Gill Raker Differentiation of Tui Chub,
Gila bicolor (Girard), in the Sierra and Great Basin

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Abstract

Extreme variation occurs in gill raker meristics of tui chub, *Gila bicolor* (Girard), inhabiting seven lake systems of the Sierra Nevada and western Great Basin. In general, two ecologically distinct forms exist. *G. b. obesa* is a fluvial-benthic morph with 8-19 coarse gill rakers. *G.b. pectinifer* is a lacustrine fish with 27-42 fine gill rakers. The Walker Lake population has an abundant *pectinifer* mode, and a remnant mode in the intermediate (20-26) range. Pyramid Lake has two ecologically separate populations: a surface-limnetic population having a numerical frequency distribution nearly identical to that of Walker Lake, and a bimodal inshore-benthic group with one mode representing *obesa* and intermediates and the second a discrete *pectinifer* mode. The Topaz Lake population exhibits two modes: 16-25 and 25-36 gill rakers. The Lake Tahoe inshore population exhibits a bimodal distribution, similar to that of the inshore-benthic Pyramid Lake group, with modal classes of 14 and 32. Various subpopulations in the Lake Tahoe system exhibit different gill raker distributions; e.g., a Taylor Creek sample was unimodal in the 12-20 range. The Eagle Lake tui chub sample collected in 1981 was similar to historical data; i.e., bimodal in the *obesa* and intermediate categories. A tributary to Honey Lake has a unimodal distribution, primarily in the 15-19 range. The Lake Almanor population may represent fish introduced from either the Sacramento or Lahontan systems; it exhibits a numerical distribution primarily is the *obesa* range, with a small proportion in the intermediate range. The results from the lake populations are compared to historical data from fluvial Great Basin populations.

Introduction

The tui chub, *Gila bicolor*, exhibits extreme evolutionary
plasticity evidenced by the fact that almost every drainage system
in California, Nevada, and Oregon which is at least partially isolated
supports one or more distinctive form (Moyle 1976). The entire tui
chub complex is called *Gila bicolor* (Girard), by the American Fisheries
Society (AFS) Committee on Names of Fishes (Robins et al. 1980). The
species is represented by at least seven local forms in the Lahontan
system, however, several problems exist in this nomenclature (Hubbs
et al. 1974). The Lahontan complex was treated under the generic
name *Siphateles* which is endemic to the central Great Basin, until
recently, when Uyeno (1960) synomymized that taxon with *Gila*. Bailey
and Uyeno (1964) revised the nomenclature of the blue and tui chub,
and regard the Humboldt River (fluvial) tui chub as *Gila bicolor obesa*
(Girard). This taxon is listed by the AFS Endangered Species Committee
as being "Of Special Concern" (Deacon et al. 1979).

Two forms of tui chub are known to exist in remnant Lahontan
waters, i.e., *G.b. obesa* (Girard), which is characterized by coarse
gill rakers and *G.b. pectinifer* (Snyder), which exhibits fine gill
rakers. The great fluctuation (8-42) in gill-raker numbers for *Gila
bicolor* within the Lahontan basin, and the concomitant variation in
size, texture, and structure is attributable to trophic divergence;
however, it is widely recognized that gill raker development is usually
fixed to some extent genetically (Hopkirk 1973; Hubbs et al. 1974; Lindsey
1981).

Disagreement exists among contemporary authorities whether or not these two forms represent discrete taxa, opinions have varied over the entire spectrum: two genera, two distinct species, two subspecies, hybridization between two subspecies, or a single subspecies. Snyder (1917) was so impressed with the differentiation of the limnetic planktiverous *pectinifer* that he regarded it as a distinct Genus, *Leucidius*. Due to sympatry of the two types in large lakes (e.g., Tahoe and Pyramid), Hopkirk and Behnke (1966) consider the two forms to be distinct species. R.G. Miller (doctoral thesis, Stanford University 1951) and Hubbs, Miller and Hubbs (1974) consider the two types to be subspecies which exhibit intraspecific intergradation. Kimsey (1954) considers the tui chub population occurring in Eagle Lake as hybrids best described by the scientific name *G. bicolor: obesa X pectinifer*. Hopkirk (1973) reports that *obesa* and *pectinifer* also hybridize in Lake Tahoe. LaRivers and Trelease (1952) state *pectinifer* has no valid standing as a taxonomic unit. A further taxonomic complication exists since *G. bicolor* are known to hybridize with *Richardsonius egregius* and *Rhinichthys osculus* in Lake Tahoe (Evans 1969), and with *Orthodon microlepidotus* in a Truckee Meadows pond (LaRivers and Trelease 1952).

In addition to finer, more numerous gill rakers, the *pectinifer* form has a more oblique mouth and more concave head than the *obesa* form (Moyle 1976). The coloration of *obesa* is brassy or brownish, whereas, *pectinifer* is comparatively untinted, being blackish or of a silvery hue (Miller 1951).

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Judging from its diet in a variety of habitats *G. bicolor* can
be classified as an opportunistic omnivoir (Snyder 1917; Miller 1951;
Kimsey 1954; LaRivers 1962; Hubbs et al. 1974; Bird 1975; Moyle 1976;
Cooper 1978; Kucera et al. 1978; Langdon 1979; Marrin and Erman 1982;
Galat and Vucinich 1983a). However, the differential morphology of
the tui chub is correlated with its ecological niche. *G.b. obesa*
typically inhabits rivers and lake bottoms and feeds primarily on
benthic organisms and limited amounts of zooplankton (Snyder 1917);
in contrast, *G.b. pectinifer* inhabits the limnetic zone of large lakes
and feeds almost exclusively on zooplankton (Miller 1951; Langdon 1979).

Regardless of the taxonomic designation given the two forms,
their areal distribution and food preferences indicate they occupy
separate ecological niches and therefore, can be recognized at least
as distinct ecotypes (Galat and Vucinich 1983b). However, spatial
overlap does, at least partially, occur and a key question is if
reproductive isolation exists. If morphological differentiation
does not coincide with reproductive isolation there is no simple and
satisfactory resolution to the systematic problem, and species status
must be based on a broad evaluation of the particular case (Mayr 1966).

The purpose of this paper is to summarize all available information
on gill raker differentiation of tui chub in the Lahontan basin. We
are comparing previously unpublished data on Walker Lake, Topaz Lake,
Pyramid Lake, Lake Tahoe, Honey Lake, Eagle Lake and Lake Almanor
with the available literature.

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All of the study lakes are or have been connected with the
Lahontan System with the exception of Lake Almanor (Figure 1). Eagle,
Honey, Tahoe, Pyramid, and Walker Lakes have native fishes character-
istic of the Lahontan fauna. Topaz Lake does not have a true native
fauna since it was an intermittant playa before a canal and reservoir
were constructed. However, it can be assumed that the fish in the
upper Walker River have access to Topaz. Lake Almanor is a reservoir
on the Feather River in the Sacramento River System; tui chub were
apparently introduced from an unknown source. Lake Almanor is the
second largest (area) reservoir in California.

Pyramid Lake and Walker Lake are the deepest remnants of Lake
Lahontan which occupied an area of about 5 million ha from west-
central Nevada north to the Oregon border during the Pleistocene
Pluvial period some 10-15 thousand years ago (Russell 1885). Pyramid
Lake is the largest (volume) saline terminal lake in North America.
Lake Tahoe is at the headwaters of the Truckee River some 192 km
upstream from Pyramid Lake; it is the third largest (volume) lake
in North America. Eagle Lake probably had a discharge into the
Honey Lake arm of Lake Lahontan during Pleistocene pluvial periods
via Willow Creek Valley (Hubbs et al. 1974). Hubbs and Miller (1948)
observed a gravel beach some 18.3 above the 1924 level. The surface
connection is evidenced by the fact that four of the five native

species occuring in Eagle Lake are of Lahontan origin. Honey Lake
is a shallow ($\bar{z} \approx 0.5$ m) fluctuating, alkaline-saline (≈ 800 mg/ℓ) playa
lake which was previously occupied by the western arm of Lake Lahontan
(Russell 1885). Honey Lake periodically desiccates; its tributaries
are the Susan River to the northwest and Long Valley Creek to the
south. The comparative physical descriptions of six study lakes are
presented in Table 1.

Methods

Tui chubs were sampled from several habitats by different workers
from 1940 to 1983. Gill nets and beach seines were the primary methods
used to capture fish. We sampled tui chubs from Walker Lake on 29 May
1981 and 5 October 1981. The May sample was taken at the "cliffs"
on the west shore of the lake from a large spawning school in shallow
water ($<$ 1 m) using a (1 X 10 m) beach seine. The October sample was
taken on the northwest shore about one km from the mouth of the Walker
River using variable mesh gill nets in 5-10 m of water. We collected
tui chubs from Eagle Lake using 2.54 cm bar mesh and variable mesh
gill nets at a depth of 2-4 m near Stones Landing on 1 August 1981.

R.W. Langdon (1979) provided gill raker counts from tui chubs
taken at a mid-lake station with vertical gill nets and inshore
surface-bottom gill net samples at 23 m. These fish represent a

subsample of the catches from intensive fishing conducted by one of us (SV) during 1977; refer to Vigg (1978) for detailed methods.

Dr. D.L. Galat gave us permission to present published data on size-specific gill raker distributions derived from juvenile Pyramid Lake tui chubs collected during 1979. These distributions represent both wild young of year tui chubs sampled with beach seines at intervals throughout the growing season and a cohort of young of year tui chubs raised in microcosms (Galat and Vucinich 1983b).

California Department of Fish and Game provided data on gill raker counts of tui chubs sampled with gill nets from Topaz Lake and Lake Almanor. The Topaz collection was made in 22 June 1971 and the Almanor collections on 21 October 1971 and 12 May 1972.

Data provided by Dr.R.R. Miller are from collections made by G.I. Murphy and Dr. C.L. Hubbs. Murphy's collections include two samples in the Honey Lake Basin (Long Valley Creek) during April 1940; and four samples in the Lake Tahoe Basin: Upper Angora Lake and Babcock Pier during June 1970, and Taylor Creek and offshore in Lake Tahoe during 1942. Hubbs' collections include two samples from Eagle Lake (near Pine Creek) and a sample from the northwest shore of Walker Lake during July 1942. The latter collection is referred to in Hubbs (1961, pp 13-14) and Hubbs et al. (1974, p. 144).

Dr. R. G. Miller provided unpublished gill raker frequency distributions from his doctoral dissertation. The fish were sampled from Lake Tahoe in 1949 with bottom set gill nets at depths to 46 m.

We dissected the first left gill arch from tui chubs which were preserved in the field with 10% formalin. The gill arches were placed in a vial of 70% ethanol for latter enumeration. The fork length of each fish was recorded. Gill raker (branchiospine) counts were made on the anterior side of the gill arch using a dissecting microscope. Care was taken to include rudimentary elements at the extreme top and bottom of each arch.

RESULTS

Walker Lake

The Walker Lake tui chub population exhibits a unimodal gill raker frequency distribution in the range of 29-42 (Figure 2). A small proportion of the fish sampled had gill raker counts <28. An inshore spawning school sampled in May 1981 had < 3% represented by tui chubs with 21-22 gill rakers. In contrast a sample taken about one km from the Walker River delta in October 1981 was comprised of about 11% in the range 20-27; and a sample taken by Dr. C.L. Hubbs near the river inflow in 1942 was comprised of about 13% in the range of 20-25 and one fish had 16 gill rakers. The overall mean of the 1981 samples was 33.0 and that of the 1942 sample was 31.9 gill rakers. For both time periods the modal class was 34.

Topaz Lake

Tui chubs from Topaz Lake exhibit a bimodal distribution of gill rakers (Figure 3). The modes ranged 16-25 ($\bar{x}$ - 21.2) and 25.36($\bar{x}$ = 30.4). The overall mean gill raker number of the sample was 26.3.

Pyramid Lake

Two principal habitats exist for tui chubs in Pyramid Lake: offshore-open water and inshore (Vigg 1978, 1981). Langdon (1979) made gill raker counts of these groups of tui chubs and studied their diet. The limnetic sample was almost entrirely comprised (98%) of fish with >28 gill rakers (Figure 4); the mean number of gill rakers for this sample was 34.1. In contrast the inshore (23 m) sample was bimodal; it exhibits modes of 10-24 ($\bar{x}$ = 15.2) and 27-40 ($\bar{x}$ = 34.1). The overall mean of the inshore sample was 26.4 gill rakers. Surface and bottom subsamples were taken on the inshore 23 m station. The surface inshore sample was similar to the limnetic one; it was comprised predominantly (82.5) of fish with >26 gill rakers. In contrast the 23 m bottom sample was nearly half <25 and half >26 gill rakers. The proportion of the two forms inshore was somewhat biased since Langdon selected for coarse rakered fish.

Galat and Vucinich (1983a,b) studied the diet of young of the year tui chubs in the littoral zone of Pyramid Lake. Their work provides information on size specific gill raker distributions of sub-adult tui chubs sampled at intervals from the eulittoral zone (< 1 m) (Figure 5) and a sample raised for 120 days in microcosms (Figure 6).

These data illustrate that young of the year tui chubs (< 30 mm) have
< 28 gill rakers and do not exhibit well defined modes; i.e., their gill
raker development is incomplete. As the fish grow the range of gill
rakers increases and the modes diverge. Galat and Vucinich (1983b)
describe the largest size group (≈ 70 mm) as having "...the character-
istic nonoverlapping bimodal gill raker distribution..."; however, it
may be more accurately called trimodal. The mode in the 25-38 range
of both the wild and microcosm tui chubs is relatively discrete and
unambiguous. Within the ≤ 22 range, however, two submodes are apparent.
In fact with a little imagination one can visualize three modes through-
out the development sequence.

On 11 February 1983 a sample of adult tui chubs was collected with
four bottom-set gill nets within two km of the Truckee River delta at
depths of about 15 m (Gill and Vigg, unpublished manuscript). Nearly
half of these fish had > 30 gill rakers ($\overline{x}$ = 35.3), and about half had
< 23 ($\overline{x}$ = 15.6). Within the lower range, the primary submode was in the
range 12-16 ($\overline{x}$ = 14.0); about 12% of the sample consisted of a group of
tui chubs with 20-22 gill rakers (Figure 7). Although this sample is
represented by a limited number of fish (n = 33), it also suggests
three modes.

Lake Tahoe

Nearshore tui chubs sampled by R.G. Miller in 1949 at depths
≤ 46 m exhibited a bimodal distribution of gill rakers (Figure 8).

The left gill arch ranged 10-23 ($\overline{x}$ = 15.5) and 25-36 ($\overline{x}$ = 30.6) gill rakers for the two modes. About 62% of the tui chubs were in the < 24 gill raker mode.

Various subpopulations apparently exist in the Lake Tahoe basin. Collections by G.I. Murphy at four locations (Figure 9) exhibited different modes than Miller's representative lake samples. The Taylor Creek population was unimodal in the 12-20 range, with a mean of 15.2 gill rakers. The samples taken in Lake Tahoe off Taylor Creek and at Babcock Pier were nearly identical, primarily in the range 17-24 ($\overline{x} \simeq$ 19.5). The latter sample had one fish with 32 gill rakers. Upper Angora Lake tui chubs had 12-16 gill rakers ($\overline{x}$ = 13.4); this may represent an introduced stock (Needham and Sumner 1942).

Honey Lake

Two samples of tui chubs were taken by G.I. Murphy in Long Valley Creek during 1940; one at the mouth where it enters Honey Lake and the other about 3 km upstream (Figure 10). The distribution of gill rakers in the two samples was quite similar; unimodal (13-26) with means of 17.9 (mouth) and 17.7 (upstream).

Eagle Lake

Kimsey (1954) described the gill raker distribution of Eagle Lake tui chubs as a bimodal curve. His data are compared to an earlier sample collected by C.L. Hubbs and a recent one collected during this study

(Figure 11). The mean gill raker counts for the three samples are 20.8,
21.3, and 21.7 for 1942, 1954, and 1981, respectively. For all data
combined (n = 382) the modes can be defined as 12-20 ($\overline{x}$ = 17.3) and
20-32 ($\overline{x}$ = 24.1).

Lake Almanor

The gill raker distribution of tui chubs from Lake Almanor can be
described as unimodal (Figure 12). Most of the fish exhibit 11-19 gill
rakers ($\overline{x}$ = 14.9). A small submode (10.7%) exists, however, in the
21-25 range ($\overline{x}$ = 22.6).

Discussion

We have previously presented background information on the contro-
versy among ichthyologists regarding the taxonomic status of the tui
chub populations in the Lahontan Basin. In our discussion we use the
subspecific designation for the two forms for clarity and simplicity;
however, at the present state of the knowledge this usage is not
intended to be judgemental. *Gila bicolor obesa* and *pectinifer* are
distinct in terms of their morphology, meristics, and ecological niches.
Gill raker distributions of various lacustrine populations are different
in terms of range, overall parametric mean, number and relative abundance
of modes, and mean gill raker number within each mode.

Criteria to separate *obesa* and *pectinifer*

    The attributes of gill raker distributions (e.g., mean, mode, and range) of samples have commonly been used to differentiate between *obesa* and *pectinifer*. Miller (1951) cites a natural break between *obesa* and *pectinifer* at 26 gill rakers; this is generally true for remnant lacustrine populations in the Lahontan basin (Table 2). We agree with Miller's interpretation of ≤ 19 as *obesa*, and ≥ 27 as *pectinifer*.

    The number of gill rakers on the first left gill arch is the only criterion analyzed in this paper. Obviously there are limitations to using a univariate analysis on a multivariate problem, but we believe a comparison of gill raker meristics from various lake populations will serve to clarify the issue of tui chub speciation. Neff and Smith (1979) conducted a multivariate analysis of traits of two species of cyprinids and their hybrids and found that gill raker number is an important determinant. They caution however, that gill rakers increase in divergence more posteriously in the branchial basket, and the anterior side of the first gill arch represents the least discriminating count. Miller (1951) stated that form of gill rakers (shape, spacing, length) gives a clearer picture than numbers. Thus it should be recognized that multiple criteria (from disciplines such as morphology, systematics, population genetics, physiology and ecology will be required to resolve the taxonomy of the tui chub.

<u>Fluvial *obesa* populations</u>

Hubbs et al. (1974) analyzed gill raker counts of various fluvial populations of *G. bicolor*, including *obesa* from the Lahontan basin (Table 3). In the Humboldt River system, gill raker counts exhibit a sharp upstream decrease, in a regular cline, with means of 14.9 > 13.6 > 12.6. Hubbs et al. (1974) attribute this to past hybridization of downstream *obesa* populations with *pectinifer* and subsequent back-crossing with *obesa*. Occurrence of intergrades between *obesa* and *pectinifer* in ancient Indian caches near Lovelock demonstrates past intermixing near the lower end of the Humboldt River (Hubbs and Miller 1948). The Carson River sample (12-23, $\overline{x}$ = 16.4) is also considered by Hubbs et al. (1974) to be a *G. b. obesa* population with some introgression with *pectinifer*.

Tui chubs from Long Valley Creek, tributary to Honey Lake were predominantly in the *obesa* gill raker category (Figure 10). A substantial proportion (18.3%), however, was in the 20-29 range. The mean number (17.8) is slightly higher than that of the lower Carson River (Table 3). A similar case of introgression with *G. b. pectinifer*, which Hubbs et al. (1974) postulated for other fluvial populations could have occurred in Long Valley Creek. One can hypothesize that as Lake Lahontan desiccated, a remnant *pectinifer* population remained in Honey Lake, and *obesa* in its tributaries. As Honey Lake experienced periodic changes from lake to playa the *obesa* and *pectinifer* populations interbred, but the *obesa* form was generally selected for.

Hubbs et al. (1974) concluded from the remnants of Pluvial lakes Diamond, Newark and Clover that either these previously lacustrine populations did not evolve high gill raker number, or that rakers reverted back to low numbers when the populations subsequently became isolated in springs and creeks. Williams and Williams (1980) found that the gill raker morphology of *G. boraxobius* (≈ 16 rakers) and *G. alvordensis* (≈ 20 rakers) which exist in remnant springs and ponds in southeastern Oregon and northwestern Nevada is similar to that of *G. b. obesa*.

The samples taken at Fallen Leaf Creek - Upper Angora Lake and Taylor Creek (12-20 rakers) indicate that *obesa* populations exist in tributaries to Lake Tahoe (Figure 9). Needham and Sumner (1942) suggested that the Upper Angora Lake population may have been introduced. If separate gene pools exist in the limnetic zone and tributaries of Lake Tahoe, this could represent a reproductive isolating mechanism.

obvious

The status of fluvial *G. b. obesa* in the major Lahontan river systems is in doubt; e.g., Walker, Carson, Truckee, and Humboldt River populations. The U.S. Fish and Wildlife Service conducted extensive sampling in the Truckee River from Lake Tahoe to Pyramid Lake during 1977; no tui chubs were captured, however one *G. bicolor* x *Richardsonius egregius* hybrid was taken in the upper river (USFWS 1978). Extensive gill net sampling in Lahontan Reservoir on the Carson River since 1980 by the Nevada Department of Wildlife has revealed the

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absence of tui chub (Michael Sevon, Nevada Department of Wildlife,
personal correspondence). Extirpation of *G. bicolor* from Lahontan
Reservoir was apparently caused by competition and/or hybridization with
Orthodon microlepidotus, which may have been introduced in the 1950's.
Ponds in the lower Carson Sink complex, which do not have a large *O.
microlepidotus* population, still support tui chubs. Rye Patch Reservoir
on the lower Humboldt River supported a *G bicolor* population prior to
desiccation in the 1960's, but recent sampling indicates that tui chubs
may be absent (Michael Sevon, Nevada Department of Wildlife, personal
correspondence). It is believed, however, that tui chubs are still
abundant downstream in the Humboldt Sink.

Lacustrine *obesa* populations

It is difficult to discuss *obesa* modes ($\leq$ 19 rakers) without
inclusion of the intermediate range (20-26 rakers) since overlap is
often observed in lake populations. An exception is the unimodal *obesa*
population observed in Lake Almanor (Figure 12); a discrete sub-mode was
present in the intermediate range. The source of the Lake Almanor
population is unknown. Jack A Hanson, Associate Fishery Biologist of
the California Department of Fish and Game, speculates that tui chubs
were introduced by bait fishermen -- because the dam was completed in
1913 and tui chubs did not become abundant until the late 1940's
(personal correspondence, letter dated 26 August 1981).

Long Valley Creek, and other tributary populations (e.g., Susan River and Willow Creek), probably recolonize Honey Lake after desiccation. Periodic forced mixing of the fluvial and lacustrine tui chubs in the system has likely resulted in essentially one population; mid-lake samples would be necessary to ascertain their identity.

Eagle Lake has a mode in the *obesa* range; however, this mode overlaps one in the intermediate range. The lack of complete separation of modes makes interpretation of the Eagle Lake population questionable. Nonetheless the bimodal nature of the gill raker frequency distribution is apparent in Kimsey's (1954) sample and our recent (1981) one (Figure 11). The Eagle Lake population will be reconsidered in the next section.

Inshore samples from Pyramid Lake and Lake Tahoe exhibit large modes in the *obesa* range with the modal class at 14 rakers. In both lakes the tail of the distribution extends into the intermediate range. (Figure 4 and 8). This may be attributed in part to a sampling artifact. Pooling of several different samples that results in a relatively large sample size ($n \approx 200$) may mask a discrete sub-mode in the 20-26 range. As previously indicated the development sequence of Pyramid Lake tui chub monitored by Galat and Vucinich (Figures 5 and 6) and the sample taken by Gill and Vigg (Figure 7) suggest three modes. Two different samples taken in Lake Tahoe (Figure 9, center) indicate that schools of tui chubs which exhibit on intermediate number of gill rakers exist.

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Intermediate modes

All of the fluvial subspecies of *G. bicolor*, including the upstream populations of *G. b. obesa* have < 18 gill rakers (Hubbs et al. 1979). Hubbs et al. (1974) interpret the extension of gill raker number into the relatively high range (>20) for the lower Humboldt and lower Carson River populations as introgression with *G. b. pectinifer* during Lake Lahontan times. Miller (1951) determined from morphological characteristics that *G. b. obesa* in Lake Tahoe has ≤ 19 gill rakers. We have observed a remnant mode in the 20-26 gill raker range in discrete samples from several lakes including Almanor, Pyramid and Walker. Abundant modes in this intermediate range are seen in the Eagle and Topaz populations, and subpopulations of Lake Tahoe. Hopkirk (1973) reports that a lacustrine sample of *obesa* (n = 41) had a mean number of 16.7 rakers, and *obesa* X *pectinifer* hybrids (n = 86) averaged 20.4 rakers.

Based on the preceding information we consider the 20-26 range as intermediate *G. b. obesa* and *G. b. pectinifer*, probably caused by limited interbreeding of two forms. This can be interpreted as either subspecific intergadation or interspecific hybridization. Hubbs et al. (1974) state that if the interchange of genes is extensive, they favor the intraspecific interpretation.

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Kimsey (1954) considered the Eagle Lake population as intergrades best described as *bicolor; obesa* X *pectinifer*. He concedes that the gill raker distribution has two modes, but bases his conclusion of a single population on a uniform intergradation of all other characteristics upon which *pectinifer* and *obesa* are differentiated. Kimsey observed two body forms; but claimed this differentiation, like their diet, was not correlated with gill raker number. Hubbs et al. (1974, p. 144) apparently concur that fusion of the two forms has occurred in Eagle Lake, resulting in "...a taxon with a distinctly bimodal, intermediate number of rakers..."

Reconsideration of the gill raker data from Eagle Lake (Figure 11) leads us to agree with previous workers that although the frequency distributions are not clear-cut, two modes exist. Only one of the modes is in the intermediate range, however; the other is clearly in the *obesa* range.

Marrin and Erman (1982) describe the Stampede Reservoir (upper Truckee River tributary impoundment) tui chub population as being the zooplanktiverous form with a superior oblique mouth and numerous slender gill rakers. Based on diet and morphology, Marrin (1980) concluded the population was exclusively *pectinifer*. It is doubtful, however, that the Stampede Reservoir (impounded since 1969) represents a truely *pectinifer* population. D.L. Marrin (personal correspondance, letter dated 5 May 1983) relates that gill raker counts on less than

20 fish consistantly fell in the 18-30 range; subsequent counts were recorded only if outside this range -- one fish had 16 and four had 32-36. Thus, based on gill raker number, we consider the Stampede population to be intermediate that of *obesa* and *pectinifer*.

Lacustrine *pectinifer* populations

Topaz, Tahoe, Walker, and Pyramid Lakes have tui chub populations which exhibit a mode in the *pectinifer* (>26) range. The mean gill raker number for this mode is 30.4, 30.6, 33.7, and 34.3, respectively. It is interesting that the *pectinifer* mode of the two high-elevation lake populations (Topaz and Tahoe) closely resemble each other and have a lower mean than that of the terminal lakes. This observation is in agreement with the data of Hopkirk (1973); he found the mean raker number of *pectinifer* from Lake Tahoe (n = 15) was 32.2, compared to 36.1 from a Pyramid Lake sample (n = 94). Thus, *pectinifer* apparently achieves its greatest expression in Walker and Pyramid Lakes.

From extensive sampling in various areas of Walker Lake during 1976 - 1977, one of us (JJC) observed that all of the tui chubs had fine, numerous gill rakers (Cooper 1978). In contrast Hubbs (1961, p 13-14) and Hubbs et al. (1974, p 144) refer to:

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"... a large collection from the inlet end of Walker Lake
that was uniformly typical of *'pectinifer'* in all characters,
except that a considerable proportion had, as an apparent
result of introgression, the low raker number of *'obesa'*,
and others had a dribbling range of counts fully connecting
the high *'pectinifer'* and low *obesa* modes".

Our interpretation of data collected by Dr. C.L. Hubbs in 1942
(Figure 2, top) is that the sample is primarily represented by a
pectinifer mode with a small proportion (≈13%) in the intermediate
range; only one fish is in the *obesa* category.

The status of the *obesa* population in the lower Walker River is
unknown; however, one can speculate that limited gene flow occurs
between the fluvial *obesa* and lacustrine *pectinifer* populations in
the Walker Lake system. The sample we collected near the river inlet
(Figure 2, bottom) was similar to Hubb's sample; it was comprised of
about 11% in the intermediate range. In contrast, the spawning school
sampled on shore in the central region of Walker Lake (Figure 2, center)
was comprised of only 3% in the intermediate range. The latter sample
was nearly identical to the limnetic Pyramid Lake sample (Figure 4,
top) This suggests that both Walker and Pyramid Lakes have a segregated
pectinifer population.

It seems likely that Lake Tahoe would also have a strictly
pectinifer limnetic population. R.G. Miller's Lake Tahoe sample was
primarily collected inshore at depths less than 46 m. The bimodal
distribution which Miller (1951) observed in Lake Tahoe (Figure 8)
corresponds to the inshore Pyramid Lake population (Figure 4, bottom).

Taxonomic Status of *obesa* and *pectinifer*

What level of differentiation exists between *obesa* and *pectinifer?*
J.O. Snyder, a conservative ichthyologist, obviously considered the
forms distinct since he placed them in separata genera. Presently
there is general agreement that the fluvial form should be considered
a subspecies; i.e., *G. b. obesa* (Bailey and Uyeno 1964; Hopkirk 1973;
Hubbs et al. 1974; Deacon et al. 1979). In fact, the population
abundance status of the fluvial *G. b. obsea* is unknown in most of its
former habitats (e.g., Walker, Carson, Truckee, and Humboldt Rivers),
and it is probably quite scarce.

The real question is what to do with the lacustrine *pectinifer*.
Only LaRivers (1962) thought *pectinifer* was not a valid taxonomic
unit, and included it with *G.b. obesa* as the Lahontan tui chub. We
reject LaRiver's opinion based on three observations. First, the
two forms have separate niches in Pyramid Lake as discussed by Galat and
Vucinich (1983b). Secondly, the fact that *pectinifer* has retained
its identity (based on a non-overlapping gill raker mode in the 27-42
range) during a sympatric existance in the inshore regions of Pyramid
and Tahoe. Thirdly, an exclusively *pectinifer* population exists in
Walker Lake away from the fluvial influence and in the limnetic regions
of Pyramid Lake. The status of a limnetic *pectinifer* population in
Lake Tahoe is uncertain since Miller (1951) did not sample in that
region. Furthermore, the introduction of the zooplanktiverous kokanee,
Oncorhynchus nerka kenerlyi, (Fraser and Pollitt 1951) and the drastic

reduction in cladoceran zooplankters associated with the introduction

of the opossum shrimp, *Mysis relictus*, (Richards et al. 1975) could

have greatly impacted the limnetic *pectinifer* population in Lake

Tahoe.

Previous interpretations of Pyramid Lake gill raker data were

that distinct *obesa* and *pectinifer* modes existed without intergrades

caused by interbreeding of the two forms. Dr. R.J. Behnke (Colorado

State University, personal communication) considers the sympatric

existance of *obesa* and *pectinifer* without intergradation in Pyramid

Lake as clear evidence of separate species. In contrast Hubbs (1961)

cited intermediate stocks in Eagle, Tahoe, and Walker Lakes as evidence

that *obesa* and *pectinifer* are subspecies. Hubbs (1943) stated it is

the degree of differentation that determines the stage of speciation;

a species is completely differentiated and a subspecies is not. Hubbs

(1943, p116) used the criterion of intergradation to determine the

degree of differentiation: "Thus, I regard intergadation of almost   / *but genetically or phenotypically.*

any type as evidence that speciation is not complete and that the forms

are on the subspecies level of differentiation."

However, as Hubbs (1943) points out natural hybrids between

species commonly occurs in fishes. Hubbs et al. (1974, p144) later

admit that:

"the interplay between *'pectinifer'* and *obesa* could be interpreted as extensive interspecific hybridization rather than subspecific intergradation." and "... the distinction is to a large degree arbitrary."

Hopkirk (1973) acknowldedges interbreeding between *obesa* and *pectinifer* but considers the latter a distinct species. According to the biological species concept as defined by Mayr (1970): "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." Hopkirk (1973, p118) concludes "... minor differences in morphology, behavior, and ecology can reproductively isolate sympatric lacustrine *(Gila pectinifer)* and fluviatile *(Gila bicolor obesa)* populations." The demonstration of a reproductive isolating mechanism in Tahoe, Pyramid or Walker Lakes would help resolve the tui chub speciation problem. Utter (1981) concludes that reliable genetic data using electrophoretic methods complimented by biological and life history data, as well as historical and geological information are necessary criteria to define a fish species.

Thus in answer to the original question, more information is necessary to determine the level of differentiation of the two tui chub morphs, particularly *pectinifer*. The demonstration of a reproductive isolating mechanism in the large lakes and determination of genetic variation via electrophoresis will be necessary to resolve the systematic issue.

24

<u>*Summary and Conclusions*</u>

Frequency distributions of gill raker counts of the anterior side
of the first left gill arch of tui chbs from Almanor, Eagle, Honey,
Tahoe, Pyramid, Topaz, and Walker Lakes are compared and contrasted.
The numerical criteria to define *obesa*, intermediates, and *pectinifer*
are 8-19, 20-26, and 27-42 gill rakers, respectively.

Fluvial Great Basin populations of *obesa* analyzed by Hubbs et al.
(1974) generally have <18 gill rakers, except where introgression with
pectinifer occurred. Likewise, Lake Tahoe tributary populations are
unimodal in the *obesa* range.   The Lake Almanor population can be
characterized as unimodal in the *obesa* range with a remnant
intermediate mode.   The Honey Lake (Long Valley Creek) population
is also unimodal in the *obesa* category extending into the inter-
mediate range.

The Eagle Lake population exhibits two abundant modes: *obesa*
and intermediate.   The inshore Pyramid Lake and Lake Tahoe populations
exhibit a bimodal distribution; the tail of the *obesa* distribution
includes an intermediate submode, while the *pectinifer* mode is discrete.
Samples from both Pyramid and Tahoe illustrate that a separate
intermediate category exists.   We interprete the existance of intergrades
as the result of limited interbreeding between the two morphs.   Limited

gene exchange between *obesa* and *pectinifer* inshore in Pyramid, Tahoe, and Walker Lakes does not preclude the existance of a reproductive isolating mechanism; natural interspecific hydridization is common in fishes.

The limnetic population of Pyramid Lake is unimodal in the *pectinifer* range, with a small remnant intermediate mode. The Walker Lake population, away from the influence of the river inlet, is nearly identical with the limnetic Pyramid Lake population. The environmental conditions in these large, saline, terminal lakes is apparently conducive to the maximum expression of the *pectinifer* morph.

The qualitative analysis of gill raker distributions presented in this paper illustrates that different patterns of gill raker phenotypes exist in remnant Lahontan waters. However, gill raker meristics can not be used as the sole criterion to evaluate the extent of speciation between *obesa* and *pectinifer*. It will be necessary to conduct a rigorous investigation of multivariate morphology, an eco-physiological analysis of reproductive isolating mechanisms, and an electrophoretic analysis of population genetics in order to resolve the systematics of the tui chub.

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Lakes, Oregon. Unpublished thesis. Oregon State Univ. 165 pp.

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TABLE 1. Limnological characteristics of six study lakes.

Parameter	Lake Almanor	Eagle Lake	Lake Tahoe	Pyramid Lake	Topaz Lake	Walker Lake
Bathymetric map	Pacific Gas and Electric	California Dept. of Water Resources	Rush (1973)	Harris (1970)	Rush and Hill (1972)	Rush (1970)
Maximum length/ width (km)	23/7	17/6.8	35.5/19.5	40/16	7/2.5	25/9
Surface area (km^2)	106.2	121.4	499	446.4	9.8	150
Volume (km^3)	1.3	0.43	150.1	26.4	0.16	3.5
Mean Depth (m)	12	7	313	59	16	20
Maximum Depth (m)	30.5	30.5	501	103	28	33
Axis	NW-SE	NE-SW	N-S	NW-SE	N-S	N-S
Origin	Reservoir (1913)	Rockslide	Graben	Graben	Reservoir/ Playa (1921)	Fault block/scarp
Elevation (m)	1,375	1,555	1,899	1,157 (1976)	1,526	1,200
Stratification (classification)	June-September (monomictic)	ill defined in summer (monomictic)	(monomictic)	June-December (monomictic)	May-October (monomictic)	May-November (monomictic)
Trophic Class	MESO	MESO	OLIGO	MESO	MESO	EU
TDS (mg/ℓ) (alkalinity)	59 (58)	(700)	62 (43)	5,350 (1,430)	105 (85)	10,700 (2,870)
Watershed (km^2)	1,277	1,290	1,310	6,500	685	10,500
Main Tributary Stream (km)	N. Fork Feather River	Pine Creek (41.8)	Truckee River (+ numerous tributaries)	Truckee River (192)	West Walker River	Walker River
Latitude/ Longitude	40° 15'N 121° 10'W	40° 40'N 120° 45'W	39° 09'N 120° 08'W	40° 00'N 119° 35'W	38° 42'N 119° 31'W	38° 43'N 118° 40'W

Table 2. Gill raker criteria for *Gila bicolor obesa* versus *pectinifer*.

Gill Raker Range		
obesa	*pectinifer*	Reference
8-20	29-36	Snyder (1917)
≤ 19	≥ 27	Miller (1951)
11-19	29-40	Hubbs et al. (1974)
8-24	29-40	Moyle (1976)
10-24	27-40	Langdon (1979)
≤ 21	≥ 27	Galat and Vucinich (1983)

TABLE 3. *Number of gill-rakers in populations of* Gila bicolor *in certain basins in Nevada* (From Hubbs et al. 1974).

| Subspecies
Pluvial lake system
Locality[1] | Gill-rakers, including all rudiments, on first gill-arch | | | | | | | | | | | | | | | | |
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	No.	Ave.
Gila bicolor obesa																		
Lake Lahontan																		
Carson River (G1)[2]	—	—	—	—	1	6	9	13	13	8	5	5	5	1	3	1	70	16.43
Humboldt River																		
Near Lovelock (G2)	—	—	—	—	3	16	32	37	29	15	5	2	2	2	2	—	145	14.90
Near Carlin (G3)	—	—	—	2	5	23	16	13	—	1	—	—	—	—	—	—	60	13.62
Bishop Creek (G4)	—	—	1	16	66	83	25	1	—	—	—	—	—	—	—	—	192	12.61
Lake Diamond																		
Birch Ranch (G5)	—	—	—	—	9	28	22	9	2	—	—	—	—	—	—	—	70	13.53
Sulphur Spring (G6)	—	—	—	—	5	22	43	12	—	—	—	—	—	—	—	—	82	13.76
Gila bicolor newarkensis																		
Lake Newark																		
Near Diamond Peak (G7)	—	1	8	23	38	22	5	3	—	—	—	—	—	—	—	—	100	11.99
Moores Ranch (G8)	—	—	2	14	39	34	11	—	—	—	—	—	—	—	—	—	100	12.23
Warm Springs (G9)	—	—	—	2	6	—	—	—	—	—	—	—	—	—	—	—	8	11.75
Gila bicolor euchila																		
Lake Newark																		
Fish Creek Springs (G10)	—	—	13	40	56	24	5	—	—	—	—	—	—	—	—	—	138	11.77
Gila bicolor isolata																		
Lake Clover																		
Independence Valley (G11)	2	9	30	53	36	18	1	—	—	—	—	—	—	—	—	—	149	11.14

[1] Expressed as numbered Locations in the G series.

[2] Some introgression from *Gila bicolor pectinifer*.

FIGURE CAPTIONS

FIGURE 1.   Location of the seven study lakes, California and Nevada.

FIGURE 2.   Gill raker frequency distributions of adult tui chubs
            sampled from Walker Lake, Nevada in 1942 (top), compared
            to May 1981 (center) and October 1981 (bottom).

FIGURE 3.   Gill raker frequency distribution of adult tui chubs from
            Topaz Lake, Nevada-California, June 1971 (California
            Department of Fish and Game, Unpublished data).

FIGURE 4.   Gill raker frequency distributions of adult tui chubs
            from the mid-lake water column (top) and inshore benthic
            and surface samples (bottom) from Pyramid Lake, Nevada,
            1977 (From Langdon 1979).

FIGURE 5.   Gill raker frequency distributions of three size classes
            of young of year tui chubs collected throughout the summer
            of 1979 in the eulittoral zone of Pyramid Lake, Nevada
            (From Galat and Vucinich 1983).

FIGURE 6.   Gill raker frequency distributions of young of year tui
            chubs sampled from Pyramid Lake, Nevada during 1979 (top),
            and after 120 days in experimental microcosms (bottom)
            (From Galat and Vucinich 1983).

