

PATTERN OF ENERGY FLOW IN FRESHWATER TROPICAL AND SUB-TROPICAL IMPOUNDMENTS

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INTRODUCTION

Energy is the capacity of doing work and all living organisms require energy in one or the other form. Several forms of energy have been recognised but those of greatest importance to living organisms are mechanical, chemical, radiant and heat. The energy source for all living organisms is sun, a vast incandescent sphere of gas, which releases energy by nuclear transmutation of hydrogen to helium in the form of electromagnetic waves. The biotic communities (producers, consumers and decomposers) in an ecosystem are linked with one another with energy chains. Unidirectional flow of energy and nutrient cycles are the two great principles of general ecology. Complete knowledge of the interrelationships among organisms, flow of energy and nutrients from one level to the other and the role of environmental parameters in the energy transformation processes is of great importance for the correct understanding of the ecosystem and better utilization of energy source. It is interesting to note that the study of productivity now receiving so much importance in ecology is only a part of energy story and the ecologists interested in energetics are concerned with efficiency with which solar energy is converted to chemical energy by producers (photosynthetic efficiency) and the efficiency with which this energy is utilised by consumer organisms (ecological efficiency). The energy flow approach leads one to view a biological system as being driven by solar energy which is trapped during photosynthesis and passed on to consumers.

India has approximately three million hectares of impoundments. This area is increasing year after year with the addition of more and more impounded surface waters. Millions of calories of energy per hectare is falling on this water mass and the study of the fate of such a vast amount of energy is essential for its proper utilization. Workers like Juday (1940), Lindemann (1942), Teal (1957), Odum (1957), Mann (1965), Odum (1975) etc., have studied the flow of energy in different biotopes. Their approach was of general type and some important deductions have been made on controlled aquatic ecosystems. In India practically no detailed study has been made on the energetic aspects of man-made lakes, which are the store houses of a large number of

organisms linked with various energy chains. Ganapati (1970), Sreenivasan (1972), Ganapati and Sreenivasan (1972) and Natarajan and Pathak (1980) studied the bio-energetics of some man-made lakes. Lack of understanding of ecological principles of energy transformations and improper management practices have resulted in very poor energy harvest (10 kg of fish/ha or approximately 12×10^7 cal/ha of energy on an average basis) from Indian reservoirs. The present paper gives a complete background of the flow of energy in freshwater impoundments taking Bhavanisagar, Nagarjunasagar, Rihand and Govindsagar as examples. These reservoirs are situated at latitudes varying from $11^{\circ}5'$ N to $31^{\circ}25'$ N and differ considerably in limno-chemical characters. Attempts have also been made to derive a methodology for evaluating the energy relationships among various processes in the biotopes. The observations reported here are based on the materials collected under All India Coordinated Research Project on Ecology and Fisheries of Freshwater Reservoirs during 1974-75 to 1978-79 by the first author as leader of the Project and second author as associate.

PROCEDURAL METHODS

Limnological procedures followed were the same as given by Jhingran *et al.* 1969 and Pathak 1979. Commercially exploited fishery data were collected from various landing centres in the impoundments. In all these impoundments fishes were mostly exploited by gill nets of different mesh sizes. Primary production or chemical energy fixed by producers was measured by dark and light bottle technique giving full day exposure (roughly 12 hours). The results were integrated to obtain the values in $\text{gC/m}^2/\text{day}$ which was later converted to $\text{cal/m}^2/\text{day}$. Average fish yield for the years was taken for comparison. The following conversion factors were used for interpreting the results.

1 g of oxygen = 0.375 g carbon.

1 g of O_2 produced during photosynthesis = 3.68 K cal.

1 g of carbon = 2 g organic matter (Ryther 1956).

1 g dry wt of organic matter = 4.5 K cal

1 g of carbon = 10 g of wet weight of fish (Rodhe 1958)

1 g C is approximately equivalent to 10 K cal.

Visible light energy for the appropriate latitude was obtained from the table furnished by the United States Weather Bureau (Kimbal, 1935). Maximum-minimum

values were calculated for every month and annual average was drawn. Energy released by decomposition and the bottom energy were calculated from hypolimnetic oxygen consumption in the reservoir (Ohle 1956). The chemical energy fixed by producers was averaged for the years. As the reservoirs have large fluctuating areas the average area was taken as half of the area of full reservoir level and dead storage level. Assuming the average composition of the freshwater reservoir fish to be 18% protein and 2% fat (the calorific value of protein and fat being 5,600 and 9,400 cal/g respectively) one gram of wet weight of the fish comes to be approximately 1,200 cal.

RESULTS AND DISCUSSION

1. Productivity considerations from limno-chemical parameters

The productivity of reservoir biotopes depends on climatic, edaphic and morphometric features. The climatic factors like rainfall, sun shine, wind velocity, air temperature etc., and edaphic factors—water and soil quality provide essential source of energy and nutrients while morphometric features like, depth, area, volume, water level fluctuation etc., regulate the supply of energy and nutrients. In addition the hydrological cycle (inflow and outflow) also play important role in the productivity of impoundments. The important limno-chemical features of the four man-made lakes are given in Table I. It is obvious from the table that the reservoirs vary widely with respect to morpho-ecological features and based on this they differ considerably in productivity. This aspect has been fully discussed by Natarajan (1979) and Pathak (1979).

Limnologists have attempted to classify lakes according to their thermal features (Welch 1952, Hutchinson 1957). Though such classifications are intended primarily for lakes they may be extended to reservoirs also, however, deep water release-character of the later, influences this physical phenomenon to a greater extent. Reservoirs, especially in the North Indian belt, Rihand and Govindsagar, come under the category of monomictic lakes with strong thermal stratification during summer. But winter circulation does not apply to them as both wind action and monsoon floods break the summer stagnation. The peninsular reservoirs, Nagarjunasagar and Bhavanisagar, generally show absence of any thermal stratification as is expected from the narrow range of seasonal variation in water temperature. Circulation of water is an important phenomenon that brings the chemical nutrients locked in the tropholytic zone upto trophogenic zone and facilitates fixation and utilization of energy. Heat dynamics of four impoundments has been

Table - I
MORPHOMETRIC AND EDAPHIC FEATURES OF RESERVOIRS

PARAMETERS	BHAVANI SAGAR	NAGARJUNA SAGAR	RIHAND	GOVIND SAGAR
MORPHOMETRY				
Latitude	11°5'N	16°34'N	24°N	31°25'N
Area at FRL (ha)	7,265	28,474	46,538	16,867
Water level fluctuation (m)	13.5	18.0	15.2	59.0
Mean depth (m)	11.2	40.6	23.9	55.6
SOIL FEATURE				
pH	5.8	7.5	7.1	8.7
Available—N (mg/100g)	41.2	15.04	14.2	16.0
Available—P (mg/100g)	3.9	3.5	1.74	0.5
WATER PHASE				
Water temperature (°C)	25.8	27.5	24.0	22.5
Transparency (cm)	107.0	260.0	54.0	112.1
pH	8.3	8.3	7.7	8.8
Dissolved oxygen (ppm)	7.5	8.0	6.2	9.7
Total alkalinity (ppm)	52.11	110.0	43.87	69.3
Sp. conductivity (μ mhos)	268.9	450.0	97.7	215.2
Nitrate (ppm)	0.16	0.70	0.40	0.27
Phosphate (ppm)	0.02	0.01	0.079	0.02
Silicate (ppm)	9.90	30.0	6.44	1.07

