Standing Crops of Fishes in Three Small Lakes Compared with C14 Estimates of Net Primary Productivity

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ABSTRACT

The standing crops of fishes which inhabited three small lakes were estimated immediately after rotenone treatment by combinations of procedures which included collections of all fish along the shorelines, from the surface waters offshore, and from the bottoms in shallow water; collections and counts from random sampling areas on shore and in shallow water; and collections and counts from randomly selected transect lines on bottom in deep water by SCUBA divers. Estimates of the net primary productivities of the lakes were made by the C^{14} method. When the lakes are ranked according to their estimated standing crops, the order of ranking is confirmed by the estimated net primary productivity of the most productive lake, but is in conflict with the productivity estimates from the intermediate and least productive lakes. Analyses of the structures of the fish populations of the lakes before reclamation and evaluations of techniques are also presented.

INTRODUCTION

Knowledge of the standing crops of fishes and the primary productivities of waters has been considered fundamental to predictable manipulation of aquatic ecosystems. The purpose of this paper is to present the numbers, weights, and species compositions of the fish populations of three potential trout lakes in Maine, and to compare the total standing crops with the net primary productivities of the lakes estimated by the C^{14} method. Also described are a method for evaluating the standing crops of fishes in small lakes following complete kill with rotenone, and a limitation of the C^{14} method for estimating primary productivity of the very soft inland waters of Maine.

The possibility of enumerating standing crops of fishes in small lakes, ponds, and segments of streams by some direct-count method has appeared attractive to fishery biologists ever since rotenone products became readily available in the late 1930's. Procedures for using rotenone to assure the killing of all fishes in suitable waters were developed rapidly, and it remained only to enumerate the fishes that had been killed. This latter problem has been approached using various procedures (Eschmeyer, 1939; Bennett, 1943; Swingle, 1954; Brown and Tatum, 1962; Boccardy and Cooper, 1963; and many others) but it appears that only Carlander and Lewis (1948) have considered seriously or taken into account the proportion of a fish popula-

tion that sinks to the bottom in deep water after rotenone treatment and is thus unavailable for counting or sampling at the surface. As will be shown, the number of rotenone-killed fish which sink to the bottom of a small lake may be as great as the number which float at the surface; therefore, a deep-water sampling procedure using SCUBA divers developed during these studies will be described in some detail.

Interest in the possible existence of a single, easily obtained index to lake productivity was increased greatly with the publication of the first description of the C^{14} method by Steemann Nielsen (1951, 1952). Later papers by Ryther (1956), Doty and Oguri (1958), Frey (1959), and Hooper, Podoliac, and Sniezko (1961) drew further attention to the method, emphasizing its relatively simple field technique. Use of C^{14} in this study has revealed an important limitation of the method for certain types of water, however, and this limitation will be discussed.

METHODS

The Marine Department of Inland Fisheries and Game has been conducting a program of potential trout lake reclamation using rotenone since 1954. Usually 6 to 10 small lakes have been reclaimed each fall. As a corollary to this program, three lakes were chosen for investigation of the standing crops of fishes that existed before reclamation and for studies of primary productivity: Shagg Lake, Oxford

TABLE 1.—*Physical and biological characteristics of Shagg, Coleback, and Hills Lakes, Maine*

Characteristic	Lake		
	Shagg	Coleback	Hills
Surface area (acres)	55	20	19
Elevation (ft above msl)	850	130	1,200
Maximum depth (feet)	40	28	31
Typical summer temperatures (°F)			
Surface	70	70	68
10 feet	70	68	67
20 feet	50	64	46
30 feet	44	59[1]	44
Typical summer oxygen levels (ppm)			
Surface	7.4	8.6	8.4
10 feet	8.0	—	8.2
20 feet	7.4	9.0	4.0
30 feet	4.4	6.8[1]	2.4
Methyl orange alkalinity (ppm)	1–4	7	3–5
pH	6.1–7.9	6.3–6.9	6.2–6.5
Color of water	Clear	Lt. brown	Clear
Turbidity	None	None	None
Date of rotenone treatment	9 Sept. 1957	3 Sept. 1958	3 Oct. 1961
Fishes present before rotenone treatment[2]	*Osmerus mordax*	*Osmerus mordax*	*Osmerus mordax*
	Catostomus commersoni	*Lepomis gibbosus*	*Chrosomus eos*
	Ictalurus nebulosus	*Anguilla rostrata*	*Ictalurus nebulosus*
	Esox niger	*Esox niger*	*Rhynichthys atratulus*
	Roccus americanus	*Catostomus commersoni*	*Salvelinus fontinalis*
	Micropterus dolomieui		

[1] Observations taken at depth of 25 feet.
[2] Fishes listed in the order of their numerical abundance in each lake.

County; Coleback Lake, Washington County; and Hills Lake, Franklin County. These lakes were chosen because (1) they had physical characteristics which assured a high probability of obtaining complete kills with rotenone; (2) they were small enough (maximum area, 55 acres) to give us confidence that the fish pickup and sampling operations could be handled in a few days with the personnel and facilities available; (3) they had negligible tributary systems and outlets and high, firm shorelines, features deemed necessary for efficient pickup of fish that floated to the surface and then drifted ashore; (4) they had clear water and depths not greater than 40 feet, features necessary to insure that the SCUBA divers would be able to see and pick up samples of fish that sank to the bottom; and (5) they were easily accessible by road and had good boat landings so that fish could be collected, counted, weighed, and disposed of rapidly and efficiently. Descriptions of the three lakes are presented in Table 1.

Commercial preparations containing 5 per cent of rotenone or 2.5 per cent of rotenone plus a synergist in an emulsifying carrier were used in the treatment of Shagg, Coleback, and Hills Lakes. Shagg and Hills Lakes received concentrations of 1.0 ppm, and Coleback Lake received a concentration of 0.75 ppm. Application procedure was simply to spray the rotenone-bearing material mixed with water onto the surfaces of the lakes using a portable pumping apparatus carried in a small boat. Spraying was continued until the amount calculated to be necessary to provide the required concentration had been applied. In addition to surface spraying, ⅓ to ½ of the rotenone-bearing material was pumped down into and beneath the metalimnions in Shagg and Hills Lakes.

Fish began to show distress within 30 minutes and to die within an hour after the rotenone applications began. Subsequent sampling operations demonstrated that all fish were killed within 24 hours or less in each lake.

Procedures for enumerating the fish that had been killed by the rotenone treatments differed among the three study lakes, and will therefore be described separately.

Shagg Lake

Recovery and enumeration of fishes killed by rotenone in Shagg Lake were divided into four distinct operations: (1) collection of all fish that floated at the surface; (2) collection of all fish that sank to the bottom in depths of

10 feet or less; (3) collection of samples of the fish that sank to the bottom in depths greater than 10 feet; and (4) counting, measuring, and recording length, weight, and species composition of the fish recovered.

Surface collections.—Because one of the objectives of the fish collection operation at Shagg Lake was to determine what proportion of rotenone-killed fish would surface and what proportion would sink, and because it was considered a possibility that some of the fish which surfaced initially might later sink if not disturbed, floating fishes were collected only after they had drifted ashore. Three two-man crews used canoes and waders to work carefully along the shore picking up all the fish they encountered. Fish began drifting ashore within several hours after the rotenone had been applied, and the shore pickup was completed during the third day after reclamation. Most of the shoreline areas had to be examined several times because of delayed surfacing of many of the fish.

Collections from the bottom in depths of 10 feet or less.—The 10-foot bottom contour of Shagg Lake was marked with buoys before application of the rotenone began. On the day after the rotenone application, three divers using snorkels and attended by a boat began picking up the fish that had settled to the bottom. The area of the 0- to 10-foot zone was 23 acres, and it required 2 full days for the divers to collect all the fish. The divers worked together more or less in line, sweeping systematically around the lake. Spot checks of the bottom in the pickup zone after the divers had passed showed that few fish had been missed.

Deep bottom samples.—Four equally spaced transect lines were laid out normal to the long axis of the deep-water zone of Shagg Lake and marked with flags on the shore. Total length of the lines from 10-foot contour to 10-foot contour was 4,023 feet. Three divers using SCUBA gear entered the water at the west end of a transect line and proceeded to pick up all fish seen in a 20-foot strip along the line. The divers worked side by side, the outer two holding the ends of a 20-foot rope to measure the width of the sampling strip while the diver in the center held the middle

of the rope and kept the team on course with a compass. All three divers picked up the fish they encountered within the 20-foot strip and carried them along in a mesh bag. It required 1 full day to complete the pickup of fish along the deep sampling lines.

The area of bottom included in the sampling strips was 1.81 acres, an area approximating 5.66 per cent of the 32 acres of Shagg Lake which have depths greater than 10 feet. Fish collected from the sampling lines were tabulated separately by line and species, and the lengths of the individual lines were known, thus allowing the data to be treated according to a method of representative sampling in irregular areas described by Schumacher and Chapman (1954, pp. 101–106). According to this method, the sampling strips were visualized as consisting of individual segments each 100 feet long, and weighted average numbers and weights of fish collected in the 40.23 segments examined were calculated. The variances of these estimates are given as

$$S^2(\bar{y}_w) = \frac{1}{\sum\limits^n (w)} \left\{ \frac{1}{n-1} \left(\sum\limits^n [w(y_w)^2] - \frac{[\sum\limits^n (wy_w)]^2}{\sum\limits^n (w)} \right) \right\},$$

and the standard errors as

$$S(\bar{y}_w) = \sqrt{S^2(\bar{y}_w)},$$

where $\bar{y}_w$ = the weighted mean, the average number or weight of fish per segment in all sampling lines, y_w = the average number or weight per segment within any one sampling line, w = the number of 100-foot segments in a line, and n = the number of lines. Expansion of the weighted means to yield population estimates for the entire area of lake bottom under consideration was done using the expression

$$P = \bar{y}_w(k),$$

where P = the required estimate of the population, and k = the total number of 100- by 20-foot units of area in the deep-sampling zone; i.e., $k = 43,560 \times 32/2,000 = 697$. The standard errors of the means were also expanded by the factor k.

Data collecting.—Collecting crews brought their fish to a data station where they were separated according to species, weighed in groups by species, and measured for classification into 1-inch or ½-inch total length groups. When numbers of fish landed at the data station became too large for length classification of each individual, large random samples were taken for measuring.

Coleback Lake

Surface collections.—It was again deemed desirable to collect fishes floating at the surface only after they had drifted ashore. However, no attempt was made to collect all fish, a stratified sampling procedure described by Schumacher and Chapman (1954, pp. 71–70) being adopted instead. Five sampling strata were established: A and C at the ends of the lake, and B, D, and E at the sides. Shoreline areas measuring 3 feet along the shore and extending out to a depth of 2 feet were designated as sampling sites. Forty sampling sites were chosen at random in stratum A, 20 in stratum B, 38 in stratum C, 20 in stratum D, and 8 in stratum E. These numbers of samples provided for pickup of fish along 11 to 12 per cent of the shoreline in strata A and C, along 7 to 8 per cent of the shoreline in strata B and D, and along 4 per cent of the shoreline in stratum E. Collection of fishes began on the day following application of the rotenone. A breeze during the previous night had drifted all floating fishes ashore, and observations showed that very few additional fish were rising to the surface. Two two-man crews worked along the shores in different strata, completing their collections in 2 days.

Bottom samples.—Sampling of fishes on the bottom in depths greater than 2 feet was done at Coleback Lake by SCUBA divers following transect lines normal to the long axis of the lake. The sampling zones were 3 feet wide, the divers maintaining this width with yardsticks held in front of them and at right angles to their direction of travel. Direction was maintained by following a compass held on the wrist of the same hand that held the middle of the yardstick. Fish collected were carried along in a mesh bag, then tagged for identification of the transect and taken to the data station. Bottom sampling began at about noon of the day following reclamation and was completed during the following afternoon. The 20 randomly chosen transects represented 3.7 per cent of the 536 choices possible, and their total length was 11,480 feet. Procedures for analysis of data were similar to those described for Shagg Lake except that the transects were subdivided into 10-foot segments rather than 100-foot segments.

Hills Lake

Surface collections.—Enumeration of fishes that floated to the surface of Hills Lake was undertaken in two steps: (1) a concerted effort was made to collect fish as they surfaced on the day the rotenone was applied, and (2) fish that rose to the surface during the first night and those not collected during the first day were allowed to drift ashore, then counted in sample areas around the shore. Sportsman assistance during the first day was solicited, and it was hoped that virtually all fish could be collected as they surfaced, reducing greatly the arduous and time-consuming shore sampling. Fifteen to 25 sportsmen and crew members simply dipped up fish whenever and wherever they could. Cooperation was excellent, and approximately 17,300 fish were collected during the first day.

Shore sampling at Hills Lake differed from that at Coleback Lake in that the fish in the sample areas were merely counted by species, not collected. Collection of the fish was not considered necessary because sufficient samples for size and weight had already been taken during the first day's operation. Merely counting the fish in the sample areas made the operation much faster than it would have been if the fish had been collected, and there was probably no reduction in accuracy. Sample areas were 24 feet long, there were only 22 of them, and no stratification plan was used. The sample areas comprised 10.5 per cent of the shoreline of the lake.

Bottom samples.—Bottom sampling at Hills Lake was by the same procedure as that used at Coleback Lake except that only 10 transect lines were used, and the fish were not picked up. Instead of collecting the fish, the divers carried pencils and 2- by 4-inch pieces of

sheet aluminum, simply tallying by species the numbers of fish they saw as they proceeded along the 3-foot sampling zones. The 10 transect lines followed at Hills Lake had an aggregate length of 4,070 feet, and they comprised 1.5 per cent of the 670 choices possible.

Productivity estimates

Estimates of net primary productivity[1] by phytoplankton during the daytime at Shagg, Coleback, and Hills Lakes were made by a C^{14} technique which differed in one important respect from that used by Steemann Nielsen (1952) and Doty and Oguri (1958), but was similar to that used by Goldman (1960). It has been shown (Jitts and Scott, 1961) that productivity calculations based on the ratio between calculated, zero-thickness count of the radiocarbon added to the lake water and the empirical count of the radiocarbon appearing in the plankton after exposure is not accurate because of the virtual impossibility of precipitating barium carbonate from the sodium carbonate solutions in layers thin enough to allow reliable extrapolation to zero thickness. For this reason, productivity calculations in this study were based on the ratios between the absolute activities of the radiocarbonate added to the lake water and the absolute activities of the plankton recovered after exposure, rather than on the relative activities as in the originally described technique. The steps in the development of this modified procedure were (1) to establish the relationship between counts of C^{14}-bearing plankton samples as observed with our REAC D-501 manual counter and the absolute activity of the plankton as determined by some direct technique, and (2) to confirm that the C^{14}–sodium carbonate ampules purchased from a commercial supplier did indeed contain the absolute activities stated on their labels.

Millipore filter discs bearing plankton which had been exposed to C^{14} were counted on the REAC D-501 to a counting error of ± 0.1 per cent. The filters were then sent to the New England Nuclear Assay Corp., Boston, Mass.,

for radioassay by means of combustion to CO_2 gas followed by direct liquid scintillation. Results allowed the construction of a regression of observed count on absolute activity through a count range of 860 to 48,000 cpm.

Samples of the 1-ml sodium carbonate ampules with nominal activities of 3 and $5\mu c$/ml purchased for the productivity studies were also sent to the New England Nuclear Assay Corp. to confirm that the labeled activities were correct. Results of liquid scintillation analyses showed that labeled activities of most lots were within ± 5 per cent of the assayed activities, an accuracy considered sufficient for the purposes of our study.

Upon completion of these preliminary steps, estimates of the fractions of the total available carbon incorporated into protoplasm and retained by phytoplankton at various stations, depths, and times in the three study lakes were made by the usual light-and-dark-bottle procedure. A sample of lake water from a given location was collected in a plastic sampling bottle, then used to fill two 225-ml glass-stoppered bottles. Each bottle was then inoculated with 1 ml of C^{14}–sodium carbonate solution from a hypodermic syringe. One bottle was covered completely with heavy aluminum foil to exclude light; then the two bottles were suspended on a buoy line at the location from which the water sample had been taken. Exposures were for periods of half a day, beginning at noon and ending at sunset. Upon termination of exposure, the plankton were removed from the water in the sample bottles by vacuum filtration onto type AA Millipore filter discs. After washing with filtered lake water (McAllister, 1961), the filters were placed in a desiccating chamber for drying and transportation to the laboratory. The fraction of the carbon available to plankton at the given site which was taken up and retained by the plankton during the time of exposure was then computed, with appropriate correction for the 6 per cent isotope effect (Steemann Nielsen, 1952).

In addition to estimates of the fractions of available carbon used by phytoplankton in given exposure times, estimates of primary productivity also require knowledge of the amount of carbon available to the plankton

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[1] *"Net primary productivity* is the rate of storage of organic matter in plant tissues in excess of the respiratory utilization by the plants during the period of measurement" (Odum and Odum, 1959).

TABLE 2.—*Counts and estimates of the total numbers and weights of fish killed at Shagg Lake, Oxford County, Maine, by application of rotenone on 9 September 1957*

Measures of standing crop	Location in lake			Totals	
	Ashore and on bottom 10 feet deep or less (totals counted)	On bottom deeper than 10 feet			
		Point estimates	Confidence limits ($p = 0.2$; df = 3)	Point estimates	Confidence limits ($p = 0.2$; df = 3)
Number	34,495	37,465	17,320 57,610	71,960	51,820 92,100
Weight (pounds)	1,307	876	614 1,183	2,183	1,921 2,490

at the given site and time. These data are obtained using equilibrium equations involving temperature, pH, and total alkalinity. Temperatures at each exposure site at Shagg, Coleback, and Hills Lakes were obtained with a thermistor, pH was determined using a Hellige pocket comparator, and total akalinity was calculated from methyl orange titration using N/50 sulfuric acid. Conversions of these data to total available carbon in mg/liter were done using a table prepared by Mr. R. W. Bachmann.[2]

The most extensive sampling program feasible for estimating net primary productivity at Shagg, Coleback, and Hills Lakes consisted of exposures performed during 4 or 5 consecutive days and at various depths and stations in each lake. At Shagg Lake sample sites were chosen 4 feet below the surface, just above the metalimnion, in the middle of the metalimnion, and in the hypolimnion over a deepwater station; and at 4- and 8-foot depths in the epilimnion over a shallow-water station. At Coleback Lake the exposures were made at one station only and at depths of 4, 14, and 23 feet. At Hills Lake the samples were exposed at one station and at depths of 4, 15, and 18 feet; the first two depths representing locations in the epilimnion and the 18-foot depth representing the metalimnion. Dates of sample exposures were: Shagg Lake—14–17 August 1962; Coleback Lake—30 July–3 August 1962; and Hills Lake—24–27 July

[2] Bachmann, Roger W. (1960) The calculation of available carbon. Unpublished typescript, Dept. of Zool., Univ. Mich., Ann Arbor, Michigan. 8 pp.

1962. It is recognized that the sampling programs were minimal.

Final calculations for each sample site yielded estimates of net primary productivity in milligrams of elemental carbon per cubic meter of lake water per daylight hour. It must be emphasized that these are estimates of *net* primary productivity, estimates of the rate at which carbon is incorporated into and retained by the plankton in their processes of growth and reproduction. Attempts to estimate gross productivity from the data obtained in this study would lead to errors because the plankton are known to lose C^{14} by respiration and probably other processes at the same time they are assimilating it through photosynthesis (Ryther, 1956; Davis, 1963). No attempts to measure any losses of carbon by the plankton were made in this study; therefore, the data provide no information on gross rate of carbon assimilation for studies of energy budgets, photosynthesis, or respiration. Estimates of daytime net primary productivity were deemed sufficient for the comparative studies reported here.

RESULTS

Shagg Lake

Standing crop of fish.—The number of rotenone-killed fish collected after they had drifted ashore at Shagg Lake or after they had settled on the bottom in depths of 10 feet and less was 34,495, and the weight was 1,307 pounds. These data are unaccompanied by any measures of variability because the collections were planned to yield complete counts. The estimated number and weight of fish that sank to the bottom in depths greater than 10 feet were 37,465 and 876 pounds, respectively. Addition of these counts and estimates yields point estimates of the total standing crop: 71,960 fish or 2,183 pounds. These values can also be expressed as mean standing crops of 1,308 fish or 39.7 pounds per acre. Confidence limits about the estimates are presented in Table 2.

Comparison of the numbers and weights of fish which sank in the deep-water zone of the lake with the numbers and weights of fish which floated ashore or sank in shallow water also can be made using the data presented in

TABLE 3.—*Estimates of net primary productivity in milligrams of carbon per cubic meter of lake water per daylight hour at various stations and depths in Shagg Lake in August 1962*

Station[1]	Depth (feet)	Stratum and temperature range (°F)	Mg C/m³/hr				Mean and standard error
			14 Aug.	15 Aug.	16 Aug.	17 Aug.	
a	4	Epilimnion	0.685	1.630	1.910	0.685	
b	4	(68°–65°)	1.106	1.640	1.350	0.512	
b	8		0.415	1.100	0.720	0.488	0.910 ± 0.127
a	12		0.307	0.663	1.048	0.310	
a	16	Metalimnion (65°–48°)	0.190	0.687	0.398	0.212	0.371 ± 0.116
a	25	Hypolimnion (48°–43°)	0.093	0.155	0.165	0.074	0.122 ± 0.023

[1] Station a was located in the center of the lake over the deepest water; station b in a sheltered cove over a depth of 12 feet.

Table 2. Thus an estimated 40 per cent by weight of the total standing crop and 52 per cent by number settled to the bottom in the deep-water zone after their deaths from rotenone. Confidence limits for these estimates also can be computed from the data in Table 2. The differences in the relative numbers and weights of fish found in the two zones can be attributed to the fact that relatively more of the smaller fish (smelts) sank after death, and relatively more of the larger fish (suckers) floated.

The precision of the estimates presented in Table 2 is discussed in a later section.

Net primary productivity.—Estimates of net primary productivity at various depths over two stations in Shagg Lake during August 1962 are presented in Table 3. Mean values and standard errors for the three strata into which the lake was divided at that time are also presented.

Productivity estimates expressed on the basis of lake surface area are considered more useful than estimates expressed on a unit volume basis because the unit-surface-area expression takes into account differences among lakes in trophogenic volume, littoral volume, turbidity, etc. Therefore, volumes of water in the three strata of Shagg Lake were computed from a hydrographic map, the volume of each stratum was multiplied by its appropriate mean productivity estimate, the products for each stratum were added, and the sum was found to be equal to 3.370 mg of carbon per square meter of lake surface per daylight hour (mg C/m²/hr). The entire volume of the lake was considered to be within the trophogenic zone for the purposes of these calculations.

Population structure.—In addition to estimates of the total fish population of Shagg Lake before rotenone treatment, independent estimates of the numbers and weights of the six species making up the total population were also made (Table 4). These estimates were made by a procedure similar to that used for the total fish population, except that the estimates from the deep-water zone were computed merely by proportional expansion of the sample sums ($k = 1/0.0566 = 17.67$). The close agreement between the sums of the species estimates in Table 4 and the total population estimates in Table 2 provides evidence that the simpler computational procedure for expanding the species counts from the deep-water zone did not lead to important errors.

The American smelt was by far the most numerous fish in Shagg Lake, but the white sucker population contributed the most weight (Table 4). Furthermore, 53 to 57 per cent of the smelt population settled to the bottom in the deep-water zone after death, and 56 to 60 per cent of the sucker population floated or settled in shallow water, explaining the high number but low weight of fishes in the deep-water zone. Finally, the general agreement between numbers and weights of the various species found in the two zones of the lake (except for the few white perch) provides evidence that size of fish was not an important factor in their final location after death and that size selectivity was not an important source of error in the sampling procedure.

TABLE 4.—*Numbers and weights of six species of fish inhabiting Shagg Lake before rotenone treatment in September 1957*

Species	Total population		Percentages of total population		Percentages of species populations			
					Recovered ashore or in shallow zone[1]		Estimated in deep zone	
	Number	Weight (pounds)	Number	Weight	Number	Weight	Number	Weight
American smelt	60,659	484	84.1	22.0	44.4	47.4	55.6	52.6
White sucker	6,122	1,200	8.5	54.5	56.2	59.5	43.8	40.5
Brown bullhead	3,314	252	4.6	11.5	92.6	94.3	7.4	5.7
Chain pickerel	1,854	201	2.6	9.1	50.2	60.2	49.8	39.8
White perch	171	61	0.2	2.9	64.9	8.2	35.1	91.8
Smallmouth bass	1	2	—	—	100.0	100.0	—	—
Totals	72,121	2,200	100.0	100.0	—	—	—	—

[1] The shallow zone is defined as the area of the lake with depths of 10 feet or less; the deep zone as the area of the lake with depths greater than 10 feet.

The zonal distribution of the brown bullheads requires comment. The SCUBA divers who made the collections in the deep-water zone reported that many bullheads apparently had burrowed into the bottom silt as they died, leaving only their tails showing. Those seen were collected, but it seems likely that others may have buried themselves completely, making the bullhead estimate significantly low. The divers reported that none of the other species evidenced this burrowing behavior to any marked degree.