FIGURE 7.   Gill raker frequency distributions of adult tui chubs
            sampled from Pyramid Lake, Nevada, February 1983 (From
            Gill and Vigg, unpublished manuscript).

FIGURE 8.   Gill raker frequency distributions of adult tui chubs
            sampled from Lake Tahoe, California-Nevada, during 1949
            (From Miller 1951).

FIGURE 9.   Gill raker frequency distributions of adult tui chubs from
            various populations in the Lake Tahoe basin, 1940-1942
            (Unpublished data, collected by G.I. Murphy).

FIGURE 10. Gill raker frequency distributions of adult tui chubs from
            a tributary of Honey Lake, California, 1940 (unpublished
            data, collected by G.I. Murphy).

FIGURE 11. Gill raker frequency distributions of adult tui chubs
            sampled from Eagle Lake, California, by C.L. Hubbs in 1942
            (top), J.B. Kimsey in the 1950's (center), and during
            August 1981 (bottom).

FIGURE 12. Gill raker frequency distribution of tui chubs from Lake
            Almanor, California, May and October 1971 (California
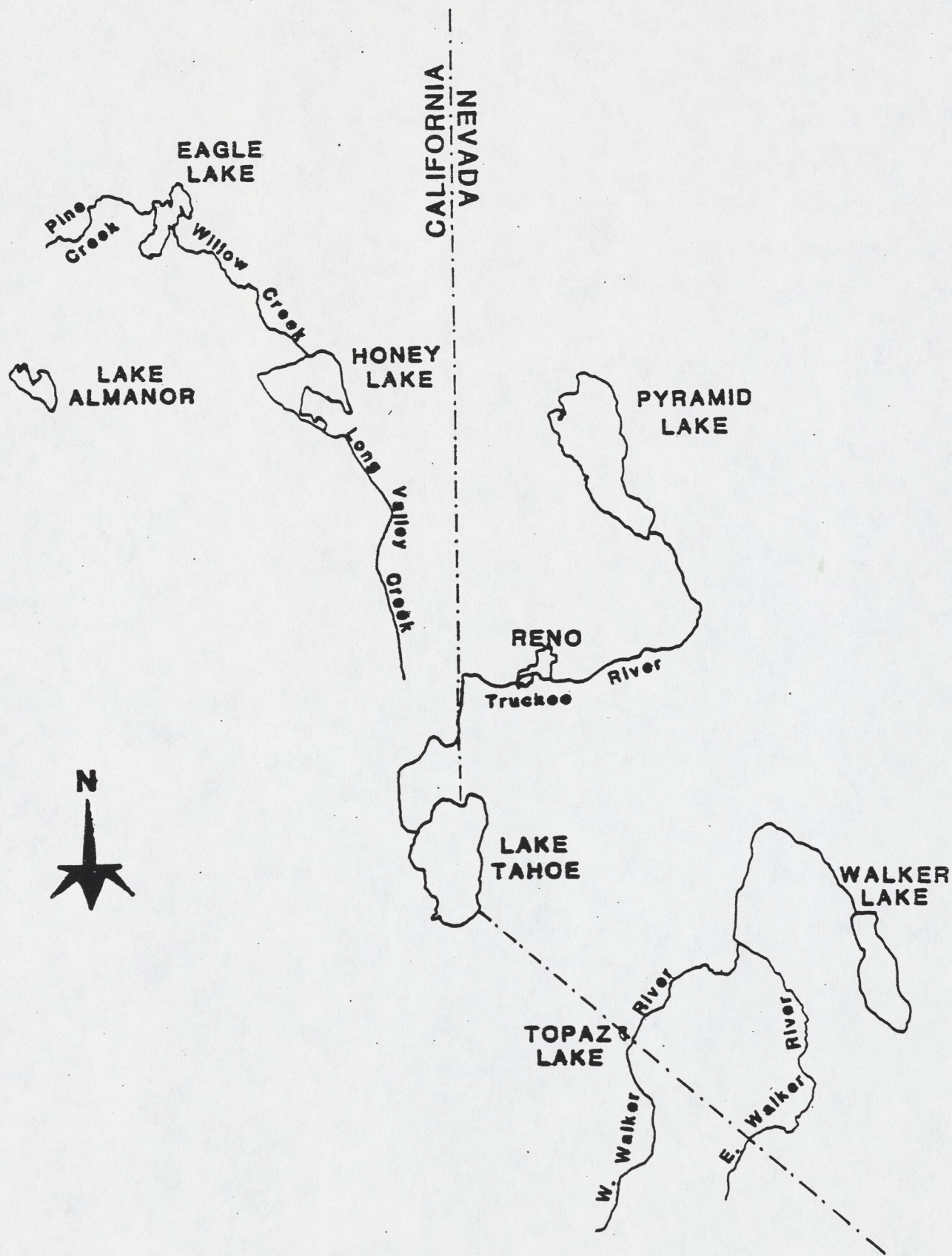   Department of Fish and Game, unpublished data).
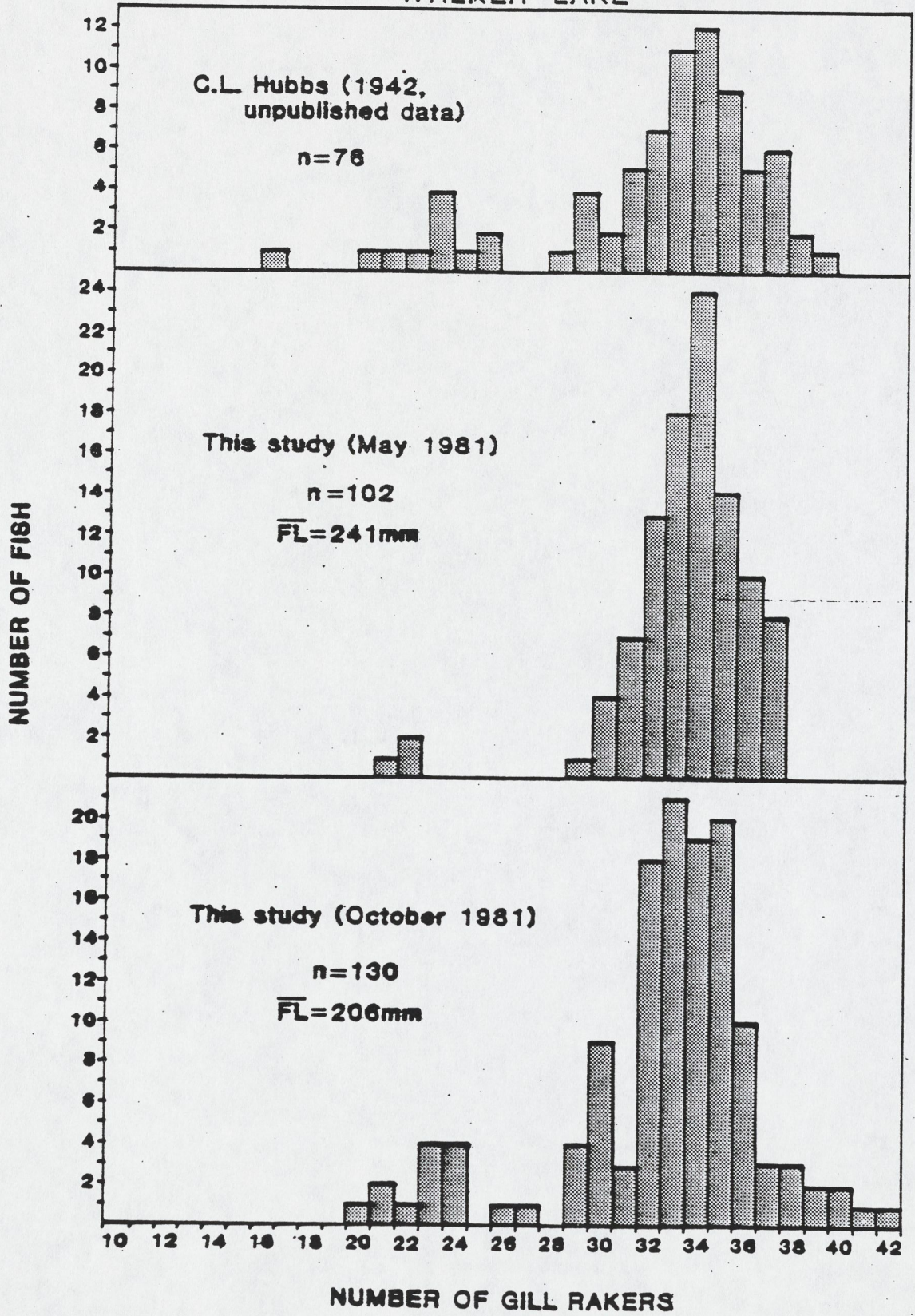
Fig 1.

WALKER LAKE

C.L. Hubbs (1942, unpublished data)

n=76

This study (May 1981)

n=102

$\overline{FL}$=241mm

This study (October 1981)

n=130

$\overline{FL}$=206mm

NUMBER OF FISH

NUMBER OF GILL RAKERS

Fig 2

TOPAZ LAKE

n=221
$\overline{FL}$=246mm

NUMBER OF FISH

NUMBER OF GILL RAKERS
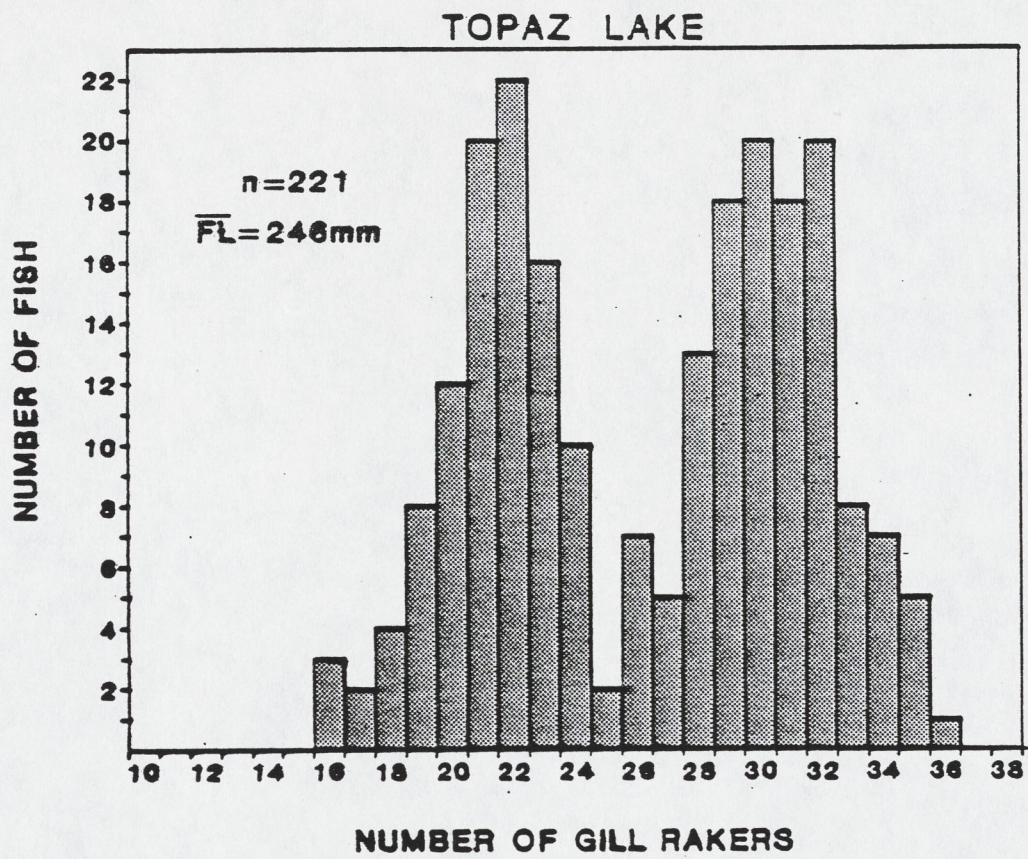
Fig 3.

PYRAMID LAKE

Fig 4.

PYRAMID LAKE

NUMBER OF FISH

n=107
FL≤25mm

n=129
FL=26-50mm

n=83
FL=51-75mm

NUMBER OF GILL RAKERS

Fig 5.

PYRAMID LAKE

n=48

$\overline{FL}$ =29mm

Wet weight $\overline{x}$=0.181g

n=120

$\overline{FL}$ =70mm

Wet weight $\overline{x}$=4.53g

NUMBER OF FISH

NUMBER OF GILL RAKERS

Fig 6.

PYRAMID LAKE

n = 33

$\vec{FL}$ = 200.4 mm

NUMBER OF FISH

NUMBER OF GILL RAKERS

Fig 7

LAKE TAHOE

NUMBER OF FISH

Right side

n = 218

Left side

NUMBER OF GILL RAKERS

Fig 8

LAKE TAHOE BASIN

Upper Angora Lake

n = 15

Babcock Pier
inshore

n = 35

Lake Tahoe
off Taylor Creek

n = 30

Taylor Creek

n = 68

NUMBER OF FISH

NUMBER OF GILL RAKERS
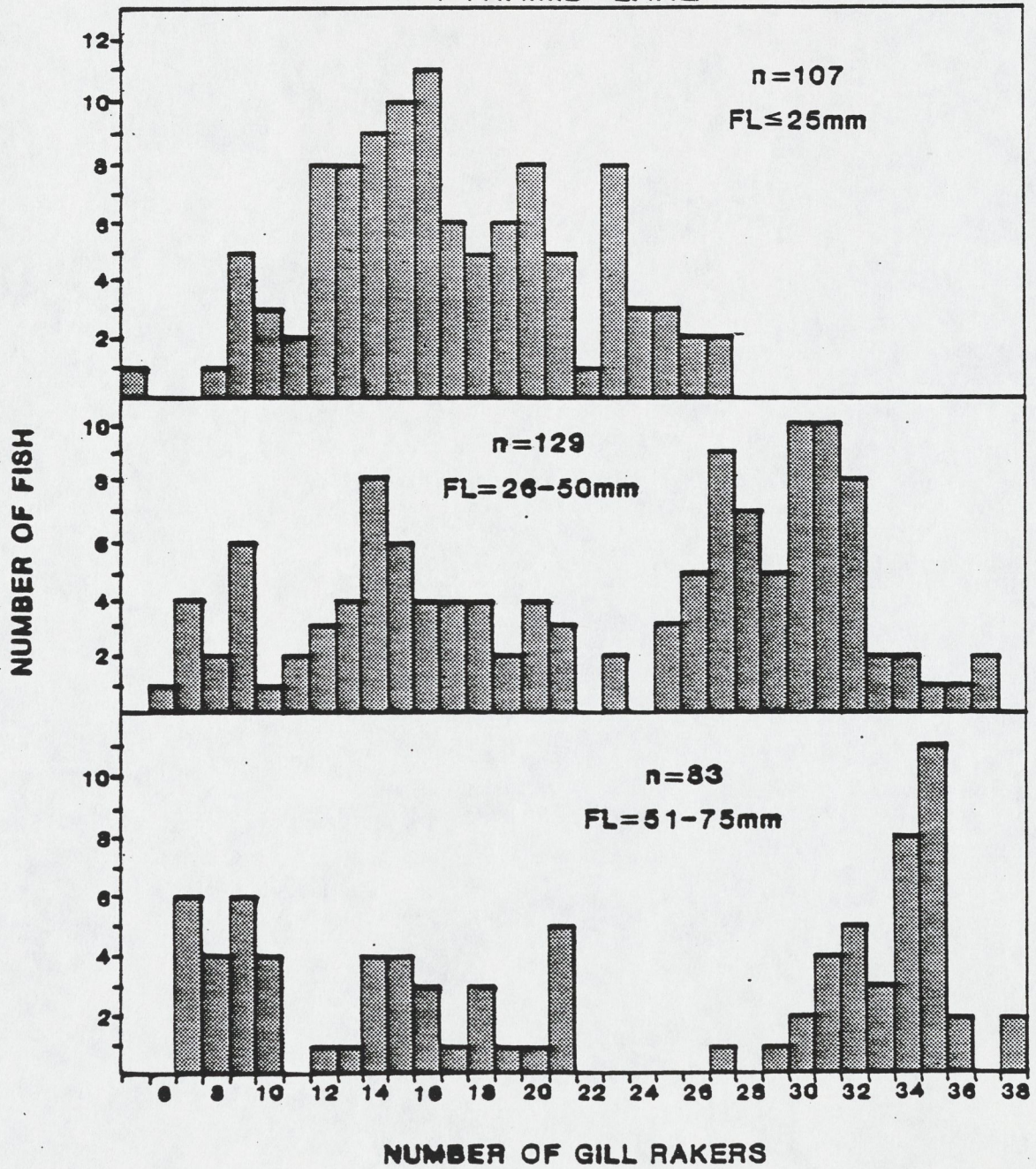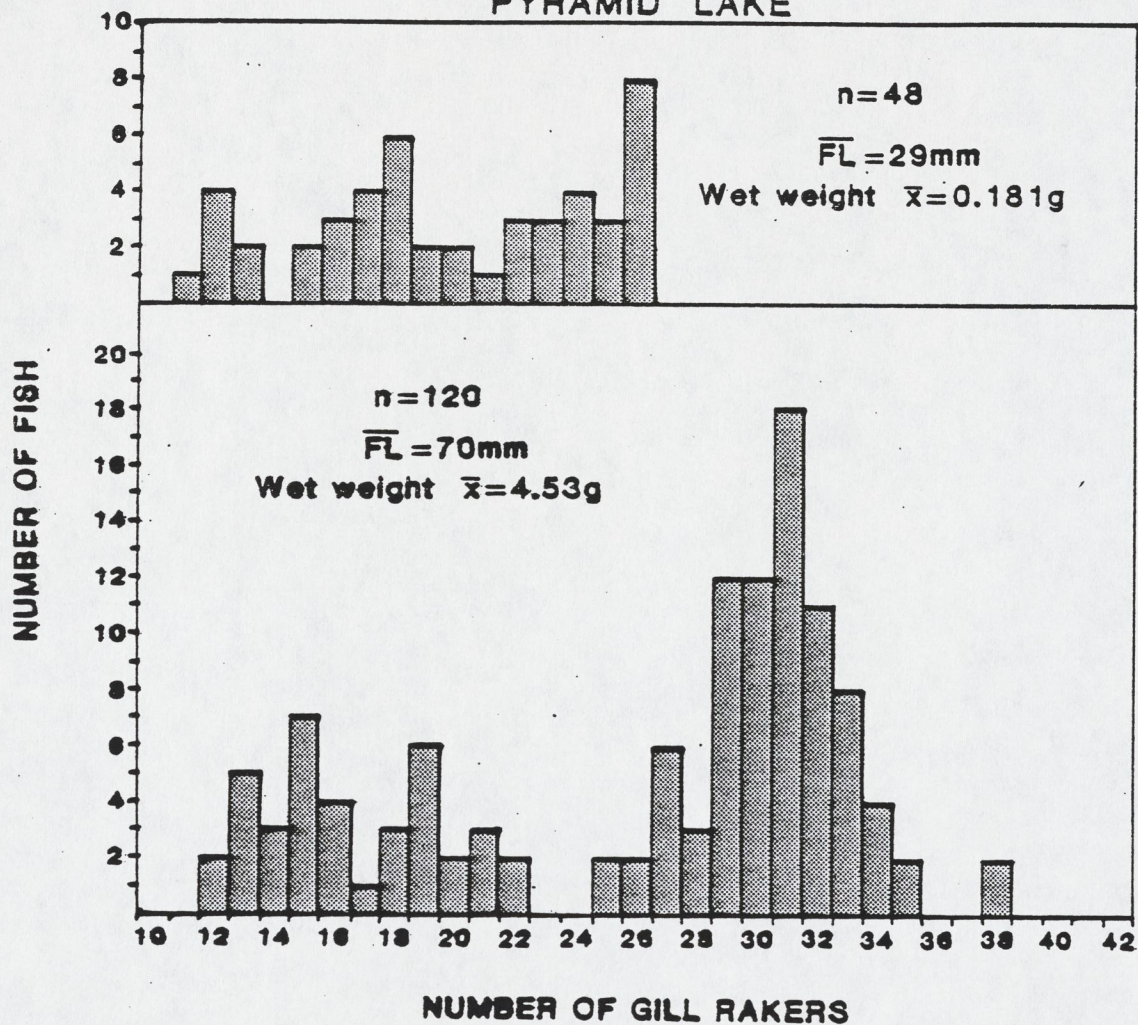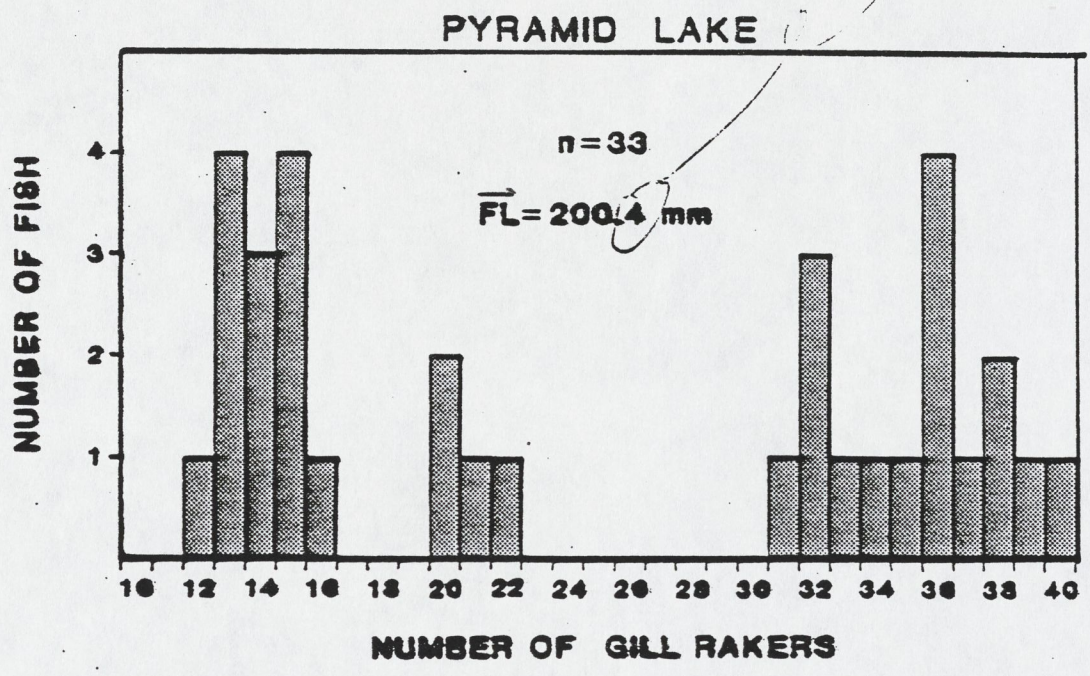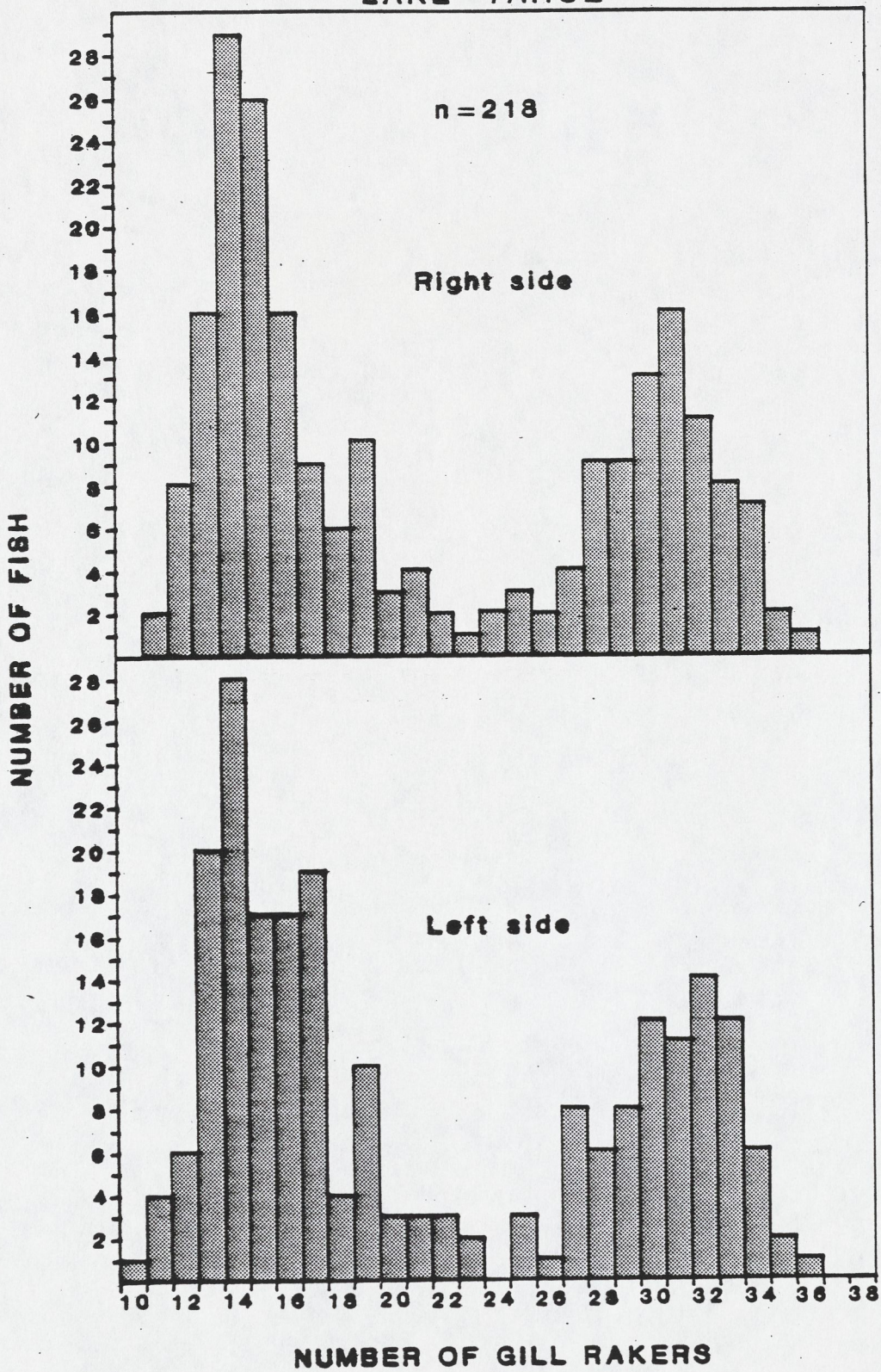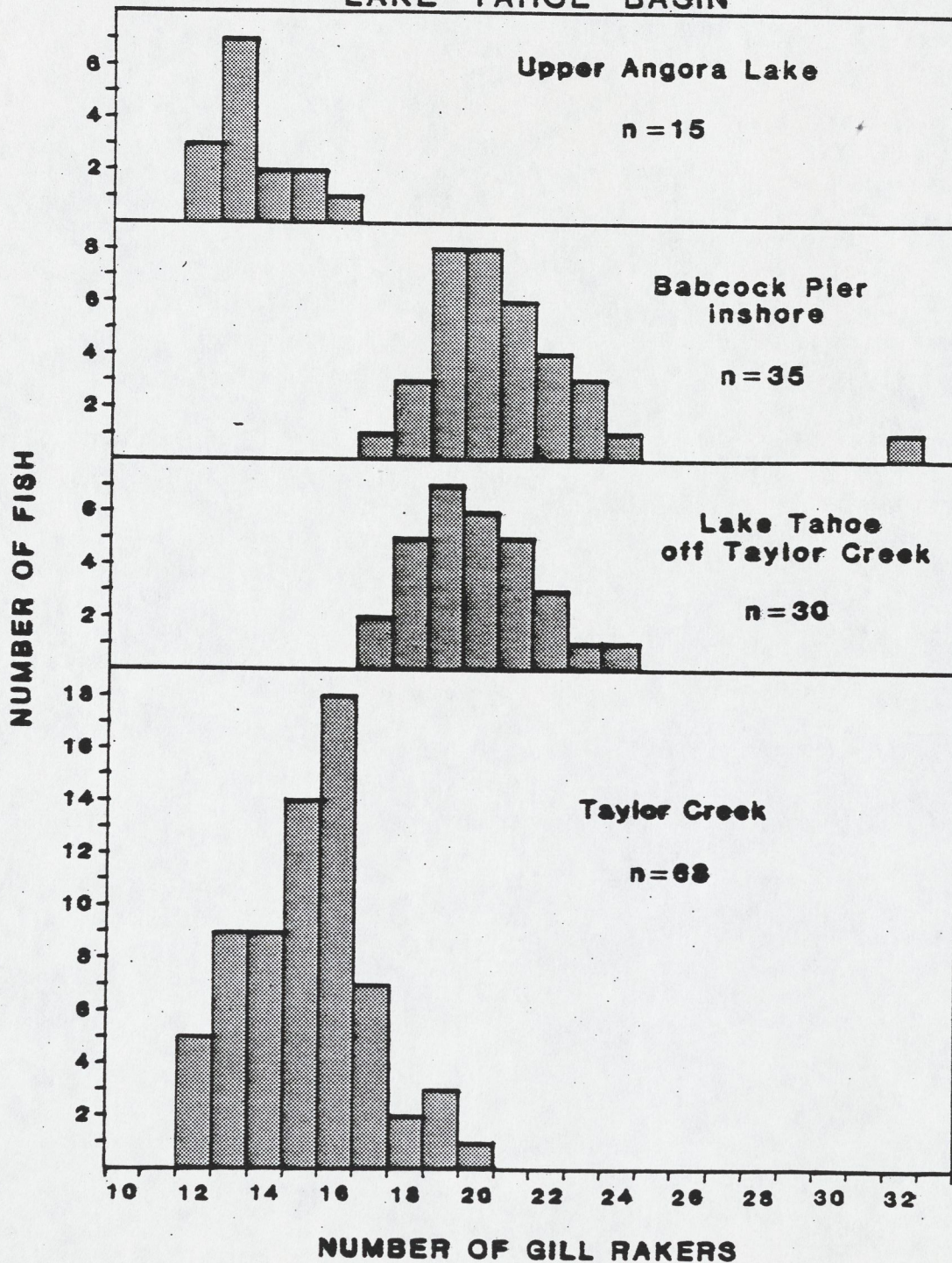
Fig 9.

HONEY LAKE TRIBUTARY

At mouth of
Long Valley Creek

n = 81

3 km upstream,
Long Valley Creek

n = 99

NUMBER OF FISH

NUMBER OF GILL RAKERS

Fig 16

EAGLE LAKE

C.L. Hubbs (1942,
unpublished data)

n=29

Kimsey (1954)

n=272

This study (August 1981)

n=81

$\overline{FL}$=167mm

NUMBER OF FISH

NUMBER OF GILL RAKERS

LAKE ALMANOR

n=131

$\overline{FL}$=290mm

NUMBER OF FISH

NUMBER OF GILL RAKERS
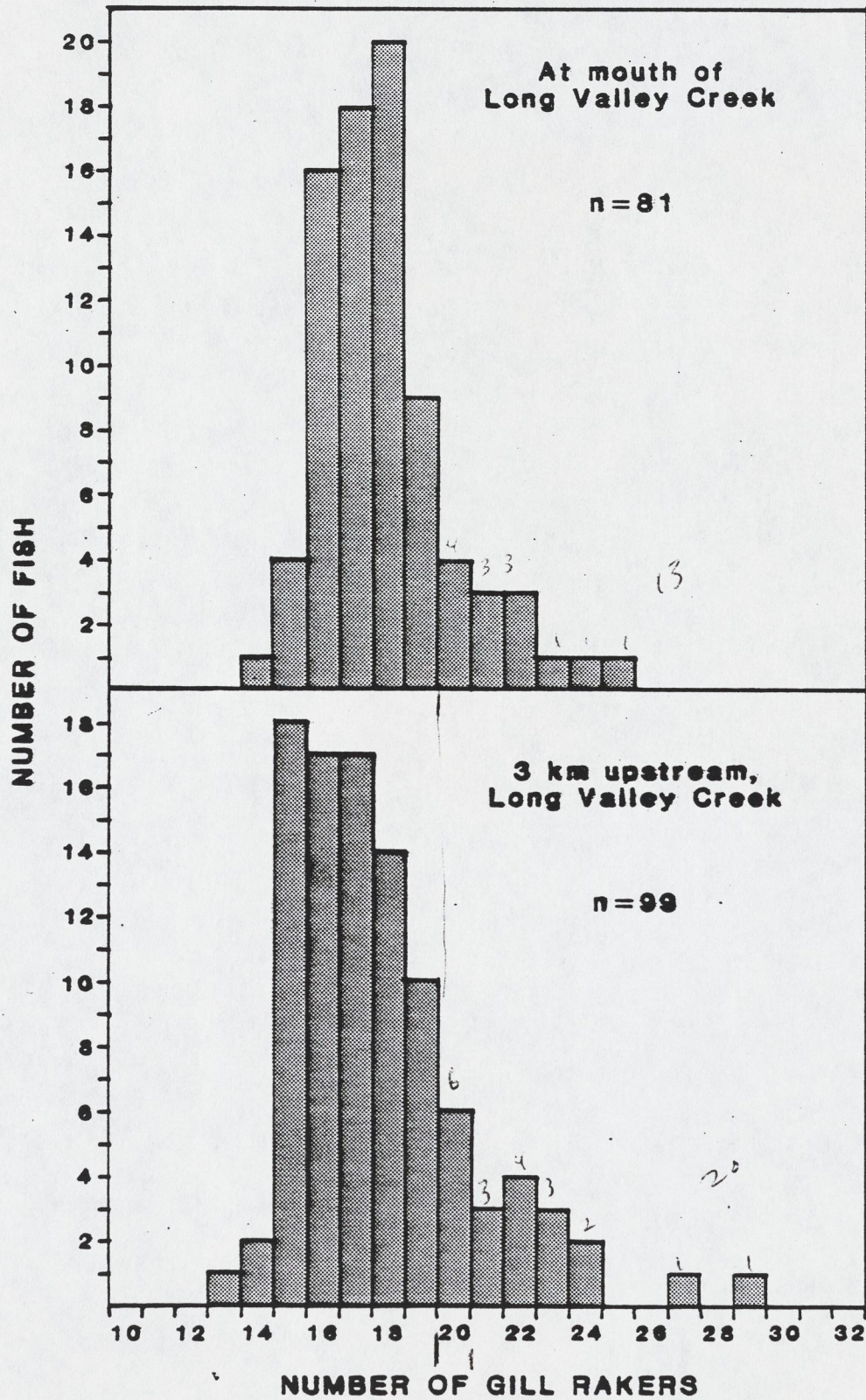
Fig. 12.

AGE, GROWTH, AND FOOD HABITS OF TUI CHUB,
GILA BICOLOR, IN WALKER LAKE, NEVADA

James J. Cooper[1]

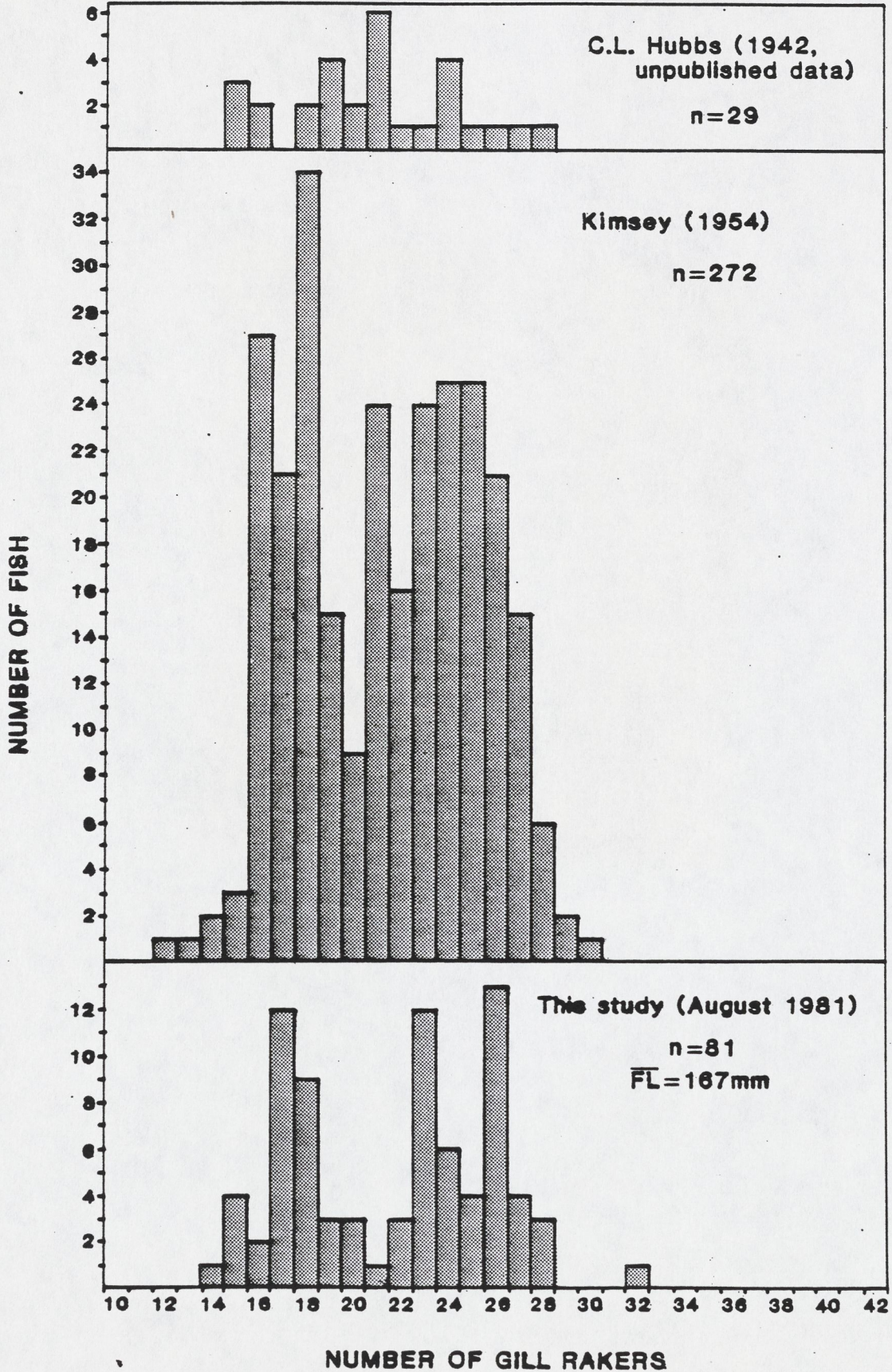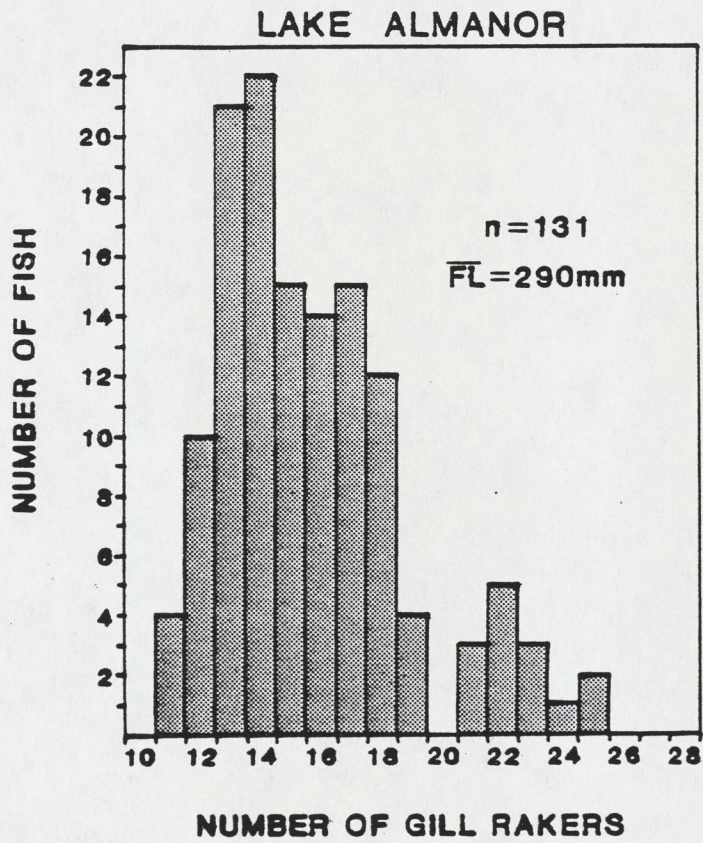ABSTRACT. —At Walker Lake, Nevada, tui chub were collected 1975–1977 for analysis of age, growth rate, and food habits. The fork length (FL)–scale radius (SR) relationship was linear and described by the equation $FL = 4.44 + 3.17$ (SR). Age I, II, III, and IV chub were 116, 176, 218, and 242 mm fork length, respectively. Maximum longevity was six years. The length weight relationship was defined by the log transformed linear equation log weight = -4.65 + 2.93 (log FL). Chub collected from pelagic regions ate mostly zooplankton, whereas chub collected from littoral areas had a diet of zooplankton and benthic organisms.