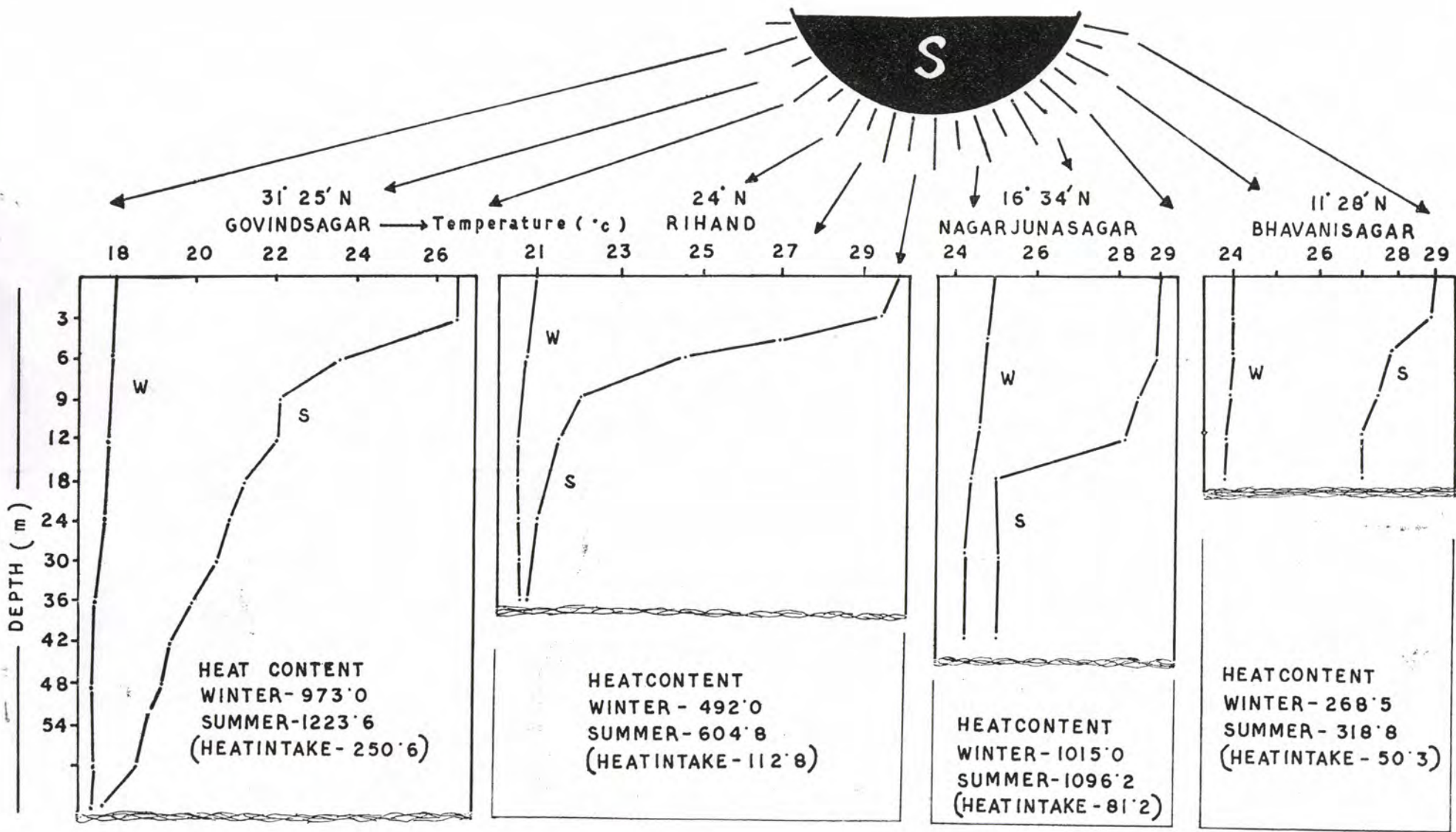


FIG-1 MEAN TEMPERATURE (°c) X MEAN DEPTH (m) = HEAT CONTENT (ton calories/m²)

HEAT DYNAMICS IN DIFFERENT RESERVOIR (ton calories/m²)

presented in figure-1. It is important to note from the figure that the subtropical reservoirs, though receive less solar energy per year, they retain more heat energy than the tropical reservoirs.

Another important feature of the reservoir is the oxygen depletion near the bottom brought about by oxidative processes. Under otherwise equal conditions a lake with richer biota will show greater oxygen deficiency in deepwaters than a poorer lake. Hence the relative productivity can be estimated from oxygen curve. Reservoirs like Bhavanisagar, Nagarjunasagar and Govindsagar have shown strong oxygen decline in the tropholytic layers and distribution of oxygen is klinograde in nature. These reservoirs can therefore be said to have high energy reserve at the bottom and as such come under the category of high productive reservoirs. On the other hand Rihand showed a near uniform distribution of oxygen from surface to bottom (orthograde) and hence can be put under the category of low productive reservoir as the bottom energy is of low order. The rate of oxygen consumption in the tropholytic layers is further influenced by temperature. According to Vant Hoff's law the rate of consumption is atleast doubled for every 10°C rise in temperature and as such oxygen consumption in tropical impoundments (where the bottom water temperature is considerably higher) will be much more than the temperate ones. This is clear in the case of reservoirs like Bhavanisagar and Nagarjunasagar. The decomposition of bottom organic sediments and decline of oxygen is accompanied by increased nitrogen levels and by the accumulation of carbon dioxide. This enriched carbon dioxide and subsequent increase in hydrogen ion ($\text{CO}_2 + \text{H}_2\text{O} = 2\text{H}^+ + \text{CO}_3^{--}$) lowers the pH of the bottom layers: Hence, the bottom accumulation of carbon dioxide, fall in pH, increase in bicarbonate and conductivity and rise in bottom nutrient levels serve to reflect the reservoir's high productivity. Productive reservoirs like Bhavanisagar, Nagarjunasagar and Govindsagar have all shown sharp changes in these parameters in the hypolimnetic regions but in Rihand the distribution of the above parameters was near uniform from surface to bottom. The distribution of physico-chemical parameters from surface to bottom in four man-made lakes have been presented in table II.