Fish collected during the Shagg Lake project were measured for classification into ½- and 1-inch total length groups, and the resulting length distributions were expanded proportionally to yield estimates of the size compositions of the total species populations. These estimated size compositions are presented in Figure 1. Numbers of fish measured were: American smelt—3,150; white sucker—2,450; brown bullhead—1,560; chain pickerel—744; and white perch—111.

Examination of scales from samples of smelts

from Shagg Lake showed that the first peak in Figure 1 corresponds with the modal length of the 0 age group, the second peak with the modal length of age-group I, and the third peak with the modal length of age-group III. Members of age-group II (the 1955 year class) had lengths ranging generally from 4.5 to 6.5 inches, and were poorly represented in the population.

Scales from suckers from Shagg Lake were not examined, but the length–frequency distribution for this species suggests strongly the presence of at least three age-classes. If the growth rate of suckers in this lake was similar to the calculated median rate in several waters reported by Carlander (1953), the distribution then has peaks representing age-groups 0, I, and III, and has also a low segment at 8 to 10 inches representing a lesser number of fish of the 1955 year class (age-group II). The absence of an ascending left-hand limb in this distribution cannot be explained.

The size distribution of the white perch population requires special comment. Shagg

TABLE 5.—*Estimated numbers and weights of fish killed by rotenone at Coleback Lake, Washington County, Maine, on 3 September 1958*

Measures of standing crop	Location in lake				Totals	
	At surface and on bottom not deeper than 2 feet		On bottom deeper than 2 feet			
	Point estimates	Confidence limits ($p = 0.1$; df = 121)	Point estimates	Confidence limits ($p = 0.1$; df = 19)	Point estimates	Confidence limits ($p = 0.1$; df = 140)
Number	48,520	36,980 60,170	64,910	41,140 84,990	113,430	85,400 141,460
Weight (pounds)	847	646 1,050	1,245	810 1,680	2,090	1,670 2,565

Lake was surveyed initially in 1954, and the survey crew did not report white perch present at that time. The 9- to 11-inch fish found in the lake in September 1957 were mature individuals, and the 1- to 4-inch fish were young-of-the-year. It can be concluded, therefore, that an unauthorized introduction of a small number of adult white perch took place sometime after 1954, and that the first successful spawning of these fish occurred in the spring of 1957. It is most probable that the introduction occurred during 1956 or the early spring of 1957.

The recovery of the one smallmouth bass from Shagg Lake cannot be explained. This species had not been known to be present at Shagg Lake prior to its reclamation.
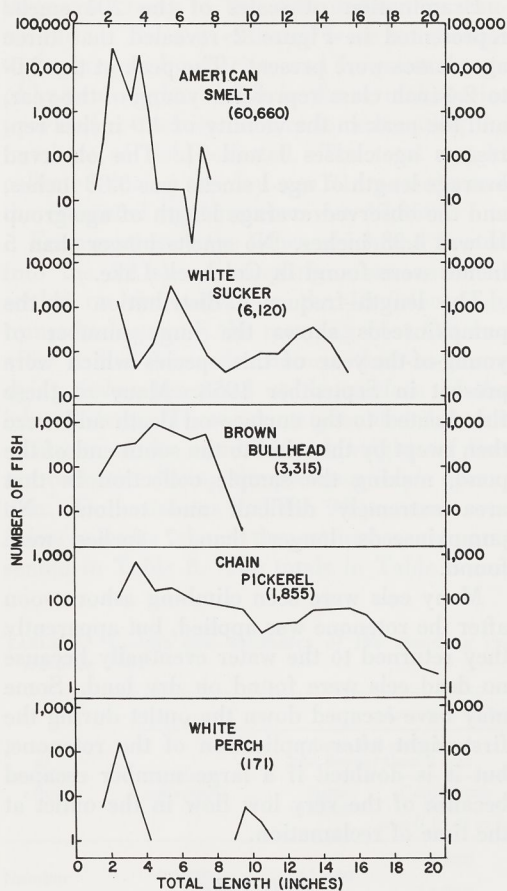

FIGURE 1.—Total length distributions of the five species populations inhabiting Shagg Lake prior to 9 September 1957.

TABLE 6.—*Estimates of net primary productivity in milligrams of carbon per cubic meter of lake water per daylight hour at three depths in Coleback Lake in July and August 1962*

Depth (feet)	Temperature (°F)	Mg C/m³/hr					Mean and standard error
		30 July	31 July	1 Aug.	2 Aug.	3 Aug.	
4	68	2.70	1.74	0.85	0.91	1.65	
14	67	1.44	1.60	0.57	0.97	0.69	1.361 ± 0.204
23	61	0.25	1.16	0.65	2.72	2.52	

Coleback Lake

Standing crop of fish.—Estimates of the number and weight of fish inhabiting Coleback Lake prior to rotenone treatment on 3 September 1958, are presented in Table 5. The estimated totals can also be expressed on an area basis, in which case they represent standing crops of 5,670 fish or 104.5 pounds per acre. Ninety per cent confidence limits about the estimates are also presented in Table 5.

The numbers and weights of fish that settled in the two sampling zones of Coleback Lake were more nearly similar than at Shagg Lake: 42.8 per cent by number and 40.3 per cent by weight were estimated to have floated ashore or settled to the bottom in depths not greater than 2 feet.

Net primary productivity.—Estimates of net primary productivity at three depths over a single station near the center of Coleback Lake during late July and early August 1962 are presented in Table 6. The estimates from the three depths were averaged to give a single, general mean because the lake was not stratified at the time the sample exposures were made.

The estimated mean net primary productivity from Table 6 was converted to a per-unit-surface-area basis by the same procedure used with the Shagg Lake data, giving a definitive estimate of 6.958 mg C/m²/hr. The entire volume of Coleback Lake was considered to be within the trophogenic zone.

Population structure.—Independent estimates of the numbers of fish belonging to each of the five species at Coleback Lake were made by the same procedure used for the total fish populations and are presented in Table 7. Ninety per cent confidence limits about the
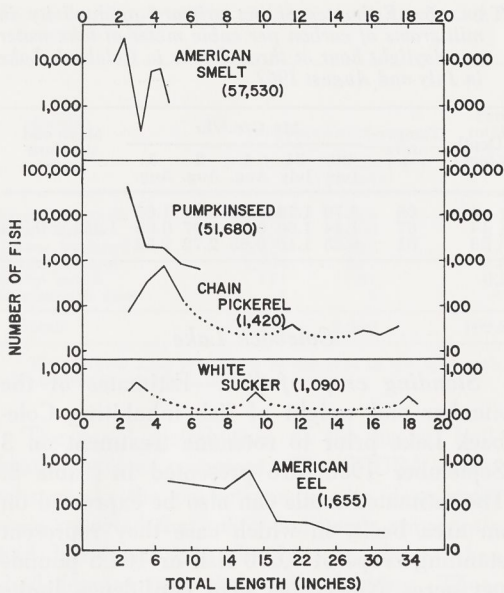
FIGURE 2.—Total length distributions of the five species populations inhabiting Coleback Lake before 3 September 1958. Dotted lines in the figure represent size classes not included in the samples.

estimates for the species populations were generally comparable to confidence limits about the estimates of the total population, and are therefore not listed. Weights of the species populations were determined from small random samples of fish from each species, and the percentage distributions of weights of fish found in the different sampling areas of the lake were therefore the same as the percentage distributions by number. This shortcut was deemed permissible because of the absence of size specificity in sampling or in ultimate location after death observed at Shagg Lake during the previous year.

Comparison of Table 7 with Table 4 shows that the locations of smelts, suckers, and pickerel after death in Shagg Lake and in Coleback Lake were essentially similar; more than half of the smelts settled in the deep zones, and more than half of the suckers and pickerel were located ultimately in the surface waters. Number–weight relationships were dissimilar, however; smelts at Coleback Lake were notably smaller than those at Shagg Lake, and pickerel and suckers were some-

what larger. The small number but great weight of the eel population at Coleback Lake is another feature of note.

Length–frequency distributions of the five species populations which inhabited Coleback Lake are presented in Figure 2. These distributions are based on 1,154 measurements which were apportioned among the five species as follows: American smelt—204; pumpkinseed—846; American eel—63; chain pickerel—20; and white sucker—21. Sample sizes were clearly inadequate in the cases of the pickerel and the suckers; however, the 111 pickerel and the 81 suckers collected during the sampling operations were grouped visually according to size, and the peaks in Figure 2 do represent the modal lengths of the major size groupings.

Examination of scales of the 204 smelts represented in Figure 2 revealed that three age-classes were present. The peak at the 2.0- to 2.4-inch class represents young-of-the-year, and the peak in the vicinity of 4.0 inches represents age-classes I and II. The observed average length of age-I smelts was 3.88 inches, and the observed average length of age-group II was 4.33 inches. No smelts longer than 5 inches were found in Coleback Lake.

The length–frequency distribution of the pumpkinseeds shows the huge number of young-of-the-year of this species which were present in September 1958. Many of these fish floated to the surface on death and were then swept by the wind to the south end of the pond, making the sample collection in that area extremely difficult and tedious. No pumpkinseeds longer than 7 inches were found.

Many eels were seen climbing ashore soon after the rotenone was applied, but apparently they returned to the water eventually because no dead eels were found on dry land. Some may have escaped down the outlet during the first night after application of the rotenone, but it is doubted if a large number escaped because of the very low flow in the outlet at the time of reclamation.

Hills Lake

Standing crop of fish.—Application of rotenone at Hills Lake began at daybreak on 3

Table 7.—*Estimated numbers and weights of five species of fish inhabiting Coleback Lake prior to rotenone treatment in September 1958*

Species	Total population		Percentages of total population		Percentages of species populations[1]	
	Number	Weight (pounds)	Number	Weight	Located ashore or in shallow zone[2]	Located in deep zone
American smelt	57,530	140	50.7	6.7	39.3	60.7
Pumpkinseed	51,680	265	45.6	12.6	45.9	54.1
American eel	1,655	850	1.4	40.7	22.2	77.8
Chain pickerel	1,420	150	1.3	7.2	86.8	13.2
White sucker	1,909	685	1.0	32.8	50.9	49.1
Totals	113,375	2,090	100.0	100.0	—	—

[1] Percentages listed apply to both numbers and weights. See text for explanation.
[2] The shallow zone is defined as the area of the lake with depths of 2 feet or less; the deep zone as the area of the lake with depths greater than 2 feet.

October 1961, and dying fish began appearing at the surface within 2 hours. Sportsmen and crew members collected the dying fish as rapidly as they could, periodically bringing their collections to the data station for enumeration. The fish collected were weighed in the aggregate by species, and frequent counts of known weights of fish in the several species provided conversion factors for estimating the numbers of fish collected. The total weight collected during the day was 314 pounds, and the estimated total number was 17,350.

Enumeration of the fishes which had floated into the 22 shore sampling areas and had settled on the bottom in the 10 3-foot-wide transects began on the morning of 4 October after it had been determined that no more dying fishes remained at the surface of the lake offshore. These counts provided data for estimates of the numbers and weights of fish not collected during the previous day's operation. The estimates and the 90 per cent confidence limits about the estimates are presented in Table 8. The totals in Table 8 can

be expressed as standing crops of 2,863 fish or 62.5 pounds per acre.

Net primary productivity.—Estimates of the net primary productivity by volume at a single station in Hills Lake during July 1962 are presented in Table 9. Total productivity per unit of surface area, calculated from the means presented in Table 9 and the volumes of the two strata sampled, was estimated as 1.886 mg $C/m^2/hr$. Epilemnetic volume determined from a hydrographic map for these calculations was 220 acre-feet (depth: 0 to 17 feet), and the volume of the metalimnion was 34 acre-feet (depth: 17 to 25 feet). The very small volume of water comprising the hypolimnion (5 acre-feet) was not sampled and was not, therefore, included in the calculations.

The maximum probable error in the estimated total productivity per unit area caused by neglecting possible productivity in the hypolimnion is very small. If productivity per cubic meter in this stratum had been as high as that in the metalimnion, the final estimate

Table 8.—*Counts and estimates of the standing crop of fish inhabiting Hills Lake before reclamation on 3 October 1961*

Measures of standing crop	Surface collection	Location in lake				Totals	
		Ashore and on bottom not deeper than 2 feet		Bottom deeper than 2 feet			
		Point estimates	Confidence limits ($p = 0.1$; df $= 21$)	Point estimates	Confidence limits ($p = 0.1$; df $= 9$)	Point estimates	Confidence limits ($p = 0.1$; df $= 30$)
Number	17,350	11,440	8,650 14,220	25,620	13,190 38,050	54,400	42,580 66,240
Weight (pounds)	314	78	59 97	796	410 1,182	1,188	908 1,466

TABLE 9.—*Estimates of net primary productivity in milligrams of carbon per cubic meter of lake water per daylight hour at Hills Lake during July 1962*

Depth (feet)	Stratum and temperature range (°F)	Mg C/m³/hr				Mean and standard error
		24 July	25 July	26 July	27 July	
4 15	Epilimnion (69–68)	0.73 0.30	0.75 0.59	0.41 0.23	0.43 0.37	0.476 ± 0.068
18	Metalimnion (68–46)	0.48	0.52	0.11	0.40	0.378 ± 0.093

would have been increased only to 1.916 mg C/m²/hr. Because it is likely that productivity per unit volume in the hypolimnion was less than in the metalimnion, it follows that total areal productivity probably was somewhat less than 1.916 but possibly greater than 1.886 mg C/m²/hr. In any case, the maximum inaccuracy is small.

Population structure. — Estimates of the numbers of fish belonging to the five species inhabiting Hills Lake prior to rotenone treatment (Table 10) were made by the same procedures described previously. Numbers of fish were estimated from measured weights collected during the first day's operation, and weights were determined from numbers estimated by sampling during the second day. The species of dace were not distinguished when collected or counted; rather, relative abundance of the two species was determined by sampling later at the data processing station. Blacknose dace comprised 4.43 per cent of the total dace collections, and redbelly dace comprised 95.57 per cent.

American smelts were the most numerous fish inhabiting Hills Lake before reclamation,

and they also made up the greatest weight. Dace were almost equally as numerous as smelts, but they were small and made up only a minor part of the total weight of the fish population. Only five brook trout were recovered from Hills Lake despite the fact that the lake had been stocked with this species for many years.

Comparison of the relative numbers and weights of fish collected as they surfaced during the day the rotenone was applied with the relative numbers estimated to have settled in other parts of the lake after the first day allows an appraisal of the effectiveness of the attempted surface pickup. As shown by Table 10, most of the smelts and many of the bullheads that might have remained at the surface after death were collected, while less than half of the dace remaining at the surface were collected. This result might have been expected because the dace surfaced in very shallow water near shore, and the sportsmen who helped with the collections were more interested in the smelts and bullheads. Nevertheless, Table 10 shows that the surface pickup operation was more effective than the authors thought it would be while it was in progress.

Total length measurements of 197 smelts, 201 brown bullheads, 112 redbelly dace, and 73 blacknose dace were recorded to provide data on size compositions of the populations (Figure 3). Examination of the scales of the smelts showed that the first peak in Figure 3 represents young-of-the-year, and the second peak represents I-, II-, and III-year-olds. The I-year-olds were the most abundant fish in this group, with the II's and III's numbering

TABLE 10.—*Estimated numbers and weights of the five species of fish inhabiting Hills Lake before 3 October 1961*

Species	Total population		Percentages of total population		Percentages of species populations[1]		
	Number	Weight (pounds)	Number	Weight	Collected at surface	Sampled ashore or in shallow zone[2]	Sampled in deepwater zone
American smelt	26,128	686	48.0	57.7	18.4	0.7	80.9
Brown bullhead	5,450	412	10.0	34.7	35.3	7.5	57.2
Redbelly dace[3]	21,804	85	40.1	7.2	46.5	47.6	5.9
Blacknose dace[3]	1,010	4	1.9	0.4	46.5	47.6	5.9
Brook trout	5	1	—	—	100.0		
Totals	54,397	1,188	100.0	100.0	—	—	—

[1] Percentages listed apply to both numbers and weights.
[2] The shallow zone is defined as the area of the lake with depths of 2 feet or less.
[3] Sportsmen and crew members did not differentiate between the two species of dace at the time the collections or counts were made. Rather, subsequent sampling of the fish collected showed that 4.43 per cent were blacknose dace, and the remainder were redbelly dace.

only approximately 1,000 and 150, respectively. Average total lengths of I-, II-, and III-year-old fish were 4.65, 5.30, and 5.6 inches, respectively. It is thus evident that the growth rate of smelts in Hills Lake dropped markedly after the second summer of life.

Ages of bullheads were not determined, but it is perhaps worth noting that the range in lengths of bullheads from Hills Lake was similar to the length range of this species in Shagg Lake. Bullheads commonly attain lengths as great as 12 and 14 inches in Maine's more productive warmwater environments.

DISCUSSION

Critique of methods

Standing crop.—Efforts to determine the numbers and weights of rotenone-killed fish that floated to the surfaces of the study lakes after death were made by three different procedures: at Shagg Lake by exhaustive collection along the shoreline and on the bottom in shallow water after all floating fish had drifted ashore or settled; at Coleback Lake by stratified random sampling on and near shore after drifting fish had settled; and at Hills Lake by surface collecting offshore, followed by nonstratified random sampling along the shore to estimate the number of fish not collected offshore. The two latter procedures provided satisfactory data, but the procedure used at Shagg Lake was clearly inadequate.

The inadequacy of the Shagg Lake procedure resulted from our ill-advised attempt to collect all the fish that floated ashore or settled in water 10 feet deep or less; the task in this 55-acre lake was much greater than we had imagined it would be, and there was no objective way to evaluate our results. Spot checks showed that most of the fish had been collected, but the spot checking was minimal and depended wholly on visual observation. An additional factor contributing to uncertainty about the completeness of the collection procedure was the advancing decomposition of the rotenone-killed fish by the last day of the operation. In short, three two-man crews and a three-man team of divers were unable after 3 days of work to be certain that all fish had been collected. Their results are regarded
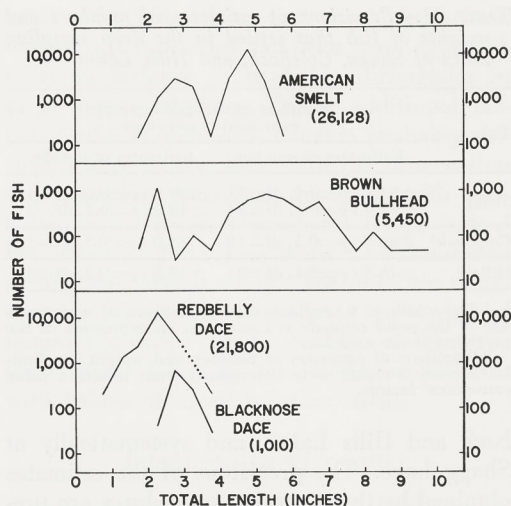

FIGURE 3.—Length–frequency distributions of four fish species which inhabited Hills Lake prior to reclamation with rotenone on 3 October 1961. The dotted line in the figure represents size classes not included in the samples.

as minimal estimates of the number and weight of fish actually present, and the estimates cannot be accompanied by any measures of probable error.

At Coleback and Hills Lakes, on the other hand, the sampling and collecting procedures yielded satisfactory results. The 90 per cent confidence limits about the estimates from stratified random sampling at Coleback Lake were ±23.9 per cent. At Hills Lake approximately 60 per cent of the dead and dying fish which floated to the surface were collected before they floated ashore, and nonstratified random sampling yielded estimates of the remainder, whose 90 per cent confidence limits were ±24.3 per cent. The sampling plan at Hills Lake involved sample areas which were larger and fewer than at Coleback Lake, an economy which evidently was permissible because of the large number of fish collected from the surface before they drifted ashore.

Sampling to estimate the number and weight of fish which sank to the bottom in deep water at Shagg Lake was done using 4 transects each 20 feet wide, at Coleback Lake using 20 transects each 3 feet wide, and at Hills Lake using 10 transects each 3 feet wide. Locations of transects were chosen at random at Cole-

TABLE 11.—*Precisions of estimates of numbers and weights of fish that settled in the deep sampling zones of Shagg, Coleback, and Hills Lakes*

Lake	Width of confidence intervals expressed in per cent[1]	
	Estimates of number	Estimates of weight
Shagg	±53.8 (p=0.2, df=3)	±29.9 (p=0.2, df=3)
	±77.2 (p=0.1, df=3)	±42.9 (p=0.1, df=3)
Coleback[2]	±36.6 (p=0.1, df=19)	±35.0 (p=0.1, df=19)
Hills[2]	±48.5 (p=0.1, df=9)	±48.5 (p=0.1, df=9)

[1] The width of a confidence interval given as a percentage of the point estimate is considered an expression of the precision of the estimate.
[2] Precisions of estimates of number and weight are similar because weights were determined from numbers using conversion factors.

back and Hills Lakes, and systematically at Shagg Lake. The precisions of the estimates obtained by these varying procedures are presented in Table 11. The data show that the procedure used at Coleback Lake provided the most precise estimate and that the Shagg Lake procedure provided the least precise estimates. The total area of bottom examined at Shagg Lake was greater than the area of bottom examined at Coleback Lake, but the Coleback estimate was more precise because of increased replication. Replication of bottom sampling at Hills Lake was reduced because of limitations in personnel and time, and the precision of the bottom estimate at Hills Lake was reduced correspondingly.

None of the confidence intervals described in Table 11 are considered entirely satisfactory. Plans for future deep-water sampling of rotenone-killed fish should provided for increased replication of samples, and also possibly for stratification.

All sampling at Shagg and Coleback Lakes was done by collecting the fish in the sample areas for later enumeration and weighing. At Hills Lake the numbers of fish in the sample areas were counted by species, but they were not collected. This latter procedure was much more efficient than the former, and it is believed that there was no loss in accuracy. Samples of the various species populations needed for determining length, weight, and age structure were obtained from fish not in the sampling areas.

Net primary productivity.—Calculations of net primary productivity by the C^{14} method require (1) measurement of the total inor-ganic carbon available for uptake by phytoplankton during a specific time in a known volume of lake water at a given site, and (2) measurement of the fraction of the available carbon actually assimilated and retained by the phytoplankton during the specific time, in the known volume, and at the given site. C^{14} is used as tracer to determine the fraction of the available carbon assimilated and retained by the phytoplankton, and ordinary chemical water-analysis methods are used to determine the total carbon available. Errors in either phase of the procedure will cause errors in the result.

No important difficulties were encountered in the tracer phase of the productivity studies at Shagg, Coleback, and Hills Lakes, but the calculation of total available carbon did present problems. Total available carbon is obtained from equilibrium equations which require measures of pH, water temperature, and total alkalinity. Total alkalinity was determined by methyl orange titration, and was subject to all the uncertainties usually experienced with this difficult and unsatisfactory end point. Total alkalinities of natural waters can run as high as several hundred ppm, but are seldom found above 10 ppm in Maine waters. Error or uncertainty of the order of 2 or 3 ppm is unimportant from the point of view of the entire range of alkalinities possible in natural waters, but when considered from the narrower point of view of the range expected in Maine, 1 or 2 ppm could be equivalent to 10 or 20 per cent.

The effect of an error in alkalinity determination of only 2.5 ppm is illustrated below, where pH is 6.4 and water temperature is 15° C:

Total alkalinity	–	3.0	5.5
Milligrams available carbon per m^3	–	1.47×10^3	2.70×10^3
Fraction of tracer taken up in 8 hours	–	3.8×10^{-3}	3.8×10^{-3}
Milligrams of C taken up per m^3 in 8 hours	–	5.586	10.260
Mg C/m^3/hr	–	0.698	1.282

Thus an error of 2.5 ppm in measurement of total alkalinity has resulted almost in a doubling of the estimated net primary productivity. Again, the difference between 0.698 and 1.282 mg of carbon could be unimportant if we were estimating a parameter with a normal range of several hundred, but in Maine waters it is unlikely that productivity values above 10 mg will ever be encountered. Thus errors of 10 to 50 per cent can be expected as usual occurrences under even the most ideal conditions, and hopes to correlate net primary productivity with other attributes of Maine lakes appear somewhat dim. It must be concluded that the C^{14} technique at its present state of development provides productivity estimates which are too crude to be expected to indicate reliably the small differences which exist among Maine's generally soft, infertile waters.

Another considerable difficulty in estimating the net primary productivity of lakes is found in the sampling problems involved. As pointed out by Davis (1963), ". . . the results apply not to the ecosystems as a whole, but only to that particular portion of the area sampled on a particular day; hence they depend upon local temporary weather conditions, and upon the local quality and quantity of those photosynthetic and chemosynthetic organisms that are present. . . ." Rodhe (1958) also discussed the difficulties associated with attempts to measure primary productivity and emphasized the need for exhaustive sampling.