Tui chub, *Gila bicolor*, is the most abundant of the three species of fish currently found in Walker Lake, Nevada. It is common to the Walker, Carson, Truckee, and Humboldt river systems of the Lahontan basin (La Rivers 1962). Various subspecies of tui chub occur in other endorheic basins in the drainages of pluvial lakes Railroad, Toiyabe, and Dixie, and lakes in the White Mountains in west central Nevada. Other forms occupy lake basins in California, southeastern Oregon, and southeastern Washington (Hubbs et al. 1974). In Walker Lake tui chub are an important component of the ecosystem bioenergetics and are preyed upon heavily by the piscivorous Lahontan cutthroat trout, *Salmo clarki henshawi* (Cooper and Koch, 1984). The vast number of fish-eating birds that annually visit the lake are also predators of tui chub.

Most of the life history information reported in the literature for the Lahontan form of tui chub has been collected from Eagle Lake, California, and Pyramid Lake, Nevada. Kucera (1978) and Kennedy (1983) studied the reproductive biology and growth of Pyramid Lake tui chub. Kimsey (1954) described the life history of the Eagle Lake tui chub population. Cooper (1978, 1982), working on Walker Lake, described various aspects of tui chub life history. Notes on the species can be found in other articles (Snyder 1917, La Rivers 1962, Vigg 1978, 1980, 1981, Galat et al. 1981, Galat and Vucinich 1983a, 1983b). The objectives of this study are to present data on the age, growth rate, and diet of tui chub from Walker Lake.

STUDY AREA

Walker Lake, a remnant of pluvial Lake Lahontan, is in west central Nevada 209 km southeast of Reno. The lake has a surface area of 15,000 ha, is 25 km long and 9 km wide, and has a maximum and mean depth of 33 and 20 m, respectively. It is the second largest remnant of Lake Lahontan. The lake's drainage basin is endorheic and receives water from the eastern Sierra Nevada via the Walker River. Because Walker is a terminal lake, it has a relatively high total dissolved solids (TDS) content of 12,500 mg/l that has increased rapidly in historic times. During the past 45 years the lake has had an average increase in TDS of 152 mg/l per year, and the cutthroat trout sport fishery appears to be in jeopardy. The primary factor responsible for the increasing salinity has been surface evaporation exceeding tributary inflow; since 1915 the lake's elevation has dropped at an average rate of 0.58 m per year (Cooper and Koch, 1984). Agricultural and urban diversion of the Walker River is hastening desiccation of the lake.

METHODS

The scale method was used to analyze the age of tui chub at various sizes (Ricker 1971, Everhart et al. 1975). Scales were taken from the left side of the body above the lateral line and below the dorsal fin. In the laboratory scales were placed between two plastic slides and run through a roller press to form an impression. Scales were read using an Eber-

Errata for Jenkins and Burkhead. 1984. Bull. Ala. Mus. Nat. Hist. 8:1-30

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Description, Biology and Distribution of the Spotfin Chub, *Hybopsis monacha,* a Threatened Cyprinid Fish of the Tennessee River Drainage

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ABSTRACT: Jenkins, Robert E. and Noel Burkhead, 1984. Description, biology and distribution of the spotfin Chub, *Hybopsis monacha.* Bulletin Alabama Museum of Natural History, Number 8:1-30, 6 tables, 7 figs. Anatomy and color of the distinctive spotfin chub, *Hybopsis monacha* (Cope), are described in detail for the first time. This species currently is in the subgenus *Erimystax,* but *Erimonax* may warrant resurrection as a subgenus for its sole reception. The following appear to be closely linked phyletically: *H. monacha, Erimystax s. s.,* additional eclectic species and species-groups presently in *Hybopsis,* the genus *Phenacobius,* and the subgenus *Cyprinella* of *Notropis.*

Major food items of *H. monacha* are benthic immature insects, primarily Diptera. Maximum longevity is about three years, maximum known size 89.5 mm SL; males attain larger size than females. Spawning probably extends from May into August. Number of ripe ova present in females at one time (150–800; 0.8–1.4 mm diameter) increases with size of female, but may greatly underestimate fecundity in one spawning season if *H. monacha* is a fractional spawner.

Hybopsis monacha typically inhabits medium to large, relatively clean, warm streams. It is closely associated with riffles and runs with various largely unsilted substrate types. During the past 100 years, it was generally rare or uncommon.

The spotfin chub is endemic to the Tennessee River drainage, in which it had a wide range: five states, four physiographic provinces, and 12 tributary systems. It has disappeared from most of this range, being extant and localized in only four systems: Little Tennessee, North Carolina; Duck and Emory, Tennessee; and North Fork Holston, Tennessee and Virginia. Probable or possible reasons for reduction or extirpation of populations include impoundments, cold tailwaters, channelization, pollution, turbidity, siltation, stream renovation by ichthyocide, localized intensive collecting, and interspecific competition. The spotfin chub merits protection status of Threatened nationally, as designated in 1977.

Introduction

The spotfin chub, *Hybopsis monacha* (Cope), is a small cyprinid fish, poorly known until recently. Currently, it is placed in the subgenus *Erimystax,* but its exact relationships to this and other species-groups of eastern minnows are unclear. Cope (1868) thought it had solitary habits, but the specific epithet connoting monastic is appropriate only to its occurrence as generally localized, small populations. The nuptial male of brilliant blue body and blue and white fins has been seen rarely.

Hybopsis monacha is endemic to the Tennessee River drainage of Alabama, Georgia, North Carolina, Tennessee, and Virginia. Its original range includes varied upland-montane habitats in four physiographic provinces comprising 12 tributary systems: Blue Ridge (French Broad River and Little Tennessee River systems), Ridge and Valley (Clinch River, Powell River, North and South forks of Holston River, and Chickamauga Creek systems), Cumberland Plateau (Emory River and Whites Creek systems), and Interior Low Plateaus (Shoal Creek, Little Bear Creek, and Duck River systems). However, since 1960 *H. monacha* is known only from the Duck, Little Tennessee, Emory and North Fork Holston systems, North Carolina, Tennessee and Virginia. Based on its wide extirpation, and

on localization and vulnerability of the extant populations, it has been designated as a Threatened species nationally since 1977.

With recognition of wide decline of *H. monacha,* Jenkins was contracted in 1975 by the Office of Endangered Species, U.S. Fish and Wildlife Service, to perform a study of morphology, life history, habitat, and distribution. The data were used in brief accounts of the species (Jenkins and Burkhead, 1980; Jenkins and Musick, 1980; Starnes and Etnier, 1980; Parker and Dixon, 1981), and as a basis for granting it protection status. In 1981, we performed further work for the U.S. Fish and Wildlife Service to determine the current status of populations of *H. monacha* and to supplement previous life history work.

Here presented is a detailed account of historical and current biogeography from museum specimens, ecological data files, and our fieldwork through 1982. This was greatly enhanced by major contributions of collection data by numerous ichthyologists, several with special interest in *H. monacha.* Additionally, the first detailed description of the species is given, and its complex phylogenetic relationships are discussed on the basis of continuing study by Jenkins.

A critical feature of this study is presentation of geochronographic figures. These depict, for single rivers or river systems with extant populations, the past and current distribution of the species, give numbers of specimens captured by specific collection sites, and summarize numbers of collections that did and did not include the species. In so doing, we attempted, and at least closely approached, a review of the entire history of ichthyological survey in the streams treated. Inclusion with the maps of data indicating apparent absence of the species ("negative" data) provides an aspect of the historical record often needed but missing or lightly treated in similar studies. We regard the maps as a valid starting point for future studies of the same species (and to have application in study of associated species). Investigators would not need to repeat the tedious and pitfall-replete process of regathering and resynthesizing the original data, which are highly scattered, often esoteric, and largely unpublished.

and Inland Fisheries, courtesy Jack M. Hoffman.

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Methods

External, sensory, and trophic anatomy. — Lengths of specimens are expressed as mm SL (standard length), measured to the nearest 0.1 mm with needlepoint dial calipers, or as size classes of 2 mm SL. Measurements of body parts were read to the nearest 0.1 mm, except for basal diameters of tubercles and brain dimensions, which were measured under a binocular microscope with dial calipers to the nearest 0.05 mm. Standard methods (Hubbs and Lagler, 1958) generally were used for counts and measurements of body parts, but some of our methods warrant qualification when alternative methods may be in common practice or implied by Hubbs and Lagler. Head and postorbital lengths were measured to the bony posterior margin of the operculum. Snout and postorbital lengths were taken from the bony ortibal rim. Orbit length and interorbit width were measured from the fleshy orbital rim. Upper lip length includes the anterior expansion of the lip and excludes the barbel. Nuptial tuberculation, the cephalic lateral line system and cutaneous taste buds were examined under strong light with a binocular microscope and compressed air. Snelson (1972) was followed for terminology of the lateral line system. Gill raker counts are of the total, including rudiments, on the outer portion of the first right arch. The intestine and swim bladder were extracted for measurement.

Food. — Diet was determined from contents of the first descending section of the intestine. Percent fullness of this section was visually estimated.

Aging. — Attempts to age specimens by recognition of annuli on scales often resulted in great uncertainty. Usually 6–10 scales were removed from the dorsolateral area below the dorsal fin. For 56 specimens, scales were mounted between glass slides. For 28 additional specimens, scales were placed in a watch glass with alcohol. Scales were examined under a 30x stereomicroscope and/or a 100x microprojector. Attempts to age many problematic specimens were made during well separated periods, to allow a fresh opinion each time, but no clear advantage was gained.

For some specimens, regarded as aged with some certainty, periods of rapid or slow growth were recognized by groups of widely or closely spaced circuli (each group with four to many circuli) in the lateral and posterior fields, and/or by cutting over of one to three lateral field circuli. However, for many other specimens, adjacent similarly spaced circuli numbered only two or three, rendering it highly uncertain that a full period of rapid or slow growth for the year was indicated. In some of these specimens, posi-

tion of a putative annulus often varied distinctly among the scales. The first annulus generally was the least distinct or unrecognizable annulus. Of 84 specimens we attempted to age by scales, 36 were deemed unageable, and 48 were aged with some certainty. Hereafter the latter are termed "scale-aged" specimens. We did not back-calculate lengths of scale-aged specimens because a single circulus marking an annulus often was unrecognizeable (particularly at the first annulus), and because of potential bias from using a subsample that in this case was particularly selective.

Length frequency also presented unsolved problems in aging individual specimens and recognition of a general growth pattern. The composite of 317 specimens (Table 3) from throughout the species range, the vast majority from extant populations, did not clearly identify age groups, despite separate analysis of the sexes and only moderate latitudinal/altitudinal range. Separate frequency distributions for the Little Tennessee, Emory, and North Fork Holston populations did not enhance aging due to smaller samples and possible year-class differences in growth. Apparent protraction of the spawning season also probably adversely affected length frequency analysis.

In the Age and Growth section, age groups are recognized on combination of the pooled length frequency and the 48 scale-aged specimens, with emphasis on the latter.

Reproductive paramenters. — Specimens were sexed by examination of gonads or, for some nuptial males, by presence of well-developed tubercles. Size of gonads was recorded as minute, small, medium, large, or very large, by comparison with maximum gonad size of the respective sex. GSI refers to gonosomatic index, calculated by total weight of both ovaries divided by eviscerated body weight X 1000. Weights were determined after blotting, to the nearest 1 mg for ovaries and to the nearest 10 mg for bodies, with a Mettler analytic balance. Numbers of Class I ova were determined by direct count from both ovaries. Numbers of Class II ova were estimated by counting a total of 125–200 ova of classes I and II from each specimen, subsampled from different areas of the ovaries, to determine the ratio of Class II to Class I in the pooled subsamples of the specimen; the ratio was then multiplied by the total number of Class I ova in that specimen. Ova diameters were measured with an ocular micrometer in a stereomicroscope. Ten randomly selected ova of each class from seven specimens were measured, to the nearest 0.1 mm for Classes I and II, nearest 0.05 mm for Class III.

Substrate. — Size ranges in cm of certain substrate types mentioned herein are: pea or small gravel, 0.3–3.0; medium gravel, 3–5; large gravel, 5–8; small rubble, 8–15; medium rubble, 15–22; large rubble, 22–30; boulder, greater than 30.

Geochronographic figures: data base, collecting methods, and interpretation. — These figures are maps showing loca-

tions, years, numbers of collections, and results of collecting in rivers with three of the extant populations (Figs. 5–7). Collection sites generally are 0.1–0.4 km length. The center of each site usually is located to the nearest 0.1 Rkm (River kilometer). A few sites were located approximately, generally when distance/bearing descriptors and site names given by the collector disagreed slightly. In such cases, the most likely site was chosen. A few localities shown as one actually comprise 1-3 separate sites whose centers are usually 0.5 km apart at most. For USGS/TVA topographic quadrangles that omit North Fork Holston River mileages, we determined these with a map measurer using checkpoints provided by the TVA; some of these may be slightly inaccurate. In a few cases the number of specimens is approximate; this occurs for specimens released without careful count or those observed instream. In instances when a range of number of specimens was given to us, the low estimate was used. Locality data for all records are given under Materials. Data for collections lacking *H. monacha* are available from Jenkins.

Interpretation of qualitative (presence/absence) and quantitative (number/density) catch results, particularly for determination of stability or changes in distribution and abundance, should include consideration of objectives, technique, and intensity of collecting. These in turn may be affected by substrate, turbidity, and discharge and by habitat preferences of target species. We did not sample by electroshocker or ichthyocide when turbidity would have reduced specimen capture. High discharge from heavy rains caused us to abort collecting trips. However, under favorable conditions, we believe that for *H. monacha,* one intensive collection by either seine, shocker, or ichthyocide at a site generally provides adequate qualitative information, i.e. the species is either present or absent (or uncollected but extremely rare, virtually absent). Most collections made by seine and shocker since 1970 in the upper Little Tennessee, Emory, and North Fork Holston were aimed particularly, often solely, at securing *H. monacha* by expending greater effort in its preferred habitat, or they involved chemical treatment (rotenone or creosol of fairly large areas, sodium cyanide in small, swift areas). Several sites in the above rivers have been sampled often, lending greater strength to qualitative results. Further, although some sites were sampled only once or twice, generally these were near more frequently worked sites. Data from low sampling intensity tended to be consistent with those from high intensity, and combination of data from both intensities usually yielded a clear pattern for 10–20 km river sections concerned.

Seining often is criticized as yielding too little or invalid qualitative and quantitative data. Many collections treated herein were made by seine, virtually all of those from the 1800s to 1950, and many of ours since 1970. We think the seine yielded adequate qualitative data in most situations. We emphasize that seining effectiveness is greatly enhanced by knowledge of specific habitat associations and by good execution of techniques appropriate for these habitats.

Population of *H. monacha* in North Fork Holston River are often centered at major areas of gravel in or near swift current. Such relatively smooth surfaced substrate is readily sweep-seined. An indication of our apparent effectiveness is depletion by seining of *H. monacha* at North Fork Holston Rkm 10.1 and 41.2. Also, at North Fork Holston Rkm 3.2, we first surveyed a wide area by snorkeling, locating only two juveniles at one spot of rough bottom; immediately subsequent seining of the entire snorkeled area took one juvenile from the exact spot where the two were sighted.

The prevalent methods used in the Little Tennessee and Emory were electroshocking and ichthyocide, probably more effective methods therein than seining because of higher frequency of large rubble and boulder than in the North Fork Holston. In the latter, most of our 1981 collections and all of our 1982 collections were by shocker. Kick-seining, of course, yields useful results for benthic fishes among large substrate and was employed in much of our work.

Two types of quantitative information derive from numbers of specimens in a collection: general or relative abundance (compared with associated species, or with other efforts for target species alone) and population density. Estimates of the latter for *H. monacha* resulting from random community sampling generally have little significance because of its distinct tendency to localize. Density estimates are treated under Distribution, Emory system.

Abundance descriptors used herein, from numbers captured or seen while snorkeling, are rare (1–4 specimens), uncommon (5–10), and common. These interpretations are fairly firm for some North Fork Holston sites because we tended to equalize efforts at specific sites (each generally worked 1–2 h, some on 4–8 dates). We made similar interpretations of most recent data by others because we are aware of their collecting strategies.

For pertinent background and documentation of collecting efforts, we review under Distribution major or otherwise important collecting programs, with indication of methods when known. These and additional collections from three of the four systems with extant populations are summarized in Figs. 5–7.

Materials

A virtually complete record of capture, repository or release, or observation is given. Institutional acronyms are under Acknowledgements. NMB and REJ prefix our field numbers, with which series are identified at Roanoke College. RC denotes series at Roanoke College not collected by us. Number of specimens (in parentheses) follows the catalog or field number, or acronym. For more than one number in parentheses, the first is of extant specimens, the others released or observed specimens, as indicated. Brackets signify all specimens were released or observed. Asterisk denotes extant specimens not examined by us. Notation ''nonextant'' refers to specimens, none examined by us, that

apparently no longer exist. All specimens indicated as unexamined, released, observed, or nonextant are regarded as competently identified. The few misidentifications of this distinctive species that have occurred were resolved.

The 841 total specimens (96 collections and/or observations) comprise 333 extant, examined by us (part or all of 55 series); 199 extant, unexamined (part or all of 36 series); ca. 63 released (part or all of 12 collections); ca. 113 observed (6 sessions); and ca. 133 unlocated, probably nonextant (forming part of 1, all of 4 collections). Numbers taken in two additional nonextant collections are unknown.

Within each tributary system, collections are listed in sequence progressing upstream, all main river sites first. Collections from the same site are listed in chronological order. Nonoriginal locality data, except for conversions to metric, are bracketed. For collectors, generally only party leader or agency is given.

Duck River System. *Tennessee*: LEWIS COUNTY: NLU 39464 (4*) Buffalo River 0.4 km below to 0.4 km above Grinders Creek mouth, 8-9 April 1978, Douglas. UMMZ 105181-105182 (3) Grinders Creek at TVA site 579, 41SE, 42NE, 50SW [6.4 airkm NW of Napier], 24 May 1937, TVA.

Little Bear Creek System. *Alabama*: COLBERT COUNTY: UMMZ 132502 (1) Little Bear Creek at TVA site 620 [5.6 airkm SW of Tuscumbia], 19 November 1937, TVA.

Shoal Creek System. *Alabama*: LAUDERDALE COUNTY: UMMZ 192582 (orig. Indiana Univ. 4787) (1), USNM 36664 (2) Shoal Creek at [probably near] Florence, 1884, Gilbert, Swain.

Chickamauga Creek System. *Georgia*: CATOOSA COUNTY: (nonextant) [South] Chickamauga Creek at Ringgold, summer 1877, Jordan.

Little Tennessee River System. *Tennessee*: MONROE COUNTY: UMMZ 113292 (1) Citico Creek near mouth, 16.1 km E of Madisonville, 11 November 1936, Holloway. UMMZ 165598 (1) Citico Creek 10 miles above mouth, near Tellico Plains, 16 September 1940, Holloway. BLOUNT COUNTY: UMMZ 129466 (37) Abrams Creek ca. 1.6 km above mouth, ca. 0.4 km above and below Panther Creek mouth, 6 September 1937, Hubbs. UMMZ 163294 (1) Abrams Creek near Panther Creek mouth, 31 March 1941, Hubbs. UMMZ 163280 (3), UMMZ 163280S (1* cleared, stained) Abrams Creek at Happy Valley, ca. halfway between mouth and falls, 31 March 1941, Hubbs. KFW (32) Abrams Creek within ichthyocided zone, below falls, 9 June 1957, Whitney. *North Carolina*: SWAIN COUNTY: UMMZ 131474(2) Tuckasegee River at Noland Creek mouth, 29 June 1940, Hubbs. Little Tennessee River: RC (4, 4 rel.) Rkm ca. 144.4, vic. end of Co. Rt. 1125, including Halls Ford, 0.5 km below Sawmill Creek, near or just within upper arm of Fontana Reservoir, 6 November 1975, Eager. (TVA 68.16, 1* specimen, from this site on ''12'' November 1975 probably is one of the ''released'' specimens, misdated). RC (4) same site as preceding, 26 November 1975, Eager. UT 44.1424 (1*) same site as preceding, 8 July 1977, Etnier. UF 26374 (1*) same site as preceding, 1 October 1977, Etnier. RC (1) Rkm 154.9, 50 m above Rattlesnake Creek mouth, 10 April 1980, Crittenden. UT 44.1424 (1*) Rkm 156.1, along Co. Rt. 1113, at swinging bridge, 1 October 1977, Etnier. MACON COUNTY: Little Tennessee River: UF 24085 (2*) Rkm 159.3, along Co. Rt 1113 near county line, 7 July 1977, Etnier. UT 44.1110 (3*, 3 rel.) Rkm 160.9 near Stiles, vic. Lost Creek Bridge, between Rts. 28 and 1370, ca. 2.9 km above Co. line, 6 November 1975, Eager. TVA (2*) same site as preceding, 25 November 1975, Eager. UF 26423 (1*) same site as preceding, 8 July 1977, Etnier. TVA 68.15 (1*, 1 rel.) Rkm 170.6, Coggins Bend, access via Welch Farm, ca. 0.8 km above Rose Creek mouth, 6 November 1975, Eager. RC (2) same site as preceding, 25 November 1975, Eager. NCSM 6894 (1*) Rkm ca. 177.0, Rt 28 bridge near Iotla, just below Iotla Creek, 6 November 1975, Eager.

French Broad River System. *North Carolina*: MADISON COUNTY: USNM 40499 (1) Spring Creek at Hot Springs, 13-14 August 1888, Jordan. BUNCOMBE COUNTY: UMMZ 192584 (orig. Indiana Univ. 8132) (2) Swannanoa River at railroad station to ca. 3.2 km above, near Asheville, 15, 17 August 1888, Jordan.

Whites Creek System. *Tennessee*: RHEA-ROANE COUNTY LINE: USNM 190644 (7) Whites Creek 1.6 airkm SW of Glen Alice, 29 August 1959, Taylor.

Emory River System. *Tennessee*: **Emory River**: ROANE COUNTY: UMMZ (44*), UMMZ (16), UMMZ 157704 (2) Rkm ca. 20.9, vic. Avery Branch mouth, 12-13 October 1941, TVA. MORGAN COUNTY: UT 44.189 (2) Rkm ca. 29.0, at Oakdale, 16 October 1967, Etnier. UT 44.563 (4) Rkm 35.1, at Hall Bridge near Camp Austin, 4 September 1968, TVA. TVA 68.8 (6*) same site as preceding, 11 December 1974, TVA. UT (2*) same site as preceding, 6 November 1975, Etnier. BHB (6*) same site as preceding, 18 August 1981, Crittenden. UF 15919 (4) Rkm ca. 44.2-46.0, near Nemo Bridge between mouths of Obed River and Island Creek, SW of Wartburg, 12 June 1968, Etnier. UT 44.564 (36 plus 11 nonextant) same site as preceding, 16 August 1968, TVA. (1 nonextant) same site as preceding, 5 August 1969, Etnier. UT 44.552 (21) same site as preceding, 6 August 1970, Etnier. UT 44. 1031 (19*) same site as preceding, 8 May 1974, UT students. UT 44.1092 (23*) and WCS 265-01 (8*) same site as preceding, 24 July 1974, Starnes. TTU (38), AU 12167 (1*) same site as preceding, 14 and/or 19 September 1974, Riddle. [2 obs.] same site as preceding, 10 December 1974, Saylor. TVA 68.7 (1*) same site as preceding, 12 December 1974, Saylor. UAIC 4897.02 (11*) same site as preceding, 6 June 1975, Boschung. AU 11026 (24*) same site as preceding, 27 August 1975, Ramsey. [ca. 80 obs.] same site as preceding, 15 August 1979, Beets, Smith. NMB 601 (9, ca. 20 obs.) same site as preceding, 10 August 1981, Burkhead. BHB 887 (4*), UT 2377 (4*) same site as preceding, 19-20 August 1981, Crittenden.

Emory River tributaries. *Tennessee*: MORGAN COUNTY: USFWS (2*) Island Creek just above mouth in Emory River, 23 August 1979, Smith. (27 nonextant?) Obed River, tributary of Emory River, Rkm 0.6, fide Riddle (1975), 1974, Riddle. AU 11449 (2*) Obed River, Rkm 15.0, at Daddys Creek mouth, 3 July 1974, Riddle. UT 44.2359 (3*) Clear Creek, tributary of Obed River, Rkm 2.3, at Lilly Bridge, 7 August 1981, Crittenden. TTU (4), AU 11474 (1*) Clear Creek, Rkm 6.4, at Jett Bridge, Rt 4252, 27 June 1974, Riddle. UT 44.2361 (2*) same site as preceding, 5 August 1981, Crittenden. (89 nonextant) Clear Creek, Rkm 14.2, at Waltman Ford Bridge, White Creek mouth, August 1968, TVA. UT 44.2360 (3*) same site as preceding, 6 August 1981, Crittenden. UT 44.2363 (2* and 1 hybrid) Daddys Creek, tributary of Obed River, Rkm 0.0-0.5, 16 July 1981, Crittenden. (5 nonextant?) Daddys Creek, Rkm 0.3, 1974, Riddle. TTU (2*) Daddys Creek, Rkm ca. 3.9, near Devil's Breakfast Table in Catoosa Wildlife Management Area, 16 November 1979, Abbott. UT 44.2378 (3*) same site as preceding, 20 August 1981, Crittenden. UT 44.2362 (1*) Daddys Creek, Rkm ca. 5.6, unnumbered Co. Rt. at Cumberland-Morgan Co. line, 28 July 1981, Crittenden.

Clinch River System. *Tennessee*: CLAIBORNE-UNION COUNTY LINE: USNM 117361 (1) Clinch River at Walkers Ford, [Rkm ca. 203], 12 October 1893, Evermann. CLAIBORNE COUNTY: (nonextant) Ball Creek near Tazewell, 12 October 1893, Evermann.

Powell River System. *Tennessee*: CLAIBORNE COUNTY: USNM 70581 (2) Indian Creek near Cumberland Gap, 17 October 1893, Gurley.

North Fork Holston River System. North Fork Holston River: *Tennessee*: HAWKINS-COUNTY LINE: UMNH 17606 (orig. VPI 554) (4) Rkm 0.3-1.2, near Sullivan Rt 11 bridge, 12 June 1954, Ross. USNM 177657 (orig. VPI 558) (1) same site as preceding, 9 July 1954, Ross. CU 46397 (2) same site as preceding, 9 August 1963, Zorach. TVA 68.21 (2*) same site as preceding, 23 August 1977, TVA. USNM 231355 (orig. REJ 701) (1, 1 obs.) Rkm 3.2, 0.5 km. below Sensabaugh Branch mouth, 26 August 1975, Jenkins. CU 50382 (orig. VPI 559) (1) Rkm 7.5, Cloud Ford, above bridge on Cleveland-Morrison City Road, 9 July 1954, Ross. *Virginia*: SCOTT COUNTY: REJ 376 (7) Rkm 10.1, Click Island, 1 August 1970, Jenkins. TVA 68.6 (1*) same

site as preceding, 13 March 1972, TVA. TVA 68.27 (1*) same site as preceding, 21 April 1976, TVA. (1 rel.) same site as preceding, May 1981, TVA. REJ 568 (1) Rkm 37.7, Holston Mill along Co. Rt 689, 4 June 1972, Jenkins. REJ 931 (1) same site as preceding, 18 June 1981, Jenkins. REJ 552 (18) Rkm 41.2, island off Blue Springs Branch mouth, along Co. Rt 689, 16 May 1972, Jenkins. REJ 569 (10) same site as preceding, 4 June 1972, Jenkins. TU 96409 (orig. REJ 668) (3) same site as preceding, 20 May 1974, Jenkins. USNM 231356 (orig. REJ 707) (2) same site as preceding, 27 August 1975, Jenkins. REJ 928 (2, 2 rel.) same site as preceding, 17 June 1981, Jenkins. REJ 947 (1, 1 rel., 4 obs.) same site as preceding, 19 May 1982, Jenkins. REJ 948 [1 rel.] Rkm 45.9, along Co. Rt 689, 0.5 km above Cove Cr. mouth, 19 May 1982, Jenkins. WASHINGTON COUNTY: NMB 614 (3, 7 rel.) Rkm 59.2, island off Co. Rt 615, 0.7 airkm S of Jct. Co. Rts 614-615, near Mendota, 14 August 1981, Burkhead. REJ 949 (2, 1 rel.) Rkm 62.9, Co. Rt 614 bridge at Mendota, 19 May 1982, Jenkins. NMB 613 (6, 16 rel.) Rkm 68.2, Hobbs Ford off Co. Rt 614, 1.6 airkm E of Mendota, 14 August 1981, Burkhead. REJ 950 (1, 20 Rel.) same site as preceding, 20 May 1982, Jenkins. NMB 612 (3, 6 obs.) Rkm 71.6, Fleenor Mill Ford off Co. Rt 614, 3.9 airkm ENE of Mendota, 14 August 1981, Burkhead. REJ 951 (4, 6 rel.) same site as preceding, 20 May 1982, Jenkins. SMYTH COUNTY: ANSP 2036-2040 (5 syntypes) Rkm ca. 132, vic. of Saltville; see Types section, October 1867, Cope. USNM 40475 (3) same site as preceding, or nearby, 9 August 1888, Jordan. ANSP 74181 (1) Rkm 142.6, at Co. Rt 633 bridge 5.8 km. E of Saltville, 21 June-4 July 1954.

South Fork Holston River System. *Tennessee:* SULLIVAN COUNTY: UMMZ 157561 (3) South Fork Holston River 0.4 km above South Holston Dam site, 23 September 1947, Bailey. Formerly UMMZ 157534, exchanged (2*) South Fork Holston River near Fish Dam Creek mouth, 3.2 km ENE of dam site, 22 September 1947, Bailey. UMMZ 159595 (3) South Fork Holston River 1.6 km below state line, 23 September 1947, Bailey. UMMZ 157506 (1) Jacob Creek, tributary of South Fork Holston River, from mouth to ca. 200 m upstream, 20 September 1947, Bailey.

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Hybopsis monacha (Cope)
Spotfin Chub
Figs. 1-3

</div>

Cope (1868) described the spotfin chub as *Ceratichthys monachus* from an unspecified number of specimens seined in October 1867 with W.A. Stuart. The five syntypes found by Fowler (1924) and us are subadult to adult, 52–79 mm SL, in fair condition. Orthography of the specific epithet was clarified by Hubbs and Crowe (1956).

The types are from North Fork Holston River, Virginia, the locality being the vicinity of Saltville located in Smyth County just above the Washington County line. Cope (1868) stated that the species occurs in the channel of the Holston in Washington County, but stated he collected in Saltville, and often seined "...for some miles at a time." We arbitrarily plotted the type locality, and the second Saltville area record (Jordan, 1889), at Saltville (Fig. 7: Rkm 131.9).

Description

Diagnosis. — Body elongate, slightly compressed; eye small, lateral; mouth inferior, upper lip expanded anteriad; terminal labial barbel minute or absent; teeth 4-4; scales moderately small, lateral line 52–62; anal rays 8; caudal spot with distinctive shape; posterior part of dorsal fin with dark area or moderate amount of melanin in membranes; no blot-
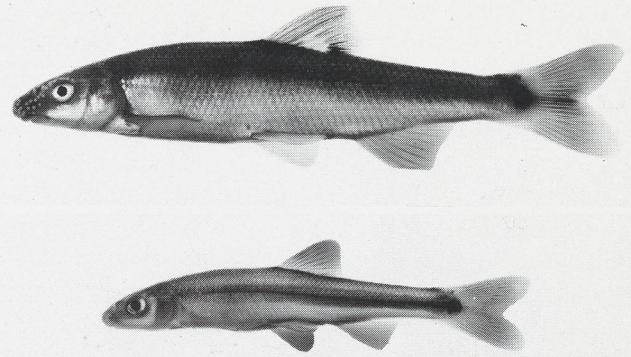
Fig. 1. *Hybopsis monacha:* Upper - tuberculate male 74 mm SL taken 4 June 1972 (REJ 569). Lower - juvenile male 44 mm SL taken 16 May 1972 (REJ 552). Both from North Fork Holston River.

ches or speckling on body. Nuptial male with medium to large, antrorse tubercles on most of head dorsum; smaller tubercles on front and side of snout; body with iridescent blue prominent above lateral line; fins blue with white margins.

External morphology. — Morphometry: Physiognomy of head and body and form and location of fins are shown in Fig. 1. Proportional measurements (Table 1) show slight but significant sexual dimorphism only in lengths of the dorsal, anal and pelvic fins (longer in males) and predorsal and postdorsal lengths (dorsal fin inserted more anterior in males). It is surprising that a significant difference was not found in pectoral fin length (expected longer in males), as this fin is tuberculate only in males and probably used to aid in maintenance of contact with females during the spawning act. The probability of a significant difference between the sexes in pectoral length was less than 0.1 but not less than 0.05. The juveniles in the measured sample may have reduced the pectoral fin difference of adults. Sexual dimorphism in position of the dorsal fin insertion in certain other American cyprinids was found by Snelson (1972), Hubbs et al. (1974), and Snelson and Pflieger (1975).

Scale counts: Lateral line 53 (in 1 specimen), 54(2), 55(5), 56(4), 57(5), 58(3), 59(3), 60(4), 61(2), $\bar{x} = 57.2$ (range of 52-62 given by Hubbs and Crowe, 1956). Rows across back 15(2), 16(2), 17(20), 18(2), 19(3), $\bar{x} = 17.1$. Rows across belly 13(5), 14(9), 15(12), 16(1), 17(1), $\bar{x} = 14.5$. Circumferential rows (last 2 counts + 2) 30(1), 31(1), 32(5), 33(8), 34(9), 35(1), 36(3), 38(1), $\bar{x} = 33.5$. Predorsal rows crossing middorsum 24(3), 25(4), 26(11), 27(3), 28(1), $\bar{x} = 25.7$. Caudal peduncle 15(2), 16(7), 17(12), 18(6), 20(1), $\bar{x} = 16.9$. Breast squamation (% scaled area) 10-100, $\bar{x} = 48$. Scale radii only in posterior field; counts from 38 total scales from upper body beneath dorsal fin of 5 specimens 50-77, $\bar{x} = 65$ mm SL: primary radii 3-11, $\bar{x} = 4.7$, secondary radii 0-6, $\bar{x} = 2.1$, total radii 3-12, $\bar{x} = 6.9$; larger specimens tended to have higher counts.

Fin ray counts: Pectoral 13(3), 14(13), 15(10), 16(1),

Table 1. Proportional measurements (expressed in thousandths of SL) of well preserved larger juveniles and adults of *Hybopsis monacha:* 9 females 46-78, x = 62.7 mm SL; 13 males 48-76, x = 65.6 mm SL. Student's t-test was used to test the significance between means. Levels of probability (P) greater than 0.05 were considered not significant (ns).

Character	Sex	Range	x	SD	t value	P
Head length	F	213–234	228	0.60	1.632	ns
	M	216–235	223	0.68		
Head depth	F	131–141	138	0.60	0.607	ns
	M	133–145	139	0.35		
Head width	F	112–129	120	0.55	1.167	ns
	M	108–128	117	0.52		
Snout length	F	75–84	79	0.32	1.027	ns
	M	73–89	81	0.50		
Postorbital	F	80–94	88	0.45	0.766	ns
	M	79–99	90	0.56		
Orbit length	F	39–60	51	0.67	0.892	ns
	M	40–54	49	0.43		
Upper lip length	F	58–67	63	0.46	0.109	ns
	M	60–68	63	0.23		
Gape width	F	46–62	52	0.51	1.710	ns
	M	46–65	56	0.53		
Interorbital width	F	69–83	74	0.46	0.320	ns
	M	69–82	75	0.36		
Caudal peduncle length	F	182–239	206	1.57	0.056	ns
	M	194–218	206	0.83		
Caudal peduncle depth	F	78–92	84	0.41	1.750	ns
	M	81–101	88	0.53		
Dorsal fin length	F*	164–193	175	1.03	3.335	0.01
	M**	177–194	186	0.53		
Anal fin length	F*	129–161	144	1.06	3.348	0.01
	M**	146–169	159	0.93		
Pectoral fin length	F*	139–170	158	1.10	1.994	ns
	M**	151–177	166	0.75		
Pelvic fin length	F	128–151	138	0.070	2.824	0.02
	M	138–153	145	0.38		
Body depth	F	151–219	190	2.16	0.101	ns
	M	175–221	191	1.25		
Body width	F	114–153	131	1.36	1.958	ns
	M	116–136	123	0.65		
Predorsal length	F	515–543	526	0.87	2.557	0.02
	M	493–529	516	0.99		
Postdorsal length	F	476–510	494	1.13	2.518	0.05
	M	494–528	506	0.95		
Prepelvic length	F	471–499	492	0.92	1.298	ns
	M	474–505	487	0.98		
Preanal length	F	673–718	698	1.39	1.170	ns
	M**	682–712	692	0.85		

*8 specimens; **12 specimens

x = 14.3. Pelvic 8-8(27), 8[left]-7(2), 9-8(1), x = 16.0. Anal 7(2), 8(35), x = 8.0. Dorsal 8(32). Branched caudal 17(24).

Nuptial tuberculation: twenty-eight highly tuberculate males, 60-89, x = 73.2 mm SL (KFW, Abrams Cr.; REJ 569, 950, North Fork Holston R.; UF 15918, Emory R.), were examined. Fig. 2 is of a male with basically typical distribution of head tubercles; its head dorsum tubercles are larger, less crowded and fewer than in most specimens. Distribution of cephalic tubercles (and range of tubercle counts of 11 specimens) are: head dorsum from internasal region to occiput (58–142); anterior snout (38–64); sides of snout, over lachrymal bone (12–41); jaw rami and lower cheek with a few tubercles in some specimens (0–5, 0–6 respectively). Total head tubercles range 112–244, x = 183; the figured specimen has 118. Larger specimens tend to have higher counts, resembling certain species of *Notropis (Cyprinella)* in Gibbs (1963:Fig. 2, upper two specimens). A narrow to broad (Fig. 2) hiatus occurs between internasal and anterior snout tubercles in most specimens; in some specimens, generally those with relatively high tubercle numbers, the area of the hiatus has tubercles spaced about equally as in the internasal region. Size of most head tubercles is medium-small to medium-large (compared with cyprinids in general), basal diameter of largest ones 0.9% SL. Tubercle size tends to be smallest, and density greatest, on the snout tip. Some specimens with relatively few, less crowded tubercles on the dorsum behind the snout have suggestion of alignment of many of those tubercles into two rows, each slightly lateral to the midline (as on left side in Fig. 2); no specimens have a straight row. (See also description of small, weakly tuberculate specimens, below.) Most dorsum and lateral snout tubercles are antrorse, except supraorbitally where tubercle tips more frequently curve laterad; most on the snout tip are erect.

The body, although most roughened, is weakly tuberculate. Its tubercles are generally very small to minute; they tend to be more widely distributed in larger specimens. Most specimens have moderate to low density of tubercles in most dorsal and lateral areas and relatively few tubercles on the belly. The anterior nape tends to be the most heavily tuberculate area, with tubercles scattered over all exposed scale fields; a few tubercles approach the size of smaller head tubercles. Elsewhere tubercles tend to occur only marginally and submarginally on scales. The midlateral body tends to be more tuberculate than the upper body except for the nape. When tubercles are present on the lower half of the caudal peduncle, they tend to be slightly larger than those on the upper half. Firm, pronouncedly thickened, probably keratinized epidermis extends over the scales in the ventrolateral area from the pectoral to caudal fin. Thickening increases toward the posterior margin of each scale, effecting a rough surface. Thickening is greatest over the urosome, where in peak development the surface of each scale is further roughened by 3–10 longitudinal ridges apparently of the same tissue as general epidermal thickening. Some specimens with pronounced urosomal skin thickening apparently lack tubercles in that area; the function of tubercles probably is served by elevation of skin at scale margins and surface ridging.

