Life History and Ecology of the Humpback Chub (Gila cypha) in the Colorado River, Grand Canyon, Arizona

Supplement No. ~~III~~ V
Population Model

PRELIMINARY SUBJECT TO REVIEW & CHANGE

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Cover drawing from Powell (1875)

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CHAPTER 1 - INTRODUCTION

BACKGROUND

This report describes the development of a population model for the endangered humpback chub (Gila cypha) in the Colorado River and its tributaries in Grand Canyon, Arizona. Development of a population model is one component of the Native and Endangered Fish Studies of the Glen Canyon Environmental Studies (GCES), designed to evaluate the operation of Glen Canyon Dam. This report identifies five elements necessary for model development and presents a conceptual population model for humpback chub in Grand Canyon. State and rate variables for a model are identified along with data availability and data needs. Construction of a population model is not presently advised until all fisheries data from the Colorado River and Little Colorado River in Grand Canyon are made available to GCES.

Joint GCES Studies

Comprehensive studies of the life history and ecology of the humpback chub in Grand Canyon are being completed under Phase II of GCES for the Bureau of Reclamation. These studies are being conducted jointly by Arizona Game and Fish Department (AGFD), Arizona State University (ASU), University of Arizona (UOA), U.S. Fish and Wildlife Service (FWS), and BIO/WEST (B/W). The purpose of the joint studies is to:

Determine the ecological and limiting factors of all life stages of humpback chub in the Colorado River, Grand Canyon, and the effects of Glen Canyon Dam operations.

The objectives of the joint studies are to:

- Determine resource availability and use (habitat, water quality, food, etc.),
- Determine reproductive capacity and success,
- Determine survivorship of early life stages,
- Determine distribution, abundance and movement, and effects of dam operations,
- Determine important biotic interactions with other species, and
- Develop a population model from empirical data.

These investigations were designed to provide input to state and federal agencies charged with management and protection of this endangered species, and to address two of seven conservation measures arising from the 1978 Biological Opinion on the operation of Glen Canyon Dam. An Environmental Impact Statement (EIS) on the Operation of Glen Canyon Dam and a Biological Opinion were developed by Bureau of Reclamation and the EIS is expected to become Record of Decision in 1996.

Purpose and Objectives of Modelling Program

The purpose of this modelling program is to provide an integrated quantitative characterization of the humpback chub population in Grand Canyon. The objectives of the modelling program are to:

- Provide the framework for a comprehensive assimilation and integration of data and information for humpback chub in Grand Canyon,
- Provide a tool to help understand humpback chub population dynamics and environmental interrelationships,
- Identify missing life history information as guidance to core research,
- Evaluate the efficacy of long-term monitoring in detection of biological responses, and
- Evaluate population viability.

MODELLING PROGRAM OVERVIEW

Role of Models

The role of models varies with program objectives and goals. Modelling programs are best used as tools to:

- Help researchers and decision-makers define problems and organize thoughts (Starfield and Bleloch 1986),
- Quantify factors that are not easily or directly measurable (Vaughan and Saila 1976),
- Integrate factors to assess their effects on system dynamics (Forrester 1961), and
- Examine the consequences of complexity (Thornley and Johnson 1990).

These tools are best utilized along with laboratory and field experimentation in the problem solving/decision-making process (Beyschlag et al. 1994). While models allow for investigation and integration of system dynamics, their outputs are of minimal value unless they can be supported or validated by at least some findings from direct measurement (i.e., empirical data).

The role of modelling the humpback chub population in Grand Canyon is primarily as an organizing and integrating tool to assist research, integration, and monitoring efforts. A modelling effort will provide the framework for data integration, identify additional research needs, provide guidance to long-term monitoring, and act as an organizational tool for the Integrated Humpback Chub (HBC) Final Report (Fig. 1). A population model can also be used as a predictor of population dynamics, depending on the reliability of data input.

Approaches To Modelling

Population studies are usually approached in one of three ways (Smith and Fowler 1981). The first is a natural history study, which is primarily descriptive in nature, and best describes much of the work on humpback chub, to date. Descriptive information is essential to defining a population, its distribution, and basic ecology, and to formulate concepts and hypotheses on the dynamics of the population. The second approach is development of conceptual models which are usually compartmental flow diagrams accompanied by written narrative. These conceptual models are designed to visualize interrelationships of various components of the population with the environment. The third approach is to develop formal mathematical models to describe population components and functions, and their dynamics. All three approaches overlap, to some extent, and a holistic approach to the study of population dynamics involves the integration of all three. This integrated approach is recommended for humpback chub in Grand Canyon, in which conceptual and mathematical models will be developed from past and present life history information on the species in Grand Canyon, as well as other populations.

Suitability of Modelling Program to Humpback Chub

Of the four mainstem Colorado River endangered fish species--Colorado squawfish (Ptychocheilus lucius), razorback sucker (Xyrauchen texanus), bonytail (Gila elegans) and humpback chub--the humpback chub in Grand Canyon is best suited for development of conceptual and mathematical population models for the following reasons:

- The species is relatively accessible for study, and sample methods have been developed and refined for reliably capturing all life stages.
- Much research has been conducted on this species, prior to and including the present studies, and a sizable database exists for identifying parameters and interactions.
- Humpback chub in Grand Canyon, as in other populations, exhibit a high fidelity for a relatively small geographic region that permits use of closed-systems analyses, and minimizes problems with random immigration and emigration.
- The life history of humpback chub is similar to that of many freshwater forms, and strategies and results of prior modelling efforts could be applicable.

The population model for humpback chub in Grand Canyon will consist of a series of linked mathematical and logical relationships that can be used to provide inferences into various aspects of the population. Generally only submodels of an overall model will be used to address specific objectives. We do not expect that any aspect of this model can or will be used to precisely describe or predict specific elements of the population. Instead, these submodels are expected to provide insight into the relationships between various population parameters and the environment, as well as the behavior of the population over time. These submodels will also aid in estimation of parameters and rates that are difficult to measure.

PROGRAM ELEMENTS

Modelling efforts are often conducted as a series of work elements, in which performance of one can depend upon completion of previous elements. This stepwise approach allows for periodic and regular evaluation of suitability and appropriateness of a modelling program for a particular species, and provides useful interim products throughout the modelling effort. Once developed, these models can be used to identify needed core research, guide and interpret monitoring data, and evaluate population viability. Five program elements composed the organizational framework for this population modelling program and are described in the following chapters.

I. Determine the feasibility of a population model,
II. Develop a conceptual population model,
III. Identify and assimilate data for important state and rate variables,
IV. Develop a series of mathematical and logical relationships, and
V. Develop and implement the population model.

CHAPTER 2 - FEASIBILITY OF A POPULATION MODEL

The feasibility of developing a population model for humpback chub in Grand Canyon was evaluated according to the following criteria:

1. Does the scientific community perceive a need for developing a population model for humpback chub in Grand Canyon?
2. Are there sufficient data available for developing a population model?
3. What type of population model(s) would be most suitable and valuable?
4. How would a population model be used?

THE NEED FOR A POPULATION MODEL

The need for a population model for humpback chub in Grand Canyon was identified early in Phase II of GCES by the Aquatic Coordination Team (ACT), i.e., a group of scientists from AGFD, FWS, BOR, ASU, and B/W. The ACT perceived the need to pursue a model development program as a mechanism for assimilating data on the species in Grand Canyon, as well as elsewhere in the basin, and for achieving some predictability in biological response to operations of Glen Canyon Dam. The ACT recognized that many data gaps were likely, but that the process of model development would benefit future research by defining data availability and needs for state and rate variables most important to the species.

The need for developing population models for three species of Colorado River endangered fishes (i.e., humpback chub, Colorado squawfish, razorback sucker) was also identified as part of the Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin (J. Hamill and P. Nelson, Pers. Comm.). Gilpin (1993) conducted a population viability analysis (PVA) on Colorado squawfish, and identified many state and rate variables for the population in the upper basin. This PVA was considered as only one component of a modelling effort for the species. Work on a common population model for Colorado squawfish and razorback sucker is being conducted at Utah State University by T. Crowl, although a separate modelling effort is not currently known for humpback chub. Hence, a population model for humpback chub in Grand Canyon would be very valuable in understanding species dynamics in upper basin populations as well.

DATA AVAILABILITY

The population of humpback chub in the Little Colorado River in Grand Canyon is the most intensively studied of the six populations in existence. Recent studies of the species in the mainstem, under GCES Phase I and Phase II, also produced valuable data for the species in the mainstem Colorado River in Grand Canyon. Historic and recent data collections were summarized by Valdez and Ryel (1995) and Valdez and Wasowicz (1995). Although the five populations of humpback chub in the Upper Colorado River Basin have been surveyed since 1979 (Tyus et al. 1982, Valdez et al 1982), and monitored since 1987 (McAda 1995), there is little known of the demographics of these populations, e.g., age-growth, survival, predation, etc.

While many state variables are known for the Grand Canyon population (e.g., number of eggs per female, relative numbers and distributions of fish by age group), few rate variables have been measured (e.g., survival, movement). Hence, there appears to be sufficient data available to construct a conceptual diagrammatic model by identifying state variables, but many rate variables remain unknown. Data recently collected from the Little Colorado River were not available for this model development program. The data from this component are vital to understanding the population in Grand Canyon. Model construction is not advised until these data are available.

SUITABLE POPULATION MODELS

Age-structured models appear to be more useful than simple birth-death models for characterizing humpback chub in Grand Canyon. Previous studies indicate that many environmental factors affect the species differentially by age group, e.g., survival seems highest for older fish, while predation is highest for younger, smaller fish. A more detailed description of simple birth-death models and age- and stage-structured models is provided in Chapter 6.

USES FOR A POPULATION MODEL

This modeling effort has been identified by scientists as a valuable tool to:

- Identify and integrate existing data,
- Identify and quantify important state and rate variables,
- Identify and evaluate population and environmental parameters that most affect population response,
- Help guide and interpret monitoring,
- Evaluate population viability, and

- Provide insight to population behavior under adaptive management.

The process of developing a population model can help scientists identify available data and integrate historic with present information. The framework for a population model can serve as an organizational tool by providing a conceptual picture of the relationships among state and rate variables. This conceptualization helps to identify and evaluate those parameters that most affect the population. A population model is also a valuable monitoring tool for identifying important parameters and as a predictor of response. Performing a population viability analysis is also an important and valuable exercise for determining the long-term trajectory of the population and the need for immediate management actions. The relationships identified in the population modelling effort can provide valuable insight into the behavior of the population in response to actions taken under adaptive management.

CHAPTER 3- CONCEPTUAL POPULATION MODEL

OVERVIEW OF A CONCEPTUAL POPULATION MODEL

Development of a population dynamics model begins with the recognition that organisms are part of a much larger system. In its simplest form, a conceptual model for humpback chub in Grand Canyon consists of the chub population and factors (abiotic, biotic and man-influenced) that affect this population (Fig. 2). However, these factors may affect distinct portions of the population in different ways, and a useful model construct should include information about these population components.

A common approach to modelling population dynamics is to divide a population into distinct groups (state variables) based upon age, sex, and distribution. The model then considers the numbers of individuals in each of these groups and transition rates (rate variables) between groups, or the influence of one group size on another (Fig. 3). These fluxes are rates such as physical movement between spatially-separated population components or survival rates between age classes. The influence of one group size on another can occur through reproduction, mortality, or competition.

By separating the population into distinct groups, the effects of abiotic, biotic, and man-influenced factors can be assessed for individual groups within the population. These effects can be direct in their influence (Fig. 4a) or can be indirect and involve feedback between two or more variables (Fig. 4b). While ideal, it is impossible to identify all the factors that affect the number of fish in each group and the fluxes between groups, as the number of factors can be dynamic and essentially infinite. The set of factors to be included for a given model application is determined by the study objectives.

The purpose of this work is not to identify external factors that affect state or rate variables, but to propose a conceptual model that divides the population into separable groups based upon sex, age, and distribution, and identifies transitions and influences between these groups. This division is designed to provide a working structure for population assessment through a consensus of involved researchers. The resulting conceptual model will provide the framework upon which to assess the effects on humpback chub of pertinent abiotic, biotic, and anthropogenic elements.

COMPONENTS OF A CONCEPTUAL POPULATION MODEL

In the initial conceptual model proposed here, all humpback chub in Grand Canyon are considered one population, distinct and isolated from those in the upper Colorado River basin. The Grand Canyon population was divided into five components (Table 1) which have various degrees of interaction and influence (Fig. 5). Some of these components may function as interrelated units with other components, or they may be separate and subject to extinction and recolonization dynamics. Based on the current knowledge of the species in Grand Canyon, the LCR component is considered to be the center of the metapopulation.

Table 1. Components of the humpback chub population in Grand Canyon.

a. Colorado River Upstream (CRU) of LCR component.
b. Colorado River/LCR inflow (CRI).
c. Colorado River Downstream (CRD) of LCR component.
d. Little Colorado River (LCR).
e. Tributaries (TRI).

Within these components, groups of fish were divided into age groups (Fig. 6). Survival, reproduction rates and movement were identified as the principal rate variables to link numbers between age groups of each component. The initial linkages between state variables are based upon our present understanding of the population.

One or more of the five components identified above may not be significant contributors to overall numbers of humpback chub in Grand Canyon. Nevertheless, all known components, and associated state and rate variables are identified so that all probable population intrarelationships are considered. We also recognize that many of these variables may be insignificant. Where these relationships are determined to not exist, state or rate variables will equal zero, and may be removed from the flow diagram. The conceptual model flow diagram (Fig. 6) does not partition the fish into groups by sex. While sex-specific rates and numbers may be important, and distinct, partitions by gender were not a part of this model development program.

Component a. Colorado River Upstream (CRU)

Only 5 percent of the humpback chub captured by B/W in the Colorado River in Grand Canyon, from 1990 through 1993, were found in regions of the Colorado River outside of the 30-km area around the LCR inflow (RM 58-77). Little is known about these fish, including their origin, abundance, distribution, movement, reproduction, and survival. An aggregation was found near South Canyon (RM 30) and small numbers of individuals were found downstream to RM 57. The aggregation associated with warm springs near RM 30 is the largest upstream of the LCR inflow (mark-recapture population estimate shows about 50 fish). We believe that there are no significant numbers of humpback chub upstream of this aggregations to contribute to this component. Larvae and age 0 from this component may move downstream into the CRI component, but extensive marking programs show no exchange of age I fish and older between components.

Component b. Colorado River/LCR Inflow (CRI)

Recent research by Valdez and Ryel (1995) shows that about 95 percent of the humpback chub in the mainstem Colorado River in Grand Canyon are found within a 20-mile (32-km) area around the LCR inflow (RM 57-77). The relationship between this Colorado River/LCR inflow component and the LCR component is not clear. Radiotelemetry and extensive mark-recapture studies in the mainstem show that the majority of adults from the CRI component ascend the LCR annually to spawn in February-May, and descent in June-July. These fish spawn simultaneously with adults of the LCR component in the lower 13 km of the LCR. It is not presently known if some adults of the CRI component remain for one or more years in the LCR before returning to the mainstem. The number of adults ascending from the CRI component to the LCR to spawn is approximately 3,480.

Large numbers of young humpback chub (age 0 and age I) descend annually from the LCR into the mainstem Colorado River. It is not known if these fish are primarily the progeny of the CRI component, of the LCR component, or a mixture of the two. Large numbers of young (age 0, age I), subadult (age II), and adult (age III, III+) humpback chub remain in the LCR year around.

Component c. Colorado River Downstream (CRD)

Humpback chub downstream of the CRI component have been found as individuals and small aggregations at RM 83-84 (Clear Creek), RM 92-93, RM 108-109 (Shinumo Creek), RM 114-115, RM 119-120, RM 143-144 (Kanab Creek), RM 156-157 (Havasu Creek), and RM 195 (Valdez and Ryel 1995). The largest aggregation downstream of the CRI component occurs at RM 126-129 (mark-recapture population estimate shows about 100 adults). Low numbers of larvae and small age 0 humpback chub in these regions indicate some successful reproduction or transport from the LCR. Most fish in this region probably originated from the LCR component, although some successful mainstem reproduction or local tributary reproduction cannot be discounted. There is little evidence of reproduction by humpback chub in Grand Canyon outside of the LCR, primarily because cold water released from Glen Canyon Dam prevents maturation of eggs and survival of larvae in the mainstem.