The authors do not consider that the sampling programs followed at Shagg, Coleback, and Hills Lakes were adequate. Measurement periods were too short, they did not include either the spring or fall plankton pulses, and they sampled the productivity of Coleback and Hills Lakes during periods of unusual local weather.[3] Exposure times were from noon to sunset to insure that the plankton would be metabolizing under the full range of solar radiation appropriate to the season and latitude, but the results obtained

may differ from those that would have been obtained if exposures had been from daybreak to noon because of probable differences in physiological rhythms. Many additional factors could be discussed, but it is probably sufficient here to conclude with the observation that sampling problems involved with estimates of net primary productivity are indeed herculean, and that they were not surmounted during the present study. The data are therefore useful mainly to indicate an order of magnitude which can be used for ranking the three study lakes or for gross comparisons with values obtained in other areas.

Interpretation of results

Estimates of standing crop of fish and net primary productivity during the daytime from Shagg, Coleback, and Hills Lakes are summarized in Table 12. From the table it is clear that Coleback Lake ranks highest in standing crop and productivity. Which lakes occupy the intermediate and lowest ranks is not so clear; the estimated productivity of Hills Lake was lowest, but this estimate might be in error because of the sampling and technique difficulties discussed above or because of the unfavorable weather that prevailed when the estimate was being made; the estimated standing crop of Shagg Lake was lowest, but this estimate might also be in error because of the unsatisfactory sampling procedures used. The authors believe that the estimate of the primary productivity of Hills Lake is likely to be in greater error than the estimate of the standing crop of Shagg Lake; therefore, they conclude provisionally that Hills Lake occupied the intermediate rank in standing crop and productivity before reclamation, and Shagg Lake occupied the lowest rank.

[3] Continuous rain and dense cloudiness during the productivity sampling at Hills Lake, continuous clear and unusually hot weather during the sampling at Coleback Lake, and variable weather during the sampling at Shagg Lake.

TABLE 12.—*Summary at standing crop and productivity data from three potential trout lakes in Maine*

Lake	Surface area (acres)	Average depth (feet)	Standing crop of fish		Net primary productivity in midsummer (mg C/m²/hr)
			Number per acre	Weight per acre (pounds)	
Shagg	55	19	1,308	39.7	3.370
Coleback	20	17	5,670	104.5	6.958
Hills	19	17	2,863	62.5	1.886

Failure of standing crop and primary productivity estimates from Shagg and Hills Lakes to conform with the proposed ranking of the lakes may not be wholly the result of errors in the measurements. There seems to be general agreement among biologists (Rounsefell, 1963; Davis, 1963; McConnell, 1963; Odum and Odum, 1959) that there is no a priori reason why standing crop of fish and productivity of phytoplankton should be correlated. Thus the data in Table 12 may not be misleadingly inaccurate, but may merely demonstrate again that productivity of phytoplankton is not a satisfactory index to standing crop of fish, or vice versa. Indeed, standing crop of fish is considered a poor index even to the productivity of a fish population (Ricker, 1958; McConnell, 1963), suggesting even more strongly the unreality of expecting a close correlation with productivity of phytoplankton. Other factors probably operating to make close correlations unlikely are the differing species compositions of the fish populations that inhabited the lakes and their differing interspecific interactions, the differing food webs probable in the three lakes, and the varying amounts and types of extraneous nutrient materials reaching the lakes from their drainage basins.

In view of the above considerations it is doubtless unrealistic to imagine that a single index to the basic fish-producing capacity of a lake exists. Certainly the most we can hope for with measures presently available is that individual habitats can be ranked. That the ranking tentatively assigned to Shagg, Coleback, and Hills Lakes after consideration of Table 12 may be correct is suggested by the average total lengths attained by brook trout in the lakes subsequent to reclamation and restocking. Management policy for reclaimed trout lakes in Maine calls for annual mid- or late-summer stocking with 0-age trout (2 to 4 inches, total length) beginning in the first summer after the pond has become nontoxic. The number of trout stocked at Shagg Lake was 236 per acre, at Coleback Lake 250 per acre, and at Hills Lake 253 per acre. Average total lengths attained after 1 year at large were: Shagg Lake—7.04 inches, Coleback Lake—8.63 inches, and Hills Lake—7.99 inches. These differences are statistically significant at or above the 95 per cent level; thus the lengths attained in the three lakes conform with the proposed ranking of the lakes.

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BIOLOGICAL MEANS OF INCREASING PRODUCTIVITY IN PONDS

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Many techniques must be employed by the fish culturist to obtain highest possible yields of fish from ponds. Unproductive natural waters and soils may be improved by the chemical means of liming and fertilization. Production can be further increased by supplemental feeding, and to the highest plateau by feeding in flowing waters to dispose of wastes.

At all levels of fishculture, stock manipulation and other biological means of increasing productivity are of greatest importance in obtaining maximum efficiency in use of the water and pond space. The various techniques found to be of importance in obtaining high productivity at this Station include use of efficient species, species combinations, disappearing species, rates of stocking, delayed stocking, control of reproduction, control of wastes, and use of cover.

1 USE OF EFFICIENT PONDFISH

Under this heading come three principal subheadings - species that are efficient because of their feeding habits, because of selective breeding or because of freedom from parasites and disease.

1.1 Efficient species of pondfishes

It is well known in biology that highest production may be obtained by use of those species with the shortest food chains. In general this indicates that highest production may be obtained by use of plant-feeding species of fish. Results from a wide variety of species indicate that in general this is true. Maximum production obtained at this Station with species of various feeding habits in fertilized ponds were as follows:

Species	Feeding habit	Maximum production kg/ha
Laregmouth bass[1]	piscivorous	196
Channel catfish[2]	insectivorous	370
Bluegill[3]	insectivorous	560
Java tilapia[4]	plankton-feeder	1612

[1]Micropterus salmoides
[2]Ictalurus punctatus
[3]Lepomis macrochirus
[4]Tilapia mossambica

However, it should be pointed out that the Java tilapia is a plankton-feeder and not purely a plant-feeder. In fact, work by Tay (Prowse; 1961) has indicated that several species of phytoplankton ingested by this tilapia are apparently not digested. It is probably true that no species of fish is entirely herbivorous.

The mere fact that a species is at least in part herbivorous does not indicate that it will give highest production under various systems of management. The Congo tilapia (Tilapia melanopleura) feeds extensively upon submersed aquatic plants. However, when placed in an environment (fertilized water) where the plants are microscopic, it gives relatively low production because its gill rakers are too widely spaced to enable it to strain and utilize the phytoplankton. It does appear to hold true

that highest production is usually obtained with plankton-feeding species.
Where supplemental feeding was used, maximum production with Congo tilapia
was 2240 kg per ha and with Java tilapia was 6048.

Again, it must be emphasized that a more efficient species at one
level of management may not be the more efficient at another level. For
example, the bluegill and the channel catfish are both principally in-
sectivorous. In fertilized ponds, the bluegill was the more efficient,
yielding 560 kg per ha as compared with 370 kg for the channel catfish.
When placed in ponds receiving supplemental feeding, however, the order
was reversed, with the channel catfish yielding up to 2,688 kg per ha and
the bluegill 896. It appeared probable that the smaller mouth-size of
the bluegill made it the more efficient in harvesting natural fish-food
organisms, but this was no advantage when supplemental feed was supplied
in the form of pellets.

These results emphasize that each species must be tested experimentally
for efficiency at different levels of pondculture - in unfertilized ponds,
in ponds receiving fertilization, and those receiving feeding. It is very
important that this testing be done with the principal species present in
each country to identify the most efficient fishes. There are at present
relatively few species of fishes known to be suitable for pond culture,
although many species in the great river systems of each continent would
appear suitable. It is important to have a number of efficient yet different
species to select from for use in ecologically different waters and for
different human preferences.

1.2 Selection for efficiency

Most fish used in pondculture today have not been selectively bred
for any purpose, let alone for efficiency. The common carp Cyprinus carpio

have been selectively bred for shape, for extent of coverage by scales, and for color. Most other species used may be considered to be unselected strains of wild fish, although the fishculturist probably selects each year the larger individuals for spawning.

Prather (1951) selectively bred largemouth bass for efficiency of food conversion at this Station. Individual bass in circular pools were fed weighed amounts of small fish twice weekly for periods of 5 to 12 weeks, and efficiency of gain was determined by dividing weight of fish consumed by gain in weight. The most efficient individuals were spawned and the more rapid-growing of these progeny tested as above for efficiency. This was repeated during a 6-year period. Conversion ranged from 1.5 to 24.2 the first year, and the mean conversions were as follows:

Year	Mean Conversion	Standard deviation
1941	7.3	1.20
1942	3.1	0.28
1943	3.9	0.16
1946	5.1	0.50
1947	2.1	0.15
1948	3.4	0.26

Apparently after 1 year, the most inefficient individuals were eliminated and little change was produced subsequently. The work was discontinued because it was evident that little more could be done without an intensive fish breeding and selection program.

The changes that have occurred in agricultural animals through selection and breeding suggest that this should be a fertile field for improvement of fish stocks.

1.3 <u>Use of parasite - and disease-free fingerlings for stocking</u>

All fishculturists have experienced loss of all or part of a fish

crop from parasites and/or disease. The most effective way to reduce
or prevent such losses in ponds is to stock only fingerlings that are
relatively free of parasites and disease. Clean fingerlings can be
provided principally by two procedures. The first is the use of brood
fish examined and treated where necessary to rid of parasites and/or
disease, followed by early separation of the eggs or young from the parents,
and their culture in uncontaminated waters. The second is the chemical
treatment of all fingerlings for parasite and disease control before
stocking them into production ponds.

At this Station, the earliest experiments with channel catfish were
conducted with fingerlings obtained from a river and no treatments were given
to free them of parasites. During a 3-year test period, each year 50
percent of all catfish died and it was concluded that this species was
not suitable for culture in ponds. However, in later years channel
catfish fingerlings were treated with acriflavin, formalin and potassium
permanganate to rid them of external parasites and disease organisms,
followed by treatment with di-n-butyl tin oxide to rid them of intestinal
parasites before they were stocked into production ponds. When this
was done, survivals ranged from 95 to 98 percent during their growth
to marketable size (Swingle, 1958).

Allison (1957) has developed pond treatments that can be applied
to control the protozoan ectoparasites on fish when epizootics develop in
the production ponds. External parasites of catfishes have caused poor
feed conversions or even extensive fish kills in ponds.

2 SPECIES COMBINATIONS

While the highest production of a single species may be obtained by
raising a plankton-feeding fish, highest total fish production per hectare

can only be obtained by using a combination of species of different feeding habits.

One of the most important problems in fishculture is to determine just what combinations of species are the most efficient in utilizing available fish feeds. Again, this can be determined only by testing in experimental ponds although a certain amount of preselection is possible.

The traditional fishcultures of China and India used species combinations, but these combinations resulted because of occurrence of these species in rivers from which the fish eggs and fry were obtained. Whether these combinations were the most efficient available in each country was not measured.

2.1 Combinations of fishes of different feeding habits

2.1.1 Channel catfish and Java tilapia

The channel catfish is insectivorous and utilizes efficiently pelleted fish feeds containing vegetable and fish meals. It was postulated that this species with Java tilapia, a plankton feeder, should make an efficient combination. Where the pond received supplemental feeding, the results per hectare were as follows in a 191-day experiment:

Species Stocked	Production kg	Catfish Feed Conversion
1. Channel catfish (4400)	1400.0	1.7
2. Channel catfish (4400)	1568	1.7
plus Java tilapia (1250)	266	-

The combination of the two species yielded 1834 kg compared with 1400 from the channel catfish alone. There was no difference in feed

conversion, assuming all feed was utilized by catfish. The tilapia apparently fed on plankton, wastes, and other fish feeds not utilized by channel catfish.

Both the Java and Nile tilapia (T. aurea) have been used repeatedly with channel catfish receiving supplemental feeding. Addition up to 2,500 tilapia with 7,500 channel catfish per ha has not measureably affected growth of catfish or feed conversion where it is assumed that catfish consumed all the feed added.

2.1.2 Common carp[1] and bigmouth buffalofish[2]

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[1] Cyprinus carpio

[2] Ictiobus cyprinella

The common carp stocked at rates over 240 per ha into fertilized ponds often muddy the water during their feeding activities to such an extent as to interfere with phytoplankton growth. The buffalofish is an omnivorous feeder, which does not burrow in the pond bottom. The results per ha of a 10-month test were as follows when the pond received 10 applications of 8-8-2 fertilizer:

	Stocking		Production, kg
1.	2500 common carp		313.6
2.	2500 buffalofish		896.0
3.	2250 buffalofish	745.0	
	plus 250 common carp	179.2	925.1

Here the combination of buffalofish-carp gave slightly higher yield than buffalofish alone, and much higher than carp alone; also the pond water remained translucent enough for good plankton production.

2.1.3 Fish and freshwater mussel

Other animals may be combined with fish in stocking to obtain higher total protein production. An edible soft-shelled mussel, <u>Lampsilis</u> <u>claibornensis</u>, was introduced into bluegill-largemouth bass ponds to determine if it could be successfully cultured along with fish. This mussel was used fried or in soups and considered to be a desirable species for this purpose.

Production of mussels (including shells) per ha in a 12-month period was as follows:

Unfertilized ---------------- 58.2 kg
Fertilized ------------------1010.2 kg

The mussel was stocked into an 0.8-ha pond along with a standard stocking of per ha of 2500 bluegills, 1250 redear sunfish, and 250 largemouth bass. Mussels became very abundant over the pond bottom and were harvested for a period of 5 years along with the fish. At the end of the 6th year, the pond was drained with the following recovery per ha.

Total fish   464.4 kg
Total mussel meats   399.6 "

The total weight of mussel plus shells was 1270.8 kg per ha, of which the shucked weight of meats was 31.5 percent. In addition to the fish recovered on draining, an additional 139.7 kg per ha had been removed by fishing. The average standing crop of fish where no mussels were present was 316.6 kg per ha (Swingle, 1961). In this case the presence of mussels appeared to increase fish production.

It is postulated that the apparent increase was real and probably caused by cleaner water resulting from the filtering action of the 49,440

mussels per ha distributed over the pond bottom. Their combined effect in filtering out the detritus and organisms upon which they feed should have helped to reduce the waste materials that are limiting factor in fish production. The effectiveness of these and other animals in maintaining cleaner pond waters should be a rewarding field of research.

It is noteworthy that the difference in production obtained from Congo and Java tilapia receiving daily feeding, as mentioned in Section 1.1, appeared to depend upon their relative ability to maintain clean water. The Java tilapia feed upon artificial feeds, decaying organic matter, their own feces and upon plankton. Consequently, they can be fed at a high daily rate because the pond bottom and waters are kept clean.

2.2 Combination with fishes that disappear from the combination

A problem in maximum utilization of all food in a pond is that when fingerling fish are stocked, and their combined weight is small, much food currently available is not utilized. Food is lost by emergence of adult insects, by decay and incorporation into the bottom muds, by denitrification, and other processes. A small amount is recycled into fish foods at a later date, but not in amounts to make up for inability of fish to utilize it during this early period.

One solution would be to stock more fingerlings, but if too many are stocked, none may reach a desirable size. Another solution is to stock the desired species in combination with another species that reproduces very early, is efficient in harvesting the otherwise wasted fish-food organisms, and that remains small enough to be consumed when the principal species becomes larger and food per individual is more scarce.

2.2.1 Bluegills plus Gambusia

In a 7-month experiment in fertilized ponds using 3,900 bluegill plus 1623 Gambusia affinis per hectare, average production per ha was:

Bluegill   186.4 kg

Bluegill plus Gambusia   349.4 "

The 2-inch bluegills plus Gambusia adults were stocked May 2. The Gambusia began producing young on June 1, and became very abundant by late July, when their numbers began declining. When the pond was drained November 14, practically all topminnows had been consumed by bluegills.

2.2.2 Bluegill-bass plus fathead minnows

The fathead minnow (Pimephales promelas) appeared more desirable for this purpose than Gambusia since the former began spawning in March and the latter in June. Average production per ha for a 12-month period in fertilized ponds stocked with 3750 bluegill fingerlings (5cm), 134 largemouth bass (2cm), and with or without fathead minnows (1000 and 2500) were as follows:

Bluegill-bass   282.6 kg

Bluegill-bass-fatheads   470.6 "

The fathead minnows and bluegill fingerlings were stocked in December, with the small fingerlings bass added in May. Fatheads spawned in March and became exceedingly abundant. The numbers began to decline early in July, from predation upon them by both the bass and the bluegills. Few remained when ponds were drained in October-December. Their presence harvested enough extra fish foods to increase average production by approximately 66 percent.

2.2.3 Tilapia-bass plus fathead minnows

Tilapias at this Station are carried overwinter in warm water and stocked into ponds in April. Largemouth bass fingerlings are added in May. One year a pond was stocked with 2,500 Nile, 2500 Java tilapias plus 500 largemouth bass per ha. The next year it received the same stocking of Nile, Java tilapias and bass, plus 2500 Congo tilapia and fathead minnows. The fathead minnows were in the pond in January of the same year, being escapees from draining a fathead pond above. They were used to harvest fish-food organism produced in the pond prior to stocking the tilapias. Since tilapias were primarily plankton feeders, the fatheads plus any young tilapias hatched in the pond were principally feed for the young bass. Each year the fish received supplemental feeding from May to November, when the pond was drained. The results per ha were as follows:

Experiment	Production, kg	
	Tilapias	Bass
Without fathead minnows	2118.0	21.2
With " "	2182.7	108.6

The addition of fathead minnows resulted in an increase of 87 kg largemouth bass per ha, without reducing the production of tilapias.

2.2.4 Channel catfish-bass plus fathead minnows

Originally, 2,500 fathead minnows were added with 7,500 channel catfish per ha in ponds receiving supplemental feeding with the expectation that they would be eaten by catfish. This did not occur; therefore, they were utilized by stocking 125 largemouth bass per ha. In a period of 7 years this had added an average of approximately 45 kg per ha of bass to each crop of catfish without interference with the growth or production

of the latter.

This method of making more efficient use of unused fish feeds in ponds would appear worthy of more extensive testing and use.

3 RATES OF STOCKING

Rates of stocking of fish are extremely important at all levels of fishculture. If too few are stocked, the results are large fish and low production. If too many are stocked, the result may be high production, with fish of undesirable size.

3.1 In unfertilized and fertilized ponds

The problem of how many fish to stock is most troublesome in unfertilized and in fertilized ponds. If the number of fingerling carps is stocked so that 200 g carp will be produced by the end of the growing period, then fish foods produced by the pond are being wasted during a considerable portion of this time. This is true because the carp normally eats not more than 5 to 8 percent of its own weight daily, and when small, little feed is required. In natural populations, this problem is solved by spawning; then thousands of young fishes are available for harvest of the fish-food organisms. As fish grow larger and require more feed, this problem is solved by reduction in small fishes by predation. This is a similar solution to that presented in section 2.2 by use of the fathead minnows as a disappearing species.

If sufficient carp are stocked to consume current fish-food production, then there will be insufficient food to raise them to a desirable size.

This was illustrated by experiments at this Station on rates of stocking Java tilapias in fertilized ponds during a 4-month period (Swingle, 1960). The results per ha were:

Number stocked	Fish production, kg [1]		Percentage harvestable
	Total	Harvestable	
5,000	316.2	309.1	97.5
10,000	403.2	203.4	50.4

[1]
Tilapias averaging 45 g or more.

In experiments with various rates of stocking bigmouth buffalofish, results from a 6-month growing period in fertilized ponds (Swingle, 1957b) were per ha:

Number stocked	Average weight stocked, g	Production kg	Average size g
300	22.7	151.6	636
600	22.7	273.5	603
1080	22.7	656.5	590

In this case, since the final sizes were approximately equal, the maximum rate of stocking probably could have been somewhat higher. The two lower rates of stocking (300 and 600) required another 7 month of growing season to reach approximately the same standing crop as was achieved in 6 months at the highest rate of stocking. It is evident that in determining rates of stocking for various levels of management, a range in rates of stocking must be tested to enable selection of the maximum rate producing desirable-sized fish in a minimum time period.

3.2 In ponds with feeding

Supplemental feeding enables the fishculturist to use natural fish-food organisms more efficiently. In a direct way he can do what nature does in natural populations in a round-about way. In section 3.1 it was

pointed out that in natural populations small fishes hatching in the

spring harvested economically the fish-food organisms and as some

became larger, a larger share of the food was made available to them by

reduction in the numbers of fish. This reduction is accomplished by

predation, often ably assisted by various other causes of "natural

mortality". With supplemental feeding, the fishculturist can stock

larger numbers of fish per ha to more fully utilize natural fish-food

organisms. As fish grow larger, he can supply increasing amounts of

supplemental feed to bring them to harvestable size.

3.2.1 Experiments with catfishes

With daily supplemental feeding, large numbers of fingerling fish,

or larger fish, must be stocked if high production is to be achieved.

In early experiments at this Station, the channel catfish was stocked

at 560 fish per ha and given supplemental feeding. The species was dis-

carded as of little value for commercial use because production per ha

was only 302 kg. Later work with the speckled brown bullhead (Ictalurus

nebulosus marmoratus) demonstrated the important relationship between

stocking rates and production with feeding (Swingle, 1957a). Results

per ha are given below for a 1-year period during which fish received

daily supplemental feed while water temperatures remained above 16° C:

Rate stocked	Fish produced, kg
2,500	631.7
5,000	840.1
7,500	1,011.8
15,000	1,387.0

With this information, it was immediately suspected that low production

obtained with channel catfish and feeding was the result of the low rate of stocking. Testing with this species was then resumed at various rates of stocking and with supplemental feeding. The channel catfish was then found to be a high producer and most economical in food conversion, directly contrary to the former conclusion. Results for an 8.5-month experiment per ha were as follows (Swingle, 1958):

Rate stocked	Kg fish produced
2,500	1,076.7
5,000	1,709.7
7,500	2,646.6

3.2.2 Experiments with tilapias

Similar results were obtained in experiments with both the Java and Nile tilapias (Swingle, 1960). Fingerlings were stocked at various rates per ha in ponds that had been fertilized. In addition, the fish were fed a supplemental pelleted fish feed. Production per ha in a period from 111 to 123 days was:

Species	Number stocked	Production kg	A_T	"S" Conversion
Java tilapia	10,000	563.6	98.7	2.57
"	20,000	1,601.7	99.7	1.67
"	25,000	1,999.9	88.9	1.10
"	50,000	3,299.1	67.7	1.10
Nile tilapia	20,000	1,546.7	98.5	1.80
"	40,000	2,665.5	91.9	1.35

The fishculturist still has several factors that limit the number of fish he can grow to harvestable size. He must stay within the feeding

rates that give economical conversion, and the maximum amount of feed
he can add daily is limited by the type of feed and by the "sewage
disposal" system in his pond. With flowing water to remove wastes and
and to supply oxygen, safe feeding rates rise to a high level. Without
flowing water to remove wastes, he is limited by the capacity of his
pond system to minimize and to destroy wastes. The Java and Nile
tilapias are among the most efficient of fishes in minimizing wastes;
consequently they can be fed at high rates to obtain high production.
However, even here a limit exists beyond which it is not safe to feed.
Although the stocking per ha of 50,000 fingerling Java tilapias gave
highest production, it was not possible to increase feeding to where
more than 67.7 percent (A_T) of the weight was fish of harvestable
size (i.e. weighing 45 g or more). Combinations of species giving
more efficient disposal of wastes in impounded water or other methods
of waste destruction are needed to attain higher levels of production.

4 CONTROL OF REPRODUCTION

While control of reproduction would probably decrease weight of
the entire standing crop, it makes possible production of fish of desirable
size. This is especially important with the use of supplemental
feeding where the feed must be utilized to produce marketable fish.
Various methods of population control have been used in fisheries.

4.1 Change of environment

This method is widely used in pondfish culture. Milkfish (<u>Chanos
chanos</u>), which spawn only in the oceans, are cultured in brackish water
ponds along the Asiatic Coast. Chinese and Indian pondcultures used
carps that spawned in flooded rivers but would not spawn in ponds. Channel

catfish and buffalofish used at this Station also were river fishes and seldom spawned in production ponds. Lack of ability to spawn in the pond environment made many of these fish excellent species for pondculture.

4.2 Repressive factor

Both common carp and buffalofish normally failed to spawn in waters in which they had been held for several months prior to the spawning period, but spawned readily when transferred to fresh water. This effect was attributed to the repressive effect of excretions from these species (Swingle, 1956). A method of culture for speckled bullhead was devised by stocking fingerlings at different rates to determine the rate at which there was no or little spawning while the fish were still not too crowded for satisfactory growth. For this species the stocking rate of 7,500 per ha accomplished this purpose (Swingle, 1957a).

Nile tilapia fingerlings stocked at 20,000 or more per ha grew satisfactorily with supplemental feeding, but failed to reproduce (Swingle, 1960). However, Java tilapias still reproduced at stocking rates of 50,000 per ha.

4.3 Use of fish too young to spawn

A culture method was devised for the brown bullhead by stocking 2 to 5 cm fingerlings in June, feeding to obtain rapid growth, followed by harvest the next May before reproduction could occur (Swingle, 1957a).

