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Endemic Whitefishes of Bear Lake, Utah-Idaho: A Problem in Systematics

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ENDEMIC WHITEFISHES OF BEAR LAKE, UTAH-IDAHO:

A PROBLEM IN SYSTEMATICS

by

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of the requirements for the degree

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Robert G. White

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ABSTRACT

Endemic Whitefishes of Bear Lake, Utah-Idaho:

A Problem in Systematics

by

Robert G. White, Doctor of Philosophy

Utah State University, 1974

Major Professor: Dr. William T. Helm
Department: Wildlife Science

The systematic status of whitefishes endemic to Bear Lake, Utah-Idaho, has remained tenuous since their original description. Clarification of this problem was the major objective of the present study. The general approach was an integrated one, including examination of morphological, biochemical and ecological parameters; artificial hybrids were produced and compared with questionable groups from the natural population.

Morphological analysis revealed five forms of Bear Lake whitefishes. Prosopium gemmiferum (Bonneville cisco) and P. abyssicola (Bear Lake whitefish) were well differentiated from other forms and were treated as originally described. The P. spilonotus (Bonneville whitefish) group, however, was found to be made up of two morphologically distinct populations, referred to as P. spilonotus (small form) and P. spilonotus (large form). The fifth group referred to as P. gemmiferum-like (represented by only five specimens) was intermediate between P. gemmiferum and either P. spilonotus (small form) or P. abyssicola and was hypothesized to be of hybrid origin. Multiple discriminant function analysis of the four major

groups and P. williamsoni (mountain whitefish) (Logan River) confirmed morphological differentiation between forms.

Hybridization studies among Bear Lake Prosopium and P. williamsoni involved 50 homo - and heterospecific crosses (17 combinations). Of 12 experimental hybrid combinations attempted, all those involving simultaneously ripe specimens of two groups (five crosses) showed maximum fertilization success equalling that of pure crosses. No evidence that interspecific crosses are less successful than conspecific crosses, with the possible exception of P. williamsoni ♀ x P. gemmiferum ♂ (W x G), was obtained. Culture methods were developed and morphological comparisons made.

Origin of P. gemmiferum-like hybrids in the lake population was not consistently explained by morphological comparison of known P. spilonotus (small form) ♀ x P. gemmiferum ♂ (S x G) hybrids or P. abyssicola ♀ x P. gemmiferum ♂ (A x G) hybrids; morphometric characters were more like S x G hybrids while meristic characters were more closely associated with A x G hybrids. Based on evidence available, no definitive statement could be made concerning the origin of P. gemmiferum-like hybrids except that they are hybrids among combinations of P. gemmiferum and either P. spilonotus (small form) or P. abyssicola. No known hybrid explained the origin of either group of P. spilonotus.

Electrophoretic analysis of general proteins and several enzyme systems of various tissues showed much similarity among Bear Lake Prosopium; only P. williamsoni was totally unique. Biochemical evidence did not support or refute separate consideration of the two forms of P. spilonotus but did establish that neither were phenotypic variants of P. williamsoni.

Ecological characteristics of Bear Lake Prosopium revealed important distinctions between forms. Growth histories of P. abyssicola, P. spilonotus (small form) and P. spilonotus (large form) showed pronounced differences. Distinct differences in growth and in age and size at maturity of forms of P. spilonotus provided further evidence supporting their separate consideration. Spatial overlap of spawning activities was marked between forms of P. spilonotus and P. gemmiferum; P. abyssicola was well separated spatially. Temporally, slight overlap was observed between ripe females of one group and ripe males of the succeeding group to spawn. The only observation of the simultaneous occurrence of ripe females of two forms was between P. spilonotus (large form) and P. spilonotus (small form); in this instance, the number of ripe females of each form was extremely small. No evidence of mass hybridization among forms was observed. A combination of temporal, spatial and ethological premating isolating mechanisms are thought to be important in reproductive isolation of Bear Lake whitefishes while postmating mechanisms are nonfunctional with the possible exception of hybrid sterility.

