THE DEVELOPMENT OF FISHERY COMPARTMENTS AND POPULATION RATE COEFFICIENTS FOR USE IN RESERVOIR ECOSYSTEM MODELING

PART I: INTRODUCTION

1. In 1973, personnel at the Environmental Effects Laboratory (EEL), of the U. S. Army Engineer Waterways Experiment Station (WES), at Vicksburg, Mississippi, began to assess and improve a comprehensive mathematical river basin model. One component of the river basin model is the reservoir system model. This model, *when* complete, will integrate information on the physical, chemical, and biological relationships of reservoirs. The model will allow theoretical aspects of reservoir dynamics to be tested and evaluated, as well as the impacts of proposed reservoir management plans.

2. Because reservoirs are complex systems continually in a state of flux, they are difficult to model. One approach toward simplifying this complexity, and the approach used in the *reservoir* model, is to divide the system into smaller, more manageable subsystems. Each subsystem can then be studied and, once understood., related to other subsystems. In this manner, the entire reservoir system can be reconstructed from component parts. This paper presents the data base for one of the reservoir subsystems--fish.

3. The purpose of this report is to provide the data base necessary for the development of a fishery model that will simulate

fish population dynamics in various types of Corps of Engineers (CE) reservoirs on a regional basis. The CE reservoirs have been classified as either hydropower or nonhydropower. Nonhydropower reservoirs do not have hydroelectric generation and are used for flood control, irrigation, water supply, recreation, and other purposes.

4. Major u.s. drainage areas (Figure 1) for which regional fishery data were developed are:

New England (including Great Lakes and St. Lawrence)
Middle Atlantic
Gulf and South Atlantic
Ohio Basin (inclUding the Tennessee Valley)
Upper Mississippi Basin (including Souria and Red)
Lower Mississippi
Rio Grande and Gulf
Arkansas-White-Red
Missouri Basin
Columbia Basin
North Pacific
Central Valley
Central and South Pacific

No information was available to develop regional fishery data for the Colorado Basin or the Great Basin.

5. The remainder of the report consists of two parts. The first part describes the chemical and physical characteristics of all CE reservoirs in the United states larger than 500 acres. in area. Where available, information on fish species present and the sport and commercial harvest is also provided. Mathematical formulas are presented that allow the prediction of fish standing crop and sport fish harvest in CE reservoirs. The second part describes the data base to be used

*For conversion to the metric system, see page 7.

Figure 1. Major drainage areas of the United states (from U.S. Water Resources Development Map, U.S. Geological Survey, 1963).

in developing the reservoir fishery model on a regional basis. Presented are:

1) Fish and fish food compartment descriptions
2) Fish carrying capacity and production
3) Fish reproduction, recruitment, and harvest
4) Fish growth and mortality rates
5) Fish digestive efficiencies and half-saturation constants
6) Fish respiration rates
7) Fish temperature tolerances
B) Fish chemical composition

PART II: DESCRIPTIVE DATA FOR CE RESERVOIRS

Physical and Chemical Descriptions of Reservoirs

6. Physical and chemical characteristics of 187 CE reservoirs are presented in Appendix A. Only reservoirs larger than 500 surface acres at normal pool were included (see Appendix A for definitions of tems). Most run-of-the-river (storage ratio <0.01) navigation impoundments were excluded. All reservoirs were grouped by major drainage areas. Table 1 summarizes the numerical and areal distributions of CE reservoirs by drainage area. Reservoirs included in this study total 3,510,000 acres, or 36 percent of the total reservoir area (reservoirs larger than 500 acres) in the U.S. (National Reservoir Research Program 1976*).

Fishery Description of CE Reservoirs

7. One purpose of this study was to develop fishery statistics on a regional basis. However, it was first necessary to test the assumption that regionalization by major drainage areas would show sufficient differences in fish species composition and standing crop to warrant regional treatment. It was assumed that all reservoirs within a drainage area would have similar fish species present and that the species composition of reservoirs in one drainage area would vary to some extent from those in other drainage areas.

8. A list of fish species present was compiled for 61 CE

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* All references cited in the text and appendices are listed alphabetically by author in Appendix N.

Table 1

Numerical and Areal Distributions of CE Impoundments by Drainage Area

Drainage Area	Number of Reservoirs	Total Surface Area, acres
New England	2	1,610
Middle Atlantic	1	68,941
Gulf and South Atlantic	12	308,050
Ohio Basin	49	328,484
Upper Mississippi	14	356,241
Lower Mississippi	5	18,510
Arkansas-Red-White	40	782,118
R10 Grande and Gulf	16	241,609
Missouri Basin	18	1,164,201
North Pacific	1	1,135
Columbia Basin	16	162,105
Central and South Pacific	2	2,380
Central Valley	5	14,550

reservoirs where data were available. Species composition data were not available for reservoirs in the following drainage areas:

New England
Upper Mississippi Basin
Columbia Basin
North Pacific
Central Valley
Central and South Pacific

Data were available on only one reservoir each in the Middle Atlantic, Rio Grande and Gulf, and Missouri Basin drainage areas. The reservoir sample thus includes primarily eastern and southern impoundments.

9. A cluster analysis computer program (University of Arkansas Computing Center) was used to compare the species composition of each reservoir with all other reservoirs and to group reservoirs with similar species together. The comparison was based on the presence or absence of 125 fish species. The results showed, with exceptions, that the species composition of the fish in reservoirs within drainage areas were si.mi.lar. Furthermore, they showed that some drainage areas contained fish species not found in other areas. For example, yellow perch were found only in reservoirs or the Middle Atlantic and the Gulf and South Atlantic drainages. Freshwater drum were not found in reservoirs or these drainages, but occurred in all others. lack or fish species information for all of the western drainage areas prevented testing the regional approach to modeling for those areas. Many western reservoirs with salmonids, especially cold-water reservoirs, would be expected to be markedly dissimilar to eastern and southern reservoirs.

10. Differences among drainage areas in species composition are most pronounced when examined on a species presence or absence basis. However, for modeling purposes, various fish species were grouped together on the basis of feeding similarities. At this level, regional dil'ferences in species composition were less obvious. Appendix B summarizes by drainage area, fish species composition and standing crop data for 61 CE reservoirs. Only predominant fish species or groups of closely related species were tabulated. As expected, considerable variation exists among reservoirs in standing crop of fish. Standing crop is defined as the amount, in pounds per acre, of fish biomass present at the time measurements were made. If all of the reservoirs were compared solely on the basis of presence or absence of the major fish groups, such as suckers, black basses, or sunfishes, little variation would be apparent. On this basis, only the Middle Atlantic and the Gulf and South Atlantic drainages differed from other drainages in the absence of freshwater drum. At this level of examination, there was not much support for regionalizing reservoirs by drainage areas because the fine distinctions in fish species composition among different areas had been masked.

11. Within drainage areas most reservoirs had similar fish species and total standing crops, although the standing crops of individual species or species groups varied widely. There were notable exceptions to this generalization. Within the Ohio Basin, two reservoirs, John W. Flannagan and Summersville, had total standing crops well below those

of other reservoirs in the basin. These two reservoirs also had fewer fish species than most other impoundments. Likewise, in the Lower Mississippi drainage area, Wappapello had a much greater standing crop than other reservoirs. Species composition was also different. In the Arkansas River *Basin*, standing crop was extremely variable among reservoirs, and several reservoirs were appreciably different from the norm.

12. Variation was to be expected in the biological characteristics of reservoirs within a drainage area. Changes *in* environmental variables over the large geographical area encompassed by each drainage area influence reservoir fish populations. Furthermore, year-to-year changes occur in the fish populations of each reservoir in response to changing environmental conditions. The difficulty in accurately describing reservoir fisheries results from the use of static descriptors in analyzing a dynamic system. Finally, the data base upon which conclusions were drawn may be inadequate, as demonstrated for many drainage areas where little or no data are available. Single point measurements of a biological system like many of the fish population measurements used in this study should be viewed with caution.

13. Most of the drainage areas examined had one or more reservoirs with characteristics significantly different from those of most of the impoundments. It was difficult, therefore, to make firm statements on the fishery of reservoirs within a given drainage. In this study, reservoirs showing major differences from the norm were treated

separately when it was felt that the effect of their influence on an analysis would bias the results and conclusions.

Field Estimates of Fish Standing Crop

14. Estimates of fish standing crop used in this study were derived by sampling reservoir coves with rotenone, a fish toxicant that has been used in the United states for fishery management purposes since 1934. Cove sampling involves selecting coves that usually represent a variety of fish habitats and range from 1 to 5 acres in size. Escape of fish from the cove is prevented by using block nets at the end opening to the reservoir proper. Cove area and depth are accurately measured and a rotenone dosage is calculated on the basis of water volume and water temperature. Finally, rotenone is applied throughout the cove and all fish appearing at the surface are collected. Fish are normally collected for two days after treatment. To estimate the percentage of fish actually present that are recovered, workers place marked fish in the cove before it is treated. In some studies, scuba divers collect fish that do not float to the surface. All fish collected are sorted by species and length classes and weighed. Standing crop, usually expressed as pounds of fish per acre, is calculated from the collected data. Most cove sampling schemes involve sampling three coves of nearly similar area so that variability in samples can be estimated and a mean standing crop value determined. Cove rotenone sampling is normally parforned in the summer, usually in August.

15. Even carefully planned and executed cove rotenone samples usually underestimate or overestimate the standing crop of some species for two primary reasons. First, some species of fish are not recovered adequately because they do not float to the surface where they can be collected. Fish underestimated in this manner are primarily benthic species such as catfishes, carp, suckers, and freshwater drum. *Small* fish of various species are also underestimated usually because they are overlooked in pickup operations. This is especially true for small shad, sunfishes and minnows. Second, some species of fish are more abundant in the coves than in the open water of the reservoir. Cove samples overestimate the abundance of these species in the reservoir. Gars, bowfin, various sunfishes, perches, and pickerels are normally more abundant in coves than in open water. Likewise, other species which are more abundant in open water than in coves, are underestimated; such species are various suckers, temperate basses, and freshwater drum.

