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A survey of the biological limnology of Lake Titicaca

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With 4 figures and 2 tables in the text

Lake Titicaca, at 3800 m altitude and 16° S.L., impounds 820 km^3 of water with a total surface area of 7,800 km^2 and a maximum depth of 280 m. The lake supports an abundant and varied flora and fauna and serves as an important resource for nearly one million peasants living in the area. Rainbow trout and silversides supply the restaurant trade of nearby Peruvian and Bolivian cities (EVERETT 1971).

The most comprehensive work to date was published by members of the PERCY SLADEN Trust Expedition lead by H. C. GILSON (1939, 1940, 1955). MONHEIM (1956) published an extensive report on the climatology and hydrology of the Titicaca basin. These authors have reviewed the sparse earlier literature.

During 1973, twenty-one measurements of primary production were made approximately twice monthly. Phytoplankton and zooplankton populations were sampled simultaneously. Most of the work was done in waters of 100 meters depth, off Isañata Island near the village of Capachica. The position of this station is indicated by I (index station) on Fig. 1. Limited synoptic observations (Tab. 1) at stations M, W, X, Y

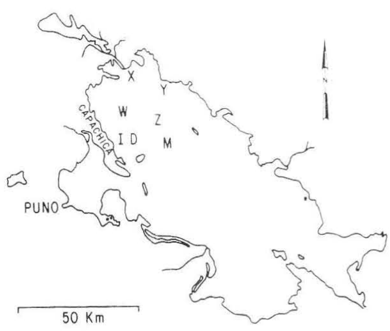

Fig. 1. The location of sampling stations in Lake Titicaca. I identifies the routine index station and D the nearby, deeper, station where temperature profiles were made.

and Z, suggest that our data from the index station are representative of the Lago Grande basin which reportedly accounts for 99 % of the volume of the lake (GILSON 1964). The physical and chemical measurements, made in conjunction with the biological work, are described in a second paper (RICHERSON et al. 1975).

Methods

Primary production was measured by the 14-C method of STEEMAN-NIELSEN (1952) as modified by GOLDMAN (1963). Water was obtained from 9 depths (usually 0, 3, 5, 7, 10, 12, 15, 20, 30 m) and incubated in situ four hours near midday.

Insolation data were obtained from pyrheliographs provided by the weather station at Puno, about 40 kilometers from station I. These data were used to convert production per hour to a daily value, assuming that the photosynthesis per unit light was the same during the incubation period as during other times of the day. Photosynthetic efficiency was computed by dividing the caloric equivalent of the incubation period primary production by the incubation period insolation.

Samples of the phytoplankton were obtained from lake water and were fixed with LUGOL's solution. The phytoplankton were filtered on to Millipore filters with 0.45 μ pore size, fixed, and mounted on slides according to DOZIER & RICHERSON (1975). Biomass was calculated from phytoplankton counts and converted to units of carbon using the relations of MULLIN, SLOAN & EPPLEY (1966). Diversity was calculated using the information theoretic index (PIELOU 1969).

Zooplankton were collected in 100 meter vertical hauls with a net (23 threads per centimeter). The samples were preserved in formol and later identified and counted. Zooplankton biomass was converted to carbon units by assuming that 4.5 ‰ of wet weight is carbon.

Results and discussion

The primary production pattern, with depth and time, is summarized in Fig. 2. The form of most of the curves is typical of mesotrophic waters. In sum-

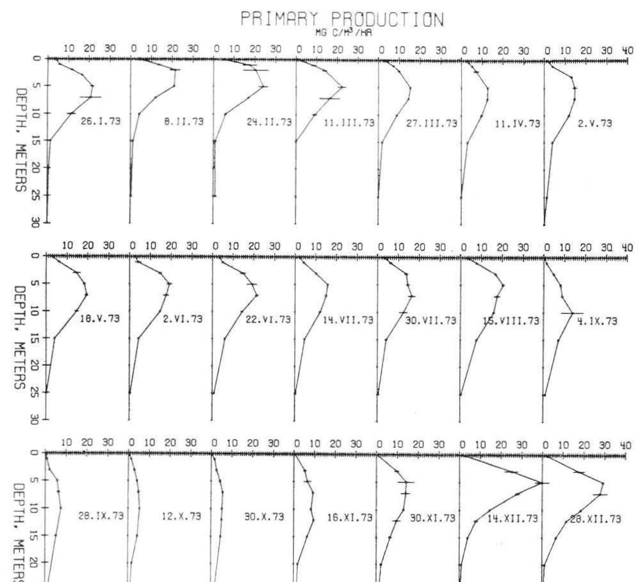

Fig. 2. Profiles of primary production. Hourly values are averages for the incubation period.

mer, high algal biomass and tubidity from riverine sources probably accounted for the production maxima near 5 m. Transparent winter conditions allowed production to extend downward. The strong inhibition at shallower depths was caused by the high light intensities and high ultra-violet radiation at Titicaca's latitude and altitude. The low springtime production occurred several weeks after the disappearance of thermal stratification (RICHERSON et al. 1975) when biomass was minimal. Shortly after the lake became isothermal (July 30), photosynthetic activity first increased and then declined sharply (Tab. 2, Fig. 3). Initially, isothermy seems to have stimulated production by permitting mixing of nutrients into the photic zone. On September 4, however, biomass and production fell sharply and remained low until after stratification was re-established. Production then rose rapidly as the rainy season began in December. The only reliable nutrient measurements made were of silicate, using a Hach Kit model DR-EL. Values of SiO_2 in the photic zone rose only slightly during isothermy (Tab. 2).