2. Energy Transformation from light to Chemical

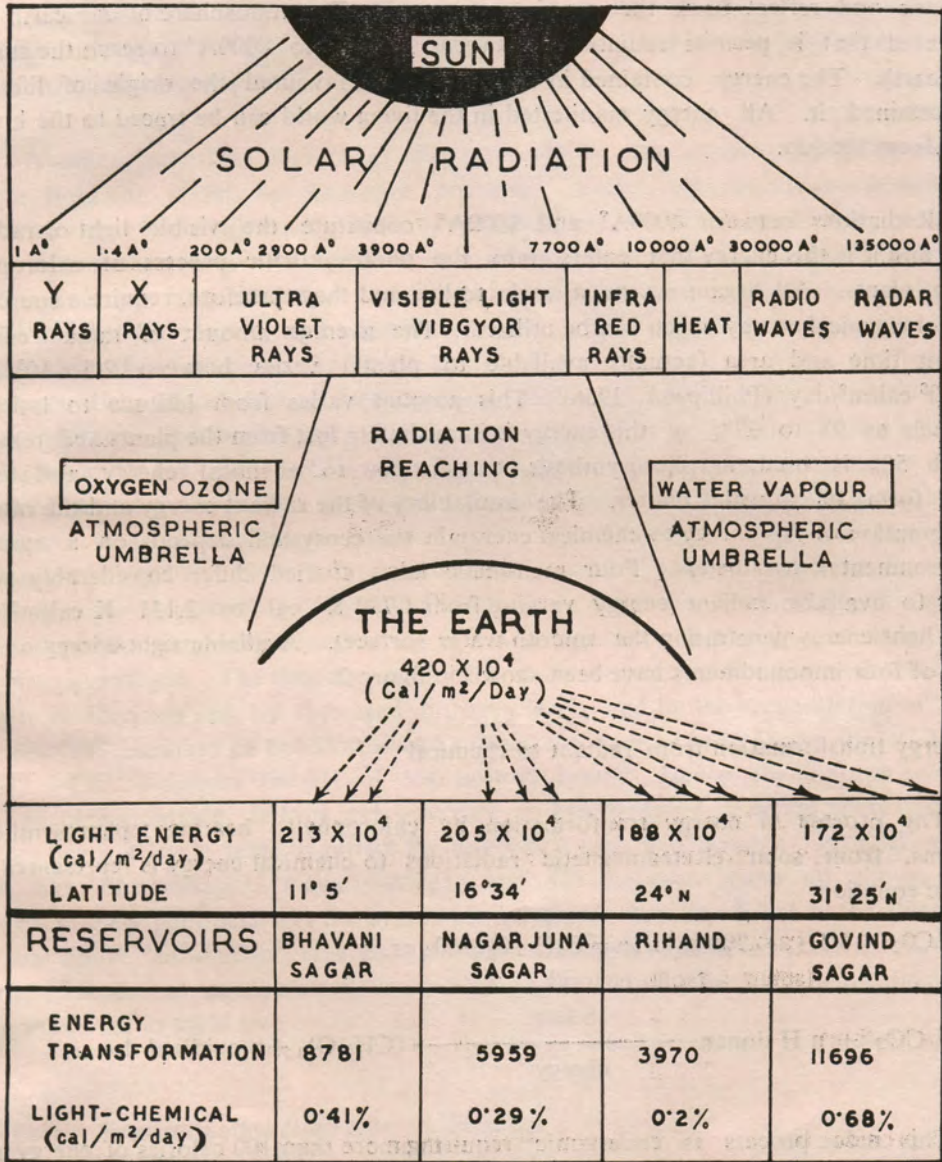
a) Radiant energy available on the lake surface

Sun sends kinetic energy in the form of electromagnetic radiations of different wave lengths ranging from 1A° to $1,35,000\text{A}^\circ$. The planets absorb some of these

Table—II
DYNAMICS OF CHEMICAL CONSTITUENTS
IN THE RESERVOIR BIOTOPE

Depth (m)	Govindsagar				Nagarjunasagar			
	DO (ppm)	pH	CO ₂ (ppm)	HCO ₃ (ppm)	DO (ppm)	pH	CO ₂ (ppm)	HCO ₃ (ppm)
0	8.3	8.2	Nil	62.0	5.98	8.6	Nil	125.0
3	8.3	8.2	Nil	63.0	5.98	8.6	Nil	125.0
6	6.9	8.0	Nil	65.0	5.98	8.6	Nil	127.0
9	6.0	7.85	2.0	65.0	5.6	8.6	Nil	127.0
12	5.7	7.85	2.0	70.0	5.6	8.6	Nil	130.0
15	5.7	7.85	2.0	72.0	5.6	8.5	Nil	130.0
18	5.0	7.85	6.0	78.0	2.9	8.2	5.04	141.0
21	5.0	7.85	6.0	80.0	2.9	8.2	5.04	143.0
24	4.5	7.85	6.0	80.0	2.9	8.2	5.04	143.0
27	4.5	7.85	6.0	80.0	2.9	8.2	5.04	150.0
30	4.5	7.85	6.0	80.0	2.9	8.2	5.04	150.0
33	4.5	7.65	8.0	82.0	2.6	8.2	5.04	150.0
36	4.2	7.65	8.0	82.0	2.6	8.2	5.04	150.0
39	4.2	7.65	8.0	82.0	2.6	8.2	5.04	152.0
42	2.8	7.65	8.0	82.0	2.5	8.2	5.04	152.0
60	2.0	7.50	11.0	84.0	—	—	—	—
Depth (m)	Bhavanisagar				Rihand			
	DO (ppm)	pH	CO ₂ (ppm)	HCO ₃ (ppm)	DO (ppm)	pH	CO ₂ (ppm)	HCO ₃ (ppm)
0	7.9	8.35	Nil	34.0	8.2	8.0	8.0	44.0
3	7.5	8.35	Nil	34.0	8.2	8.0	8.0	44.0
6	5.0	7.30	4.5	44.0	8.0	8.0	10.0	44.0
9	3.5	6.90	6.0	48.0	7.0	7.9	10.0	40.0
12	2.0	6.8	9.0	51.8	7.0	7.9	10.0	40.0
15	1.0	6.8	11.0	56.0	6.5	7.9	10.0	38.0
18	—	—	—	—	6.5	7.9	12.0	38.0
21	—	—	—	—	6.5	7.9	12.0	36.0
24	—	—	—	—	6.5	7.8	13.0	36.0
42	—	—	—	—	6.3	7.7	13.5	34.9

Fig 2



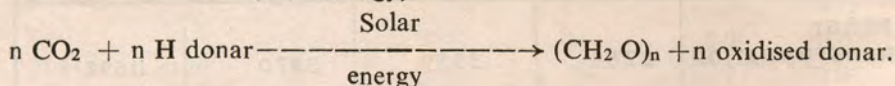
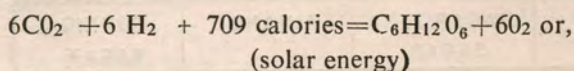
AVAILABLE LIGHT ENERGY IN DIFFERENT RESERVOIRS AND ITS TRANSFORMATION TO CHEMICAL ENERGY BY PHOTOSYNTHETIC ORGANISMS.

radiations and reflect back the rest into the space. The atmosphere of our earth is so constituted that it permits radiations between 3700\AA to 8000\AA to reach the surface of the earth. The energy contained in this band has favoured the origin of life and has sustained it. All energy manifested in the living world can be traced to the kinetic energy from the sun.