16. Adjustments must then be made for nonrecovery of species and for cove to open-water habitat. Adjustment factors for the previous sources of error have been estimated for a number of southern reservoirs (Hayne et 81.. 1967; Jenkins and Morais 1977) and are presented in Table 2. By applying the adjustment factors to the initial standing crop estimates, an adjusted standing crop value can be obtained. AU standing crop estimates used in this report have been adjusted, with

Table 2

Adjustment Factors Used in Estimating Standing Crop from Cove Rotenone Samples

Species or Species Group	Adjustment for fish not recovered in cove rotenone sampling	Adjustment from cove sample to open water	Adjustment from unadjusted standing crop to adjusted standing crop	Adjustment from unadjusted standing crop to carrying capacity
Gars	1.44	0.8	1.15	0.81
Bowfin	1.80	0.8	1.44	1.01
Shad	1.25	1.0	1.25	0.88
Pickerels	1.37	0.8	1.10	0.77
Carp	1.40	1.2	1.68	1.18
Minnows and Silversides	1.50	0.8	1.20	0.84
Catostomids	1.34	2.3	3.08	2.17
Catfishes	1.47	1.0	1.47	1.04
Temperate basses	1.18	2.0	2.36	1.66
Sunfishes	1.46	0.6	0.88	0.62
Black basses	1.40	1.1	1.54	1.08
Crappies	1.39	1.5	2.09	1.47
Perches	1.52	0.8	1.22	0.86
Freshwater drum	1.40	2.4	3.36	2.37
All other species	1.40	0.8	1.12	0.79

the exception of estimates derived by multiple regression analysis.

Field Estimates of Fish Harvest

17. Jenkins and Morais (1971) examined in detail the relation of sport fishing effort and fish harvest to envi.ronmental variables. Their results, based on the analysis o£ 103 reservoirs throughout the U.S., showed that the average annual harvest of all reservoirs combined on an area-weighted basis was 14.6 pounds per acre. Area-weighted harvest values were used because Jenkins (1967) found that sport fish harvest was negatively related to reservoir area. A previous study by Jenkins (1967) showed the average annual area-weighted sport fish harvest for 127 U.s. reservoirs to be 13.9 pounds per acre. An average of 7.0 pounds per acre of commercial fish was harvested from 45 reservoirs. sport fish harvest for individual reservoirs ranged from less than 1 to as many as 169 pounds per acre. Commercial fish harvest ranged from less than 1 to as many as 55 pounds per acre.

18. Current sport fish harvest estimates are based on a resurvey of all harvest data available in the files of the National Reservoir Research Program (NRRP). Data as recent as 1975 and representing 164 reservoirs throughout the country are summarized in Appendix C. Commercial fish harvest vas not reanalyzed, but only rearranged to a form more useful for modeling. Appendix C, Part II, lists sport fish harvest by major drainage areas of the U. S. Within each drainage area. data are given on the number of reservoirs in the sample. total

reservoir area, simple and area-weighted sport fish harvest, and area-weighted harvest by species groups. Under each species group, the annual harvest is shown in pounds per acre and as a percentage of the total harvest. Only reservoirs with data on the harvest of individual fish species were included in the analysis. Harvests of less than 0.05 pound per acre were excluded. About 23 percent of the total reservoir area in the U. S. is represented in the analysis.

19. sport fish harvest varied considerably among drainage areas, both in total harvest and in species composition. Some of this variability can be attributed to an inadequate number of reservoirs sampled within each drainage area and to a limited number of harvest estimates per reservoir. The area-weighted sport fish harvest for all reservoirs combined was 12.1 pounds per acre, as compared with a previous estimate by Jenkins and Morais (1971) of 14.6 pounds per acre. Harvest data on 48 CE reservoirs subsampled from the data set showed an unweighted average harvest of 22.6 pounds per acre and an area-weighted harvest of 13.6 pounds per acre.

20. Data on the harvest of commercial fish species were not as readily available as those for sport fish. The infonnation compiled by Jenkins (1967) has been used in this analysis (Appendix C, Part III). Many drainage areas lacked reservoirs supporting commercial fisheries. For drainage areas with four or more reservoirs with commercial fisheries, exclUding the Termessee Valley, commercial fish harvest was low, ranging from 1.0 to 4.2 pounds per acre (area-weighted mean). The Tennessee

Valley reservoirs supported a high conmercial harvest of 14..6 pounds per acre. Buffalofishes made up 65 percent of the corrrnercial.ly harvested species, catfish 25 percent, and carp 10 percent.. The conmercial fishing statistics were from reservoirs representing about 16 percent of the total reservoir area of the U. S. (three per cent of the total number of reservoirs).

21. Reservoir age has a significant effect on harvest estimates. Many reservoirs become less productive of sport fish with age (Ellis 1937). Because most of the harvest estimates used in this analysis were collected when the reservoirs were relatively new, the average harvest values given may overestimate current conditions for some drainage areas, such as the White River Basin and the Rio Grande and Gulf drainage reservoirs.

Predicted Standing Crop and Soort Fish Harvest for CE Reservoirs

22.. Since 1963, biologists of the NRRP have compiled and analyzed available pertinent infonnation on the biological, physical, and chemical characteristics of U.S. reservoirs. A primary purpose of NRRP is to describe and correlate differences in fish production in terms of standing crop as estimated by cove rotenone samples and by sport and commercial fish yields with such variables as climate, reservoir size, age, uses, shore developnent, water depth, water level fluctuation, water chemistry, storage ratio, outlet depth, thermocline depth, dissolved organic matter, plankton and benthic fauna crops, and other biological characteristics.

23. This research program has resulted in the development of a series of multiple regression formulas for use in predicting fish standing crop and angler harvest and effort *in* U.S. reservoirs (NRRP 1974). Selected multiple regression fonnulas from this series were used in the present study to estimate standing crop and sport fish harvest for CE reservoirs for which a fishery data base was available. The results, as well as explanatory material, are presented *in* Appendix D, Parts I and II. For a review of the relationships between environmental variables and fish standing crop and harvest, as well as a history of the development of multivariate analysis as a method for estimating crop and harvest, see Jenkins (1967; 1974; 1976) end Jenkins and Morais (1971).

PART III: THE FISHERY MODEL DATA BASE

Fish and Fish Food Compartments

24. Reservoirs contain many fish species which differ in some degree from others in environmental requirements. Foremost among the many requirements tor survival of each species is food. Sometimes the differences in types of food eaten among species are striking. For instance. adult striped bass normally feed on other fish, whereas adult bigmouth buffalo primarily feed on zooplankton. Among similar fishes, sunfish for example, the different species often overlap in their food habits. Food preferences also change as fish grow; for example, largemouth bass feed on zooplankton when newly hatched but on other fish and benthic organisms when they become adults. Food preferences often change daily and seasonally, as any frustrated fisherman can testify. To complicate this picture still further, the same species of fish may eat different foods in different reservoirs. In attempting to describe reservoir fish populations and their food for modeling, it is necessary to simplify the above relationships by generalization.

25. Before any simplifications can be attempted, the food of the diff'erent fish species must be known. Appendix E details the f'ood of 78 reservoir fish species. Generalized food categories were used to simplify the classification of hWldreds of different food items eaten by fish. Results are expressed as a percentage of the total volume of

food in the stomach of each fish.

26. Food. information was abWldant for some well-studied species but scarce for many more. The variability in foods eaten with age of fish, season, and location of reservoir was high. To develop a reasonably manageable model of fish species and their foods, this variability was reduced to general statements on the food of' .fish. Table 3 details the food for 26 major groups of reservoir fish. The estimates presented in this table represent an attempt to average the food of each fish group by species, season, age, and geographical location. These results should be interpreted to represent the diet of the average adult fish in each group over an annual cycle. It is reemphasized that the tabulated data do not represent absolute values. Many of the data developed in the remainder of this study rest on these general assumptions of what fish eat. Because of the high variability *in* the foods eaten, no regional trends could be detennined.

Description of fish food compartments

27. On the basis of infonnation collected from food studies, the food resources of reservoirs were generalized to fonn five food compartments (Figure 2). In the fishery model, all reservoir fish feed from one or more of these compartments. A description of each food compartmem follows.

28. Prey fishes. All prey species eaten by a predatory fish (piscivore) are included in this category. Young-of-the-year fish, minnows, and clupeids are the major prey resources.

Table 3

Fish Food Expressed as a Percentage of the Diet by Volume*

Species or Species Group	Food					
	Plant	Detritus	Benthos	Zooplankton	Fish	Terrestrial
Gars					100	
Bowfin					100	
Gizzard shad	10	80	5	5		
Threadfin shad (young)	30	50	10	10		
Threadfin shad (adult)	30	5	15	55		
Rainbow trout	5		60	15	10	10
Brook trout			90	5		5
Pickerels					100	
Carp	30	40	20	10		
Minnows	20		20	60		
Carpsuckers	15	65	5	15		
Suckers	15	65	5	15		
Hog suckers		80	5	15		
Buffalofishes	5	40	5	50		
Redhorses			100			
Bullheads	10	25	50		15	
Catfishes	10		10		80	
Madtoms		27	55		18	
Silversides			20	80		
Temperate basses			20	10	70	
Sunfishes	10	5	65		5	15
Black basses			8		86	6
Crappies	5	5	20	15	55	
Perches			20	20	60	
Freshwater drum		8	58		34	
All other species			100			

* Food categories are described in the text.