Morphological and ecological analyses, combined with results of experimental hybridization, provided abundant evidence supporting separate recognition of the two forms of P. spilonotus. Karyotypes of P. gemmiferum, P. abyssicola and P. spilonotus (small form) have been determined (Booke, 1974) and are unique for each species. If the karyotype of P. spilonotus (large form) is found to also be unique, there should be no question that the two forms of P. spilonotus represent distinct species. Final clarification of the taxonomic status of these forms will not come until karyotype data is available; however, based upon present evidence, tentative recognition of a new species is recommended.

(209 pages)

INTRODUCTION

Whitefishes have long been regarded as being among the most intriguing and controversial of all animal groups investigated by biologists (Lindsey and Woods, 1970). The diversity and variability of whitefishes is so great that despite persistent studies, there is no universal opinion among ichthyologists concerning the rank of the whole group or its members. The basis for much of the existing taxonomic confusion lies in the extreme phenotypic plasticity often expressed by whitefishes of the same species occupying different environments (Behnke, 1970; Svardson, 1949 through 1970; Smith, 1957; Chellevold, 1970; Vladydov, 1970; and others). Frequent hybridization and subsequent introgression of genes from one species into another are other probable sources of confusion (Svardson, 1970).

Although some authors maintain that the whitefishes should have full family status (Gosline, 1960; Vladydov, 1963, 1970), the majority are in agreement that a more realistic classification is to place them as a subfamily (Coregoninae) within the family Salmonidae. This subfamily contains three genera: Coregonus, Stenodus, and Prosopium (Behnke, 1972, 1970; Norden, 1961; Booke, 1968; Shaposhnikova, 1970).

Traditional morphometric analysis has fallen short of properly evaluating the species status of many coregonine fishes. Modern systematists have made remarkable advances owing to increased knowledge of genetics and ecology and the application of an integrated morphometric-ecologic-genetic approach. Behnke (1970, p. 239) emphasizes that

> final judgement on the validity of a species and proper classification should be based on all the information of the whole

integrated organism, its ecology, behavior, reproductive isolation, total phenotype and any biochemical and cytogenetic evidence of divergence contributing to our knowledge.

The present study deals with the systematic evaluation of the endemic species flock of whitefishes inhabiting Bear Lake, Utah-Idaho. These fishes are members of the genus Prosopium Milner which is distinguished from other whitefish genera by the presence of a single narial flap, a basibranchial plate and parr marks in juveniles (Norden, 1961).

The Bear Lake endemics comprise an interesting facet of the zoogeography of the genus Prosopium in that they represent three of its six recognized species. These species are the Bonneville cisco, P. gemmiferum; the Bonneville whitefish, P. spilonotus; and the Bear Lake whitefish, P. abyssicola. A fourth species of Prosopium, the mountain whitefish, P. williamsoni, has been reported to be indigenous to Bear Lake (McConnell, Clark and Sigler, 1957).

Subsequent to the original description (Snyder, 1919) only P. gemmiferum had been the subject of any comprehensive investigation (Perry, 1943). This species is sharply divergent, both morphologically and ecologically, from the other Bear Lake whitefishes and its slim, terete body form, large mouth and distinctly superior jaw make identification positive.

Aside from data presented in the original description (Snyder, 1919) and sparse data collected during a few cursory surveys concerning the Bear Lake fish fauna (McConnell et al., 1957; Hassler, 1960; Loo, 1960), no information on the biology of P. spilonotus and P. abyssicola was available at the conception of the present study. Close morphological similarity between species, considerable variation within species and the occurrence of a suspected intergrade in the natural population are

thought to be responsible for this neglect. Indicative of the poor understanding of the systematic status of these fishes and the extent of their evaluation by previous investigators is the statement from Loo, Sigler and Workman (1964, p. 30) that "identification of the whitefishes, excluding the Bonneville cisco, proved uncertain and the two species were considered as a single group." In the original description of these fishes, the taxonomic problem was alluded to when Snyder (1919, p. 6) stated

> Locally these two forms (small and large forms of P. spilonotus) are regarded as distinct, but a considerable series of specimens . . . supplies examples intermediate in size and age, and seems to demonstrate without much doubt that they belong to the same species. The question need not be considered as settled, however, until more complete data have been obtained.

Each of the recognized species of Bear Lake Prosopium was included in the recently published list of threatened freshwater fishes of the United States (Miller, 1972). Comprehensive research on habits, ecology and life history of these fishes is important in ensuring their long-term existence in the face of man's continued disturbance of the lake ecosystem. Before such studies can be initiated, the taxonomic status of the group must be defined.