Radiations between 4000\AA and 8000\AA constitute the visible light or radiant energy and it is this energy that enters into the photosynthetic process of chlorophyll bearing plants. All organisms must work to live and they therefore, require a source of potential chemical energy which can be utilized. The average amount of radiant energy per unit time and area (actually available to plants) varies between 2.5×10^8 and 6.0×10^8 cal/m²/day (Phillipson 1966). This amount varies from latitude to latitude. As much as 95 to 99% of this energy is immediately lost from the plants and remaining 1 to 5% is used in photosynthesis, transformed to chemical energy and stored in the form of organic matter. The availability of the radiant energy and the rate of transformation of this energy to chemical energy in the ecosystem depends on a number of environmental parameters. Four man-made lakes studied differ considerably with respect to available radiant energy varying from 1,720 K cal to 2,131 K cal/m²/day (visible light energy penetrating the smooth water surface). Available light energy on the surface of four impoundments have been shown in figure 2.

b) Energy transformation from radiant to chemical

The process of energy transformation by chlorophyll bearing photosynthetic organisms, from solar electromagnetic radiations to chemical energy is represented by the basic equation



This redox process is endergonic requiring more than 100 calories of energy per mole of CO₂ reduced and consequently through photosynthetic process of plants can store large amount of energy in the form of energy rich organic compounds. From the above equation it is apparent that energy associated with gross liberation of oxygen is roughly 3.68 calories/mg of oxygen liberated and hence measurement of gross

liberation of oxygen will give a measure of the radiant energy trapped as chemical energy during the process.

$$WO_2 \text{ (mg/cm}^2\text{/day)} = \frac{F \times S}{3.68}$$

$$\text{or, } WO_2 \text{ (g/m}^2\text{/day)} = 2.71 \times F \times S$$

where WO_2 = the weight of oxygen liberated.

F = the efficiency with which light energy is transformed to chemical energy.

S = visible light energy & 3.68 = oxycalorific value for algal photosynthesis.

Assuming that all nutrient substances of biological significance are available for algal photosynthesis in any piece of natural water, the capacity of that water to produce oxygen can be predicted from a knowledge of the amount of solar radiation actually received at the water surface. The visible or photosynthetically active portion of sun light (wave length approximately 4000\AA to 8000\AA), the prime factor for photosynthetic oxygenation can be easily obtained from the table furnished by United States Weather Bureau (Kimble 1935).

c) Calculation of photosynthetic efficiency, F.

The actual photosynthetic efficiency 'F' is nearly equal to the calories of energy 'H,' in the algal cells produced per unit space per day divided by the amount of visible solar energy 'S' received at the water surface per unit space and day (or $F = H/S$). H can be determined either from oxygen values or from the algal weight which may be found out by dividing the oxygen values by 1.63 (Ganapati 1970).

The general formula for calculating photosynthetic efficiency is

$$\text{Photosynthetic efficiency} = \frac{L_n}{L_n - 1} \times 100$$

where $L_n - 1$ = solar radiation.

and L_n = energy in primary producers.

The energy fixed by producers can be obtained either from oxygen produced during photosynthesis (3.68 calories are required to produce one mg of O_2) or by converting oxygen to carbohydrates by multiplying with 0.937 (based on the heat of com-

bustion of carbohydrates as glucose) and as one gram of carbohydrate is equivalent to 4.1 K cal of energy, multiplying the carbohydrate values with 4.1 gives the energy fixed by producers as carbohydrate. There are many ways in which the sun light could be treated total incident sun light, the visible radiation useful for photosynthesis, light penetrating to the community after correcting for reflection and back scattering, light absorbed by the specific photosynthetic pigments. Each one of these leads to a different index of efficiency. Four man-made lakes studied differ considerably with respect to their efficiency to convert light energy to chemical energy varying between 0.2 % in Rihand and 0.7% in Govindsagar. Factors limiting the rate of energy fixation during primary production are light and nutrients such as phosphate, nitrogenous substances and silicates. Where nitrogen fixing blue green algae are seen nitrogen alone is rarely a limiting factor. Carbondioxide can be a limiting factor where there is permanent bloom of blue green algae such as *Microcystis* spp. in tropics where pH may be as high as 9 or 10.

The magnitude of energy fixation differs considerably in four man-made lakes being maximum (11,696 cal/m²/day) in Govindsagar and minimum (3,802 cal/m²/day) in Rihand. Gessner (1960) observed that euphotic lakes of temperate rsgions show a gross production of the order of 1,840—18,400 cal/m²/day during the seasons of maximum growth. For the Lake Victoria the average daily estimate is of the order of 26,054 cal/m²/day (Talling 1961). Ganapati & Sreenivasan (1972) noted average daily production of 20,054 cal/m²/day in Amaravati and 10,598 cal/m²/day in Stanley, the two man-made lakes in Tamil Nadu, showing a photosynthetic efficiency between 0.27—0.67% and 0.3—0.59% respectively. The efficiency in these two tropical impoundments is quite comparable with the values obtained in the four man-made lakes under the present study.

The transformation of light energy to chemical energy confirms the laws of thermodynamics.

$$\begin{array}{ccc} \lambda_{n-1} & \lambda_n & H \\ \text{(light energy)} & = & \text{(energy fixed by producers)} + \text{(energy lost to the environment)} \end{array}$$

λ_n is known as gross energy fixation or gross primary production. A part of this energy is used by the plants themselves for their own metabolic activities (measured by respiration) and remaining is stored by them. The storage of energy by plants is termed as net energy fixation or net primary production and according to the thermodynamic

laws.

$$\text{Gross energy fixation} = \text{Energy assimilated} + \text{Energy of respiration}$$

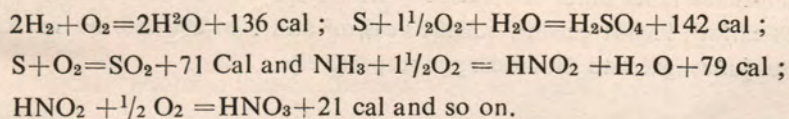
$$\lambda_n = A_n + R$$

Studies made in four impoundments revealed that 41.7 to 65.2% of energy fixed by producers (gross energy) stored by the producers and the rest is lost as energy of respiration.

3. Other sources of energy input

a) Chemo-synthetic source of energy in the ecosystem

Photosynthetic organisms represent one group of autotrophic organisms which store energy from inorganic raw materials. There is another group of autotrophic organisms which rely on inorganic substances as electron donors. These organisms derive their energy from inorganic chemical bonds, rearrangement of electrons e.g., oxidation of H_2 , N_2 , S, NH_3 , NO_2 and so on (chemosynthesis).