Component d. Little Colorado River (LCR)

The LCR component is the largest of the five components of the humpback chub population in Grand Canyon. Past and current research indicates that a large proportion of humpback chub in Grand Canyon reside in the LCR (LCR component), all or most of the year. The numbers of adults and juveniles that remain in this tributary year around, and the numbers that ascend annually from the mainstem to spawn are approximately known from population estimates in the LCR (Douglas and Marsh 1996) and population estimates and movement information from the mainstem Colorado River (Ryel and Valdez 1996).

The LCR component probably consists of a resident population, with reproduction from age III+ fish. Adults, resident to the mainstem, also ascend and spawn in the LCR annually. The proportion of larvae, age 0, age I, and age II fish from each of these components that remains in the LCR or descends to the mainstem is unknown.

Although the lower LCR is a low to moderate gradient stream, it is unlikely that larvae, age 0, or age I fish from the CRI component ascend upstream into the LCR. Also, it appears that the majority of larvae, age 0, and age I fish transported from the LCR into the mainstem are downstream of that inflow.

Component e. Tributaries (TRI)

Small numbers of humpback chub have been historically and recently captured in a number of tributary inflows, including Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek (Valdez and Wasowicz 1995). Thorough sampling in these tributaries indicate that these fish are primarily emigrants from another component of the Grand Canyon population. Young humpback chub captured in these tributaries indicates either local successful reproduction or ascent by mainstem fish attracted to warmer tributary temperatures. Some reproduction may be occurring in these tributaries (e.g., Bright Angel, Shinumo, Kanab, Tapeats, Havasu creeks), but evidence--such as gravid fish, incubating eggs, and larvae--has not been found in these streams recently.

CHAPTER 4 - STATE AND RATE VARIABLES

It is important to identify state and rate variables as part of the development of a conceptual population model, as well as to assess the availability and types of data. The objectives of this element were to:

1. Identify important state and rate variables.
2. Assimilate empirical data for important state and rate variables.
3. Identify missing and needed information.

IMPORTANT VARIABLES

State and rate variables wee identified for each population component in development of the conceptual model (Fig. 2, Chapter 3). State variables for this model development are defined as the age-specific elements, and include estimated numbers of eggs, larvae, age-0, age I, age II, age III, and age n (age IV+). Rate variables are those functions that link the state variables, and include fecundity, survival, and movement. The relative importance of each of these variables is best determined when the relationships between variables are defined and understood.

EMPIRICAL DATA

Past and present research has accumulated a sizeable database on life history parameters of humpback chub in Grand Canyon, as well as from five other populations (Black Rocks, Westwater Canyon, Desolation Canyon, Cataract Canyon, and Yampa Canyon). While this database cannot provide estimates for all parameters identified in a conceptual model, it will likely provide much of the needed information.

Recent studies in both the mainstem Colorado River and the LCR have supplied information on many of these parameters. For many of the rate and state variables for mainstem Colorado River populations, initial parameter estimates have been made (Table 2). Most of these estimates were obtained from work presented in Valdez and Ryel (1995). Estimations of adult population size and survival are detailed in Appendix A. Estimates of parameters from other researchers will be added to Table 2 as they become available. A more detailed discussion of the mathematical and logical relationships used to describe these state and rate variables is presented in Chapter 5.

Table 2. Descriptions and available data for state and rate variables for each component of a conceptual population model for humpback chub in Grand Canyon. A description of the data available is presented in Chapter 5. Blank lines indicate no data are available.

Component State & Rate Variables	Description	Data Available
Component a: Colorado River Upstream (CRU)		
State Variables		
Eggs	No. eggs in CRU	52 adults at RM 30; 26-female x 2,500 eggs = 65,000 eggs
Larvae	No. of larvae in CRU	None found
Age 0	No. of fish less than 1 year old in CRU	~100 found in July 1994
Age I	No. of fish less than 2 years old in CRU	Few found (<50)
Age II	No. of fish less than 3 years old in CRU	Few found (<25)
Age III	No. of fish less than 4 years old in CRU	Few found (<10)
Age n	No. of fish n years (age IV...age n) in CRU	Estimated 52 near RM 30
Rate Variables		
F_{IIIa}	Fecundity of Age III fish in CRU	1,000 eggs/female
F_{na}	Fecundity of Age n fish in CRU	2,500 eggs/female
S_{ea}	Survival of eggs in CRU	
S_{la}	Survival of larvae in CRU	
S_{0a}	Survival of Age 0 in CRU	100 of 65,000 = 0.0015
S_{Ia}	Survival of Age I in CRU	
S_{IIa}	Survival of Age II in CRU	
S_{IIIa}	Survival of Age III in CRU	
$S_{IIIa}...S_{na}$	Survival of Age n in CRU	assume 0.755 for all adults
M_{la}	Movement of larvae from CRU to CRI	
M_{0a}	Movement of Age 0 from CRU to CRI	
M_{Ia}	Movement of Age I from CRU to CRI	
M_{IIa}	Movement of Age II from CRU to CRI	
M_{IIIa}	Movement of Age III from CRU to CRI	
M_{na}	Movement of Age n from CRU to CRI	
M_{IIba}	Movement of Age II from CRI to CRU	
M_{IIIba}	Movement of Age III from CRI to CRU	
M_{nba}	Movement of Age n from CRI to CRU	

Component State & Rate Variables	Description	Data Available
Component b: Colorado River/LCR Inflow (CRI)		
State Variables		
Eggs	No. eggs in CRI	
Larvae	No. of larvae in CRI	
Age 0	No. of fish less than 1 year old in CRI	For LCR to Lava Chuar (RM 61.0-65.4)=66,000; to 230,000 in 1991 and 1992; 858,000 in 1993
Age I	No. of fish less than 2 years old in CRI	same as above
Age II	No. of fish less than 3 years old in CRI	same as above
Age III	No. of fish less than 4 years old in CRI	Total estimates for adults = 3,480 (RM 57-65.4)
Age n	No. of fish n years (age IV...age n) in CRI	same as above
Rate Variables		
F_{IIIb}	Fecundity of Age III fish in CRI	1,000 eggs/female
F_{nb}	Fecundity of Age n fish in CRI	2,500 eggs/female
F_{IIIbd}	Fecundity of Age III fish from CRI to LCR	1,000 eggs/female
F_{nbd}	Fecundity of Age n fish from CRI to LCR	2,500 eggs/female
S_{eb}	Survival of eggs in CRI	
S_{lb}	Survival of larvae in CRI	
S_{0b}	Survival of Age 0 in CRI	0.010/yr
S_{Ib}	Survival of Age I in CRI	0.010/yr
S_{IIb}	Survival of Age II in CRI	0.010/yr
S_{IIIb}	Survival of Age III in CRI	0.755 for all adults
$S_{IIIb}...S_{nb}$	Survival of Age n in CRI	same as above
M_{lb}	Movement of larvae from CRI to CRD	
M_{0b}	Movement of Age 0 from CRI to CRD	246,000 to 738,000 subadults moving below Lava-Chuar in 1991, 1992; 3,920,000 in 1993
M_{Ib}	Movement of Age I from CRI to CRD	same as above
M_{IIb}	Movement of Age II from CRI to CRD	same as above
M_{IIIb}	Movement of Age III from CRI to CRD	2 of 356=0.6% of adults
M_{nb}	Movement of Age n from CRI to CRD	same as above
M_{IIcb}	Movement of Age II from CRD to CRI	0
M_{IIIcb}	Movement of Age III from CRD to CRI	0
M_{ncb}	Movement of Age n from CRD to CRI	0

Component State & Rate Variables	Description	Data Available
Component c: Colorado River Downstream (CRD)		
State Variables		
Eggs	No. females x wt.:no. eggs in CRD	175 adults (RM 65.4-225) ~88 female x 2,500 eggs = 220,000 eggs
Larvae	No. of larvae in CRD	~0 (few if any produced in this area)
Age 0	No. of fish less than 1 year old in CRD	~1,000 (few if any produced in this area)
Age I	No. of fish less than 2 years old in CRD	~300 (few if any produced in this area)
Age II	No. of fish less than 3 years old in CRD	~300 (few if any produced in this area)
Age III	No. of fish less than 4 years old in CRD	~175 adults from Lava Chuar (RM 65.4) to Diamond Creek (RM 225)
Age n	No. of fish n years (age IV...age n) in CRD	same as above
Rate Variables		
F_{IIIc}	Fecundity of Age III fish in CRD	1,000 eggs/female
F_{nc}	Fecundity of Age n fish in CRD	2,500 eggs/femlae
F_{IIIce}	Fecundity of Age III fish from CRD to TRI	1,000 eggs/female
F_{nce}	Fecundity of Age n fish from CRD to TRI	2,500 eggs/female
S_{ec}	Survival of eggs in CRD	~0
S_{lc}	Survival of larvae in CRD	~0
S_{0c}	Survival of Age 0 in CRD	~0
S_{Ic}	Survival of Age I in CRD	0.01/yr
S_{IIc}	Survival of Age II in CRD	0.01/yr
S_{IIIc}	Survival of Age III in CRD	0.755/yr
$S_{IIIc}...S_{nc}$	Survival of Age n in CRD	0.755/yr
M_{lc}	Movement of larvae from CRD to Lake Mead	~0
M_{0c}	Movement of Age 0 from CRD to Lake Mead	~0
M_{Ic}	Movement of Age I from CRD to Lake Mead	~0
M_{IIc}	Movement of Age II from CRD to Lake Mead	~0
M_{IIIc}	Movement of Age III from CRD to Lake Mead	0
M_{nc}	Movement of Age n from CRD to Lake Mead	0

Component State & Rate Variables	Description	Data Available
Component d: Little Colorado River (LCR)		
State Variables		
Eggs	No. females x wt.:no. eggs in LCR	
Larvae	No. of larvae in LCR	
Age 0	No. of fish less than 1 year old in LCR	
Age I	No. of fish less than 2 years old in LCR	
Age II	No. of fish less than 3 years old in LCR	
Age III	No. of fish less than 4 years old in LCR	
Age n	No. of fish n years (age IV...age n) in LCR	
Rate Variables		
F_{IIId}	Fecundity of Age III fish in LCR	
F_{nd}	Fecundity of Age n fish in LCR	
S_{ed}	Survival of eggs in LCR	
S_{ld}	Survival of larvae in LCR	
S_{0d}	Survival of Age 0 in LCR	
S_{Id}	Survival of Age I in LCR	
S_{IId}	Survival of Age II in LCR	
S_{IIId}	Survival of Age III in LCR	
$S_{IIId}...S_{nd}$	Survival of Age n in LCR	
M_{ld}	Movement of larvae from LCR to CRI	
M_{0d}	Movement of Age 0 from LCR to CRI	All subadults: 246,000 to 738,000 in 1991 and 1992; 3,918,000 in 1993
M_{Id}	Movement of Age I from LCR to CRI	same as above
M_{IId}	Movement of Age II from LCR to CRI	same as above
M_{IIId}	Movement of Age III from LCR to CRI	All adults returning from spawning = 3,480 adults annually
M_{nd}	Movement of Age n from LCR to CRI	same as above
M_{IIIbd}	Movement of Age III from CRI to LCR	All adults: ~3,480 adults ascent LCR to spawn annually
M_{nbd}	Movement of Age n from CRI to LCR	same as above
Component e: Tributaries (TRI)		
State Variables		
Eggs	No. females x wt.:no. eggs in TRI	0
Larvae	No. of larvae in TRI	0
Age 0	No. of fish less than 1 year old in TRI	0

Component State & Rate Variables	Description	Data Available
Age I	No. of fish less than 2 years old in TRI	0
Age II	No. of fish less than 3 years old in TRI	0
Age III	No. of fish less than 4 years old in TRI	0
Age n	No. of fish n years (age IV...age n) in TRI	0
Rate Variables		
F_{IIIe}	Fecundity of Age III fish in TRI	1,000 eggs/female
F_{ne}	Fecundity of Age n fish in TRI	2,500 eggs/female
S_{ee}	Survival of eggs in TRI	
S_{le}	Survival of larvae in TRI	
S_{0e}	Survival of Age 0 in TRI	0
S_{Ie}	Survival of Age I in TRI	0
S_{IIe}	Survival of Age II in TRI	0
S_{IIIe}	Survival of Age III in TRI	0
$S_{IIIe}...S_{ne}$	Survival of Age n in TRI	0
M_{le}	Movement of larvae from TRI to CRD	0
M_{0e}	Movement of Age 0 from TRI to CRD	0
M_{Ie}	Movement of Age I from TRI to CRD	0
M_{IIe}	Movement of Age II from TRI to CRD	0
M_{IIIe}	Movement of Age III from TRI to CRD	0
M_{ne}	Movement of Age n from TRI to CRD	0
M_{IIIce}	Movement of Age III from CRD to TRI	None reported
M_{nce}	Movement of Age n from CRD to TRI	None reported

Mainstem tagging studies provided estimates of population size, as well as survival rates and sex ratios of adults living in the mainstem in the vicinity of the LCR. Similar estimates will soon be available from the LCR. The combination of data from the LCR and mainstem should provide an estimate of the exchange of fish between the two systems. Movement rates of subadult and adult humpback chub in the mainstem downstream of the LCR component has also been estimated, but survival estimates may be more difficult to obtain.

Assessing abundance of younger chubs is likely to be more difficult. However, within the LCR, estimates of population size and survival may be possible through tagging studies--at least for individuals greater than 150 mm total length. In addition, the rate of emigration from the LCR may be possible through coordinated efforts between the LCR and mainstem studies. Estimates of survival in the LCR may also be possible through tagging or catch-effort studies.

MISSING AND NEEDED INFORMATION

The most important partition of data missing from this model development effort is for the state and rate variables associated with component d (Little Colorado River). Many of these data have been collected but are not currently available to GCES.

The effects of environmental changes on life-history parameters will be difficult to measure directly in most circumstances. However, such changes in parameter values can be investigated by hypothesizing bounds on the parameter value as affected by environmental change. These exercises are often beneficial to assess relative magnitude of an environmental change or perturbation.

Where data gaps continue to exist, other methods can be employed to provide parameter estimates. Empirical data from historical studies may be used where available, and literature will be researched for similar species to fill data needs. Where data are missing for important variables, Grand Canyon researchers may be asked, through a Delphi approach (Pill 1971, Crance 1987), to provide best estimates.

Alternately, life history parameters that are difficult to measure can be estimated using preliminary model results. With information on some life history parameters, others can be estimated using a model with stated assumptions of population trajectory (Vaughan and Saila 1976, Van Winkle et al. 1978, Deangelis et al. 1980, Manly 1990). For example, if estimated adult population size and survival rates are known, the recruitment rate needed to maintain a stable, or increasing, population can be calculated. Such calculated rates can be compared with estimates from field measurements to determine if recruitment is sufficient to maintain the population, and to assess the effect of high variation in recruitment on population dynamics. Significant deficiencies in important parametric data may result in recommendations for future research efforts.

Also, rate functions affected by density of some aspect of the population (density dependence) may be identified with a model (Van Winkle et al. 1978, Manly 1990). For example, the robust condition of adult chubs in the mainstem Colorado River suggests that factors affecting survival of younger age groups (perhaps density) may be limiting the number of fish that reach maturity as hypothesized for other fish species (Gulland 1965).

Despite intensive studies of humpback chub in the LCR since about 1980, data sets have not been fully analyzed to quantitatively describe the state and rate variables for the component of that tributary. These relationships are important to understanding the entire population of humpback chub in Grand Canyon. Without these relationships, model development cannot proceed past the descriptive phase of state and rate variables for the mainstem Colorado River.

CHAPTER 5 - MATHEMATICAL AND LOGICAL RELATIONSHIPS

The purpose for this element is to integrate the assimilated information on humpback chub from Grand Canyon into a series of mathematical and logical relationships. The objectives of the element are to:

1. Analyze data for describing important state and rate variables,
2. Identify parameters that most affect changes in the population, and
3. Assess available and missing information on state and rate variables.

DATA ANALYSIS

Data assimilated under Element III will be synthesized and analyzed to provide mathematical or logical relationships for important state and rate variables. These relationships describe the state variables and define the linkages between these variables. Many databases from Grand Canyon do not contain the type of information necessary for population modelling. Some state and rate variables can be gleaned from existing data through analysis and interpretation, which are best performed by investigators responsible for initial data collection. However, the availability of this information in progress reports is very limited. This modelling program may need to work with researchers to provide guidance in data analyses necessary for model input.

PARAMETERS THAT MOST AFFECT CHANGE

The relative change in potential population growth rate caused by changes in life history parameters can be effectively assessed with population models (Horst 1977, Caswell 1978, Caswell 1988). This "sensitivity analysis" will help focus the monitoring effort by identifying key monitoring parameters to ascertain the status and trajectory of the population. In addition, it will help identify life history parameters that may have the biggest effect on the population in response to environmental change. This may include investigating environmental changes that have detrimental effects (e.g., reducing food supply, increasing predation), or management schemes that may prove beneficial to the population (e.g., temperature and flow modifications, predator reduction).