The primary objective of the present study was to clarify the taxonomic relationships among Bear Lake whitefishes. The general approach was an integrated one, including examination of morphological, biochemical and ecological parameters. In addition, artificial hybrids were produced and compared with suspected hybrids from the natural population.

Specific objectives of this study were:

1. To examine the systematics of the Bear Lake coregonines, genus Prosopium, using morphometric measurements, meristic counts, and

electrophoretic analysis with emphasis on P. spilonotus, P. abyssicola and suspected intergrades.

2. To make all possible hybrid crosses among P. spilonotus, P. abyssicola, P. gemmiferum and P. williamsoni.

3. To compare progeny of successful hybrid crosses with suspected hybrids from the natural population.

4. To document important life history characteristics of Bear Lake Prosopium for the purpose of gaining insight into the degree of ecological and reproductive isolation.

STUDY AREA

Bear Lake valley is a long, narrow valley lying north and south across the Utah-Idaho boundary about 19.3 km (12 mi) west of the Wyoming border. The valley is bounded on the west by the Bear River Range, approximately 3,048 m (10,000 ft) in elevation and on the east by the Bear Lake Plateau about 2,440 m (8,000 ft) high (Perry, 1943). Bear Lake (Figure 1) occupies a tectonic basin in the southern half of the valley. Slightly more than one-half of its 30 km (19 mi) length is in Utah, the remainder in Idaho. Its width ranges from about 6.4 to 12 km (4-7½ mi). Maximum surface elevation is 1,805.5 m (5,923.5 ft) above mean sea level. Bear Lake is an oligotrophic lake, characterized by clear, deep, cold water, usually saturated with oxygen (McConnell et al., 1957; Nyquist, 1968).

The lake is oval in shape and its 77 km (48 mi) shoreline is regular, with no major coves or bays. Large natural beach bars form the north and south shores (McConnell et al., 1957). The lake is relatively deep, with an average depth of over 30.5 m (100 ft). The greatest depth of about 63.4 m (208 ft) lies approximately one-fourth mile off the east shore and just north of South Eden delta. This area is part of a deep trough which runs parallel to the east shore for a considerable distance, causing a steep declivity on that side of the lake basin. This steep slope is a continuation of the noticeably steep escarpment formed by the Bear Lake fault along much of the east shore (Perry, 1943). An almost continuous line of scarplets in recent sediments and displacement of the delta fans at the mouth of North and South Eden

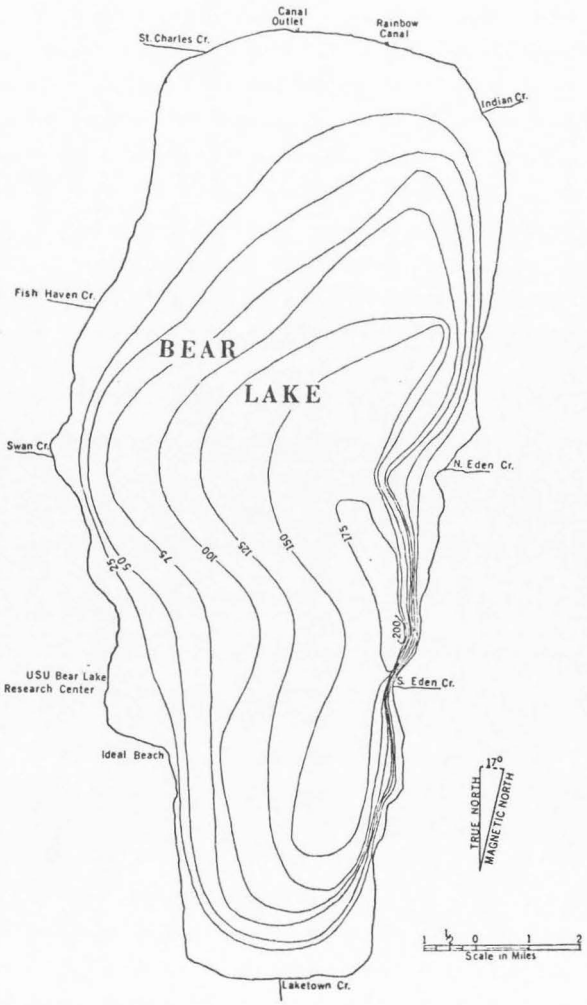

Figure 1. Map of Bear Lake, Utah-Idaho.

canyons is evidence that the fault is presently active (Kaliser, 1972).