Tab. 1. Comparison of production rates from several stations in Lake Titicaca.

Station	Date	Primary production mg C m^{-2} day^{-1}	Efficiency units $\times 10^{-3}$
M	3 May	1,189	2.82
W	15 May	1,559	4.59
X	15 May	1,112	3.27
Y	17 May	1,569	3.50
Z	17 May	1,470	3.28
I	18 May	1,544	3.77

The data suggest that only moderate amounts of nutrients were mixed upward while the lake was unstratified and that the high production late in 1973 was associated with nutrients carried into the lake by runoff as the rainy season began.

Photosynthetic efficiency, daily primary production, and phytoplankton biomass were strongly related throughout the year (Fig. 3). Nutrients seem to limit cell growth rather than carbon fixation per unit biomass during the spring minimum.

Using average values for 14-C production and areal data from GILSON (1964), we have calculated the annual primary production for the main basin to be 3.11 million metric tons, and for the total lake, 4.02 million. The latter figure might be conservative since the shallow waters included are likely to be more productive than those of the main body of the lake. The annual primary production of 529 grams C per m^2 is in reasonable agreement with the regression equation predictions of BRYLINSKY & MANN (1973) and BRYLINSKY (pers. comm.).

The annual patterns of distribution of the dominant phytoplankton and zooplankton populations are summarized in Fig. 4. Zooplankton species were identified from HARDING's (1955) and UÉNO's (1967) descriptions. Phytoplankton have only been tentatively identified, so generic designations are used in Fig. 4.

Changes in phytoplankton populations tend to reflect changes in production. *Coscinodiscus* sp. for example, disappeared during the production and SiO_2 minima in spring. *Oocystis* sp. and one *Ulothrix* sp., however, reached maximum levels during this period. Diversity changed considerably from time to time, as indicated in Tab. 2. Low diversity was associated with high production and rising biomass.

Zooplankton populations varied little throughout the year. *Boeckella titicacae* HARDING was always strongly dominant; all other species together seldom made

Tab. 2. Primary production — Lake Titicaca 1973. Biomass and diversity are based on counts from 0,7, and 15 m only.

Date	Primary production mg-C m^{-2} day^{-1}	Insolation Kcal m^{-2} day^{-1}	Efficiency units $\times 10^{-3}$	Phytoplankton biomass (av.) mg-C m^{-3}	Phytoplankton diversity bits $indiv.^{-1}$	Silica (5 m) ppm SiO_2
Summer						
26 Jan	1,345	3,363	4.00	17.40	1.8	0.82
8 Feb	1,177	3,382	3.48	30.81	1.6	1.10
24 Feb	1,041	3,630	2.87	27.71	2.6	1.05
11 Mar	1,189	5,017	2.37	36.75	3.1	1.14
Autumn						
27 Mar	1,320	5,431	2.43	22.02	4.0	1.00
11 Apr	1,174	5,798	2.02	23.47	3.7	0.84
2 May	1,395	4,666	2.99	22.54	3.3	0.67
18 May	1,544	4,093	3.77	39.27	3.7	0.49
2 Jun	1,614	4,630	3.49	32.46	3.2	0.47
Winter						
22 Jun	1,673	4,557	3.67	29.32	3.2	0.13
14 Jul	1,264	3,818	3.31	29.25	3.2	0.06
30 Jul	1,701	5,140	3.31	26.91	3.3	0.44
15 Aug	2,014	5,480	3.68	29.26	3.7	0.11
4 Sep	1,391	5,571	2.50	19.14	3.2	0.20
Spring						
28 Sep	1,004	5,526	1.82	14.28	3.4	0.20
12 Oct	756	4,948	1.53	13.11	2.9	0.23
30 Oct	720	5,908	1.22	13.89	3.2	0.17
16 Nov	985	6,868	1.43	12.71	2.1	0.23
30 Nov	1,579	6,715	2.35	17.60	1.2	0.22
14 Dec	2,711	6,939	3.91	27.76	1.4	0.25
Summer						
28 Dec	2,861	5,317	5.38	28.18	1.1	0.25
Average	1,450	5,086	2.93	24.47	2.8	0.48

Yearly primary production: 529 grams C m^{-2}
Main basin (Lago Grande): 3.11×10^6 metric tons   Total lake: 4.02×10^6 metric tons