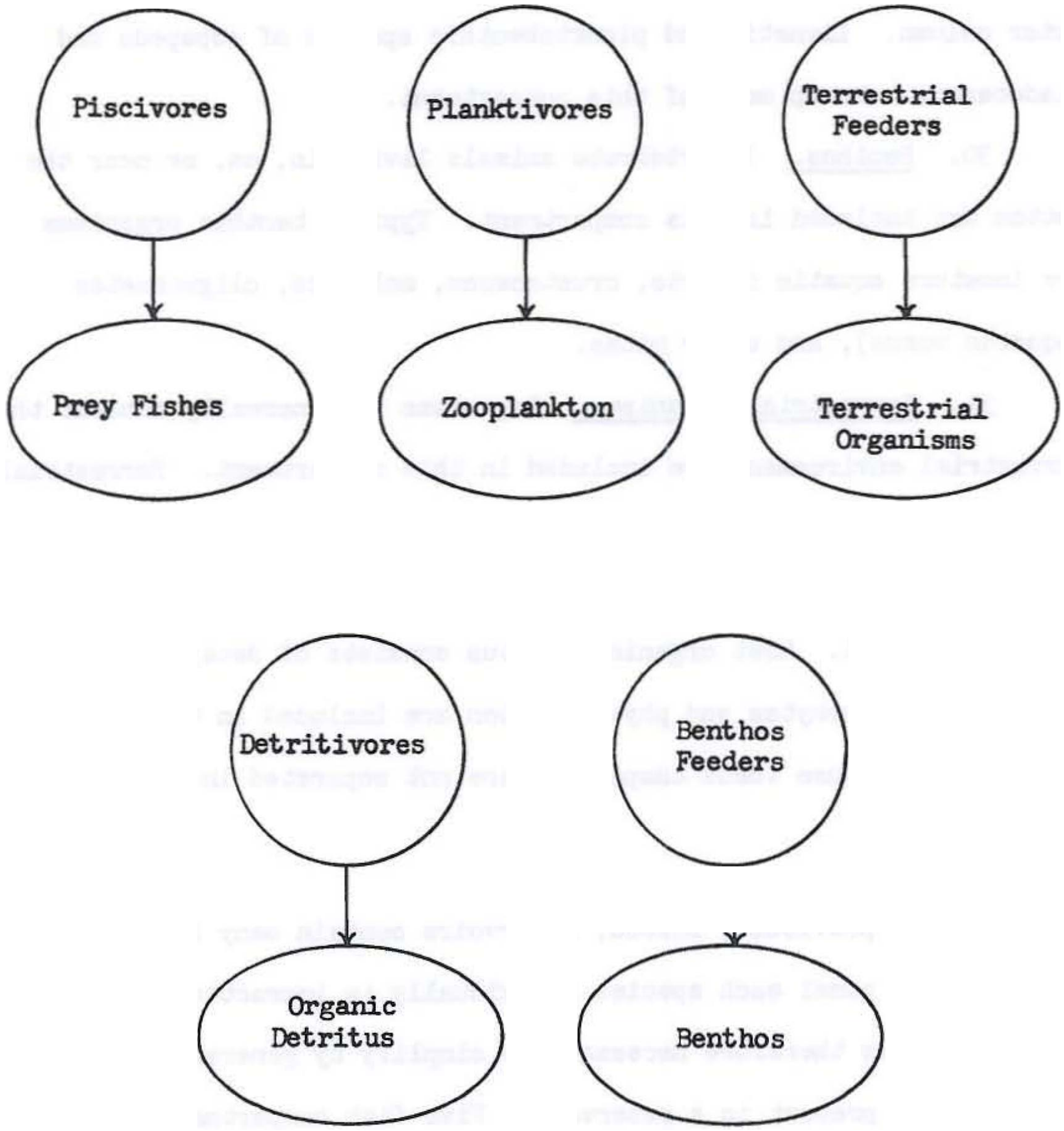

Figure 2. Schematic diagram of the relationship between fish and fish food compartments. (Circles represent fish compartments and ellipses represent fish food compart.ments)

29. Zooplankton. Zooplankters are small microscopic or nearly microscopic animals that drift passively or have weak mobility in the water column. Umnetic and planktobenthic species of copepods and cladocerans make up most of this compartment.

30. Benthos. Invertebrate animals living in, on, or near the bottom are included in this compartment. Typical benthic organisms are immature aquatic insects, crustaceans, molluscs, oligochaetes (aquatic worms), and water mites.

31. Terrestrial organisms. Organisms that nonnally inhabit the terrestrial environment are included in this compartment. Terrestrial and adult aquatic insects are the primary food items.

32. Organic detritus. Detritus is defined as unidentifiable organic matenal. Most organic detritus consists of decayed plant material. lo'.acrophytes and phytoplankton are included in the detritus compartment because these components are not separated in most food studies.

Description of fish couroartments

33. As prev1.ously stated, reservoirs contain many fish species. Attempting to model each species individually is impractical for obvious reasons. It is therefore necessary to simplify by generalization the types of fish present in a reservoir. Five fish compartments developed to correspond to the five fish food compartments outlined above are described here.

34. Piscivores. This group contains fish species that are all or in part piscivorous. Included are black basses, temperate basses,

crappies longer than 10 inches, catfishes longer than 18 inches, freshwater drum longer than 16 inches, and gars, bowfin, pickerels, pikes, and walleye. This group feeds on the prey fishes food compartment.

35. Planktivores. Fish included in this group are zooplankton feeders and include young-of-the-year fish of most species. Clupeids are the predominate fish group.

36. Benthos reeders and detritivores. Fish in these two groups are primarily bottom feeders. Most species included here are both detritivores and benthos feeders. The predominate species are adult shad, carp, freshwater drum less than 16 inches long, buffalofishes, carpsuckers, catfishes shorter than 16 inches, redhorses, crappies shorter than 10 inches, and various species of sunfish.

37. Terrestrial feeders. Fish that feed on terrestrial organisms primarily at the water surface are included in this compartment. Sunrishes and young black basses are the predominant terrestrial reeders.

Distribution or Fish Biomass Among Model Compartments

38. The fishery model is a mass balance model. For component parts of the model to be compatible, the units of measurement must be the same. The units used are biomass units expressed as pounds per acre. After fish and fish food compartments are established for modeling, a procedure was developed to distribute fish biomass to the appropriate compartment.

39. It was evident from Table 3 that, based on food habits, most

fish could be placed in several of the fish compartments. The biomass of each species or species group was proportioned among all of the compartments that characterize the foods eaten based on the percentage of food taken from each compartment. For example, temperate basses are benthos feeders, planktivores, and piscivores (Table 3). Twenty percent of the total biomass of temperate basses was assigned to the benthos feeder fish compartment, because 20 percent of the total diet of temperate basses was benthos. Likewise, 10 percent was distributed to the planktivore compartment and 70 percent to the piscivore compartment. Another way of stating the same infonnation is that 20 percent of the temperate bass biomass is supported by the benthos food compartment, 10 percent by the planktivore food compartment, and 70 percent by the prey fishes food compartment. It was assumed that all foods are of equal nutritional value by volume.

40. Similar manipulations of fish biomass were perfonned for all fish species or species groups on a regional level. In this manner, fish biomass was distributed among the fishery model compartments. This distribution technique allowed a greater degree of realism in accounting for the tremendous variety in fish food habits than would a method that simply assigned the total biomass-of each fish species to a fish compartment based only on the predominant food item eaten. Appendix F details the distribution of fish biomass, including annual production (see paragraphs 42 through 48, below), supported by each food compartment on a regional basis. The lack of sufficient infonnation prevented completion of the analysis for all regions.

Concepts of Fish Carrying Capacity and Fish Production

Carrying Capacity

41. Fish carrying capacity is a useful concept in reservoir management. It is defined as the standing crop of fish at the most critical period of the year for fish survival. This period is normally late winter or early spring. The concept of fish production is complementary to that of carrying capacity. Production is defined as the total living fish biomass produced in a given time interval. The elaboration of sex products has been excluded from the production definition. In practical terms, the time interval corresponds to seasonal growth from late spring to late rall of each year. Surplus production constitutes fish biomass added during the growing season minus natural mortality. Under stable conditions, surplus production does not survive the critical period of the year but is lost through natural and angling mortality and body weight loss.

Production and the re:lationshi:o to growing season

42. Thompson (1941) hypothesized that because fish production may be expected to be proportional to total digestion, digestion being a function of temperature-influenced metabolic rates, it should be possible to express the relationship of production to carrying capacity at different latitudes. Thompson used digestive rates determined by Markus (1932) to derive values of maximum annual p1!Oduction as a percentage of carrying capacity, based on mean monthly air temperatures. Production varied from 21 percent of carrying capacity in Vilas County, Wisconsin, to liB percent at New Orleans, IDuisiana.

43. Jenkins and Morais (1971) found highly positive correlations between length of growing season and sport fish harvest, which prompted them to explore Thompson's hypothesis in relation to reservoir fish standing crop and harvest. They derived a curvilinear relation for growing season (frost-free period *in* days) versus the latitudinal production estimates of Thompson (Figure 3). This relation approximated the relationship found between standing crop of sport fishes and harvest in 15 predominantly southern reservoirs. The above relation is useful in estimating carrying capacity and annual fish production for reservpirs and has been used extensively in this study.

44. The growing season-production relation can be used to estimate carrying capacity and annual production not only for individual species and reservoirs but also for drainage areas, as the following example illustrates.

EXAMPIE: The average standing crop for all reservoirs in the White River Basin is 300 pounds per acre at the time of cove sampling in August. By August, 60 percent of the annual growing season of 200 days is over. The relation between growing season and production predicts that the maximum annual production for a 200-day growing season will be about 70 percent of carrying capacity (Figure 3). The relation of carrying capacity to August standing crop can be written:

Carrying capacity + 0.6 (0.7 carrying capacity) • standing crop, (1)

which rearranges to:

Carrying capacity = standing crop/1.42

e.g.:

White River reservoir carrying capacity .. 300/Lk2 • 211 lb/acre

and the expected maximum annual surplus production is:

Annual production. 0.7 (211) • 148 1b/acre

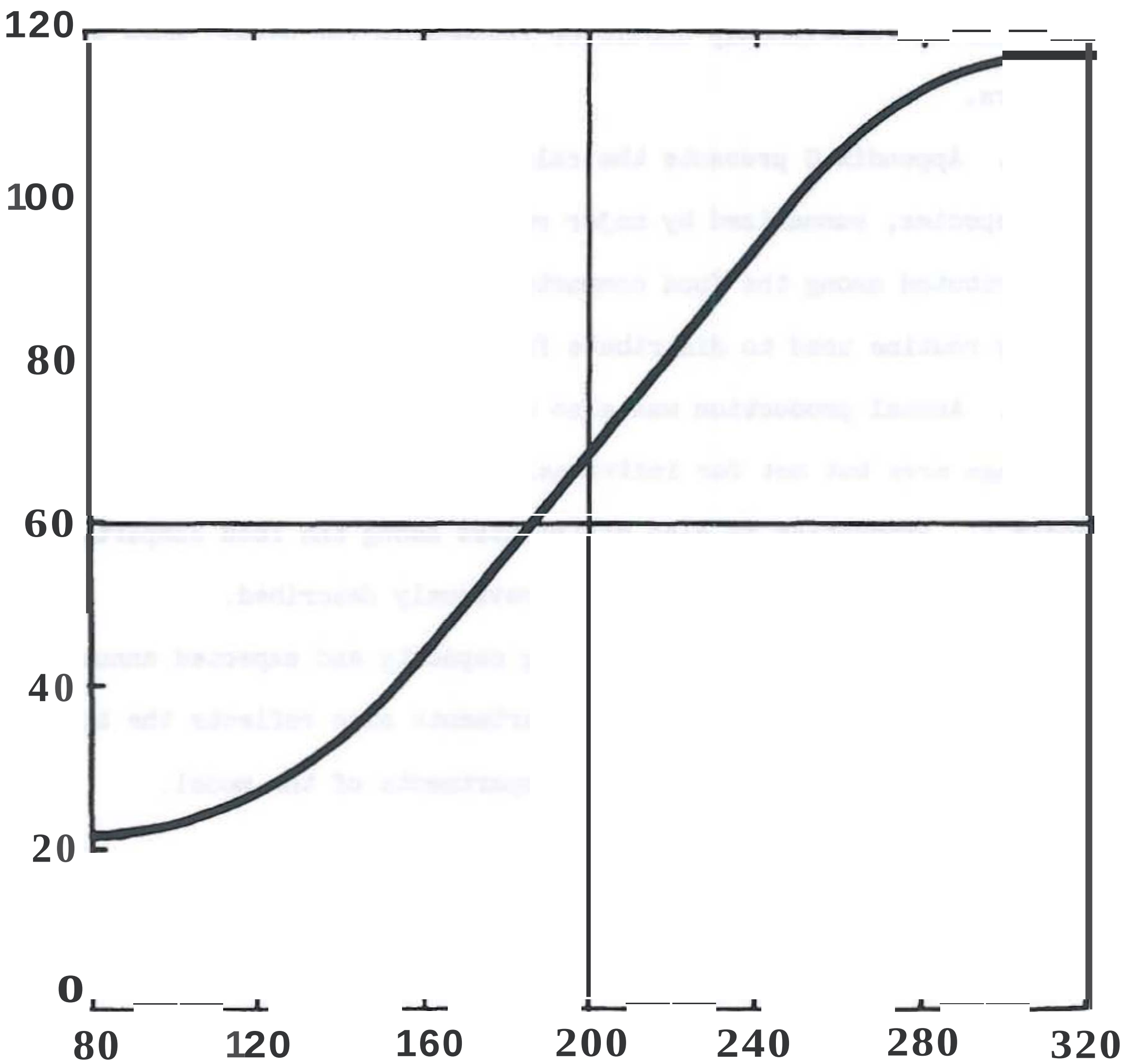

Figure 3. Hypothetical relationship of average annual length of growing season (frost-free period in days) to maximum annual fish production as a percent of carrying capacity. (The regression formula, where X is growing season in days and Y is maximum production as a percent of carrying capacity, is $Y = 81.73 - 1.516X + 0.01099X^2 - 0.00001845X^3$.)

45. The growing season-production relationship may not predict sound estimates for new reservoirs. These reservoirs have initial high fertility and fast turnover rates and may produce more than predicted. The postulated relationship should be reasonabl.e for older, more stable reservoirs.

46. Appendix G presents the calculated carrying capacities of various species, surrmarized by major reservoir groups. Carrying capacity was distributed among the food compartments on the basis of the proportionality routine used to distribute fish biomass.

47. Annual production was also determined on a regional basis by drainage area but not for individual species; it is presented in Appendix F. Production is also distributed among the food compartments based on the proportionality routine previously described.

48. The distribution of carrying capacity and expected annual surplus production among the food compartments also reflects the biomass distribution among the fish species compartments of the model.

Fish Reproduction

49. For modeling purposes, fish reproduction has been defined as the biomass of young fish existing just before the beginning of their second growing season. This corresponds to the time of annulus formation when the fish are not quite one calendar year old. To rephrase the definition of reproduction, it is the production of young fish that survive from hatching through the critical period of the following spring.

50. Published data on fish reproduction in a fonn and detail necessary for the fishery model are not available in the literature. Therefore, the growing season-fish production relationship shown in Figure J was used to estimate fish reproduction in CE reservoirs.

Estimating fish reproduction

51. Data for 21 Predator Stocking Evaluation (PSE) reservoirs (Jenkins and Morais 1977) were used to estimate fish reproduction 'rates in CE reservoirs. These reservoirs are in the eastern and southern United states. For each reservoir, two years of data (1972, 1973) were avai..lable on the standing crop of young-of-the-year fish. The growing season-production relationship was applied to these data and the expected annual production of all young-of-the-year fish was calculated. Annual production of young-of-the-year fish, after being corrected for mortality, was defined 85 fish reproduction for modeling purposes. Table 4 summarizes the results for all reservoirs in the sample in tenns of carrying capacity. Considerable variability existed among reservoirs examined, but when all values were pooled and averaged, reproduction was estimated to be about 28 percent of carrying capacity, or 37 percent of the total annual production.

52. Two reservoirs from the above sample, Beaver and Bull Shoals, both on the White River in Arkansas, have extensive data on young-of-the-year production available. Data for 10 years on Bull Shoals and 8 years on Beaver were analyzed to develop an estimate 01' year-to-year variability in reproduction. Table 5 presents the results of this analysis, which indicate that total reproduction as well as reproduction

Table 4

Estimated Reproduction as a Percentage of the Carrying Capacity for 21 PSE Reservoirs in 1972 and 1973

	Year		
Reservoir and State	.illl	1973	1972-73 Average
Jordan, Alabama	16.5	21.0	18.8
Mitchell. Alabama	36.2	25.5	30.8
Beaver, Arkansas	26.0	27.1	22'
Bull Shoals. Arkansas	27.8	67.7	33**
Greeson. Arkansas	23.2	46.2	34.7
Jackson. Georgia	34.3	24.8	29.5
Sinclair. Georgia	57.1	35.8	46.5
Deep Creek. Maryland	36.3	44.8	40.5
Barnett. Mississippi	32.6	61.8	47.2
Enid. Mississippi	26.1	14.4	20.3
Grenada. Mississippi	17.1	29.6	23.4
Okatibbee. Mississippi	24.0	23.8	23.9
Sardis. Mississippi	15.7	17.4	16.5
Badin. North Carolina	29.4	28.4	28.9
Gaston. North Carolina	9.6	17.7	13.6
Cherokee. Tennessee	31.8	29.1	30.4
Dale Hollow. Tennessee	7.5	20.7	14.1
Watauga. Tennessee	14.0	7.0	10.5
Bastrop. Texas	21.7	30.0	25.9
Cypress Springs. Texas	15.5	27.7	21.6
E. V. Spence. Texas	43.2	58.8	51.0
Average of all reservoirs			27.8
Average of all reservoirs. excluding Beaver and Bull Shoals			27.8

* Eight-year average.

** Ten-year average.

[redacted]

Table 5

Production and Reproduction Estimates for
Beaver and Bull Shoals Reservoirs.

Item	Beaver		Bull Shoals		Average of Two Reservoirs
	Range of Values	Average Value	Range of Values	Average *Value*	
Production of all Y-O-Y•• fish as a percentage of the total annual production.	8-50	33	5-95	57	45
Reproduction 8s 8 percentage of the carrying capacity.	16-30	22	3-163	33	28
Reproduction of y-o-y shad as a percentage of the total y-o-y reproduction.	38-93	79	6-76	48	64
Reproduction of Y-O-Y predators as a percentage of the total Y-O-Y reproduction.	5-60	18	7-88	36	27
Reproduction of all other Y-O-Y fish as 8 percentage of the total Y-O-I reproduction•	<1-7	3	5-59	16	9

• Estimates are based on 10 years of data for Bull Shoals and 8 years of uata for Beaver.
•• Y-O-Y is the abbreviation for young-of-the-year (fish).

by various types of fishes is highly variable from year to year. The average value for total reproduction for both reservoirs in combination was 28 percent, which was identical to the average reproduction of all 21 reservoirs discussed previously.

53. If fish reproduction in Beaver and Bull Shoals reservoirs can be considered typical of the White River Basin, the following relationships would apply regionally: the White River Basin carrying capacity is 211.4 pounds per acrej reproduction is then 52.9 pounds per acre. Of this reproduction, 64 percent or 33.8 pounds per acre is contributed by shad; 27 percent or 14.3 pounds per acre by predatorsj and 9 percent or 4.8 pounds per acre by all other species.

Regional variations

54. Insufficient data exist at present to statistically demonstrate regional variation in reproduction rates. Data are lacking for most areas of the country, but it can be anticipated that regional differences *in* reproduction rate do exist. The above data suggest that reservoirs of the lower Mississippi drainage and Tennessee Valley have lower reproduction than the average value derived in this analysis.

55. The contributions of the various fish compartments to total reproduction can change, depending on fluctuating environmental characteristics and reservoir fish species compositi0!1. Because the contribution of each fish compartment to total reproduction cannot be determined directly from the data available, an indirect method has been used. Reproduction by each fish compartment has been assumed to make the same percerrt.age contribution to total reproduction as the percentage

recruitment contribution by each compartment makes to total recruitment (see Fish Recruitment). It is assumed that recruitment to a f'ish compartment is directly proportional to that compartment's reproduction. A further assumption is that there is no differential mortality of prerecruits among the fish compartments. Data for the 21 reservoirs examined previously were analyzed by this technique (Table 6).

56. Most young-of-the-year fish produced by the fish compartments do not feed on the same food. as adults. This created a problem in data analysis because most young fish did not belong to the same fish compartment as the adults. The apportionment of young-<lf-the-year fish among the food compartments was achieved by using the proportion-of-diet method employed to distribute fish biomass and production, except that the diet of young-of-the-year fish was substituted. Table 7 summarizes the results for drainage areas or particular reservoir groups on the basis of CE reservoir data. Most drainage areas were excluded from analysis because few or no fishery data were available.