MISSING INFORMATION

This element will also help to identify missing information on important state and rate variables, which may not become evident until attempts are made to integrate analyzed data. Differences in data collection methods, spatial or temporal discrepancies, or data-type mismatches may preclude integration of certain data partitions into a comprehensive modelling program. The following provides a description of the mathematical and logical relationships available or missing for the state and rate variables of each population component, as identified in Chapter 4.

COMPONENT A: COLORADO RIVER UPSTREAM (CRU)

State Variables

Eggs - No. Eggs in CRU

The number of eggs potentially deposited on an annual basis by humpback chub in the Colorado River upstream of the LCR is based on the estimated number of adults associated with the warm springs near RM 30. With an estimated 52 adults, or approximately 26 females (captures indicate about a 50:50 sex ratio), each with an average of 2,500 eggs (Hamman 1982), the total number of eggs potentially deposited annually is 65,000.

Larvae - No. Larvae in CRU.

Larval humpback chub have not been found upstream of the LCR component.

Age 0 - No. Fish <1 Year Old in CRU.

In July of 1994, approximately 100 humpback chub (18-31 mm TL, n=14) were captured in a warm spring at RM 30.8 (Valdez and Masslich, In review).

Age I - No. Fish <2 Years Old in CRU.

Very few fish have been found upstream of the LCR component that are believed to be less than 2 years of age.

Age II - No. Fish <3 Years Old in CRU.

Very few fish have been found upstream of the LCR component that are believed to be less than 3 years of age.

Age III - No. Fish <4 Years Old in CRU.

Very few fish have been found upstream of the LCR component that are believed to be less than 4 years of age.

Age n - No. Fish Age IV+ in CRU.

The only aggregation of humpback chub upstream of the LCR component is the estimated 52 adults associated with the warm springs near RM 30.

Rate Variables

F_{IIIa} - Fecundity of Age III Fish in CRU.

Relationship of fish body weight to number of eggs is expressed as:

$$EPF = -4443 + 14.53W \quad (R^2 = 0.96)$$

where: EPF = numbers of eggs per female, and
W = body weight of fish.

With humpback chub first reaching maturity at about 200 mm TL or about 85 g, the number of eggs per female cannot be computed from the above relationship, which was developed for larger fish. Hence, the minimum fecundity of 1,000 eggs per female is used for age III fish.

The length-weight relationship for female humpback chub in the Colorado River in Grand Canyon is:

$$\log_{10}W = 4.556 + 2.817 \log_{10}TL \quad (R^2 = 0.82)$$

The logarithmic growth curve for humpback chub in the Colorado River in Grand Canyon is:

$$TL = 143.92 * \log_e(Age+1) + 1.0938 \quad (R^2 = 0.99)$$

F_{na} - Fecundity of Age n Fish in CRU.

Relationship of fish body weight to number of eggs for all sizes and ages is presented above for F_{IIIa}.

S_{ea} - Survival of Eggs in CRU.

The survival of eggs in the Colorado River upstream of the LCR component is unknown. Survival of eggs in the mainstem is expected to be insignificant since no survival of eggs is reported at a temperature of less than 12°C (Hamman 1982); the Colorado River upstream of the LCR varies from about 8°C to 10°C. Survival of eggs is expected in inchannel warm springs, but the rate is unknown.

S_{la} - Survival of Larvae in CRU.

The survival of larvae in the Colorado River upstream of the LCR component is unknown, but is expected to be low because of cold water temperature and large numbers of predators; Hamman (1982) reported 15% survival of larvae reared at 12-13°C.

S_{0a} - Survival of Age 0 in CRU.

The survival of Age 0 in the Colorado River upstream of the LCR component is unknown. Survival of egg to Age 0 could be inferred from observations in July 1994, or 100 age 0 of 65,000 eggs (0.0015).

S_{Ia} - Survival of Age I in CRU.

The survival of Age I in the Colorado River upstream of the LCR component is unknown.

S_{IIa} - Survival of Age II in CRU.

The survival of Age II in the Colorado River upstream of the LCR component is unknown.

S_{IIIa} - Survival of Age III in CRU.

The survival of Age III in the Colorado River upstream of the LCR component is unknown.

S_{na} - Survival of Age n in CRU.

The survival of Age n or adults in the LCR component is 0.755 (95% C.I. = 0.627-0.896), and is assumed to be the same for the CRU component.

M_{la} - Movement of Larvae From CRU to CRI.

Movement of larvae from the CRU component to the CRI component is unknown, but is probably insignificant considering the susceptibility of humpback chub larvae to cold water temperature.

M_{0a} - Movement of Age 0 From CRU to CRI.

Movement of Age 0 from the CRU component to the CRI component is unknown, but is probably insignificant considering the susceptibility of young humpback chub to cold water temperature.

M_{Ia} - Movement of Age I From CRU to CRI.

Movement of Age I from the CRU component to the CRI component is unknown.

M_{IIa} - Movement of Age II From CRU to CRI.

Movement of Age II from the CRU component to the CRI component is unknown.

M_{IIIa} - Movement of Age III From CRU to CRI.

Movement of Age III from the CRU component to the CRI component is unknown.

M_{na} - Movement of Age n From CRU to CRI.

Movement of Age n from the CRU component to the CRI component is unknown.

M_{IIba} - Movement of Age II From CRI to CRU.

Movement of Age II from the CRI component to the CRU component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which reduce the swimming ability of the fish (Bulkley et al. 1982).

M_{IIIba} - Movement of Age III From CRI to CRU.

Movement of Age III from the CRI component to the CRU component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which could reduce the swimming ability of the fish (Bulkley et al. 1982).

M_{nba} - Movement of Age n From CRI to CRU.

Movement of Age n from the CRI component to the CRU component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which could reduce the swimming ability of the fish (Bulkley et al. 1982).

COMPONENT B: COLORADO RIVER/LCR INFLOW (CRI)

State Variables

Eggs - No. Eggs in CRI.

The number of eggs potentially deposited on an annual basis by humpback chub in the Colorado River in the vicinity of the LCR is probably low. The majority of adults of the CRI component ascend the LCR to spawn (as part of the LCR component). Some spawning may occur in the warm LCR inflow, but survival is probably low because fluctuating mainstem flows frequently bath the eggs in cold mainstem water.

Larvae - No. Larvae in CRI.

The number of larval humpback chub originating from the Colorado River in the vicinity of the LCR is probably low because of limited spawning success. The majority of larvae in this component are probably immigrated from the LCR component, but these numbers are unknown.

Age 0 - No. Fish <1 Year Old in CRI.

The number of Age 0 humpback chub originating from the Colorado River in the vicinity of the LCR is probably low because of limited spawning success. The majority of Age 0 in this component are probably immigrated from the LCR component; peak numbers of juveniles (Age 0, I, II) in the CRI component in 1991, 1992, and 1993 were 66,000; 230,000; and 858,000.

Age I - No. Fish <2 Years Old in CRI.

The number of Age I humpback chub originating from the Colorado River in the vicinity of the LCR is probably low because of limited spawning success. The majority of Age I in this component are probably immigrated from the LCR component; peak numbers of juveniles (Age 0, I, II) in the CRI component in 1991, 1992, and 1993 were 66,000; 230,000; and 858,000.

Age II - No. Fish <3 Years Old in CRI.

The number of Age I humpback chub originating from the Colorado River in the vicinity of the LCR is probably low because of limited spawning success. The majority of Age I in this component are probably immigrated from the LCR component; peak numbers of juveniles (Age 0, I, II) in the CRI component in 1991, 1992, and 1993 were 66,000; 230,000; and 858,000, respectively.

Age III - No. Fish <4 Years Old in CRI.

The estimated number of adult humpback chub (Age III+) in this component in 1993 was 3,480, (95% C.I.=2,682-4,281) with an approximately 50:50 sex ratio.

Age n - No. Fish Age IV+ in CRI.

The estimated number of adult humpback chub (Age III+) in this component (mean for 1991-93) was 3,480, (95% C.I. = 2,682-4,281) with an approximately 50:50 sex ratio.

Rate Variables

F_{IIIb} - Fecundity of Age III Fish in CRI.

Relationship of fish body weight to number of eggs is expressed as:

$$EPF = -4443 + 14.53W \quad (R^2 = 0.96)$$

where: EPF = numbers of eggs per female, and
W = body weight of fish.

With humpback chub first reaching maturity at about 200 mm TL or about 85 g, the number of eggs per female cannot be computed from the above relationship, which was developed for larger fish. Hence, the minimum fecundity of 1,000 eggs per female is used for age III fish.

The length-weight relationship for female humpback chub in the Colorado River in Grand Canyon is:

$$\log_{10}W = 4.556 + 2.817 \log_{10}TL \ (R^2 = 0.82)$$

The logarithmic growth curve for humpback chub in the Colorado River in Grand Canyon is:

$$TL = 143.92 * \log_e(Age+1) + 1.0938 \ (R^2 = 0.99)$$

F_{nb} - Fecundity of Age n Fish in CRI.

Relationship of fish body weight to number of eggs for all sizes and ages is presented above for F_{nnb}.

S_{eb} - Survival of Eggs in CRI.

The survival of eggs in the Colorado River for the LCR component is unknown. Survival of eggs in the mainstem is expected to be insignificant since no survival of eggs is reported at a temperature of less than 12°C (Hamman 1982); the Colorado River upstream of the LCR varies from about 8°C to 12°C. Survival of eggs might occur in the warm LCR inflow.

S_{lb} - Survival of Larvae in CRI.

The survival of larvae in the Colorado River for the LCR component is unknown, but is expected to be low because of cold water temperature and large numbers of predators; Hamman (1982) reported 15% survival of larvae reared at 12-13°C. The majority of the larvae in this component probably immigrate from the LCR.

S_{0b} - Survival of Age 0 in CRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRI component is 0.01. Predation of juvenile humpback chub by other fish species is described by Valdez and Ryel (1995); brown trout (10.4%), rainbow trout (5-10%), channel catfish (1.5%).

S_{Ib} - Survival of Age I in CRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRI component is 0.01. Predation of juvenile humpback chub by other fish species is described by Valdez and Ryel (1995); brown trout (10.4%), rainbow trout (5-10%), channel catfish (1.5%).

S_{IIb} - Survival of Age II in CRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRI component is 0.01. Predation of juvenile humpback chub by other fish species is described by Valdez and Ryel (1995); brown trout (10.4%), rainbow trout (5-10%), channel catfish (1.5%).

S_{IIIb} - Survival of Age III in CRI.

The survival of Age III+ or adults in the CRI component is 0.755 (95% C.I. = 0.627-0.896).

S_{nb} - Survival of Age n in CRI.

The survival of Age n or adults in the CRI component is 0.755 (95% C.I. = 0.627-0.896).

M_{lb} - Movement of Larvae From CRI to CRD.

Movement of larvae from the CRI component to the CRD component is unknown, but is probably insignificant considering the susceptibility of humpback chub larvae to cold water temperature.

M_{0b} - Movement of Age 0 From CRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRI component to the CRD component in 1991, 1992, and 1993 were 246,000; 738,000; and 3,920,000, respectively.

M_{Ib} - Movement of Age I From CRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRI component to the CRD component in 1991, 1992, and 1993 were 246,000; 738,000; and 3,920,000, respectively.

M_{IIb} - Movement of Age II From CRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRI component to the CRD component in 1991, 1992, and 1993 were 246,000; 738,000; and 3,920,000, respectively.

M_{IIIb} - Movement of Age III From CRI to CRD.

Of 1,360 uniquely PIT-tagged humpback chub (Age III+) captured and released in the CRI component from October 1990 through November 1993, a total of 356 were recaptured, but only 2 fish had moved from the CRI component to the CRD component for a movement rate of 2/356 = 0.006.

M_{nb} - Movement of Age n From CRI to CRD.

Of 1,360 uniquely PIT-tagged humpback chub (Age III+) captured and released in the CRI component from October 1990 through November 1993, a total of 356 were recaptured, but only 2 fish had moved from the CRI component to the CRD component for a movement rate of 2/356 = 0.006.

M_{IIcb} - Movement of Age II From CRD to CRI.

Movement of Age II from the CRD component to the CRI component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which reduce the swimming ability of the fish (Bulkley et al. 1982).

M_{IIIcb} - Movement of Age III From CRD to CRI.

Movement of Age III from the CRD component to the CRI component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which could reduce the swimming ability of the fish (Bulkley et al. 1982).

M_{ncb} - Movement of Age n From CRD to CRI.

Movement of Age n from the CRD component to the CRI component is unknown, but expected to be insignificant because of swift water currents and constant cold water temperatures which could reduce the swimming ability of the fish (Bulkley et al. 1982).

COMPONENT C: COLORADO RIVER DOWNSTREAM (CRD)

State Variables

Eggs - No. Eggs in CRD.

The number of eggs potentially deposited on an annual basis by humpback chub in the Colorado River downstream of the LCR is probably low. The majority of adults of the CRD component may not attempt to spawn because of constant cold temperatures, i.e., 8-16°C. The total number of adults in the CRD component is about 175 with about 88 females. At an average fecundity of 2,500 eggs, total number of eggs is about 220,000.

Larvae - No. Larvae in CRD.

The number of larval humpback chub originating from the Colorado River downstream of the LCR is probably low because of limited spawning success. The majority of larvae in this component are probably immigrated from the LCR component, but these numbers are probably low because of cold temperatures and numerous predators.

Age 0 - No. Fish <1 Year Old in CRD.

The number of Age 0 humpback chub originating from the Colorado River downstream of the LCR is probably low because of limited mainstem spawning success. The majority of Age 0 in this component are probably immigrated from the LCR component. Based on total captures, the number of Age 0 in this component is about 1,000 individuals.

Age I - No. Fish <2 Years Old in CRD.

The number of Age I humpback chub originating from the Colorado River downstream of the LCR is probably low because of limited mainstem spawning success. The majority of Age I in this component are probably immigrated from the LCR component. Based on total captures of juveniles (Age I and II), the number of juveniles in this component is about 300 individuals.

Age II - No. Fish <3 Years Old in CRD.

The number of Age II humpback chub originating from the Colorado River downstream of the LCR is probably low because of limited mainstem spawning success. The majority of Age II in this component are probably immigrated from the LCR component. Based on total captures of juveniles (Age I and II), the number of juveniles in this component is about 300 individuals.

Age III - No. Fish <4 Years Old in CRD.

The estimated number of adult humpback chub (Age III+) in this component in 1993 was about 175 individuals, with an approximately 50:50 sex ratio.

Age n - No. Fish Age IV+ in CRD.

The estimated number of adult humpback chub (Age III+) in this component in 1993 was about 175 individuals, with an approximately 50:50 sex ratio.

Rate Variables

F_{IIIc} - Fecundity of Age III Fish in CRD.

Relationship of fish body weight to number of eggs is expressed as:

$$EPF = -4443 + 14.53W \quad (R^2 = 0.96)$$

where: EPF = numbers of eggs per female, and
W = body weight of fish.

With humpback chub first reaching maturity at about 200 mm TL or about 85 g, the number of eggs per female cannot be computed from the above relationship, which was developed for larger fish. Hence, the minimum fecundity of 1,000 eggs per female is used for age III fish.

The length-weight relationship for female humpback chub in the Colorado River in Grand Canyon is:

$$\log_{10}W = 4.556 + 2.817 \log_{10}TL \; (R^2 = 0.82)$$

The logarithmic growth curve for humpback chub in the Colorado River in Grand Canyon is:

$$TL = 143.92 * \log_e(Age+1) + 1.0938 \; (R^2 = 0.99)$$

F_{nc} - Fecundity of Age n Fish in CRD.

Relationship of fish body weight to number of eggs for all sizes and ages is presented above for F_{IIId}.

S_{ec} - Survival of Eggs in CRD.

The survival of eggs in the Colorado River downstream of the LCR component is unknown. Survival of eggs in the mainstem is expected to be low since no survival of eggs is reported at a temperature of less than 12°C (Hamman 1982); the Colorado River downstream of the LCR varies from about 8°C to 16°C. Survival of eggs might occur in warm tributary inflows or during warmest water temperatures in late July and August.

S_{lc} - Survival of Larvae in CRD.

The survival of larvae in the Colorado River downstream of the LCR component is unknown, but is expected to be low because of cold water temperature and large numbers of predators; Hamman (1982) reported 15% survival of larvae reared at 12-13°C. While the majority of the larvae in this component probably immigrate from the LCR, a few may survive from local spawning, but numbers are expected to be insignificant to the overall population.