A similar culture was used for Java and Nile tilapias by stocking in May and harvesting at 15 to 20 cm total length the following October (Swingle, 1960). Light spawning occasionally occurred with the Java tilapia, but insufficient young were produced before draining to interfere with production of larger fish.

These cultures have the disadvantage of producing relatively small

harvestable fish (50 to 200 g), and harvest must be in a fixed period just before spawning. This prevents the fish culturist from holding his crop to obtain higher prices when the market is low.

4.4 Use of piscivorous fishes

Piscivorous fishes are used in a number of cultures to reduce the numbers of young so that the older fish may reach a desirable size. In European carp culture, the pike Esox lucius or pike-perch Lucioperca sandra was used to eliminate small carp that resulted from unexpected spawning and wild fishes that entered the pond (Schaeperclaus, 1933).

At this Station largemouth bass have been used with catfishes, tilapias, carp, and other species for a similar purpose and also to increase overall production of desirable species (Swingle, 1957a,b) 1958; 1960).

5 ADDITIONAL SURFACE FOR FISH-FOOD ORGANISMS

In many fertilized ponds, almost the entire bottom contains individual fish-food organisms in close proximity. It appeared, therefore, that "floor" space was a limiting factor and that the addition of various materials would greatly increase surface for attachment and might increase production.

5.1 Freshwater shrimp and bluegills

Experiments were conducted with freshwater shrimp Palaemonetes kadiakensis and the bluegill in ponds with and without cover in the form of brush piles or a mixture of aquatic plants Chara, Najas, and Cabomba. The stocking May 2 per hectare was 3750 bluegills weighing 53.7 kg and/or 65,000 shrimp weighing 21.7 kg; ponds were drained in November. Fertilized ponds received 10 applications of 7-8-2 fertilizer at the rate of 112

kg per ha. The results per ha were as follows:

Unfertilized ponds	Production, kg/ha	
	Shrimp	Bluegill
A Shrimp	45.4	
B Shrimp with plants (less than 50% cover)	236.7	
C Bluegill		112.0
D Bluegill plus plants		140.7
C Bluegill plus shrimp plus plants	182.0	263.9
Fertilized ponds		
A Shrimp	637.7	
B Bluegill plus shrimp	104.9	235.9
C Bluegill		154.3
D Bluegill plus shrimp plus brush	1,173.5	236.8

The presence of rooted or attached aquatic plants filling less than 50 percent of the water volume increased both shrimp and bluegill production in unfertilized ponds. Subsequent experiments indicated that the increase came principally from the presence of <u>Chara</u>, while <u>Najas</u> did not increase production. Highest bluegill production was with <u>Chara</u> plus shrimp.

In fertilized ponds, the presence of shrimp increased bluegill production 60 percent. When cover (attachment surface) was provided by filling the pond to water level with loosely-piled brush, the added surface caused production of 10 times the weight of shrimp but no increase in weight of bluegills above that in the shrimp-bluegill pond without cover. However, all bluegills in the pond with cover were large, while those in the pond without cover included a high percentage of small bluegills. Cover was thus effective in greatly increasing a fish-food

organism, the freshwater shrimp, and increased the harvestable crop
of bluegills.

5.2   Bluegill-largemouth bass

Four ponds were each stocked per ha with 3750 bluegills in December
plus 300 largemouth bass fingerlings in May. Three of these ponds were
without cover and one was filled with brush to the water level in the
shallow half of the pond. After draining in October, the latter pond
was restocked the following season exactly as above, except 600 largemouth
bass fingerling were added. All ponds received standard fertilization.
The average results per ha were:

Stocking *Fertilized ponds*	Cover	Production kg/ha
A Bluegill plus bass (300)	None	282.6
B Bluegill plus bass (300)	Yes	492.8
C Bluegill plus bass (600)	Yes	439.0

Again, it is quite evident that "cover" or added surface provided by
brush was effective in increasing total fish production very materially
(65 percent). The amount of added surface or "cover" needed for highest
production and methods of supplying it are interesting subjects for research.
These experiments suggest that submersed aquatic plants and brush
served the same purpose. It is postulated that the increased pro-
duction resulted because of increased attachment surface for fish-food
organisms. Since brush or flooded trees decay rapidly, they lose most
of their effectiveness within a few years. It would appear that submersed
rooted aquatic plants would be the cheapest and best for adding attachment
surface, provided species can be found that do not become so abundant

as to exclude fish from large areas of the pond.

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Aquatic Primary Production

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SYNOPSIS. The ecosystem concept has been particularly useful and extensively employed in the study of aquatic primary productivity. The flow of energy through the system is an attractive area of investigation when it involves some process, but has a more restricted value when units of biomass are simply converted to calories. Although we are able to measure primary productivity in terms of the carbon fixed, we are not yet able to measure the actual change in the oxidative state of the newly fixed carbon. The fate of photosynthate as food for higher trophic levels is therefore dependent upon a considerable array of biological and environmental variables. Primary productivity is considered in terms of its evolution from measures of standing crop and yield, which have been gradually replaced by measures of rate of carbon uptake or oxygen production, or by measure of nutrient loss, or by change of CO_2 in the environment. Data from five lakes are used to illustrate the evolutionary thread of eutrophication and the great range in primary productivity to be expected on the basis of either unit volume or unit surface area at different trophic states. Light and nutrients are important in limiting primary productivity, and are contributing factors to the great variability which one may encounter within a given lake. Only with a sounder understanding of productivity at the base of the food-chain can we have any real hope of controlling the productivity of aquatic environments for the benefit of man.

The concept of "primary productivity" is one aspect of the more general concept of the "ecosystem." Judging from the historical development of ecological theory, ecosystems as conceptual divisions have been most easily studied in the form of standing bodies of water. Eighty years ago Forbes (1887) published his classic "The Lake as a Microcosm," in which he displayed remarkable insight into the interdependence of the plants and animals in a lake. If he appeared less aware of the great importance to his microcosm of such abiotic factors as erosion and domestic pollution, it is probable that in 1887 they were considerably less visible than they are today. The ecosystem concept continued to develop through the work of other aquatic biologists such as Thienemann (1925), and eventually gained maturity in papers by Hutchinson (1941) and Lindeman (1942). The last author considered productivity the focal point of activity within his dynamic ecosystem.

One result of this historical development is that the productivities of aquatic systems have been more intensively examined and more carefully measured than terrestrial ones. A further result was the realization that the physical and chemical environment must be studied concomitantly with the biological. This was a major step forward, but with the spectacular availability of new research tools and methods for measuring vast arrays of biological and physical parameters, the researcher now finds himself in a new and sometimes serious dilemma. What is to be measured, why should it be measured, and what is it likely to add to our understanding of the ecosystem? In the following I give, and sometimes illustrate, my impressions of the direction that primary productivity studies have taken, what progress has been made along the way, and what some of the opportunities are for gaining a better understanding of the first level of the aquatic food-chain.

The object of conducting a study of the primary productivity of a particular aquatic environment is to obtain quantitative information about the amount of energy available to support what Ohle (1956) has called the "bioactivity" of the system. This is considered to be the system's capacity for the formation of potential energy and the subsequent reconversion of this to kinetic energy on a unit volume or area basis. In terms of Lindeman's trophic-dynamic model, one measures productivity in order

to compute efficiency of energy transfer within the system. In this kind of analysis, some value derived from the measured primary productivity is used to express the input of energy into the herbivore level.

Lindeman (1942) developed a model in which he introduced the concept of energy flow, illustrating it with data collected in natural ecosystems. It was consistent with his purpose to express the data as energy units (calories). Subsequent workers have continued to probe the concept of energy flow. However, advances in biochemistry, physiology, and ecology require an elaboration of the model of energy flow to the point where data relating it to the natural world are extremely difficult to acquire.

Energy is interesting to talk about when the discussion is referred to some process. In an imaginary world in which the functional units are discrete trophic levels, it is not only possible but stimulating to describe the flow of energy through the system. But when the functional units of the system being investigated are conceived of as macromolecules there seems to be only limited merit in translating what amount to rate measurements of biomass accumulation into energy units.

As an illustration, the widely used C^{14} method for estimating primary productivity measures the physical incorporation of carbon atoms into living cells. Neither this method nor any other practical technique adequately measures the change in oxidative state of the carbon fixed. Moreover, the subsequent ecological role of newly fixed carbon is even less amenable to quantitative study. Photosynthate may be used in numerous ways by the photosynthetic organism. The subsequent ecological role of the photosynthate depends on which of these possibilities is realized. Even if we could specify completely the fate of newly fixed carbon in producer organisms, we would be unable to describe its transfer to heterotrophic organisms in any but the most general terms. In particular, we are still not in a position to describe the energy conversions which take place when a population of natural zooplankton grazes a natural population of phytoplankton. Present-

ly, we are barely in a position to list some of the factors which may be significant. Among these factors are those relative to the immediate history of the organisms, the past and present condition of the environment, and the trend of growth in both populations. Not only do the primary producers themselves have rather different abilities to utilize the available light energy, but the consumers of this trophic level are not bomb calorimeters and have very different abilities to utilize the calories that they consume.

Disregarding for the moment this problem of how best to present data, let us consider how much of primary production is available to the rest of the food-chain. Perhaps the best way to answer this is to consider how much is not available. The community of phytoplankton has a definite respiratory need which obviously must be met before any energy can be passed on to higher trophic levels. The magnitude of this need is impossible to determine with samples of natural phytoplankton because of the presence of bacteria. However, a minimum figure of 10% seems acceptable from studies using the oxygen light-and-dark bottle (*e.g.*, Patten, 1966). In such a study the difference between gross productivity and net productivity represents the rate of community respiration, and ranges from 10% of gross productivity to several hundred percent. An appreciable part of this respiration is due to phytoplankton, and there seems to be no reason to make the assumption that algal respiration remains at some fixed percentage of gross photosynthesis while community respiration fluctuates widely in response to changing conditions. Bunt (1965) measured oxygen consumption of bacteria-free algal cultures with a mass spectrometer and recorded values between 20 and 100% of gross photosynthesis. The results were influenced by quality of the light and temperature. The number of factors likely to influence the ratio of algal respiration to photosynthesis is large and any figure arbitrarily taken to represent this ratio is not apt to be very reliable.

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trophic production for respiration, phyto-plankton communities must also reserve a portion for the maintenance of community structure. This "information cost" has never been measured directly but there is some indirect evidence that it must be paid. When an aquatic system is altered with the aim of increasing the production of fish, zooplankton and fish production may increase disproportionately more than does the production of phytoplankton (McConnell, 1965; Goldman, 1967). A possible interpretation of this observation is that a large amount of primary production is unavailable to grazers but remains with the phytoplankton community as "information" necessary for the maintenance or development of community structure. Grazers remove production which is in excess of this threshold level. If the magnitude of the information cost is high relative to primary production and is not itself a fixed percentage of primary production, then a small increase in the rate of growth of the phytoplankton will provide a relatively larger increase in the food supply of grazers and eventually the fish which consume them.

There are additional difficulties that must be met in the course of fitting measurements of primary productivity to the trophic-dynamic model. It is now known that a highly variable, yet often significant, portion of the photosynthate produced during a C^{14} light-and-dark-bottle experiment is not retained by the producer organisms, but moves into the environment in soluble form (Fogg and Watt, 1965; Watt, 1966; Hellebust, 1965). It is impossible to measure the absolute magnitude of such excretion by a community of natural plankton because the excreta can serve as a substrate for bacterial growth (Hobbie and Wright, 1965) and thus find their way back to particulate or inorganic form during the incubation period. To be sure, the material so formed is rightly considered primary production, and it ultimately serves as a source of energy for organisms at the higher trophic levels. The pathway along which this energy flows, however, is quite different from that usually modeled for the transfer

of energy from phytoplankton to herbivorous zooplankton, and there is evidence that the amount of energy involved may sometimes be of the same order of magnitude as that recovered in particulate form in routine C^{14} productivity studies (Fogg and Watt, 1965).

Another factor that should be considered in studies of energy flow is the role of allochthonous material in supporting the energy requirements of consumer organisms. This material is included in Ohle's (1956) definition of bioactivity. No natural aquatic ecosystem is entirely closed. Potential energy enters in the form of organic solutes and debris. Parsons and Strickland (1962) and Sorokin (1965) have discussed the role of bacteria in incorporating organic solutes into particulate matter. Moreover, Sorokin has shown that this type of production of particulate matter can be the most important as far as producing food for filter-feeding crustaceans is concerned. Organic matter, both particulate and dissolved, may also appear in the water as a result of chemosynthesis. This mode of formation should be considered primary production, but is not usually measured. Its magnitude is probably not great in many systems, but Sorokin has found it to be very important in the Rybinsk reservoir and in the Black Sea.

EVALUATION OF METHODS

Before continuing with a discussion of primary productivity and succession in lakes it is important to turn our attention to methods of measuring primary productivity, for much of the current research in aquatic primary productivity is still directed toward achieving more accurate measurements or toward greater understanding of the methods already in use. Methods of measuring primary productivity are reviewed and discussed in greater detail in Ryther (1956), Odum (1956), Strickland (1960), Doty (1963), Goldman (1963), and Strickland and Parsons (1965). Although some methods of measuring primary productivity have preceded the great development in instrumentation in the last two decades, they have been greatly acceler-

ated by the use of modern instruments, radioactive isotopes, and computers for analysis of data.

Standing Crop and Yield

The standing-crop method has been used by aquatic biologists for the longest time and is still used for estimating the productivity of rooted plants (Westlake, 1965), and for periphyton growth on slides. Primary productivity is the conversion of inorganic matter into organic matter. Standing crop is that part of the production which is physically present in the system, and does not include what is lost in respiration. Findenegg (1965) has made useful comparisons between the standing crop and productivity. Biologists in the early part of this century were, for the most part, content to look at biological systems at rest. To set the whole scheme of biological interactions in motion took several more decades. Preoccupation with measuring standing crop dominated the interests of both freshwater and marine scientists during the long period when nets were yielding a myriad of exciting new plankton organisms to be described. Standing-crop measures were most frequently reported in terms of numbers of organisms. Recognition of the lack of precision in equating large phytoplankters to smaller forms led to the more precise practice of converting counts to biomass or to volumes, and eventually thought was given to production in terms of yield of organisms. This introduced the time factor, and fisheries biologists, like farmers, expressed yields in terms of tons of fish produced per acre of water surface per year.

Productivity is defined as the rate at which biological production occurs. Thus an operational definition of primary productivity is the rate at which photosynthesis occurs. An early attempt at estimating phytoplankton productivity was made by Lohman (1908) from changes in the standing crop. Estimates of phytoplankton productivity are still made today from periodic measurements of standing crop (*e.g.*, Maciolek and Kennedy, 1964), but the

method is of limited use because changes in standing crop of phytoplankton reflect only the net effect of many biological and physical events. For example, standing crop may be greatly diminished by predation and water movements, while at the same time photosynthetic rates may remain high. The measurement of plant pigments, also a standing-crop measurement, is frequently used (Richards, 1952). Some problems in the estimation of chlorophyll *a* are discussed by Talling and Driver (1963).

UPTAKE OF NUTRIENTS

An early attempt at measuring the rate of production in aquatic ecosystems was made by measuring the materials removed in a given aquatic system and calculating how much biological production would be required to absorb this amount. In the North Sea, the decreases in CO_2 and phosphate were used by Atkins (1922, 1923), and Cooper (1938) considered decreases in oxygen and nitrate. Steele (1956) has estimated the annual cycle of plant production in a northern portion of the North Sea (Fladen Ground) by considering changes in the inorganic phosphate in relation to vertical mixing of the water mass. Phosphorus is considered by many to be a particularly difficult element to use because it is often taken up and stored by organisms well in excess of their requirements for optimum growth (Gerloff and Skoog, 1954). These methods were, of course, indirect and were influenced to an uncertain extent by the interactions of both plants and animals. Still they were of real importance in directing the field towards attempting to achieve more precise measurements of a dynamic system.

Methods of Measuring Oxygen and CO_2

In moderately to highly productive aquatic environments it is feasible to measure short-term fluctuations in dissolved oxygen directly in the environment. As a first approximation, it is assumed that as each mole of carbon dioxide is reduced in photosynthesis a mole of oxygen is released into the water. Thus, if suitable correc-

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tions can be made for the diffusion of oxy-
gen across the air-water interface this meth-
od can be used to estimate the net rate at
which the community is incorporating CO_2,
without enclosing it in a bottle (Odum,
1956). If measurements are made at regu-
lar intervals over a 24-hr period, the aver-
age hourly decrease in oxygen during
hours of darkness can be determined. It is
then assumed that respiration removes this
amount of oxygen each hour throughout
the day, making it possible to estimate the
gross rate at which the community incor-
porates CO_2. There is an analogous meth-
od in which fluctuations in CO_2 are re-
corded.

The pH meter, which was thought for a
while to be the panacea for the afflictions
of aquatic biologists, was quickly brought
to bear on the problem of measuring pho-
tosynthesis. As carbon dioxide is removed
from an aquatic system during photosyn-
thesis, the pH rises. This shift has been
used to estimate both photosynthesis and
respiration. The sea and some fresh waters
are too buffered against changes in pH to
make this method useful in all environ-
ments, but it has been employed with suc-
cess in lakes (Verduin, 1956), and for con-
tinuously monitoring the growth of cul-
tures (Beyers, 1965). CO_2 may also be meas-
ured by standard volumetric or gasometric
techniques.

Although CO_2 and O_2 can be measured
with relative precision, the overall preci-
sion of productivity measurements made by
these techniques is not generally great be-
cause of uncertainties in the corrections for
diffusion, water movements, or extended
enclosure time. Some of the oxygen pro-
duced may not be immediately released
from higher aquatic plants, thus causing a
lag period in the evolution of oxygen. The
big advantage of this method relative to
the more sensitive C^{14} method is the esti-
mate one gets of community respiration.

Light-and-Dark-Bottle Methods

Some of the uncertainties just mentioned
can be reduced by making the measure-
ments on samples which have been en-
closed in glass bottles for a time just long

enough for measurable changes to occur,
but not long enough for depletion of nu-
trients or bacterial growth on the bottle
surface. Respiration can be estimated by
pairing each "light bottle" sample with a
"dark bottle" from which light is excluded.
Pütter (1924) and Gaarder and Gran
(1927) were apparently the first to use this
method. They recorded the oxygen in the
initial sample and then, after incubation,
the change in oxygen that occurred in the
light and the dark bottles. From this they
calculated net and gross productivity.

In methods dependent on measurements
of oxygen one has to make some assump-
tion about the photosynthetic quotient
(moles O_2 liberated/moles CO_2 incorpo-
rated). For the photosynthesis of carbo-
hydrate the ratio is unity. For the synthesis
of an algal cell, however, the expected ratio
is higher, and presumably varies with the
physiological state of the algae and the nu-
trients available (Myers and Cramer, 1948;
Ryther, 1956).

Oxygen methods in general have rather
poor sensitivity and are of no use if the
gross incorporation of inorganic carbon
during the test period is less than about
20 mgC/m^3. In many of the less produc-
tive aquatic environments several days may
be required for this much photosynthesis to
occur. During this time bacteria may de-
velop on the insides of the container, in-
validating the results.

Photosynthetic rates can also be meas-
ured in light and dark bottles by determin-
ing the amount of radioactive carbon fixed
in particulate form after a short incubation
with $Na_2C^{14}O_3$ (Steemann Nielsen, 1952).
Sensitivities with this method are much
greater, and much shorter periods of incu-
bation are possible. By adjusting the speci-
fic activity of the $Na_2C^{14}O_3$ inoculums it is
possible to obtain easily measurable
amounts of C^{14} in particulate form after
only 2 hr. Unlike the oxygen method, how-
ever, the result with the dark bottle does
not provide an estimate of community res-
piration and for this reason the C^{14} meth-
od gives the ecologist somewhat less to
work with.

Because the C^{14} method is so sensitive

and rapid, it has been widely used. One outcome of its popularity has been a great deal of scrutiny of the method itself. After 15 years of use, however, it is still not clear whether the C^{14} method estimates gross productivity, net productivity, or something in between. One of the latest papers on the subject (Bunt, 1965) concludes that the results most closely estimate net productivity, but also suggests that the problem may only be resolvable in terms of a particular set of experimental conditions.

There are other uncertainties associated with the C^{14} method already mentioned. There is now ample evidence that a portion of the C^{14} fixed during incubation may seep out of the algal cells in the form of water-soluble organic compounds (Fogg and Watt, 1965). This material is part of the primary production although it follows a different path through the food-chain, presumably being utilized by bacteria (Hobbie and Wright, 1965). The amount of photosynthate liberated extracellularly is large enough to be measured with precision and a number of workers, including the author, are now routinely including quantitative studies of extracellular products of photosynthesis as part of the measurements of primary productivity.

A serious technical problem associated with C^{14} concerns the calibration of radioactive sources and of instruments used for measuring radioactivity. In order to calculate productivity in terms of carbon uptake it is necessary to know accurately the amount of C^{14} initially in the sample, the amount of C^{14} added in microcuries, and the number of microcuries recovered in particulate form by filtering the sample through a membrane filter. Steemann Nielsen (1966) and Goldman (1963, 1968) describe different approaches to solving these problems.

Arthur and Rigler (1967) confirm the warning of Guillard and Wangersky (1958) that another possible source of error exists in the C^{14} method. These authors found evidence that under certain conditions phytoplankton cells are damaged during the filtration, and if steps are not taken to circumvent this loss, calculated productiv-

ities will be less than the actual rates.

These comments on methods have been presented as a caution to those ecologists who might be tempted to rely too heavily on published values of primary productivity in generalizing about the transfer of energy through aquatic food-webs. In this regard, it is significant that those of us who are measuring primary productivity are still spending a disproportionate amount of time on simply finding out more precisely what is being measured.

PRIMARY PRODUCTIVITY AND SUCCESSION IN LAKES

Having briefly discussed methods of measurement, I shall consider succession in five lakes which exemplify major differences in primary productivity and trophic state. The concept of eutrophic and oligotrophic types of lakes is not a new one. It was used by Naumann (1919) to indicate the difference between the more productive lakes of the cultivated lowlands and the less productive mountain lakes. The trophic state of five different aquatic environments is summarized in Figure 1. It should
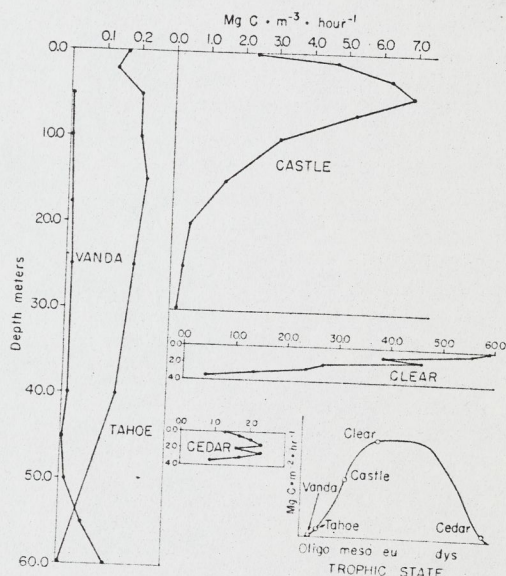

FIG. 1. Profiles of the change in photosynthesis with depth in five lakes during summer. The general trophic state of these lakes is also indicated in relation to their relative carbon assimilation per unit of surface area.