The contribution of chemosynthetic energy as an energy source may not be so significant for other heterotrophs but it is important from the point of view of the organisms which get energy through this source.

b) Energy import in the reservoir biotope from allochthonous source

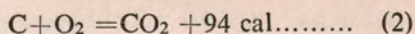
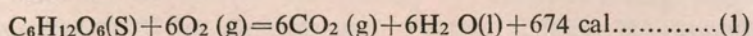
If there is no other source of energy, then the energy fixed by autotrophs gives the available energy for the ecosystem. But in aquatic ecosystems like man-made lakes the energy represented by primary producers gives only a part of the available energy as large amount of energy is imported from the catchment by inflowing waters. Hence, to account for the total energy available in the reservoir ecosystem, the energy other than that fixed by producers must also be accounted for and thus.

$$\text{Energy available at the lowest trophic level} = \text{Chemical energy fixed by producers} + \text{Energy imported from allochthonous source}$$

Direct measurement of allochthonous import of energy is very difficult in man-made lakes. Some indirect methods with limitations have been discussed later in this paper.

c) Energy release during decomposition process

Most of the bacteria responsible for decomposition obtain energy for their metabolic processes by oxidation of carbohydrates and related organic materials, as illustrated by the equation below :



The Value of ΔH in the above equation (1) will depend on whether the H_2O is in the l or g state. At $25^\circ C$ and one atmospheric pressure when H_2O is in l state, O_2 in the g state and $C_6H_{12}O_6$ in the S state, $\Delta H = -674$ cal/mole of glucose i. e., 674 cal of energy is released by the oxidation of one mole of glucose. In the equation (2) $\Delta H = -95$ cal/mole CO_2 evolved. The consumption of oxygen and the liberation of CO_2 are therefore, a measure of the energy at the bottom. Birge and Juday (1911), Ruttner (1953) and Waldichuk (1956) have all shown that the intensity of decomposition in the tropholytic zone reflected by the decline of oxygen can be used as a measure of productivity or energy resource at the bottom. Four man-made lakes differ considerably with respect to bottom energy being of the order of 36,328 cal/m², 93,641 cal/m², 1,39,010 cal/m² and 3,04,690 cal/m² in Rihand, Bhavanisagar, Nagarjunasagar and Govindsagar respectively.

4. Secondary Production

(Energy utilization in the impoundments)

a) Biotic communities present in the lakes

Impoundments generate qualitative transformation of plankton population, rheophil species giving way to limnophil species. The biotic communities are linked with one another by energy chains and a dynamic equilibrium exists between producers, consumers and decomposers. As the flow of energy is unidirectional, entering from one end and living through the other, it is essential to know the various organisms present and their mode of obtaining

Bhavanisagar :

Phytoplankters of this reservoir are represented by Cyanophyceae, Chlorophyceae,

Bacillariophyceae and Dinophyceae. Among the four groups, Cyanophyceae generally contributed the bulk. The main constituents of the group were species of *Anacystis* or *Microcystis*, *Oscillatoria* and *Anabaena* of which *Anacystis* was the most dominant. Next in the order of abundance was Chlorophyceae which was represented by species of *Pediastrum* and *Spirogyra*. Bacillariophyceae was represented by *Synedra* and Dinophyceae by *Ceratium*. The zooplankton was represented by *Cyclops* and *Diaptomus* among copepods, *Brachionus*, *Keratella* and *Polyarthra* among rotifers, *Arcella*, *Actinosphaerium* among protozoans and *Daphnia* among cladocerans. The biota were represented by oligochaetes, *Chironomus* and *Chaoborus* larvae and mayfly nymphs. The important fishery of this reservoir included *L. calbasu*, *C. mrigala*, *C. catla*, *L. rohita*, *P. dubius*, *L. fimbriatus*, *L. bata*, *M. aor* and *W. attu*. *L. fimbriatus* and *L. bata* started forming minor fishery from 1973-74 onwards. Among carps *L. calbasu* and among catfishes *M. aor* and *W. attu* dominated.

Nagarjunasagar :

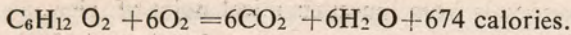
Among the phytoplanktons *Anacystis* or *Microcystis* (Myxophyceae) was the most dominant followed by *Pediastrum* (Chlorophyceae), *Fragilaria*, *Gyrosigma*, *Navicula*, *Synedra* and *Tabellaria* (Bacillariophyceae). The zooplankton was mainly represented by rotifers like *Keratella* and *Filinia*, copepods like *Cyclops* and *Diaptomus* and cladocerans like *Daphnia* and *Chydorus*. Biota was mainly constituted by gastropods, bivalves, insect larvae, chironomids and oligochaetes. Bays, which were generally richer in biota, showed large population of bivalves and gastropods. Commercial fishery in the reservoir was mainly constituted by *L. fimbriatus*, *L. calbasu*, *C. catla*, *L. rohita*, *C. mrigala*, *T. khudree*, *P. pangasius*, *W. attu*, *M. seenghala*, *M. aor* and *S. childreni*. The present fishery structure shows that catfishes have established a clear dominance (70 to 75%) over carps (25%).

Govindsagar :

The phytoplankton of this reservoir is mainly represented by Dinophyceae (*Ceratium*). Other groups that occur are Myxophyceae (*Microcystis*), Chlorophyceae and Diatomaceae. Zooplankton is mainly represented by *Diaptomus*, *Cyclops* and their nauplii. Benthic organisms are represented mainly by dipteran larvae (*Chaoborus* and *Chironomus*) and mayfly nymphs. Among the fishery, the Gangetic carps have shown a marked improvement. *C. catla*, *C. mrigala*, *L. rohita*, *T. putitora*, *C. carpio*, *L. dero*, *M. seenghala* are the dominant species in commercial catches. Silver carp, *H. molitrix*, which got stocked in the reservoir rather accidentally during 1972, has greatly improved its abundance during recent years.

selective feeding on phytoplanktons. As such all the energy represented by primary producers is not always utilised by the consumers directly and the unutilized energy reach the bottom after the death of the producer organisms. This energy can be utilized by detritus feeders through detritus chains. Workers like Teal (1957), Odum (1957) and Odum (1975) etc., have studied the flow of energy through both the chains and highlighted the importance of detritus path. Studies made in the four man-made lakes have shown that in the tropical reservoirs, Bhavanisagar and Nagarjunasagar, the flow of energy is more through detritus chain than grazing chain, specially in Bhavanisagar, where about 65% of the energy utilization is through primary detritus consumption. In both the reservoirs *Microcystis* is the dominant primary producer but it is not much utilized directly by the existing fishes. As a result the energy represented by this primary producer reach the bottom where it is utilized by detritivores. In Bhavanisagar, the major fishery is *L. calbasu* which utilises the primary energy not directly but through detritus. Similarly in Nagarjunasagar, which is dominated by a secondary consumer, a catfish, *P. pangasius* the detritus energy is utilised through moluscs (gastropods and bivalves, primary consumers getting detritus energy). In Govindsagar, the energy utilization is both through detritus and grazing chains but in Rihand the flow of energy is mainly through grazing chain.

Heterotrophs get their nutritional energy from the breakdown (oxidation) of organic material stored by the producers and passed on to consumers, the process of energy liberation being represented by the equation.