S_{0c} - Survival of Age 0 in CRD.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRD component is unknown, but could be the same as survival of juveniles in the CRI component, i.e., 0.01 per year.

S_{Ic} - Survival of Age I in CRD.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRD component is unknown, but could be the same as survival of juveniles in the CRI component, i.e., 0.01 per year.

S_{IIc} - Survival of Age II in CRD.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the CRD component is unknown, but could be the same as survival of juveniles in the CRI component, i.e., 0.01 per year.

S_{IIIc} - Survival of Age III in CRD.

The survival of Age III+ or adults in the CRD component is unknown, but is assumed to be the same as survival of adults in the CRI component, i.e., 0.755 (95% C.I. = 0.627-0.896).

S_{nc} - Survival of Age n in CRD.

The survival of Age III+ or adults in the CRD component is unknown, but is assumed to be the same as survival of adults in the CRI component, i.e., 0.755 (95% C.I. = 0.627-0.896).

M_{lc} - Movement of Larvae From CRD to Lake Mead.

Movement of larvae from the CRD component to Lake Mead is unknown, but is probably insignificant considering the small numbers of larvae likely to be in this component and the susceptibility of humpback chub larvae to cold water temperature.

M_{0c} - Movement of Age 0 From CRD to Lake Mead.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRD component to Lake Mead is unknown, and is not expected to be significant since no subadults and only one adult humpback chub were found between Diamond Creek (RM 226) and the Lake Mead inflow (RM 280) during 1992, 1993, and 1994 (Valdez and Ryel 1995, Valdez 1995).

M_{Ic} - Movement of Age I From CRD to Lake Mead.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRD component to Lake Mead is unknown, and is not expected to be significant since no subadults and only one adult humpback chub were found between Diamond Creek (RM 226) and the Lake Mead inflow (RM 280) during 1992, 1993, and 1994 (Valdez and Ryel 1995, Valdez 1995).

M_{IIc} - Movement of Age II From CRD to Lake Mead.

Estimated numbers of juveniles (Age 0, I, II) moving from the CRD component to Lake Mead is unknown, and is not expected to be significant since no subadults and only one adult humpback chub were found between Diamond Creek (RM 226) and the Lake Mead inflow (RM 280) during 1992, 1993, and 1994 (Valdez and Ryel 1995, Valdez 1995).

M_{IIIc} - Movement of Age III From CRD to Lake Mead.

Estimated numbers of adults (Age III+) moving from the CRD component to Lake Mead is unknown, and is not expected to be significant since no subadults and only one adult humpback chub were found between Diamond Creek (RM 226) and the Lake Mead inflow (RM 280) during 1992, 1993, and 1994 (Valdez and Ryel 1995, Valdez 1995).

M_{nc} - Movement of Age n From CRD to Lake Mead.

Estimated numbers of adults (Age III+) moving from the CRD component to Lake Mead is unknown, and is not expected to be significant since no subadults and only one adult humpback chub were found between Diamond Creek (RM 226) and the Lake Mead inflow (RM 280) during 1992, 1993, and 1994 (Valdez and Ryel 1995, Valdez 1995).

COMPONENT D: LITTLE COLORADO RIVER (LCR)

State Variables

Eggs - No. Eggs in LCR.

The number of eggs potentially deposited on an annual basis by humpback chub in the Little Colorado River would have to be based on the numbers of adults estimated to be resident in the LCR as well as the numbers of adults entering the LCR from the mainstem to spawn. The number of adults entering from the mainstem is about 3,480 with an approximately 50:50 sex ratio. The number of adults residing in the LCR is unknown.

Larvae - No. Larvae in LCR.

The number of larval humpback chub in the LCR is unknown. The numbers are expected to be high since this is the major spawning area for this population.

Age 0 - No. Fish <1 Year Old in CRI.

The number of Age 0 humpback chub in the LCR is unknown. The numbers are expected to be high since this is the major spawning area for this population.

Age I - No. Fish <2 Years Old in LCR.

The number of Age I humpback chub in the LCR is unknown. The numbers are expected to be high since this is the major spawning area for this population.

Age II - No. Fish <3 Years Old in LCR.

The number of Age II humpback chub in the LCR is unknown. The numbers are expected to be high since this is the major spawning area for this population.

Age III - No. Fish <4 Years Old in LCR.

The number of adult humpback chub (Age III+) in the LCR is unknown. Estimates by three areas of the LCR and by season were made by Douglas and Marsh (1996), and these estimates need to be converted to total numbers for a given time t.

Age n - No. Fish Age IV+ in LCR.

The number of adult humpback chub (Age III+) in the LCR is unknown. Estimates by three areas of the LCR and by season were made by Douglas and Marsh (1996), and these estimates need to be converted to total numbers for a given time t.

Rate Variables

F_{IIId} - Fecundity of Age III Fish in LCR.

The relationship of fish body weight to number of eggs for humpback chub in the LCR is unknown, but is assumed to be similar to that for the mainstem Colorado River, expressed as:

$$EPF = -4443 + 14.53W \ (R^2 = 0.96)$$

where: EPF = numbers of eggs per female, and
W = body weight of fish.

With humpback chub first reaching maturity at about 200 mm TL or about 85 g, the number of eggs per female cannot be computed from the above relationship, which was developed for larger fish. Hence, the minimum fecundity of 1,000 eggs per female is used for age III fish.

The length-weight relationship for female humpback chub in the LCR is unknown, but is assumed to be similar to that for the mainstem Colorado River, expressed as:

$$\log_{10}W = 4.556 + 2.817 \log_{10}TL \ (R^2 = 0.82)$$

The logarithmic growth curve for humpback chub in the LCR (Valdez and Ryel 1995), from data from Minckley (1992) is:

$$TL = 114.43 * \log_e(Age+1) + 14.921 \ (R^2 = 0.97)$$

F_{nd} - Fecundity of Age n Fish in LCR.

Relationship of fish body weight to number of eggs for all sizes and ages is presented above for F_{IIId}.

S_{ed} - Survival of Eggs in LCR.

The survival of eggs in the LCR component is unknown.

S_{ld} - Survival of Larvae in LCR.

The survival of larvae in the LCR component is unknown.

S_{0d} - Survival of Age 0 in LCR.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the LCR component is unknown.

S_{Id} - Survival of Age I in LCR.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the LCR component is unknown.

S_{IId} - Survival of Age II in LCR.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in the LCR component is unknown.

S_{IIId} - Survival of Age III in LCR.

Survival of adult humpback chub (Age III+) in the LCR component is unknown.

S_{nd} - Survival of Age n in LCR.

Survival of Age n or adults in the LCR component is unknown.

M_{ld} - Movement of Larvae From LCR to CRI.

Movement of larvae from the LCR component to the CRI component is unknown.

M_{0d} - Movement of Age 0 From LCR to CRI.

Estimated numbers of juveniles (Age 0, I, II) moving from the LCR component to the CRI component is unknown.

M_{Id} - Movement of Age I From LCR to CRI.

Estimated numbers of juveniles (Age 0, I, II) moving from the LCR component to the CRI component is unknown.

M_{IId} - Movement of Age II From LCR to CRI.

Estimated numbers of juveniles (Age 0, I, II) moving from the LCR component to the CRI component is unknown.

M_{IIId} - Movement of Age III From LCR to CRI.

Estimated numbers of adults (Age III+) moving from the LCR component to the CRI component is unknown.

M_{nd} - Movement of Age n From LCR to CRI.

Estimated numbers of adults (Age III+) moving from the LCR component to the CRI component is unknown.

M_{IIIbd} - Movement of Age III From CRI to LCR.

Most adults (Age III+) from the CRI component ascend into the LCR on an annual basis to spawn in that tributary. The estimated number of adults in the CRI component is 3,480 individuals with a 50:50 sex ratio.

M_{nbd} - Movement of Age n From CRI to LCR.

Most adults (Age III+) from the CRI component ascend into the LCR on an annual basis to spawn in that tributary. The estimated number of adults in the CRI component is 3,480 individuals with a 50:50 sex ratio.

COMPONENT E: TRIBUTARIES (TRI)

State Variables

Eggs - No. Eggs in TRI.

The number of eggs potentially deposited on an annual basis by humpback chub in tributaries other than the LCR is unknown. No resident populations are reported for tributaries in Grand Canyon other than the LCR (Mattes 1993, Otis 1994, Weiss 1993, Allan 1993).

Larvae - No. Larvae in TRI.

The number of larval humpback chub in the LCR is unknown. The numbers are expected to be low since very few larvae are reported from tributaries other than the LCR.

Age 0 - No. Fish <1 Year Old in TRI.

The number of Age 0 humpback chub in the TRI component is unknown. The numbers are expected to be very low since no spawning is reported from tributaries other than the LCR.

Age I - No. Fish <2 Years Old in TRI.

The number of Age I humpback chub in the TRI component is unknown. The numbers are expected to be very low since no spawning is reported from tributaries other than the LCR. Small numbers of juveniles reported from Shinumo Creek and Kanab Creek (Kubly 1990) may have been spawned in the respective tributary or originated from mainstem immigration to the warm tributaries.

Age II - No. Fish <3 Years Old in TRI.

The number of Age II humpback chub in the TRI component is unknown. The numbers are expected to be very low since no spawning is reported from tributaries other than the LCR. Small numbers of juveniles reported from Shinumo Creek and Kanab Creek (Kubly 1990) may have been spawned in the respective tributary or originated from mainstem immigration to the warm tributaries.

Age III - No. Fish <4 Years Old in TRI.

No adult humpback chub have been reported recently from tributaries above their respective inflows, other than the LCR (Mattes 1993, Otis 1994, Weiss 1993, Allan 1993).

Age n - No. Fish Age IV+ in TRI.

No adult humpback chub have been reported recently from tributaries above their respective inflows, other than the LCR (Mattes 1993, Otis 1994, Weiss 1993, Allan 1993).

Rate Variables

$F_{III\bullet}$ - Fecundity of Age III Fish in TRI.

The relationship of fish body weight to number of eggs for humpback chub in the tributaries of Grand Canyon is unknown, but is assumed to be similar to that for the mainstem Colorado River, expressed as:

$$EPF = -4443 + 14.53W \quad (R^2 = 0.96)$$

where: **EPF = numbers of eggs per female, and**
W = body weight of fish.

With humpback chub first reaching maturity at about 200 mm TL or about 85 g, the number of eggs per female cannot be computed from the above relationship, which was developed for larger fish. Hence, the minimum fecundity of 1,000 eggs per female is used for age III fish.

The length-weight relationship for female humpback chub in tributaries is unknown, but is assumed to be similar to that for the LCR, which is based on the mainstem Colorado River and expressed as:

$$\log_{10}W = 4.556 + 2.817 \log_{10}TL \ (R^2 = 0.82)$$

The logarithmic growth curve for humpback chub in the LCR (Valdez and Ryel 1995), from data from Minckley (1992) is as follows, and is assumed to be approximately the same for other tributaries:

$$TL = 114.43 * \log_e(Age+1) + 14.921 \ (R^2 = 0.97)$$

F_{ne} - Fecundity of Age n Fish in TRI.

Relationship of fish body weight to number of eggs for all sizes and ages is presented above for F_{IIIe}.

S_{ee} - Survival of Eggs in TRI.

The survival of eggs in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{le} - Survival of Larvae in TRI.

The survival of larvae in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{0e} - Survival of Age 0 in TRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{Ie} - Survival of Age I in TRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{IIe} - Survival of Age II in TRI.

Estimated annual survival of juvenile humpback chub (Age 0, I, II) in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{IIIe} - Survival of Age III in TRI.

Survival of adult humpback chub (Age III+) in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

S_{ne} - Survival of Age n in TRI.

Survival of Age n or adults in tributaries, other than the LCR is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

M_{le} - Movement of Larvae From TRI to CRD.

Movement of larvae from the TRI component to the CRD component is unknown, but is expected to be insignificant to the overall population in Grand Canyon.

M_{0e} - Movement of Age 0 From TRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the TRI component to the CRD component are unknown, but are expected to be insignificant to the overall population in Grand Canyon.

M_{Ie} - Movement of Age I From TRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the TRI component to the CRD component are unknown, but are expected to be insignificant to the overall population in Grand Canyon.

M_{IIe} - Movement of Age II From TRI to CRD.

Estimated numbers of juveniles (Age 0, I, II) moving from the TRI component to the CRD component are unknown, but are expected to be insignificant to the overall population in Grand Canyon.

M_{IIIe} - Movement of Age III From TRI to CRD.

Estimated numbers of adults (Age III+) moving from the TRI component to the CRD component are unknown, but none have been reported recently.

M_{ne} - Movement of Age n From TRI to CRD.

Estimated numbers of adults (Age III+) moving from the TRI component to the CRD component are unknown, but none have been reported recently.

M_{IIIce} - Movement of Age III From CRD to TRI.

Estimated numbers of adults (Age III+) moving from the CRD component to the TRI component are unknown, but are expected to be insignificant to the overall population in Grand Canyon.

M_{nce} - Movement of Age n From CRD to TRI.

Estimated numbers of adults (Age III+) moving from the CRD component to the TRI component are unknown, but are expected to be insignificant to the overall population in Grand Canyon.

CHAPTER 6 - THE POPULATION MODEL

A population model will be developed as a series or family of mathematical and logical relationships that will describe the conceptual model presented in Chapter 3. These relationships will be primarily age-structured models, with model formulation that meet each of the program objectives.

This family of relationships cannot be developed at this time because of the unavailability of data or described relationships for the LCR. Information from the LCR are vital to this model development since that component is the center of this population of humpback chub in Grand Canyon, i.e., most of the fish reside or spawn in the LCR and contribute to most of the recruitment of the canyon.

Hence, instead of devoting this chapter to model development, we discuss the types of models available and best suited to this program, model applications, and the concept of population viability. We have proceeded only to this point in model development because to proceed any further by employing inferences and assumptions on existing data would be a wasted effort.

TYPES OF MODELS

The formalization of conceptual models into mathematical expressions generally produces one of two basic types of fish population models:

- Simple birth-death models, and
- Age- and stage-structured models.

Both can be structured as deterministic (non-random) or stochastic (random components) models and can include the effects of density on various rates. Each of these model types is evaluated for its applicability in modelling humpback chub population dynamics to meet the stated objectives.

Simple Birth-Death Models

These models characterize the rate of change in population size in terms of average population birth and death rates (Renshaw 1990). The population can be characterized by unbounded growth or decline, or its growth rate can be limited by the feedback of density--as in the familiar logistic population growth model. These models are characterized by the lack of any age structure, and assume average rates of reproduction and survival across the entire population. Time lags are often built into these models in an attempt to account for lengthy maturation times (Goel et al. 1971, Braddock and Van Den Driessche 1981). These models are most applicable when all life stages of a species are subject to similar ecological pressures.

The uses of birth-death models are varied, and may include characterization of population growth or decline of many organisms (Goel et al. 1971, Starfield and Bleloch 1986, Renshaw 1990), or to calculation of persistence times in viability analyses (Leigh 1981, Belovshy 1987, Allen et al. 1992). One significant use of these models in fisheries is development of catch-based models for harvested fish populations (Gulland 1983, Schnute 1985). Stock-recruitment or surplus-yield models have been significant components of fisheries management based on the assumption of density-limiting population growth (e.g., Ricker 1973, Getz 1980, 1984, Gatto and Rinaldi 1980, Walter 1981, Fowler et al. 1982, Policansky 1986).

Use of simple birth-death models is limited for characterizing humpback chub populations in Grand Canyon. The major drawback is the inability to separate life stages because of our inability to accurately age the fish. These life stages may behave differently and are subject to different ecological needs and environmental conditions. In addition, the large body of catch-based models, which are applied to harvested fish populations, has limited value in assessing the humpback chub population. However, these birth-death models may be used to assess dynamics of specific age categories of chubs (i.e., eggs, larvae, YOY, juveniles, adults), and in a general way, to assess population persistence.

Age- and Stage-Structured Models

Age- and stage-structured models have their foundations in the work of Bernardelli (1941), Lewis (1942) and Leslie (1945). These models are based on division of a population into distinct age, size, or stage classes, and allow for assessment of population dynamics assuming different reproductive and survival rates for each class. They were developed for populations with age- or stage-specific differences between classes.

