time spillage is very small -- Fig. 4). The time needed for water to cover this distance is probably not shorter than the renewal time of lake water below the level of 60 m above sea level, which at this time corresponds to 14.4 m depth, i.e. below the thermocline (Fig. 2). Renewal time for this water is about 20 days in this period (Fig. 4). It seems, therefore, that 20 days are needed for a decrease in oxygen concentration of 2.5 mg/liter in the water covering this distance (average oxygen concentrations below 14.4 m depth are 6.5 and 4.0 mg 0_2/liter at the 20th km and by the dam, respectively – Fig. 3). So, the rate of oxygen consumption in this water is 0.125 mg 0_2/liter per day, i.e. about 5 mg $0_2/m^3$ per hour. This value corresponds exactly to the values of the entire plankton community respiration rates *R* observed in June and October below the thermocline (Fig. 5).

It may be concluded then, that as a consequence of the steep density gradient layer in Madden Lake, all the easily oxidizable organic matter is decomposed in the euphotic layer, whereas only unreadily oxidizable organic matter falls to the deeper layers, where it is either quickly carried away by the "fast flowing" river below or deposited on the bottom without exhausting large amounts of oxygen from the hypolimnion. The former seems more probable though, since the rate of cumulation of bottom deposits in Madden Lake is unexpectedly low in comparison with nearby Gatun Lake which is unstratified and significantly less productive (Gliwicz in press). This is evident from data collected in 1973–1974 by Meteorological and Hydrographic Branch, Panama Canal Company (A. Gonzales, pers. comm.):