57. The above data represent the total production of age 0 fish. only a portion of this total was present in the system at a given time and an undetermined amount represented production that would be lost during the year through mortality and anabolic activities. An example is offered to illustrate this point: if' the average growing season were 215 days, as it is for the 21 PSE reservoirs used to estimate reproduction, about 25 percent of the annual production would have occurred by 1 June, 50 percent by 1 July, 75 percent by 1 August,

Table 6

Contribution of Each Fish Compartment to Total Reproduction

Fish Compartment	% Contribution to Total Reproduction
Piscivores	20
Planktivores	30
Benthos Feeders	25
Terrestrial Feeders	5
Detr1tivores	20

Table 7

Annual Reproduction Supported by Each Food Compartaent

Drainage Area or Reservoir Group	NUlllber of Re!lervoirs	Detritus lb/acre	Detritus %TR	Benthol lb/acre	Benthol %TR	Zooplankton lb/acre	Zooplankton %T'	Fish lb/acre	Fish %TR	Terrestrial lb/acre	Terrestrial %T'	Total lb/acre	Total !..!!
White River	●	17.8	26.7	'.3	14.0	35.9	53.9	2.4	3.'	1.2	1.8	66.6	100
Il.ed River	●	16.6	26.8	8.6	13.9	33.4	54.0	2.2	3.'	1.1	1.8	61.9	100
Arkansas River**	15	35.7	25.4	19.5	13.8	76.1	54.0	S.O	3.'	2.S	1.8	140.8	100
Blue Mt., N1.Jllrod. and Wister	3	44.3	27.8	30.2	18.9	71.8	45.0	8.'	S.'	4.4	2.8	159.5	100
Green and Cumberland Riven and Dewey Reservoir	8	16.3	26.7	8.S	13.9	33.0	54.0	2.2	3.'	1.1	1.8	61.1	100
Lower Mississippi Valley	S	22.0	27.6	14.2	11.8	37.5	47.0	4.1	S.l	2.0	2.S	79.8	100
Gulf and South Atlantic	10	,•,	27.8	'.4	18.0	16.8	47.2	1.8	S.O	0.'	2.S	35.6	100
Buckhorn. Sutton, Summerville, and Flannagan	4	3.'	29.5	3.8	28.8	J.S	26.5	1.3	'.8	O••	4.S	13.2	100
Weighted Average		21.6	26.4	12.4	15.2	42.2	51.6	3.3	4.1	1.7	2.1	81.7	100
Percent of average total carrying capacity (260.6 lb/acra)		8.3		4.8		16.2		1.3		0.'		31.4	

Food Compartments*

• TR - Total Reproduction.

*. Excluding Blue Mountain, NilllfOd, Wister, and Great Salt Plaina.

and 100 percent by 1 November (Figure 4). A net loss in biomass would occur after November, until the next growing season.

58. Figure 4. illustrates the simplest case where carrying capacity is stable and does not change annually. In reality, carrying capacity may vary widely from year to year depending on environmental conditions. The carrying capacity of biomass elaborated during the growing season is determined by the environmental conditions of the succeeding winter and spring.

59. Caution should be exercised in using any of these results. No information is currently available for testing the assumptions of the analysis.

Fish Recruitment

60. Recruitment was defined as the addition of new fish to the vulnerable population by growth from among smaller size categories (Ricker 1975). The vulnerable population consisted of those size classes of fish subject to the sport or commercial fishing effort. For modeling purposes, biomass was recruited rather than numbers of fish. Estimating recruitment by using standard techniques such as recruitment curves, required information on the spawning stock, fecundity, and mortality of each species. These data were unavailable for mixed species populations of reservoir fishes. An alternative method of estimating recruitment, and the one used in this study, was to set a minimum size at which each species was recruited.

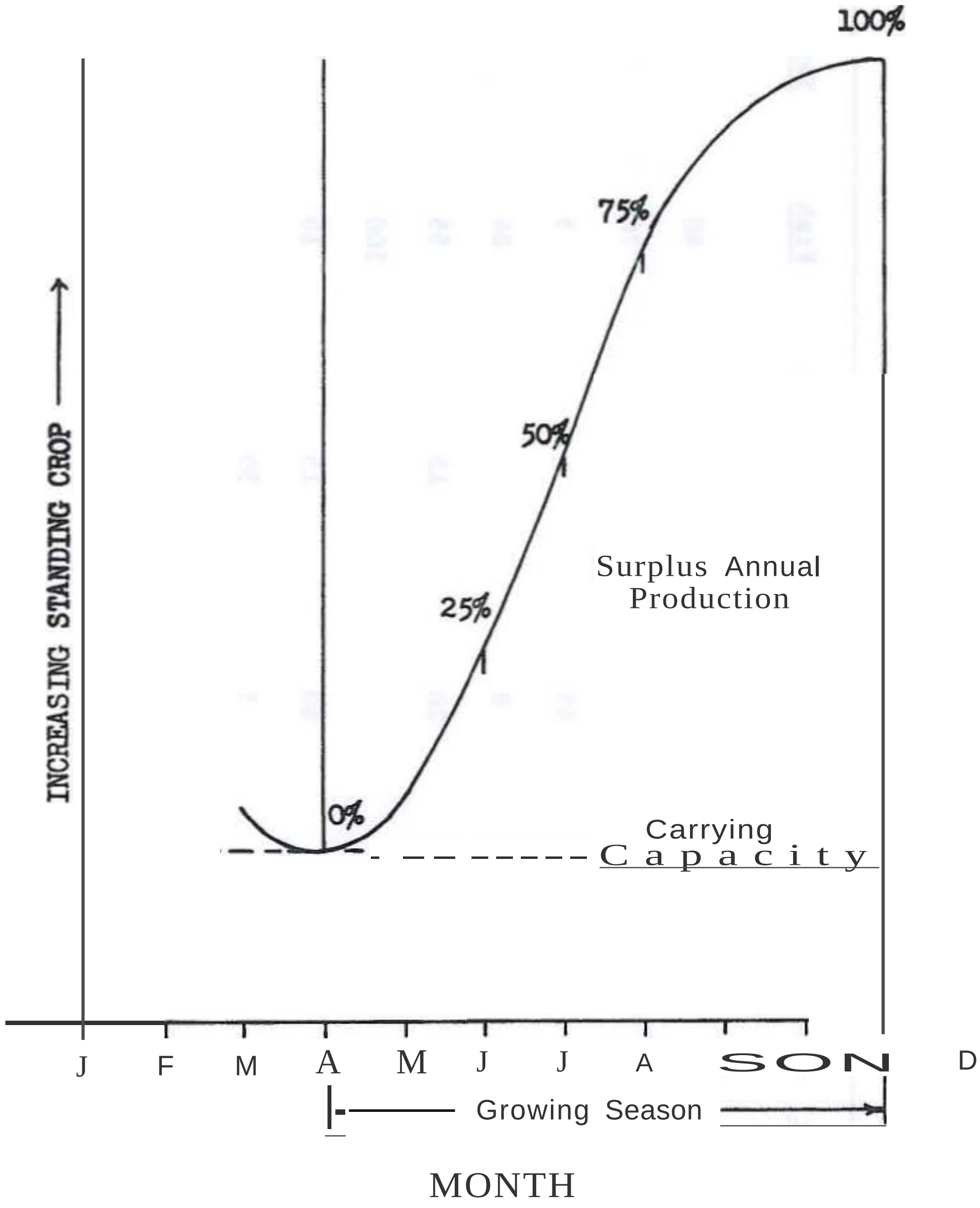

Figure 4. Relationships among standing crop, surplus annual production, carrying capacity, and time of year for 21 PSE reservoirs.

Table 9

Fish Food at Recruitment Expressed as a Percentage of the Diet by Volume

Species or Species Group	Food					
	Plant	Detritus	Benthos	Zooplankton	Fish	Terrestrial
Carp	30	40	20	10		
Catfishes	10	5	40	5	40	
Temperate basses			20	10	70	
Sunfishes	10	5	65		5	15
Black basses			8		86	6
Crappies	5	5	20	15	55	
Walleye					100	
Salmonids	5		60	15	10	10
Buffalofishes	5	40	5	50		

Table 10

Distribution of Recruitment by Food Compartments and Date for 23 PSE Reservoirs

Category of Fish and Date	Food Compartments. Plant Material Ib/acre	%TCC	Detritus Ib/acre	%TCC	Bentbos Ib/acre	%TCC	Zooplankton Ib/acre	%TCC	Fish Ib/acre	%TCC	Terrestrial Ib/acre	%TCe	Total Ib/acre	% TCC
Sport Fisb-.														
1 April	2.8	1.0	1.9	0.6	13.8	4.8	1.3	0.4	9.2	3.2	2.4	0.8	31.3	10.8
1 Jun	3.3	1.1	2.3	0.8	16.3	5.6	1.5	0.5	10.9	3.8	2.9	1.0	37.2	12.9
1 July	3.9	1.3	2.6	0.9	18.9	6.5	1.8	0.6	12.6	4.4	3.3	1.1	43.1	14.9
1 August	4.4	1.S	3.0	1.0	21.5	7.4	2.0	0.7	14.3	4.9	3.8	1.3	48.9	16.9
1 November	4.9	1.7	3.4	1.2	24.1	8.3	2.2	0.8	16.0	5.5	4.2	1.4	54.8	18.9
Commercial Fish t tt														
1 April	1.3	0.4	2.9	1.0	4.1	1.4	2.8	1.0	3.7	1.3	0	0	14.8	5.1
1 June	1.6	0.5	3.4	1.2	4.9	1.7	3.3	1.1	4.4	1.5	0	0	17.6	6.1
1 July	1.8	0.6	4.0	1.4	5.6	1.9	3.8	1.3	5.1	1.8	0	0	20.4	7.0
1 August	2.1	0.7	4.5	1.6	6.4	2.2	4.4	l.S	5.7	2.0	0	0	23.1	8.0
1 November	2.4	0.8	5.0	1.7	7.2	2.5	4.9	1.7	6.4	2.2	0	0	25.9	9.0

* TCC • Total Carrying Capacity· 289.2 Ib/acre.