The simplest form of these models are projection models or Leslie matrices used to calculate population size in each of m age groups in time t+1 from the population in time t (Fig. 7). The square projection matrix A contains rates of reproduction and survival for each of the m age groups. The model structure has been modified slightly to account for stage-based populations-- those whose structure is more readily assessed by size or developmental stage instead of age (Lefkovitch 1965, Caswell 1982, 1988). This may be the most appropriate structure for humpback chub in Grand Canyon because of our inability to age the fish.

These models have been refined substantially since their original formulation (Usher 1972). The application of these models has assumed that rates in the projection matrix are stochastic in nature (Pollard 1966, Getz and Haight 1989), with functions of density (Leslie 1948, 1959, Smith 1973, Pennycuick 1969, Fowler 1987), and functions of environmental factors (Horst 1977, Vaughan 1981). The flexibility of this modelling structure is in the ability to make each element of the projection matrix a function of any factor affecting it.

Age- and stage-based models have been used for a variety of organisms, including insects (Lefkovich 1965, Horst 1976), large mammals (Fowler and Smith 1973, Ryel 1980, Fowler 1981), and trees and herbaceous species (Hartshorn 1975, Meagher 1982, Law 1983). Fish populations have also been evaluated with these models to assess harvest yield (Walters 1969, Jensen 1974, Quinn 1981, Law and Grey 1988), to quantify effects of environmental factors (Horst 1977, Vaughan 1981), to estimate life history parameters (Vaughan and Saila 1976, Van Winkle et al. 1978), and to evaluate the significance of changes in life history on population growth rate (Caswell et al. 1984).

The age-structured model formulation would be the most useful in a modelling effort of humpback chub in Grand Canyon. The model format readily adapts to a conceptual model framework, and past and present studies will provide initial estimates of many of the model parameters. Environmental and density-dependent effects on various parameters can readily be incorporated into the model structure.

A complete model formulation for humpback chub in Grand Canyon--including parameter estimation of all the state and rate variables--is unlikely. Instead, formulations will be based on needs, objectives and to some extent on available data. Thus, a general formulation of the population used in viability or sensitivity analyses, may contain much of the structure included in a conceptual model, while a much reduced formulation may be used to estimate parameter values, or assess certain monitoring data where only a segment of the population is of interest.

MODEL APPLICATIONS

Applications of a population model are based on the objectives outlined for the GCES integration phase and long-term monitoring. Four general applications are identified for a population model of humpback chub in Grand Canyon:

1. Assist integration phase of GCES program,
2. Help evaluate management alternatives,
3. Help guide and interpret long-term monitoring, and
4. Help determine population viability.

These applications have not been identified as specific program elements because implementation of the population model for these and other applications will depend on model suitability and appropriateness for various program objectives, such as long-term monitoring. Similarly, a population viability analysis may or may not be appropriate or necessary, depending on the objectives of recovery program elements for humpback chub in Grand Canyon.

Assist Integration Phase of GCES Program

The conceptual model (see Chapter 3) provides the basis for an integrated understanding of humpback chub populations in the Grand Canyon. With this as a framework, a more complete picture of the biology and ecology of the species can be developed. Achieving this understanding requires the integration of information from all studies in Grand Canyon.

Model simulations can be used to address a variety of biological and ecological questions. These range from parameter evaluation and estimation to understanding the relationship between the population components. Additionally energetics aspects may be incorporated into the modelling effort if necessary to evaluate the effects of other trophic levels on chubs.

Ideally, data collected by various investigators should be analyzed by the respective scientists and made available as logical or mathematical relationships for identified state and rate variables of the population. Analyses and presentation of data by respective scientists are important to insure proper interpretation and use of those data incorporated into the modeling program.

Alternatively, raw data sets can be procured and used to develop the necessary relationships, but this process involves the risk of misuse of data sets, erroneous data partitioning, or data misinterpretation by a scientist unfamiliar with data collection objectives and methodologies. This use of data should be strengthened through close collaboration with investigators responsible for the original sampling design and data collection.

Evaluate Management Alternatives

As objectives of the GCES integration program are developed, applications of the population model will be identified to assist in meeting these objectives. These applications may involve assessing population dynamics and energetics effects of management alternatives, or assessing the dynamics of a second population. Specific modelling efforts will be developed when these objectives are formalized.

Guide and Interpret Long-term Monitoring

A long-term monitoring plan has been identified as an important aspect of adaptive management of Glen Canyon Dam. This population model could provide guidance for the plan, and aid in data interpretation. Monitoring activities will realistically be limited to parameters that are readily measurable, but not likely to totally portray population trajectory. Population modelling will provide one way to interrelate monitoring parameters with population status.

The combined endeavor of linking the modelling effort with the monitoring program, will provide a better assessment of population status and the means to modify the monitoring program, as well as identify areas needed for further research. This will be particularly useful when monitoring results do not fit expected model outputs, based on the present level of understanding of the population. Model formulations can be used to identify important measurable parameters, and to compare these with field validation data from long-term monitoring.

Population Viability

The analysis of species viability--or vulnerability to extinction--is rooted in the theory of island biography (MacArthur and Wilson 1963,1967), which contends that persistence of plant and animal species is related to island size. This theory became the basis for later work in defining refuge sizes (Diamond 1976, Diamond and May 1981, Soulé 1987). The probability of species persistence has been assessed for whole systems (Forman et al. 1976, Lovejoy 1980), as well as individual populations (Frankel and Soulé 1981, Shaffer 1981). Persistence of whole systems and individual populations are generally interrelated, and key species are sometimes used to assess the viability of whole systems (Frankel and Soulé 1981, Soulé and Simberloff 1986). Population viability could be used to assess the probable success of a second spawning population of humpback chub in Grand Canyon, as well as its effects on the existing population.

The vulnerability of a population is often expressed as the minimum viable population (Soulé 1987) that would have a high probability of surviving for a long period of time, e.g., a 95% probability that the population survives for 1000 years (Allen et al. 1992). Because species have different life history strategies, the minimum viable population size, and number and sizes of refuges is not easily generalized (Simberloff and Abele 1976, 1982, Soulé 1987).

Shaffer (1981) listed four sources of uncertainty that affect population viability:

- Demographic uncertainty,
- Environmental uncertainty,
- Natural catastrophes, and
- Genetic uncertainty.

Demographic uncertainty of humpback chub would result from random changes in survival, recruitment, and population distribution. Environmental uncertainty would result from changes in food supply, populations of competing or predatory fishes, parasite infestation, and water flow regimes from Glen Canyon Dam and the LCR (as flows affect water temperature, turbidity, and volume). Catastrophes affecting chub populations may include the release of toxic chemicals into the river system, introduction of a deadly disease or debilitating parasite, and major storm events that cause significant habitat changes. Genetic uncertainties result from changes in gene pool caused by genetic drift, and inbreeding that may affect reproductive or survival rates.

Environmental (Allen et al. 1992, Shaffer 1987) and demographic uncertainties--as related to population distribution and connectivity (Gilpin 1987)--are the most likely factors affecting the persistence of humpback chub in Grand Canyon, although catastrophic uncertainty can not be discounted. Modelling efforts to assess population viability should include investigating the effects of demographic and environmental uncertainties, as well effects of catastrophic events. Genetic uncertainty is unlikely to affect the present humpback chub population in Grand Canyon, because of the absence of congeneric species (i.e., roundtail chub, Gila robusta, and bonytail, Gila elegans), and because present population size likely exceeds that considered necessary for maintaining genetic diversity (Frankel and Soulé 1981, Franklin 1980).

RECOMMENDATIONS

1. Familiarize Grand Canyon researchers with this modelling program by providing this report.

2. Solicit input from Grand Canyon researchers for refinement of a conceptual population model.

3. Request data and mathematical and logical relationships from Grand Canyon researchers for important state and rate variables.

4. Use an age- or stage-based population model structure in modelling efforts on humpback chub.

5. Define objectives for the GCES integration program and identify where population modelling will be necessary and beneficial.

6. Integrate the modelling effort to help determine future data needs, core research needs, and as guidance for long-term monitoring.

7. Conduct a viability analysis for humpback chub in Grand Canyon after Program Elements I-V are completed. Include in this analysis, the effects of different environmental changes and perturbations, and the significance of adding a second spawning population.

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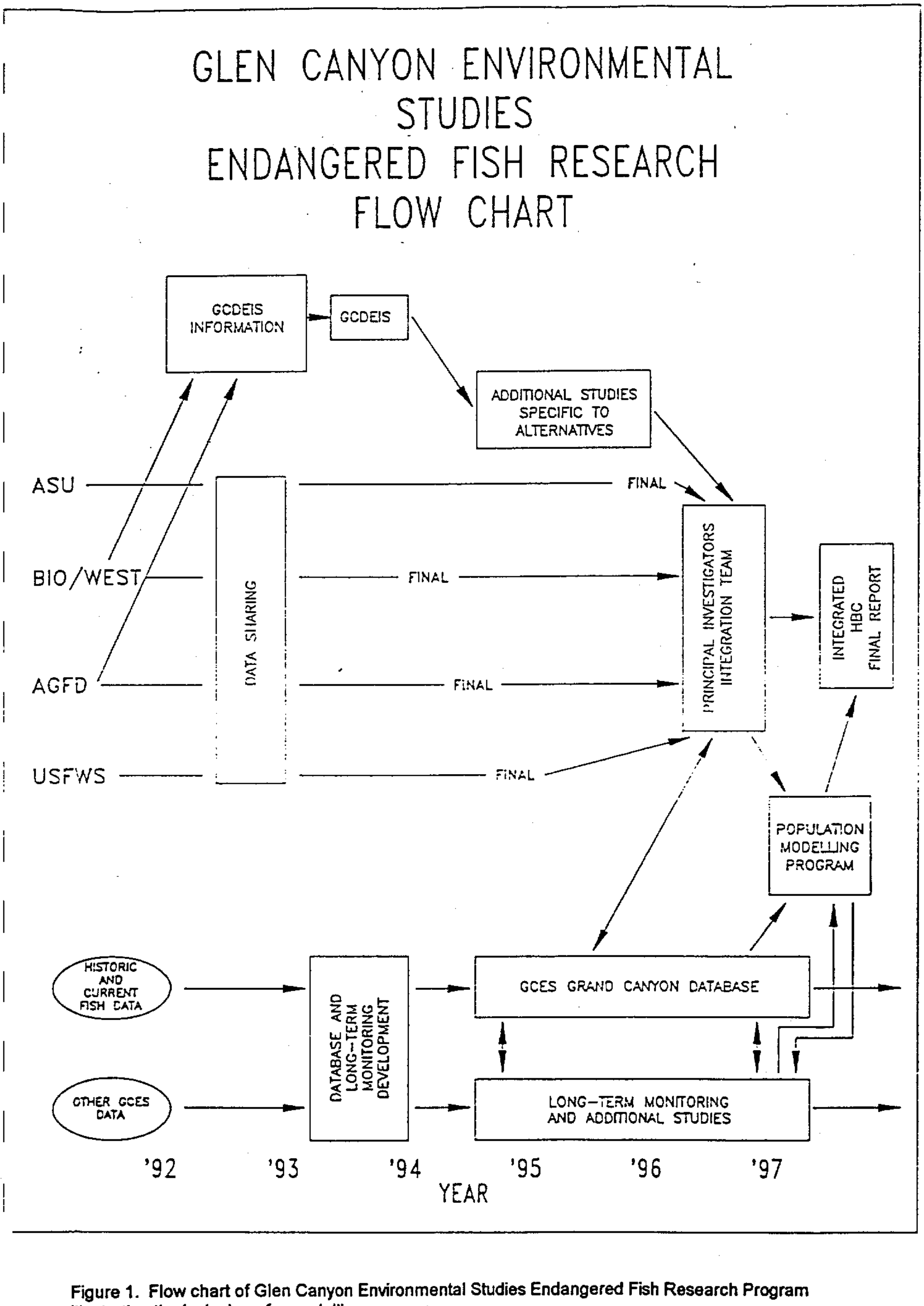

Figure 1. Flow chart of Glen Canyon Environmental Studies Endangered Fish Research Program illustrating the inclusion of a modelling program.

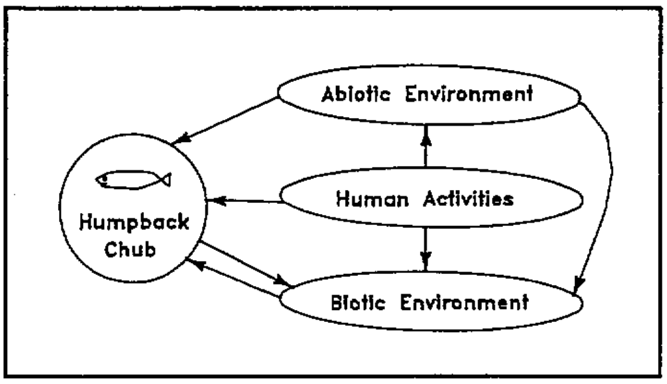

Figure 2

Figure 2. Conceptual model for humpback chub population showing abiotic, biotic and man–influenced effects.

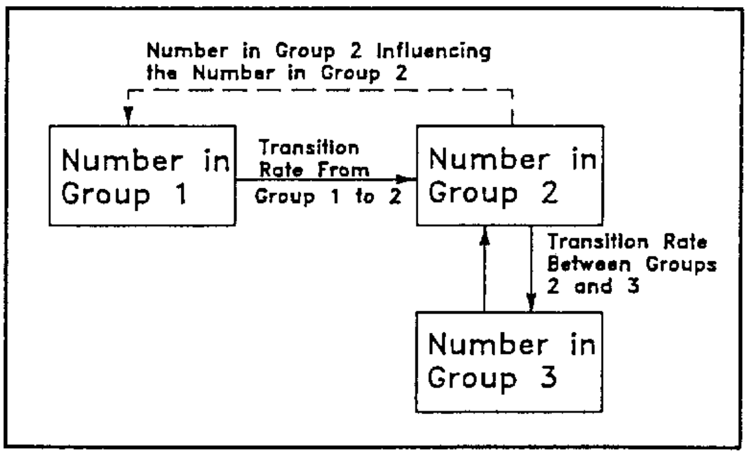

Figure 3

Figure 3. Population model for species with distinct groups showing transition rates (solid line) and influences (dashed line) between groups.

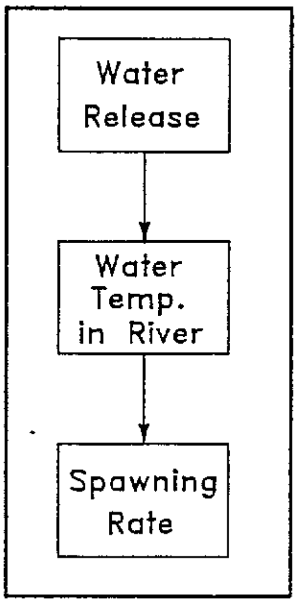

Figure 4a

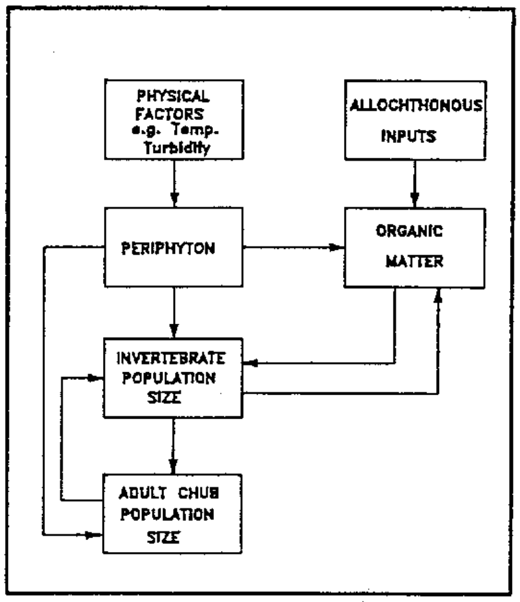

Figure 4b

Figure 4. (a) Example of direct effect of physical factor on population rate showing the hypothesized effect of present water release on humpback chub spawning in the mainstem Colorado River in Grand Canyon; (b) Example of one feedback interaction between components using a simplified trophic structure for humpback chub in Grand Canyon.

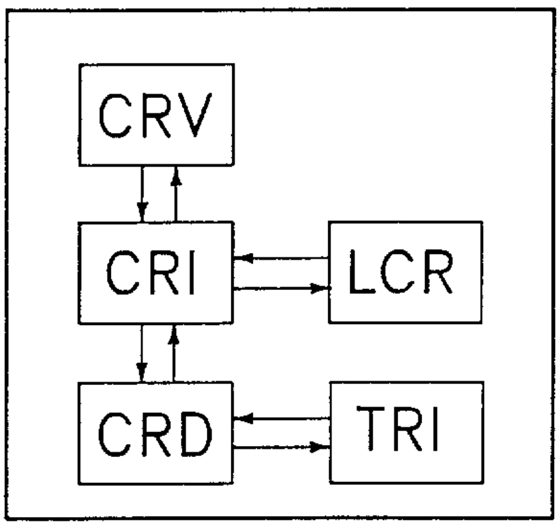

Figure 5

Figure 5. Basic linkages between the five identified ~~subpopulations~~ components of the humpback chub population in Grand Canyon.