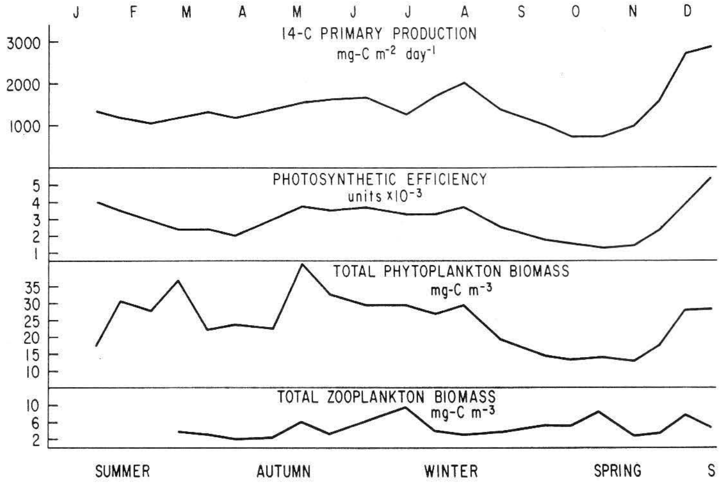

Fig. 3. Comparison of basic rate and biomass measurements, averaged over all depths from which data was collected, except phytoplankton which represents 0, 7, and 15 m only.

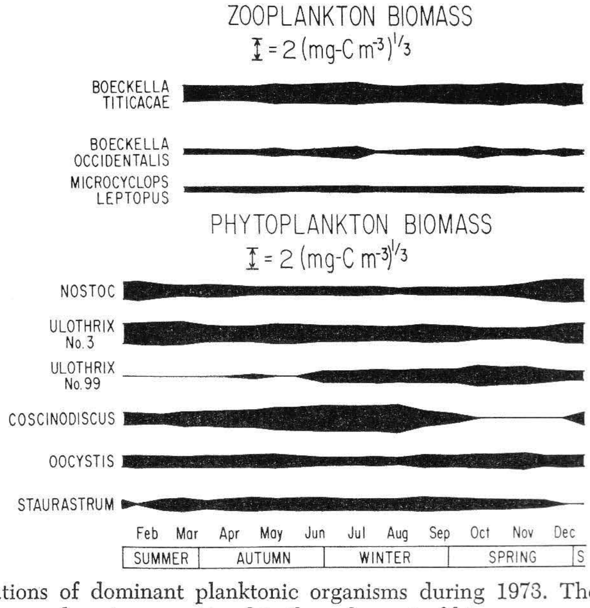

Fig. 4. Populations of dominant planktonic organisms during 1973. The width of the bars is proportional to the cube root of biomass.

up as much as 10 % of the biomass. Biomass data for the three commonest crustacea are shown in Fig. 4. The three planktonic cladocera found in the lake (UÉNO 1967) were always minor constituents of the community.

The general patterns of biological processes in Lake Titicaca resemble those of the tropical East African lakes, especially Lake Victoria (TALLING 1965, 1966, 1969). The low seasonality dampens the usual annual patterns of higher latitude lakes. Productivity varies relatively little and seasonal changes in the phytoplankton are muted. The extreme monotony of Lake Titicaca's zooplankton may also stem from reduced seasonality. BURGIS (1969) describes a similar zooplankton fauna in Lake George (Uganda). The general stimulatory effect of tropicality on species diversity seems to be directly reversed in the lacustrine zooplankton assemblages of both lakes, perhaps because of a strong temporal component in zooplankton niches.

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Discussion

FEE: Were the data used to infer potential yield of the L. Titicaca fishery? How?

WIDMER: Yes. We have estimated that if the harvested species were primary carnivores, the lake should yield 250,000 metric tons. If the fish harvested were secondary carnivores the maximum sustainable yield should be approximately 38,000 metric tons. These values were estimated by assuming that grazers have an overall ecological efficiency of 10 %, that predators have a 15 % efficiency and that sustained yield is about 50 % of production.

LEWIS: Ecological efficiency of photosynthesis will not be directly affected by changes in incident light, but will be affected by the depth of circulation, which can be an important aspect of light limitation in large lakes. I therefore do not feel that you are justified in concluding that the basis of changes in ecological efficiency is nutrient limitation alone.

WIDMER: True. We found that during the season of thermal stratification phytoplankton were very sparse below the thermocline and that after isothermy a significant proportion of the biomass was found below the compensation point.

STOERMER: How was biomass of individual phytoplankton populations determined?

WIDMER: Numbers of cells of individual species were counted and cell volume estimated by approximation to geometrical solids. The amount of cell carbon was estimated as described in the text.

GELIN: Is there some relationship between phytoplankton diversity and SECCHI disk transparency?

WIDMER: Only an indirect one. When algal biomass is increasing, diversity falls. During periods of increasing biomass the SECCHI depth also rises.

KILHAM: Prof. GILSON in his account of the phytoplankton of Lake Titicaca states that *Stephanodiscus astraea* is the dominant diatom. Is the *Coscinodiscus* species you found possibly mis-identified?

WIDMER: As best we can make out, the species in our samples is *Coscinodiscus lacustris*. We would be glad to provide material to other workers for expert determination.