On the pectoral fin, small tubercles occur along most of the dorsal surface of ray 1 and succeeding 7-10 rays; they are arranged uniserially (except biserial at proximal ray fork), and number 1–2 per ray segment. Tips are curved posteriad or medioposteriad when the fin is abducted 90°.

Pelvic fin tubercles are minute and occur on the dorsal surface of rays, from ray 2 through 4-8. No other fins are tuberculate.
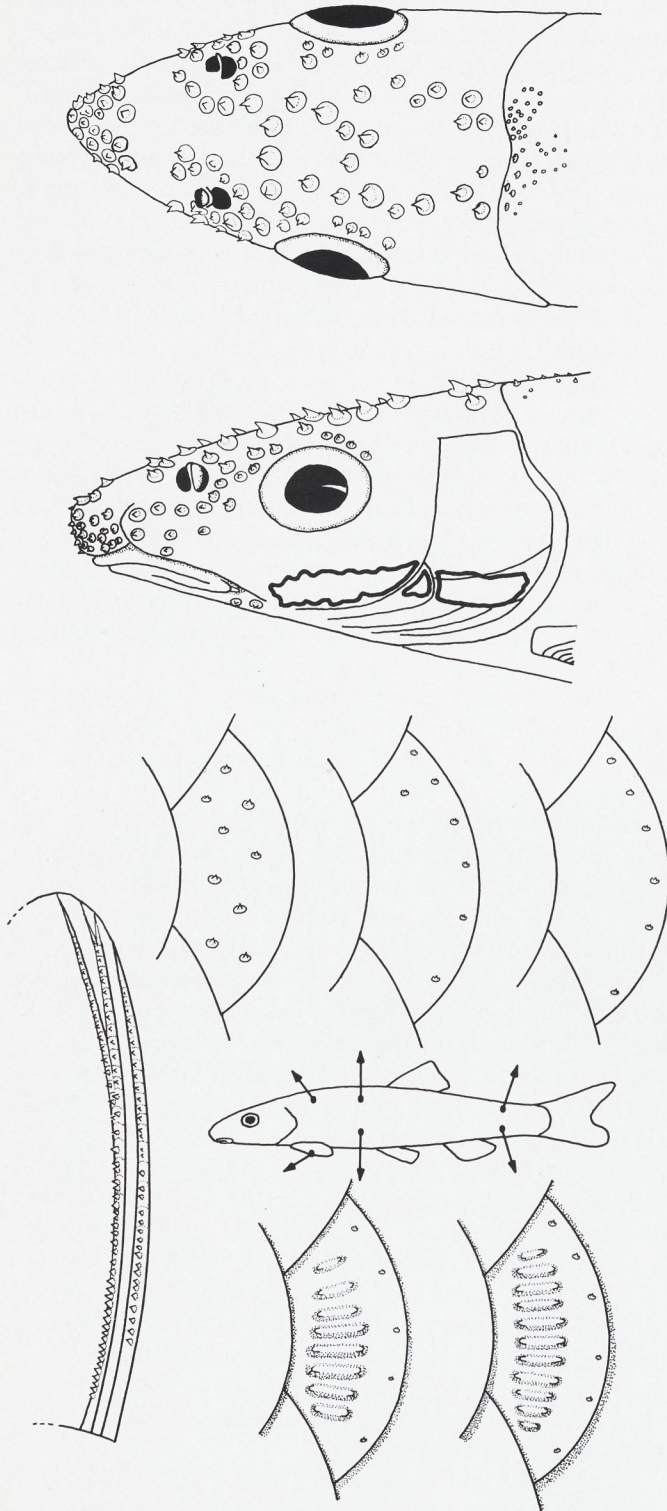
Fig. 2. Highly tuberculate males of *Hybopsis monacha*. Dorsal and lateral head from same specimen as in Fig. 1, upper. Bold outline on lower side of head indicates location of nuptial pad. Tuberculation of representative scales and dorsal surface of first two pectoral fin rays based on composite of specimens in KFW series from Abrams Creek, 9 June 1957.

A nuptial cheek pad is present in two males (REJ 569, UF 15918). It is a pale, flat, smooth surfaced (under 10X magnification) area of firm (not hard), possibly keratinized tissue on the lower cheek and operculum (Fig. 2). The pad is only moderately developed in one male (74 mm, REJ 569) compared with nuptial males of other species of the subgenus *Erimystax* and the genus *Phenacobius* and is barely discernible on another male (72 mm, UF 15918). Oddly, all 25 Abrams Creek tuberculate males appear to lack the pad, although it is hinted in one of the larger. It is absent in the 89 mm North Fork Holston male (REJ 950), which on the lower cheeks has 6 tubercles on one side, 11 on the other. The pad probably increases friction between spawning individuals, and may be a contact pad.

Other large, apparently adult size, males and females, and some smaller which may be large immatures or have just matured (taken from spring to mid-summer, sometimes with highly tuberculate males), have weakly developed tuberculation. Their tubercles are small or, in most specimens, minute (possibly in "bud" stage, Lachner and Jenkins, 1971) on the head, anterior nape and, present only in larger males, minute on pectoral and pelvic fins. A nuptial pad and coloration were not detected on any. These males tend to have better developed tuberculation than females of similar size with which they were collected. Some adults of both sexes taken in later summer and fall have obvious, somewhat keratinized buds or old tubercle cores on the head. Smaller specimens tend to have fewer head tubercles than larger specimens, and often most of their dorsum tubercles are arranged into 2 or 4 longitudinal rows.

Sensory and trophic anatomy. — The form of the dorsal surface of the brain of species of *Hybopsis* was studied by Davis and Miller (1967), but they lacked *H. monacha.* Compared with data and figures by Davis and Miller, *H. monacha* has a large cerebellum and optic lobes and small facial and vagal lobes (Fig. 3), adapting it for manuverability and placing it in the "sight feeder" group, although the orbit is small. Brain proportions (thousandths of total brain length) of one specimen (REJ 522) 65 mm SL, total brain length 7.45 mm are: forebrain length 336, width 134; total optic width 523; cerebellum length 282, width 282; facial lobe length 107, width 121; vagal lobe length 161, width 67, total vagal width 215; rhomboid fossa length 80, width 101.

Lateral line on body complete, uninterrupted. Preoperculomandibular (PM) and supraorbital (SO) canals always incomplete. Pore counts from 15 adults: infraorbital (IO, including common pore, when rarely present, at infraorbital-supratemporal (ST) junction) 11(1), 12(4), 13(4), 15(1), 11 + 2(1), 8 + 2 + 3(1), 11 + 3(1), 5 + 5 + 2 + 3(1), 9 + 5 + 2(1); PM 7(1), 8(1), 2 + 5(2), 3 + 5(10), 3 + 6(1); SO 8(12), 9(3); ST 5(11), 3 + 3(1), 4 + 1(1), 1 + 2 + 2(1), 1 + 2 + 2 + 1(1). Canal locations, pore sizes, and canaliculus lengths are as described and illustrated from three specimens by Reno (1969b), with the following modifications. Often the third

IO canaliculus is slightly shorter and joins the IO slightly posterior to the position figured by Reno. Often the cephalic lateralis dips moderately ventrad from the IO-ST junction, not from above the posterior end of the opercle.

FOREBRAIN

OPTIC LOBE

CEREBELLUM

FACIAL LOBE

VAGAL LOBE
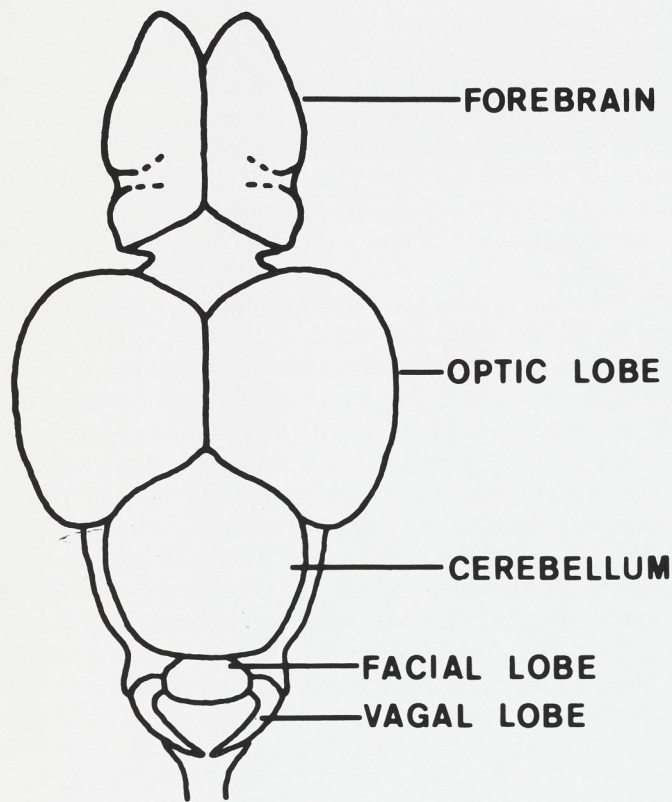
Fig. 3. Dorsal view of brain of *Hybopsis monacha,* 64.9 mm SL (REJ 522), North Fork Holston River.

The mouth is distinctly inferior. The lips are thick and heavily papillose; the central portion of the upper lip is extended anteriad. The barbel generally is only a minute, tapered extension or nub on the posterior end of the lip symphysis. Infrequently it is separated by a cleft and excised or clearly pendant from the lips (Reno, 1969b: fig. 10, ventral view). No specimens have more than one barbel on a side, and often there is no trace of a barbel on one or both sides. Cutaneous taste buds are obvious only on the ventral surface of the head and barbel, where they are densely distributed. The rugose area of moderate to large buds depicted with stipple by Reno (1969b:750) should have included the lower edge of the snout and isthmus.

Gill rakers 5(2), 6(6), 7(3), 8(3), 9(1), x = 6.7; upper rakers short, acute; lowers rudimentary, blunt. Pharyngeal teeth 4-4 in the 10 specimens studied. Fowler (1924) gave the dental formulae of syntypes as 4-4, rarely 5-4. Our examination of the 5 syntypes showed all have 4-4 teeth. All teeth hooked at tip in some specimens. With wear, teeth apparently lose hooks and become acutely tipped, the tips grading basad into a smooth, flat grinding surface. Some teeth, possibly only when recently ankylosed, have serrations along

the lower portion of the inner curve of hooks and on a flange slightly below, where the grinding surface develops. Thickness of teeth and arch and length of the upper and lower edentulous processes are moderate. As is typical of cyprinids, a true stomach is apparently absent in *H. monacha;* the bile duct enters the alimentary canal just posterior to the esophagus. The intestine is short and S-shape, unwhorled. In 8 adults 53–72, $\bar{x} = 62$ mm SL, the ascending section is only 8.2–17.5, $\bar{x} = 13.8\%$ SL, and total intestinal length is 55.3–77.9, $\bar{x} = 68.4\%$ SL. The inner lining of the intestine has folds arranged in a herringbone-like pattern. The peritoneum is medium brown to partly silvery (melanophores not contiguous), usually light brown.

Other internal characters. — Gas bladder large, two chambered; total length 28.4–31.8, $\bar{x} = 29.9\%$ SL, posterior chamber length 18.9–20.6, $\bar{x} = 19.6\%$ SL, in 8 adults with abdominal cavity length 38.5–47.6, $\bar{x} = 42.8\%$ SL. Peritoneal tunic (Rosen and Greenwood, 1970) covers anterior chamber. Pneumatic duct uncoiled, attached to anterior portion of posterior chamber. Bladder lacks spiral markings, striations, and intrinsic or extrinsic muscles.

Post-Weberian vertebrae (subtraction of 4 from counts in Jenkins and Lachner, 1971) 37(3), 38(15), 39(1), $\bar{x} = 37.9$.

Coloration. — In life: Hand held nonnuptial adult males, adult females and juveniles are pale to medium green or dusky grey above the lateral line, silvery on the lower sides. An iridescent stripe of green, sometimes with gold suffusion, occurs middorsally and one on each side dorsolaterally. The dorsal spot is obvious and black in large specimens. The black caudal spot is obvious in juveniles, but not as predominent as when preserved; in large specimens the spot tends to be partly masked by silvery. When observed underwater, the ground colors of juveniles and small adults appears medium grey throughout the body, and the iridescent stripes on the upper body and dark dorsal and caudal spots are obvious.

Nuptial color is shown in photographs by Jenkins (Deacon et al., 1979) and W.C. Starnes (Parker and Dixon, 1980). The respective specimens are 74 mm taken 4 June from North Fork Holston River and 76 mm, 24 July, Emory River. The blue color of the former specimen had faded markedly in 15 min. between placement in formalin and photographing, and the slide was underexposed. The 76 mm specimen may have lost some blue prior to photographing.

The 74 mm male was deep metallic turquoise to royal blue on the body from the dorsolateral area to about the lateral line, from occiput to tail, and over the entire caudal base. Contrasting with the upper body, an iridescent blue wash extended from the lateral line to the ventrolateral area and was present on some belly scales. The dorsum was iridescent greenish. An iridescent oblique dark blue bar occurred just behind the head. On the head a band of blue, more brilliant than on the upper body, extended along the dorsal

margin of the operculum. The dorsal fin spot was blue. With rapid fading of the blue in formalin, the back became darker green and the mid and lower sides a lustrous silvery white.

All fins had satiny white distally, least in the pectoral (margin only) and caudal (tips only), best developed in the pelvics and anal, which had a broad white marginal band and white extending proximad along anterior rays. Tubercles were whitish.

A 72 mm nuptial male taken 12 June from Emory River was described (D.A. Etnier, C.R. Gilbert, pers. comm., 1968) as having an iridescent deep sky blue upper body and silvery lower body; no blue or milkly colors were noted in the fins.

The probable peak nuptial color was seen in one of the largest known males, 89 mm from the North Fork Holston on 20 May 1982. Although bluish did not extend below midside, most of the upper body was iridescent aqua to turquoise, changing rapidly to steel blue in formalin. The dorsum was brownish olive when the living specimen was viewed from directly above, but bluish when observed laterally. All fins had satiny turquoise, with some golden glints, distributed throughout the pelvic, anal and dorsal, mostly along the first three rays and margin of the pectoral, and narrowly margining the caudal. Upon death turquoise disappeared from the fins, revealing satiny white in the same areas.

An additional color pattern, possibly developed only during courtship/spawning, was seen in aggressive tuberculate males on 15 August in Emory River (underwater observation by J.P. Beets, in litt.). Two large whitish zones occurred on the anterior half of the body, extending from the lower sides to the dorsolateral area. Between and posterior to the zones, the body was blue. The whitish zones were most distinct dorsolaterally, where the remainder of the body was deepest blue, rendering males highly obvious. This pattern was obvious in the 89 mm male in life; it faded rapidly in formalin, remaining slightly developed in the alcoholic specimen due to differential intensity of melanophore pigmentation. It is slightly developed in a few of the 25 highly tuberculate preserved males from Abrams Creek on 9 June. It is faintly suggested in the preserved 74 mm male (Fig. 1) but was not detected in life.

As indicated under Reproduction, some small mature males may lack blue color during the spawning season. Females lacked nuptial color.

In preservative: The head and body are dark above, pale below (Fig. 1). Scales above the lateral line are marked, inevidently in larger specimens, moderately obviously in small specimens, by a smoothly curved intensification of melanophores parallel and submarginal to the rounded posterior margins of scales. Thus the dorsolateral area lacks the diamond-shape pattern of pigmentation characteristic of many *Notropis (Cyprinella)* species. The lateral stripe on the posterior half of the body is centered along the horizontal myoseptum, but the stripe is prominent usually only below

this myoseptum. In adults, which have a darker back than juveniles, the upper edge of the stripe is less discrete (often indistinct) than in juveniles. Frequently the stripe is interrupted by a narrow, pale, obliquely oriented line over each transverse myoseptum. On the anterior body of adults the stripe generally is poorly developed or absent; occasionally it is quite dusky with the darkest portion centered just above the horizontal myoseptum. The anterior portion of the stripe is usually faint in juveniles, which typically have a narrow dark line over the horizontal myoseptum. Just above and below each lateral line pore on the anterior body is a small area of slight intensification of pigment. A middorsal stripe is well developed from head to tail, widest before the dorsal fin.

The caudal spot is particularly diagnostic. It is prominent in young, juveniles and smaller adults, but occasionally it is broadly connected with the lateral stripe in large specimens with a dark stripe; the adult male in Fig. 1 has a well developed, distinct spot. In young and small juveniles the spot usually is disconnected from the lateral stripe. The spot has two contiguous components, one over caudal base musculature, one in the area of the basal exposed portion of the medial 3-4 caudal rays. The anterior, larger component usually is round or oval, the longest axis vertical. On caudal rays generally it is quadrate or subtriangular, the apex anterior. The two components are nearly disconnected in young and small juveniles. In large juveniles and small adults the components generally are moderately to broadly connected, and the dark area often appears somewhat bell shaped. Large adults normally have the components completely connected, and the dark area is ovoid or amorphous.

The size and intensity of the dorsal fin spot correlates positively with body length, as in many cyprinids and shown for *Notropis (Cyprinella)* by Gibbs (1975b) and for total fin pigmentation in *Notropis (Lythrurus)* by Snelson (1972). The spot is best developed in nuptial males and is obvious in other large males and females. It is formed by concentration of melanophores in membranes between the last 3 rays and between the forks of each ray, and centered mid-third of the length of the rays. Melanophores are sparse in the central portion of the membranes between the medial rays, and absent in anterior membranes (except lining rays). Some nuptial males have a clear "window" in the basal part of the dorsal fin, effected by a nearly pigmentless area below and slightly anterior to the spot, thus highlighting the spot. Young and small juveniles have relatively few melanophores in the posterior membranes; hence, they lack a definitive spot.

Relationships

Hybopsis monacha is a distinctive species, described once and never synonymized. Due to its distinctiveness and because critically important nuptial color and tuberculation were long unknown, its relationships have been unclear. It was described in the genus *Ceratichthys* Baird, in which most

barbeled chubs were sometimes placed during the 1800's. It has generally been placed in *Erimystax* Jordan, which at times was recognized as a genus, and essentially since 1956 as a subgenus of *Hybopsis* Agassiz. Jordan (1924) described *Erimonax* as a genus for the sole reception of *H. monacha*, but was not followed. Reviews of the taxonomic and nomenclatural history of *Hybopsis* are by Reno (1969a), Clemmer (1971) and Lachner and Jenkins (1971).

Evidence of close relationship of *H. monacha* to the other four species of *Erimystax (sensu stricto,* type species *Hybopsis dissimilis,* including *H. cahni, H. insignis, H. x-punctata*) is their sharing of two distinctive, probably apomorphic character states: nuptial pad and anteromedial upper lip expansion. Additionally the five species have a terminal labial barbel. As indicated by Jenkins and Lachner (1971), these five species are phyletically linked to *Hybopsis (Hybopsis) storeriana, H. (Platygobio) gracilis, H. (Macrhybopsis) gelida,* and the five species of suckermouth minnows, genus *Phenacobius.* All of these also develop a nuptial pad and, except for *Phenacobius,* terminal labial barbels. *Phenacobius* also has an upper lip expansion. The large majority of these fishes are elongate, live in moderate to swift currents, and are adapted for benthic feeding.

Hybopsis monacha appears to be most closely allied to *Cyprinella,* one of the largest subgenera (ca. 25 species) of *Notropis,* by possessing several diagnostic features of *Cyprinella* (in part, Gibbs, 1957a): cephalic dorsum tubercles antrorse and tending to align in longitudinal rows; hiatus present between snout and internasal tubercles; lower urosome with tubercles larger than adjacent body areas, or with distinctive keratinization; pectoral fin tubercles uniserial, first ray tuberculate; distinctive head physiognomy; white in fins and iridescent blue upper body color of nuptial males; blackened posterior dorsal fin membranes. The only known hybrid of *H. monacha* involved a species of *Cyprinella* (Reproduction section).

Features of *H. monacha* in which it diverges from *Erimystax s.s.* and/or *Cyprinella* are small size of eye and scales, distinctive shape of caudal spot, and anal ray count of 8 (7 in all species of *Erimystax s.s.,* 8-11 in *Cyprinella*). Although *H. monacha* lacks the diamond-patterned scale coloration typical of *Cyprinella,* this is also absent in some *Cyprinella* species.

Pending further study of the *Hybopsis - Notropis* complex, particularly the barbeled *H. (Hybopsis) labrosa* species-group which also probably is closely related to *Cyprinella* (Jenkins and Lachner, 1980), *Erimonax* may warrant resurrection to at least subgeneric level for sole reception of *H. monacha.* We leave *H. monacha* in *Erimystax* until conclusions are firm. Regardless of taxonomic rank, *H. monacha* seems phyletically linked, in an undetermined way, to two large, complex groups of eastern American minnows - shiners *(Notropis)* and certain non-nestbuilding barbeled "chubs" *(Hybopsis).*

Diet and Feeding Behavior

Food of 39 specimens collected during daylight is summarized in Table 2. The diet comprises a relatively nondiverse assemblage of virtually entirely immature aquatic insects. Of the 2539 insect items found, 89.8% were dipterans. The bulk were midge larvae (48.0% of total insects, some in cases) and pupae (0.4%) and blackfly larvae (41.0%) and pupae (0.1%); all other dipterans were cranefly larvae, *Antocha* (0.4%). Mayfly larvae were commonly taken, formming 6.8% of total items. Of these, *Baetisca* and heptageniids were rarely taken; the remainder (6.2% of total items) were tiny baetids, probably *Baetis* and/or *Pseudocloeon,* and unidentifiable genera probably at least largely baetids. At least most insects unidentified to order (1.5%) probably also were baetids. The following orders formed small portions of the diet: Trichoptera 1.6% of total items (some hydroptilids in purse cases); Lepidoptera 0.2% (all *Parargyractis*); Plecptera 0.08%; Coleoptera 0.04%; all were larvae except one of the 40 trichopterans was a pupa.

Dipterans dominated gut contents of most specimens oc-

Table 2. Food contents of first descending section of intestine of *Hybopsis monacha.* Total insect items = 2539. Total fish sample 39 specimens: 23 small specimens, ranging 27-48, x = 38.2 mm SL; 16 large specimens, 51-87, x = 63.6 mm. River systems subsamples: 11 from North Fork Holston River, 20 Emory system, 7 Little Tennessee River, 1 Abrams Creek. Number of specimens by month: 1 in April, 2 May, 5 June, 1 July, 17 August, 7 September, 6 November. Omitted are 6 specimens (5 from Little Tennessee in November) that lacked insects and Algae.

Items	% of total insect items	No. spms. with item — Small fish	No. spms. with item — Large fish	Range — Small fish	Range — Large fish	x̄ both sizes
Insecta, undet.	1.5	7	6	1–12	2–33	7.1
Ephemeroptera, undet.	5.0	8	8	1–17	1–26	10.6
Baetidae	1.2	1	6	1	1–23	6.5
Heptageniidae, undet.	0.3	1	3	3	1–3	2.3
Epeorus	0.2	0	1	0	3	3.0
Stenonema	0.04	0	1	0	1	1.0
Baetiscidae, *Baetisca*	0.1	1	1	1	1	1.0
Plecoptera, undet.	0.04	0	1	0	14	14.0
Taeniopteryx	0.04	1	0	100	0	100.0
Trichoptera, undet.	1.0	6	10	1–8	0.4–67	14.8
Hydropsychidae	0.2	0	3	0	2–14	6.0
Hydroptilidae	0.4	0	5	0	0.4–67	14.7
Lepidoptera, *Parargyractis*	0.2	0	3	0	0.2–1	0.7
Coleoptera, undet.	0.04	0	1	0	1	1.0
Diptera, Tipulidae, *Antocha*	0.4	0	4	0	0.4–3	1.6
Chironomidae	48.4	20	15	1–100	4–81	61.9
Simuliidae	41.0	13	10	2–100	15–96	37.6
Nematoda	—	0	1	—	—	—
Filamentous Algae	—	2	0	—	—	—
Detritus	—	4	2	—	—	—
Sand, mica	—	5	2	—	—	—

casionally, usually in specimens with few items, mayflies and caddisflies were found in moderate percentages, and one specimen had consumed only a stonefly.

Insect choices were essentially uniform in the four river systems sampled. Analysis of diet by subdivision of fish into two size groups (Table 2; small fish group includes one or few young, mostly juveniles; large fish group composed of subadults and adults) indicates that small and large fish have similar preferences. Number of insect items in large fish (2-460, $\bar{x} = 115$ items) was generally greater than in small fish (1-96, $\bar{x} = 39$). The somewhat greater taxonomic diversity of items consumed by large fish probably reflects greater food intake due to larger gut capacity, and possibly a wider range of foraging habitat, including current swifter than that typically occupied by small fish.

Insects consumed were generally minute, usually 1 mm or less. Large midge and blackfly larvae were rare. Most mayfly larvae seemed to be early instars. The notable exception was one stonefly larva, *Taeniopteryx* nearly of emergence size, the only item eaten, and occupying 30% of anterior gut lumen of a 37 mm specimen. The generally much larger number of items taken by large fish also indicates that large fish generally do not select larger insects than do small fish. An average difference in size of insects consumed by large and small fish was not discerned by observation of gut contents.

Non-insect items were rarely found. One adult had one nematode, possibly parasitic. Filamentous algae was taken by only two juveniles, both in a November collection from Little Tennessee River; the algae filled 10% of gut volume in one specimen, 40% in the other. Detritus, other than probable shredded midge larvae cases, was recognized in only six specimens (three from Little Tennessee River in November), forming 5-80%, $\bar{x} = 28\%$ of gut volume. Sand, one to several grains, occurred in only seven specimens, four from Little Tennessee River in November. Two of the latter also had a few mica flakes, the only specimens in which mica was found. All of these items, certainly the inorganic matter, may have been consumed incidentally while foraging for insects.

Regarding seasonality, the data are largely from the warmer half of the year. In 32 specimens taken from mid May to mid September (Table 2), volume of insects was 10-100%, $\bar{x} = 71\%$ of anterior gut space. Only one additional specimen (July) from this period lacked food. Some distinct differences occurred with specimens collected from Little Tennessee River during colder months, mid April (1 specimen) and early to late November (10). The April specimen, a large adult, had the gut only 5% full (two insects). Of the November specimens, only five had insects, total of nine items composing 1-30%, $\bar{x} = 12\%$ of gut volume. Three of these specimens also consumed algae, detritus and/or inorganic materials, composing an additional 1-50%, $\bar{x} = 26\%$ of gut volume. Two other specimens had only detritus and/or inorganic matter, the sum of which

was trace-10% of gut volume. The remaining three specimens lacked material in the anterior gut. Food intake probably is generally low throughout the range during colder times. From snorkeling during December 1974 in Emory River, C.F. Saylor (pers. comm.) found *H. monacha* to be under and among large rubble and boulder, not in swift current; they were very sluggish in the cold water. The differences, particularly consumption of inorganic matter by the November Little Tennessee specimens, may relate to reduced chub activity and insect availability, the latter possibly effected by both low temperature (this is the highest altitude population) and heavy sand-mica deposition.

The following are observations of feeding habitat and behavior, all but the first instance by snorkeling.

Abrams Creek, 13 Sept. 1937, C.L. Hubbs (fieldnotes M37-917 at UMMZ): "Under and about flat boulders of riffles; observed sliding over bottoms, feeding on rock surface with inferior mouth."

North Fork Holston River, Rkm 41.2, 1700-1730 h, 20 May 1974, Burkhead, Jenkins: Two adults and one or two juveniles were in a gravel run, 0.3-1.0 m depth. They almost always remained very close to substrate, more frequently than closely associated benthic feeding *Hybopsis dissimilis*, and moved about less rapidly than most other species. Generally they picked at the upper surface of gravel, apparently feeding on material indistinguishable to observers. Often one fish mouthed branched algae. Once one made an apparent feeding movement about 10 cm above bottom. Common associates were *H. dissimilis, Notropis galacturus, N. rubellus* and *Notropis* sp. (sawfin shiner).

North Fork Holston River, Rkm 3.2, 1420-1500 h, 26 Aug. 1975, Jenkins, Dudley: In a run floored largely with bedrock, two juveniles were seen briefly near a school of shiners. The latter were feeding actively in midwater on material dislodged by our wading. The spotfin chubs remained at or near the bottom, and their probable feeding movements were slow compared to the shiners.

Emory River, Nemo Bridge, 10 Aug. 1981, 1305-1410 h, Burkhead: Two small groups and a few isolated specimens, totaling ca. 20 probable juveniles, were watched. Some were over small gravel, some among boulders, all slightly silted at most, in dpeths of 0.3-0.6 m and slow to moderate current. All chubs were in close association with the substrate, usually only a few cm above. Most were feeding, only from substrate, by lateral movements of the head.

Emory River, Nemo Bridge, 15 Aug. 1979, 1000-1700 h, Beets, Smith (in litt.): Approximately 1.6 km of river was intensely searched and only about 80 *H. monacha* were seen. None were observed in several large, heavily silted pools nor at the Obed River mouth in an area of swift current and large rubble and boulder, which virtually lacked small substrate particles. Most chubs were sighted in the area just above the pool which extends under the bridge. Some young and/or small juveniles were feeding at large bedrock shelves in quiet water, ca. 1 m deep, just below a shoal. Others were feeding nearby on large, flat smooth-surfaced rocks beside the stream bank in 0.1-0.2 m depths. Rocks were coated with a thin film of algae or sediments, but appeared cleaner than those in the pool proper. The chubs were in small, loose groups; they remained very close to and continuously picked from the substrate. They exhibited no territoriality and were commonly associated with young *Notropis coccogenis*. About 20-30 adults, including females and highly colored, tuberculate males, and several juveniles were concentrated a short distance above the juveniles, in midstream of a riffle-run area of bedrock, boulder, rubble and small patches of gravel; depths were 0.2-0.6 m. When not feeding, most chubs swam individually up in the water column with other cyprinids, particularly *N. coccogenis* and *N. leuciodus*. These were generally above the near-benthic level occupied by *Campostoma anomalum* and *Nocomis micropogon*. Often they darted from midwater to feed at the substrate for periods varying from

a few picks to nearly continuous picking. Once an adult male swam rapidly to the surface of a boulder to briefly tug a probable caddisfly larva, then quickly resumed midwater position. Chubs generally fed with the body very close to the substrate, at angles of ca. 10–20%, unlike the shiners whose bodies were at higher angles to the substrate. Feeding was restricted to the bottom; chubs were not observed taking particles in the water column, not even those stirred up by hand from the substrate. Some adults exhibited territoriality, treated under Reproduction.

In summary, *H. monacha* is an insectivore and, as indicated by instream observations, diet and trophic morphology, it feeds benthically in areas of slow to swift current and varied substrate but only slight siltation at most. Deep drift may be taken occasionally; no terrestrial forms were found, suggesting that midwater and higher drift is not often sought. It is a diurnal feeder; it may also feed nocturnally but no data are available. The general absence of detritus and inorganic material in the gut indicates *H. monacha* is a sight feeder and/or an efficient taste-sorter of insects from other material in the oropharyngeal cavity. It seems morphologically equipped to detect food by taste and sight. The dash by one specimen to take a benthic organism indicated ability to visually detect food. The relatively high frequency of algae, detritus and sand/mica

in early winter Little Tennessee specimens may be due to different feeding habits in cold water and/or to lower quality of habitat, with an overload of such materials.

Age and Growth

Problems of age determination by scales and composite length frequency (Table 3) are treated in the Methods section. We make frequent reference below to position of many of the 48 scale-aged specimens in the frequency distribution. For convenience, we often use the term age for age group. Young are age 0 specimens taken in the calendar year they hatched. Subsequent age groups begin at January 1.

Four age groups (0-III) were found. Young first appeared in August collections and ranged 19–37 mm, the latter scale-aged from a November collection.

Age I specimens ranged 20–48 mm through May, 27–50 mm in June, 27–59 mm in August (27 mm and 30 mm based on one and two scale-aged specimens respectively; 59 based on one scale-aged specimen), 34–60 mm in September, and 41–62 mm in October-November. The apparent separation within this age group around 49–50 mm in August-September is judged artifactual based on three specimens, 53, 58, and 59 mm, scale-aged as age I, and on the overall frequency distribution.

Table 3. Length frequency by month and sex of 317 specimens of *Hybopsis monacha* from throughout its range. (unsex = unsexed)

SL, mm	Mar. un-sex	Mar. F	Apr. M	May un-sex	May M	May F	June un-sex	June M	June F	July M	July F	Aug. un-sex	Aug. M	Aug. F	Sept. un-sex	Sept. M	Sept. F	Oct. un-sex	Oct. M	Oct. F	Nov. M	Nov. F
89–88					1		1														1	
87–86			1				1														1	
85–84							1															
83–82							4														1	
81–80							3					1										
79–78							4					1						1				
77–76					1			3	1					1								
75–74								3	1							1						
73–72					1			5		1		1							3			
71–70								1					1	1	1				1	1		
69–68								1	4					2	2							
67–66								2	1	1					1	1			2			
65–64					2			3				1				1	1	1				
63–62								2	1			2					1					
61–60								1					1	1		2	4	1		1		
59–58		1											3	2		1	4	2				
57–56								2	1				4	1		1	5					
55–54					1			3	1			2				1	4	1				
53–52	1				1								1	4	1		3	1	1	1	2	
51–50							1						3	3	1				2		1	
49–48					1			2	1				1	1		2				2		
47–46	1				2								1	1	2	6	4		1	1	1	1
45–44					3			1					1			3	4				1	
43–42					1								2	1		1	5				1	
41–40					1				1			1	5	1		3	3				1	
39–38					2								3	1		2	4					
37–36					1	1			1				3	1		3	2		1			1
35–34					1				1			1	6	3		2	2		1			2
33–32									2				3	3				1				2
31–30					1	1	3					1	2	3							1	
29–28					1		1					2	1		1	1						
27–26							1					1			1							
25–24												3						1				
23–22					1							2										
21–20	1																					
19															1							

Age II and III specimens show considerable overlap in length based largely on the following scale-aged specimens. Three of age II ranged 55–65 mm in May; minimum size was 56 mm in June, 67 mm in August; maximum size was 89 mm in May, 88 mm in June, 89 mm in November. The smallest of age III were 72 mm in May, 76 mm in August; the largest were 77 mm in May, 86 mm in June, 80 mm in August. The greater overlap in length of age II and III specimens, compared with age I and II, suggests that age III specimens grow relatively slowly. The latest month of capture of age III specimens (two males, one female) was August, hence maximum longevity is about three years.

Maximum length of *H. monacha* was thought to be ca. 77 mm SL. (Jenkins and Musick, 1980), based on study through summer 1975. More recent acquisitions from Abrams Creek (1957 collection), Little Tennessee River, Clear Creek of Emory system and North Fork Holston River have significantly larger specimens. Size attained in these populations seems about equal. All four produced males in the 85–89 mm range (about equal numbers of ages II and III). The largest known specimen is a male 89.5 mm (92.5 mm SL freshly preserved, R.B. Eager, pers. comm.) of age II taken in November from Little Tennessee River.

The six largest females range 70–77.7 mm SL, the three aged being age III. The data suggest that longevity of the sexes is about equal, and that males grow faster, attaining larger size. Males generally are larger than females in many highly sexually dimorphic/dichromatic cyprinids, notably at least most species of *Cyprinella*.

Reproduction

Sex ratio of all age groups combined was 128 males: 120 females. The data exclude 32 specimens (29 males) taken by massive poisoning of Abrams Creek; selective preservation of colorful tuberculate males apparently occurred.

Age at attainment of maturity was determined only from scale-aged specimens. Only males with well developed nuptial tuberculation (and coloration if known) were regarded mature. Such males are all those of age III and some of those of age II. All 28 highly tuberculate (aged and unaged) males studied are relatively large, 60–89 mm, $\bar{x} = 73.2$ mm. It is possible that most or all age II and some age I males mature before or in the spawning period, but do not exhibit obvious sexual dimorphism and hence may not be recognized as mature. This is based on some medium size males, 45–59 mm, with tubercles in an early developmental (or possibly postnuptial) stages. Recent maturation would be difficult, at best, to detect by size of testes, as most large nuptial male *H. monacha* have small testes. Gale and Gale (1977) found that some spawning males of *Notropis (Cyprinella) spilopterus* lack observable tubercles and have only slight nuptial color.

Mature females are those with mature ova. All age II and III specimens taken May-August were mature (3 and 7 scale-aged specimens, respectively). The two other large females

(75, 76 mm, at least age II based on length) taken during the spawning season were also mature. These 12 specimens ranged 67–77 mm, $\bar{x} = 71.3$ mm. Many specimens of 35–47 mm (probable age I) taken mid-May to early June were immature, as were many of 40–59 mm (probable age I) taken in mid-August. However, three other mid-August specimens, 53, 57, 58 mm, scale-aged as age I, had many mature ova, indicating that some females mature around the end of their first full year of life. Other small, 55–66 mm, mature unaged (age I and/or II) females were gravid during mid-June to early August.

The extent of the spawning period was estimated from dates of capture or observation of apparently reproductive males (highly tuberculate, nuptial color) and females (ovaries large, some ova mature). Dates for males range 20 May–15 August, females 16 May–14 August. Hence the spawning period appears to be protracted, possibly mid-May to mid-August. Unsuitable conditions such as turbidity may interrupt spawning during this general period.

Hybopsis monacha may be a fractional, crevice spawner. All seven species of *Cyprinella* whose reproduction is known (Outten, 1958; Wallace and Ramsey, 1981 and references therein) spawn partly or entirely in crevices of rocks, logs and other cover. Evidence of crevice spawning is the only known hybrid involving the spotfin chub: one specimen of *H. monacha* x *Notropis (Cyprinella) galacturus* from Daddys Creek (Burkhead and Bauer, 1983). The latter is a crevice spawner (Outten, 1958). For adequately studied species of *Cyprinella,* multiple or fractional spawning is typical, with some females spawning up to 11–12 times over three months (Gale and Gale, 1977; Gale and Buynak, 1978). Advantages of fractional spawning (increased fecundity) and crevice spawning (localization and protection of eggs from predation, mechanical damage and siltation) were discussed by Gale and Gale (1977).

Three classes of ova are recognized in preserved adults from the spawning period (Table 4). Class I ova are opaque, yellow or pale orange, and 0.8–1.4 mm in diameter. Class II ova are opaque, white or slightly yellowish, and 0.4–0.8 mm. Class III ova are translucent and 0.09-0.2 mm. Class I ova are apparently mature. Some of the Class II approached apparent maturity and may have matured during the current spawning period. Class II ova were 3.3–5.0 times more numerous than Class I ova. Class III ova were not counted, but appeared much more numerous than Class II ova. Ova of all classes seemed evenly intermixed throughout ovaries.

Numbers of Class I and II ova increased markedly with increase in female size. Numbers of Class I ova per female (157-791) may not adequately indicate fecundity because of possible spawning prior to capture. Further, counts of Class I ova present at one time in a female may grossly underestimate fecundity over a spawning season if *H. monacha* is a fractional spawner. Total Class I and II ova at the start of the spawning season may be a better index

Table 4. Reproductive parameters of seven female *Hybopsis monacha,* from N. Fk. Holston River (May, August) and Abrams creek (June). GSI = gonosomatic index. Ova classes (Roman) head right side five columns.

Date	Age group	SL, mm	Body wt., g, evis.	GSI	No. ova I	No. ova II	Diameter, mm I		10 ova, x, II		Range III	
May 16	III	77	4.4	—	791	—	—		—		—	
	III	72	3.2	—	589	—	—		—		—	
June 9	II	69	3.1	—	408	1120	1.03,	.9–1.2	.53,	.4–.7	.12,	.1–.2
	II	69	3.0	125	425	1145	1.08,	.9–1.3	.48,	.2–.7	.12,	.1–.2
	II	68	3.4	147	403	2029	1.26,	1.2–1.4	.56,	.5–.8	.09,	.1–.2
Aug. 14	I	57	1.9	—	170	739	1.22,	.9–1.4	.69,	.6–.8	.09,	.05–.13
	I	53	1.6	—	157	522	1.01,	.8–1.2	.60,	.5–.7	.09,	.05–.15

of fecundity for this species.

Possible reproductive behavior was observed in Emory River at Nemo bridge in afternoon of 15 August 1979 (Beets and Smith, in litt.). Highly colored, tuberculate males and adult females were associated in a riffle-run area with structurally diverse habitat, including large and small rocks. Both sexes often fed during the period. Males were loosely aggregated and exhibited aggressive behavior toward other cyprinid species by rapid chases.