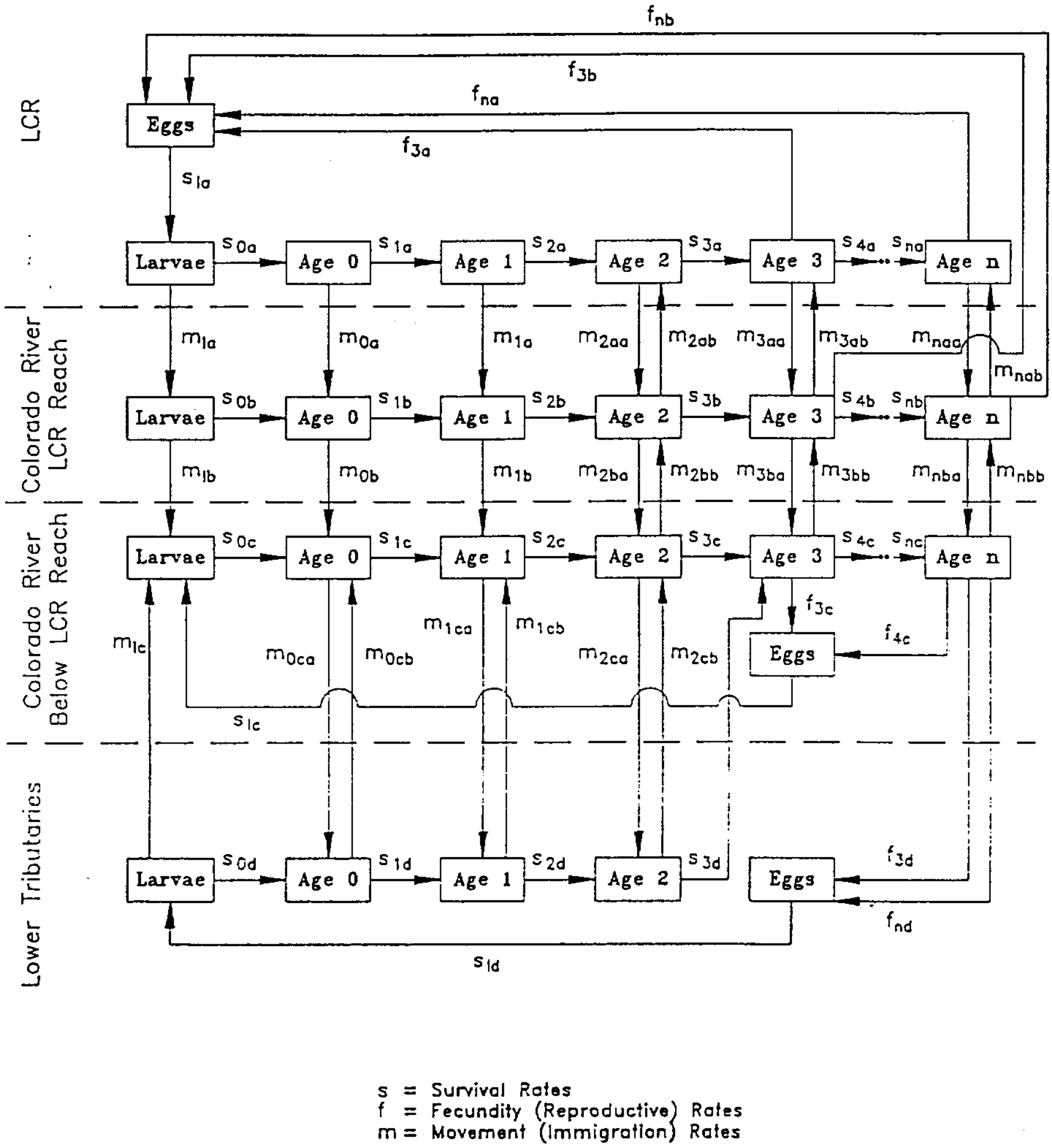

Figure 6. Conceptual model of humpback chub population in Grand Canyon.

$$
\begin{bmatrix}
f_1 & f_2 & \cdots & f_m \\
p_1 & 0 & \cdots & 0 \\
\vdots & p_2 & & \vdots \\
 & & \ddots & \\
0 & \cdots & p_{m-1} & 0
\end{bmatrix}
\begin{bmatrix}
n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{m,t}
\end{bmatrix}
=
\begin{bmatrix}
n_{1,t+1} \\ n_{2,t+1} \\ \vdots \\ n_{m,t+1}
\end{bmatrix}
$$

$$A \qquad N_t \qquad N_{t+1}$$

Figure 7. Projection matrix model for calculating the population of a species at time **t+1** (**N_{t+1}**) from the population at time **t** (**N_t**) using the projection matrix **A** (from Fowler and Ryel 1978).

APPENDIX A

Population Estimation of Adult Humpback Chubs in Mainstem Colorado River, Grand Canyon, Arizona

APPENDIX A - Population Estimation of Adult Humpback Chubs in Mainstem Colorado River, Grand Canyon, Arizona

INTRODUCTION

Population estimates of adult humpback chub in Grand Canyon were made using both open and closed population estimators. Estimates wre made for adults in six distinct aggregations within the mainstem Colorado River from data collected October 1990 to November 1993. Survival estimates for adult chubs in the Little Colorado River Inflow (LCRI) aggregation were also made using open population models.

METHODS

Population Estimates - Adult Humpback Chub

Numbers of adult humpback chub (TL≥200 mm) in six distinct aggregations in the mainstem Colorado River were estimated. Eleven estimators in two classes (open and closed population) were used for estimating numbers of adults in the LCR aggregation. Fewer population estimators were used for the other aggregations as numbers of recaptures were much lower.

Adult humpback chub were captured with nets or electrofishing,marked (with PIT tags) and released in 32 monthly sampling trips October 1990-November 1993. Sampling was not conducted in December 1990, August, October and December 1991, and October and December 1992. Radio-contact information on chubs from radio telemetry was not used as these 'captures' are not from methods which sample all adult chubs. Only chubs captured by B/W personnel were considered in these population estimates. It is important to note that capturing adult humpback chub for population estimation was not a high priority (distributional and radio-tagging studies were highest priority), and capture-recapture data did not reflect an optimal sampling design.

Closed Population Models

Closed population models are used to estimate the size of populations where there is no mortality, recruitment, immigration or emigration, and population size remains constant during the sampling period. No animal population is permanently closed as mortality, recruitment, emigration and/or immigration will eventually occur, but the sampling period can be often be chosen to minimize the influence of these factors (White et al. 1982). Assumptions associated with models for estimating the size of closed populations are outlined by Seber (1982) and Otis et al. (1978).

Familiar estimators for population size of closed populations are the Lincoln-Peterson index (Le Cren 1965), and its extension the Schnabel estimator (Schnabel 1938). More recently, Otis et al. (1978) has developed a framework of models for estimating the size of closed populations under variations in capture probabilities. These models, while assuming demographic closure, permit variation in capture probabilities due to time, behavioral response to sampling, and individual heterogeneity.

Estimators presented by Otis et al. (1978) for each model emphasize the use of maximum likelihood estimators (MLE) as the most desirable formulation. The following is a brief overview of these models and the estimators used in this study to estimate the population of adult humpback chub in the mainstem Colorado River in Grand Canyon. The reader is referred to the cited references for specific equations for each estimator of population size and associated variance. The comprehensive computer program CAPTURE (Otis et al. 1978, White et al. 1982, and Rexstad and Burnham 1991) calculates estimates for all of the following estimators except Schnabel M_t, many of which require iterative methods to solve for N.

Model M_o This model assumes constant capture probabilities at each sampling period and for all individuals. The MLE's of population size (N) and capture probability (p) for this model are derived in Otis et al. (1978:105).

Model M_t This model assumes that all individuals of the population have the same probability of capture, but that the capture probability may change from one sampling period to the next. Such changes in capture probability may result from different sampling effort, different sampling methods, seasonal or weather effects, or combinations of all factors. The MLE's of N and p_i (i=1, number of sample periods) for this model are derived in Otis et al. (1978:106), and variance of N, derived by Darroch (1958), is presented in Otis et al. (1978:107). This formulation is referred to in this study as the Darroch M_t estimator.

The Schnabel estimator is the original formulation for model M_t, but it is only an approximation of the MLE for N (Otis et al. 1978:51). This formulation is most appropriate when p_i are less than 0.1 at each sampling period, a condition met with this study (Seber 1982). Estimates using Schnabel estimator are presented in this study for comparative purposes since this is a commonly used estimator. Equations for this estimator of N and associated variance developed by Chapman (1952) are presented in Seber (1982:139).

A third estimator for model M_t was developed by Chao (1989). This formulation was developed to reduce bias in the Darroch M_t estimator of N that can occur when p_i is small. Equations for the bias-corrected Chao M_t estimator of N and associated variance are presented in Chao (1989:430).

Model M_h This model allows capture probabilities to vary by individual within the population. Such variation may result from different accessibility of individuals to traps or nets, or age and sex differences in behavior and activity (Otis et al. 1978). Use of estimators which do not assume such heterogeneity in capture probabilities, when such heterogeneity is prevalent, result in underestimation (negative bias) of the population size (e.g., Edwards and Eberhardt 1967, Carothers 1973). MLE estimators for model M_h can be developed only when the distribution of capture probabilities is known (unlikely). An alternative approach to estimating N, using the generalized 'jackknife' statistic (Gray and Schuncany 1972), was developed by Burnham and Overton (1979). Equations for jackknife estimates of N and associated variance are presented in Otis et al. (1978:109).

Chao (1987) developed another estimator for N under the assumptions of model M_h. This development was in response to the underestimation of N by the jackknife estimator when most individuals were captured only once or twice, the case with captured adult humpback chubs in this study. Equations for estimated N and variance are shown in Chao (1989:431-432).

Model M_b This model allows capture probabilities to change after the initial capture, although the probability of capture of all individuals are the same prior to initial capture. Otis et al. (1978) derives the MLE estimator of N which is nearly equivalent to the Zippin removal estimator (Zippin 1956, 1958). This estimator relies only on first capture records, and is most appropriate in removal sampling (physically removed or 'removed' through marking) where the number of newly captured individuals must decline over the study period. Equations for this estimator are contained in Otis et al. (1978:107-108).

Models M_{tb}, M_{th}, M_{bh}, M_{tbh} Combinations of models M_t, M_b, and M_h have been also been proposed. Estimators for all but M_{tbh} have been developed. Program CAPTURE contains an unpublished estimator for M_{tb} (referred to as Burnham M_{tb}) where the probability of recapture (r) is related to the probability of initial capture (c) as follows: $c=p^{1/\theta}$ (Rexstad and Burnham). An iterative procedure is used to find the MLE's of N, c and θ.

Chao (1992:205-207) proposed an estimators of N for M_{th} based on a nonparametric approach. The bias-corrected estimator N_3 in Chao (1992) was used in this study.

Estimators for model M_{bh} are presented in Otis et al. (1978:112-113) and Pollick and Otto (1983). As with the Zippin estimator for model M_b, these estimators are best suited to removal experiments, requiring a decline in numbers of newly captured individuals over the course of the study.

Estimations In this study closed population estimates were made for adult humpback chubs captured within a single calender-year (1991, 1992 and 1993) where additions and losses to the population were assumed to have minimal effect on the population estimate. Each monthly sampling trip was considered to be a sampling period. Sample periods were 9 in 1991, 10 in 1992 and 11 in 1993. Program CAPTURE was used to calculate most of the parameter estimates except for the Schnabel M_t estimator. A FORTRAN program was created to make calculations to estimate parameters with the Schnabel M_t estimator using equations from Seber (1982:139). The assumption of population closure for the LCR aggregation for each year was supported by statistical tests for closure performed by CAPTURE. Closure could not be rejected for any of the three years of capture data. Meaningful closure tests could not be performed on the data from the other aggregations due to minimal capture data.

Model Selection Program CAPTURE contains an extensive routine to aid in the selection of the best closed population model for the data collected. Statistical comparisons between models and goodness-of-fit tests of individual models are made using the supplied capture data. When capture probabilities are low, however, the effectiveness of this selection routine is limited (Menkens and Anderson 1988, Pollock et al. 1990). When applied to much of the capture-recapture data from this study, CAPTURE was often unable to perform one or more of the tests due to insufficient data. This problem combined with the ineffectiveness of the selection routine with low capture probabilities resulted in very limited use of these test results in this study. Instead, estimates produced by estimators robust to low capture probabilities, Chao M_h and M_t (Chao 1989) were considered to be the most reliable. However, estimates and confidence intervals of N produced with these models were compared with those of the other estimators to provide a more complete evaluation of the estimated N.

Confidence Intervals Confidence intervals around individual estimates of N were calculated as suggested by Burnham et al. (1987). This method is based upon the assumption that the number of individuals in the population not captured is log-normally distributed. Chao (1989:429) and Rexstad and Burnham (1991:19) provide the necessary equations for the 95% confidence intervals about N. Confidence intervals of the mean of two or more estimates of N were calculated assuming the variance of the means is a linear combination of the variances of each mean (Blum and Rosenblatt 1972).

Open Population Models

Demographically open population models provide estimates of population size without the constraints of assuming no additions or losses to the population. Pollock et al. (1990) provides a series of estimators for open populations, within the framework the general Jolly-Seber model (Jolly 1965, Seber 1965). Estimates are made of the population size (N_i), survival rate (ϕ_i) number of additions to the population (B_i), and capture probability (p_i) at each sampling period *i*. While these open models are not subject to the closure restriction of closed population models, estimation of additional parameters (i.e., ϕ, B and N at each time period), often result in less precise estimates.

Models A, A', B, C, D MLE's of five related models are presented by Pollock et al. (1990). Model A assumes time specific survival (ϕ_i) and probability of capture (p_i). Model A' is the same as model A but assumes no immigration (B = 0). Model B assumes constant probability of capture (p) and time specific survival (ϕ_i). Model C assumes constant survival (ϕ), but time specific probability of capture (p_i). Model D assumes constant survival (ϕ) and constant probability of capture (p). All five models assume no differences in capture probability by individual or changes in capture probability after initial capture. Equations for MLE of models A and A' are contained in Pollock et al. (1990:20-21, 36). Jolly (1982:304-309) provides equations for MLE of models B, C and D.

Estimations The comprehensive computer program JOLLY was used to estimate parameters for models A, C and D in this study. Because insufficient data existed from each monthly sampling trip, sampling periods were combined into seasonal sampling periods to provide sufficient numbers of chubs captured to estimate N and ϕ. This resulted in 13 sampling periods between October 1990-November 1993. December-February was defined as the winter sampling period, March-May as the spring period, June-August as the summer period and September-November as the fall period.

Model Selection Program JOLLY (Pollock et al. 1990) provides parameter estimates and associated confidence intervals for models A, B, and D, as well as tow other related models. Goodness-of-fit tests and tests between models are conducted by JOLLY to aid in model selection. Estimators for the simplest model that fits the data are usually selected for parameter estimation.

Confidence Intervals Confidence intervals for N_i and ϕ_i were calculated by program JOLLY as ±1.96 times the standard error of the parameter. Confidence intervals of the mean of two or more estimates of N were calculated assuming the variance of the means is a linear combination of the variances of each mean (Blum and Rosenblatt 1972).

Survival Estimates - Adult Humpback Chub

Survival estimates of adult chubs were calculated in conjunction with N_i using estimators for the open population models A, B and D presented in the previous section. Brownie et al. (1985) provide estimators of survival from band recovery data which could also be applied to estimating survival of adult chubs. They show, however, that estimators of survival derived from their methods are equivalent to those of the Jolly-Seber model estimators discussed in the preceding section (Brownie et al. 1985:170-175).