*. Carrying capacity of aport fisb recruits - 31.3 Ib/scre. Expected annual surplus production of sport fish recruits - 23.5 1b/acre.

t Carrying capacity of commercial fish recruits - 14.8 lb/acre. Expected annual surplus production of commercial fish recruits. 11.11b/acre.

tt Catfishes and carp are included here as well as in the sport fish recruitment estimate. Shad are excluded.

Table 11

Percentage of Total Annual Recruitment Supported by Each Food Compartment

	Plant Material	Detritus	Zooplankton	Benthos	Fish	Terrestrial	Total
Sport Fish	9	6	4	44	29	8	100
Commercial Fish	9	19	19	28	25	0	100

The recruitment values in Table 10 for 1 April represent the initial standing crops of the recruits at the beginning of the growing season, which is also the carrying capacity. The carrying capacity of sport fish recruits averaged 11 percent of total carrying capacity for all reservoirs combined for both years. Individual values varied from 2.1 to 28.5 percent. Reservoirs of the Arkansas and White Rivers appeared to have lower recruitment rates than the other reservoirs. However, insufficient data exist to statistically demonstrate the validity of these rates. Corrr.lercial fish species had a carrying capacity of recruits that is about 5 percent of the total carrying capacity.

64. Recruitment estimates were based on a predominantly southern sample of reservoirs. Caution must be exercised in attempting to extrapolate these data to other regions of the country. For instance, salmonids were not represented in sport fish biomass in the reservoirs sampled. They were, however, the predolId.nant sport fish in other areas of the country (Appendix C, Part I). A further complicating factor was the length of grorlng season. Jenkins (1974) has described the hypothet-ieal relationship of growing season to fish production. Generally, the longer the growing season, the greater the fish production (Figure 3). The PSE reservoirs had an average growine season of 215 days, which meant that the fish production during the growing season would be about 75 percent of the carrying capacity. This relationship would not be true of a reservoir, say in the Missouri Basin, that had a groWing season of 160 days where fish production would be about 40 percent of carrying capacity.

65. Data are lacking for the *estimation* of recruitment for reservoirs in other regions of the cOW'ltry. The suggested approach for estimating recruitment when a data base is lacking is to use the relationship between recruitment and total carrying capacity. For example, benthos-feeding sport fish recruits on 1 July made up 6.5 percent of the total carrying capacity in PSE reservoirs (Table 10). Assuming that the 6.5-percent relationship is relative and is a reasonable estimate regardless of geographical location, carrying capacity and growing season can vary. It is necessary to know carrying capacity, which has already been determined (Appendix G). Only the calendar dates between Which growth occurs need to be reset and the percentage of total growth occurring by a given date properly proportioned.

66. The technique used in estimating recruitment may, in some cases, overestimate the correct value. This is especially true if much of the sport fish biomass is contributed by sunfishes, since sunfish recruited at a length of 5 and 6 inches are near their maximum size. At this size, sunfish of several year classes tend to accumulate. Fish recruited in previous years showing little additional growth could conceivably still be within this size range and hence recounted in the recruitment estimate.

67. A comparison of estimated recruitment rates (Table 10) with estimated harvest rates (Appendix C) indicates that sufficient fish are usually recruited to replace those that are harvested.

Distribution of Fish Harvest Among Model Compartments

68. Sport and conrnercial fish harvests for CE reservoirs were described in Part II of this paper. The mass balance nature of the fishery model required that the biomass of harvestable fish be distributed among the appropriate fish cocpartments. The apportiorunent was achieved in this analysis, as before, by distributing the biomass of each harvested species among compartments in direct proportion to the percentage of diet by volwne eaten in each food compartment (Table 9). For example, black basses at recruitment ate 8 percent benthos, 86 percent fish, and 6 percent terrestrial food items. Therefore, 8 percent of the biomass of black basses harvested was ass1JJned to have come from the benthic-feeding fish compartment, f!f1 percent from the piscivorous fish comparlment, and 6 percent from the terrestrial-feeding fish compartment. Plant raaterial has been separated from detritus in this analysis, but it may be desirable to combine these two food compartments. The division between plant material and detritus is usually made by an arbitrary judgment. Appendix H, Parts I and II, summarizes the distribution of harvest among the food, and hence, f'ish compartments.

Fish Growth Rates

69. Esti.mates of specific growth rates under laboratory conditions and for long time periods were available for only a few fish species. Many laboratory investigations in which growth rates were studied were not concerned principally with determining the maximwn rates attainable.

Those studies att.empting to determine maximum growth rates under varying conditions (i.e., photoperiod, temperature, or food ration) usually tested young fish less than age II. These fish have high growth rates and the application of their maximum growth rates to mixed species and mixed aged populations in reservoirs may not be valid. A further hindrance to using results from the literature, whether they be from laboratory or field, was that most results were presented in terms of growth in length, not in weight. t-!any authors failed to indicate the length-weight relationships so that the data cannot be converted. others failed to include the exact time period over which growth occurred.

70. The data presented in Appendix I represent the, maximum growth rates found in the literature for 46 reservoir fish species. The literature survey was not exhaustive but represented an examination of over 230 papers dealing with fish growth in weight. Some species are represented by only a single citation while others have as many as 30 ref'erences with data for all major climatic areas of' the country. Growth had to be expressed as a rate between age classes, because infonnation on growth *in* weight between length classes that included *time* period information necessary to derive per-day rates was unavailable. The tabular data under "age-elass Itl represent growth rates for fish from age 0 to age I, and under "age-class lItI, for fish from age I to age II, and so on. Papers cited in Carlander (1969 and W1published) represented 60 percent of the papers examined in compiling growth rate data.

71. The youngest fish, both in the laboratory and in the field, have the highest specific growth rates and the oldest fish the lowest.

Ideally, to derive a maximum growth rate for a reservoir fish population, one would weight the *maximum* growth rate of each species at each age class by the corresponding biomasses and arrive at an overall weighted average. Insufficient data exist to attempt this for any reservoir, so an alternative approach must be used. In a mixed species reservoir population, the greatest biomass of fish is usually in age-class II or III. Therefore, to obtain the best estimate of maximum growth rate for the reservoir fish population as a whole, it is necessary to determine the maximum growth rate for fish in age-class II or III. This value should be less than the high growth rate of fish younger than age II but greater than the low growth rate of fish older than age III. Field study data must be relied upon heavily in estimation because laboratory data are scant. The authors believe that the estimates will approximate the maximum population growth rate. Higb specific growth rates of young fish that make up a small percentage of the total biomass are balanced by the low specific growth rates of old fish that usually make up a greater percentage of the biomass.

72. At this time there appears to be no difference statistically in maximum specific growth rates among the proposed fish compartments of the model. Reasonable estimates for the maximum specific growth rate range from 0.007 to 0.015 per day, with the most favored value being 0.010 per day.

Half-Saturation Constants for Fish Growth

73. The concept of half-saturation constants or dissociation constants, has its origins in enzyme-substrate kinetics theory as first expressed by Michaelis and Menten (1913). They developed an equation to express the relationship of the rate of a chemical reaction as a function of the maximum reaction rate possible, the concentration of the material reacting, and a constant, known as a dissociation or half-saturation constant. Biologists have used the Michaelis-Menten relationship, as it is known, to describe many rate-dependent phenomena in living systems.

74. The fishery model uses half-saturation constants to adjust the growth rate of fish to the available food supply. The half-saturation constant is actually the amount of food ingested that results in fish growing at half the maximum growth rate. This relationship can be described as follows:

$$v = V_{max} \left(\frac{S}{K_s + S} \right)$$

where: v = actual growth rate

V_{max} = maximum growth rate

S = food concentration ingested

K_s = half-saturation constant

75. It was found that the relation of fish growth to food consumption does not closely follow the above Michaelis-Menten relationship.

76. Transformations of fish growth-food consumption data, following Michaelis-Menten (Case I) (Lineweaver and Burk 1934), indicate

that fish growth can obtain infinite velocity at a finite food level. Obviously, this is Wltrue. Further transformations developed to analyze more complex enzyme-substrate interactions (Cases II through VI) fail to accurately model fish growth-food consumption relationships. Case VIr (Diffusion) most closely fits the available data. The fonn of this relationship is:

$$v \cdot V_{max} k_1' (S)/(V_{max} + k_1' K_s (S) - v)$$

where: k_1' = velocity constant

This relationship was used to estimate the half-saturation constant K_s for all data sets.

77. Numerous laboratory studies have examined the influence of food ration quantity on fish growth. However, few of these studies have examined the growth-food consumption relationship in enough detail to allow an estimate of the half-saturation constant to be made. Many studies are statistically unreliable because conclusions are drawn from small sample sizes. Others fail to distinguish between the growth efficiencies of fish of different ages. Only Brett et ala (1969) examined the temperature effects on the growth-food consumption relationship and also included sufficient detail to estimate half-saturation constants.

78. Data drawn from six laboratory studies were analyzed to estimate half-saturation constants; the results are presented in Table 12. Young fish were tested by Williams (1959), Gammon (1963)t Brett et al. (1969), and Andrews and Stickney (1972). Because the growth rates of these fish are higher than for older, slower growing fish, the estimated

Table 12

Estimated Half-Saturation Constants for Fish Growth

Species	Length and/or Weight	Water Temperature °C	Calculated Maximum Growth Rate Expressed as % of Body Weight Gained Per Day	Calculated Half-Saturation Constant (Kg) Expressed as % of Body Weight Consumed Per Day	Type of Food	Reference
Largemouth bass	24.5 cm	21	3.9	4.6	minnows	Thompson (1941)
Smallmouth bass	8.3-20.2 cm 4-112 g (x • 40 g)	21.3	4.7	7.2	minnows	Williams (1959)
Muskellunge	17.0 cm 17.0 g	19.5	3.9	5.6	minnows	Gammon (1963)
Reticulate sculpin	1.2g	11.6	1.7	4.4	midge larvae	Davis and Warren (1965)
Channel catfish	4 g	30	3.4	3.1	mixed diet	Andrews and Stickney (1972)
Sockeye salmon	6.9 g	10	1.8	3.9	mixed diet	Brett et al. (1969)
Sockeye salmon	7.1 g	15	4.2	7.9	mixed diet	Brett et al. (1969)

half-saturation constants will be high. Thompson (1941) presented data for a lO-inch largemouth bass. A bass of this size represents a typical reservoir predator. only two data sets were available for benthos-feeding fish: the channel catfish data of Andrews and Stickney (1972) which are limited and should be treated cautiously; and the Davis and Warren (1965) investigation, which studied yearling reticulate sculpins under cold-water conditions.