Parasites

The only ectoparasites found were blackspot metacerariae of strigeid trematodes. These were rarely hosted, and when spots were found they almost always numbered one or two per fish; the largest number noted was five. Examination of the first descending section of the intestine of 43 specimens revealed only one minute nematode, possibly nonparasitic.

Habitat

Certain habitat parameters of the 24 stream sections in 12 tributary systems historically occupied by *H. monacha* are given in Table 5. All records are from freely flowing sections, some later impounded. Occupation of lentic habitat is very unlikely due to its habitat preference. Elevations are 200–600 m, gradients moderate to moderately high. Its range extends across the Blue Ridge gradient barrier (Gilbert, 1980) into the upper Little Tennessee and French Broad systems. Water is moderately soft to moderately hard. Stream temperatures in summer are generally warm (diurnal maxima greater than ca. 20 C); some populations in maxima of 18–20 C may be thermally limited. Submersed macrophytes are absent or, occasionally, scant to abundant; the spotfin chub does not appear to be closely associated with higher plants, although often it is found along bars with stands of emergent water willow, *Justicia,* and occasionally near or among submerged pondweed, *Potamogeton.*

The large majority of records are from medium to large streams, average widths of occupied sections ca. 15–0 m. Most records from smaller streams are within a few km of the mouth in much larger ones, and may represent forays of individuals, or populations largely reliant upon recruitment from main rivers. If the latter were untrue, more tributary populations would likely have survived modification of main rivers. No records are from Tennessee River or lower sections of its largest major tributaries (Duck, Elk, Hiwassee, Little Tennessee, French Broad, Holston and Clinch rivers). However, prior to impoundment and other changes of these large rivers, only generally scant collecting efforts were made for small, benthic, rheophilic fishes (in part, Etnier et al., 1979).

Stream sections inhabited have riffles, runs and pools, with *H. monacha* nearly always found during warmer times in or near moderate to swift current, depth usually 0.3–1 m. Young and juveniles tend to occupy slower current than adults, although much overlap seems typical. During midwinter, adults tend to inhabit slower current than in warm seasons (C.F. Saylor, pers. comm.). Common substrates (Table 5) in populated sections are silt, gravel, rubble, boulder and bedrock; occasionally small amounts of sand are present. The spotfin chub occupies all these substrates, but apparently only where siltation is slight at most. Jenkins and Musick (1980) stated that *H. monacha* shows a strong proclivity for large areas of small (pea) to medium gravel in North Fork Holston River. Of 89 specimens, taken or observed in this river during 1970–1981 by Burkhead and Jenkins, about 55 were over small-medium gravel; most of the remainder were from uniform or mixed coarse sand, large gravel, rubble, boulder and bedrock. However, the disproportionate numbers of chubs found on gravel bars and flats may relate partly to our preference and ease of seining over gravel. In the North Fork during 1982, with approximately equal electrofishing effort in gravel, rubble and small boulder, we took 41 chubs: ca. 15 from large gravel, 17 in large gravel-small rubble mix, 4 from rubble, 5 among rubble-boulder. No streams are known to have been typically turbid when occupied by *H. monacha,* although many become quite turbid from intense precipitation.

Descriptions of feeding habitat, comprised in that described above, are given under Feeding. Although Cope (1868)

Table 5. Habitat parameters of all specific stream sections with record of *Hybopsis monacha,* with years populations are known. Numbers of specimens without parentheses refer to those with at least partial habitat data; those in parentheses lack original habitat data (although in most cases they are from stream sections of the former category). Bracketed habitat data were not originally associated with records and may be incomplete, as are some originally associated data. ? = estimate of width without observation of stream, or data unknown. Substrate types defined under Methods: Sd sand, Gr gravel, Ru rubble, Bo boulder, Bd bedrock; dominate type(s) italicized when known; siltation excluded here, treated in text.

System	Stream	Year(s)	No. of Specimens	Width,m	Substrate: General	Capture/Obs.	Source
Duck	Buffalo	1978	4	[20-30]	Sd Gr *Ru*[Bo] *Bd*	?	Douglas [Anon., 1973]
	Grinders	1937	3	7	*Bd*	?	UMMZ
Lit. Bear	Lit. Bear	1973	1	3-6	Gr Rb	?	UMMZ
Shoal	Shoal	1884	3	[20-40]	Gr Rb	?	Gilbert, 1891 [Williams, Howell]
Chickamauga	S. Chickamauga	1887	("abt.")	[30-40]	[Sd Gr Bo]	?	Jordan and Brayton, 1878 [Etnier et al., 1981.]
Lit. Tennessee	Citico	1936 1940	2	[4-10]	[Gr *Rb Bo* Bd]	?	[Bauer et al., 1983]
	Abrams	1937-1957	42(32)	10-12	Sd Gr *Rb Bo* Bd	Rb Bo	UMMZ; Lennon and Parker, 1959
	Tuckasegee	1940	2	60	Gr Bo Bd	Gr	UMMZ
	Lit. Tennessee	1975-1980	29(4)	75-100	Sd Gr *Rb Bo Bd*	Sd Gr Bo Bd	Eager, Crittenden, Etnier, NMB
French Broad	Spring	1888	1	[8-12]	[Sd *Gr Rb Bo* Bd]	?	Jordan, 1889 [REJ]
	Swannanoa	1888	2	[?15-30]	Gr Rb	?	Jordan, 1889 [REJ]
Whites	Whites	1959	7	15-30	Rb Bo Bd	Rb Bo	USNM
Emory	Emory	1941-1981	174(225)	10-40	Sd Gr Ru *Bo Bd*	Gr Ru Bo Bd	Anon., 1970; Beets, Crittenden, NMB
	Island	1979	2	Small	?	?	Smith
	Obed	1968-1974	29	[20-25]	Sd Gr *Ru Bo*	?	[Anon., 1970; Crittenden]
	Clear	1968-1981	94(8)	15-30	Sd Gr *Ru* Bo *Bd*	?	Anon., 1970; Crittenden
	Daddys	1974-1981	3(10)	5-15	Gr *Ru Bo* Bd	?	Crittenden [Anon., 1970]
Clinch	Clinch	1893	1	[?40-70]	[Gr] Ru Bo Bd	?	Evermann and Hildebrand, 1916 [REJ]
	Ball	1893	?	[Small]	?	?	Evermann and Hildebrand, 1916 [REJ]
Powell	Indian	1893	2	[10-15]	Gr Ru Bo Bd	?	Evermann and Hildebrand, 1916 [REJ]
N. Fk. Holston	low. N. Fk. Holston	1954-1982	130(13)	20-40	Sd Gr Ru Bo Bd	Sd *Gr Ru* Bo	REJ, NMB
	up. N. Fk. Holston	1867-1954	4(5)	[25-35]	[Gr *Ru* Bo Bd]	?	Cope, 1868; Jordan, 1889; Patrick 1961 [REJ]
S. Fk. Holston	S. Fk. Holston	1947-1949	8	45-90	Sd Gr Ru Bo Bd	?	UMMZ
	Jacob	1947	1	2-6	Gr *Ru* Bd	?	UMMZ

thought *H. monacha* had solitary habits, it was commonly observed in small, loose to tight aggregations. Often 2–4 specimens were captured per short seine haul, and none taken in most other parts of a locality, suggesting localization.

Distribution, Abundance and Population Status

Hybopsis monacha is known from 12 upland or montane tributary systems located widely in the Tennessee River drainage, most in the upper half (Fig. 4). Populations in apparently only four systems are extant (in part, Figs. 5–7). Generally the species was rare or uncommon (Table 5), probably relating to decline in availability of, and localization at, preferred habitat. Recently it was found to be common only at few sites in Emory and North Fork Holston rivers. It was reported abundant only in South Chickamauga Creek in 1877 (Jordan and Brayton, 1878). Although their specimens were not found, the identification is probably correct as Jordan and Brayton reported the other species with which *H. monacha* would likely be confused.

Reviewed here and in Tables 5 and 6 are distribution within and status of populations and habitat of the tributary systems, with comments on certain associated, sensitive or localized species. Year of dam closures, filling of reservoirs, and associated parameters are from Anon. (1940, 1949, 1963, 1964a, b), Louder and Baker (1966) and Fitz (1968).

Duck River System. — Extreme localization and tenuity may apply to the spotfin chub in this large lower Tennessee River tributary system, western Tennessee. Only two records are known, from a small area, with a major hiatus between years of capture. Three specimens were taken in middle Grinders Creek, a small Buffalo River tributary, in 1937 by the TVA. Four specimens were caught in Buffalo River at Grinders Creek mouth in 1978 by N.H. Douglas. *Hybopsis monacha* has been very rare at the latter. Douglas (pers. comm.) made an intensive collection there once each year from 1970–1981, totaling some 50,000 fishes. The site also was worked by D.A. Etnier in 1970, the TVA in 1971 (Anon., 1973), and W.C. Starnes in 1977. Other one-time records from there for the entire Duck system are of *Nocomis micropogon* (UT) and *Ammocrypta vivax* (Starnes et al., 1977). Douglas also seined lower Grinders Creek several times but did not find *H. monacha*.

The spotfin chub may be localized within the Buffalo subsystem of the Duck, based on absence from 58 additional collections from throughout it during 1937-1981 (TVA, UMMZ file; Anon., 1973; Etnier, Feeman, in litt.; UAIC).
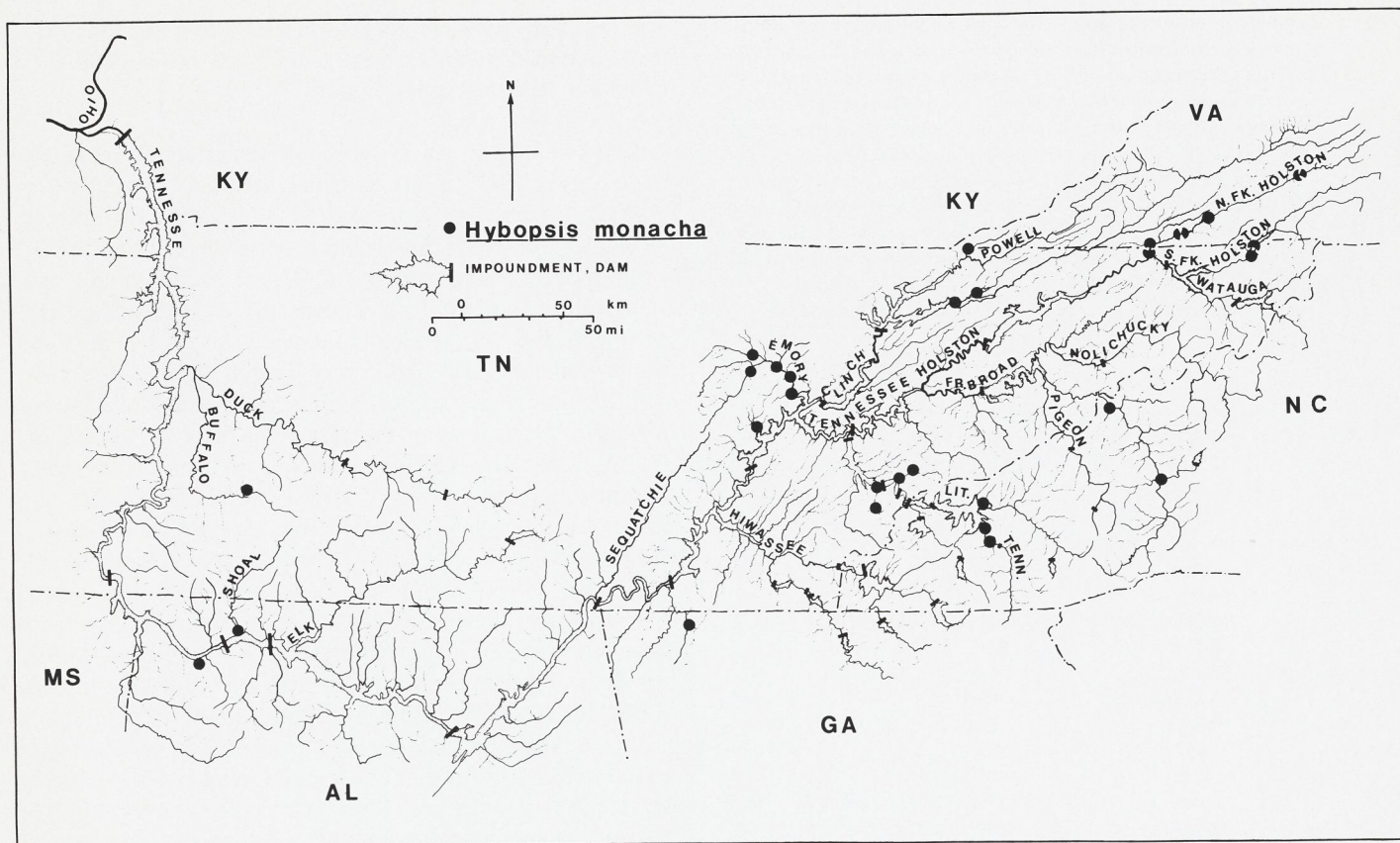
Fig. 4. Distribution of *Hybopsis monacha,* showing all known extant and extirpated populations. Some dots cover more than one record locality. Records from three of four extant populations are shown in detail in Figs. 5–7.

However, only ca. 12 of these are from the ca. 160 km of main channel below Grinders Creek. Buffalo River lacks impoundment and it and its tributaries are typically clean, clear and of varied substrate. Isom and Yokely (1968) and Starnes et al. (1977) opined that Buffalo River is essentially pristine, and Anon. (1973) stated it is considered one of the most unspoiled rivers in the Southeast. Isom and Yokely (1968) found its mussel fauna in poor condition, and speculated a cause to be changes in the fish fauna of the lowermost reach induced by embayment of Tennessee River. However, the subsystem still has moderately high species richness and diversity of fishes (in part, Anon., 1973). *Hybopsis monacha* may be temperature limited by numerous high volume, cool springs in the system.

The puzzling apparent absence of *H. monacha* from the much larger Duck subsystem casts doubt upon its possible wider occurrence in the Buffalo. It is absent from over 350 collections from throughout the Duck subsystem, many from Duck River proper (Anon., 1975; Nieland, 1979; J.C. Feeman, pers. comm., 1981). Habitat quality and diversity in the subsystem appear to remain high, and Duck River sustains the most speciose ichthyofauna in the Tennessee drainage (Etnier and Jenkins, 1980), perhaps the most diverse in North America. It includes relict populations of *Noturus stanauli* and *Etheostoma tippecanoe.*

Hybopsis monacha may never have been particularly successful in the Duck system. Many natural differences are known between the upland faunas of the lower and upper Tennessee drainage (summary for fishes, Jenkins et al., 1972; bivalve mollusks, Ortmann, 1925, van der Schalie, 1939, and Stansbery, 1964; crayfishes, Hobbs, 1969).

Little Bear Creek System. — The single specimen was taken in the lower part of this small northwestern Alabama stream in 1937 during preimpoundment survey of the southern bend region of Tennessee River. The only change of which we are aware that may affect the stream is impoundment, at its mouth, of Tennessee River by Pickwick Dam in 1938. Apparently the creek has not been recollected. The population may have been supported by recruitment from a hypothetical one in the Muscle Shoals section of Tennessee River, a former extensive haven of rheophilic life whose preimpoundment fish fauna is virtually unknown.

Shoal Creek System. — Three specimens represent the single record from lower Shoal Creek, Alabama in 1884 by Gilbert (1891), who regarded *H. monacha* as rare and had sampled other western tributaries of the southern bend. The system was widely surveyed over the past 20 years (Wagers, 1974). Although the lower 10 miles were impounded by

Table 6. Length (km) of stream sections with extant populations (probable discontinuities between record sites included), and anthropogenic and natural limiting factors (some only suspected) on all known populations of *Hybopsis monacha*. "Indirect" impacts are on stream sections receiving populated tributaries (some of the former also were or remain populated). Impacts: 1 impoundment, 2 cold tailwater, 3 channelization, 4 siltation and/or coal fine sedimentation, 5 pollution (inorganic and/or organic), 6 population renovation, 7 localized collecting, 8 natural cool temperature, 9 small stream size. Impact may not refer to all parts of occupied section.

System	Stream	Length	Impact: Direct	Indirect
Duck	Buffalo	1	?8	—
	Grinders	—	?8,?9	?8
Lit. Bear	Lit. Bear	—	?9	1
Shoal	Shoal	—	1	1
Chickamauga	S. Chickamauga	—	1,3,4,5	1
Lit. Tennessee	Citico	—	8,?9	1,2
	Abrams	—	1,6,8	1,2
	Tuckasegee	—	1,4,5,?8	1,4,5,?8
	Lit. Tennessee	33	1,2,4,5,?8	—
French Broad	Spring	—	?5,?8,?9	4,5
	Swannanoa	—	4,5	4,5
Whites	Whites	—	1	1
Emory	Emory	25	1,4,5	1
	Island	0.2	?9	4,5
	Obed	15	4,5	4,5
	Clear	14	4,5	4,5
	Daddys	6	4,5	4,5
Clinch	Clinch	—	1,2,4,5	1
	Ball	—	?9	1
Powell	Indian	—	4	4
N. Fk. Holston	low. N. Fk. Holston	72	4,5,7	4,5
	up. N. Fk. Holston	—	4	4,5
S. Fk. Holston	S. Fk. Holston	—	1,2	4,5
	Jacob	—	1,?8,9	1

Wilson Dam in 1924, the mainstream above is of size that probably would support *H. monacha* and has stretches of clean gravel and rubble (W.M. Howell, J.D. Williams, pers. comm.). Wagers (1974) considered the lower section of the watershed, in Alabama, to be in good condition (contrasting with some upper parts, in Tennessee).

All Alabama populations of *H. monacha* were regarded as extirpated by Ramsey (1976). Some streams in the bend region have been or are scheduled for channelization (Ramsey et al., 1972). The ichthyofauna of the bend region (in part, Armstrong and Williams, 1971) is somewhat transitional between the lower and upper Tennessee faunas. *Hybopsis monacha* is known only from the western part of the bend, and the populations may have been marginal, as in the Duck.

Hybopsis monacha probably populated the eastern sector of the bend region, perhaps more so than the western. Although recent survey of the former found two relict species, *Notropis* sp., the palezone shiner of upper Tennessee affinity, and the snail darter, *Percina tanasi* (R.G. Biggins,

J.C. Feeman, pers. comm.), earlier sampling was much less than than of the western part, insufficient to locate the then probably receding spotfin chub.

Chickamauga Creek System. — This system was collected once during 1877, in South Chickamauga Creek at Ringgold, by Jordan and Brayton (1878), yielding the sole *H. monacha* record for the system and Georgia. It was said to be abundant. Some springs and West Chickamauga Creek were sampled in 1893 by Evermann and Hildebrand (1916), who took the only record from the latter of *Phenacobius uranops* and *Noturus flavipinnis* (Taylor, 1969). The system was sparsely collected, often at springs, beginning about 1960, and extensively surveyed in 1979-1980 by Etnier et al. (1981), who reviewed most previous collections. Recently *Notropis ariommus* (Gilbert, 1969), *P. uranops* and the snail darter (Etnier et al., 1981) were discovered in South Chickamauga Creek at or below Ringgold. However, *H. monacha, N. flavipinnis,* and the extinct *Lagochila lacera,* the latter also taken only by Jordan and Brayton, apparently have not persisted. From description by Etnier et al. (1981), stream size (becoming a medium size river at Ringgold) and substrate (except for siltation) of lower South Chickamauga Creek seem appropriate for *H. monacha*. However, the extreme lower section in Tennessee is impounded or partly leveed and channelized. This portion and the section in Georgia up to about Ringgold has a history of heavy floods, siltation and domestic and industrial pollution (Anon., 1964c; Etnier et al., 1981).

Little Tennessee River System. — A population is extant in the upper section of only one of the four streams that yielded records. Lower Little Tennessee River is treated first as it bears on the extirpated populations of two of its tributaries in Tennessee.

Lower Little Tennessee River: At least part of the lower 80 km of Little Tennessee River in Tennessee probably supported *H. monacha* prior to impoundments. Suitable structural habitat appeared to have been present based on Kingman et al. (1900), Etnier (1976), Starnes (1977) and Hickman and Fitz (1978). However, other than probable gamefish sampling, we know of only one early collection, from Rkm ca. 60 in 1937 by Hubbs (UMMZ file). This was below the two earliest constructed dams, Calderwood at Rkm 71 (filled in 1930), Cheoah at Rkm 80 (1919). Some warmwater fishes were taken in the 1937 collection, and although Calderwood reservoir had typically warmwater habitat at the time (Dendy and Stroud, 1949), maximum temperature in the river below may have declined somewhat as both reservoirs were deep. River temperature below Calderwood was greatly lowered by operation of Fontana Dam, the highest east of the Mississippi River, at Rkm 96.5 in North Carolina (closed in 1944). Water released from Fontana passed relatively quickly through Cheoah and thence Calderwood reservoirs as thick density currents,

highest temperature 20 C, generally much lower, and sometimes with very low oxygen content (Dendy and Stroud, 1949). Chilhowee Dam, built at Rkm 53 (closed in 1957), effected a 92 km series of impoundments that further extended cold tailwaters. The upper section of the lower freely flowing 53 km was sampled five times in 1964, not showing a typical warmwater riverine fauna (Etnier, in litt.). Etnier (1976) indicated that the lowermost 32 km was unsampled until 1973, when *P. tanasi* was discovered, and had a predominance of warmwater fishes. Collections reported by Hickman and Fitz (1978) indicated a somewhat depauperate warmwater fauna, and R.B. Eager (in litt.), who was involved in the TVA study, stated that the lower Little Tennessee was sparsely populated, with numbers of fishes largely restricted to areas of tributary mouths. Temperature was depressed far down the river, not exceeding 20 C at Rkm ca. 11 (Hickman and Fitz, 1978). Virtually the remainder of lower Little Tennessee River was impounded by Tellico Dam in 1979.

Citico Creek: This lower Little Tennessee tributary yielded one specimen in 1936 near the mouth, and one in 1940 from its middle section. It is entirely within Cherokee National Forest, Tennessee, and has remained in good condition (Bauer et al., 1983). Its fauna and that of neighboring tributaries are well known from collections made in 1969-mid 1970's (Etnier, Crittenden, in litt.). More recently, *Noturus baileyi,* formerly believed extinct, *N. flavipinnis* and the duskytail darter, *Etheostoma (Catonotus)* sp., were discovered in lower Citico Creek (Bauer et al., 1983; Etnier, pers. comm.). Middle Citico is trout water and may have been marginal, too cool and small, for *H. monacha*. Only lower Citico may have provided preferred habitat, but because of longevity of good conditions and apparent current absence of *H. monacha* therein, we suspect the population was at least partly reliant on a hypothetical one in lower Little Tennessee River. Although the Little Tennessee was freely flowing at the Citico Creek mouth until 1979, it was a cold tailwater since at least 1944.

Abrams Creek: Spotfin chubs populated at least the lower, warmer half of the lower 23.5 km, below Abrams Falls, of this Great Smoky Mountains National Park, Tennessee stream. It was taken in three of four collections from below the falls in 1937 and 1941, the negative result from near the falls. It was next (and last) taken at an unknown site(s) below the falls in 1957 (KFW series misidentified as *Notropis stigmaturus [= venustus]* by Lennon and Parker, 1959). We do not know the stream to have been worked by an ichthyologist during 1942-1956.

The stretch ca. 1.0-1.8 km above the mouth was described in 1937 by C.L. Hubbs (UMMZ file) as long pools and long riffles, substrates mud, sand, gravel, boulders and bedrock, water "exceptionally clear and not easily roiled." At ca. 12 km above the mouth, it was nearly all rapids with small amounts of sand and mud. The lower 23.5 km was characterized (Lennon and Parker, 1959) as short cascades and very long, deep pools; water clear, slightly brown, and soft. Descriptions by Hubbs and the latter differ somewhat, suggesting varied physical features; all agreed regarding water clarity. The chub population of the lower creek was probably resident: the stream is slightly larger and probably warmer than nearby Citico Creek; the 1957 collection postdates by 13 years cooling of Little Tennessee River with closure of Fontana Dam.

Hybopsis monacha was regarded as common in Great Smoky Mountains National Park by Lennon (1962). Although he used the 1937 and 1941 records (KFW series still misidentified), the statement is at least partly erroneous as Abrams Creek had supported the only known Park population. Spotfin chubs may have been only locally common in lower Abrams Creek. Although 37 specimens were taken near the mouth in 1937, the sampling effort spanned ca. 0.8 km. and 5.5 h. Only five specimens were caught in 1941, one near the mouth, and four about halfway to the falls. Results of the extensive ichthyocidal treatment in 1957 are inconclusive regarding abundance. Only 3233 specimens, including 2237 game and food fishes, from the lower 23.5 km were "checked" (Lennon and Parker, 1959); nuptial *H. monacha* apparently were selectively preserved (Reproduction section).

The spotfin chub apparently was extirpated from Abrams Creek in 1957 by rotenone treatment of the stream from the falls to the mouth and of many tributaries. The "reclamation" was intended to reduce competition of nongame and warmwater sport fishes with introduced trout, an action difficult to reconcile with Park policy of preservation of native biota. Although Abrams Creek remains in good condition, and many native species have reestablished naturally (Miller, 1968; Bauer et al., 1983) its populations of *N. baileyi, Percina burtoni, Etheostoma blennioides* and duskytail darter vanished with *H. monacha*. Impoundment of the lower four km of Abrams Creek by Chilhowee Dam in 1957 (and prior and later impoundment of Little Tennessee River) sealed their fate.

Upper Little Tennessee River sytem: Fig. 5 shows 41 and 42 collections, respectively, from 18 and 12 sites in upper Little Tennessee River and its largest tributary, Tuckasegee River, North Carolina. Early or major surveys are reviewed first. Their tributaries also have been surveyed extensively.

In 1930, J.S. Gutsell surveyed Tuckasegee River and tributaries; the actual number of collections is unknown. Hildebrand (1932) reported the collections and mentioned six sites on the main river; we considered that one collection was made at each. During 1937-1940, C.L. Hubbs and/or TVA personnel collected two sites in upper Little Tennessee River that now are impounded, and three sites in Tuckasegee River, two of which are inundated. In 1947, J.R. Bailey made a fishery survey, including two and three collections, respectively from Little Tennessee and Tuckasegee rivers. In 1961, a North Carolina Wildlife

RKM
16.1
O 1977,1

RKM
20.9
O 1930,1

O 1937,1

O 1975,1

O 1976,1

RKM
122.3
O 1937,1

RKM
4.8
O 1937,1

RKM
29.0
O 1930,1

RKM
41.8
O 1930,1

O 1967,1

O 1977,1 RKM
47.5
O 1930,1

FONTANA

RES.

O 1937,1
RKM
96.5

LITTLE

O 1967,1

O 1975,1

TUCKASEGEE

● 1940,2

O 1947,1
RKM
9.7

O 1947,1

● 1975,8,4

● ;O 1977,1,1;1

O 1980,2
RKM
144.4

O 1961,1

O 1930,1

O 1980,1
RKM
57.9

O 1947,1
RKM
66.0

O 1977,1

O 1980,1
RKM
53.1

O 1980,2
RKM
153.3

● 1980,1
RKM
154.9

● 1977,2

O 1980,2
RKM
159.3

O 1930,1
RKM
67.6

● ;O 1977,1;1
RKM
156.1

O 1977,2
RKM
167.3

O 1977,1
RKM
175.5

O 1975,1

O 1976,1
RKM
74.8

● 1975,6,2

● ;O 1977,1;1

O 1980,1
RKM
160.9

● 1975,2,2
RKM
170.6

O 1961,1

O 1962,1

O 1967,1

FRANKLIN

● ;O 1975,1;1

O 1977,1

O 1980,1
RKM
177.0

O 1977,1
RKM
189.9

TENNESSEE

O 1961,1
RKM
197.9

N

TN

NC

GA

O 1980,1
RKM
207.6

O 1947,1
RKM
210.8

O 1980,1
RKM
213.2
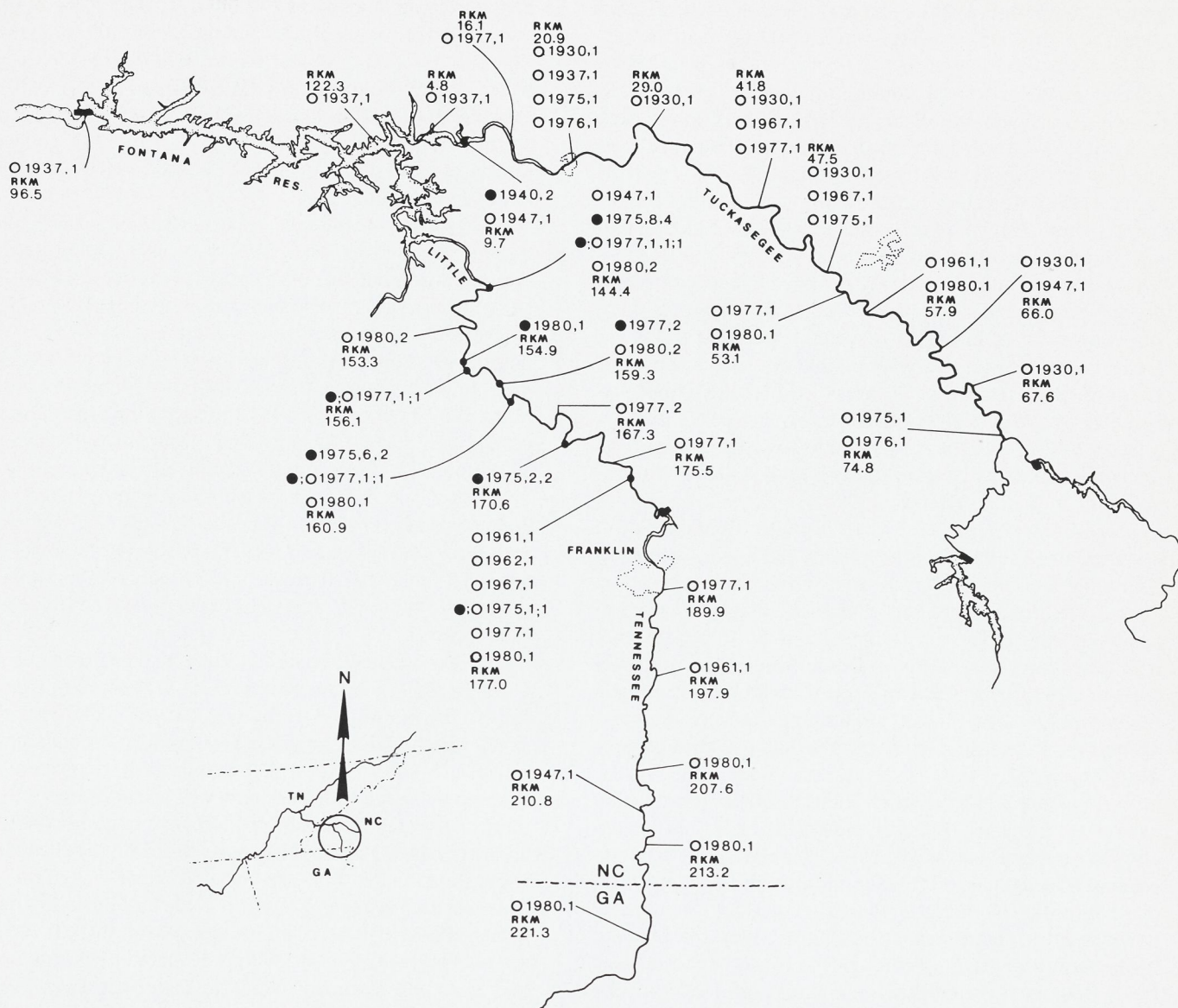
NC
GA

O 1980,1
RKM
221.3

Fig. 5. Geochronography of *Hybopsis monacha* in Little Tennessee and Tuckasegee rivers, North Carolina. Map shows all collections known from their main channels from Fontana Dam up to headwaters (except for one collection each from three unspecified lower and middle Tuckasegee sites in 1975). Collections from reservoir area were made prior to impoundment. Solid dots on rivers indicate capture sites, but not necessarily extant subpopulations. Offriver data are: year of collection(s, preceded by (1) solid dot if *H. monacha* taken, (2) open circle if not taken; following the year are: (3) number of specimens taken, if any (if specimens were taken more than once in a year, the number of specimens in each collection is given separately, hence indicating the number of collections yielding specimens), and lastly (4) the number of collections not yielding specimens (this number is separated by a semicolon from number of specimens).

Resources Commission crew poisoned 60 stations, two in Little Tennessee River, three in Tuckasegee River (Messer and Ratledge, 1963). In 1969, a TVA crew creosoled 19 sites, all in tributaries (Anon., 1971). In November 1975 R.B. Eager and TVA crew kick-seined four Little Tennessee River sites, on two occasions at each site, yielding the first specimens of *H. monacha* from the river proper. During 1975-1976, Eager or other TVA biologists made one or two collections from each of three places (plus one collection each from three unspecified sites) on Tuckasegee River and two collections in Cullasaja River, a major Little Tennessee

River tributary. Upon discovery of *H. monacha* in the first 1975 collection, the subsequent TVA collections were particularly aimed for this species. During 1977, in a survey for *H. monacha,* D.A. Etnier made 19 collections, including 13 from Little Tennessee River and three from Tuckasegee River, by seine, electrofisher or ichthyocide. Burkhead worked on 14 of these collections. For a status assessment of *H. monacha,* E. Crittenden, USFWS, made a broad survey of the system during summers of 1978-1980. The inhouse report is confusing regarding number of collections; apparently 64 were made, including 10 from the Little Ten-

nessee, two from Tuckasegee and eight from Cullaseja rivers. The year of collection is unavailable for all collections except the one in which *H. monacha* was taken, in 1980; the year of all collections is given as 1980 in Fig. 5. Methods were kick-seine or electrofisher. R.B. Eager worked with Crittenden on several days. Fish identifications were verified by Etnier or others at the University of Tennessee.

Tuckasegee River: The two spotfin chubs from this river are from the Noland Creek mouth in 1940. The demise of the lower river population was spelled in 1945 by filling of Fontana Reservoir. However, *H. monacha* probably had previously declined widely as it was not taken in other preimpoundment collections, and never above the reservoir. The river has a history of marked pollution (Hildebrand, 1932; Messer and Ratledge, 1963; Anon., 1971) and its lower section is considerably silted.

Upper Little Tennessee River: The reach of Little Tennessee River, North Carolina, inhabited by *H. monacha* spans ca. 32.5 km, from the markedly fluctuating head of Fontana Reservoir to near Franklin Dam just below the town of Franklin (Fig. 5). Within this section, *H. monacha* was found at seven sites since 1975 and generally was rare; the most taken at one time was eight. Three once-sampled sites yielded no specimens. The population may have long been tenuous. It was not taken in four collections in 1947–1967 from the currently occupied section nor earlier in three preimpoundment collections. Varied success is suggested at some localities during 1975–1981. The section above Franklin was searched sparsely but specifically for *H. monacha* with negative results, indicating enclosure of the population by two impoundments.

Several factors beset the biota. Much of the substrate is covered with mobile fine sand and mica, the former found commonly only in the gut of Little Tennessee specimens, the latter appearing only therein. Messer and Ratledge (1963) stated that the river below Franklin is a turbid stream, with heavy sedimentation emanating widely from farming, mining and other sources, and it carries domestic and industrial pollution from the Franklin area and industrial pollution from Georgia. The *H. monacha* population may also be thermally limited; it occupies the altitudinal extreme for the species (520–600m), where temperature maxima may normally be 18–20 C (Messer and Ragledge, 1963).

Regarding Franklin Dam, the following is from correspondence in 1976 from an official of Nantahala Power and Light Company, Franklin, to R.B. Eager. The dam was constructed in 1925 at Rkm 182, impounds ca. 4.5 km of the Little Tennessee to form Lake Emory, and generates electrical power. Most of the reservoir usually is fully sedimented, hence much of the incoming alluvial load passes through turbines and floodgates. It was estimated that if the reservoir was fully desilted, it would refill in less than five years. Since the reservoir is not used for storage, it is lowered only for maintenance such as clearage of plant intake racks by sluicing. This is done once within one to two year periods, at no set schedule but generally during low river stage, usually in fall. (At such times the reservoir is drained and at least the lower part of its main channel flushed to near base level, with heavy sediment load released below. fide J. Davies, North Carolina Wildlife Resources Commission, pers. comm., 1982).

The dam may have varied impacts related to timing and intensity of sediment passage. It may have been a primary factor in persistence below of *H. monacha*. Its formation of a sedimentation basin (although generally ineffective) would be beneficial particularly during the spring-summer spawning period. However, a major load released then and at other times probably would cause population reduction, and could be devastative at least locally. Despite uncertainty regarding relative effects of lake drainage, general siltation and pollution from and above Franklin, it seems didactic that only one spotfin chub was caught in the total of eight collections from the two sites nearest Franklin.

French Broad River System. — The lower reach of two widely separate tributaries in the Blue Ridge, North Carolina yielded three specimens in 1888 to Jordan (1889), who regarded *H. monacha* as uncommon. He described the lower Swannanoa and Spring Creek sites as clear. In 1972 we found the lower 100 m of Spring Creek to be very clear and have scant siltation. Lower Swannanoa River, in the populous Asheville area, now is heavily silted and received domestic and industrial pollution (Richardson et al., 1963). Although lower Spring Creek seemed in good physical condition in 1972, it was somewhat small for *H. monacha,* and fish species richness was low (10 species). It may periodically receive contaminants from the town of Hot Springs. French Broad River was heavily polluted from Brevard, just above the Swannanoa mouth, to the Tennessee state line, just below the Spring Creek mouth (Richardson et al., 1963).

Whites Creek System. — The single series was taken in 1959 at the foot of Cumberland Plateau Escarpment, Tennessee (just below Emory River mouth, Fig. 4). Although only seven spotfin chubs were caught, W.R. Taylor (USNM file) regarded it as common based on difficult seining conditions and small total catch. The site is three km above the eight km Whites Creek arm of Watts Bar Reservoir created on Tennessee River in 1942. (The record in Jenkins and Burkhead, 1980, on Tennessee River between the mouths of Whites Creek and Emory River is erroneous, and should be deleted).

Negative collecting results for *H. monacha* in Whites Creek follow. One rotenone collection each from three different sites in the later impounded section, made by the TVA in 1941 (Etnier, in litt.), yielded 19–35 species including expected species of darters and a sculpin, suggesting good effort; the fauna of lower sections of Tennessee River tributaries in that area is not particularly diverse. Lower Whites Creek was inspected above and below the record site

by diving in January 1975 by TVA biologists. Shiners and darters were plentiful, but *H. monacha* was not found, somewhat opposite of results from lower Emory River the previous month by the same crew (C.F. Saylor, in litt.). In 1981 E. Crittenden and USFWS crew unsuccessfully sought *H. monacha* at four sites in Whites Creek, two below the Escarpment.

The population may have been restricted to below the Escarpment and, based on absence in the 1941 collections, was generally sparse or localized. Immediately above, the system branches into a network of apparently small streams. During dry periods the stream in the Escarpment gorge recedes to pools (Anon., 1938), probably forcing the chub into marginal habitat and intensified interspecific competition. We are unaware of human-caused stresses in the system other than impoundment, which it survived for at least 17 years. However, impoundment probably constricted its range, and it may have died out during a time of drought.

Emory River System. — This largely Cumberland Plateau system, Tennessee, has been well surveyed, mostly recently (82 collections, 37 sites, Fig. 6). In 1941, seven collections from five sites were taken by the TVA. At least three of these sites were later impounded; the exact location of the Little Emory site is unknown. Three wide surveys were made: In 1968, 16 sites were ichthyocided by R.B. Fitz and TVA crew (Anon, 1970). In 1973–1975, Riddle (1975) sampled by various methods; probably only his 14 ichthyocide collections would have sampled *H. monacha* (extant series of *H. monacha* taken in 1974; year unspecified for general collections, regarded as 1974 in Fig. 6 herein; latter collections examined by Bauer or Etnier). In 1981, 26 collections specifically for *H. monacha*, mostly by ichthyocide, a few by electroshocker, were made by E. Crittenden and USFWS (collections identified by and all data obtained from Bauer; data also in USFWS Asheville office report). Etnier seined Emory River intermittently since 1968, mostly in the Obed River mouth-Nemo Bridge area (Rkm 44.2–46.0), and several others worked the latter. Beets and Smith (in litt.) made important observations in the latter section in 1979, as did Burkhead in 1981.