The energy consumed by heterotrophs is channeled in many ways and the energy transformation is represented as :

$$\begin{array}{ccccccc} \text{Energy of food} & = & \text{Energy of} & + & \text{Energy of} & + & \text{Energy of} \\ \text{uptake (C)} & & \text{growth (P)} & & \text{respiration} & & \text{faeces (F)} \\ & & & & \text{(M)} & & + \\ & & & & & & \text{urine (U)} \end{array}$$

Winberg (1956) showed that for freshwater fishes the energy of urine and faeces combined is nearly 20% of the energy of food uptake. The above equation may then be modified as :

$$\text{Energy of food (C)} = 1.25 (\text{Energy of growth (P)}) + \text{Energy of metabolism (M)}$$

The storage of energy in the heterotroph's tissue, secondary production or secondary accumulation of energy can be obtained by knowing the calorific value of the representative

fishes and the total yield. In controlled aquatic ecosystems, it is possible to calculate the energy involved in various processes but in man-made lakes the complexity of organisms present and their complex mode of feeding and energy assimilation put restrictions on energy calculations. In some reservoirs dominated by single species (*Tilapia* in Amara-vati and *Catla* in Rihand) the energy calculations are quite easy but in other reservoirs the energy harvest as fish can be used in production efficiency calculations.

c) Comparison of productivity efficiencies among the reservoir biotopes

By their very location the radiation reaching these waters vary considerably. The impoundments also differ in the efficiency of photosynthetic utilization of light energy being maximum in Govindsagar and minimum in Rihand. Sreenivasan (1972) has noted better utilization of light energy in small ponds. Comparison of the photosynthetic energy with the energy harvest as fish shows an interesting pattern. A good conversion indicates the efficiency of harvest of fish and of management practices. The two tropical impoundments Bhavanisagar and Nagarjunasagar receive almost similar light radiation and have quite high photosynthetic efficiency but the energy harvest as fish is much higher in Bhavanisagar than in Nagarjunasagar. The conversion of Photosynthetic energy fixation to fish and light to fish is 0.22% and 0.0009% respectively in Bhavanisagar but in Nagarjunasagar the values are 0.043% and 0.00013% only. This clearly indicates that the management has failed in Nagargunasagar and the energy harvest is much less than expected though the limnochemical features of the two lakes show their productive nature. Govindsagar, another productive reservoir from limno-chemical point of view, also shows high values of conversion from chemical energy fixed to energy harvest (0.15%) or light to fish (0.001%). In fact this reservoir has highest light energy conversion to fish, though the incident light energy is less in comparison to other reservoirs. The energy harvest and the two efficiencies are minimum in Rihand.

It is interesting to note that Bhavanisagar and Govindsagar are dominated by primary consumer carps and hence, the energy conversion is higher. In Nagarjunasagar, though the limno-chemical features have shown its productive nature, the fishery is dominated by catfishes which feed at higher trophic levels causing greater loss of energy and poor energy harvest. Similarly Rihand is dominated by a single species *C. catla* and the energy harvest is very poor in this reservoir. Limno-chemical features of the reservoir also indicate its poor productivity. Nicolsky (1963) stated "the nearer the useful end product stands to the first link in food chain the higher the yield from the water mass". Elster (1961) recorded a yield of 300 kg/ha (mainly *Tilapia*) from two lakes in Egypt. Hopher (1962) noted that the ratio of algal weight to fish weight in fertilized fish ponds

in Israel was 100 : 1.3 to 2.3. Lindemann (1942) recorded that as against 480 cal/cm²/yr of primary production the secondary consumer were 2.3 and tertiary consumer (fish) 0.3 cal in lakes Mondeta.

The energy conversions in four man—made lakes studied have been presented in Table III. The studies of conversion efficiencies, light to chemical (photosynthesis), chemical to fish and light to fish clearly indicate the extent of utilization of the energy resource and the management measures to be adopted for maximising the energy output from man—made ecosystems. The low energy output from the various reservoirs in the country is due to lack of understanding of the energy relationships at various levels and the improper management practices resulting in partial utilisation of the energy resource.

5. Trophic Dynamic Models of Productivity of Reservoirs

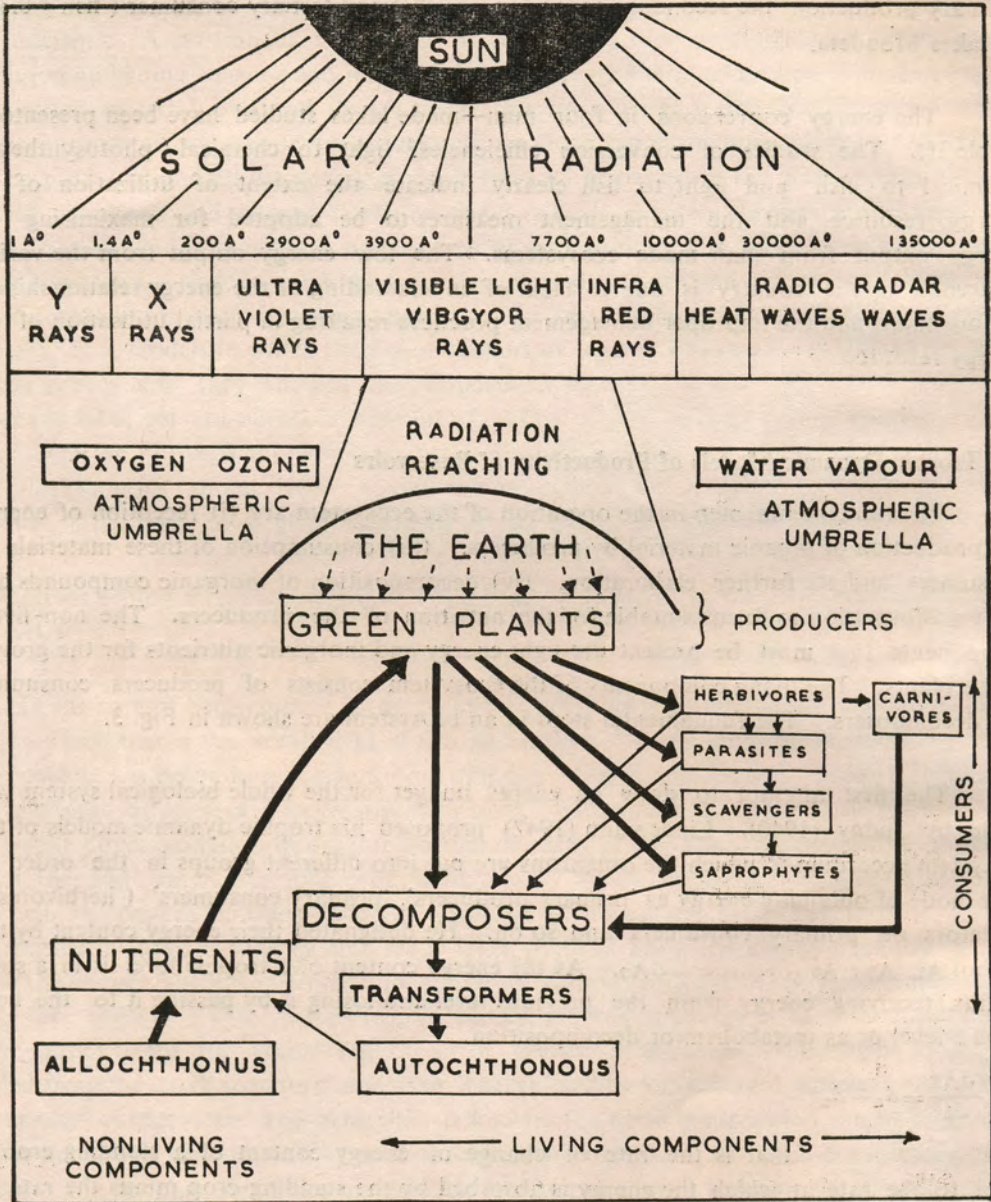
The fundamental step in the operation of the ecosystem are (i) reception of energy, (ii) production of organic material by producers, (iii) consumption of these materials by consumers and its further elaboration, (iv) decomposition of inorganic compounds and (v) transformation to forms suitable for the nutrition of the producers. The non-living components that must be present are light energy and inorganic nutrients for the growth of the plants. The living components of the ecosystem consists of producers, consumers and decomposers. The fundamental steps in an ecosystem are shown in Fig. 3.