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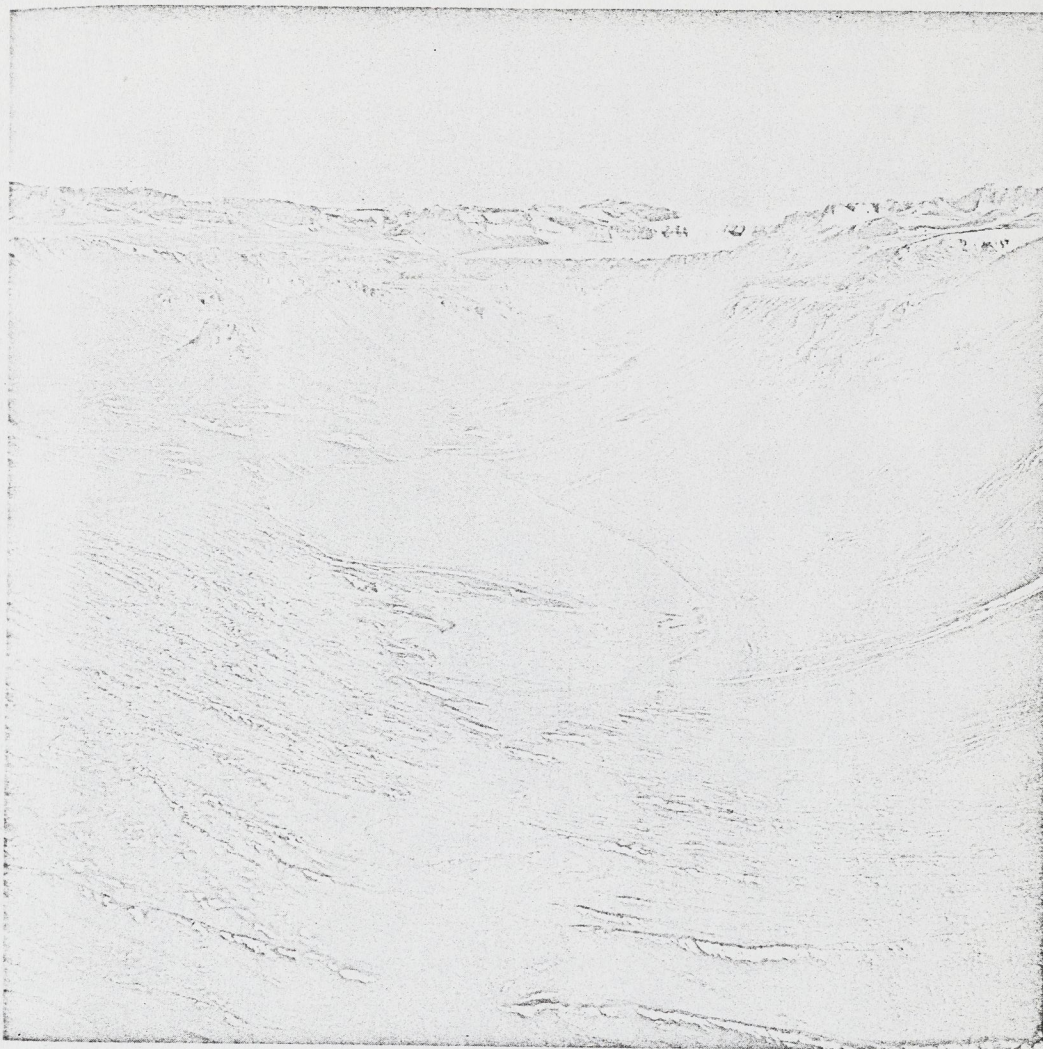
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FIG. 2. Permanently frozen Lake Vanda in the Wright dry Valley, Antarctica (77°32′S lat. 161°33′E long.). Previous shorelines are evident along the right side of the lake. Official U. S. Navy photograph.

be kept in mind that the general progression from an oligotrophic to eutrophic and finally to a dystrophic lake is as much a result of the original basin shape, climate, and edaphic factors, as it is of geologic age. It is unlikely that some shallow lakes ever passed through a stage that could be considered oligotrophic, and it is just as unlikely that the first lake to be considered here (Vanda) will ever become eutrophic.

Lake Vanda, located in "dry" Wright Valley near McMurdo Sound in Antarctica, is one of the least productive lakes in the world (Fig. 2). The lake is permanently sealed under 3 to 4 m of very clear ice, which transmits 14 to 20% of the incident radiation to the water below. This provides enough light to power the photosynthesis of a sparse phytoplankton population to a depth of 60 m (Goldman, et al., 1967). Lake Vanda can be classified as ultraoligotrophic, since its mean productivity is only about 1 mgC/m²/hr (Fig. 1).

Lake Tahoe in the Sierra Nevada of California and Nevada is an alpine lake long esteemed for its remarkable clarity.

FIG. 3. Castle Lake as viewed from the west rim. This cirque lake with a surface area of 19.5 hectares is located in Siskiyou County, California. T.39N.,R.5W.,S13 at an elevation of 5600 feet.

Although it is more productive than Lake Vanda, it is still oligotrophic. The lake is characterized by a deep euphotic zone, with photosynthesis occurring in the phytoplankton (Fig. 1) and attached plants to a depth of about 100 m. Although the production under a unit of surface area is not small, the intensity of productivity per unit of volume is extremely low. Lake Tahoe's low fertility (as inferred from its productivity per unit volume) is the result of a restricted watershed, whose granitic rocks provide a minimum of nutrient salts. This situation is rapidly being altered by human activity in the Tahoe basin. The cultural eutrophication of the lake is accelerated by sewage disposal in the basin and by the exposure of mineral soils through road building and other construction. Since Lake Tahoe's water is saturated with oxygen all the way down, the decomposition of dead plankton sinking slowly towards the bottom is essentially complete. This means that nutrients are returned to the system and because of a water retention time of over 600 years the increase in fertility will be cumulative.

Castle Lake, located at an elevation of 5600 feet in the Klamath Mountains of northern California, shows some of the characteristics of Lake Tahoe as well as those of more productive environments (Fig. 3). It is, therefore, best classified as mesotrophic. Although the lake has a mean productivity of about 70 mgC/m²/hr (Fig. 1) during the growing season, it shows a

depletion in oxygen in its deep water during summer stratification and also under ice cover during late winter.

Clear Lake is an extremely eutrophic shallow lake, with periodic blooms of a bluegreen alga (*Aphanizomenon*) and inorganic turbidity greatly reducing the transparency of the water. The photosynthetic zone is thus limited to the upper 4 m (Fig. 1), with a high intensity of productivity per unit volume yielding an average of about 300 mgC/m²/hr during the growing season. Because Clear Lake is shallow, it does not stratify for more than a few hours at a time during the summer, and the phytoplankton which sinks below the light zone is continuously returned to it by mixing.

Cedar Lake lies near Castle Lake in the Klamath Mountains (Fig. 4). Its shallow basin is nearly filled with sediment and it is nearing the end of its existence as a lake. Numerous scars of similar lakes found in the area presage Cedar Lake's future. Terrestrial plants are already invading the lake, and higher aquatic plants reach the surface in many places. The photosynthesis beneath a unit of surface area amounts to only about 6.0 mgC/m²/hr during the growing season as the lake is now only about 4 m in depth (Fig. 1). Cedar Lake may be considered a dystrophic lake. Some lakes of this type pass to a bog condition before extinction. In others, their shallow basins may go completely dry

FIG. 4. Cedar Lake, Siskiyou County, California. The lake has a maximum depth of just under 4 m and the invasion of the lake basin by rooted plants is well underway.

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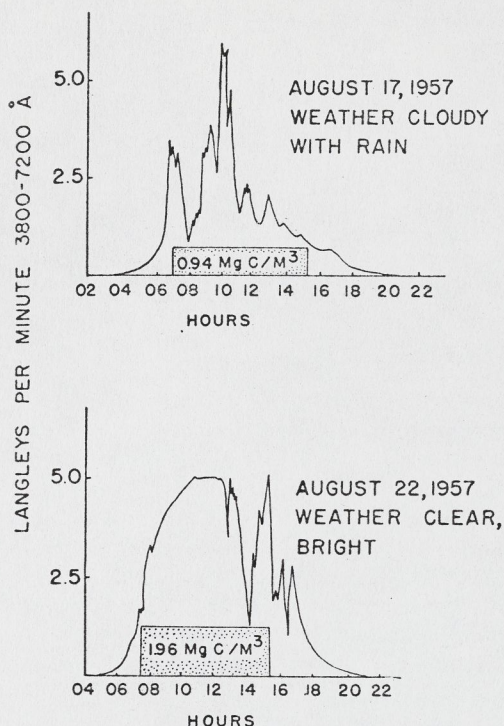...e lake basin by rooted plants

FIG. 5. Average photosynthetic carbon assimilation with variation in solar radiation at Brooks Lake, Alaska. The primary productivity on a cloudy day is compared with that occurring on a bright day. Values are from the average of two stations run simultaneously. (Goldman, 1960a)

during summer, and their flora and fauna become those of vernal ponds.

In examining some aspects of the productivity of these five lakes, the variation in both the intensity of photosynthesis and the depth to which it occurs is evident (Fig. 1). The great importance of the total available light can scarcely be overemphasized. This was first made apparent to the author during studies of primary productivity and limiting factors in three oligotrophic lakes of the Alaskan Peninsula, where weather conditions imposed severe light limitations on the phytoplankton productivity (Goldman, 1960a). The average photosynthesis (mgC/m³/day) on both a cloudy and a bright day was essentially proportional to the available light energy (Fig. 5).

In Figure 1, photosynthesis with depth has been presented for five lakes of greatly differing trophic character. These values

of photosynthesis per hour are all based on 4-hr experiments made at mid-day during summer. Had the experiments been performed during a different time of day, the results would have appeared quite different. A diurnal study of photosynthesis with depth is therefore particularly instructive because it reflects this variation in photosynthesis as the light pattern changes throughout the day (Fig. 6). If photosynthesis-depth curves such as those shown in Figure 6 are integrated, we can plot the diurnal course of photosynthesis beneath a unit of surface area. This has been done for six diurnal studies at Castle Lake, California (Fig. 7). The light curve is included to show the very close relationship between photosynthesis and light during the months of June through September. The consistent symmetry of these curves enables an investigator to make rather accurate conversions of short term experiments to a day's productivity on the basis of measured light.

Theoretical curves have been developed by Talling (1965), Vollenweider (1965),
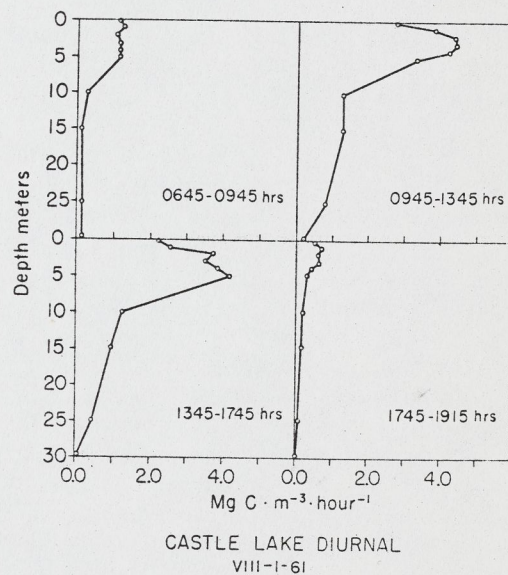

CASTLE LAKE DIURNAL
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FIG. 6. Diurnal photosynthesis-depth curves at a single station in Castle Lake, California. Measurements were made under different light conditions occurring during the four time intervals noted on 1 August 1961. For the light curve for this day see Figure 7.
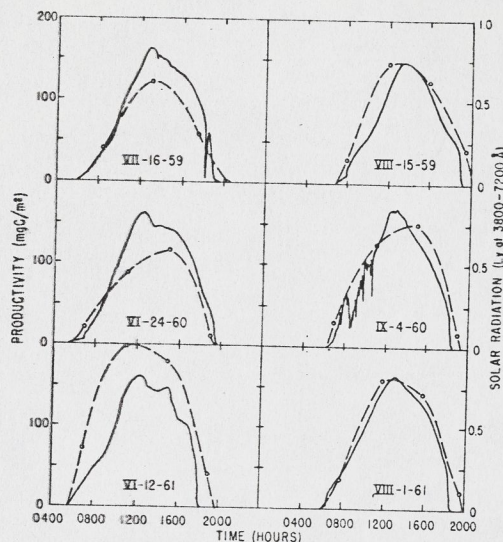
FIG. 7. Integral diurnal productivity curves (broken lines) and photosynthetically active radiation (solid lines) based on measurements made at Castle Lake, California. All curves were developed from the integration of vertical productivity profiles such as the one constructed for 1 August 1961 shown in Figure 6.

and Rodhe (1965) to express the integral photosynthesis. These give rather good estimates if there is not too great an asymmetry in the distribution of the phytoplankton population and if the light curve decreases uniformly with depth. This procedure has very limited usefulness, however, in a lake like Clear Lake where the percentage of light transmitted per meter varies greatly in the euphotic zone (Fig. 8), or in a lake such as Naknek, Alaska, which receives volcanic ash from tributary streams and has a strongly asymmetrical curve of photosynthesis with depth (Goldman, 1960a).

Nutrient limiting factors have been reviewed by Lund (1965) and examined by the author in a number of lakes (Goldman, 1960a, b; 1964; 1965). In Brooks Lake, Alaska, a sequence of the most limiting factors ranged from magnesium in the spring, through nitrogen in the summer, to phosphorus in the fall (Goldman, 1960a). In Castle Lake, potassium, sulfur, and the trace element, molybdenum, were found to be the most limiting. In Lake Tahoe, iron and nitrogen gave greatest photosynthetic

response, with nitrogen of particular importance. Trace elements, either singly or in combination, have been found to stimulate photosynthesis in a variety of lakes. In general, some component of the phytoplankton will respond positively to almost any addition of nutrients, but the community as a whole will tend to share some common deficiencies. Justus Von Liebig did not intend to apply his law of the minimum as rigidly as some have interpreted it, and we can best envision limitation of nutrients from the standpoint of the balance and interactions of the whole nutrient medium with the community of organisms present at any given time. Much about the nutrient requirements of phytoplankton can be gleaned from the excellent treatise of Hutchinson (1967).

It must be borne in mind that the primary productivity of a given lake may vary greatly from place to place, and measurements made at any one location may not provide a very good estimate for the lake as a whole. This problem has been explored in reservoirs by Sorokin (1959), and in Brooks Lake, Alaska, by the author. In the rather sterile Brooks Lake the productivity per unit volume and per unit of surface area increased as one approached the major tributaries providing the lake's nutrients.

Variability in productivity beneath a unit of surface area is particularly evident in Lake Tahoe, where attached algae are already becoming a nuisance in the shallow water, and transparency is often mark-
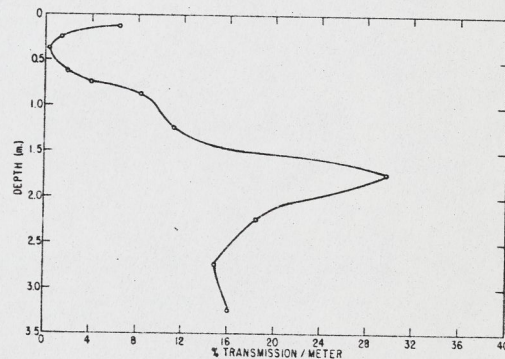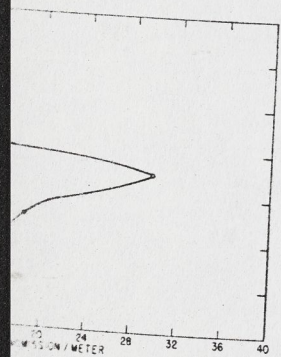

FIG. 8. Variation in the percentage of light transmission with depth in Clear Lake, California. Values computed for each successive depth interval.

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have been found to stimu-
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edly reduced near streams which drain dis-
turbed watersheds. In July, 1962, the pro-
ductivity of Lake Tahoe showed great in-
crease near areas of high nutrient inflow
(Goldman and Carter, 1965). This condi-
tion was even more evident in the summer
of 1967 when Crystal Bay at the north end
of the lake, and the southern end of the
lake showed different periods of high pro-
ductivity. This variability in productivity
may be influenced by discharge of sewage
and land disturbance. Were it not for the
great volume of the lake (155 km³), it
would already be showing more severe
signs of eutrophication.

In the foregoing, I have attempted to
give my impressions of aquatic primary
productivity, treating the subject both as
a research task and as a body of informa-
tion to be interpreted. I believe that bio-
logical productivity can no longer be con-
sidered a matter of simple academic inter-
est, but must be recognized as a problem
of unquestioned importance for survival.
The productivity and harvest of most of
the world's terrestrial and aquatic environ-
ments must be increased if the world popu-
lation is to have any real hope of having
enough to eat. This increase is not pos-
sible unless we gain a much better under-
standing of both aquatic and terrestrial
productivity. Only with a sounder under-
standing of the processes which control
productivity at the level of the primary
producers can we have any real hope of
understanding the intricate pathways by
which energy moves and biomass accumu-
lates in various links of the food-chain.

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How To Be a Predator

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SYNOPSIS. This paper discusses what would appear to be the optimal strategy of a predator given two alternative objectives: (1) maximum yield commensurate with the long-term mainte- nance of the prey species, and (2) extinction of the prey species. The problem is examined in terms of past research on *Daphnia* and *Hydra,* and takes into account estimates of ecological efficiency, population efficiency, and growth efficiency based on many laboratory experiments. It is shown that there may be distinct differences in the effects of removing different kinds of indi- viduals from a prey population. The optimal system for a predator wishing to insure the con- tinued availability of its prey is to take animals which are about to die anyway, *i.e.,* to alter the natural pattern of mortality as little as possible. It is concluded, with some reservations, that predators in nature generally act in this manner. Conversely, if one's intent is to exterminate a prey species (*e.g.,* an objectionable pest), the animals removed should be those which natural predators do not select.

It is obvious that the welfare of man is in part dependent on the kind and abun- dance of some of the other animals on earth. The life, death, and abundance of the completely domesticated animals (*e.g.,* the cows, horses, and pigs) are completely in man's hands. If there are economic rea- sons for having a large population of cows this can be arranged by normal husbandry, and if new means of transportation appear the number of horses is appropriately re- duced. There are, in addition, non-domes- ticated species whose abundance is of sig- nificance. Some of these animals are of great value, and populations of them con- stitute resources occasionally equal in po- litical and historical significance to min- eral resources. Others are pests. Included among the pests are the direct nuisances and hazards, like biting insects and disease vectors, and the indirect nuisances, like ter- mites and stored grain eaters, which tend to lower the wealth and living standards of human populations. While the abun- dance of both pest and resource popula- tions is of great interest to man, and is par- tially under his influence, it typically is not under human control. With regard to these populations even modern man is a hunter, not a farmer.

There is an intuitive feeling that there are wise and foolish ways to be a hunter. A hunter may have as his goal the exter- mination of his prey, or he may be con- cerned with satisfying his own needs at the expense of the prey over a long period of time. Clearly, we expect the behavior of the exterminator to differ from that of the manager, and the behavior of hunters of different species of animals also differs. Is there a general theory which will permit us to distinguish between the behavior of a clever pest killer and a clever resource manager? Or are the differences between the various prey species so great that they overwhelm the hunters' behavior, and ob- scure the differences between exploitation and extermination? The answer to this question is of major importance on a very practical level. As the world's human popu- lation expands, greater pressures are put on specific resource populations. Occasion- ally in the past, and increasingly in the future, these populations are, or will be, altered so as to be in danger of extinction. When such dangers are recognized, research is begun on ways to modify the exploitation of the resource, and any possible shortcuts that might be made in such research are of obvious practical value. If each resource population is a unique problem then no shortcuts are possible.

It would be extremely pleasant if we could discover some basic mathematical law of predation, which would permit us to evaluate in the field a list of constants, and from these parameters derive an opti- mal process of rational predation or effec-

tive pest control. Various workers in fisheries institutions, pest infestation laboratories, and university biology departments around the world have been exploring this possibility for many years. I will not attempt a historical summary but will discuss some of the experimental approaches that have been made to the problem, largely in my own laboratory. I will then derive a rather tentative general theory of predation.

It should be noted that man is not the only hunter to benefit from a prudent policy of predation. The various carnivorous animals also face the same problems. Obviously, for both man and animals the first problem is how to catch prey. Once that has been successfully solved the next problem is how to avoid catching the prey in such a way as to eliminate the resource completely. If we succeed in developing a general theory of prudent predation, it becomes of great biological interest to know if non-human predators mimic this prudent behavior.

It is extremely difficult to experiment with a natural fishery. Aside from the intrinsic difficulties in dealing with large populations of wild animals in nature, any attempt to alter actual fishing procedures involves social and economic problems of major magnitude. Some "natural" experiments can be found, e.g., the cessation of fishing during wars or the introduction of new technology. Unfortunately these are generally lacking in replication and controls and can only be analyzed in a limited way. British and European workers have carefully analyzed the effect of two world wars on the North Sea fisheries.

Rather than wait for accidental experiments it is possible to derive some information from laboratory experiments. These experiments must use animals which are short-lived and which are amenable to relatively simple procedures for laboratory culture. Once the culture problems have been solved, animals placed in a laboratory container will alter their abundance so as to accommodate to the environment. So long as culture conditions remain constant such laboratory populations can be maintained

for generation after generation. It is possible to set up arbitrarily different systems of predation and determine the effect of these on laboratory populations.

In the laboratory, "reality" and immediate applicability are sacrificed for ease of experimental manipulation and repetition. Both natural and laboratory populations are, however, self-regulating systems in which the abundance of a population is determined by the environmental circumstances and the interactions between the organism (given the physiological and genetic properties of the individual animals themselves). If there exists a unique general theory of predation it should be applicable to both natural and laboratory systems and derivable, in principle, from either.

In my laboratory we have used, at various times, populations of flatworms, *Daphnia,* and *Hydra.* All of these species are aquatic and capable of asexual reproduction. In fact sexuality is essentially negligible during these experiments. The experiments are singularly simple, even for laboratory situations, because we deal with behaviorally simple animals in a transparent medium, and are not confronted with genetic recombination and selection during the course of each experiment. In *Daphnia,* for any given physical environment, the size of the population is dependent on the rate of food supply in an essentially linear fashion (Slobodkin, 1954). This is also true of *Hydra* and is convenient for analysis.

It is also generally true that the number of animals maintained in steady-state populations is lower at higher rates of predation. For such populations there is no unique optimal predatory procedure. This becomes obvious if we recognize that a prudent predator must maximize both its yield from the prey population and the probability of future survival of the prey. Other things being equal, an increase in the rate of predation increases the yield but also reduces the number of animals in the prey population—making the continued survival of the prey population increasingly less probable. The rate of predation to

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be chosen in any particular case depends on the amount of weight to be given these two considerations.

Assuming for the moment that the predator is concerned with maximal steady-state yield, it need only leave behind enough of the prey population to just replace itself. What are the limits on this process? The ultimate limit is the maximal possible rate of increase of the prey population. In a constant environment all populations tend to come to constant abundance or fluctuate cyclically. The period of constancy is obviously characterized by equal rates of natality and mortality. The actual size of the population at any time is a resultant of the number born and the life expectancy of each animal. For example, if ten animals per day are born into a population and ten animals die, we know that the population is not changing in abundance. But we do not know how many animals are in it unless we know how long the average animal lives. If an average animal lives ten days there will be one hundred animals in the population—ten times as many animals as there would be if the average animal born lived one day.

Predation acts initially to increase the mortality rate above the birth rate. If there were no compensatory increase of the birth rate the prey population would be completely eliminated. However, there is for all species a certain resilience in the reproductive rate. This resilience is primarily due to the fact that in any population the removal of some of the animals leaves unutilized the resources these individuals would have used. This increases the available resources for the survivors. The number of young born tends to be higher than in the absence of predation, and the mean life expectancy of the animals that are not taken by the predator may be higher than it otherwise would have been. However, the *mean* life expectancy of a newborn animal will be less than in the absence of predation.

As predation becomes more intense and the prey population becomes smaller, a further increase in the rate of predation diminishes the increase in reproductive

rate and longevity of survivors. That is, the physiological limits of fecundity and longevity are approached. Once these limits have been reached there is no further compensatory mechanism available, and further predation will simply destroy the prey population. At the physiological limit the population can be thought of as attempting to increase at a rate equal to the rate of predation. This rate (computed as the immediate increase in population that would occur should predation cease) is the maximal rate of natural increase of the population. It can be computed readily from data on life expectancy and fecundity, and varies between and within species according to the quality of the environment. If we consider that what is taken per unit of time by any predator represents the increase for that environment, it becomes apparent that in the absence of all predation the rate of increase is zero.

While a predator can remove animals at a rate up to the maximum intrinsic rate of natural increase in that environment, it is not advantageous to do so. Not only does such an intense rate remove all resilience from the prey population, but it also usually involves a reduction of the rate of yield to the predator over that achieved by a lower rate of predation.

A predator, in general, uses its prey population to manufacture some commodity from raw materials which are otherwise of no immediate use. For example, a fur trapper uses the fox or beaver population to manufacture furs from the raw material of lemmings or poplar bark, and a herring uses microcrustacea to manufacture food from phytoplankton. The predator is therefore best off if the rate of predation is adjusted to maximize its yield. The process of predation increases the rate of manufacture per unit of prey population while it diminishes the size of the prey population. An extremely small prey population cannot produce the same total quantity of yield to the predator as a somewhat larger one, even if the larger one is producing at a slower rate per animal. Excessive predation therefore diminishes yield even if it does not destroy the prey population.

Our experiments provided a rather surprising result with regard to the maximum rate of yield possible in a predator-prey relationship. In the experiments with *Hydra* and *Daphnia*, the amount of food provided the experimental populations could be measured with fair precision. The *Daphnia* were fed on unicellular algae grown on sterile agar medium. The algae were washed off the medium, the density of algae in suspension was measured photo electrically, and a constant amount of food added to each culture. Richman (1958) determined by direct combustion the caloric content of the algae and of *Daphnia* of different sizes. With this information, and the number and approximate size of the *Daphnia* that had actually been taken from the populations, the ratio of the energy (as calories) in the *Daphnia* removed to the energy in the algae eaten can be calculated. This is, in effect, the efficiency of the *Daphnia* population in taking algal energy and converting it into energy in the form of yield to the predator.