The known range of *H. monacha* is Emory River up to about the Obed River mouth (largest Emory tributary), Obed River to the Daddys Creek mouth, and the lower portions of Clear and Daddys creeks (largest Obed tributaries). Generally *H. monacha* was nearly consistently taken at record sites worked at least twice. Usually it was uncommon or rare; numbers greater than 20 generally were from collection and/or observations of ca. 0.8 km at a time. Effort in the unsurveyed ca. 10–30 km sections above the uppermost record localities may reveal greater upstream extension, notably in Clear Creek. The upper limit in this stream is suggested as the White Creek mouth, implying improved water quality by influx of White Creek. However, in 1981 lowermost White Creek had much silt, algae and

sewage odor; *H. monacha* was not found.

Uncertainties regarding collection data attend the range statement for Obed River, which is based on the following two records. Riddle (1975:table 12) listed 27 specimens from Rkm 0.6, but none was located by us. The record is accepted based partly on long establishment of *H. monacha* in Emory River in the Obed River mouth area, and on occurrence in lower Clear Creek. Riddle did not list *H. monacha* at Rkm 15.0 (Daddys Creek mouth), but two specimens with such data and taken by Riddle in 1974 are at AU. Although *H. monacha* was not found there in 1968 and 1981, it was found consistently (1974, 1981) in lowermost Daddys Creek; perhaps the AU specimens were caught by a method other than those yielding the data in Riddle's Table 12.

Problems are here considered for the 1968 TVA population density estimates (Anon., 1970: table 5). The spotfin chub was misidentified as suckermouth minnow, *Phenacobius mirabilis*. Two series of *H. monacha* (UT 44.563, 44.564, originally labeled *P. mirabilis*) from Emory River sites were found by Etnier at the Norris TVA laboratory. We assume, and R.B. Fitz (in litt., 1974) thought it probable, that the other *P. mirabilis* record, from lower Clear Creek (from which we have examined *H. monacha)*, was also the latter. *Phenacobius mirabilis* is superficially similar to *H. monacha,* absent from the upper Tennessee, and not expected in habitat typical of the Emory. The numbers of specimens reported from the three sites, supposedly double the actual catch for each one-half mile section (expresed as density per mile, Anon., 1970:table 5), are also in error based on reexamination by Fitz of the original data: 24 specimens were reported at the lower Emory site, 4 are listed in original data, 4 are extant; 677 reported at middle Emory, 47 originally, 36 extant (the 11 missing may have been among those discarded at streamside, Anon., 1970); 176 reported from Clear Creek, 89 originally, none extant. Only the number reported from Clear Creek approaches doubling of the original, and Fitz (in litt., 1975) cautioned usage of even original numbers for population estimates. Relative abundance would also be clouded if data reported for other species are also defective.

The range of *H. monacha* in the system has been reduced. The lower 21.4 km of Emory River was impounded in 1942 by Watts Bar Dam. Upper Emory River, which did not yield a record, has been disturbed primarily by silt from coal mining, which also affects lower Emory River at least by high sulphate concentration (Anon, 1970; Riddle, 1975). Tackett (1963) noted Emory River is the only sizeable Tennessee drainage tributary that drains extensive sandstone areas and is consistently acidic. Although Anon. (1970) reported pH at widely located stations in August to be 7.1–7.8 at 11 stations (6.4–6.9 at 5 other stations), Riddle's 84 readings from throughout the system and year ranged 6.41–6.95. Low buffering capacity was also indicated by conductivities and alkalinities reported by Anon. and Riddle. Rock Creek, a small tributary entering Emory River at

RKM 7.1 O1974,1

RKM 11.3 O1974,1

RKM 0.2 O1981,1

RKM 65.6 O1968,1

O1974,1

RKM 44.2–46.0 ●1968,4,47

●1969,1

●1970,21

●1974,1,2,38,1,31,19

●1975,24,11

●;O1979,80;1

●1981,29,4,4

RKM 46.7 O1968,1

O1974,1

RKM 14.2 ●1968,89

●;O1981,3;1

CLEAR

WHITE CR

RKM 2.3 O1968,1

●1981,3

GREASY CR

RKM 0.5 O1968,1

EMORY

RKM 6.4 ●1974,5

●1981,2

CR

O1981,1

RKM 15.0 ●1974,2

O1981,1 O1968,1

RKM 25.1 O1981,1

RKM 0.6 ●1974,27

R

RKM 32.7 O1981,2

OBED

RKM 39.4 O1968,1

O1974,1

EMORY

RKM 6.4 O1981,1

FK

CR

O1981,1 RKM 0.2

O1981,2

OTTER

CR

O1974,1 RKM 0.3

ISLAND CR

●1979,2 RKM 0.2

●;O1968,4;1

●1974,6

●1975,2

●1981,6 RKM 35.1

CROOKED FK

LITTLE EMORY R

RKM 64.4 O1968,1

●1974,5 RKM 0.3

●1981,2

O1974,1 ROCK CR RKM 3.9

ORCHARD

RKM 17.4 O1981,1

O1981,2 RKM 3.7

O1941,1

OBED

●1981,1 RKM 5.6

CRAB

CR

O1968,1

O1974,1

●1979,2

RKM 3.9 ●1981,3

O1968,1

O1981,1 RKM 14.8

●1967,2 RKM 29.0

CLIFTY

O1941,1 KING CR RKM 0.8

O1941,1 SWAN POND CR RKM 0.3

O1981,1 RKM 32.2

O1968,1

O1974,1

O1981,1 RKM 43.4

DADDYS

O1981,1 RKM 27.7

O1941,1 RKM 0.3

●1941,44,2,16 RKM 20.9
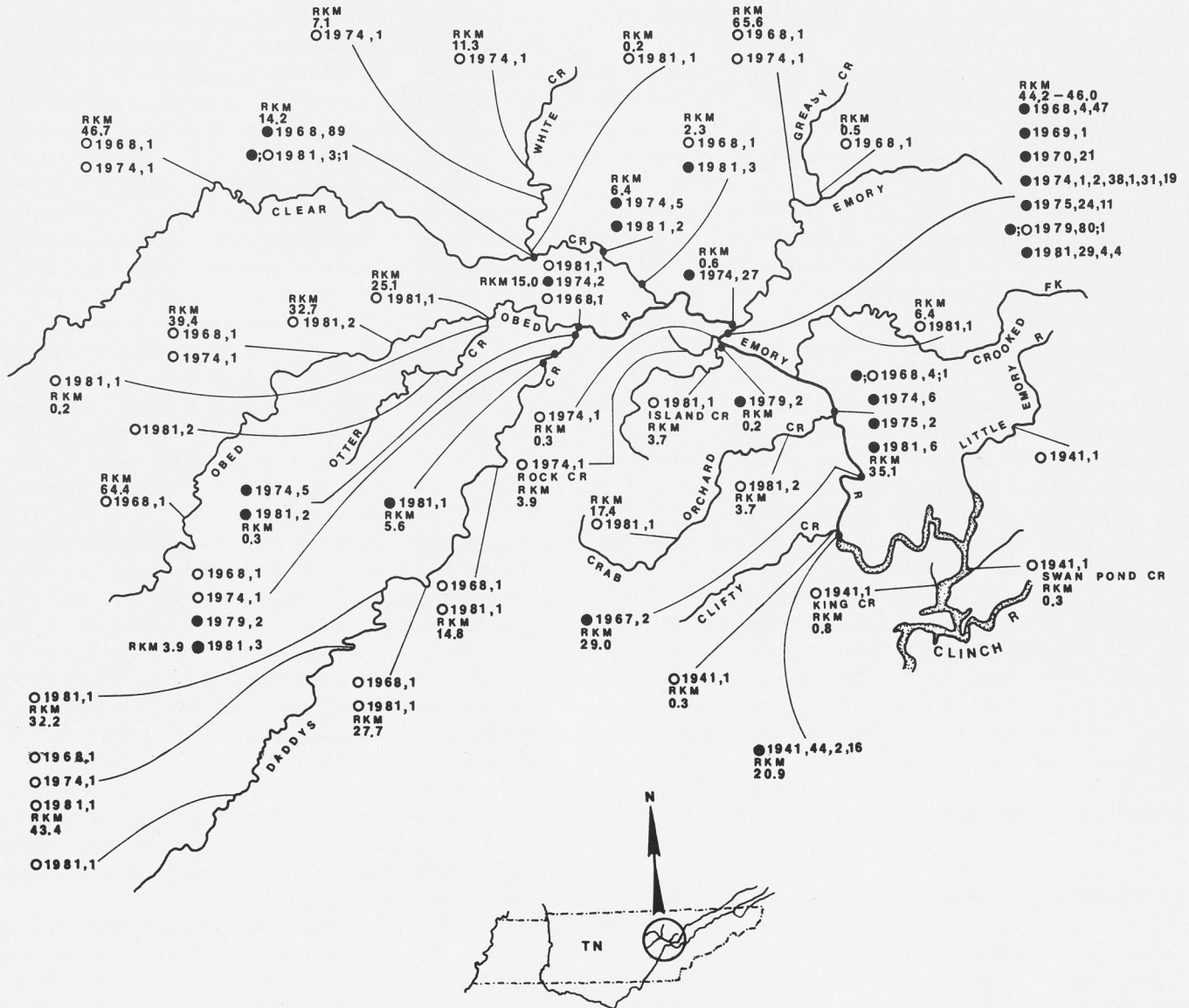
CLINCH R

O1981,1

N

TN

Fig. 6. Geochronography of *Hybopsis monacha* in the Emory River system, Tennessee. Map shows virtually all collections known from the system made by methods of sampling small fishes. Data format explained in Fig. 5.

Nemo Bridge, carries acid discharge from active coal strip mines (Smith, in litt., 1979). Smith collected the Emory at its mouth during a heavily turbid time and did not take *H. monacha*, but concurrently found two young in clear-running lowermost Island Creek, entering Emory River just below Rock Creek. (Smith's and Beets' observations of *H. monacha* made one week prior in Emory River were from just above Rock Creek.) Major parts of the system, additional to upper Emory, afflicted by silt and chemical discharge from mines and/or domestic and industrial pollution are Crooked Fork, Crab Orchard, White and Daddys creeks and upper Obed River.

It appears that dilution of wastes upgrades quality of lower Obed River, Clear and Daddys creeks, in turn enhancing recovery of lower Emory River. It is only these sections where *H. monacha* remains, and to which native muskellunge are largely confined (Riddle, 1975; Crossman, 1978). Parts of these stream sections (except Clear Creek) form boundaries of the Catoosa Wildlife Management Area, which apparently benefits the watershed.

Clinch River System. — Only one specimen is known from Clinch River. Evermann and Hildebrand (1916) reported six *H. monacha* taken in 1893 from Walkers Ford, Tennessee, but five were reidentified (Hubbs and Crowe, 1956) as *H. cahni*. The Walkers Ford and other probable populations in the lower Clinch may have been waning in the late 1800s-early 1900s. Collecting effort is insufficient for judgement. Their demise was sealed by filling of Norris Reservoir in 1936, temperature depression and often very low discharge

of its tailwater, and Melton Hill Reservoir created in 1963 farther down the Clinch.

Hybopsis monacha probably was an early occupant of Clinch River above Norris Reservoir, but was undetected; extensive survey occurred after 1965 (Masnik, 1974; Jenkins et al., in prep.) and produced no specimens. This section of the river in Tennessee and Virginia has long been adversely affected by sedimentation of coal fines from coal washing operations in Virginia (Tackett, 1963; Wollitz, 1968). The ichthyofauna was virtually eliminated in 106 km of the Virginia section and some kill occurred in the upper ca. 50 km in Tennessee, from a major spillage of alkaline waste in 1967 (Jaco, 1967; Wollitz, 1970; Crossman et al., 1973). Perhaps surprisingly, the Clinch from Norris Reservoir to somewhat into Virginia still supports a highly diverse fish fauna (Masnik, 1974; Etnier and Jenkins, 1980). Apparently sensitive species that persist in this section in Tennessee include *H. cahni, Notropis ariommus, Noturus stanauli, Ammocrypta clara* and *E. tippecanoe.*

The single record from a Clinch system, Tennessee tributary also dates from 1893. It is from an unspecified site in Ball Creek, a small tributary of Big Sycamore Creek, which enters Clinch River ca. one km below the Ball Creek mouth. Evermann and Hildebrand (1916) did not give number of specimens, and the collection apparently is not extant. The site probably was in lower Ball Creek. Young of a nearly strictly riverine species, *Moxostoma carinatum* (misidentified by Evermann and Hildebrand as *M. aureolum*) were taken in the same collection. Lower Big Sycamore and Ball Creeks now are impounded by Norris Reservoir.

Powell River System. — As for the Clinch, the only Powell system record is from 1893. Three specimens (Evermann and Hildebrand, 1916), two located, were from Indian Creek, Tennessee, the locality descriptor being unspecific and habitat not described. We found lower Indian Creek to be 10-15 m width and of varied habitat, somewhat silted but not heavily in swift areas. This major unimpounded tributary has been moderately sampled. The Powell itself has been extensively sampled, including collections at the Indian Creek mouth by us and others, and still supports a diverse fauna, notably *H. cahni, Notropis ariommus, N. flavipinnis* and *A. clara* (Taylor et al., 1971; Masnik, 1974; Starnes et al., 1977; recent TVA collections reviewed by Jenkins et al., in prep). However, its lower portion is impounded by Norris Reservoir, and through much of Virginia and part of Tennessee it is plagued with coal and silt deposits.

North River Holston River System. — Results of 205 collections from 50 main river sites, three in Tennessee, 47 in Virginia, are in Fig. 7. Extensive sampling in tributaries (in part, Ross and Carico, 1963) did not reveal *H. monacha.*

The early seiners, Cope (1868), Jordan (1889) and Becker

(in 1928, UMMZ), provided a good qualitative concept of the fauna in the Saltville vicinity, upper river. Patrick (1961) listed fishes in a 1954 collection above Saltville. During 1954–1958, R.D. Ross (Ross and Carico, 1963) made 69 collections by shocker or seine at 36 localities (with lumping, 24 herein) throughout the river. Unfortunately the qualitative value of many of Ross' collections is suspect; although some sites were more adversely impacted by pollutants in the 1950s than currently, species numbers (some augmented by us from original data and specimens at VPI) from less perturbed sites often are well below those usually found by recent intensive sampling. However, we include all Ross' data as they agree with patterns found by others, and he collected some sites 3–13 times.

During 1970–1977, the TVA established 22 stations which were netblocked and poisoned 1–4 times a year for 1–6 years, totaling 67 collections. Burkhead aided with four of these. Hill et al. (1975) analyzed collections made during 1970–1973 at some of the stations, and Feeman (1980) discussed 1973 collections. Feeman transmitted to us original fish data from all of 1970s collections and four TVA collections taken in 1981 from one of the original stations (Click Island). Each 1981 collection was made by electroshocker and a novel seine-snorkel method, partially described and figured by Hickman and Fitz (1978) and Hickman (1981). The operation involved four snorkelers moving abreast, over transects of ca. 8 m at a time, toward a seine held by other workers. Fishes were herded toward the seine by the snorkelers with aid of poles held end to end, forming a line generally perpendicular to the current. Feeman (pers. comm.) regarded this method to be very effective for inventory of benthic fishes. A major part of the Click Island area was covered on each date.

In 1963 Jenkins electrofished two sites with Ross. None of the above efforts were particularly aimed for *H. monacha,* but they provided firm ground for conclusions on its distribution and abundance. The following efforts by Burkhead and/or Jenkins were made especially or entirely for *H. monacha.* In 1970–1975 nine sites were worked mostly by seine, yielding 19 collections; in 1976 one site was widely inspected by snorkeling; in 1981 10 localities were sampled once by shocker or seine; in 1982 six were shocked.

Although the populations of the lower and upper river probably were contiguous, for convenience they are discussed separately.

Lower North Fork Holston River: The reach currently populated is from the mouth in Tennessee, through Scott County, Virginia to the Mendota area, western Washington County, comprising 72 km. Populations are discontinous partly due to avoidance of frequent long pools.

In Tennessee and Scott County, *H. monacha* was found at 7 of 15 sites. At least five record sites had a significant area(s) of small to medium gravel, and sites lacking a record generally lacked such areas. A striking exception was apparent absence of *H. monacha* in an extensive area of clean,
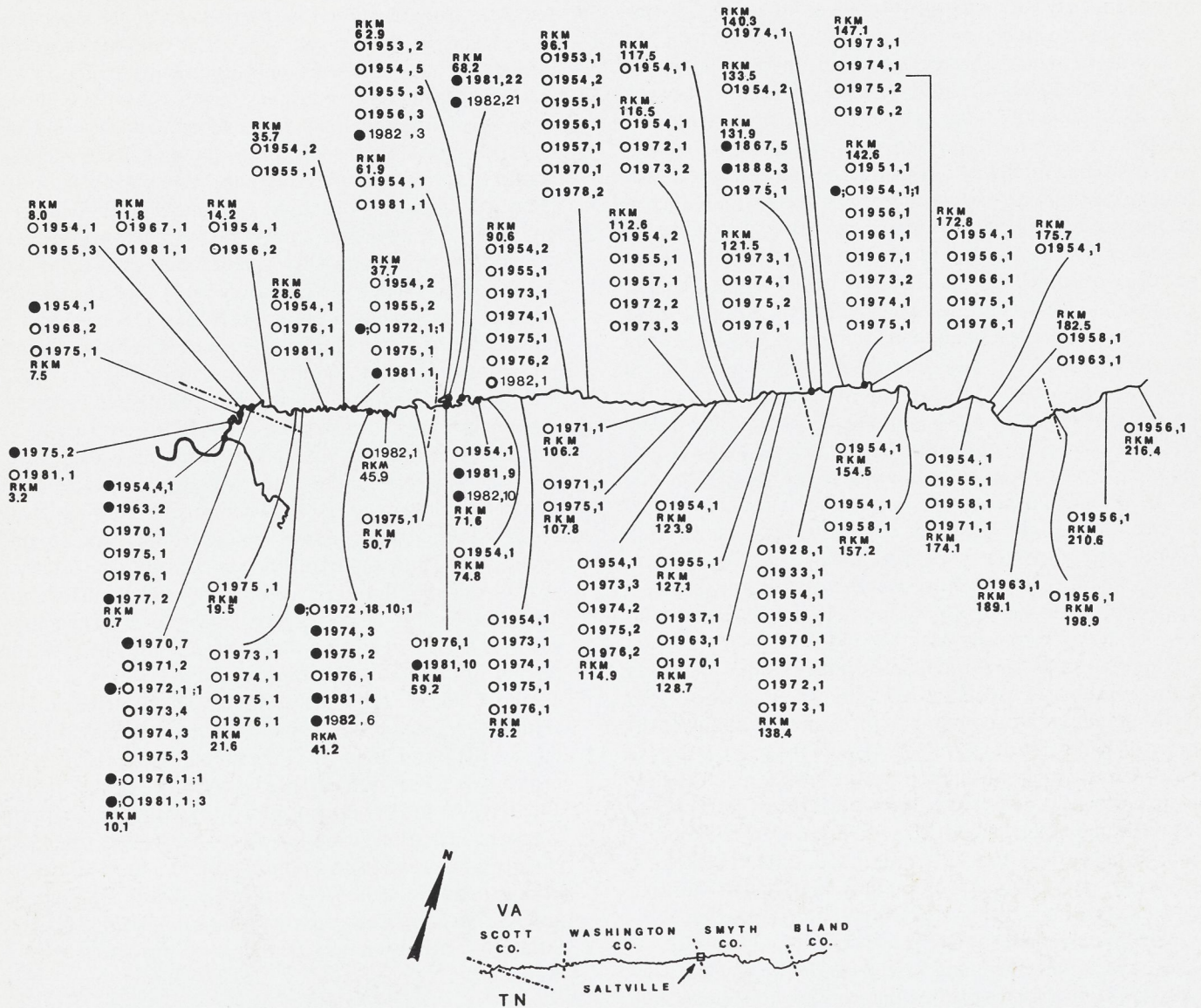
RKM 62.9
O1953,2
O1954,5
O1955,3
O1956,3
●1982 ,3

RKM 68.2
●1981,22
●1982,21

RKM 96.1
O1953,1
O1954,2
O1955,1
O1956,1
O1957,1
O1970,1
O1978,2

RKM 117.5
O1954,1

RKM 133.5
O1954,2

RKM 116.5
O1954,1
O1972,1
O1973,2

RKM 140.3
O1974,1

RKM 131.9
●1867,5
●1888,3
O1975,1

RKM 147.1
O1973,1
O1974,1
O1975,2
O1976,2

RKM 142.6
O1951,1
●;O1954,1;1
O1956,1
O1961,1
O1967,1
O1973,2
O1974,1
O1975,1

RKM 35.7
O1954,2
O1955,1

RKM 61.9
O1954,1
O1981,1

RKM 8.0
O1954,1
O1955,3

RKM 11.8
O1967,1
O1981,1

RKM 14.2
O1954,1
O1956,2

●1954,1
●1968,2
O1975,1
RKM 7.5

RKM 37.7
O1954,1
O1955,2
●;O1972,1;1
O1975,1
●1981,1

RKM 28.6
O1954,1
O1976,1
O1981,1

RKM 90.6
O1954,2
O1955,1
O1973,1
O1974,1
O1975,1
O1976,2
O1982,1

RKM 112.6
O1954,2
O1955,1
O1957,1
O1972,2
O1973,3

RKM 121.5
O1973,1
O1974,1
O1975,2
O1976,1

RKM 172.8
O1954,1
O1956,1
O1966,1
O1975,1
O1976,1

RKM 175.7
O1954,1

RKM 182.5
O1958,1
O1963,1

●1975,2
O1981,1
RKM 3.2

RKM 45.9
O1982,1

O1971,1
RKM 106.2

O1954,1
RKM 154.5

O1954,1
O1955,1
O1958,1
O1971,1

●1954,4,1
●1963,2
O1970,1
O1975,1
O1976,1
●1977,2
RKM 0.7

RKM 19.5
O1975,1

RKM 50.7
O1975,1

RKM 71.6
O1954,1
●1981,9
●1982,10

O1971,1
O1975,1
RKM 107.8

O1954,1
RKM 123.9

O1954,1
O1958,1
RKM 157.2

RKM 174.1

O1956,1
RKM 216.4

RKM 74.8
O1954,1

●1970,7
O1971,2
●;O1972,1;1
O1973,4
O1974,3
O1975,3
●;O1976,1;1
●;O1981,1;3
RKM 10.1

O1973,1
O1974,1
O1975,1
O1976,1

●;O1972,18,10;1
●1974,3
●1975,2
O1976,1
O1981,4
●1982,6
RKM 21.6

RKM 41.2

O1976,1
●1981,10
RKM 59.2

O1954,1
O1973,1
O1974,1
O1975,1
O1976,1
RKM 78.2

O1954,1
O1973,3
O1974,2
O1975,2
O1976,2
RKM 114.9

O1955,1
O1954,1
RKM 127.1

O1928,1
O1933,1
O1954,1
O1959,1
O1970,1
O1971,1
O1972,1
RKM 128.7

O1937,1
O1963,1
O1970,1
O1973,1
RKM 138.4

O1954,1

O1958,1

O1956,1
RKM 210.6

O1963,1
RKM 189.1

O1956,1
RKM 198.9

N

VA

SCOTT CO.   WASHINGTON CO.   SMYTH CO.   BLAND CO.

SALTVILLE

TN

Fig. 7. Geoghronography of *Hybopsis monacha* in North Fork Holston River, Tennessee and Virginia. Map shows virtually all known collections from the river. Data format explained in Fig. 5.

small-medium gravel (and large gravel-rubble) near Weber City (Rkm 11.8, where Rt. 614 reaches the river), seined in 1981. We give data in the Habitat section indicating *H. monacha* has an affinity for gravel in the North Fork Holston. However, even at record sites *H. monacha* generally was rare when found, and more frequently it was not taken at most record sites. At five sites its rarity apparently was natural. Reduction at the other two sites, in Scott County, probably relates partly to collecting; the sequence of collections and numbers taken is instructive concerning slow population recovery, here reviewed.

When the Click Island (Rkm 10.1) population was discovered in 1970 by Jenkins, seven specimens were quickly seined along the gravel bar at its tail. Further sampling yielded no more, nor did our effort at that spot and closeby the tail of the island in 1971, 1975 and 1981. The 13 Click Island rotenone collections by the TVA in 1971–1976 took only two specimens; all collections were from the narrower channel along the main island, with larger substrate than at the tail. The data suggest the island population was initially small, largely concentrated at the tail, depleted by the 1970 seining, and that recruitment was insignificant (our seine collection in May 1971 predated the 1971 rotenoning). It is possible that incomplete neutralization of rotenone inhibited population increase at the tail during 1971–1976, but recovery during the subsequent five years hiatus in all collecting was insignificant based on capture of only one specimen in five collections in 1981. Throughout the seven years of collecting, fishes in general remained common.

The island at Rkm 41.2 is similar to Click Island in having a bar and then a flat bed of small-medium gravel extending well below the tail. The remainder of the island is sur-

rounded mostly with large gravel-rubble. When we first seined the island, widely on 16 May 1972, *H. monacha* was somewhat common; 18 were taken, only in the tail area. On 4 June 1972, 10 were seined; only the tail area was sampled. On 12 June 1972, the full periphery of the island and below were seined without finding *H. monacha*. Collecting conditions had improved through the period and other fishes remained common. We conclude that a good population for *H. monacha*, small compared to many species, first occupied the lower island area, and that seining effectively depleted, perhaps temporarily extirpated it. We seined three specimens at the tail in 1974, and two in a slow run to the right of the tail in 1975. The left channel of the island was rotenoned by the TVA in 1976, without capture of *H. monacha*. In 1981, we seined two in the tail and one on each side of the island. In 1982, we shocked completely around the island and below for 1.5 h, and snorkled near the end of the island; six specimens were taken or seen, all at the lower right side of the island. Obviously the population had not returned to near the initial 1972 level, suggesting that, as at Click Island, recruitment occurs slowly at best. The dam at Holston Mill, Rkm 37.7, would prevent distant dispersal upstream to the island. Possibly the initial island population level was atypically high for the site.

The western Washington County populations, in a 13 km section bracketing Mendota, were discovered by us in 1981. It was uncommon to common at three sites, probably most dense at Hobbs Ford (Rkm 68.2) where the most extensive area of clean, small-medium gravel we have seen in the river occurs. It was not found in 1954 and 1981 at Barker Mill Dam (Rkm 61.9), where substrate averaged larger. Ross' 13 collections in the 1950s at Mendota (Rkm 62.9) lacked *H. monacha*; perhaps only a slow, deep section was worked; we took three specimens there in 1982, over rubble.

North Fork Holston River has had a long history of industrial pollution emanating from Saltville (Kent, 1955; Higgins, 1978), just above the Washington-Smyth County line. Toxic waste spillage apparently was chronic, and the effects of breakage in 1924 of a lateral dam, impounding a large area of dissolved alkaline waste and sediment over the flood plain at Saltville, must have been catastrophic. Residents along the river in Scott County and Tennessee told us fish kills extended through that section since at least the 1940s. Although the polluting industrial operation closed in 1972, and the ichthyofauna recovered somewhat (Hill et al., 1975; Feeman, 1980), sediments throughout the river and assayed fish species are contaminated with mercury. Mercury and other toxic chemicals continue to enter the river from extensive, abandoned waste storage ponds (Bailey, 1974; Toole and Ruane, 1976; Milligan and Ruane, 1978; Turner, 1981). Although many fish species exhibit normal size, vigor and population density, at least in Scott and western Washington counties, fishing has been banned in the river since 1970 (Anon., 1981).

The question arises concerning past longevity of the populations below Saltville, particularly those most proximate (ca. 60 km below, near Mendota). They may have been long extant but at low level, or intermittently extirpated with reestablishment via recruitment - from above Saltville (but population probably long tenuous there, and it would have had to traverse the heavily stressed zone); from the lesser impacted lower section (if milldams were passable); and/or from tributaries. Although a tributary population is unknown in the system, a few streams may have provided refuge from toxic slugs. Dispersal in recent years from lower South Fork Holston River was unlikely due to impoundment of that river and pollution from the Kingsport area (at junction of North and South Forks), which also degrades upper main Holston River (Anon., 1961; Higgins, 1978). The latter is identified by the Environmental Protection Agency as one of the 34 most polluted urban rivers in the United States (Anon., 1981). The range gap between Mendota and Saltville may be real. Although an undetermined number of the included 14 collection sites lack significant areas of small gravel, some do not (Feeman, pers. comm.), and sampling intensity probably is sufficient to have detected at least one population. The data imply *H. monacha* may have just recently achieved population level large enough to allow detection around Mendota, and may be extending farther up Washington County.

Upper North Fork Holston River: The spotfin chub was regarded as "rather rare" and "scarce" in the Saltville area during 1867 and 1888 by Cope (1868) and Jordan (1889) respectively. Both seined lengthy sections. Becker in 1928 and the TVA in 1933 did not find it. Patrick (1961) reported one specimen from seven km above Saltville in 1954. The early results suggest a low population, and the 44 other collections made in 1954–1976 indicate it vanished. *Lagochila* and *N. flavipinnis*, taken only by Jordan, also disappeared. Siltation possibly rendered the area unsuitable for *H. monacha*.

South Fork Holston River System. — Eight specimens came from the 21 km section of main channel in Tennessee whose upper end is the Virginia state line, and one specimen was from Jacob Creek, a small tributary of this section. All were taken in preimpoundment survey, including lower Watauga River, during 1947 by R.M. Bailey and the TVA; the 21 km section was also collected in 1949. Bailey noted (UMMZ file) for one collection of three *H. monacha* that it was rare, and that the Jacob Creek specimen was from a pool ca. 200 m above the mouth.

The population apparently was extirpated with filling of South Holston Reservoir in the early 1950s (dam just below lowermost *H. monacha* site), other mainstream reservoirs and cold tailwaters (Jenkins and Burkhead, 1975), and pollution of the extreme lower river (Anon., 1961; Higgins, 1978). the duskytail darter and *P. burtoni* also disappeared. The rare *Etheostoma acuticeps* was thought to have been eliminated, but was found in 1972 in South Fork Holston

River, Virginia within two km above the impoundment (Jenkins and Burkhead, 1975). The *E. acuticeps* population appeared tenuous then, and specimens were not found in 1976 and 1977. Although the freely flowing lower 15 km of South Fork Holston in Virginia is in fairly good condition, and was collected by Bailey once in 1947 and moderately well surveyed during 1959–1977, *H. monacha* is not known to have extended into it.

Discussion

Although the spotfin chub is endemic to one drainage, the 1050 km long Tennessee River is fed by numerous extensive tributary systems with upland or montane habitat, and the chub probably occupied all of these. In fact, the 12 tributary systems known to have been populated span the limits of the drainage except for extreme western lowlands. Many hypothetical populations, now extirpated, would have been undiscovered due to prior lack of collecting, or were undetected due to localization and general rarity during early survey. Its first recorded capture in 1867 postdates much of the general deforestation and consequent siltation of the basin. The evidence of extirpation of most known populations is good to strong, based on habitat modification(s) and, except for Little Bear Creek, negative results from collecting that has been extensive and often intensive over the past 20 years. The long persistence or recent recovery of numerous associated, apparently sensitive fishes is noted throughout the Distribution section. Although some of these are faring no better overall than *H. monacha,* the trend for the latter clearly has been decline.

Hybopsis monacha survives in about 166 total km of four isolated tributary systems: one site in Buffalo River of the lower drainage; and in the upper drainage, one section each of Little Tennessee and North Fork Holston rivers, and essentially four streams of the Emory system (Table 6). Although current ranges identified within three of these systems (Little Tennessee excepted) may actually be somewhat greater, many subpopulations probably are discontinuous and no population is generally flourishing. Given the history of demise of *H. monacha,* and stresses affecting at least three of the remaining populations (Buffalo possibly excepted), their survival is remarkable and tenuity is suggested.

Hybopsis monacha is a victim of numerous impacts, generally at least two on each population (Table 6). For the 24 formerly or currently inhabited stream sections (and inferred downstream extension through formerly suitable habitat in some), the following anthropogenic stresses are invoked to have adversely impacted or exterminated populations, followed by number of streams directly affected: silt or coal fine sedimentation 12; pollution 10; inundation by reservoir 10; temperature depression of dam tailwater 3; and channelization 1. Most of these factors also affect master streams of tributaries; some tributary populations may have been dependent upon immigration from the master streams.

Massive application of ichthyocide wiped out the entire Abrams Creek population. Localized seining in the North Fork Holston may have sharply depleted populations. Natural factors such as cool maximum temperature and small stream size probably limited some populations. The latter two conditions tend to coincide, and when so, populations may have been truly marginal.

The spotfin chub seems to be extinction prone. We could expect this of a large species when confined to a limited area, because of intrinsically low population density, and of predators at the top of food chains (Terborgh, 1974), but such clearly are unapplicable to *H. monacha*. Its competitive abilities, however, may be low. Except for one observation possibly more related to reproductive territoriality, its feeding activity seemed unaggressive and unopportunistic compared with several syntopic *Notropis* species, *Hybopsis dissimilis, Nocomis micropogon* and *Phenacobius uranops*. Spotfin chubs did not alter their benthic feeding to take drifting food stirred up from the substrate by observers; other fishes did. Specimens cupped in a net and held in a bucket remained quiet on the bottom, contrasting behaviorally with many shiners. However, such behaviors may be typical of many benthic insectivores such as *H. monacha*. Size and number of eggs are in the range of small cyprinids (Carlander, 1969), and the spawning period appears to be protracted. Fecundity may be much greater if it is a fractional spawner, and enhanced hatching success may attend crevice spawning, suggested in the Reproduction section. However, in North Fork Holston River self-recovery of and recruitment into depleted subpopulations were slight at best.

The surviving populations are in streams with low to moderately diverse fish faunas. Intensive inventory by ichthyocide of sections occupied by *H. monacha* found the usual range of species number to be 12–21 in the Emory system (Anon., 1970; Riddle, 1975:table 12), and 25–35 in North Fork Holston River (Feeman, in litt.; our data). In Little Tennessee River species numbers range 15–25 based on often repeated sampling at each site (det. from collection summary by Etnier, in litt., 1978; only seven species at two sites by Messer and Ratledge, 1963). In Buffalo River at the Grinders Creek mouth the number of species was 23; at two sites below, 31 and 34 (Anon., 1973). Species richness in spotfin chub streams is significantly less than in Clinch, Powell and Duck rivers, where in some sections 40–60 species are taken at a time (Etnier and Jenkins, 1980). Faunal recovery after environmental stress probably favored species more competitive than *H. monacha*, which seems to have persisted mainly only in moderately diverse fish communities.

Concerning *H. monacha* in the lower Tennessee, we postulate in the Distribution section that it may have been relatively unsuccessful due to natural factors. Based on most known populations being in the upper Tennessee (possibly an artifact), *H. monacha* may qualify as a "Cumberlan-

dian" species. Stansbery (1964) and Isom (1969) found that Cumberlandian species of bivalve mollusks tend to be more susceptible to environmental changes in the Tennessee drainage, compared with Ohian or Mississippian components of that fauna.

In 1977 *H. monacha* was designated as a Threatened species nationally, with Critical Habitat being Little Tennessee River, Swane (sic, Swain) and Macon counties, North Carolina; Emory River and specified portions of (most of) Obed River and Clear and Daddys creeks, Morgan, Cumberland and Fentress counties, Tennessee; North Fork Holston River, Hawkins-Sullivan County line, Tennessee, and Scott and Washington counties, Virginia (Fed. Reg., 1977). Critical Habitat comprises all known extant populations except for the Buffalo in Tennessee. The latter, rediscovered in 1978, should not alter Threatened status, which Deacon et al. (1979), Williams (1981) and we deem appropriate for the species nationally.

The spotfin chub is considred Endangered in three states (Bailey, 1977; Jenkins and Musick, 1980; Starnes and Etnier, 1980). The more precarious category is applied as each state contains fewer than the four known tributary system populations (one in North Carolina and Virginia; three, one barely, in Tennessee). It is extirpated in Alabama (Ramsey, 1976) and Georgia.

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Addendum

Hybopsis monacha is a crevice spawner. Eggs were observed being deposited on the under surface of a flat, small rock that formed a crevice by lying nearly vertical against a larger rock, in Emory River on 8 July 1983. The findings are further evidence that *H. monacha* is closely related to *Notropis (Cyprinella)*. Details of behavior and habitat will be reported elsewhere by the observers, Burkhead, W.H. Haxo and S.P. McIninch.

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27 December 1982

Mr. Steven Vigg
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Dear Mr. Vigg:

Thank you for sending a copy of your tui chub paper. It contains the most comprehensive treatment on this fish yet compiled. I would urge that you prepare a paper for publication, and, with this in mind, I'll offer some comments.

The direction of future work relating to evolution and taxonomy of tui chub should aim to establish the rationale of recognition of pectinifer as a species or subspecies. Are all chub populations with high numbers of gill rakers in several lakes monophyletic in origin? If so, then there is no doubt that pectinifer should be given full species status. The alternative hypotheses are that pectinifer evolved from obesa populations independently in each lake where they occur after the desiccation of Lake Lahontan, or that they are only a part of an obesa population exposed to different environmental conditions, or that obesa has a dimorphic expression for high and low gillraker counts in each lake.

I reject the latter two hypotheses out of hand; a degree of genetic-environmental plasticity previously unknown would be necessary. Thus, the most probable hypothesis is that an obesa ancestral population diverged in the Lahontan basin during one of the pluvial periods of the Pleistocene so that by the final desiccation two distinct species occurred in Lake Lahontan, G. obesa, and G. pectinifer. G. pectinifer, as Chasmistes, is specifically lacustrine adapted and persisted only in lakes (contemplate on Brook's ideas on intralacustrine speciation).

If this hypothesis is correct, then all pectinifer populations are more closely related to each other than any of them are to any obesa population. The ideal method to test this hypothesis is electrophoresis. But, as I believe I cautioned you previously, do not expect electrophoresis to yield clear-cut results for verification of monophyletic origins for diverse populations when the divergence initiating two or more distinct evolutionary lines occurred less than a million years ago or so.

This is due to the fact that the enzyme systems that can be sampled by electrophoresis are evolutionarily conservative and resist change. It takes considerable time, generally on the order of a million years or more,

before two lines diverging from a common ancestor establish a "species specific" (essentially a gene locus where no alleles are shared between the two species) distinction that can be found from an electrophoretic survey of about 15 or 20 loci.

Thus, the regulatory part of a genome governing morphology and life history adaptations may undergo relatively rapid evolution that would not be detected by electrophoresis. See papers by Clayton (p. 1515-22), Dehring et al. (1738-46), and Todd (1808-13) in the Can. J. Fish. Aquat. Sci. 1981 38(12) (STOC symposium), that demonstrate the limitations of electrophoresis to document or verify the evolutionary evidence apparant from morphology and life history distinctions.

I can see no need to "verify" a genetic basis for pectinifer and obesa of Pyramid Lake. The magnitude of these differences certainly have a hereditary basis on empirical evidence alone. No experimentation with any species of fish has ever induced a non genetic difference in gill raker number that comes remotely close to the difference between obesa and pectinifer. What should be done with electrophoresis is to try to find a "species specific" type of difference that then can be used to test monophyletic origins of all other obesa and pectinifer pairs in all other lakes. You mentioned that Riska and Lugaski failed to find such a distinction and perhaps there is none, but a person with considerable experience and expertise should do the work.

Another possibility that can add confusion is that pectinifer may have consisted of discrete forms in Lake Lahontan and two or more distinct forms of pectinifer may exist in Pyramid Lake. The bimodal distribution of gill raker counts indicates that this is a possibility. This phenomenon is common in Whitefishes (Coregonus) living in large lakes where distinct populations have different mean and modal numbers of gill rakers.

Carl Hubbs' classification of pectinifer as a subspecies of obesa was based on a preconceived notion and his subsequent references on the matter were never supported by actual data. As you found, when one actually counts gill rakers, there is no hard evidence for hybridization or inter-gradation in specimens from any lake where they are found. The Eagle Lake gill raker distribution is clearly biomodal, not trimodal, which it would be if hybridization were common. The "overlap" in Eagle Lake is probably just that, where occasional specimens of pure obesa and pure pectinifer with extreme counts have the same number. I suspect that if you count anterior and posterior rakers on first, second, third arches of Eagle L. specimens and examine various permutations you can get complete separation of specimens. Also take some time and make detailed examination and comparison of gill raker morphology of Pyramid L. obesa and pectinifer. Are these differences consistant? Are they consistant in Eagle L. specimens? What is the gill raker morphology of specimens with intermediate number; does it indicate a hybrid origin? Are your other morphological distinctions of head and peduncle measurements consistant between obesa and pectinifer of different lakes?