The first attempt to draw an energy budget for the whole biological system was made by Juday (1940). Lindemann (1942) proposed his trophic dynamic models of the ecosystem according to which the organisms are put into different groups in the order of their mode of obtaining energy as 'primary producers', 'primary consumers' (herbivores), predators on primary consumers and so on. He designated their energy content by the symbol $\Lambda_1, \Lambda_2, \Lambda_3, \dots, \Lambda_n$. As the energy content of a trophic level is in a state of flux receiving energy from the previous level and losing it by passing it to the next trophic level or as metabolism or decomposition.

$$\frac{d\Lambda_n}{dt} = \mathcal{L}_n - \mathcal{L}_n'$$

that is the rate of change of energy content of a standing crop is equal to the rate at which the energy is absorbed by the standing crop minus the rate at which the energy is lost from it. $\mathcal{L}_n =$ rate of flow of energy from the previous level, \mathcal{L}_n and $\mathcal{L}_n' =$ rate at which the energy flows to the next trophic level plus the rate of

Fig 3



COMPONENTS OF RESERVOIR BIOTOPES AND FUNCTIONING OF THE ECOSYSTEM

TABLE - 3
PHOTOSYNTHETIC ENERGY FIXATION AND ENERGY CONSERVATIONS
IN RESERVOIR BIOTOPES

	Bhavani-sagar	Nagarjuna Sagar	Rihand	Govind sagar
1. Location (lat)	11°5' N	16°34' N	24° N	31°25' N
2. a) Total visible radiation K cal/m ² /day	2,130	2,050	1,884	1,720
b) Total radiant energy cal/m ² /yr × 10 ⁵	7,775	7,483	6,877	6,278
3. Photosynthetic production				
a) O ₂ g/m ² /day	2.38	1.619	1.003	3.178
b) O ₂ g/m ² /yr	870.89	590.93	377.04	1159.97
c) energy cal/m ² /yr × 10 ⁶	3.205	2.175	1.387	4.269
4. Efficiency of conversion of radiant energy to chemical energy (%)	0.412	0.290	0.202	0.682
5. Fish production				
a) Kg/ha/yr (average)	59.4	7.9	4.4	53.6
b) g/m ² /yr	5.94	0.79	0.44	5.36
c) as energy cal/m ² /yr	7128	948	528	6432
6. Conversion of energy %				
a) Fish/photosynthetic 5 (C)—3 (C)	0.220	0.043	0.038	0.151
b) Fish/light 5 (C)—2 (b)	0.00091	0.00013	0.000076	0.0010
7. Fish/O ₂ production 5 (b)—3 (b)	0.680	0.134	0.116	0.462
8. a) Photosynthesis gC/m ² /yr	326.58	221.6	141.39	435.00
b) Fish yield as gC/m ² /yr	0.594	0.079	0.044	0.536
c) % conversion	0.182	0.0456	0.0311	0.123

energy loss as respiration and by decomposition (by definition λ^n is negative). In the Lindemann's dynamic model primary producers are shown as fixing energy from sun light and nutrients. A portion of this energy is released by their own metabolic activities as respiration and some energy and material pass to the primary consumers (Herbivores). The unused material dies and decays transferring their energy to the decomposers. This process is repeated at each trophic level until we reach top carnivores which by definition have no predators and all the energy is either respired or passed to the decomposers. Thus material circulates and energy flows on one way basis, it enters through autochthonous energy fixation and leaves the system as heat of respiration. The Lindemann's dynamic model represents a closed system and it was supposed that all the energy available come from autochthonous photosynthesis. Subsequently Teal (1957) and Odum (1957) presented the energy flow models in which the major import of energy was from outside or allochthonous source and they showed the importance of energy flow through detritus chain. Man-made lakes get considerable amount of energy from allochthonous source. The energy entering through autotrophic photosynthetic energy fixation and the energy import from allochthonous source both should be considered to know the energy entering the lake. The gross ecological efficiency at any level in general may be written as :

Gross ecological efficiency = $\lambda^j / \lambda^i \times 100$ (where λ represents the energy available at any level).

In the case of herbivores λ^i is the chemical energy fixed by producers and λ^j is the energy output that is the total yield of fish as calories. As we move up in the chain the energy calculation becomes more and more difficult. For fishes feeding through detritus chain λ^j = total calories of detritivores harvested. Estimation of bottom energy can be done by the direct oxidation of organic bottom deposits or by measuring the redox potentials at the soil water inter-phase or indirectly by estimating the products of oxidation i. e., decline of oxygen in the tropholytic layers or accumulation of carbon dioxide. To draw trophic dynamic models of man-made lakes we must know the energy fixed by producers, the energy brought in from allochthonous source (λ^x), the energy accumulation at the lake bottom (λ^z), various trophic chains, the loss of energy at each level and the energy output from the lake. The flow of energy at different levels can be roughly obtained from the catch structure and the energy values of different species. As the total energy output from the reservoir is known, the catch composition can be used to estimate the energy contribution by each species. On the basis of various estimates we can draw the trophic dynamics models for each impoundment to know the transformation of energy in these complex biotopes. For man-made lakes the gross ecological efficiency will be energy harvest divided by energy input (energy fixed by producers +

energy brought from outside). If λx_1 , λx_2 , λx_3 and λx_4 be the energy import in the four man-made lakes Bhavanisagar, Nagarjunasagar, Rihand and Govindsagar then the gross ecological efficiency in the above lakes will be

$$\frac{7,128}{320500 + \lambda x_1} + \frac{948}{2175000 + \lambda x_2} + \frac{528}{1387000 + \lambda x_3} + \frac{6432}{4269000 + \lambda x_4}$$

(the energy harvest represents average for five years). Calculation of λx is a very difficult task and some approximate methods are to be adopted. One such method is to measure the bottom energy and the unused chemical energy from autotrophic source. The difference between the two will give some idea about the allochthonous import of energy.

6. Present energy status of the impoundments

Four man-made lakes differ considerably in the energy transformation from light to chemical and its further utilization. The flow of energy in the lakes have been presented in Table (iv) and (v).