79. One would expect the half-saturation constant to increase as water temperature increased. After the fingerling sockeye salmon studied by Brett et a1. (1969) were fed an omnivorous diet, the authors concluded that 15^0C was optimum for growth. A substantial change in the half-saturation constant as the temperature increased from 10^0 to 15^0C was noted. At present insufficient data exist to demonstrate different half-saturation constants for pisc1vores and benthos feeders. No data could be located for detritivores or planktivores.

SO. Estimates of the half-saturation constants using Lineweaver-Burk transfonnations must be treated cautiously. Based on the analysis of the estimated half-saturation constants, and considering the influence of fish size, it is suggested that initially K_s be considered 5 percent of fish wet body weight per day at 20^0C. Five percent of the body weight consumed per day corresponds closely with the food intake rate for optimum efficiency in growth (4 to 5 percent for many species). Additionally, food consumption at this level will result in a growth rate that corresponds to the maximum growth rate observed in the field for some species.

81. Because Michaelis-Menten relationships do not closely fit fishery data, it is questionable whether or not the enzyme kinetics theory is conceptually applicable to fish populations. The analysis of relations between fish food consumption and fish growth may require the development of a new theoretical framework. No attempt has been made here to advance a new approach in developing fish growth half-saturation constants.

82. V_{max} and K_s are constants under specified conditions. In nature, however, conditions rarely ever remain constant. For instance, as a fish swims through the environment, it encounters differing concentrations of different foods. Different types of food may have different palatabilities to the fish. Thus in nature K_s and V_{max} may appear to vary continually (Parker 1975). Parker has shown that if the Michaelis-Menten equation is used to describe food ingestion by fish, constant values for V_{max} and K_s do not reproduce observed stomach contents. When both V_{max} and K_s were allowed to vary with the availability of alternate foods and the relative preference of these foods, the expected stomach contents agreed closely with actual observation.

Digestive Efficiencies of Fish

83. Knowledge of energy transfer from one trophic level to another is important in understanding fish population dynamics and the relationship of fish populations to other biological systems in reservoirs. Information on energy use and transfer can be obtained by studying

fish digestive efficiencies. Digestive efficiency, in broad terms, indicates bow the food a fish eats is used for growth and other physiological functions. The energy budget for food consumed by a fish can be written (after Warren and Davis 1967) as:

$$C = F + U + R + \Delta B \qquad (3)$$

where: C = energy consumed (ingestion)

F = energy egested (egestion)

U = energy lost as excretory products (excretion)

R = energy of respiration

ΔB = energy accumulated as growth

84. In this report information on two measurements of fish digestive efficiency is summarized: ecological growth efficiency and assimilation efficiency. Data on the food consumption requirements of various fish species are also presented. 0 attempt has been made to interpret the relationship of ecological growth efficiency or assimilation efficiency to fish age, condition, food availability, or other environmental characteristics. The reader is referred to Warren and Davis (1967) for an excellent review of fish feeding, bioenergetics, and growth.

85. Ecological growth efficiency has also been called gross growth efficiency and is defined as: $\Delta B/C \times 100$. Ecological growth efficiency expresses the relationship of fish growth to total food consumption. Appendix J summarizes data on ecological growth efficiency. Values range from 4.2 percent for a wild population of bluegill to 62.5 percent for young channel catfish under controlled laboratory conditions. For

carnivorous fish species, Winberg (1956) found the average ecological growth efficiency to be 20 percent. This 20-percent value is widely accepted in the literature as representative of most fish species.

86. Assimilation efficiency is defined as

$$A/e \times 100 \tag{4}$$

where: A = energy assimilated = C - F - U

Appendix J summarizes assimilation efficiencies for fish. Assimilation efficiency in fish is high, ranging from 66 to 98 percent. Many workers consider BO-percent assimilation efficiency realistic for most fish species.

87. Appendix J also lists the daily food consumption of fish, expressed as a percentage of body weight. Data on the daily meal of fish are useful in calculating energy budgets and for determining the amount of food necessary to support a fish population. Daily meals vary widely depending upon fish age, availability of food, and other environmental variables. In general, food amounting to 1 percent of the body weight per day is needed for maintenance without growth, and 4 to 5 percent of the body weight per day is required for optimum growth efficiency.

Fish Mortality Rates

88. The fishery model currently defines mortality rate as that fraction of the fish biomass that 15 converted to detritus by death. Modifications in the model will be necessary to account for fish biomass

lost by predation to piscivorous fish. Estimates of the ecological growth efficiency of carnivorous fish indicate that 20 percent of the fish biomass lost to predators will be incorporated as new fish biomass through growth, and the remaining 80 percent will continue along the detritus pathway in the form of egested material and feces (Winberg 1956).

89. The results of a review of the natural mortality rates of 17 species of reservoir fish are presented in Appendix K. This review is not extensive. It does, however, adequately demonstrate that natural mortality can be highly variable, depending on fish species, fish age, exploitation rate, and numerous environmental variables. For exploited populations tabulated in Appendix K, the average natural mortality rate per day for all species is 0.001. There is no evidence for significantly different regional differences in mortality rate. Insufficient data are available to examine the possibility of differential mortality rates among fish compartments. In one study that was reviewed, Patriarche (1968) demonstrated seasonal differences *in* mortality rate. Seasonal mortality rates probably vary widely over the continent and from year to year within a single reservoir, depending upon fluctuating environmental conditions.

90. For an excellent review of techniques for calculating various mortality rates (total, instantaneous, conditional, natural, and fishing), the modeler is referred to Ricker (1975).

Fish Respiration Rates

91. All energy necessary for the maintenance, growth, and reproduction of fish is derived from the energy of assimilated food. Most of the energy is used in a series of chemical reactions within a fish known as metabolism. Metabolic processes keep the internal functions operating. Energy is also used in growth. An understanding of fish production processes requires a knowledge of the interactions of energy supply, metabolism, and growth (Beamish and Dickie 1967).

92. Respiration rates have been used to study fish metabolism. Metabolism is normally equated to oxygen consumption, with the assumption being that all energy is released aerobically. Small amounts of energy are, however, released anaerobically. Respiration rates can be used to determine what fraction of fish biomass is converted to inorganic carbon, nitrogen, and phosphorus by nonnal metabolic processes. Knowledge of the rate transfers of these three elements is necessary for the mass balance functions of the fishery model.

Types of respiration

93. Three types of respiration rates were examined in this study: standard, routine, and active.

94. Standard respiration. The oxygen consumed in the absence of measurable movement is standard respiration. Standard metabolism has also been termed nonactive, basal, or resting metabolism. Obviously standard metabolism can be difficult to measure as few fish species are completely quiescent for extended periods.

95. Routine respiration. The rate of oxygen comsumption of a fish shoving normal activity is routine respiration. Routine respiratiOD is often measured as the average oxygen consumption observed over a 24-hour period.

96. Active respiration. The maximum rate of oxygen consumption under continuous forced activity is active respiration.

97. It is beyond the scope of this report to attempt to review all the available information on the metabolic rates of fishes. For further information on this subject the reader is referred to the works of Winberg (1956), Fry (1957), and Beamish and Dickie (1967). This study attempted to draw general conclusions abQut fish respiration rates in support of the data requirements of the fishery model.

Effect of temperature and fish weight

98. The active metabolic rate in relation to temperature does not necessarily follow a course parallel to the curve for the standard rate. The active rate may continue increasing until the fish reaches its upper lethal temperature limit as in trout and catfish. It may reach a plateau as in goldfish, or it may actually be depressed at the higher temperatures, as in lake trout (Figure 5, Fry 1957). For these reasons, predictive equations of active metabolism based on linear regressions may not be valid, or they may be valid only over a limited temperature range (Appendix L, Part I).

99. In contrast, the standard metabolic rates of various fish species show a qualitative uniformity of response. Standard. metabolism increases with increasing temperature and therefore is usually predictable based on linear regressions (Appendix. L, Part II). Active metabolism