Various attempts have been made to evaluate this type of efficiency (which is now called "ecological efficiency") in natural populations (see Slobodkin, 1962; Engelmann, 1966). Typically these attempts involve fairly large sampling errors in estimates of the densities of the prey and predator populations. There are also a variety of more or less correct conversion constants, and other sampling errors. The values for ecological efficiency that have been derived from field studies vary rather widely, as might be expected, from 4-5% to 20-25%. There is a tendency for such estimates to cluster around 10-15%. Given the various problems in making these determinations, it is not clear whether this clustering is actually an indication of the best estimate for ecological efficiency, or whether a kind of consensus has been created because workers exercised some kind of choice in their conversion constants so as to not disagree too badly with already published work. With these qualifications, approximately 10% is a generally accepted figure for ecological efficiency in nature, and the variations reported from that value do not seem to have any particular relation to ecological situations or taxonomic groups. Many of the estimates of ecological efficiency are for "tropic levels," *i.e.*, herbivores, first-level carnivores, etc., which may involve pooling data from groups as diverse as the vertebrates and the coelenterates.

The experiments with *Daphnia* (Slobodkin, 1959) were among the first laboratory studies in which ecological efficiency could be evaluated. While there are still several conversion constants, the errors in sampling are negligible and the steady-state condition is met. In these experiments the intensity of predation is under complete experimental control. The technician operates as a predator. In the absence of predation the ecological efficiency is zero by definition, since the prey species continues to consume energy but furnishes no yield to the predator. As the intensity of predation increases, the size of the steady state population decreases and, at least for low values of predation, the ecological efficiency increases. As predation becomes more intense the relation between the population of *Daphnia* and its food supply begins to change. At low levels of predation there is a linear relation between food level and size of population. Because the food-consuming capacity of a population is proportional to the number of animals present, when the population is excessively reduced by predation it can no longer consume all of the food provided. This occurs when the ecological efficiency is approximately 8%. As predation becomes even more intense the calories of yield from the *Daphnia* become a smaller fraction of the food provided in the experimental container. However, the amount of yield provided per unit of food energy *actually consumed* by the *Daphnia* continues to rise. At the highest level of predation which we could maintain without eliminating the population completely, the ratio of yield from *Daphnia* to food consumed by *Daphnia* was approximately 12% (Slobodkin, 1959, 1961).

Thus, the first experimental evaluation of ecological efficiency, using animals

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a maximal value of ecological efficiency
which essentially coincided with the mean
of field estimates. This result is sufficiently
surprising to merit either careful theoreti-
cal analysis or extensive repetition or both.
Are we dealing with a constant value or
not, and if it is constant why should it be
so? Unfortunately no theoretical analysis
of any satisfactory sort has yet been made
and the experimental repetition has been
limited to my laboratory.

Since the generality of the agreement
between laboratory and field estimates is
of at least as much interest as the precise
value for *Daphnia,* the repetition was done
with *Hydra*, an organism as different from
Daphnia as possible in most respects. The
Daphnia are free-swimming herbivorous
crustacea. *Hydra* are normally sedentary,
carnivorous coelenterates. The results with
Hydra were not clearly different from those
obtained with *Daphnia*.

This was then tested in one further ex-
tension. I found that the green hydra,
Chlorohydra viridissima, could be main-
tained at a steady state in the same culture
vessel as the brown hydra, *Hydra littoralis,*
in the dark. A system of predation was
established on this two-species system in
which the total number of animals to be
removed was determined as a fraction of
the total increase in population, and the
number removed from each species was
proportional to their relative abundance
in the populations. Again, the maximum
ecological efficiency obtained was essential-
ly the same as given by *Daphnia* and the
generally accepted field value.

There is an immediate suspicion that the
result is some sort of artifact of the experi-
mental procedure, but this is unlikely be-
cause when a similar experiment is at-
tempted with green hydra, in the light, the
maximum ecological efficiency, calculated
as energy in the yield-animals divided by
the energy in the brine-shrimp nauplii
which were used as food, is four times
higher than in the earlier experiments.
Muscatine has shown that green hydra re-

ceive maltose from their algal symbionts
(Muscatine and Lenhoff, 1963; Muscatine,
1965). The tentative conclusion, subject to
further test by other laboratory workers
and subject to more precise analysis of field
situations, is that an ecological efficiency of
8-12% is a reasonable and safe figure to be
maintained by a steady-state population.

If this is valid, we have produced a gen-
eral criterion for exploitation. However,
even if it is valid this criterion is not a
particularly usable one for either human
or animal predators, because it requires a
global perspective on the status of preda-
tion which neither the individual predator
nor the individual fisherman can maintain.
In my experiments I can precisely adjust
my rate of predation to a fixed level with
regard to any desired characteristic of the
population as a whole, because I can ex-
amine the entire population and only then
remove the prey. This type of adjustment
on the part of the fisherman is impossible,
because during his predatory activity he
does not know the state of the entire re-
source population. It is, therefore, neces-
sary to find a procedure which will permit
the individual predator or fisherman to act
within his own local framework in such a
way as to achieve the optimal relation with
the prey population as a whole.

The solution to this problem lies in the
fact that the different kinds of animals in
the prey population have different roles in
that population. Removal of some kinds
of animals critically reduces the standing
crop of the prey population while removal
of others does not. While it is not possible,
on a local level, to assign an optimal preda-
tory rate to each predator it is possible to
imagine an optimal mode of predation.
The strategy of the predator is to take
those animals which best satisfy its needs
with minimal disruption of the prey popu-
lation if the prey species is a resource, and
take animals so as to cause maximal dis-
ruption if the prey is a pest.

In the experiments with *Daphnia* the
optimal category of prey animal to be re-
moved can be readily determined. In these
experiments the yield could be taken either
as young animals or as adult animals, the

adults could be taken either with or without eggs, and the number of eggs in the yield could be counted. For each population we knew the calories of food consumed per unit time (I), the calories of standing crop maintained during that time (P), and the yield as adults (Y_A), as eggs (Y_E), and as young (Y_Y). The yields are expressed in calories per unit time. For each population we can write an equation:

$$I = cP + \frac{Y_A}{E_{PA}} + \frac{Y_E}{E_{PE}} + \frac{Y_Y}{E_{PY}} \quad (1)$$

in which the coefficient c is the cost of maintenance, in calories, of one calorie of standing crop for one time unit. The terms E_{PA}, E_{PE}, and E_{PY} are called "population efficiencies" associated with the removal of adults, eggs, and young, respectively. We will provide a rationale for these terms below, but notice that if the value of E_{Pi} for some kind of animal, i, is large, the corresponding term Y_i/E_{Pi} is very low. If the values of population efficiency differ for two kinds of possible yield in the prey population, it is preferable to take the kind with the highest population efficiency. This is a kind of information that can be used locally without knowing the momentary global status of the prey population. For example, it may be expected that animals in the prey population differing from each other in population efficiency also differ from each other in other properties, *e.g.*, perhaps body size or behavior. A predator can now concentrate on those prey-capturing techniques which tend to take animals of the appropriate size or behavior.

We now have two problems. First, can population efficiency or the relative population efficiencies associated with different kinds of prey be evaluated in any reasonably practical way? Second, and somewhat more subtle, do natural predators take prey of maximum population efficiency, and if so how did they determine the values for population efficiency?

The simplest kind of evaluation of population efficiency can be made if data on steady-state sizes and yields are available from a series of populations, each of which is subjected to a different pattern of predation. In the experiments with *Daphnia* there were 22 populations distributed over three feeding levels (Slobodkin, 1959). At each feeding level young animals were primarily, but not exclusively, removed from some populations while adult animals were preferentially removed from others. Within each of these categories the rate of removal differed between populations. All of the populations differed from each other in standing crop and yields, but assuming that equation (1) is valid for all of them, there is a uniquely determined best set of estimates of maintenance cost and population efficiencies. That is, for each population it is possible to write an equation like (1) with four unknowns and then to solve the 22 equations for the best estimate of the four unknowns. The actual values of population efficiency for *Daphnia* were 48% for adults, 6% for eggs, and 3% for young. While the precise values are not critical, their *relative* magnitudes provide some insight as to the relative values of population efficiency when we have only a single population for study instead of a whole series.

We know that, in general, the natural mortality pattern of *Daphnia* is such that the life expectancy of a young animal is considerably greater than that of an older one. That is, *Daphnia* shares with man, mountain sheep, and horses the property of being relatively viable in their youth and becoming more susceptible to various sources of mortality when they grow older. The removal of calories of old *Daphnia* may make considerably less difference in the size of the prey population than the removal of equivalent amounts of young calories because the old animals are quite likely destined to die in the near future.

This suggests a general procedure. Animals can be removed from a prey population with essentially no danger to the continuity of the prey population, if the predator acts so as not to disturb the distribution of deaths in the prey population. Any prey population, even in the absence of a particular predator, has a normal pattern of mortality. This pattern is a safe one

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from the standpoint of continuity of the population or the population would not be there. If a predator were able to determine which animals were destined to die in the next instant and captured only those, he would be optimally prudent. The limit to this system is that the total yield per unit of time remains small. Any predatory activity which increases yield also alters the death-distribution of the prey. Nevertheless, it is possible to alter this distribution in a modest way. It seems reasonable to conclude that the kinds of prey exhibiting high population efficiency are best to take. These individuals are relatively large and have a relatively high probability of dying in the near future even in the absence of predation.

Another feature which distinguishes one prey organism in a population from another is "growth efficiency," or the ratio of energy in the animal to energy consumed in its growth and maintenance (Slobodkin, 1960). Imagine an animal living for an infinitely long time but growing only during its first year of life. Assume also that its rate of food consumption is approximately proportional to its body size. It is clear that while the growth efficiency of our hypothetical animal might be reasonably high during its first year of life, it would tend to fall with time and eventually approach zero. Other things being equal, it is better for a predator to take animals at an age when their growth efficiency is still high.

Now turn this concept around, and consider an animal that is dying at some particular age. It is possible to calculate the cost, in calories, of replacing that animal with an equivalent one, *viz.*, the number of calories in the animal's body divided by its growth efficiency summed up to its age at death. This permits us to relate growth efficiency to population efficiency. It is possible to show that E_{Pi}—the population efficiency used in (1)—for any animal of type *i* is precisely equal to:

$$E_{Pi} = \frac{Y_K}{\Sigma K_i D_i - P'/P \Sigma K_i D_i} \qquad (2)$$

in which Y_K is the caloric content of the animal, K_i is the cost of replacing an animal of age *i* in the absence of predation, and D_i the number of such animals dying per unit time. K_i and D_i are the corresponding values in the presence of predation and P' and P are the calories of standing crop maintained with or without the removal of the animal of kind *i*.

Equation (2) may not appear to have simplified anything, but it has the virtue of permitting evaluation of population efficiency from data which, at least in principle, can be derived from a single population. Even if no precise evaluation can be made, it is a fairly safe procedure to take a large animal (with a decreasing growth efficiency and a high probability of dying in the near future) rather than a small animal with an increasing growth efficiency and a long life expectancy. Population efficiency is more or less inversely proportional to reproductive value, as defined by Fisher (1958) and used by population geneticists, but the precise relation is not obvious.

We have now shown that there is always an optimal kind of prey for a predator to take. Although it is possible, at least in principle, to choose between kinds of prey on the basis of information from a single population, a large problem remains. Do non-human predators actually take the optimal kinds of animals that would be indicated by our theory? Unfortunately we face a shortage of direct data. The problem can be resolved, however, by recognizing that if a particular predator is a major source of mortality for a particular prey, there is strong selection for some kind of adjustment to the activity of that predator. The adjustment must be expressed in some way rendering the predator's activities less significant. This result can be attained in either of two ways. The more obvious is in the development of escape behavior or protective mechanisms. Because the evolutionary machinery available to predators is essentially the same as that available to prey, this results in an endless evolutionary race unless some stabilizing process is found. The alternative procedure for the

prey is to adjust its mortality, fecundity, and growth patterns so as to maximize the population efficiency of those animals most subject to predation.

Selection is not concerned with an animal's body except as this is a container for future generations. If the fecundity and growth patterns are suitably adjusted, older animals (although still nourishing or valuable from the predator's standpoint) can be made into empty husks from the standpoint of selection. Comfort (1961) has suggested that animals of this sort may be expected to show various kinds of senile degeneration. Being of no value from the selective standpoint permits the degenerative changes that result in death from all causes, in particular from predation. A predator that took only this sort of animal would appear to be highly prudent and would appear to be choosing animals of high population efficiency.

It is possible to raise the objection that predators may prefer younger, more perfect specimens. In any case this is a possibility that should be considered. A shift to younger prey by predators constitutes a selective change on the prey and may be met in the same way as the initial selective change. If this cannot be done I would judge that the prey has been destroyed at some time in the past and is not now available for study. There are many cases in which prey are taken at relatively early ages, before any reproduction at all has occurred (*e.g.*, many of the marine animals with small larvae). It is generally true that these stages are also those that die rapidly in the absence of predation. Errington (1946) suggested, on the basis of studies of muskrat populations, that the chief impact of predators on these animals is borne by the excess animals—those that are wandering and have no territory. In both of these situations, although the animals taken have the physiological potentiality for reproductive life before them, the activities of the predators do not seriously alter the normal survivorship distributions of the prey populations. The predators are merely competing with other sources of mortality. Again we are seeing the removal

of animals with high population efficiency.

In some field situations violent fluctuations of prey are correlated in time with great increases of predatory activity. Among the best studied of these is the lemming population of Point Barrow, Alaska. It is suggested by the work of Pitelka (1957) and his students that the numerical decline of lemmings would actually occur even in the absence of predators.

Of course, in some cases (*e.g.*, the Kaibab deer), elimination of all predators results in a radical alteration in number and condition of the prey. Cases in which the elimination of only one predatory species has clearly resulted in an increase of a prey population, seem relatively rare. The reverse situation is well known in the field of biological control where new predators are sought deliberately so that they may reduce some prey species. It has been frequently pointed out that the prey species is almost always an exotic, and the successful controlling predator is usually from the same country of origin as the prey. This does not necessarily imply that elimination of the controlling predator would cause an outbreak of the prey in the country of origin. It must be emphasized, however, that this experiment (to my knowledge) has not been attempted.

I conclude, with a series of reservations and qualifications (only some of which have been listed here), that predators generally act as if they were behaving prudently. This apparent prudence is essentially forced on them by the selective effect of predation on the prey population, and does not represent any form of rationality on the part of the prey itself. In designing a system of predation for man, we are behaving with maximum prudence if we also take the kind of prey that natural predators seem to prefer. Conversely, in designing a control system we ought to take the kind of prey natural predators do not take.

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Energy Flow in Ecosystems: A Historical Review

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SYNOPSIS. A generalized model of energy flow applicable both to individual populations and food chains is discussed. The basic ideas of energy flow and trophic levels are described, and it is emphasized that the concept of trophic level is not primarily applicable to individual species. The efficacy of rates of population energy flow as a measure of importance in community function is stressed, and the disadvantages associated with measures of density and biomass are pointed out. Finally, the historical development of energy-oriented thinking in ecology is traced in a series of ten steps dating from the late 19th century. The growing importance of systems analysis and the use of computer models to simulate ecological functions are recognized as major areas of emphasis during the next decade.

The study, understanding, and intelligent manipulation of our environment requires systematic investigation of the structure and function of ecological systems at various size levels ranging from simplified microcosms to the biosphere as a whole. In a recent article (Odum, 1962) I suggested that ecology could best be defined as the study of the relationships between structure and function in nature, and that the following breakdown might provide a simplification of the first order for purposes of study.

A. Structure.
1. Composition of the biological community (species, numbers, biomass, life-history, dispersion, etc.).
2. Quantity and distribution of abiotic materials (nutrients, water, etc.).
3. Range or gradient of conditions of existence (temperature, light, etc.).

B. Function
1. Range of energy flow through the system (eco-energetics).
2. Rate of material cycling (eco-cycling).
3. Regulation by physical environment and by organisms (eco-regulation).

Thus, we review in this refresher course one of the several fundamental approaches to ecology—one that lends itself especially to the teaching of the subject to student and citizen alike. My paper is concerned with a brief history of this approach as an introduction to the five papers which follow. Before going into history, I believe it would be well to delimit and define our subject.

The behavior of energy in ecosystems can be conveniently shorthanded as "energy flow" because energy transformations are directional in contrast to the cyclic behavior of materials. The potential and kinetic components of energy flow through an ecological system are lumped under the designations, production (P) and respiration (R), respectively. Consequently, energy flow (E) can be very broadly defined as the sum of P and R, or $E = P + R$. We need, of course, to further subdivide P and R into their ecologically significant subcompartments. Since terminologies have not been standardized and the usage of equation-symbols varies so widely as to be confusing, I believe the best way to establish communication, especially in the teaching arena, is to fall back on a graphic model that shows relationships in the form of an easily understood picture.

In Figure 1, I present what might be called a "universal" model of energy flow, one that is applicable to any living component whether it be plant, animal, microorganism—or individual, population, trophic group. Linked together, such graphic models can depict food-chains (as shown in
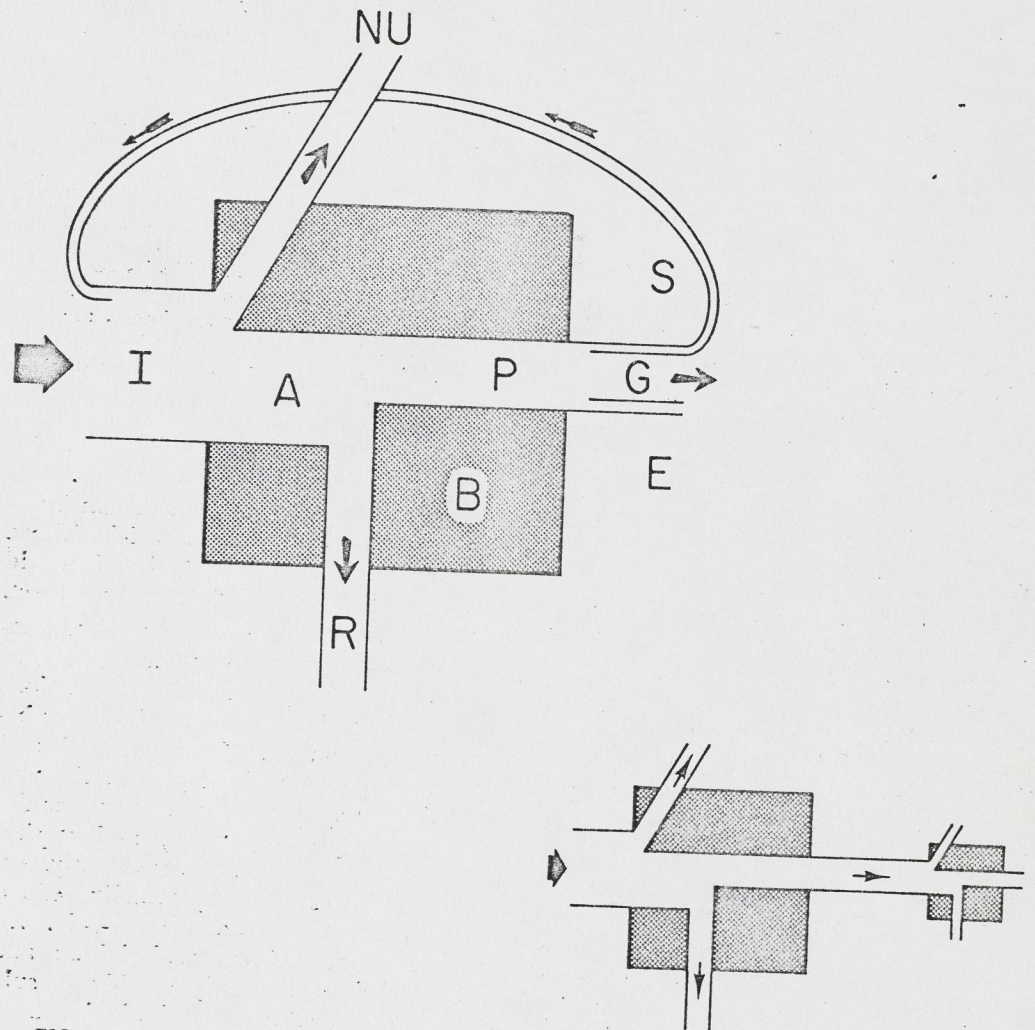
FIG. 1. Components for a "universal" model of ecological energy flow. See text for explanation of symbols.

the lower right of Fig. 1), or the bioenergetics of an entire ecosystem.

In Figure 1, the shaded box labelled "B" represents the living structure or "biomass" of the component. The designation, "standing crop," is a comparable term often used when we wish to speak of the total mass of a population or trophic grouping such as phytoplankton in a column of water or phytophagous insects in a grassland. Biomass is usually measured and expressed as some kind of weight: either total living (wet) weight, dry weight, or ash-free weight. Varying usages here and the lack of good

conversion factors often pose problems. From the standpoint of energetics it is also desirable to express biomass in terms of calories so that relationships between the rates of energy flow and the instantaneous or average standing-state biomass can be established. As will be briefly noted further along in this article, the ratios B/E, B/P, and B/R are of great theoretical interest with respect to community development and ecological succession.

The total energy input or intake is indicated by "I" in Figure 1. For strict autotrophs this is light, and for strict hetero-

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trophs organic food. Some species of algae and bacteria can utilize both energy sources, and many may require both in certain proportions. A similar situation holds for invertebrate animals and lichens which contain mutualistic algae. In such cases the input flow in the energy flow diagram can be subdivided accordingly to show the different energy sources, or the biomass can be subdivided into separate boxes if one wishes to keep everything in the same box at the same energy level (*i.e.*, the same trophic level).

Such flexibility in usage can be confusing to the beginner. In teaching, I find that it is important to emphasize that the *concept of trophic level is not primarily intended for categorizing species.* Energy flows through the community in stepwise fashion due to the second law of thermodynamics, but a given population of a species may be (and very often is) involved in more than one step or trophic level. The universal model of energy flow illustrated in Figure 1 can be used in two ways. The model can represent a species-population, in which case the appropriate energy inputs and links with other species would be shown as a conventional species-oriented food-web diagram. Or the model can represent a discrete energy level, in which case the biomass and energy channels represent all or parts of many populations supported by the same energy source. Foxes, for example, usually obtain part of their food from eating plants (fruit, etc.) and part by eating herbivorous animals (rabbits, field mice, etc.). A single diagram of energy flow could be used to represent the species or the whole population of foxes if our objective is to stress intrapopulation energetics. On the other hand, two or more boxes (such as shown in the lower right of Fig. 1) would be employed should we wish to apportion the metabolism of the fox population into more than one trophic level. In this way we can place the fox population into the overall pattern of energy flow in the community. When an entire community is modeled one cannot mix these two usages unless all species happen to be restricted to single trophic levels (*e.g.*, a highly simplified blue-grass-cow-man ecosystem).
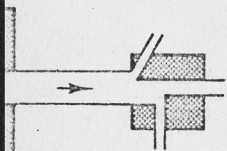
So much for the problem of the source of the energy input. Not all of the input into the biomass is transformed; some of it may simply pass through the biological structure, as occurs when food is egested from the digestive tract without being metabolized, or when light passes through vegetation without being fixed. This energy component is indicated by "NU" ("not utilized"). That portion which is utilized or assimilated is indicated by "A" in the diagram. The ratio between these two components, *i.e.*, the efficiency of assimilation, varies widely. It may be very low, as in light-fixation by plants or food-assimilation in detritus-feeding animals, or very high as in the case of animals or bacteria feeding on high energy food such as sugars and amino acids.

In autotrophs the assimilated energy ("A") is known as "gross production" or "gross photosynthesis." Historically, the term, "gross production," has been used by some authors for the analogous component in heterotrophs. However, since the "A" component in heterotrophs represent food already "produced" somewhere else, the term "gross production" should be restricted to primary or autotrophic production. In higher animals, the term, "metabolized energy," is often used for the "A" component.

A key feature of the model is the separation of assimilated energy into the "P" and "R" components as previously described. That part of the fixed energy ("A") which is burned and lost as heat is designated as respiration ("R"), while that portion which is transformed to new or different organic matter is designated as production ("P"). This is the "net production" or "net photosynthesis" in green plants and simply "production" or "secondary production" in animals. It is important to point out that the "P" component is energy available to the next trophic level, as opposed to the "NU" component which is still available at the same trophic level.

The ratio between "P" and "R" varies widely and is of great ecological signifi-

cance. In general, the proportion of energy going into respiration or maintenance is large in populations of large organisms, such as men and trees, and in mature (*i.e.*, "climax") communities. Conversely, the "P" component is relatively large in active populations of small organisms, such as bacteria or algae, and in the young or "bloom" stages of ecological succession.

Production may take a number of forms. Three subdivisions are shown in Figure 1: "G" refers to additions to the biomass or growth. "E" refers to assimilated organic matter which is excreted or secreted (*e.g.*, simple sugars, amino acids, urea, mucus, etc.). This "leakage" of organic matter, often in dissolved or gaseous form, may be appreciable but is often ignored because it is hard to measure. Finally, "S" refers to "storage," as in the accumulation of fat which may be reassimilated at some later time. The reverse "S" flow shown in Figure 1 may also be considered a "work loop" in that it depicts that portion of production which is necessary to insure a future input of new energy (*e.g.*, reserve energy used by a predator in the search for prey).