Bhavanisagar

About 68.6% of the energy output in this reservoir is contributed by primary consumers, 3.4% by secondary and 28% through by consumers. Of the total 68.6% energy utilised through primary consumption only 5.4% is through grazing chain and the rest 63.2% through detritus chain. The bottom energy in the reservoir is considerably high ($9,53,00 \times 10^6$ cal/ha) and as the major flow of energy is through detritus chain, the reservoir shows high energy of conversion from light to fish or chemical to fish and correspondingly better energy harvest.

Nagarjunasagar

Only 26.4% of the energy output from this reservoir is contributed by primary consumers (12.5% through grazing and 13.9% through detritus chains respectively) and the remaining 73.6% by secondary (34.5%) and tertiary (39.1%) consumers. The reservoir has very high energy resource at the bottom ($14,00,000 \times 10^6$ cal/ha) but this is not all utilised through primary consumption. It needs to be mentioned here that *Pangasius pangasius* is the domianating catfish in the reservoir and it utilises bottom energy through secondary consumption contributing 34.5% of the energy obtained. The non utilisation of the vast energy at the bottom specially through primary consumption has

Table—IV

Flow of Energy in Different Impoundments

Man made Lakes	Incident light energy Cal/hr/yr X10 ⁶	AVAILABLE ENERGY		ENERGY UTILIZATION		Secondary consumption Cal/ha/yr X10 ⁶	Tertiary consumption Cal/ha/yr X10 ⁶
		Chemical energy fixed by producers Cal/ha/yr X10 ⁶	Bottom energy Cal/ha/yr X10 ⁶	Primary Consumption			
				Through gra- zing chain Cal/ha/yr X10 ⁶	Through detri- tus chain Cal/ha/yr X10 ⁶		
Bhavni Sagar	77,75,000	32,050	9,53,000	3.60	43.80	2.40	19.30
Nagarjuna Sagar	74.83,000	21,7	14,00,000	1.05	1.10	2.90	3.59
Rihand	68,77,000	13,900	3,60,000	3.8	—	1.3	—
Govind Sagar	62,78,000	42,700	30,70,000	23.00	16.90	24.70	0.80
	Efficiency of conversion			% Utilization of energy			
Bhavani Sagar	0.412%			5.4	63.2	3.4%	28%
Nagarjuna Sagar	0.290%			12.5	13.3	34.5%	39.1%
Rihand	0.202%			80.0	—	10 to 15%	—
Govind Sagar	0.682%			35.1	25.0	37.8%	2.1%

Table—V

Important Fisheries of Different Impoundments and their energy contribution

NAGARJUNASAGAR			RIHAND		
Species	Average yield kg/ha/yr	Cal/ha/yr x10 ⁶	Species	Average	Cal/ha/yr x 10 ⁶
<i>L. fimbriatus</i>	0.82	0.98	<i>C. catla</i>	3.97	4.68
<i>L. rohita</i>	0.06	0.07	<i>Others</i>	0.43	0.62
<i>L. calbasu</i>	0.67	0.80			
<i>C. mrigala</i>	0.09	0.11			
<i>T. khudree</i>	0.17	0.20			
<i>C. catla</i>	0.16	0.19			
<i>P. pangasius</i>	2.26	2.71			
<i>M. seenghala</i>	0.54	0.65			
<i>M. aor</i>	1.20	1.44			
<i>S. childreni</i>	1.05	1.26			
<i>W. attu</i>	0.20	0.24			

GOVINDSAGAR			BHAVANISAGAR		
Species	Average yield kg/ha/yr	Cal/ha/yr x10 ⁶	Species	Average yield kg/ha/yr	Cal/ha/yr x 10 ⁶
<i>L. rohita</i>	10.0	12.0	<i>L. rohita</i>	3.5	4.2
<i>L. dero</i>	8.7	10.4	<i>L. fimbriatus</i>	0.1	0.12
<i>H. molitrix</i>	0.5	0.6	<i>C. mrigala</i>	7.2	8.6
<i>C. mrigala</i>	3.7	4.4	<i>P. dubius</i>	2.6	3.1
<i>C. carpio</i>	10.4	12.5	<i>L. calbasu</i>	26.8	32.1
<i>C. catla</i>	13.5	16.2	<i>C. catla</i>	2.4	2.9
<i>T. putitora</i>	7.1	8.5	<i>M. cor</i>	12.5	15.0
<i>M. seenghala</i>	0.8	0.9	<i>W. attu</i>	6.8	8.2

led to the poor harvest of energy from this reservoir, thus demanding the adoption of suitable management practices to enhance the output of energy from the reservoir.

Govindsagar

About 60% of the energy output from this reservoir is contributed by primary consumers of which 35.1% through grazing and 25% through detritus chains. The remaining 39.9% of energy is obtained mainly as secondary consumers. Owing to the proper utilisation of energy by the existing fishes this reservoir shows quite high conversion ratio either from light to fish or chemical to fish. However, both the bottom energy ($30,70,000 \times 10^6$ cal/ha) and autotrophic chemical energy ($42,700 \times 10^6$ cal/ha/yr) being very high, there is still enough scope to enhance the energy harvest from the reservoir.

Rihand

Almost 90 to 98% of the energy in this reservoir is utilised by a single species *C. catla*. Owing to the single species and single size group dominance this reservoir has shown minimum energy output. The reservoir also has minimum energy reserve at the bottom in comparison to other reservoirs. However, its proper utilisation by stocking the reservoir with multiple species at shorter food chain, will improve the yield.

7. Management practices for maximising energy output

Reservoirs are man-made ecosystems without parallel in nature. The impoundment deviates from a conventional evolutionary course and commences with a "trophic burst" during the first 2 or 3 years after the dam is sealed. When vegetated areas with rich soil are flooded, the initial biological processes are dominated by the microbial utilization of the flooded organic matter and by the large quantities of biogenic substances (nutrients) released from the soils and from the organic matter on decomposition. The great oxygen demand of these microbial processes generally results in low oxygen levels. Large population of algae, particularly the blue greens, develop reaching such large concentrations as to interfere with the use of water for domestic and industrial purposes. This is the most critical phase for management. The ecosystem has very high amount of available energy. If the proper management is not done at this stage it may lead to enormous population of weed fishes which ultimately create the condition for the large population of catfishes feeding at higher trophic levels. Once these catfishes get a foothold in the system the management will be more difficult. It is therefore, essential to

manipulate the system during the early stages so that the vast amount of available energy is properly utilised by stocking with fishes feeding at lower trophic chains (the energy utilization through primary consumption is essential for better conversion efficiencies). This can be seen by taking Nagarjunasagar and Bhavanisagar as examples. In Nagarjunasagar catfishes have established to such an extent that only 20 to 25% of the available energy is utilised by primary consumers and 75% by catfishes (secondary or tertiary). The reservoir shows poor energy harvest as fish though limnochemical features indicate its high productivity. In Bhavanisagar, where 68% of energy is utilised through primary consumers, the energy harvest is far better than that of Nagarjunasagar.

Hence proper management of the impoundments to utilise maximum energy by short circuiting the food chain, is the primary requirement for maximising energy output. From the above consideration it is apparent that the poor yield from Nagarjunasagar and Rihand is due to improper management whereas the other two reservoirs Bhavanisagar and Govindsagar, the proper management practices have increased the energy harvest to a large extent.

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