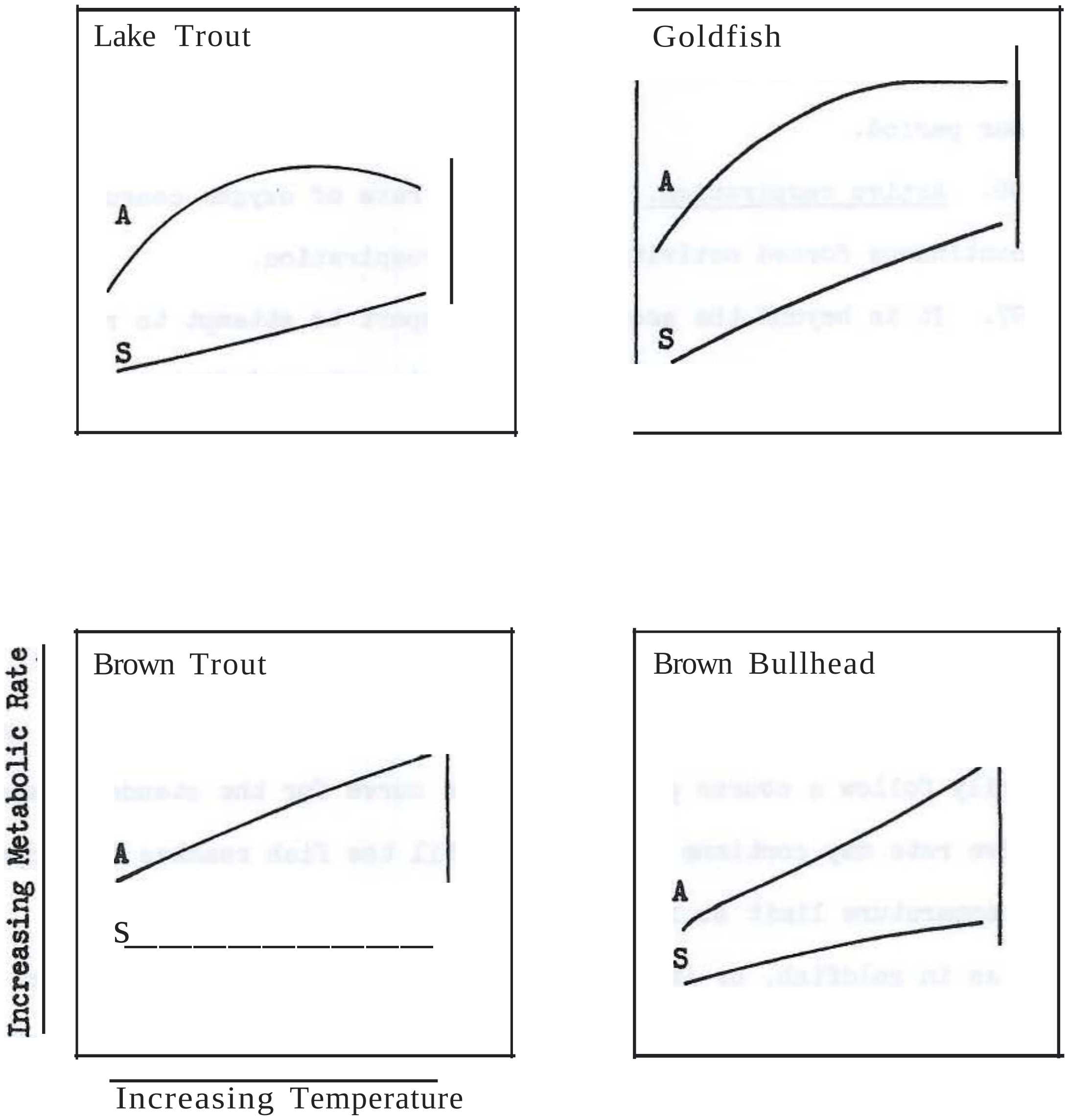

Figure 5• Active and standard metabolic rates of thermally acclimated fish (After Fry 1957). S = standard metabolic rate; A = active metabolic rate. Vertical lines represent upper lethal temperatures.

cannot be predicted a priori from the standard metabolism or the routine metabolism (Norstrom et al. 1976). Additionally, both active and standard metabolism are related to fish weight in most species. Metabolism increases with increasing weight of the fish, whereas, metabolism per unit weight usually remains the same or decreases with increasing weight. Both fish weight and temperature must be considered *in* predicting active and standard metabolism.

Effects of fish activity

100. Fry stated (Brown 1957), "An interesting point in connection with the oxygen consumption of fish is that the active rate of oxygen uptake is restricted to a few multiples of the standard rate." His data for several species showed that the greatest increases of the active rates are only of the order of four times the standard rates. However, for very active migrating species such as the sockeye salmon, Brett (1964, 1965) has shown that the active/standard ratio can exceed 16, depending on fish age. Most reservoir fish species are not as active as the sockeye salmon and consequently would have much lower active metabolic rates.

101. Winberg (1956) and Mann (1969), as well as other workers, are of the opinion that the metabolic rate of fish in confinement should be doubled to correct for activity in nature. The literature review given by Winberg (1956) indicates that this routine metabolism is approximately 1.7 times the standard metabolism (Appendix L, Part III). The relationship relating routine metabolism to standard metabolism is successful in predicting respiration rates over at least part of the normal temperature

range of various fish species (Solomon and Brafield 1972).

102. It would appear that the best estimate of the rate of respiration for normally active reservoir fish would be values for routine metabolism, such as those tabulated in Winberg (1956). Active metabolism rates as expressed in Appendix L, Parts I and III, indicate the maximum respiration rates for short time intervals. Fish do not usually respire at these rates for long periods, and therefore the values giYen overestimate the true average metabolism of normally active fish. Norstrom et al. (1976) considered active metabolism to be three times the routine metabolism.

103. It is suggested that routine respiration rates be used to estimate respiration in active fishes (Appendix L, Part IV). Routine metabolism can be estimated to be two or three times standard metabolism for reservoir fishes and four or five times the standard metabolism for active cold-water fish like salmonids.

Temperature Tolerances of Fish

104. Temperature tolerance limits define the range in which fish will grow and survive. Because the rates of most biological processes are temperature dependent, it is important to know the temperature limits an organism can tolerate and also its preferred temperature range for optimizing various physiological fWlctions.

105. Temperature tolerance data for 45 reservoir fish species are presented in Appendix M, Part I. Appendix M, Part II, summarizes the

many temperature tolerance studies by species, and Table 13 presents a generalized temperature tolerance swmnary by fish groups. For most warm-water species, upper and lower temperature tolerances are similar, the lower limit being reached at OOC and the upper limit attained between 33^0 and 37°C. The optimum temperature for growth is centered close to 27°C. Cold-water species, such as salmonids, also reach a lower lethal limit at OOC, but the upper lethal limit is near to 25^0C and optimum growth occurs at about lAoC. Temperature tolerance values presented in Appendix M were determined at various acclimation temperatures. In summarizing temperature tolerance limits (TL) by species (Appendix M, Part II), when more than one value was cited. the extreme temperature tolerances reported resulting in the survival of half the test fish for at least 24 hours are listed (24-hour TL 50)* if known.

Chemical Composition of Fish

106. Chemical composition data were used in the fishery model to maintain continuity of mass within the reservoir ecosystem by adding an appropriate amount of a particular constituent to the fish compartments through feeding and consequent growth and by returning mass due to fish respiration and decomposition as detritus.

107. Knowledge of the carbon, nitrogen, and phosphorus composition of fish is necessary for the mass balance functions. Table 14 presents these data for a variety of freshwater and saltwater fish species. In general, fish are 48 percent elemental carbon by dry weight (dry weight = weight after desiccation at 60^0c for 48 hours), 16 percent elemental

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* A 24-hour TL 50 is the median toxicity that occurs within a 24-hour period.

Table 13

Temperature Tolerances for Various Fish Groups*

Species Group	Lower Lethal	Optimum for Growth	Upper Lethal
Pickerels	0	25.4	34.4
Minnows	0	27	33.4
Catfishes	0	30	37.1
Sunfishes	<2.5	27.5	35.7
Black basses	<1.6	27	36.5
Crappies		≈23	32.5
Yellow perch	0	24.2	30.9
Average values	0	26.3	34.8

* All values expressed in degrees Centigrade.

Table 14

Chemical Composition of Fish

Element and Species	% Composition: Dry Weight	Wet Weight	Reference
Nitrogen (N)			
Ocean sunfish (Mala . ola)	16.6-18.2		Green (1899)
Bluegill	16.7		Calculated from data by Geng (1925), Gerking (1962), and Maynard (1951)
Bluegill		2.72	Gerking (1962)
Carp		2.'	Bull and MacKay (1976)
Northern squawfilh		2.5 + 0.1	
Largescale sucker		2.4 -	
Rainbow trOut		2.9	
Channel catfish		2.35	Worsham (1975)
General average	16.3		Bailey (1937), Nottingham (1952)
Carbon (C)			
Ocean sunfish (Hola mola)	48.2		Green (1899)
Phosphorus (P)			
Salmon		0.59	Atwater (1892) As P_2O_5
Trout		0.81	
Cod		0.60	
Eel		0.68	
Haddock		0.97	
Halibut.		0.44	
Herring		0.56	
Mackerel		0.56	
Turbot		0.48	
Average of above species		0.63	
Bluegill	4.75+0.70 4.73+0.85		Kitchell et al. (1975) + 1 S.E.
Bluegill	4.2 -		Hall et a1. (1970)
Channel cat.fish		0.86	Worsham (1975)
Carp		0.5 + 0.01	Bull and MacKay (1976)
Northern squaw[1ah		0.4 -	
Largescale sucker		0.3	
Rainbow trout		0.'	
General average (for fiah fleah)		0.22 (range: 0.1-0.4)	Clauseret (1962)

nitrogen, and 5 percent elemental phosphorus.

Recommendations

108. The recommendations presented suggest areas for further research to improve the fishery model data base. No attempt has been made to recommend improvements in the model itself or to address the problems of reservoir operation relating to fisheries management.

109. No matter how well conceived a model may be, its success in application depends largely on the quality of the data used to develop it. Large deficiencies in the data base exist for parts of the fishery model, and these deficiencies have been emphasized where applicable.

liO. The authors have not attempted to present final answers to the many topics examined in this paper. Much of the material presented is developed for the first time and represents an attempt to provide a starting point in solving some very difficult and little studied aspects of modeling fish population dynamics. It is anticipated that some of the methodologies used will be subjected to criticism, and it is hoped that out of such criticism new approaches to modeling and a better understanding of fish populations will develop and be useful in future modeling ef-forts.

I..II. It is recommended that the following areas be studied further to improve the model data base:

1) Additional information needs to be collected and analyzed on the fishery resources of CE reservoirs, especially those reservoirs located in the northern and western United States. Of the 187 CE

reservoirs for which physical and chemical data were available, only 33 percent had any type of fishery statistics available. Most of the reservoirs with useable data were located in the south. For those reservoirs where fishery data were available, much of the information was fragmented. Most recent data covering more years need to be obtained to develop regional fishery coefficients.

2) A continuing program of analyzing fish food habits will help refine the fishery model compartments. These data should be gathered on CE reservoirs when possible. As much of the model is developed upon fish feeding habits, a good data base is critical.

3) Further work should be directed toward improving the method of distributing fish biomass among the food compartments. Improvement should attempt to account for the nutritional value and useable energy content of different food sources.

4) The data base for estimating fish reproduction is poor and an attempt should be made to obtain further information on fish reproduction, especially from nonsoutbern reservoirs. New finds vill probably be the source for this information.

5) Except for the southern United States, there is a complete lack of fish recruitment data of a type suitable for the model.. New approaches toward estimating both reproduction and recruitment should be investigated.

6). The concept of half-saturation constants for fish growth may need to be developed from a new theoretical framework. The current data base for estimating half-saturation constants is poor, and further refinements of these constants may be necessary.

7) Further data collection on the natural mortality rates of reservoir fishes is needed, especially seasonal mortality.

8) It is reconunended that a continuous effort be made to review new literature for data directly applicable to fisheries modeling. New concepts in thinking about fish population dynamics should be explored. This may lead to improved model design and greater predictive precision.