RESULTS

Population Estimates - Adult Humpback Chub

LCR Aggregation

Closed Population Estimators Estimates of total population (N) for adult humpback chub (TL≥200 mm) in the LCR aggregation for 1991, 1992 and 1993 using 11 estimators for 7 closed population models, and summary statistics in Table 1, are shown in Table 2. Population estimates for estimators M_0, Darroch M_t, Schnabel M_t, Chao M_t, Chao M_h, and Chao M_{th} are very similar for each year, and were not significantly different (z-test, $p>0.05$). The other five estimators produced estimates of N which were generally much lower and often significantly different than the first six (z-test, $p<0.05$). The Zippin M_b estimator failed to meet the necessary requirements for declining numbers of newly caught individuals in 1991 and 1992. The jackknife M_h estimator produced intermediate estimates of N in 1991 and 1992. Chao (1987, 1989) and Pollock and Otto (1983) indicate that the jackknife M_h estimator can severely underestimate N when the probability of capture of many individuals is low, and when many individuals are captured only once or twice. This was the situation with captures of adult chubs in the LCR aggregation (all other aggregations as well).

As discussed in METHODS, the program CAPTURE was not able to effectively select an appropriate model for estimation of N. However, the estimates of N under models M_b, M_{bh}, and M_{tb} are likely underestimates as during the course of the study, 1267 distinct fish were captured. In addition, the sampling of adult chubs did not effectively meet the requirements for a removal study (note failure of Zippin M_b estimator in 1991 and 1992), casting doubt on estimates produced under models M_b and M_{bh}. Finally, significant behavioral changes due to capture are not likely unless humpback chub can effectively sense nets and relate nets to the capture experience.

Estimates using models M_t and M_h and M_{th} are probably most appropriate (except jackknife M_h with its negative bias with sparse data) as sample intensity varied between trip based upon research objectives and study design (model M_t), and different capture probabilities between individual fish were very possible (model M_h). If both sources of heterogeneity in capture were significant, model M_{th} would be the most appropriate. However, similarities in estimates for models M_t, M_h and M_{th} do not suggest one model over another to best fit the data. The Chao M_h estimator suggested by Chao (1989) as robust to low capture probabilities (independent of underlying model M_t, M_h or M_{th}) consistently produced the highest estimation of N, although estimated N was less than 10% higher than the next highest estimate. Estimated N using Darroch M_t and the estimator under model M_0 were noticeably lower in 1992 suggesting that capture data from this year may have been more affected by heterogeneity in catchability than in the other two years. With the exception of these two estimators in 1992, the population estimates under models M_t, M_h and M_{th} were relatively constant (and not significantly different: z-test, $p>0.05$) 1991-1993.

Since estimates of N for the LCR aggregation were relatively constant from 1991-1993, the estimates were averaged for the three years (Table 2). Results of estimation under closed population models suggest a population of adult chubs in the LCR aggregation of 3000-3500, with 95% confidence intervals approximately $\pm$20% of estimated N.

Population size was also estimated using estimators for closed population model M_0, M_t, M_h, and M_{th} for all data October, 1990-November, 1993 (Table 2). These estimates of N were about 1000 chubs higher (significantly higher, z-test, $z=2.58$, $p=0.0049$) than the corresponding average of estimates for separate years. This higher total resulted from the violation of closure as the number of marked chubs was reduced by mortality, and sizable recruitment likely occurred. Disproportionately low numbers of recaptures related to inflated numbers of marked chubs would cause inflated estimates of N. This phenomenon was clearly seen with the Schnabel M_t estimator when the number of marked individuals was corrected by estimated mortality (see section on Adult survival). Estimated N for this period, correcting the number of marked fish for mortality, was 3035 (se(N)=171, 95% ci=2681-3465), nearly the same as the average of Schnabel M_t estimate of 2994 based on averages of individual years. (Statistical note: It is important to note that the estimated se(N) with mortality assumes the number of marked fish (M_i) was exact. This was not the case, however, as M_i has its own probability structure related to the probability of survival. Including such variability would increase the true se(N). See Seber (1982:139) for Schnabel M_t estimator for N). When mortality was considered in Schnabel M_t estimates of N for individual years 1991-1993, estimates ranged from 2570-2886 and averaged 2711. This mean was only 9.4% below the mean Schnabel M_t estimate of N assuming closure (2994), and well within the 95% confidence intervals of 2329-3660. This analysis clearly shows the importance of approximating closure when applying these estimators.

Open Model Estimators Seasonal population estimates from estimators for open population models A, B and D using summary statistics in Table 3 are shown in Table 4. Estimated N from all models were highly variable. This variability reflects the low numbers of fish sampled and recovered in each of the 13 sampling periods, and that N was estimated for each sampling period instead of a single estimate over an extended period as with estimators for closed population models. The mean N's calculated for each model, however, were not significantly different (z-tests, $p>0.05$) and ranged from 3080 for model A to 3192 for model D. These means were nearly identical to mean estimates of N estimated from close population estimators (z-tests, $p>0.05$), although the 95% confidence intervals were greater at ±25%. The similarity of this estimate and estimates for closed population models M_0, M_t, M_h (Chao estimator) and M_{th} strongly supports the validity of these estimates over estimates under assumptions of models M_b, M_{bh} and M_{tb}.

Tests of model goodness-of-fit tests performed by program JOLLY indicated that all models fit the data at the $p=0.05$ level (χ^2 test), but model D (constant capture probabilities and survival) failed to fit the data at $p=0.10$. Tests between models B and D, and between A and D showed significant differences (χ^2 test, $p\leq0.05$), indicating variability in capture probabilities between sampling periods, consistent with the variable sampling program. No significant differences were found between model A and B (χ^2 test, $p=0.20$), indicating model B was the simplest to fit the data, and that suggests survival was relatively constant over the course of the study (see section on adult survival).

MGG Aggregation

Estimates of total population (N) for adult humpback chub (TL≥200 mm) in the LCR aggregation for 1993 using 7 estimators for closed population models M_0, M_t, M_b and M_{th}, and summary statistics in Table 5, are shown in Table 6. Estimates were conducted on 1993 capture data as this was the only relatively complete annual dataset. All estimators provided similar and not significantly different (z-test, $p>0.05$) estimates, ranging from 89-103. The ranges of 95% confidence intervals place this estimate between 68-155, or 3-5% the estimated population size of the LCR aggregation (Tables 2, 4). Data was insufficient to use open population estimators.

Estimates were also calculated using all capture data for the MGG aggregation (Table 6). Estimates were 16-77% higher than for 1993. This higher estimate was likely the result mortality and recruitment (lack of population closure) as was the case with similar estimates for the LCR aggregation.

Other Aggregations

Population size was estimated for 4 other aggregations (Table 7) from limited capture-recapture data (Table 8). Three other aggregations did not have recaptures between sampling periods (all had 2 captures of a single chub within one sampling period, however), and estimations of N could not be made (Table 8). Only 5 estimators for 3 models were used as sufficient data did not exist to calculate estimates with other estimators. Estimates ranged from 4 adult chubs in the Pumpkin Springs area to roughly 50-60 in the 30-mile and Shinumo inflow aggregations. All aggregations had population estimates less than 2% of the LCR aggregation. Sufficient data did not exist to apply open population estimators to any of these aggregations.

Survival Estimates

Adults

Estimates of adult survival were made for the LCR aggregation using estimators for open population models A, B, and D (Table 4). These estimates were made simultaneously with estimates of N. Model B, the simplest model that fit the data produced a survival estimate of 0.932 (95% ci=0.890-0.973) between seasons which translates to annual survival of 0.755 (95% ci=0.627-0.896). As with seasonal estimates of population from model A, seasonal estimates of survival were also highly variable and often greater that 1.0. The estimated mean seasonal survival rate with model A was 0.979 (95% ci=0.861-1.097) translating to an annual survival rate of 0.919 (95% ci=0.5496-1.4482). The rate estimated for model A was higher than estimated for model B, but the estimated variance was higher and the 95% confidence intervals for model A included the entire 95% confidence intervals for model B. In addition, the geometric mean (perhaps more appropriate) of seasonal survival rates for model A was 0.931, nearly identical to that of model B.

The mean estimated number of recruits for model B of 238 chubs per season (Table 3) was very similar to the number lost based upon a seasonal survival rate of 0.932. With this survival rate, 204-238 chubs would be lost each season out of a population size of 3000-3500. On an annual basis, roughly 735-857 adult chubs (TL≥200 mm) could be lost from the population each year, and be replaced with a similar number of recruits.

Analysis of Adult Humpback Chub Length Frequency

Inherent to good population estimation is availability of most individuals to capture. If sampling gear or methods do not effectively capture a significant portion of the population, population estimates may be low. The length frequency distribution for adult humpback chubs in the LCR aggregation suggest that individuals of TL 200-300 mm may be under-sampled (Fig. 1, 6-2##). When length distributions were created for an assumed stable population using the estimated annual survival of 0.755 and the growth and age-length relationships in Fig. 6-11 and Table 6-8, the number of chubs captured with TL between 200-300 mm appear greatly underrepresented (Fig. 1). Even using survival rate equal to the upper 95% confidence interval (0.896), the numbers of chubs 200-300 mm seem undersampled, relative to the number with TL>300 mm.

Two possible explanations for the low number of captures of chubs TL=200-300 mm in the LCR aggregation in the mainstem were addressed: 1) sampling gear is unable to capture many of these chubs, either through inadequate mesh size of nets, or differential habitat distribution of chubs TL=200-300 mm which make sampling difficult; 2) much lower survival rates for chubs TL=200-300 mm than for chubs TL>300 mm. These hypotheses were assessed by calculating population and survival estimates for the individual groups TL=200-300 mm and TL>300 mm. Annual population estimates for 1991-1993 using estimators for closed population models for each group are contained in Tables 9 and 10. Mean population size for adults TL>300 mm ranged from 2172-2764 depending on the estimator (Table 9). Mean estimates for adults 200-300 mm were more variable (Table 10), and were influenced by highly variable estimates in 1992 when only one chub within this length class was recaptured. However, variability of estimates was much less between estimators for 1991 and 1993, when more chubs were recaptured (Table 10), and may more accurately reflect the size of this size class.

Whether estimates from 1992 were included or not, the estimated mean population of chubs TL=200-300 mm (Table 10) were much lower than expected by the stable size distributions shown in Fig. 1. The combined total population estimates by summing the two separate estimates (Table 11) were very similar (z-test, $p>0.05$) to estimates for this aggregation made using capture data for all chubs TL≥200 mm (Table 2). Exceptions (although not significant, z-test, $p>0.05$) were estimates using the Chao M_h and M_{th} estimators when the mean estimate 1991-1993 for chubs TL=200-300 was used. However, the estimates from these estimators was much closer to the other estimates when the 1992 estimates for chubs TL=200-300 mm were excluded (Table 11).

These results indicate that the number of chubs TL=200-300 were lower in the mainstem than chubs TL>300 mm, and much lower than would be expected by a stable size distribution. In addition, estimates of adult chubs in the LCR aggregation using capture data for all chubs TL≥200 mm appear adequate. Estimated mean capture probabilities from program CAPTURE, however, indicate that the chubs TL=200-300 had lower capture probabilities (mean prob. capture for Chao M_h=0.0094 per sampling period) than chubs TL>300 mm (mean prob. capture for Chao M_h=0.0143 per sampling period), but these differences did not significantly affect the population estimate or suggest a vast undersampling of chubs TL=200-300 mm.

Survival estimates were also calculated for chubs TL>300 mm to assess whether these chubs may have a much higher survival rate than smaller chubs. Unfortunately, similar estimates could not be calculated for chubs TL=200-300 mm because of insufficient data. Seasonal survival estimates for chubs TL>300 mm using estimators for open models were 0.974 for model A and 0.927 for model B, nearly identical (z-test, $p>0.05$) to those calculated for all chubs TL≥200 mm in the LCR aggregation (Table 4). Thus it does not appear that substantially lower survival rates for chubs TL=200-300 biased the survival estimates for chubs TL>300 mm. However, rates for these smaller chubs could be less, but not likely enough to cause the disparity in the length-frequency distribution (Fig. 1).

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Table 1. Capture-recapture statistics for adult humpback chub (TL≥200 mm) in LCR aggregation for closed model population estimation. n_i=total chubs captured in sample period **i**, M_i=total marked chubs in population at start of sampling period **i**, u_i=number of newly marked chubs in **i**, and f_i=number of chubs captured with frequency **i**. M_{t+1} refers to the total number of chubs captured during the year.

	1991					1992					1993				
i	Sample Period$_i$	n_i	M_i	u_i	f_i	Sample Period$_i$	n_i	M_i	u_i	f_i	Sample Period$_i$	n_i	M_i	u_i	f_i
1	Jan '91	75	0	75	402	Jan '92	24	0	24	312	Jan '93	103	0	103	519
2	Feb '91	3	75	2	28	Feb '92	6	24	6	15	Feb '93	74	103	72	45
3	Mar '91	111	77	108	0	Mar '92	43	30	43	1	Mar '93	47	175	44	2
4	Apr '91	7	185	7	0	Apr '92	38	73	37	0	Apr '93	28	219	26	0
5	May '91	26	192	25	0	May '92	41	110	39	0	May '93	70	245	64	0
6	Jun '91	35	217	34	0	Jun '92	36	149	36	0	Jun '93	64	309	60	0
7	Jul '91	69	251	67	0	Jul '92	65	185	61	0	Jul '93	73	369	68	0
8	Sep '91	88	318	76	0	Aug '92	5	246	5	0	Aug '93	38	437	30	0
9	Nov '91	44	394	36	0	Sep '92	35	251	30	0	Sep '93	52	467	41	0
10						Nov '92	52	281	47	0	Oct '93	36	508	3011	0
11											Nov '93	30	538	28	0
	M_{t+1}		430					328					566		

Table 2. Estimated total population (N) of adult (TL≥200 mm) humpback chub in the LCR aggregation using 11 estimators for closed populations models. Estimates are shown for individual years 1991, 1992, and 1993 (upper) and for all samples collected 1990-1993 (lower center). Mean estimates for the years 1991-1993 are also shown (lower left).

	1991			1992			1993		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	3191	570	2280-4550	2276	452	1571-3380	3331	444	2587-4347
Darroch M_t	2817	463	2066-3910	2151	364	1564-3013	3358	458	2593-4408
Schnabel M_t	2941	567	2051-4317	2819	706	1772-4624	3223	465	2454-4299
Chao M_t	2749	492	1967-3927	2986	732	1893-4843	3186	453	2438-4233
Chao M_h	3315	619	2334-4803	3572	917	2213-5913	3558	521	2699-4764
Jackknife M_h	1826	96	1650-2028	1582	93	1411-1779	2659	145	2393-2964
Chao M_{th}	3126	554	2239-4447	3362	868	2078-5586	3320	489	2515-4456
Zippin M_b	-- failed to run --			-- failed to run --			856	69	748-1025
Otis M_{bh}	566	69	483-777	1234	1457	426-8629	905	393	621-2632
Pollick M_{bh}	718	51	634-836	751	65	641-898	846	55	756-977
Burnham M_{tb}	922*	403	551-2435	708	361	407-2158	1058*	433	677-2737

	Mean 1991-1993			1990-1993		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	2933	284	2375-3490	4176	241	3740-4687
Darroch M_t	2775	249	2287-3263	4616	283	4105-5218
Schnabel M_t	2994	339	2329-3660	4111	269	3630-4689
Chao M_t	2974	331	2325-3622	4208	297	3681-4852
Chao M_h	3482	408	2682-4281	4564	327	3982-5269
Jackknife M_h	2022	66	1893-2152	4870	252	4408-5399
Chao M_{th}	3269	380	2524-4014	4681	300	4142-5321
Zippin M_b	-- not calculated --			-- not run --		
Otis M_{bh}	902	504	538-1889	-- not run --		
Pollick M_{bh}	772	33	706-837	-- not run --		
Burnham M_{tb}	896	231	538-1349	-- not run --		

Table 3. Capture-recapture statistics for adult humpback chub (TL≥200 mm) in LCR aggregation for open model population estimation. n_i=total chubs captured in sample period **i**, m_i=total marked chubs captured in sample period **i**, r_i=number of chubs released during sample period **i** that are captured again (**i**=1,12), z_i=number of chubs captured before **i**, not captured at **i**, and captured again later (**i**=2,12).

i	Sample Period	n_i	m_i	r_i	z_i
1	Oct-Nov, '90	83	0	25	--
2	Jan-Feb, '91	74	3	18	0
3	Mar-May, '91	138	5	29	22
4	Jun-Aug, '91	97	7	17	35
5	Sep-Nov, '91	110	17	22	57
6	Jan-Feb, '92	23	7	7	72
7	Mar-May, '92	110	10	18	69
8	Jun-Aug, '92	90	16	28	71
9	Sep-Nov, '92	69	18	12	81
10	Jan-Feb, '93	146	29	23	64
11	Mar-May, '93	118	25	13	62
12	Jun-Aug, '93	134	39	6	36
13	Sep-Nov, '93	75	42	--	--

Table 4. Estimated total population (N) and survival (ϕ) for adult humpback chub (TL≥200 mm) for LCR aggregation for 13 seasonal periods, 1991-1993 using estimators for open population models A, B, and D. The estimated number of chubs recruited into the adult population (B) and estimated total number of marked chubs at the beginning of each sample period (M) are also shown. Survival rates are expressed on a seasonal basis.