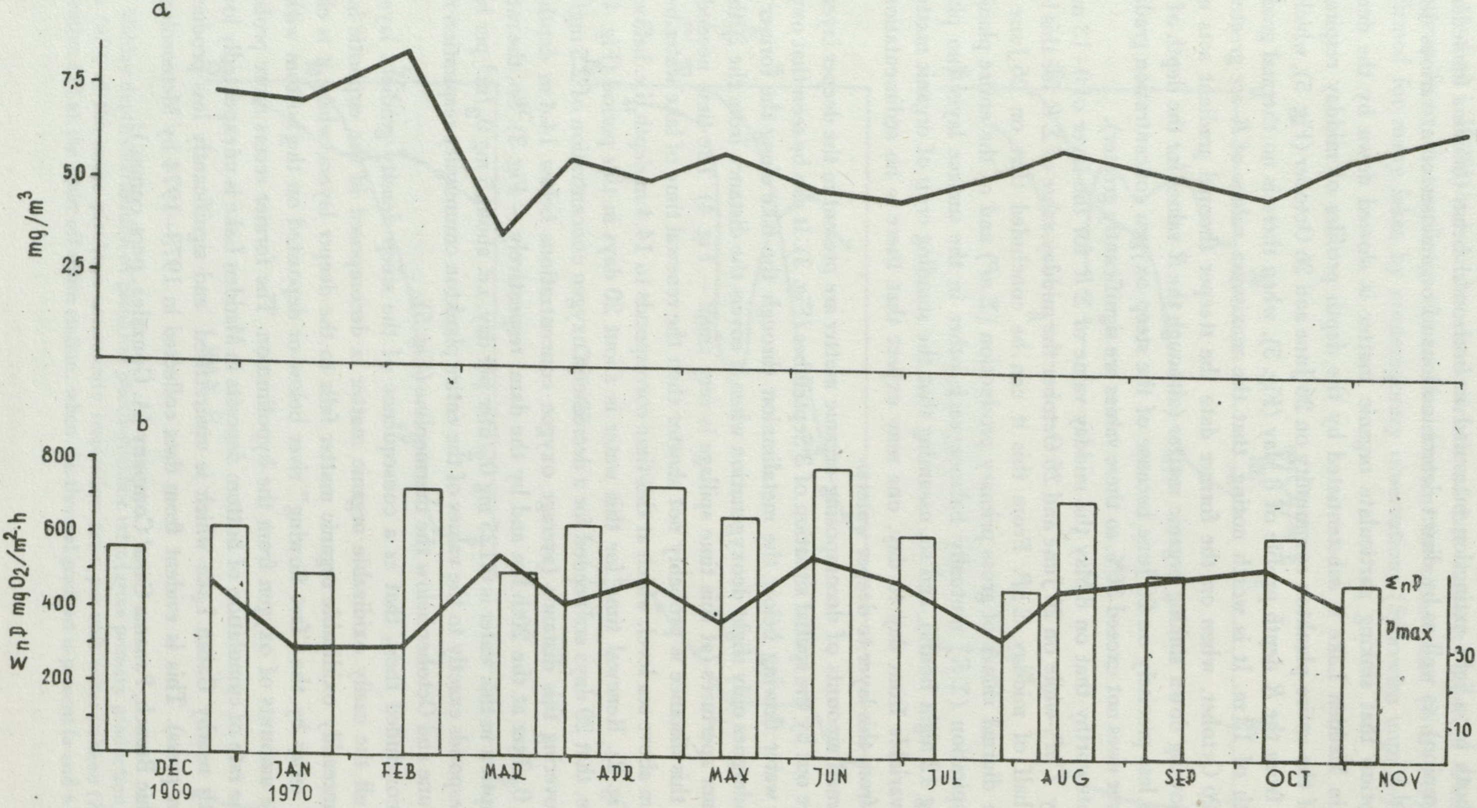

Fig. 6. Phytoplankton standing crop (*a*) as chlorophyll a concentration (*n*); b – values of integral photosynthesis (gross primary production) per unit area (ΣnP) shown as histograms and photosynthetic activity per unit of chlorophyll a (P_{max}) throughout the year at the main offshore station.

4.4. Density gradient layer and lake productivity

The density gradient layer in Madden Lake must therefore take the role of the lake bottom to some degree. Sinking dead organic matter is held by this "secondary bottom", is decomposed to a great extent there, and is capable of returning quickly to the euphotic zone in the form of nutrients.

Although the most intensive decomposition probably takes place slightly below the depth of surface mixing, i.e. where the rate of sinking is slowed to the greatest extent, it seems that recycling of a greater part of the nutrients is possible because of the continuing, albeit slight, changes in the depth of the thermal gradient. Each increase of epilimnion depth should cause an enrichment of the euphotic zone in nutrients, each decrease should cut off the euphotic zone from the nutrient supply.

This might be a contributory reason for the increase of phytoplankton biomass (Fig. 6) from January to February as well as from October to November, when an increase in depth of epilimnion was observed (Fig. 2). The drop in phytoplankton biomass at the beginning of March, despite the most favourable light conditions, might be connected with the disappearance of the "secondary bottom" in the preceding, windy period, as a result of which decomposition processes of organic matter had moved down to the deeper layers, from where surface mixing is not able to draw nutrients or organic matter up to the euphotic zone.

The presence of the density gradient, almost within the range of the euphotic zone, creates a situation in Madden Lake similar to the one observed in shallow, polymictic tropical lakes, which like Madden Lake, are rich in phytoplankton and have high values of primary production (Lake George: Ganf 1972; Lake Tchad: Lévêque et al. 1972).

Not incidently, perhaps, both the algal standing crop and primary production in Madden Lake is also maintained, except for the period of stratification break-down, at a constant level throughout the year (Fig. 6), as it is in the above mentioned lakes. In addition, as in Lake George and Lake Tchad, the phytoplankton in Madden Lake is permanently dominated by blue-greens (Gliwicz in press), and the zooplankton by cyclopoid copepods (Gliwicz and Biesiadka 1975).

5. CONCLUSIONS

The presence of a steep thermal gradient at the depth corresponding to the lowest extent of the euphotic zone, and the resulting formation of a "secondary bottom" partitioning the lake into two zones, may be found to be a rule in every dam-lake of the tropics, having a short renewal time and not particularly exposed to winds which might break the stratogenic forces of the cool influents.

The occurrence of this phenomenon in another Neotropical dam-lake (Brokopondo Lake, Surinam) might be indicated by some oxygen depth profiles included in the report by Leentvaar (1966). In other tropical lakes, for which relevant data are available, the formation of this phenomenon is not favoured by strong surface mixing or by small through-flow, so the density gradient is not steep enough to succesfully prevent sinking of organic matter (e.g. some Rhodesian lakes: Mitchell and Marshall 1974), or the through-flow is too slow to allow the river waters moving toward the dam to remain oxygen saturated (e.g. Lake Kariba: Harding 1966; D. S. Mitchell, pers. comm.). An anaerobic layer occupying all the hypolimnion is formed in these lakes for long periods of stratification characteristic of the summer.

It is not impossible though, that the thermal gradient also plays a significant role in these lakes by preventing loss of nutrients from the trophogenic zone. If this was not the case, a gradual decrease of both phytoplankton biomass and primary production would be observed during the stratification period in these lakes. But no such tendency is observed in those tropical lakes stratified for a long period of time (Talling 1966, 1969). Although there is usually some increase in algal number or biomass in periods of overturn, it is however short-lived, and, as soon as the lake is restratified, the standing crop of algae is back down at its former level and does not exhibit any further tendency to decrease.