Figure 1 shows only a few of the ecologically useful subdivisions of the basic pattern of energy flow. In practice, we are often hampered by the difficulties of measurement, especially in field situations. A primary purpose of a model, of course, is to define components that we want to measure in order to stimulate research into methodology. Even if we are not yet able to chart all the flows, measurements of gross inputs and outputs alone may be revealing. Because energy is the ultimate limiting factor, the amounts available and actually utilized must be known if we are to evaluate the importance of other potentially limiting or regulating factors. Many of the controversies about food limitation, weather limitation, competition, and biological control could be resolved if we had accurate data on energy utilization by the populations in question.

Concepts of energy flow provide not only a means of comparing ecosystems with one another, but also a means of evaluating the

TABLE 1. *Density, biomass, and energy flow of different organisms.*

	Approximate Density (m²)	Biomass (g/m²)	Energy Flow (Kcal/m² /day)
Soil bacteria	10^{12}	0.001	1.0
Marine copepods (*Acartia*)	10^5	2.0	2.5
Intertidal snails (*Littorina*)	200	10.0	1.0
Salt marsh grasshoppers (*Orchelimum*)	10	1.0	0.4
Meadow mice (*Microtus*)	10^{-2}	0.6	0.7
Deer (*Odocoileus*)	10^{-5}	1.1	0.5
Insectivorous birds	10^{-3}	0.02	0.02
Blue grass (*Poa*)	40	200	20.0

relative importance of populations of diverse sizes and rates of metabolism. Table 1 lists estimates of density, biomass, and energy flow rates of eight populations differing widely in size of organism and trophic position. These estimates are based on densities and weight-specific metabolic rates (including an estimate for the "P" component) that one might expect to find in a temperate community of moderate nutrient fertility. For the first six populations listed, the estimated energy requirements are similar, even though the densities vary over 17 orders of magnitude and the biomass over five. This indicates that all six populations are functioning at approximately the same energy level (*i.e.*, as primary consumers or herbivores). The higher rates estimated for blue grass and the lower rates for insectivorous birds are indicative of their different trophic roles in the ecosystem. Because numbers overemphasize the importance of small organisms (*e.g.*, bacteria) and weight or biomass overemphasizes the importance of large organisms, we cannot use either as a reliable criterion for comparing the functional role of populations that differ widely in size-metabolism relationships. The rate of energy flow, however, provides a suitable index for comparing the importance, ener-

..., and energy flow of ...organisms.

Biomass (g/m²)	Energy Flow (Kcal/m² /day)
0.001	1.0
2.0	2.5
10.0	1.0
1.0	0.4
0.6	0.7
1.1	0.5
0.02	0.02
200	20.0

...of populations of di-
...of metabolism. Table
...density, biomass, and
...eight populations dif-
...ze of organism and
...ese estimates are based
...ight-specific metabolic
...estimate for the "P"
...e might expect to find
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...the first six popula-
...mated energy require-
...ven though the densi-
...ers of magnitude and
...e. This indicates that
...are functioning at ap-
...e energy level (*i.e.,* as
...or herbivores). The
...ed for blue grass and
...insectivorous birds are
...different trophic roles
...Because numbers over-
...rtance of small organ-
...and weight or biomass
...importance of large or-
...use either as a reliable
...ing the functional role
...differ widely in size-
...ships. The rate of en-
...provides a suitable in-
...the importance, ener-

getically speaking, of any and all components of an ecosystem.

The idea of looking at nature as an energy-flow system is deeply rooted in the early history of science. Interest in the "fires of life" goes back to antiquity. Many of the concepts that we now apply to the population and community level had their origin in the physical sciences and in the early history of physiology and medicine. For the purposes of this refresher course, I believe we can trace the recent history of ecological energetics in about ten steps. It should be emphasized that the following outline was prepared primarily as a chronology of ideas and not as a historical review of names and literature. Only a few samples of the latter are suggested for their value as background reading.

1. *Qualitative description of food webs.* The idea that organisms in nature are linked together in network fashion through food was expressed in various ways in the writings of 19th century naturalists. Stephen A. Forbes' classic essay on "The Lake as a Microcosm" (1887) is a good example, and provides an appropriate beginning for this historical review.

2. *Trophic levels and ecological pyramids.* In the 1920's, August Thienemann (1926) described trophic levels in terms of "producers" and "consumers," and Charles Elton (1927) wrote about the "ecological niche" and the "pyramid of numbers" in terms of organization of the food chain. As emphasized earlier in this paper, criteria of energy flow should replace numbers if the "Eltonian pyramid" is to remain a valid concept for all types of ecosystems.

3. *Application of thermodynamic principles.* The 1920's also saw the beginning of the influence that the second law of thermodynamics was to have on ecological theory. A. J. Lotka's book, "The Elements of Physical Biology" (1925), was a milestone. His concepts of the non-equilibrium steady state and the "law of maximum energy in biological systems" were forerunners of important ecological generalizations, *e.g.,* the theory of H. T. Odum and Pinkerton (1955) that nature's low efficiency of energy transfer is a consequence of the

tendency for optimum efficiency for maximum power output to be less than maximum efficiency.

4. *Energy budgets and the concept of primary productivity.* Limnologists were among the first to develop these concepts, perhaps because lakes provide such convenient units for study and because heat and gaseous exchanges are more easily measured in standing bodies of water than in other ecosystems. The work of Birge and Juday in the 1930's comes to mind in this connection (see Juday, 1940). As instrumentation improved, it later became possible to deal with energy budgets of terrestrial environments, and even of the whole biosphere, as suggested in David Gates' little book, "Energy Exchange in the Biosphere" (1962).

To a considerable extent, progress in the study of primary productivity depended on the development of field methods. The following is a brief chronology of methods (together with one or more pioneer methodologists):

a. CO_2 uptake in terrestrial enclosures. Transeau (1926).

b. Dark and light bottle method (aquatic). Gaarder and Gran (1927).

c. The diurnal curve method (aquatic). Sargent and Austin (1949), H. T. Odum (1956).

d. Harvest methods. Penfound (1956), Ovington (1957), E. P. Odum (1960).

e. The pH method (aquatic). Verduin (1956), Beyers, and H. T. Odum (1959).

f. The light-chlorophyll method. Ryther and Yentsch (1957).

g. Infra-red gas analyzer measurement of CO_2 (enclosed terrestrial vegetation). Lemon (1960), Mooney and Billings (1961).

h. CO_2 vertical gradient method (unenclosed terrestrial vegetation). Monteith (1962).

5. *Trophic-dynamic concepts and energy flow by trophic levels.* Raymond Lindeman's classic paper on the "Trophic-dynamic Aspect of Ecology" (1942) ushered in the 1940's and did more than any other single contribution to bring concepts of energy flow to focus at the level of the ecosystem. One should not forget, how-

ever, the contributions to this synthesis by G. E. Hutchinson (1948), George Clarke (1946), Amyan Macfadyen (1949), and others.

6. *The energy-flow diagram and community metabolism.* The diagram of energy flow might be referred to by some as an "Odum" device (H. T. Odum, 1956, 1957; Odum and Odum, 1959; E. P. Odum, 1963), although flow-diagrams are routine in physics and engineering. The basic unit of the ecological energy-flow diagram has been described in this paper. In modified form, flow-diagrams have proved useful in emphasizing the fundamental partition of flow into grazing and detritus food-chains (E. P. Odum, 1962; 1963), and as a basis for models of electrical analogue circuits (H. T. Odum, 1960). The latter approach, which considers the energy channels to be the "invisible wires of nature," is especially appropriate for analogue computer manipulation (see item 10 below).

Studies during the 1950's demonstrated that important generalizations could be derived from measurements of the metabolism of whole communities without necessarily having detailed information on all component populations (Odum and Odum, 1955; H. T. Odum, 1957; Teal, 1957).

7. *Secondary production and energy flow in populations.* It is only natural that success in the study of primary production should be followed by increased interest in the energy flow of heterotrophs and concern with the utilization of net primary production. Here again, background experience in laboratory physiology was the basis for the first attempts at field measurements. I cite only a few examples of efforts to combine laboratory respirometry with field census procedures: Pearson (1954), Phillipson (1962), E. P. Odum and Smalley (1959), E. P. Odum, *et al.* (1962), Golley (1960). Ecologists are now seeking new methods which do not require "enclosement" (*i.e.,* confinement in cages or respirometers). Rates of uptake, elimination, and flux of radionuclide tracers provide the most exciting new tools (Crossley and Howden, 1961; E. P. Odum and F. B.

Golley, 1963; R. G. Wiegert, E. P. Odum, and J. H. Schnell, 1967; Reichle, 1967).

8. *Energetics of laboratory populations.* Just as some generalizations are best made from the study of "big nature" (such as a coral reef), so other useful generalizations come from the study of "little nature" in the laboratory. Ecologists are just beginning to take advantage of the precision, control, and experimental design-possibilities of the laboratory in studies that range from those focused on the energetics of populations of single species (Richman, 1958; Slobodkin, 1959) to those dealing with the community metabolism of self-sustaining micro-ecosystems (Beyers, 1963; Cooke, 1967). The latter will be of great interest in future attempts o design a regenerative ecosystem for man's space travel.

9. *The energetics of ecological succession.* H. T. Odum and R. C. Pinkerton (1955) were perhaps among the first to point out that ecological succession involves a fundamental change of the pattern of basic energy flows. As ecosystems develop toward maturity (*i.e.,* "climax"), the P/R ratio approaches one and the B/E (or B/P or B/R) ratio increases—the strategy being not to maximize efficiency of production (as is often desired by man), but to optimize the support of as large and complex a biomass structure as possible per unit of available energy flow. Margalef (1963a, 1963b) has recently documented and extended these basic ideas, and his papers should be required reading for all ecologists.

10. *Systems ecology.* The "input-output," "rate of change," and "flow chart" ways of thinking lead directly into "systems analysis," which is a state of mind as much as it is applied mathematics and computers (Watt, 1966). Because energy flow drives the complex cycles of materials that are the form, function, and diversity of life, "eco-energetics" is the core of "ecosystem analysis." It is not difficult to predict where the emphasis will be in the next decade!

EPILOGUE

Within our own exploding population,

Wiegert, E. P. Odum, 67; Reichle, 1967).

boratory populations. ations are best made g nature" (such as a useful generalizations of "little nature" in ogists are just begin- age of the precision, ental design-possibil- in studies that range on the energetics of e species (Richman, 59) to those dealing metabolism of self-sus- tems (Beyers, 1963; atter will be of great tempts o design a re- for man's space travel.

of ecological succes- and R. C. Pinkerton s among the first to logical succession in- al change of the pat- flows. As ecosystems urity (i.e., "climax"), aches one and the B/E ratio increases—the to maximize efficiency often desired by man). upport of as large and ructure as possible per nergy flow. Margalef recently documented basic ideas, and his quired reading for all

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ROGUE

exploding population,

there is increasing concern about "food ecology," which is essentially the same thing as "energy flow ecology" if we con- sider light as "plant food." The Inter- national Biological Program (IBP) now being planned worldwide around the theme, "the biological basis for produc- tivity and human welfare," is but one indi- cation of the recognition by scientist and citizen alike that a better understanding of the biosphere is urgent. The first phase of IBP, now well underway, involves the scheduling of symposia, planning of pro- grams by national committees, and the preparation of manuals on methods.[1] The definitive phase will involve intensive, mul- tidisciplinary studies of landscapes (such as forests or croplands), important processes (such as nitrogen fixation), and key prob- lems (such as human adaptation). To achieve these goals, many more trained and motivated people than are now available will be needed. Hence, training is one of the primary concerns of IBP planners. In some small way we hope that this refresher course will prove a useful adjunct to the IBP.

[1] Bulletins outlining the U. S. National Program for IBP may be obtained by writing: U. S. National Committee for the IBP, National Academy of Sci- ences, 2101 Constitution Avenue, Washington, D. C. 20418.

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Association, niche, and habitat. The only divisions of the bio-coenosis that seem to have real significance in ecological limnology are what would be termed *associations* by plant ecologists, particularly in Europe. Such parts of the biocoenosis are those that can be characterized by dominant or at least characteristic species.[5] The concept of the association is definitely useful for both plant, animal, and mixed communities. It inevitably has an arbitrary size parameter which cannot be dealt with by a concept of homogeneous diversity but must remain relative to the visual field of the investigator. The association is recognized as a patch, which on examination proves to be caused by the presence of a number of specimens of a particular species close together or to the texture of an area defined by a more scattered but nevertheless spatially restricted distribution of organisms against a nonliving background. The fact that associations so often have definite limits, although the factors determining them often vary continuously, is doubtless due primarily to the external determination of the direction of competition, as Gause and Witt (1935) first pointed out in a formal manner. The term association ordinarily is used for an assemblage of species that recurs under comparable ecological conditions in different places. There is, however, no logical reason why some associations should not have a unique representation in nature. To deny that such an assemblage is an association is to introduce hidden theory into the meaning of the word.

Chodorowski's (1959) term *taxocene* for a group of species, all members of a supraspecific taxon and occurring together in the same association, is most convenient. We may thus speak of the benthic taxocene of tendipedid larvae, the epilimnetic planktonic taxocene of calanoid copepods, or the littoral taxocene of monocotyledonous flowering plants. The populations of the species of a taxocene have obviously been defined as an assemblage or part thereof.

Within any biotope we may also recognize a series of habitats which may be characterized in terms of the various species present. The *habitat* of a species, within the geographical range, may be regarded as operationally defined by specifying those parts of the ecosystem that must be present in a biotope in order for the species to occur. The habitat is regarded as having spatial extension.

The *niche* of a species is defined purely intensively. It is assumed (Hutchinson 1957, 1959b) that all the variation of the factors required to define a habitat can be ordered linearly on the axes of an n-dimensional coordinate system. If the species S_1 requires that the variable X' have values between X_1' and X_2' . . . we can define a hyperspace N_1; any point within N_1 corresponds to values of the variables X', X'' . . . which permit the species to occur. This hyperspace is called the *fundamental niche* of the species. The space of which the niche is a part is called the niche space or, symbolically, the N-space.

The habitats of two species, being two volumes of the physical space of the biotope (B-space) defined by the presence within them of certain parts of the ecosystem, can overlap or be coextensive. It is considered by many ecologists, including myself (see pages 356–357), that under ordinary circumstances at equilibrium two species cannot co-occur in the same niche (*principle of competitive exclusion*). For example, if we consider two species (S_1, S_2) of planktonic copepod or rotifer, one feeding on large and one on small algal cells, and both requiring an identical range of temperature and chemical composition, the habitat of one species would be a volume of water in ordinary B-space of the required physicochemical properties, with small algae suspended in it; the habitat of the other could be the same water with larger algae. Any volume of water might contain both algae and so be a habitat for both species of zooplankton. In the ideal niche diagram, however, the hyperspaces N_1 and N_2, defining the fundamental niches of the two species, would be separated by the different values of the food size on the axis along which food size is measured. More elaborate, if still two-dimensional cases, are easily envisioned (Fig. 71).

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[5] The question why a few species are common and many rare, a condition essential in the characterization of an association, is a fundamental one and is discussed at greater length in Chapter 21.

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Specific Diversity in Fossil Assemblages

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ABSTRACT

Far from forming a confused jumble, some assemblages of fossils, including mammal bones in alluvium, show more ecological order than modern collections of species usually do. Under restrictions first clarified by Goulden, the equitability component of diversity (proportion of individuals per species) converges on MacArthur's Type I distribution. The important restrictions also define a *taxocene*: taxonomic as well as ecological homogeneity, and (if abundance is measured numerically) approximately uniform size. Over time, as shown by Goulden, Tsukada, and others, chydorid Cladocera form stable taxocenes of maximum equitability ($\varepsilon \cong 1.0$). So, also, do forams in deep-sea ooze (data of Phleger et al.), interglacial land snails (data of Sparks), and the rhizopods of bogs (data of Tolonen). Minor losses of equitability, e.g., from $\varepsilon = 0.95$ to $\varepsilon = 0.75$, usually result from abnormal abundance of a single common species, and are associated with *disturbance*: with shifting agriculture and with volcanism (chydorid Cladocera), with flooding and drying of marshes and bogs (land snails, testaceous rhizopods), and perhaps with oceanic cooling (forams). The relation between diversity and stability might be less enigmatic if these disturbances could be quantified geochemically. Supernormal equitability of relative abundance ($\varepsilon > 1.0$) occurs only in a few fossil taxocenes (forams, chydorids), and evidently implies postmortem redistribution.

The similarity of the concepts of energy, order, negentropy, and information led Margalef[2] and MacArthur[14] to a formulation of ecological order that expresses relative abundance in bits of information per individual. Thus, where there are s species and p_i is the abundance of the ith-commonest species in a rank-order of abundance, the total information in the system is

$$H_s = - \sum_{i=1}^{s} p_i \cdot \log_2 p_i .$$

Although I will use the model in this form, it has an alternative derivation that was independent of information theory.[15-18 et al.] The model, MacArthur's Type I or *a*, the "broken-stick model with nonoverlapping niches," assumes that abundances are proportional to the lengths of the n segments of a stick formed by cutting it at random $n-1$ times. For individuals of s species, the proportional abundance of the rth-rarest species is

$$p_r = \frac{1}{s} \sum_{i=1}^{r} \frac{1}{s-i+1} .$$

This generates a theoretical distribution of abundance (labeled "MacArthur" in Figures 1 to 3) that is essentially linear when the proportion of individuals per species is plotted against the logarithm of the rank. Such linearity is not necessarily significant, for, as Cohen[19] has shown, identical distributions are generated by several quite different mathematical models; but the heuristic value of MacArthur's broken-stick model is not impaired.

Despite the random manner of its generation, such a distribution of relative abundance, if it is more than momentary, implies a good deal of organization.[18] The species must have "jockeyed for position," over evolutionary time as well as more recently, within some definable habitat, and arrived at a harmonious apportionment of the environmental resources, whatever they are. Noting that a more even distribution (more nearly equal abundance of all species), though mathematically more orderly, is highly improbable biologically, Lloyd and Ghelardi[20] suggested that MacArthur's distribution represents the maximum *equitability* (evenness, not equality) of abundance that is to be expected in nature. Their coefficient ε, defined as s'/s, is the ratio between an hypothetical and an observed number of species, the hypothetical number s' being the one which, on MacArthur's model, corresponds to the observed specific diversity H_s. (To ease the work of computation, Lloyd et al. give tables[20] of H_s for s species, and tables[21] of $n \cdot \log_2 n$ and $n \cdot \log n$.)

To find species mutually adjusting their abundances in a real habitat, so that $\varepsilon \cong 1.0$, it is essential to give some thought to the definition of the habitat and its relation to sampling, as well as to the choice of species. For example, Lloyd et al.,[22] in their treatment of the herpetofauna of Borneo, were astonished to find an overall value of ε as low as 0.34, i.e., 28.3 equitably abundant species would give the diversity observed for 84 species. They were unable to decide whether the inhomogeneity arose from improper sampling, from lumping of heterogeneous habitats, or from the unpredictability, from a frog's point of view, of the environment on the floor of a rainforest. It is also questionable whether the frogs, lizards, and snakes of Borneo constitute a sufficiently homogeneous taxon inhabiting a sufficiently defined environment. That is, a herpetofauna seems not to be a *taxocene*, as defined by

Handler, Philip (Editor). 1970. Biology and the Future of Man. New York: Oxford University Press, xxiv + 936 pp.

Please note that the excerpt below is from Chapter 11 titled "What is Ecology" and was prepared by a panel of ecologists chaired by Dr. A. D. Hasler.

Stability and Diversity in Ecosystems

Natural communities as small as a patch of meadow have hundreds or thousands of species living together. The total number in a field, or in a wood or pond, is not known; every handful of soil is likely to contain species that have never been identified. Nevertheless, the main properties of the ecosystem, which is all the living and nonliving components that interact in a defined area, can be understood without knowing all its species, in the same way that an organism can be known without knowing all of its cells. Understandably, in so complex a system, some interactions are stronger than others; strong interactions are usually the obvious ones, long known to classical natural history. Ecologists nowadays spend most of their time evaluating weak interactions, many of which turn out to be not so weak, while the totality of a set of weak interactions is almost invariably both strong and nonobvious. The flow of matter and energy, as discussed in the previous section, are functional aspects of ecosystems. In this section we consider some organizational aspects—though if one says that a reef flat has more organization than a pine woods, it should be evident that *organization* is being used in an abstract sense, closely akin to *information content* or *order*.

Pattern of Organization. The diversity of species in an ecosystem is a function of both the number of species and the number of individuals of each species. A system of ten equally abundant species is more diverse than one with one very common species and nine rare species. Several indices have been devised to quantify diversity, some purely empirical, others founded on extremely interesting mathematical models. For many practical purposes, comparisons of diversity among ecosystems yield much the same result no matter which index is used. This sobering fact has not damped the explosion of research on the subject or diminished its excitement, but it is clear that our mathematical models are not yet adequate for the complexity of natural systems. The most ingenious and promising ones are too abstruse to be discussed in this nontechnical account of the subject.

A complete description of the pattern of a particular ecosystem must embrace three types of organization: (1) the pattern of the food web (the network through which energy flows, for example from an eaten individual to the eater), (2) the distribution and arrangement of different species in space and time, and (3) the grouping of individuals of several species into higher taxonomic units, which have varying functional roles. This last, which is also the main concern of systematic and evolutionary biology, is particularly important in ecology when one reflects that organization represents a moment in history. Evolutionary history is not irrelevant where different organisms interact; taxonomic distinctness is the product of such interaction over the whole span of the organisms' histories. The nature as well as the number of the individuals governs, among other ecological properties, the probability that populations will fluctuate with small or large amplitude through time. The following generalizations exemplify the three types of organization:

1. In general, the greater the number of species at any trophic (food-chain) level in a community, the greater the community stability at that level, and at lower and higher levels as well. Amplitudes of fluctuation of herbivore populations are determined by the number of species of plants they eat and by the number of species of predators and parasites that attack them.

2. The areal density of food plants determines the extent to which herbivore populations fluctuate, and the size of the herbivore population in turn determines population fluctuation among predators. Further, the extent to which plants of different ages and species are interspersed affects the stability of the animal populations.

3. When, in a given area, a genus or higher taxon is represented by a large number of species, all with about equal abundance, the information content (degree of organization) of the genus is high. When a genus has only one or a few species, and the commonest is much more abundant

than the rest, the information content is low. The information content of some genera of parasitic insects, so measured over a large area such as a state, has been found to be inversely proportional to the number of host species and to their average population stability.

Diversity and Succession. Ecological succession is the process by which one assemblage replaces another in time at the same site, producing a series of identifiable systems of increasing complexity, and ending with a self-replicating climax stage. The mechanisms are various, and have drawn attention for a hundred years. The significant aspects of succession and climax must be systematic changes in the flux and storage of matter and energy, but these are far from being understood. What is clear is that diversity tends to increase with maturity of the system. In one investigation, land abandoned by agriculture in 1952 was studied through 1963. The early stages were successively more diverse, producing after eight years a grass community dominated by broomsedges. During the ensuing four years the broomsedge community became more diverse, showing both an increase of plant species and an increase in the number of dominant species from eight to twenty-three. Production and diversity are not related in a simple manner, however. Production was high initially, decreased rapidly through the early stages, rose in the grass community to levels above that of the first year, and then declined slowly.

Diversity and Stability. Diversity and ecosystem stability are related, but the form of the relation is obscure and has given rise to controversy. Part of the difficulty may be that the relations differ as between animal and plant communities, and ecologists have attempted to generalize prematurely. If one thinks about a food web, for example, it is easy to see that a species' efficiency in feeding is in partial conflict with the demands of the total system. Food specialization will maximize efficiency for a given animal, but if all animals become perfect specialists, they all risk extinction during small environmental perturbations—the animal diversity may be maximal, but the stability of the system declines. For terrestrial plants, however, animal diversity may often be an unimportant epiphenomenon. With soil nutrients and air evenly dispersed over an area, competition is for space in the sunlight. And the greater the success of some species in becoming large and tall, thus obtaining more sunlight, the more different kinds of room there will be in the interstices for species like herbs and vines that are adapted to shade. So both plant diversity and the stability of the system may increase, almost without limit, as they seem to have done in tropical rainforests.

Computer simulation is a promising technique for understanding such matters, but computer models need both adequate formulation, or programming, and high-quality data, and so far their application to large

terrestrial ecosystems has had only modest success. Such systems being obviously the product of their histories, high-quality historical data are particularly important. A very large body of historical information exists in Europe and North America, covering environments of the last ten thousand years or so, or since the continental ice sheets disappeared. (The restriction is explained by the fact that basins of deposition—lakes and bogs—are mainly found in recently glaciated terrain.) Minor changes of upland vegetation are recorded in lavish detail by the sequence of pollen assemblages in lake mud and peat. Before radiocarbon dating became available, this sequence, used as a chronology, was the principal method of dating archaeological sites, sea level changes, volcanic eruptions, and many other events. Where pollen changes were synchronous over wide areas, regional climatic change is inferred; and although the role of human disturbance has probably been underestimated, there is no doubt that early postglacial changes (9000 to 7000 B.C.) were dramatic but orderly responses to climatic warming. From about 7000 B.C. onward, however, what is most impressive about this record is not the changes, but the stability: somewhat to the surprise of older plant ecologists, *climaxes* seem to have endured for millennia, not just for centuries. Unfortunately, the entire record is nonquantitative, in the sense that proportions of fossil pollen in mud have no definable relation to plant population density in any particular area. As radiocarbon dating (which also calibrates the pollen chronology) brings sedimentation rates under control, this difficulty is gradually being overcome, and the potentialities of a quantitative historical ecology can then be realized.