What is the origin of the <u>pectinifer</u> type of chub in Lake Almanor of the upper Sacramento River basin? Supposedly, only <u>obesa</u> is native to the basin.

Your reference to speciation of <u>Prosopium</u> of Bear Lake, is relevant because of similar hydrographic histories between the Bonneville and Lahontan basins suggest similar opportunities for intralacustrine speciation. The reference to Lake Llanao, however, in regards to rapid, explosive speciation of numerous species and genera in 10,000 years or so, lacks validity. George Myers did establish that the lava flow creating Lake Llanao is geologically recent, but he neglected the fact that the plateau on which the lake is located dates to Miocene times and contains other lakes, some of which, also have the endemic cyprinids. I suspect the Llanao species flock is many millions of years old and its origin was from more than one ancestral species.

Sincerely,

Robert Behnke

Mr. Steven Vigg
Desert Research Institute   cc for Dave Galat
P.O. Box 60220
Reno, NV ~~6022~~089506

Dear Mr. Vigg:

Thank you for sending a copy of
your tui chub paper. It contains the most
comprehensive treatment on this fish yet
compiled. I would urge that you prepare
a paper for publication, and, with this in
mind, I'll offer some comments.

The direction of future work relating
to evolution and taxonomy of tui chub
should aim to establish the rationale
of recognition of pectinifer as a species
or ~~subspecies~~. Are all chub populations with
high numbers of gill rakers in several
lakes ~~all~~ monophyletic in origin? If
so, then there is no doubt that pectinifer
should be given full species status. The
alternative hypotheses are that pectinifer
evolved from obesa populations independently
in each lake where they occur, after the
desiccation of Lake Lahontan, or that
they are only a part of an obesa
population exposed to different environmental
conditions, or that obesa has a
dimorphic expression for high and
low gillraker counts in each lake.
I reject the latter two hypotheses
out of hand; a degree of genetic —

environmental plasticity previously unknown
would be necessary. Thus, the most
probable hypothesis is that an ~~ancient~~
obesa ancestral population ~~became~~ diverged
in the Lahontan basin during one
of the pluvial periods of the Pleistocene
so that by the final desiccation
two distinct species occurred in
Lake Lahontan, G. obesa , and G. pectinifer.
G. pectinifer, as Chasmistes, is specifically
lacustrine adapted and persisted only
in lakes (~~consider~~ contemplate on Brook's ideas on intralacustrine
speciation)

If this hypothesis is correct, then
all pectinifer populations are more
closely related to each other than any
of them are to any obesa population.
The ideal ~~to~~ method to test this hypothesis
is electrophoresis. But, as I believe I
cautioned you previously, do not expect
electrophoresis to yield clear-cut results
~~to~~ for verification of monophyletic origins
~~for~~ diverse populations when the
divergence initiating two or more
distinct evolutionary lines occurred
less than a million years ago or so.
This is due to the fact that the
enzyme systems that can be sampled
by electrophoresis are evolutionarily conservative

and resist change. It takes considerable time, generally on the order of a million years or more, before two lines diverging from a common ancestor establish a "species specific" (essentially a gene locus where no alleles are shared between the two species) distinction that can be found from an electrophoretic survey of about 15 or 20 loci.

Thus, the regulatory part of a genome governing morphology and life history adaptations may undergo relatively rapid evolution that would not be detected by electrophoresis. See papers by Clayton (p. 1515-22), Dehring et al. (1738-46), and Todd (1808-13) in the Can. J. Fish. Aquat. Sci. 1981 38(12) (STOC symposium), that demonstrate the limitations of electrophoresis to document or verify the evolutionary evidence apparent from morphology and life history distinctions.

I can see no need to "verify" a genetic basis for pectinifer and obesa of Pyramid Lake. The magnitude of these differences are certainly have a hereditary basis on empirical evidence alone. No experimentation with any species of fish has ever induced a nongenetic difference in

gill raker number that comes
remotely close to the difference
between obesa and pectinifer. What
should be done with electrophoresis
is to try to find a "species
specific" type of difference that then
can be used to test monophyletic
origins of all other obesa and
pectinifer pairs in all other lakes.
You mentioned that Riska and
Lugaski failed to find such a
distinction and perhaps there is
none, but a person with considerable
experience and expertise should do
the work.

Another possibility that
can add confusion is that pectinifer
may have consisted of discrete
forms in Lake Lahontan and
two or more distinct forms of
pectinifer may exist in Pyramid Lake.
The bimodal distribution of gill raker
counts indicates that this is a
possibility. This phenomenon is common
in whitefishes (Coregonus) living in
large lakes where distinct populations
have different mean and modal
numbers of gill rakers.

Carl Hubbs' classification of pectinifer as a subspecies of obesa was based on a preconceived notion and his subsequent references on the matter were never supported by actual data. As you found, when one actually counts gill rakers, there is no ~~real~~ hard evidence for hybridization or intergradation in specimens from any lake where they are found. The Eagle Lake gill raker distribution is clearly bimodal, not trimodal, which it would be if hybridization were common. The "overlap" in Eagle Lake is probably just that, where occasional specimens of pure obesa ~~with~~ and pure pectinifer with extreme counts have the same number. I suspect that if you count anterior and posterior rakers on first, second, third arches of Eagle L. specimens and examine various permutations you can get complete separation of specimens. Also take some time and make detailed examination and comparison of gill raker morphology of Pyramid L. obesa and pectinifer. Are these differences consistant? Are they consistant in Eagle L. specimens? What is the ~~morphology of~~ gill rakers

morphology of specimens with intermediate member; does it indicate a hybrid origin? Are your other morphological distinctions of head and peduncle measurements consistant between obesa and pectinifer of different lakes?

~~Where cool~~ What is the origin of the pectinifer type of chub in Lake Almanor of the upper Sacramento River basin? Supposedly, only obesa is native to the basin.

Your reference to speciation of <u>Prosopium</u> of Bear Lake, is relevant because of similar hydrographic histories between the Bonneville and Lahontan basins suggest similar opportunities for intralacustrine speciation. The reference to Lake Lanao, however, in regards to rapid, explosive speciation of numerous species and genera in 10,000 years or so, lacks validity. George Myers did establish that the lava flow creating Lake Lanao is geologically recent, but he neglected the fact that the plateau on which the lake is located dates to Miocene times and contains other lakes, some of which, also have the endemic cyprinids. I suspect the Lanao species flock is many millions of years old and its origin was from more than one

ancestral species. Sincerely,

12-15-82

Dr. R. J. Behnke
Professor
Colorado State University
Fort Collins

Dear Dr. Behnke,

Enclosed is a report on tui chub gill raker differentiation. It contains a review of the literature, new data on several lakes (Topaz, Eagle, Walker, Almanor, Pyramid), and a proposal for studies to determine the basis of differentiation. I would appreciate receiving your comments on this paper.

Sincerely

Steven Vigg

sympatric speciation ? -- always argue that every possible to get 'to
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        cost a 10-or-8   allopatric - at least to 'initiate'
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†L. Almanor (Feather R. drain) - origin of tui club ?
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1 Eagle L. -- lack of gap   - nonsense.
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      not ne ~ myo   osch lake sympatri
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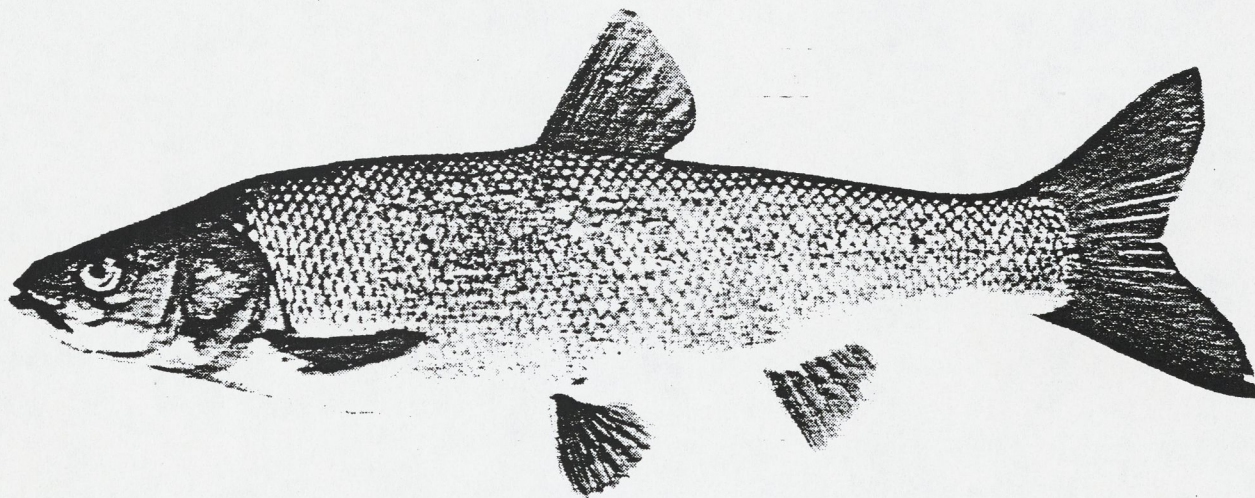   - see Tedd out in discour
                                                        - siscowet -

The Basis of Morphological Differentiation of Two
Forms of Lahontan Tui Chub: <u>Gila</u> <u>bicolor</u> <u>obesa</u> and
<u>Gila</u> <u>bicolor</u> <u>pectinifer</u>

by

Steven Vigg

for

Dr. Ayesha E. Gill
Biology 604 - Population Genetics
University of Nevada, Reno

December, 1982

The Basis of Morphological Differentiation of Two
Forms of Lahontan Tui Chub: <u>Gila</u> <u>bicolor</u> <u>obesa</u> and
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ABSTRACT

Two, apparently ecologically separate, types of Lahontan tui
chub exist in Pyramid Lake, Nevada: a (benthic) coarse gill-
rakered form-<u>Gila</u> <u>bicolor</u> <u>obesa</u>, and a (limnetic) fine gill-
rakered form-<u>Gila</u> <u>bicolor</u> <u>pectinifer</u>. It is not known if these
forms represent distinct genetic taxons or just variation within a
single gene pool. Prominent Great Basin scientists have disagreed
upon the status of the two forms of Lahontan tui chubs - opinions
have varied over the entire spectrum: one single subspecies, two
subspecies, hybridization between two subspecies, two distinct
species, or two genera. Clarification of the taxonomic confusion
would elucidate the legal status of the Lahontan tui chub; <u>G.b.</u>
<u>obesa</u> now has "special concern" status, and <u>G.b.</u> <u>pectinifer</u> is
unresolved. I will present a brief paleogeographic history, a
review of the literature on the morphology and life history of the
tui chub, and proposed experimentation to determine the basis of
differentiation of <u>G.b.</u> <u>obesa</u> and <u>G.b.</u> <u>pectinifer</u>.

INTRODUCTION

Geologic History

The "Great Basin" is an interior drainage basin bounded by
the Sierra Nevada on the west, the Columbia volcanic plateau on
the North, the Wasatach Range on the east, the Colorado River
drainage on the southeast and the Mohave Desert on the southwest
(Figure 1). The "Basin and Range Province" is a more descriptive
term for the region since it is not a single basin but a matrix of
about 90 north-south oriented valleys bounded by some 160 mountain
ranges. The most characteristic attribute of the region is that
it is an endorheic system with no outlet to the sea. This
occurred in late Pliocene when major elevation of the Sierra
Nevada took place and extensive block faulting occurred in western
Nevada. The resulting physiography set the stage for geographic
isolation and a subsequent high degree of fish endemism which
occurred when climatic changes restricted interconnections among
water systems.

During the Pleistocene (some 2.5 million years before present
- MYBP) this region contained two major lake systems; Bonneville
($51/560$ km^2) and Lahontan ($22,300$ km^2); as well as numerous
smaller ones (Hubbs et al. 1974). Utah's Great Salt Lake and Utah
Lake are the principal remnants of Lake Bonneville. Lake Lahontan
was highly dissected, consisting of nine interconnecting basins
when its surface exceeded 1,308 m above sea level (Galat et al.
1981). During the Pleistocene numerous Pluvial (wet) periods of
lake filling cycled with interpluvial (dry) periods of
desiccation. The maximum extent of the last Pluvial occurred 10-
13 thousand years BP. Since that time desiccation has reduced the
extent of aquatic habitats resulting in isolation of fish
populations.

Pyramid Lake Fish Populations

Pyramid Lake is the largest remnant of Lake Lahontan having a
surface area of 446.4 km^2, volume of 26.4 km^3, and maximum depth
of 103 m (Harris 1970). Other remnants include Winnemucca Lake
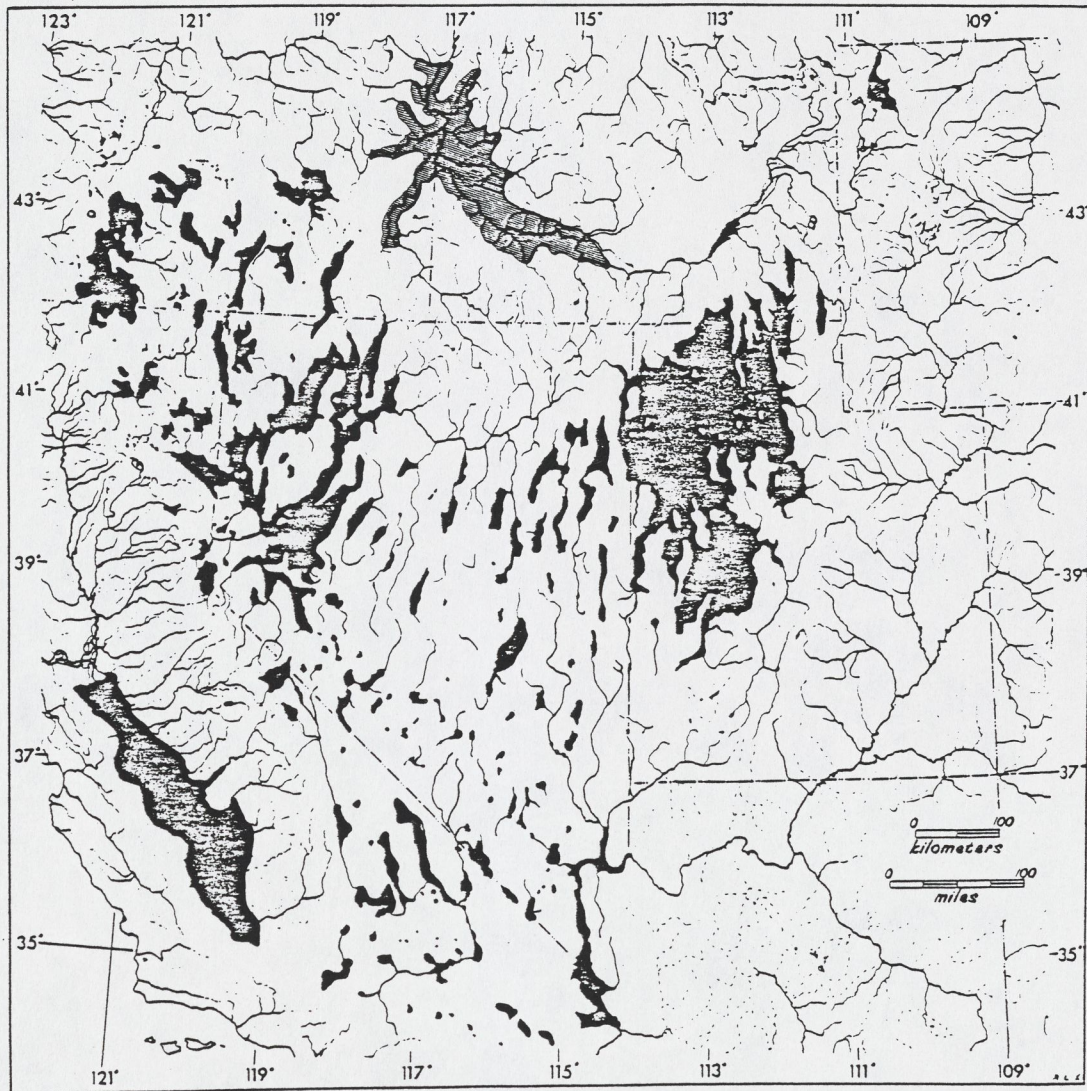(dry in 1938), Honey lake (periodically filling) and Walker Lake

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Fig. 1. Noncontemporaneous maximum extent of Late Pleistocene lakes and known fluvial connections in intermountain western North America and possible maximum extent of Pliocene Lake Idaho. Compiled and modified from Miller (1946a), Hubbs and Miller (1948), Trimball and Carr (1961), Feth (1961), Bright (193), Snyder et al. (1964), Morrison (1965), and Hubbs et al. (1974). (After Smith 1978)

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(rapidly desiccating). Pyramid Lake exhibits a characteristic fish fauna: cui-ui (_Chasmistes_ _cujus_), Tahoe sucker (_Catostomus_ _tahoensis_), Lahontan cutthroat trout (_Salmo_ _clarki_ _henshawi_), Lahontan redsides (_Richardsonius_ _egregius_), Lahontan speckled dace (_Rhinichthys_ _osculus_ _robustus_), and tui chub (_Gila_ _bicolor_), as well as an introduced species - Sacramento perch (_Archoplites_ _interruptus_ (La Rivers 1962).

Lahontan cutthroat trout and tui chub constitute a highly adapted predator - prey relationship which developed during coevolution in a continuous lacustrine environment for 50,000 to 100,000 years. The relative abundance of tui chubs has been estimated at 97.3% of the total fish population (Vigg 1981).

Tui-Chub Morphs

Gila _bicolor_ (Girard) is the taxon recognized by the American Fisheries Society Committee on Names of Fishes for the entire tui chub complex; however _G.b._ _obesa_ is recognized by the Endangered Species Committee as being "Of Special Concern" (Deacon et al. 1979). The tui chub exhibits extreme evolutionary plasticity evidenced by the fact that almost every drainage system in California, Nevada, and Oregon which is at least partially isolated supports one or more distinctive forms (Moyle 1976). The tui chub is represented by at least seven local forms in the Lahontan system; however, several complications exist in this nomenclature (Hubbs et al. 1974). Until recently, the species complex has been treated under the generic name _Siphateles_ which is endemic to the central Great Basin. On the basis of Uyeno's (1960) doctoral study, _Siphateles_ was synonymized with _Gila_. Two forms of Lahontan tui chub are known to exist in Pyramid Lake, i.e., _Gila_ _bicolor_ _obesa_ (Girard) which is characterized by coarse gill rakers and _Gila_ _bicolor_ _pectinifer_ (Snyder) which exhibits fine gill rakers. Disagreement exists among authorities whether or not these forms represent discrete taxons. Snyder (1917) regarded the two forms as generically as well as specifically

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distinct, naming the lacustrine fine-rakered form <u>Leucidius pectinifer</u>. Miller (doctoral thesis, Stanford University 1951) and Hopkirk and Behnke (1966) consider the two forms to be distinct species. Hubbs et al. (1974) consider the two types to be subspecies which exhibit intraspecific intergradation; while La Rivers and Trelease (1952) state that <u>pectinifer</u> has no valid standing as a taxonomic unit. Bailey and Uyeno (1964) revised the nomenclature of the blue and tui chub, and regard the entire Lahontan tui chub complex as <u>Gila bicolor obesa</u> (Girard). Kimsey (1954) considers the tui chub population occurring in Eagle Lake best described by the scientific name <u>G.b.</u> <u>bicolor</u>: <u>obesus</u> X <u>pectinifer</u>. A further taxonomic complication exists since <u>Gila bicolor</u> are known to hybridize with <u>Richardsonius egregius</u> and <u>Rhinichthys osculus</u> in Lake Tahoe (Evans 1969), and both of these species are present in Pyramid Lake. Only the fine-rakered form was observed in Walker Lake (Cooper 1978).

REVIEW OF FISH SPECIATION

It is useful to define various concepts dealing with fish speciation. The criteria for subspecies, species, and genera of fishes do not differ essentially from those pertinent to the tetrapod classes (Hubbs 1943). The "biological species concept" is generally accepted. According to this view species are: "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1940); or phrased another way: "systems of populations; the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of such mechanisms" (Dobzhansky 1970). White (1978) emphasizes that every species is at the same time a reproductive community, a gene pool, and a genetic system.

Speciation can be defined as the genetic changes whereby new species come into existance. Bush (1975) defines speciation as "ultimately an adaptive process that involves establishment of intrinsic barriers to gene flow between closely related

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populations by development of reproductive isolating mechanisms."
Hubbs (1967) visualized speciation as "a long-continued and often
fluctuating conflict between forces that tend to unify the gene
pool and those that tend to diversify populations genetically."
He considered the prime unifying force to be interbreeding; and
the opposing factors, which lead to isolation and speciation, to
be more numerous and complex including both intrinsic genetic
mechanisms and extrinsic environmental relations.

"Reproductive isolating mechanisms" are basic to the
definition of species. Dobzhansky (1937) coined the term
"isolating mechanisms" and classified them according to the
criteria of (1) preventing production of hybrids (reaching sexual
maturity), and (2) production of sterile hybrids. Meacham (1961)
divided isolating mechanisms into premating and postmating forms.
Mayr (1970) used these concepts to further classify isolating
mechanisms (From White 1978):

I. Mechanisms that prevent interspecific crosses (premating):
    A. Seasonal
    B. Ethological isolation
    C. Mechanical isolation (e.g. sperm transfer)

II. Mechanisms that reduce success of interspecific crosses
    (postmating):
    A. Gametic mortality
    B. Zygotic mortality
    C. Hybrid inability
    D. Partial or complete hybrid sterility.

A primary question is how populations are isolated. It is
generally accepted that geographic isolation can lead to
speciation. Mayr (1942) believes that virtually all speciation is
allopatric, i.e., that geographic isolation of two populations is
a necessary prerequisite in time to the developing of genetic
isolating mechanisms. However, many evolutionists believe that
speciation can occur in populations that occur together, i.e.,
sympatric speciation. Genetic revolution and geographic isolation

may not be required for speciation in many animals; reproductive isolation can arise during (parapatric) or even before (sympatric) new populations become adapted to new niches, without loss of contact with parent populations (Bush 1975). Seven models of speciation have been proposed by White (1978): (1) strict allopatry without a narrow bottleneck; (2) Founders principle (strict allopatry with bottleneck); (3) Extinction of intermediate populations in a chain of races; (4) clinal speciation; (5) area-effect (genic) speciation; (6) stasipotric (chromosomal) speciation; and (7) sympatric speciation.

Rivas (1964) discussed the terms allopatric and sympatric and proposed to break down the latter term into two categories. "Syntopic" refers to two or more related species which occupy the same microhabitat, are observed in close proximity, and could possibly interbreed. "Allotopic" refers to two or more related species which do not occupy the same microhabitat and could not interbreed even though they may have the same geographic distribution.

Hubbs (1961) discussed several isolating mechanisms in the speciation of fishes, citing specific examples for various groups of fishes. He conceeded that geographic isolation is a major factor in speciation and as a matter of semantics even microhabitats or niches may be termed distinct geographic entities. Regardless of semantics, Hubbs (1961) concluded that segregation and speciation of fishes may be effected in essential sympatry; this seems to be particularly true in lacustrine environments where explosive evolution may occur.

The endemic fish fauna of Lake Lanao, Philippines, is an example of "explosive evolution" of a species flock being derived from a common cyprinid ancestor. Barbus binotatus in the isolated lacustrine environment gave rise to 18 species, including four genera, possible within 10,000 years. In the Great Basin Region, the Bear Lake (Utah-Idaho) fish fauna illustrates sympatric evolution of three distinct coregonids (Snyder 1919).

Miller (1961) believes that much of the differentiation of Great Basin fishes took place in the Pleistocene. In general the

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postpluvial timespan of some 10,000 to 12,000 years is associated
with the differentiation of subspecies; however, speciation within
a few thousand years apparently occurred in exceptional cases
(Miller 1961).

The genetic bases of characters and the genetic inter-
relationships of forms can be determined more readily by experi-
ment in Pices than in most other groups because the frequent
occurrence not only of subspecific intergradation, but also of
interspecific and even of intergeneric hybridization (Hubbs 1943).
Natural hybrids between species occur more commonly in fishes than
in any other group of animals. Clark Hubbs (1970) conducted a
series of intrafamiliar hybrid experiments to illucidate
systematic relationships of Cyprinodontidae. He found the level
of hybrid survival parallels the estimate of phylogenetic
similarity as determined by morphological taxonomy. Neff and
Smith (1979) conducted a multivariate analysis of traits of hybrid
fishes and found that gill raker counts were important in
distinguishing between two species of cyprinids (Notropis) and
their hybrids.

A fully documented history of a single case of speciation
might include the following data on both forms (White 1978):
1) A precise map of present distributions
2) Geological and climatological evidence suggesting past
    distributions
3) Detailed morphological description
4) Detailed information on geographical variation, including
    multivariate biometrical studies
5) Ecological studies on habitats, niches
6) Extensive information on biochemical polymorphisms and
    the extent of allelic differences between the two forms
7) Detailed descriptions of the Karotypes
8) DNA values, including satellite DNA
9) Seasonal cycles, i.e. duration of mating season
10) Results of experimental hybridization
11) Information as to hybridization in nature
12) Information regarding any ethological isolating mechanisms

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In the following sections I will review the available data on
the ecology and life history, morphological information, and
genetic information of tui chubs in Pyramid Lake. Furthermore, I
will propose experiments to determine the basis of morphological
differentiation.

LIFE HISTORY OF TUI CHUB

Tui chub are the most abundant fish in Pyramid Lake and form
the link in the food chain between the lower levels (primary
producers, macroinvertebrates and zooplankton) - and the species
of primary economic importance, the Lahontan cutthroat trout. In
the surface-inshore and limnetic regions of Pyramid Lake tui chubs
compose 99% of the population, about 97% in the profudal zone, and
about 77% in the shallower benthic regions (Vigg 1981). Adult
chubs range from 150-350 mm fork length, have an average weight of
about 90g, and live to an age of about 6 years.

Tui chubs are generally distributed offshore in winter and
inshore and in surface waters during summer. During the summer
season about 92% of the limnetic chub population was in the top
22.5 meters of the water column, and about 88% of the benthic
population inhabited the shallow littoral zone (Vigg 1978, 1980).
During the winter tui chubs are inactive and at highest densities
in relatively deep water (46-61 m). As surface water temperatures
increase in spring there is a definite upward and inshore movement
associated with increased feeding and sexual maturation. A
hydroacoustic survey indicated that this migration had already
occurred by April (1976); the limnetic tui chub population was
concentrated in the 4-18 m strata with appreciable densities
extending to 48 m (Nunnallee et al. 1976). Concurrent zooplankton
densities exhibited a very similar vertical distribution pattern
(Lider and Langdon 1978).

Zooplankton distributions are associated with limnetic tui
chub distributions (Figure 2, Vigg 1978); congruently zooplankton
are the major food source for limnetic (fine gill raker) tui chubs
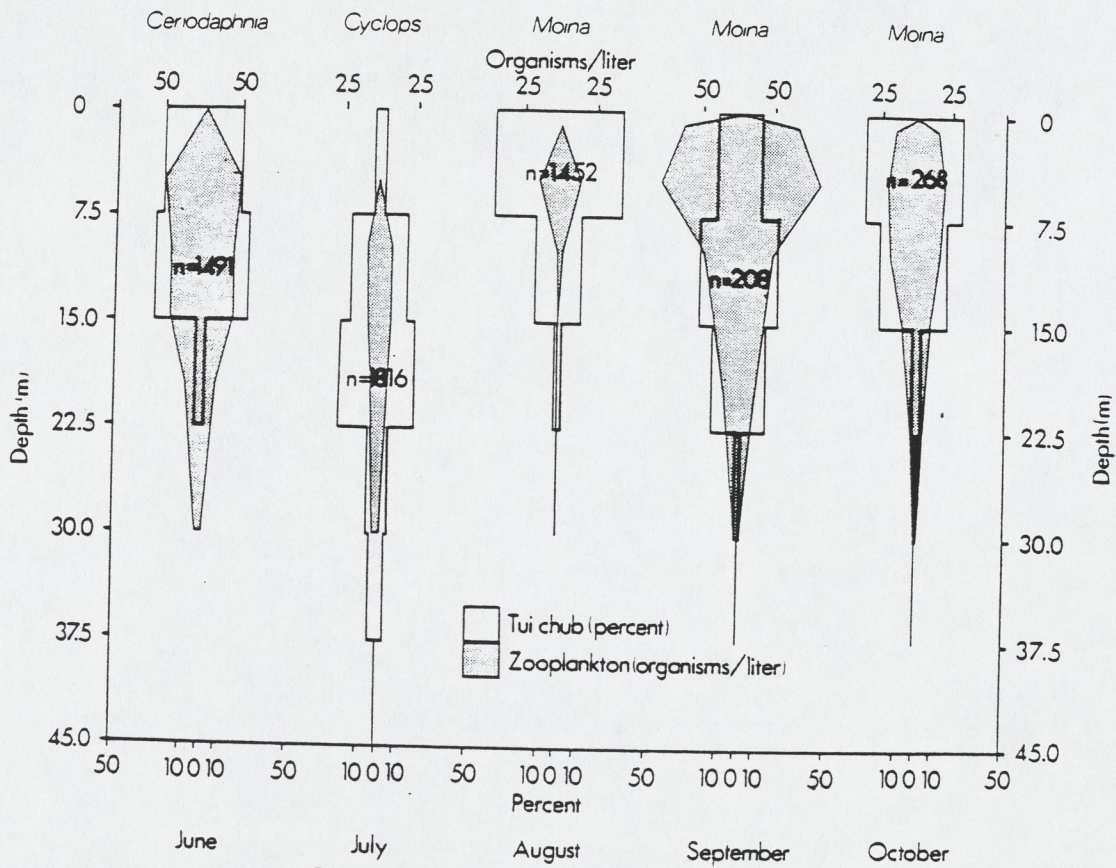(Langdon 1979). The benthic-inshore (coarse gill raker) tui

Figure 2. Vertical limnetic distribution (percent by depth interval) of tui chub in Pyramid Lake, Nevada, from June through October 1977 in relation to the vertical distribution (density by depth interval) of the zooplankton taxa selected in the diet of tui chubs (from Vigg 1978).

chubs are omnivorous, feeding on zooplankton, periphyton, and macroinvertebrates (Whaley 1978; Langdon 1980).

Spawning activity is another factor associated with inshore - surface migrations. Spawning commences near-shore in June, peaks in July, and continues through August (Kucera 1978). Tui chub fecundity ranges from 6,110 to 68,933 ova, directly correlated to fish size. Females spawn at a gonadal samatic index of 9.1% at surface water temperatures of 15.5 to 22.2 C. Males reach sexual maturity at age two, while most females mature at age three (Kucera 1978). After initiation of spawning, immeasureable numbers of juvenile tui chubs forage along the lakeshore at depths less than one meter. As individuals become larger throughout the season, they migrate progressively further offshore (Galat et al. 1981). During their first year of life juvenile chubs may approach 100 mm fork length, depending on when they were spawned relative to the growing season. Moina appears to be the principal zooplankton consumed by juveniles.

It is not known, but generally assumed, that the limnetic tui chub population moves inshore to spawn in the littoral zone. If this is the case it would be more difficult to explain reproductive isolating mechanisms; the two forms could spawn in different depths within the littoral zone (e.g., the limnetic population could spawn in deeper but still benthic areas), they could have different temporal (diel or seasonal) patterns, or differential behavior.

An alternative hypothesis is that the limnetic population spawns offshore and the benthic population spawns inshore - this would clearly constitute a reproductive isolating mechanism. One observation which may indicate limnetic spawning is the sighting of large offshore schools of tui chub beginning in March and extending through summer - during weekly aerial observations, 1976-1978 (Joseph L. Kennedy, pers. comm.). These schools are "donut-shaped" and are constantly moving in one direction. Limnetic spawning is also indicated by relatively high catches of tui chub larvae (6-15 mm) captured in offshore surface samples (Vucinich et al. 1981). The offshore catch of larvae was over

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twice that of a near-shore station; both of which peaked in July. An observation that contradicts this hypothesis is that a spawning school was sampled inshore in Walker Lake, and found to be comprised almost entirely of fine-gill rakered fish (Vigg and Cooper, unpublished manuscript). However, the benthic-coarse rakered form is apparently absent in Walker Lake.

GILL RAKER MORPHOLOGY

The taxonomic confusion concerning <u>Gila</u> <u>bicolor</u> <u>obesa</u> (coarse-gill rakers), and <u>G.b.</u> <u>pectinifer</u> (Fine-gill rakers) has been briefly reviewed in the "Introduction". Hubbs (1961) summarizes the differences:

> "One form, <u>obesus</u>, is character of streams, where it feeds on insect larvae and other bottom invertebrates and gets along with fewer than twenty stubby gill rakers. The other form, <u>pectinifer</u>, is adapted to lacustrine conditions and presumably evolved in the vast Pluvial Lake Lahontan. Its large size, strong build, upturned mouth, and very numerous and long gill rakers fit it for life in open waters feeding on zooplankton..."

In addition to finer, more numerous gill rakers, the <u>pectinifer</u> form has a more oblique mouth and more concave head than the <u>obesa</u> form (Moyle 1976). The coloration of <u>obesa</u> is brassy or brownish, whereas <u>pectinifer</u> is comparatively untinted, being blackish or of a silvery hue (Miller 1951).

At this point I will refer back to the previous discussion of fish speciation, and present Hubbs' (1943) definition of a species contrasted to subspecies:

> "I prefer to regard as full species any two completely distinct forms which do not intergrade in nature, whether or not they fail to interbreed because of their isolated ranges. If under appropriate circumstances the two forms at any time come together and interbreed regularly, I would take this as evidence that they have reverted from the specific to subspecific category of differentiation."

With these criteria in mind it is understandable why Hubbs (1961, p. 13), in his discussion of obesa vs pectinifer, regarded them as subspecies. He cited integradation of gill raker numbers in Eagle Lake, Lake Tahoe, and Walker lake populations as the reason for this designation.

In contrast Dr. Robert Behnke (Colorado State University, Pers. Comm.) considers the fact that both obesa and pectinifer exist sympatrically in Pyramid Lake without any intergradation of gill raker numbers as clear evidence of separate species. In the following discussion I will present gill raker frequency distributions from tui chub populations in various lakes.

Gill raker distribution of fluviatile populations are presented in Table 1. Hubbs et al. (1974) concluded from the remnants of pluvial lakes Diamond, Newark and Clover that either these lacustrine populations did not evolve high gill raker number, or that rakers reverted back to low numbers when the populations subsequently became isolated in springs and creeks. The raker counts exhibit a sharp upstream decrease, in a regular cline, with means of 16.4 > 14.9 > 13.6 > 12.6. Hubbs et al. (1974) attributes this to past hybridization of downstream populations with G.b. pectinifer (which has 29-40 rakers) and subsequent backcrossing with G.b. obesa. Occurrence of intergrades between G.b. obesa and G.b. pectinifer in ancient Indian caches near Lovelock demonstrates past intermixing near the lower end of the Humboldt River (Hubbs and Miller 1948).

The Pyramid Lake tui chub population clearly exhibits two modes of gill raker number: 14 (10-24) = obesa, and 34 & 38 (27-40) = pectinifer (Figure 3). Both forms are present in littoral areas while only the pectinifer form is present in offshore limnetic areas (Langdon 1979). Marrin and Errman (1982) report that the Stampede Reservoir population (tributary to the Truckee River) is comprised of the lake form characterized by numerous, slender gill rakers. Vucinich et al. (1981) demonstrated, from sampling the eulittoral zone (<1m), that the separation of the two forms becomes more distinct as the fish grow (Figure 4). The same phenomenon has been demonstrated in an experimental population

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TABLE 1. *Number of gill-rakers in populations of* Gila bicolor *in certain basins in Nevada* (From Hubbs et al. 1974).

Subspecies Pluvial lake system Locality[1]	Gill-rakers, including all rudiments, on first gill-arch																No.	Ave.
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		
Gila bicolor obesa																		
Lake Lahontan																		
Carson River (G1)[2]	—	—	—	—	1	6	9	13	13	8	5	5	5	1	3	1	70	16.43
Humboldt River																		
Near Lovelock (G2)	—	—	—	—	3	16	32	37	29	15	5	2	2	2	2	—	145	14.90
Near Carlin (G3)	—	—	—	2	5	23	16	13	—	1	—	—	—	—	—	—	60	13.62
Bishop Creek (G4)	—	—	1	16	66	83	25	1	—	—	—	—	—	—	—	—	192	12.61
Lake Diamond																		
Birch Ranch (G5)	—	—	—	—	9	28	22	9	2	—	—	—	—	—	—	—	70	13.53
Sulphur Spring (G6)	—	—	—	—	5	22	43	12	—	—	—	—	—	—	—	—	82	13.76
Gila bicolor newarkensis																		
Lake Newark																		
Near Diamond Peak (G7)	—	1	8	23	38	22	5	3	—	—	—	—	—	—	—	—	100	11.99
Moores Ranch (G8)	—	—	2	14	39	34	11	—	—	—	—	—	—	—	—	—	100	12.23
Warm Springs (G9)	—	—	—	2	6	—	—	—	—	—	—	—	—	—	—	—	8	11.75
Gila bicolor euchila																		
Lake Newark																		
Fish Creek Springs (G10)	—	—	13	40	56	24	5	—	—	—	—	—	—	—	—	—	138	11.77
Gila bicolor isolata																		
Lake Clover																		
Independence Valley (G11)	2	9	30	53	36	18	1	—	—	—	—	—	—	—	—	—	149	11.14

[1] Expressed as numbered Locations in the G series.
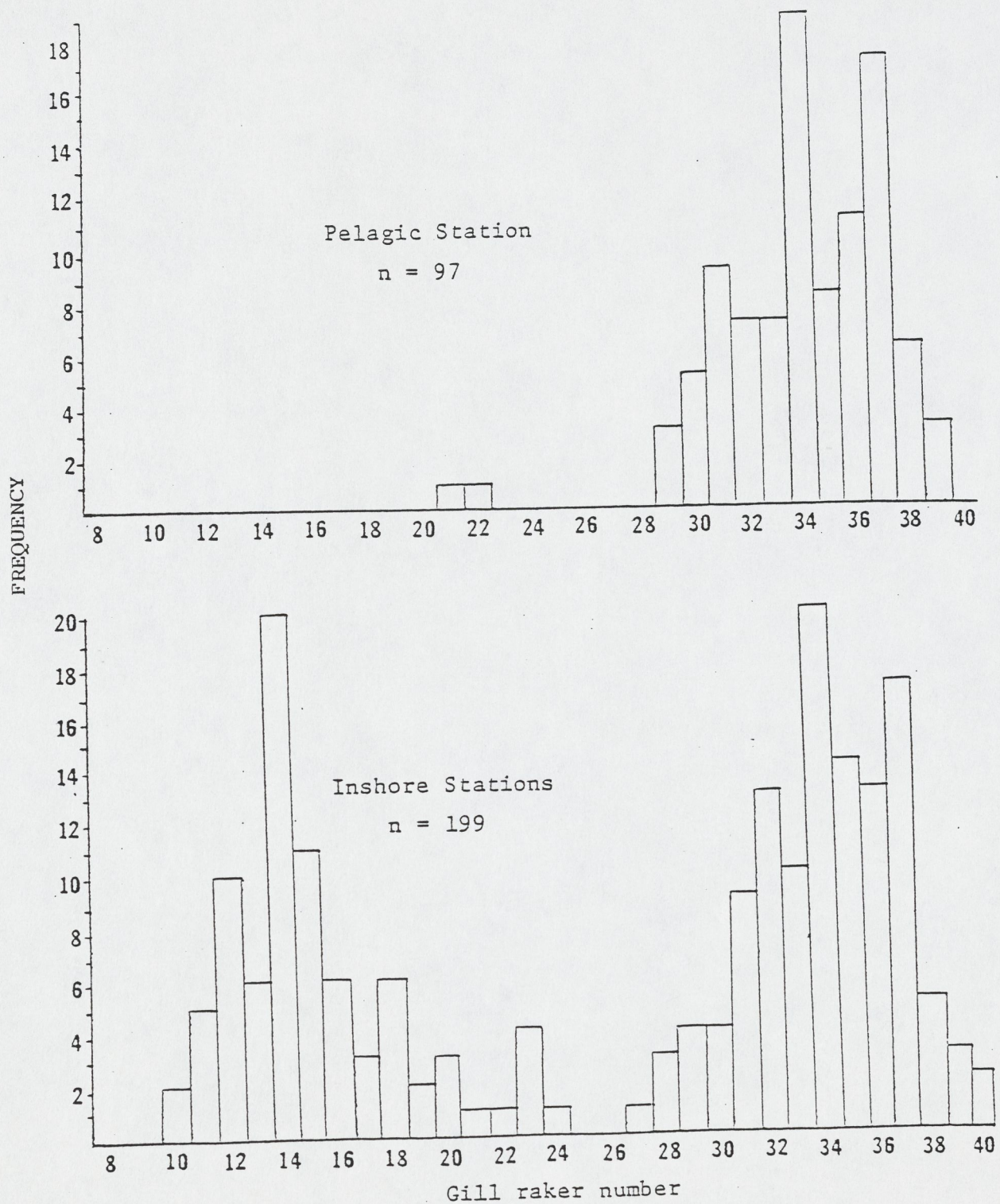[2] Some introgression from *Gila bicolor pectinifer*.