It is possible that the effect of the density gradient in the thermocline layer is also underestimated in stratified lakes of the temperate zone, where in the period of summer stagnation algal biomass or production in the euphotic zone show no tendency to decrease. Indeed the opposite occurs: the summer maxima of both standing crop and production tend to appear in August. Furthermore, during this period decomposition of organic matter and of its accumulation in situ in the euphotic zone strongly predominate over its export by sedimentation from this zone (Gliwicz and HillbrichtIlkowska 1975). The amount of sinking organic material is several times lower in this period than in the period of spring and autumn circulation (Ławacz 1969), despite the peak of primary production at this time. It is not easy, however, to assess the role of density gradient in temperate lakes, because of major changes of other environmental factors conditioning the primary production (light and temperature), and the connected seasonal succesion of phyto- and zooplankton species.

I am grateful to Dr. M. H. Moynihan and other Smithsonian Tropical Research Institute scientists for providing all facilities necessary for field and laboratory work, and to the Meteorological and Hydrografic Branch, Panama Canal Company, for providing hydrological data. Sincere gratitude is extended to Dr. D. S. Mitchell and Dr. C. H. Mortimer for their valuable critical comments, of which not all have been, unfortunately, put to use because of lack of applicable data.

6. SUMMARY

In the tropical man-made Madden Lake (Fig. 1, Table I), Panama Canal Zone, a strong thermal stratification of up to 5°C differentiation between surface and bottom layers was observed throughout the year in 1969/1970 (Fig. 2). This resulted from cool river influents filling the bottom layers of the lake (Fig. 3). The steep gradients of water density in metalimnion (0.0003 g/ml per meter depth), corresponded regularly to minima in oxygen depth profiles of a negative heterograde type (Fig. 2).

Both the steepness and the depth of the density gradient depend on the reach of vertical mixing as well as on temperature and volume of river influents (Fig. 4).

The oxygen saturated river water moving slowly below the metalimnion along the former river beds (Fig. 3) keeps in check the strong tendency toward oxygen deficiency in the hypolimnion of this highly productive lake. But this is not the only reason for a distinct oxygen vertical distribution. It was found that if the density gradient is sufficiently steep, the sinking organic matter is slowed down in the metalimnion producing oxygen minima due to high respiration intensity of the entire plankton community in the thermocline layer (Fig. 5).

The role of the density gradient in the metalimnion, which is in most cases immediately below the lowest extents of the euphotic layer, is discussed as a factor preventing a substantial part of nutrients from falling out of the cycling within the system and, therefore, providing for the nonfluctuating and high standing crop and production of phytoplankton in the limnetic zone (Fig. 6).

7. POLISH SUMMARY (STRESZCZENIE)

W tropikalnym jeziorze zaporowym Madden Lake (fig. 1, tab. I), położonym w strefie Kanału Panamskiego, obserwowano w ciągu całego roku (1969/1970) silną stratyfikację termiczną (fig. 2). Dochodzące do 5°C różnice temperatury pomiędzy powierzchniowymi i przydennymi warstwami wody były wynikiem

wlewania się chłodniejszych wód rzecznych pod bardziej ogrzane wody powierzchniowe jeziora (fig. 3). W warstwie silnego metalimnetycznego gradientu gęstości wody (0,0003 g/ml na metr głębokości) obserwowano zazwyczaj minima tlenowe (uwarstwienie tlenowe typu heterograda negatywnej – fig. 2).

Ostrość gradientu gęstości oraz płytsze lub głębsze jego położenie uzależnione było zarówno od zasięgu mieszania powierzchniowego, jak też od temperatury i objętości dopływających wód rzecznych (fig. 4).

Związana z wysoką produktywnością jeziora silna tendencja do deficytów tlenowych w hypolimnionie jest w Madden Lake osłabiana przez stały przepływ dobrze natlenionych wód dopływów w głębi jeziora, wzdłuż dawnych koryt rzecznych (fig. 3). Nie jest to jednak jedyną przyczyna charakterystycznego uwarstwienia tlenowego. Stwierdzono bowiem, że metalimnetyczne deficyty tlenowe powstają przede wszystkim na skutek znacznie intensywniejszej respiracji całej biocenozy planktonowej w warstwie metalimnionu niż powyżej lub poniżej tej warstwy. Widoczne jest to szczególnie wtedy, gdy gradient gęstości w tej warstwie jest dostatecznie ostry (fig. 5), by istotnie zwolnić tempo sedymentacji wypadającej ze strefy eufotycznej materii organicznej.

Dyskutowana jest rola występującego zazwyczaj tuż pod dolną granicą strefy eufotycznej gradientu gęstości jako czynnika zapobiegającego intensywnemu wypadaniu biogenów z krążenia, który w konsekwencji przyczynia się do mało zmiennej i wysokiej biomasy i produkcji fitoplanktonu (fig. 6) w strefie limnetycznej jeziora.

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