Diversity and Disturbance. Though stability may be hard to measure satisfactorily, it is often easy to sense, after the fact, when disturbance, the inverse of stability, has occurred. Experiments along these lines are rarely designed; most are performed inadvertently, by advancing civilization. One that *was* designed studied the role of calcium in lakes. An hourglass-shaped bog lake was divided into two lakes by an earthen barrier across the constriction. Calcium hydroxide (lime) was added to one twin, raising the pH from 5.9 to 7.3. In the first year the transparency increased by 60 percent and by the second year the well-lighted zone had thickened from 2.7 to 7.0 meters. The *Daphnia* population was found to replace itself each 2.1 weeks in the lime-treated lake, compared to 4.6 weeks in the untreated twin; both the size of the population and its rate of energy transfer were increased by liming. In addition, new species of phytoplankton and of rooted aquatic plants appeared and began to thrive (Fig. 11-4).

When field collecting is concentrated on particular taxonomic groups, the relations of common and rare species are often found to be remark-

Figure 11-4. Peter-Paul Lakes in northern Michigan were divided by a dam to make twin experimental lakes. Peter Lake was treated with calcium hydroxide, while Paul Lake served as a control. (Courtesy of A. D. Hasler)

ably orderly: a constant ratio holds between abundances, from commonest to rarest, and much the same rank order recurs from place to place and from year to year. A group of very similar species, if of about the same size and competing for similar resources, meeting similar predators, and so on, might ideally be expected to sort itself out numerically in this way, but many more departures from an ideal relation would be expected than are actually observed. The phenomenon doubtless holds the key to many puzzling aspects of ecological order, but a satisfactory general explanation has not yet been found. What is clear so far is that specific diversity, measured in this way in *taxocenes* (natural assemblages that are related both ecologically and taxonomically, like the diatoms in a stream or the mites in an acre of soil), is a sensitive measure of disturbance, especially of pollution.

The reason, probably, is that certain narrow assumptions about "ecological niches" apply best when species that occur together are genuinely similar; the larger the taxon (the birds of Massachusetts, say), the less likely that its members are truly competing for the same resources, which is to say that such a taxon is not a true taxocene. In more natural communities, under careful observation, the first hint of something abnormal

is often the discovery that some species has become abnormally common, while the rest of its relatives are abnormally rare. Diatoms, censused after settling on glass slides suspended in streams, have proved themselves to be an appropriate taxocene, in that their diversity changes in response to pollution. *Cladocera*, or water fleas, have also done so, especially the family *Chydoridae*, which are almost ubiquitous in weedy ponds and lakes. Both diatoms and chydorids have the further advantage that they fossilize readily, often quantitatively, so that quantitative historical data are easy to get. Human disturbance (slash-and-burn agriculture) in Guatemala and volcanic ashfalls in a Japanese lake have both been proved to deform the chydorid diversity systematically *and reversibly*: after each episode of disturbance, the original orderly relation is restored after a few years or decades.

ON THE PROBLEM OF THE EFFECT OF FISHERIES ON FISH STOCKS

By

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When we consider the problem how the fisheries affect the fish stocks and their reproduction the most important and principal question arises whether the fish have ever encountered the influence of any factor similar to that of the fisheries. In other words, we ask if the fish have been able to adapt themselves to some influence which can help them to stand the fishing effect, or whether the fisheries are quite a new factor to them, and they are not prepared at all.

In ichthyological literature the effect of fisheries is, to some extent, considered similar to that of predators on the fish stock. The suggestion seems to be true for small sized abundant species which are, in fact, subject to such an influence under natural conditions. However, the fishing and predatory effects differ substantially. The fishery is usually based on the adult portion of the population, and due to longer contacts between the fishery and older age groups the numerical strength of the latter is drastically reduced. The "rejuvenation" process is always a consequence of the fishery. Predators, on the contrary, take younger age groups. The predatory effect never leads to rejuvenation of the population. Thus, the fishing effect is of specific character, and the majority of fish in their development and during the adaptation process to the environment have never encountered influences resembling the fishing effect under natural conditions. Furthermore, many biologically adapted features which are acquired due to evolution and advantageous to the fish under natural conditions are turning into disadvantageous habits, thus increasing the effect of fisheries on the stocks and the reproduction.

This can be illustrated by a number of examples (Table 1). In many fish species the bodies are covered with bone knobs, hooks and thorns,

Table 1. Adapted features in fish, their biological significance and negative role under condition of intensive fishing

Adapted features	Biological significance	Negative role under fishing conditions
1. Knobs, hooks and thorns on fish bodies, thorny rays in fins	Protection of fish, especially young from predators	Tangling in nets and difficulty in escaping through meshes
2. Height and width of fish bodies	Lower predatory effect on young fishes	Enmeshing in nets with relatively large meshes
3. Shoaling	Lower predatory effect	Efficient detection of shoals by echosounders and asdics
4. Multiage composition of a population	Increase in the reproductive ability of the population	Decline in the reproductive ability as a result of rejuvenation of the stock caused by intensive fishing
5. Gradually maturation of eggs and spawning in batches	Increase in the reproductive ability of a species	Due to longer stay spawners are more easily caught on spawning grounds
6. Low metabolism in winter during the period of maturation	Savings in energy	Higher accessibility to the fisheries
7. Ability of burying themselves in the ground	Protection from predators	Failure in escaping fish nets
8. Well developed receptive system in tuna	Detection of prey	Increase in the space between hooks and extension of longlines
9. High speed of movement in tuna	Chasing for prey, escape from predators	Spread of the area fished by a longline
10. Habit of avoiding zones with high velocities of water in the river in many anadromous fishes	Savings in energy during anadromous migrations	Better access to the fisheries in shallow localities in the river

and the fins have thorny bone rays. These peculiarities can be looked upon as an adapted protection of the species, especially the young, against predators. Due to these features the bycatch of young increases under intensive fishing since it is difficult for them to escape through the meshes of nets and trawls and easy to get tangled in the meshes of the different gears. The best evidence of the negative role of the morphological peculiarities is tangling of the young of sturgeon in fixed and drift nets. This greatly affects the fish stock.

Great width and height of a fish body protect the fish from predators.

In the fishery, due to the height of the body, young specimens are entangled in nets with rather big meshes. Flounder, bream and some other species may exemplify this fact. The peculiarities of their body form impede selective fishing.

Shoaling can, to a certain extent, be considered a means to protect the fish from predators. However, the fishery with modern scouting techniques is facilitated by the shoaling and yields good catches.

A multiage composition of a spawning population leads to some increase in the reproductive ability of a species. Intensive fishing may result in a rejuvenation of the stock by reduction in the older age groups in the spawning population and finally, lowering of the reproductive ability of the species.

The fecundity of fish increases when the eggs mature gradually and is spawned in batches. This enables the fish to use much more of the energetic resources of the body as compared to the case where all the eggs ripen at the same time. Under fishing conditions a gradual maturation makes females stay on the spawning grounds much longer, chances for catch, thus, increases.

A lower rate of metabolism in winter, in the period of gonad maturation is observed in many species of fish. The phenomenon enables a species to save some energy for spawning. Low mobility of fish in this period makes them more vulnerable to fishing gear. The winter fishery for carp is based on this peculiarity as the fish are taken in deeper hollows.

Many species of flat fishes bury themselves in the ground to escape predators. The same reaction in fish to a coming trawl is observed, but all their efforts are in vain when the trawl is too near.

Tuna possess a well developed receptive system which enables them to locate prey over a radius of several dozen meters. Owing to this peculiarity hooks can be arranged with wider spaces, say 70–100 m apart, and the longline stretched to over 100 km.

The great swimming speed of the tuna causes an expansion of the efficient area of a longline, and the efficiency increases in proportion to the speed of the tuna moving over the area. As a result, a harmless gear, as it may seem at first sight, turns into one of the efficient means in the marine fisheries. Let us assume that the average speed of tuna is as low as 5 km per day when the longline is arranged in the water; a longliner then can cover the area of 500 square km. Even if not more than 20% of the fish inhabiting the area are caught, the catch per day per longliner will correspond to a yield from an area of 100 square km. Actually, the tuna is moving much faster.

The sturgeons moving upstream to their spawning areas, avoid zones with high velocities of water. To save their energy they migrate over

shallow places where they are more easily caught by seines than in deeper places of the river..

It is very likely that far more examples can be given as evidence for how adapted features, biologically advantageous, may turn into disadvantageous habits under the condition of intensive fishing.

All these facts reveal that the effect of fisheries on fish stocks is related not only to the technical progress and its excessive scale, but also with the aspect that some adapted features in fish is counteractive under conditions of intensive fishing, thus making the effect of fisheries more pronounced.

Programmes of further investigations should include examination of adapted features in fish which tend to have counteractive effect under fishing conditions, as well as comparative studies of these features under natural and fishing conditions.

SUMMARY

It is demonstrated by examples that morphological, physiological and behavioural features of fish developed evolutionary and normally of protective value are directly disadvantageous to the fish when subjected to intensive fishing.

INTRASPECIFIC STRUCTURE AND VARIABILITY IN RELATION TO FISHERIES MANAGEMENT

By

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INTRODUCTION

Cod is nothing but cod, a fish species, *Gadus morhua* L. This species is caught nowadays with trawls in the north Atlantic and on the Newfoundland banks, in the Barents Sea as well as in the northern Pacific, near the coasts of northern Asia and northern America. This fish is also caught with long lines and hooks in the Norwegian fjords and the White Sea and is known to have been fished by pomors in the last century and by middle age vikings. Cod was fished by the stone age man who populated the Norwegian coast, the Russian Murman and the Pacific coastal areas thousands of years ago.

It is yet uncertain when cod originated as a species, but as far as a number of other species of the same boreal faunistic complex, mostly fresh water fishes, are concerned, they are known to have originated in the mid tertiary period. Most zoologists nowadays regard species as an objective reality, as a form of existence of the living matter. Animal species is not a conventional concept, it is not "what a good taxonomist considers a species", but an actually existing multitude of specimens which possess some specific-qualitative properties characteristic for the given species and relatively stable in time and space. It means that a species which once originated exists a more or less long period of time (so far as the specific environment exists) retaining its specific properties.

As regards freshwater fishes, perch, pike, pike-perch, catfish and some others, they are known to have undoubtedly existed since pliocene time and possibly earlier. At approximately the same time most species representative of the boreal sea fauna complex, cod, oceanic herring, plaice and flounders, etc. were formed (NIKOLSKY 1968). However, the

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

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stability of the species over thousands, and possibly, millions of years ensured by the intraspecific variability, by its elasticity, so to say.

Stenobiotic species adapted to live under relatively stable, abiotic and biotic life conditions reveal a lower variability, lower elasticity. Usually, their intraspecific structure is simpler. An example of this type of stenobiotic fishes with a very low variability could be supplied by most of the species populating coral reefs, e.g. Pomacentridae. These species are extremely low-variable, occupying as a rule, a very limited distribution area and being adapted to very stable life conditions. They perish when these conditions change beyond the limit of this fish's very low specific adaptability.

Eurybiotic species, such as Arctic chars and cod, possess a much wider range of adaptability, a considerable intraspecific variability and more complex intraspecific structure. Thus, every species represents an open self-regulating system in a permanent interaction with the environment which incessantly keeps adapting to the changing conditions. This system possesses at the same time certain morphological, physiological and ecological characters distinctive for the species as a system.

INTRASPECIFIC VARIABILITY

For fishery biologists, endeavouring to develop a scientific basis for fish resource exploitation, the knowledge of the elasticity and the structure of the given species-system of economic importance is quite essential. Principal mechanisms operating in the populations provide changes in number and biomass due to respective environmental changes, first and foremost in the food supply rate which is manifested in growth changes. As is known, the increase in growth rate is related to a faster achievement of maturation age and an increase in fecundity. A faster growth is related to reduction of mortality rate, for, as a rule, bigger fish fall prey to predators on a larger scale than the smaller ones. Principle mechanisms of population self-regulation in connection with food supply changes have been rather well studied (NIKOLSKY 1950, 1962 and 1969, ROLLEFSEN 1953, SCHAEFER 1956 and others) and a detailed account is uncalled for here.

However, the process in question is often found not to be as direct as in the above scheme, being considerably affected by a number of factors and, in particular, by mutual interactions of fish in different number year-classes. A numerous year-class may handicap the growth rate of both preceding and following generations. The problem calls for further investigation for it is of a great theoretical and practical interest, first and foremost, in forecasting of the mature stock recruitment. A review of the data on the problem was reported by POLYAKOV (1962).

Changes in spawning periodicity appear to be an essential form of self-regulation. In fact, in years when the stock of White Sea herring is numerous a part of the females may leave out a spawning period. Due to food supply insufficiency they fail to fatten during a single feeding period (CHEPRAKOVA 1966). This phenomenon is also observed in some fresh-water species, e.g. in whitefish (RESHETNIKOV 1967). It should be noted that many species inhabiting the northern part of the distribution area reproduce every other year, southern populations reproducing annually. Besides whitefish, this has been found in bream and some other species (KOSHELEV 1966). It is interesting that in some species in the southern part of the distribution area, e.g. in bream, portioning in spawning is observed, i.e. the reproduction rate speeds up.

An essential, though yet poorly investigated, mechanism of self-regulation is change in the variability of specimens in the population. Food supply increase is, as a rule, related to a reduction in the year-class size variability. This has been most clearly demonstrated in Baltic herring larvae (ANOKHINA 1969). Strong year-classes are distinguished by a wider variability range that weaken year-classes. The food supply is determined not only by the numbers of fish in an age group, but by the development of its food resources, and equally important, the coincidence of the food plankton period with fry development. This regularity, though manifested in a more complicated way, is noted for cod fry (NIKOLSKY, BELYANINA, PONOMARENKO and SYSOEVA 1968). In the case of cod fry, the variability of characters is largely dependent on the size of the concentrations formed due to the dispersal over one or the other branch of the Atlantic current. Besides, in recent years, due to a low level of reproduction no feedback between the total number of cod fry and the food supply has been observed. This relationship was, however, revealed in specifically rich generation years, e.g. 1963.

The relationship between character variability and the quantity of cod fry is better demonstrated in coastal forms. In such stocks, as a rule, numerous populations prove to be most variable. An increase in variability makes it possible for the population to cope with more diversified environmental conditions. It has been most explicitly demonstrated for characters related to feeding and diet diversity. It is noteworthy, as was revealed in Murman coastal cod, that the diversity of characters in it slightly reduces with age in connection with a higher food supply level in fish at the age $1+$ and $2+$ as compared with specimens at the age of $0+$.

One of the most essential specific characters which secure the existence of a species as a relatively stable unit, is the intraspecific structure. To a certain extent, all the intraspecific forms can be subdivided into four groups.

1. Geographical forms or subspecies, e.g. Atlantic cod and Pacific cod. The formation of subspecies enables the species to fill in a greater distribution area.

2. Ecological forms or infraspecies, e.g. fjord and migratory cod forms. The existence of various ecological forms enables filling in diversified habitats within the distribution area.

3. Seasonal forms, e.g. spring and autumn forms in salmon, autumn and spring spawning herring forms. This means of variability ensures filling in the same biotope to a greater extent in different seasons of the year.

4. Temporary forms, the forms which originate in the same biotope under changed life conditions in a population of any species. Such temporary forms are most markedly observed in numerous freshwater species, e.g. roach in the course of transition to the life in a reservoir newly formed at the river. In mammals such temporary subspecies are found in some fossil forms from the quarternary period, e.g. in Baltic region elk. The adaptive value of temporary subspecies lies in the capability of filling in the same biotope under changed conditions.

The diversity of the four intraspecific forms may be quite different ranging from a clear cut distinguishability to a gradual transition of one form to the other, clinal variability being in evidence. It should be mentioned in this connection that I do not find justifiable the fact that in the latest edition of the zoological nomenclature code taxonomic values are solely attributed to geographical categories, subspecies, the remaining intraspecific forms, being left out. Ecological and seasonal forms, however, often prove to be distinguishable to a greater extent than subspecies.

In many cases the appearance of ecological and seasonal forms is of a parallel character. The phenomenon faced is reminiscent of Vavilov's law of homologous rows (NIKOLSKY 1969). Possibly, as was suggested by BERG (1948) it is expedient to attribute the same specimens to such similar forms in different species, e.g. deep-water forms, infraspecies profundicola, lacustrine forms, infraspecies lacustris, etc. I believe that this scheme should be employed in zoological nomenclature code, subspecific individual names being retained.

IMPORTANCE FOR FISHERIES MANAGEMENT

For fishery biologists, the existence of intraspecific group forms within a species is extremely essential. When exploiting a certain population, dynamics of its number and distribution area should be taken into consideration. For example, the Arcto-Norwegian cod stock, being a unified self-recruiting form distributed over a great area, calls for a definite

exploitation scheme. If, as in the case of the northwestern Atlantic cod, some local forms are found, rational fishery should be arranged on a different basis than in the case of the Arcto-Norwegian stock. It is interesting to note that morphological indices in different age groups of the same form do not differ greatly in local forms of western Atlantic cod. In the Arctic cod, however, the distinctions in the morphology of different age groups within a form may be quite pronounced. This appears to be accounted for by highly variable life conditions in different age groups (Popova 1968). In numerous species there occur both large migratory forms and small coastal ones distinguished by a slower growth as well as an earlier maturation onset. The degree of isolation in these forms may range widely in some cases as in north Caspian roach. A coastal, smaller form may result from reproduction by a semi-migratory fast-growing one, and, evidently, vice versa. In other cases these forms may be isolated, one not reproducing the other.

In red salmon, *Oncorhynchus nerka* (Walb.), the migratory form reproduces in lakes a land-locked form, the so-called residual. In turn from this land-locked form a migratory form can be reproduced under certain conditions (Krokhin 1967).

It should be noted that in the course of the dwarf red salmon development some caryotypic changes occur, a great number of polyploid specimens appearing. This is of particular interest if polyploidy is related to an increased morphological variability. It is noteworthy that in migratory red salmon the caryotype is peculiarly stable (Chernenko 1968). The relationships between seasonal forms prove to be likewise diversified. If, e.g. in autumn- and spring spawning Baltic herring, a partial transition of one form to the other is evidently possible, in chum salmon this appears to be out of the question. It is natural that a fishery biologist aims at elucidating the relationships between the intraspecific forms, in particular, the possibility and conditions under which specimens of one form appear from the specimens of another form, i.e. whether one form can be reproduced by another and to what extent.

Thus, investigation of the theoretical aspects of the problem of species, further elucidation of the concept of species as a self-regulating system appears to be extremely essential for the solution of a number of fishery problems, and, first and foremost, for developing the basis of a rational exploitation of commercial species.*

* Dr. Rollefsen's paper on cod and cod fishery which he kindly sent me bears the following dedication: "To Dr. Nikolsky who also struggles with these mysteries". I believe that joint efforts of scientists the world over will eventually do away with numerous mysteries that still have currency in fishery biology and help to organize rational fishery in international waters, a work which Dr. Rollefsen has been contributing greatly to.

CONCLUSIONS

Every animal species is relatively stable in time and space. This relative stability is provided by adaptive intraspecific variability which makes it possible for the species to exist under certain changes of its biotic and abiotic environment. Species is an open self-regulating system. Eurybiont species usually possess a more complex intraspecific structure and a wider range of self-regulation mechanisms than stenobiont species adapted to more stable conditions.

The knowledge of specific structure as well as its regulatory parameters is essential for rational exploitation of commercial species populations and the ensurement of their reproduction. The most essential system of regulatory mechanisms manifests itself in food supply and reproduction rate variability. Disturbances in this regulatory system affect recruitment and bring about a lack in resources of the given commercial species, i.e. overfishing in the biological sense.

An essential regulatory mechanism which secures the existence of the species is an adaptive morphological variability of its specimens. Every year-class is somewhat distinguishable from adjacent year-classes due to the specificity of its living conditions. At the same time adjacent year-classes specifically in the species with a long life cycle mutually interact, affecting the growth rate, fecundity and other year-class characters.

In specific structure the relationships between intraspecific forms is its essential property. To meet the requirements of fisheries, not only the information of the size and properties of the different species forms are essential, but also the possibilities of reproduction of one of the forms by another, i.e. the character of their relationships.

The knowledge of the peculiarities of commercial species regulatory mechanisms and their structure are prerequisite for developing productive fishery.

SUMMARY

The paper presented deals with the problem of intraspecific structure and variability in fishes. Four forms of intraspecific groups are noted. The necessity to study the intraspecific structure and variability for fishery management is emphasized.

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A note on eutrophication

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Often a distinction is drawn between natural and artificial
eutrophication, but the question now arises whether any natural
process can usefully be described as natural eutrophication.
For purposes of this note I want to use simple and direct
concepts of trophy that are more closely related to the origins
of concepts of oligotrophy and eutrophy than are some more recent
elaborations of them (see the discussions by Hutchinson and
by Rodhe, 1969).

An oligotrophic lake has a relatively small supply of nutrients,
a eutrophic lake has a large supply. Artificial eutrophication
clearly xixxxix means an increase in the nutrient supply through
some human activity. The most famous cases are those of enrichment
with sewage, but presumably any distinct increase resulting from
human activity would apply, such as deliberate fertilization
or increases based on increased erosion from cleared forest land.

Natural eutrophication, in the narrow sense, would have to
be an increase in the nutrient income of a lake brought about by
some natural agency. Such increases can happen at any time
during the life of a lake, but there is no support for the idea of
a slow, gradual, steady increase in nutrient suplly throughout the
existence of a lake. A lake newly formed by glacial action may
receive a large input of material before the surrounding land
is stabilized by a plant cover. Once this happend, the lake will
be in a sort of equilibrium with its watershed during a large
fraction of its life, receiving each year some amount of nutritional
material from the ground and from the the community in the form

of dead leaves, corpses and other objects. The income may vary from year to year with changes in weather, and some long term trends may occur as a result of succession within the terrestrial plant community and climatic changes, but there is not a steady increase in the nutrient supply. Forest fires, landslides and such events may make sudden increases, but they are tempoary and followed by decreases after the soil is stabilized again.

This idea of trophic equilibrium was introduced early by Hutchinson, and much of the paleolimnological literature supports it.

The productivity of a lake is based on its nutrient supply. In general, a eutrophic lake will be relatively highly productive, and many people have fallen into the habit of using "eutrophic" as a synonym for "highly productive". But the way a lake uses its nutrient supply in making organisms can vary widely. The rate of production and the resulting population density that is supported are affected by properties in addition to nutrient supply, such as solar radiation, exposure to wind, shape and size of the lake basin, and many other matters. Further, mean biomass or population density is only loosely coupled to productivity, although in general, lakes of higher productivity willsupport larger populations.

All this is not to say that there are not steady, progressive changes in lakes. What does happen as the lake ages is ecological succession. Just as the bare land around the lake develops a vegetation cover, so do the plankton and benthos become established in thelake. As long as the lake remains deep, with a voluminous hypolimnion, the biota of the lake remains in a fairly uniform condition. Probably one of the most important processes that dominate the conditions in the lake is the change of shape brought about by filling in, and changes begin to happen

relatively fast when the volume of the hypolimnion becomes
significantly reduced. Further, the fraction of the bottom
that is inhabitable by rooted plants increases, so the total
amount of vegetation increases. Another progressive change is
in the amount of nutrients bound up in the relatively long-lived
bulky plants, relative to that in the short-lived rapidly
turning over phytoplankton. In the later stages of succession
when the lake is very shallow, the bulk of primary production may
be contained in the massive rooted plants and associated periphyton.

The changes in biomass probably are based on increases in
production in the lake in addition to redistribution of
production among different components of the community, but
data about this point are very scarce. This note is put in
qualitative and relative terms, but obviously to develop these
points fully, would require quantities to be expressed in terms
that could be used for comparing lakes of different shape and size.

To summarize, it appears that during the development of an
initially deep lake, progressive changes take place in the rate
of production of organisms and in the distribution of material
among different kinds of organisms, the rate of change increases
In the middle period the changes may be very slow, and
toward the end of the lake's existence. This does not mean that
a corresponding change takes place in the nutrient supply.
The succession is not from oligotrophic to eutrophic, but from
low production to high production and from small abundance to
large abundance. A lake may be eutrophic shortly after its
formation if it is in a eutrophic watershed, or in Hutchinson's
sense, is part of a eutrophic system. It may never become
eutrophic, although near the end of its existence it may
be densely vegetated.

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