Figure 3.   Gill raker frequency distribution for tui chubs from inshore
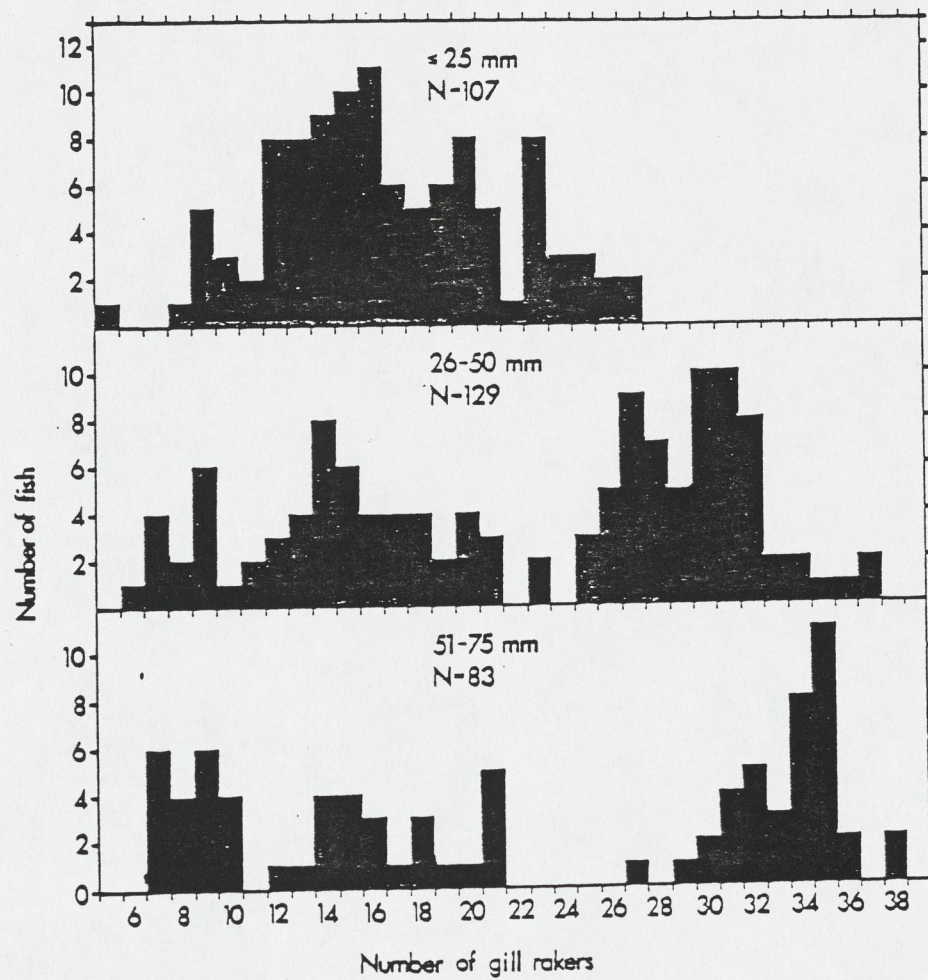and pelagic areas of Pyramid Lake, Nevada, 1977 (From
Langdon 1979).

Figure 4. Gill raker distributions for three size-categories of tui chubs collected throughout summer 1979 in the littoral zone of Pyramid Lake, NV. (From Vucinich et al. 1981).

maintained in microcosms (McConnell and Galat 1980, Figure 5);
thus change in gill raker distribution with size is not a sampling
artifact nor due to migration. As individuals of the two forms
became morphologically distinctive, the fine-rakered fish remained
obligate planktivores while the coarse-rakered fish began to feed
on macroinvertebrates as well as plankton (Vucinich et al. 1981).

A recent sample from Walker Lake was nearly identical to that
of Pyramid Lake's limnetic population (Figure 6). This is in
accord with Cooper's (1978) observation, from extensive sampling,
that the Walker Lake population is comprised almost entirely of
pectinifer. These data are in contrast to the findings of Hubbs
(1961) (also cited in Hubbs et al. 1974) that a large collection
at the inlet end of Walker Lake was comprised of pectinifer in all
characters except obesa and intermediates were present with re-
spect to gill raker counts. They inferred that introgression had
occurred and cited this as evidence of subspecific differentia-
tion.

It is possible that the Hubbs collection contained fish from
the nearby Walker River obesa population. The Topaz Lake popula-
tion, which was apparently derived from the Upper Walker River,
exhibits a bimodal gill raker distribution (Figure 7). One mode
is at 29-32 and the other at 21-22; the latter mode corresponds to
a remnant mode represented in the Walker Lake Population (Figure
6) and the Pyramid Lake limnetic population (Figure 3).

R.G. Miller (1951) considered obesa and pectinifer to repre-
sent two distinct species in Lake Tahoe. The obesa form had a
modal gill raker number of 14 (11-19), and the pectinifer form had
a mode of 32 (27-36) (Figure 8). Miller found obesa and
pectinifer in the same schools inshore. He sampled the fish with
bottom-set gill nets, minnow traps and trout stomach contents.
Miller (1951) did not demonstrate a strictly pectinifer population
like we defined in Pyramid Lake, however this may be an artifact
of sampling. It would be most interesting to take a truely
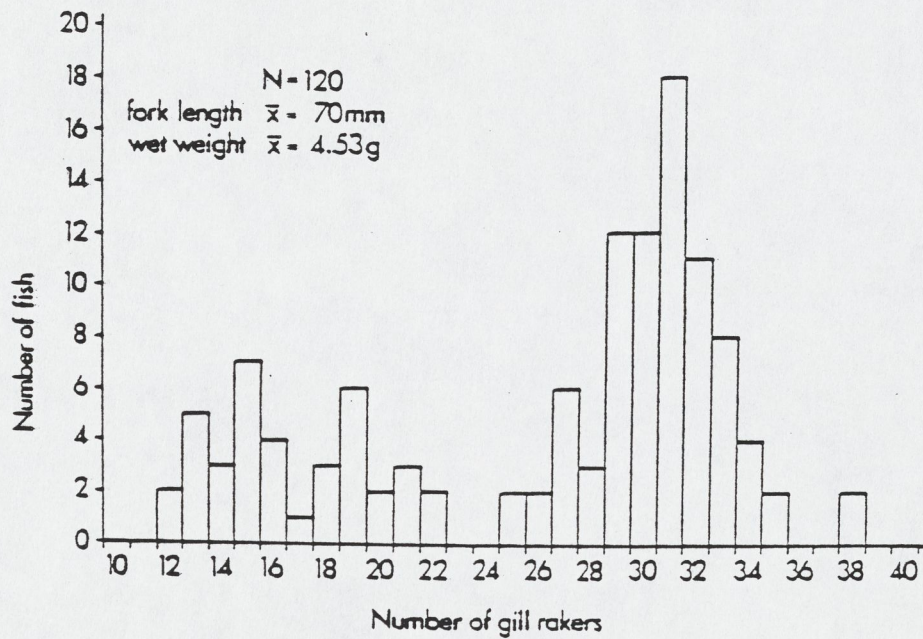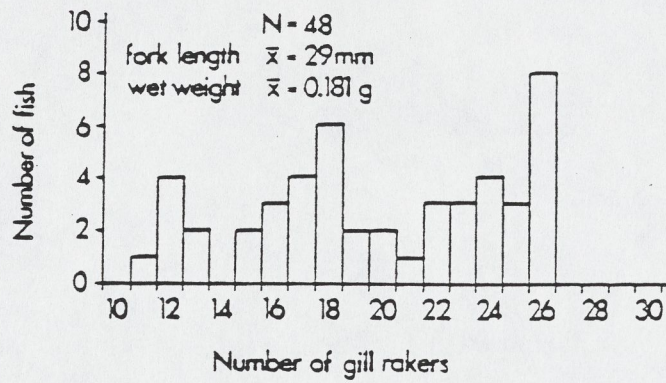limentic sample of tui chubs from Lake Tahoe (e.g. vertical

Figure 5. Gill raker frequency distribution for tui chubs when stocked into 1979 experimental microcosms (top) and after 120 days in the microcosms (bottom)(From McConnell and Galat 1980).
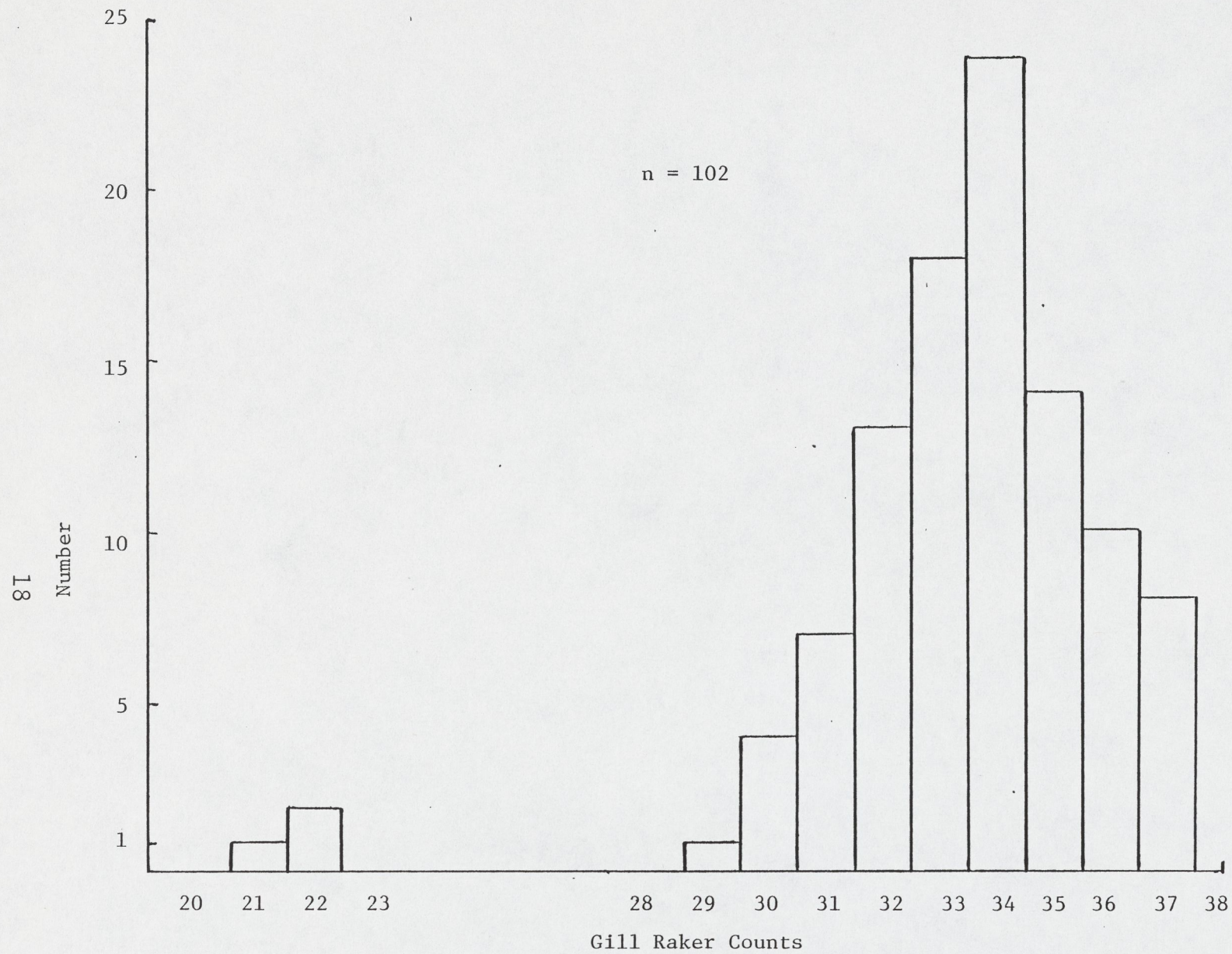
Figure 6. Frequency distribution of gill rakers of the Walker Lake tui chub population, May, 1981 (From Vigg and Cooper, unpublished).
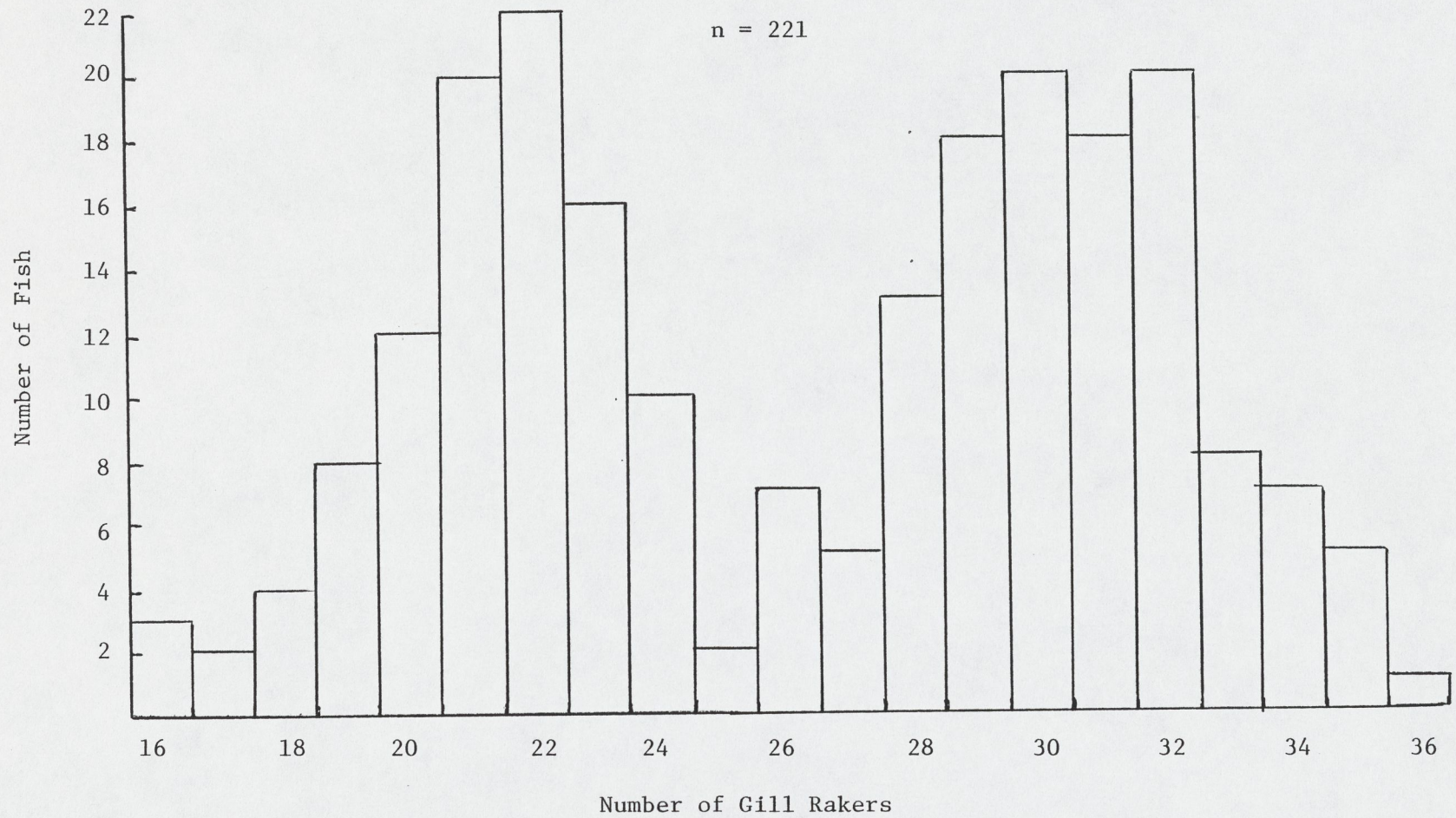
Figure 7. Gill raker frequency distribution of tui chubs from Topaz Lake, June 22, 1971 (California Department of Fish and Game, unpublished data).

GILL-RAKER COUNTS IN SPECIES OF SIPHATELES

BASED ON 218 SPECIMENS FROM LAKE TAHOE
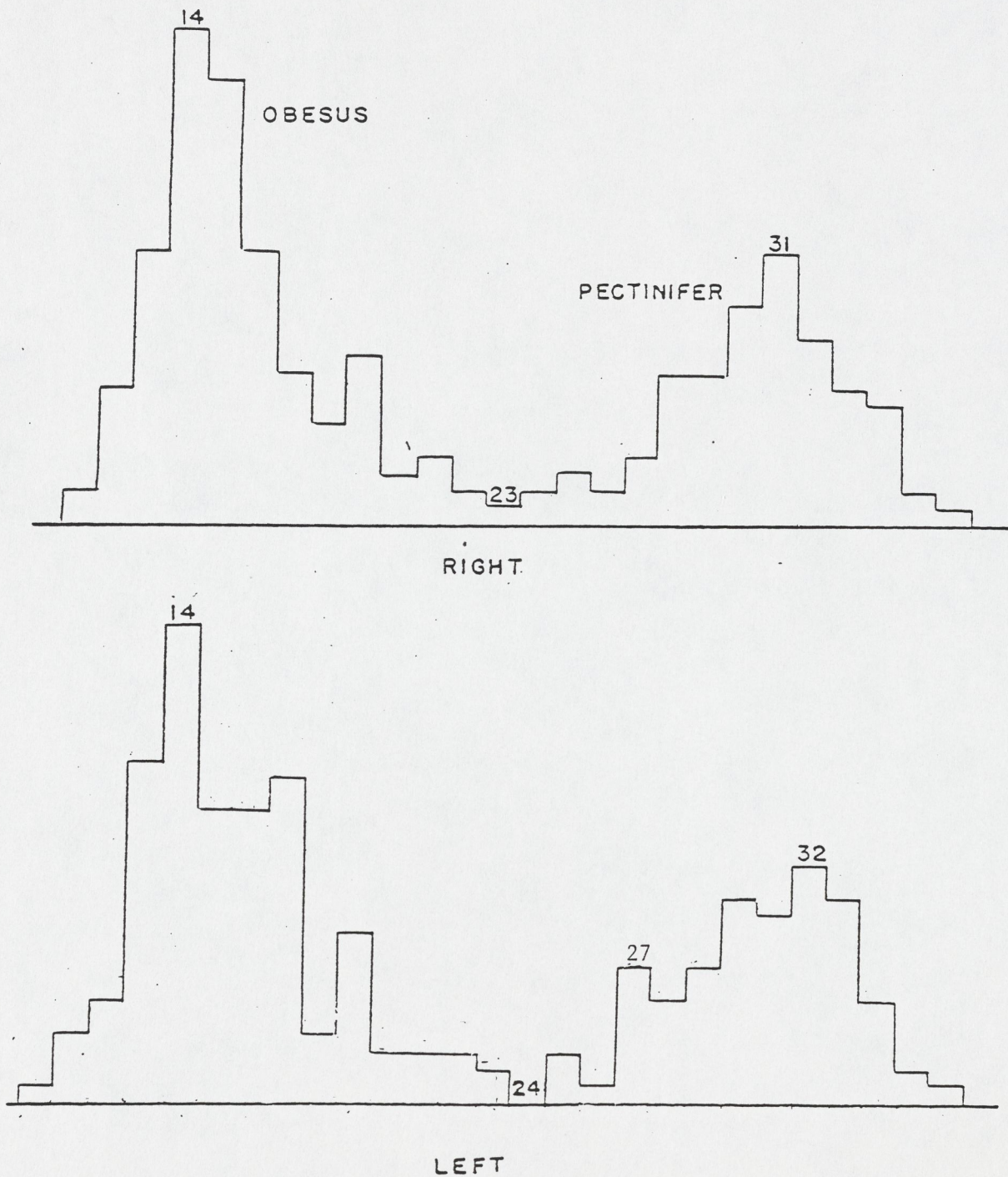
Figure 8. Frequency distribution of gill rakers of tui chubs from Lake Tahoe populations (from R.G. Miller 1951).

gill nets in the middle of the lake) and test for a limnetic
pectinifer population. Dr. John Hopkirk (Sonoma State College,
pers. comm.) believes complex interactions occur within the tui
chub population of Lake Tahoe which is represented by two species
and thier hybrids.

Eagle Lake, which was once tributary to Lake Lahontan has a
tui chub population exhibiting a bi-modal gill raker distribution
(Figure 9). Kimsey (1954) regarded the population as hybrid
between _obesa_ and _pectinifer_, apparently based on intergradation
of characters other than gill raker number. The modal class < 19
corresponds to the _obesa_ category of Pyramid Lake and Lake Tahoe;
however the 21-27 gill raker mode is intermediate the _obesa_ and
pectinifer of Pyramid and Tahoe. The gill raker distribution of
Lake Almanor (south-east of Eagle Lake) is interesting since it
has a large mode in the classical < 19 range; and a much smaller
mode in the same range (21-25) that is remnant in the Pyramid Lake
limnetic population and Walker Lake population, and well
represented in the Eagle Lake population (Figure 10).

The review I have presented on frequency distribution of gill
rakers of various populations of tui chubs represents all the
currently available data. However other criteria besides the
number of gill rakers on the first arch on the left side (the
standard measurement) should be used to differentiate between the
forms. Neff and Smith (1979) point out that gill rakers increase
in divergence more posteriously in the branchial basket, and the
anterior side of the first gill arch represents the least
discriminating count. Miller (1951) stated that the form of gill
rakers gives a clearer picture than numbers, and presented the
following descriptions:

> _obesa_ - rakers appear as a series of mounds cone-like in
> profile with the inter-raker _diastema_ as wide or wider
> than the base of the raker.

> _pectinifer_ - rakers are blade-like in structure and
> closely laid in comb-like fashion so that the inter raker
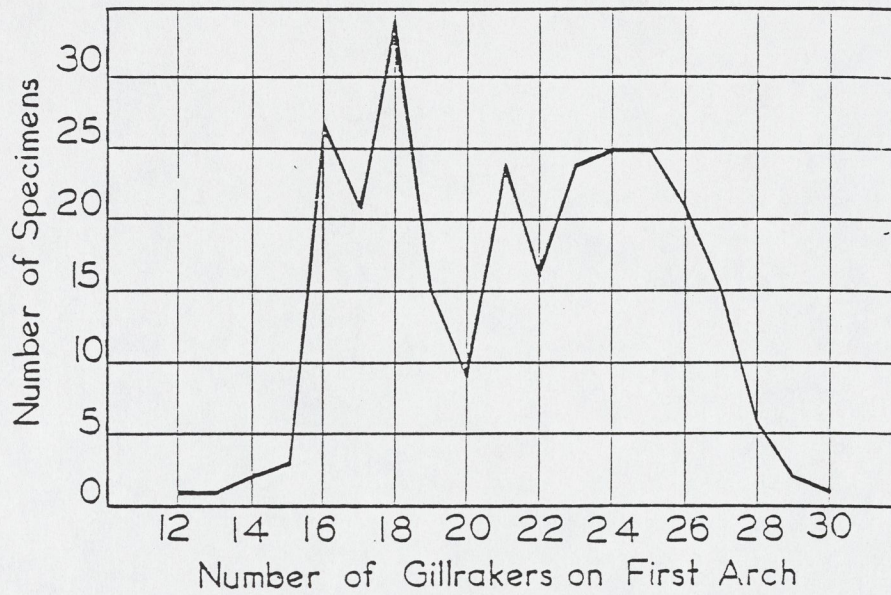> space is not so wide as the raker base.

FIGURE 2. Distribution of the number of gill rakers on the first gill arch for 272 tui chubs from Eagle Lake.
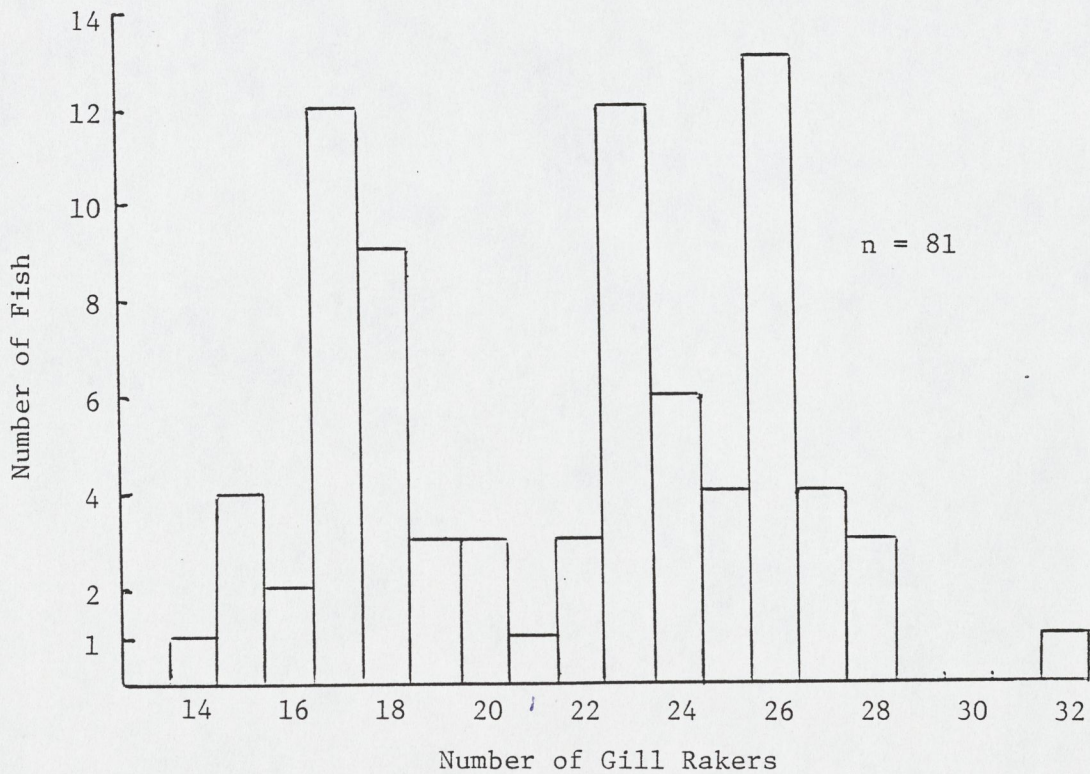

n = 81

Figure 9. Gill rakers frequency distributions of tui chubs from Eagle Lake sampled in 1949 (Kimsey 1954) compared to that of a sample taken in 1981 (Vigg and Cooper, unpublished manuscript).
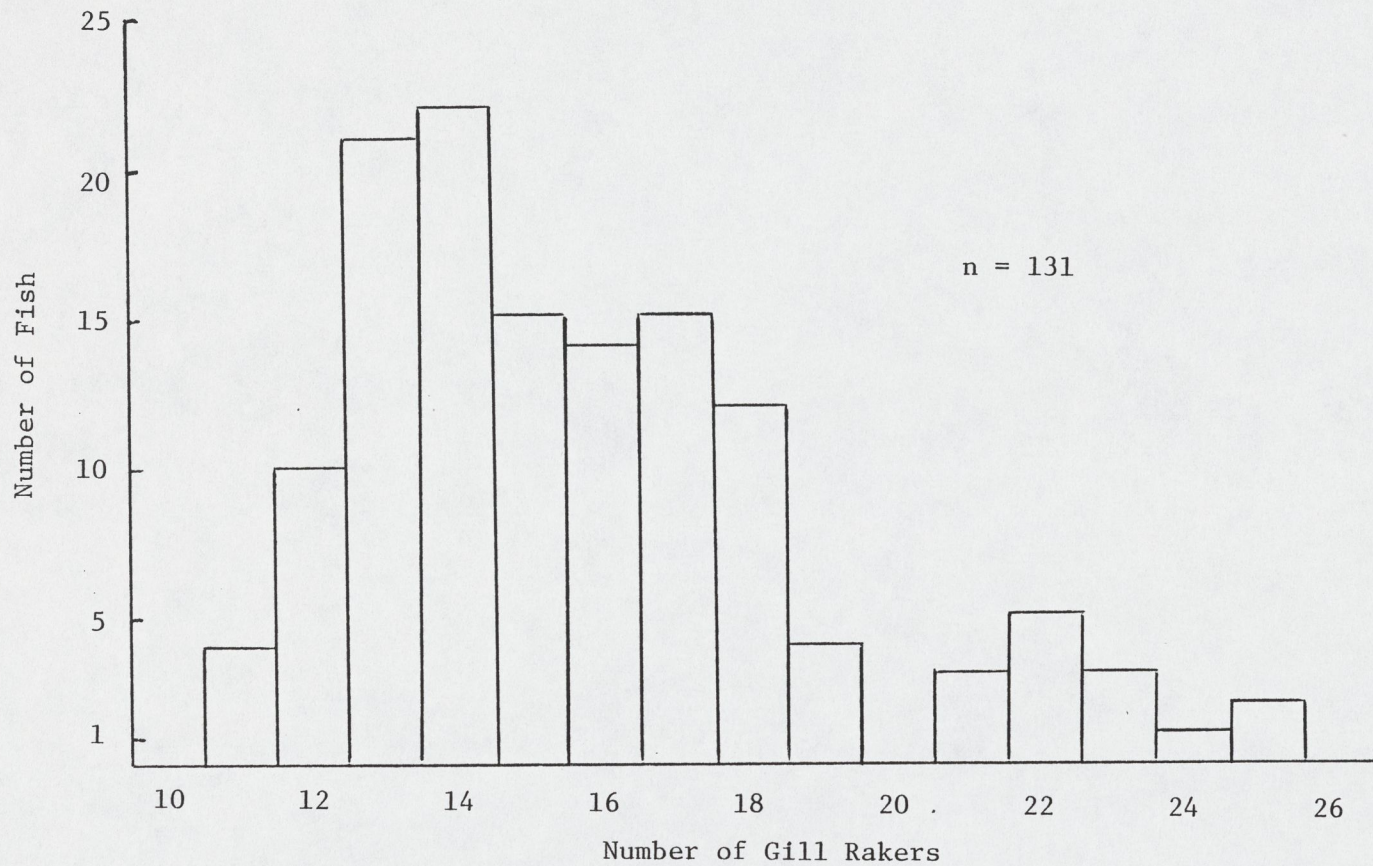
22

23

Figure 10.   Gill raker frequency distribution of tui chubs from Lake Almanor, May and October 1971 (California Department of Fish and Game, unpublished data).

The adaptations of increased number and increased length of
rakers have apparently been to a large degree independent (Hubbs
et al. 1974). Hubbs (1943) stated that species characters, if
adaptive, are generally correlated with food habits and other
biotic factors. However in an apparent contradiction, Hubbs
(1961) stated that adaptations to differential feeding are apt to
be terminal phenomena of no great phylogenetic significance. The
great fluctuation (8-40) in gill raker number for tui chub and the
concomitant variation in size, texture is attributable to trophic
divergence; however it is widely recognized that gill raker
development is usually fixed genetically (Hubbs et al., 1974).
Gill raker number is less subject to phenotypically induced
variation from environmental influences than are most
morphological characters, but gill raker differences between
populations are not necessarily purely genetic (Lindsey 1981).

EXPERIMENTS TO DETERMINE THE BASIS OF MORPHOLOGICAL DIFFERENTIATION

In the natural ecosystem of Pyramid Lake it is not possible
to determine the cause of the observed morphological differences
between the limnetic (G.b. pectinifer) and benthic (G.b. obesa)
tui chub populations. Difference in gill raker structure could be
based solely on genetics, interaction with the temperature regime
during reproduction and development (environmental), or to a
lesser extent age composition (parametric structure). The
differences between the two morphs could be manifested in terms of
their physiological response to major environmental parameters
(e.g. temperature and TDS) as well as behavior, morphology, and
biochemical composition. I have proposed three experimental
techniques to test for differences in the tui chub forms (1)
breeding experiments, and (2) physiological bioassays, (3)
electrophoresis.

Breeding Experiments - Phase I

    The primary hypothesis I wish to test is that:

    Ho(1): The Lahontan tui chub does not consist of
            two genetically distinct forms, i.e. G.b.
            obesa (coarse rakered) and G.b. pectinifer
            (fine rakered).

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For convenience I will use the symbol "O" to equal _obesa_, and
"P" to equal _pectinifer_. Simply stated, diallel matings between O
and P forms would be made under ambient and controlled environ-
mental conditions. Tests would be made for the following matings.

Table 2. Tui chub mating crosses.

Cross	O		P	
	Male	Female	Male	Female
1	X	X		
2	X			X
3			X	X
4		X	X	

A series of statistical tests would be performed on the F_1
generations:

Test 1. O x O offspring would exhibit a gill raker
distribution not significantly different
from the Pyramid Lake population.

Test 2. P x P offspring would exhibit a gill raker
distribution not significantly different
from the Pyramid Lake population.

Test 3. O x O offspring and P x P offspring would
not be significantly different with
respect to gill raker distribution.

Test 4. O female and P male and O male and P
female offspring would exhibit gill raker
distributions not significantly different
from (a) each other, (b) O x O, (c) P x P,
and (d) the Pyramid Lake population, (e)
nor intermediate the O and P forms.

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For the above tests the Pyramid Lake population would be defined as the inshore adult (>150 mm) population which includes both modes; the limnetic population is known to consist exclusively of the _pectinifer_ form. All available data on the gill raker distribution would be compiled, and in addition monthly monitoring of the inshore stock is recommended. Gill raker distributions of a minimum of 100 adult fish would be determined from representative monthly samples. These samples would be tested for temporal differences and pooled to describe the parameteric mean.

These breeding experiments would be conducted at the Pyramid Lake Research Facility in existing microcosms (1.5 x 5 m pools). The test would be conducted in Pyramid Lake water at ambient surface temperature (≈20C) during the month of peak spawning (i.e. July). Each of the four crosses would be derived from the pooled gametes of at least 10 males and 10 females. The fertilized eggs would be placed in separate pools according to treatment and allowed to grow in the semi-natural environment of the microcosm. Algae and zooplankton, and natural substrate would be present to simulate natural conditions.

Fertility of the matings, survival rate, growth rate, and behavior would be monitored. Length, weight, sex, gonadal condition, morphometric determinations, and gill raker distribution would be determined after one full year. In addition full branchial basket counts, gill raker length, and morphology, and food habits would be determined on a sub-sample.

Another series of parallel experiments would be conducted under controlled laboratory conditions to test the following hypotheses:

Ho(2):   Development and rearing temperature does not cause differences in gill raker distributions of the tui chub.

Ho(3):   Salinity level does not cause differences in gill rker distributions of the tui chub.

The same crosses and monitoring parameters would be used as in the "ambient conditions" experiment outlined previously. In contrast the hatching and rearing would be conducted at Desert Research Institute laboratories using de-chlorinated Truckee River water at four constant temperature regimes: 10, 15, 20, and 25C. Thus the effects of the two major environment parameters (temperature and salinity) on gill raker morphology could be determined.

As an integral part of the above outlined experiments, a fourth hypothesis could be tested:

Ho(4):   Age does not cause differences in gill raker distributions of tui chubs.

This hypothesis could be tested simply by taking a sub-sample (≈100 fish) of each of the treatments in either the "ambient" or "controlled" experiments. Gill raker distributions would be determined at the following age increments after hatch: 1, 4, 8, and 12 months.

Breeding Experiments - Phase II

The second phase of the breeding experiments would be to take representative samples of the F_1 generations from the Phase I crosses of O x P and backcross the heterzogotes to the O and P parental stocks, and F_1 x F_1. The allelic frequencies and dominance relationships could be determined from "classic" Mendelian ratios of phenotypic expression.

Physiological Bioassays

The response of the two different forms to pervading environmental parameters (e.g. temperature) is an important ecological consideration as well as a potential means for determination of a reproductive isolating mechanism. From the previous breeding experiments, ideal experimental material would be available to test for temperature tolerance. Tui chubs hatched and reared at the four temperature regimes, i.e. 10, 15, 20, and 25 would be used to determine temperature preference and upper lethal level in order to test the hypothesis:

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Ho(5):   There are not any differences in the tem-
          perature relationships of the O and P forms
          of tui chubs over a range of acclimation
          temperatures.

I will not go into great detail on the methodology of tem-
perature bioassays. The rearing temperatures would represent four
acclimation regimes. Basically temperature preference is deter-
mined by a linear gradient in a series of interconnected aquaria.
Temperature tolerance studies are exemplified by the classic work
by Brett (1952) on Pacific salmon. Two criteria may be applied:
critical thermal maximum (CTM) or the temperature at which the
fish lose equilibrium; and median tolerance limit (TL50) or the
constant temperature which kills half the test fish (usually
tested for 96 hrs to determine acute levels). In the latter case
the fish are tested over a series of temperatures (0-100%
mortality) and a regression equation is used to determine the
TL50.

Electrophoresis

Biochemical composition as determined by electrophoresis is
generally not a sensitive enough test to differentiate subspecies
of fish, however this is somewhat dependant on the number of
isoenzymes and loci tested. Lugaski (1980) conducted electro-
phoresis on four Great Basin genera, including Gila. Preliminary
analysis of G.b. obesa and G.b. pectinifer indicated no signifi-
cant differences between the two forms (Dr. Thomas Lugaski, pers.
comm.).

Dr. Bruce Riska conducted eletrophoresis on tui chubs from
various lakes including Pyramid, Walker, Eagle, Tahoe and Big
Soda. He analyzed 20 loci and found 3 or 4 reliably scorable;
preliminary results indicate that peptidase may differentiate
between Pyramid and Walker populations, however more work is
needed with respect to the type of stains and buffers used (pers.
comm.).

If specific isoenzymes can be identified to differentiate
between G.b. obesa and G.b. pectinifer, electrophoresis could be
effectively applied to the stocks from the breeding experiments.

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However, it is likely that, at the current state of the art, electrophoresis would not be able to differentiate between the two forms. For example, a flock of endemic species of cichlid fishes was described in the Cuatro Cienegas basin of Mexico, based on morphological feeding adaptations (Deacon and Minckley 1974). Sage and Selander (1975) found these "species" to be allelically identical at 27 gene loci and concluded that they were all morphs of the same species.

SUMMARY

I have attempted to summarize the existing data on the evolution, taxonomy, life history, and morphological variation of two forms of tui chub: <u>Gila</u> <u>bicolor</u> <u>obesa</u> and <u>G.b.</u> <u>pectinifer</u>. The "biological species concept" refers to an interbreeding population which is reproductively isolated. A documented history of speciation involves multiple criteria including paleobiogeography, morphology, ecological studies, chemotaxonomy, and hybridization studies.

The benthic <u>G.b.</u> <u>obesa</u> generally has <20 gill rakers, and the <u>G.b.</u> <u>pectinifer</u> form has 25-40. No intergrades occur in Pyramid lake. The length and morphology of gill rakers, including meristics of the entire branchial basket may be equally important as the number on the first arch - as criteria to determine differentiation. Gill raker number is one of the most reliable meristic characteristics, however it may be affected by the environment.

I have proposed breeding experiments in order to determine gill raker distributions in known F_1 hybrids under ambient and controlled conditions. The effects of temperature, salinity, and age on gill raker number may also be important. Another criteria for differentiation is the physiological response of different phenotypes to thermal stimuli. Back-crossing of F_1 hybrids is proposed to evaluate Mendelian allelic ratios. Electrophoretic techniques are proposed to evaluate genetic differences between the forms, however preliminary data are not promising.

Regardless of the taxonomic designation given the two forms, their areal distribution and food preferences indicate they occupy separate ecological niches and therefore can be recognized at least as distinct ecotypes. However, spatial overlap does, at least partially, occur and a key question is if reproductive isolation exists. If morphological differentiation does not coincide with reproductive isolation there is no simple and satisfactory resolution to the systematic problem, and species status must be based on a broad evaluation of the particular case (Mayr 1966).

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