Model A

Period	N	se(N)	N: 95% c.i.	ϕ	se(ϕ)	ϕ: 95% c.i.	B	se(B)	M	se(M)
Jan-Feb, '91	1820	1116	74-4007	1.124	0.306	0.531-1.1718	2312	2122	93	25
Mar-May, '91	4152	2003	225-8079	1.011	0.269	0.484-1.539	-11	2557	173	38
Jun-Aug, '91	4456	1946	642-8270	1.076	0.298	0.492-1.659	-913	1316	340	85
Sep-Nov, '91	2377	733	939-3814	0.738	0.216	0.315-1.162	-382	510	334	73
Jan-Feb, '92	1108	518	92-2125	0.627	0.238	0.161-1.093	3473	1756	286	97
Mar-May, '92	4944	1890	1240-8647	1.327	0.524	0.301-2.354	-620	837	449	108
Jun-Aug, '92	1750	503	764-2735	0.479	0.128	0.228-0.731	-21	812	278	50
Sep-Nov, '92	2623	910	839-4406	1.511	0.468	0.594-2.428	985	660	566	158
Jan-Feb, '93	2924	790	1375-4472	0.739	0.244	0.262-1.216	744	858	498	107
Mar-May, '93	3670	1222	1275-6065	1.001	0.327	0.360-1.642	-92	935	663	187
Jun-Aug, '93	4062	1794	545-7579	1.132	0.547	0.060-2.204	--	--	934	392
Mean	3080	405	2286-3875	0.979	0.060	0.861-1.097	547	197	--	--
Geometric Mean				0.931						

Model B

Period	N	se(N)	N: 95% c.i.	B	se(B)	M	se(M)
Jan-Feb, '91	2014	1088	-119-4148	2197	2035	96	13
Mar-May, '91	4077	1728	690-7464	96	2150	161	16
Jun-Aug, '91	3887	1358	1224-6550	-1123	1416	270	19
Sep-Nov, '91	2477	526	1444-3509	-551	776	320	23
Jan-Feb, '92	1743	520	724-2762	3220	1574	387	29
Maf-May, '92	4849	1448	2011-7687	-1357	1548	387	35
Jun-Aug, '92	3140	717	1734-4546	-395	859	440	43
Sep-Nov, '92	2579	530	1540-3619	983	749	543	53
Jan-Feb, '93	3380	622	2161-4599	615	849	564	62
Mar-May, '93	3784	729	2355-5212	-298	770	680	74
Jun-Aug, '93	3231	530	2192-4271	-764	510	748	84
Sep-Nov, '93	2224	339	1560-2889	--	--	799	94
Mean	3116	352	2425-3806	238	100	--	--

ϕ = 0.932
se(ϕ) = 0.021
95% c.i. = 0.890-0.973

Table 4. (continued)

Model D

Period	N	se(N)	N: 95% c.i.	B	se(B)	M	se(M)
Jan-Feb, '91	2081	314	1466-2697	1891	414	86	14
Mar-May, '91	3866	509	2867-4865	-797	426	146	17
Jun-Aug, '91	2862	389	2099-3625	567	374	247	22
Sep-Nov, '91	3271	432	2424-4119	-2100	408	306	26
Jan-Feb, '92	973	154	671-1276	2397	390	353	31
Mar-May, '92	3354	441	2490-4218	-293	376	389	38
Jun-Aug, '92	2906	385	2151-3662	-365	337	480	48
Sep-Nov, '92	2490	328	1846-3134	2230	434	630	62
Jan-Feb, '93	4646	573	3522-5770	-429	438	710	78
Mar-May, '93	4032	501	3049-5014	695	413	850	100
Jun-Aug, '93	4667	567	3555-5779	-1291	427	1055	135
Sep-Nov, '93	3154	420	2331-3977	--	--	1132	192
Mean	3192	330	2544-3840	228	50	--	--

$\phi = 0.953$
$se(\phi) = 0.020$
95% c.i. = 0.914-0.991

Table 5. Capture-recapture statistics for adult humpback chub (TL≥200 mm) in MGG aggregation for closed model population estimation. n_i=total chubs captured in sample period **i**, M_i=total marked chubs in population at start of sampling period **i**, u_i=number of newly marked chubs in **i**, and f_i=number of chubs captured with frequency **i**. M_{t+1} refers to the total number of chubs captured during the year.

	1993					All Years				
i	Sample Period$_i$	n_i	M_i	u_i	f_i	Sample Period$_i$	n_i	M_i	u_i	f_i
1	Feb '93	5	0	5	37	Jul '91	4	0	4	51
2	Mar '93	10	5	9	16	Sep '91	5	4	5	14
3	Apr '93	13	14	9	3	May '92	3	9	3	6
4	May '93	14	23	11	0	Jul '92	19	12	17	4
5	Jun '93	6	34	5	0	Sep '92	6	29	3	0
6	Jul '93	11	39	7	0	Nov '92	4	32	3	1
7	Sep '93	16	46	8	0	Feb '93	5	35	3	0
8	Nov '93	3	54	2	0	Mar '93	10	38	4	0
9						Apr '93	13	42	6	0
10						May '93	14	48	10	0
11						Jun '93	6	58	3	0
12						Jul '93	11	61	5	0
13						Sep '93	16	66	8	0
14						Nov '93	3	74	2	0
	M_{t+1}		56					76		

Table 6. Estimated total population (N) of adult (TL≥200 mm) humpback chub in the MGG aggregation using 7 estimators for closed population models. Estimates are shown for 1993 and for all data collected 1990-1993.

	1993			All Years		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	99	15	77-140	115	12	97-145
Darroch M_t	96	14	76-135	112	11	96-141
Schnabel M_t	91	20	68-155	106	16	86-158
Chao M_t	89	15	70-132	152	31	112-238
Chao M_h	98	19	74-153	168	37	119-273
Jackknife M_h	103	15	82-141	182	29	138-256
Chao M_{th}	96	15	75-139	167	33	122-256

Table 7. Estimated total population (N) of adult (TL≥200 mm) humpback chubs in four aggregations in the mainstem Colorado River in Grand Canyon.

Estimator	A-1: 30-mile N	se(N)	95% c.i.	A-5: Shinumo N	se(N)	95% c.i.
M_0	57	25	31-141	60	25	33-145
Darroch M_t	47	18	28-107	58	23	33-135
Schnabel M_t	41	23	23-143	48	28	26-163
Chao M_t	37	12	24-81	45	16	27-102
Chao M_h	52	23	28-136	57	26	31-149

Estimator	A-8: Havasu N	se(N)	95% c.i.	A-9: Pumpkin Spring N	se(N)	95% c.i.
M_0	10	7	5-40	4	1	4-6
Darroch M_t	8	4	5-26	4	0	4-4
Schnabel M_t	6	7	5-52	4	3	4-16
Chao M_t	7	2	5-19	4	1	4-9
Chao M_h	13	12	5-70	5	2	4-16

Table 8. Capture-recapture statistics for adult humpback chub (TL≥200 mm) in LCR aggregation for closed model population estimation for 7 aggregation in mainstem Colorado River in Grand Canyon. n_i=total chubs captured in sample period **i**, M_i=total marked chubs in population at start of sampling period **i**, u_i=number of newly marked chubs in **i**, and f_i=number of chubs captured with frequency **i**. M_{t+1} refers to the total number of chubs captured during the year.

A-1: 30-mile

i	Sample Period$_i$	n_i	M_i	u_i	f_i
1	Mar '93	1	0	1	20
2	Apr '93	4	1	4	4
3	May '93	1	5	1	0
4	Sep '93	9	6	8	0
5	Oct '93	5	14	4	0
6	Nov '93	4	18	2	0
7					
8					
	M_{t+1}		20		

A-3: Lava-Hance

Sample Period$_i$	n_i	M_i	u_i	f_i
Sep '91	2	0	2	13
Nov '91	1	2	1	0
Jan '92	1	3	1	0
Jul '92	1	4	1	0
Sep '92	2	5	2	0
Jul '93	4	7	4	0
Aug '93	1	11	1	0
Oct '93	1	12	1	0
M_{t+1}		13		

A-4: Bright Angel

Sample Period$_i$	n_i	M_i	u_i	f_i
May '91	1	0	1	8
May '92	2	1	2	0
Jul '92	2	3	2	0
May '93	2	5	2	0
Jul '93	1	7	1	0
M_{t+1}		8		

A-5: Shinumo

i	Sample Period$_i$	n_i	M_i	u_i	f_i
1	Nov '90	1	0	1	21
2	Jan '91	2	1	2	4
3	Mar '91	1	3	0	0
4	May '91	3	3	3	0
5	Jul '91	5	6	5	0
6	Sep '91	1	11	1	0
7	May '92	3	12	2	0
8	May '93	2	14	2	0
9	Sep '93	5	16	5	0
10	Nov '93	2	21	0	0
	M_{t+1}		21		

A-6: Stephen Isle

Sample Period$_i$	n_i	M_i	u_i	f_i
Jul '91	1	0	1	15
Sep '91	1	1	1	0
Jul '92	9	2	9	0
Sep '92	2	11	2	0
Jul '93	2	13	2	0
M_{t+1}		15		

A-8: Havasu

Sample Period$_i$	n_i	M_i	u_i	f_i
May '91	3	0	3	5
May '92	1	3	1	1
May '93	1	4	0	0
Sep '93	1	4	1	0
M_{t+1}		5		

A-9: Pumpkin Spring

i	Sample Period$_i$	n_i	M_i	u_i	f_i
1	Nov '90	2	0	2	4
2	Jan '91	1	2	1	2
3	Mar '91	3	3	1	0
	M_{t+1}		4		

Table 9. Estimated total population size (N) of adult humpback chub in LCR aggregation with TL>300 mm. Annual estimates of N are shown for 1991, 1992 and 1993 (upper). Mean estimates are also shown for 1991-1993 (lower left).

	1991			1992			1993		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	1999	338	1458-2803	1607	342	1085-2456	2910	419	2218-3878
Darroch M_t	2434	470	1696-3575	2013	489	1283-3257	2962	442	2235-3989
Schnabel M_t	2332	487	1583-3537	1903	510	1166-3237	2356	382	1740-3261
Chao M_t	2181	419	1526-3202	2045	533	1266-3425	2815	435	2107-3833
Chao M_h	2637	531	1810-3935	2488	685	1496-4274	3167	505	2346-4351
Chao M_{th}	2491	476	1742-3644	2372	657	1423-4091	2967	477	2198-4093

	Mean 1991-1993		
Estimator	N	se(N)	95% c.i.
M_0	2172	213	1755-2589
Darroch M_t	2470	270	1940-2999
Schnabel M_t	2197	267	1673-2721
Chao M_t	2347	269	1820-2874
Chao M_h	2764	334	2108-3419
Chao M_{th}	2610	314	1995-3225

Table 10. Estimated population size (N) of adult humpback chub in LCR aggregation with TL 200-300 mm. Annual estimates of N are shown for 1991, 1992 and 1993 (upper). Mean estimates are also shown for 1991-1993 (lower left), and for 1991 and 1993 (excluding 1992) combined (lower center).

	1991			1992			1993		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	664	315	295-1649	1637	1303	450-6567	984	309	559-1831
Darroch M_t	583	268	268-1415	738	309	352-1653	961	300	548-1782
Schnabel M_t	491	282	200-1464	1122	1485	207-8271	874	310	470-1762
Chao M_t	472	203	229-1095	1131	789	360-3968	820	251	476-1508
Chao M_h	705	350	303-1814	2738	2737	578-14136	1002	330	556-1916
Chao M_{th}	697	350	298-1812	2761	2793	576-14454	967	302	552-1793

	Mean 1991-1993			Mean 1991 and 1993		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_0	1095	459	196-1994	824	221	391-1257
Darroch M_t	761	169	429-1092	772	201	377-1167
Schnabel M_t	829	514	134-1837	683	210	271-1094
Chao M_t	808	284	250-1365	646	161	329-963
Chao M_h	1482	926	134-3298	854	241	382-1325
Chao M_{th}	1475	944	134-3325	832	231	378-1285

Table 11. Estimated total population size (N) of adult humpback chub in LCR aggregation by combining estimates for chubs 200-300 mm (Table 10) and >300 mm (Table 9). Combined estimates are sum of means of each group. Estimates are shown for all years, 1991-1993 (left), and without 1992 (right).

	Combined Estimate			Combined w/o 1992		
Estimator	N	se(N)	95% c.i.	N	se(N)	95% c.i.
M_o	3267	505	2276-4258	2996	306	2395-3597
Darroch M_t	3230	318	2606-3855	3242	337	2581-3902
Schnabel M_t	3026	580	1889-4162	2880	340	2213-3546
Chao M_t	3155	391	2388-3921	2993	313	2378-3607
Chao M_h	4246	985	2315-6176	3618	412	2810-4425
Chao M_{th}	4085	994	2135-6035	3442	390	2678-4206

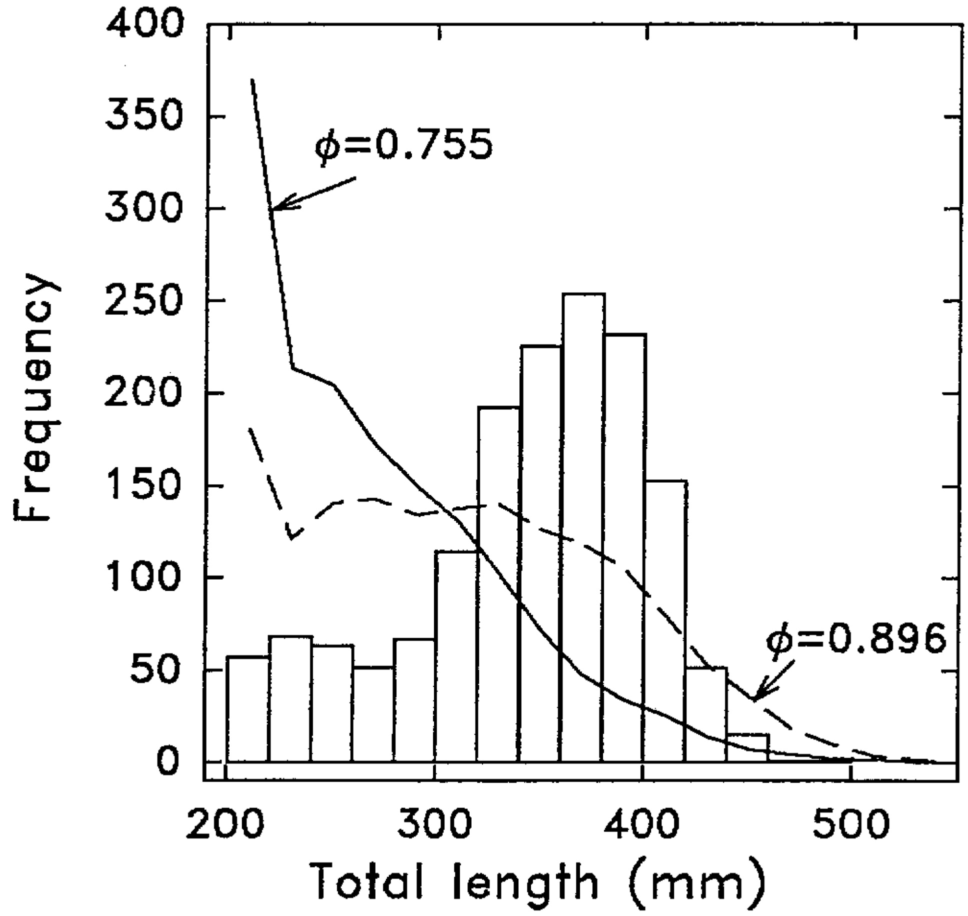

Fig. 1. Length distribution of 1545 adult humpback chub captured in the LCR aggregation, October, 1990-November, 1993 (bars), and hypothetical stable length distributions for adults assuming annual survival rates of 0.755 or 0.896 (lines). Hypothetical distributions were based upon 20,000 fish randomly assigned to a size class based on a stable age distribution, with length randomly selected from a distribution with mean as show in Fig. 6-11 and a coefficient of variation of 10%. Numbers were then standardized to 1545 for comparative purposes.