Beaches surrounding the lake are composed predominantly of sand and shells of extinct gastropods. Intermittent rocky areas occur along the southwest shore with some extensive rocky areas along the east shore. For the most part the rock does not extend far into the lake. McConnell et al. (1957) estimated that the rocky littoral zone comprises less than 0.001 percent of the total bottom area. Aside from these limited rocky areas the bottom topography is extremely regular and is composed of sand to a water depth of about 7.6 m (25 ft) and beyond this is replaced with silt and marl.

Climatically Bear Lake is located in a semi-arid zone with a mean annual precipitation of 26.9 cm (10.60 in) at Laketown (south end) and 24.4 cm (9.62 in) at the Lifton Station (north end) (Kaliser, 1972). Before the development of the lake as a reservoir, it was maintained by runoff from adjacent slopes. Bear River flows through the northern end of Bear Lake valley but in recent times has not been a natural tributary. At higher lake levels, evidenced by old shorelines, Bear River flowed directly into the lake. At the present level, however, it bypasses the lake 12.8 km (8 mi) to the north. In 1912, the Utah Power and Light Company joined the lake and river by a canal system and since that time the lake has been utilized as a reservoir for agricultural and hydroelectric purposes. Annual fluctuation in lake level as a result of man-induced control is generally between 0.9 and 1.5 m (3.0-4.9 ft) (Nunan, 1972).

The drainage basin of Bear Lake is small, covering about 650 km^2 (250 mi^2) with only three tributary streams of any consequence. With Bear River being partially diverted into the lake, the drainage area

is enlarged to about 7,770 km^2 (3,000 mi^2) (Richardson, 1941). Numerous seeps and springs occur along the west shore and some along the northeast shore; these appear to contribute a significant percentage of the total inflow (McConnell et al., 1957).

Bear Lake surface temperatures rarely exceed 21 C (70 F). A well-developed thermocline forms in late June and persists into November; water below 45.7 m (150 ft) is usually never warmer than 5.4 C (42 F). The lake freezes over about four of every five years. Freezing usually occurs in January or early February, with break-up in April. Chemical make-up of Bear Lake water follows the general pattern of inland waters with respect to the ratios of dissolved anions and cations, with one noteable exception: magnesium rather than calcium is the dominant cation (Nunan, 1972; Kemmerer, Bovard and Boorman, 1923).

A unique feature of Bear Lake is its four recognized species of endemic fishes. No other lake in western North America is endowed with such a rich endemic fish fauna. These endemics include three whitefishes and a sculpin.

Although detailed population studies have not been conducted, McConnell et al. (1957) reported that the two most numerous fishes in Bear Lake are the Bonneville cisco and the Bear Lake sculpin. Next in abundance is the Utah sucker followed by the other whitefishes collectively. Fourteen species of fish (Table 1) were collected in the present study and include all those reported by McConnell et al. (1957) with the exception of mountain whitefish, kokanee, and brown trout.

Table 1. Species of fish collected in Bear Lake, 1969-1972.

Scientific Name[a]	Common Name
Native species	
Prosopium abyssicola (Snyder)	Bear Lake whitefish
Prosopium spilonotus (Snyder)	Bonneville whitefish
Prosopium gemmiferum (Snyder)	Bonneville cisco
Salmo clarki Richardson	Cutthroat trout
Rhinichthys osculus (Girard)	Speckled dace
Richardsonius balteatus (Richardson)	Redside shiner
Gila atraria (Girard)	Utah chub
Catostomus ardens Jorden & Gilbert	Utah sucker
Cottus extensus Bailey & Bond	Bear Lake sculpin
Introduced species	
Salmo gairdneri Richardson	Rainbow trout
Salvelinus namaycush (Walbaum)	Lake trout
Cyprinus carpio Linnaeus	Carp
Lepomis cyanellus Rafinesque	Green sunfish
Perca flavescens (Mitchill)	Yellow perch

[a]Scientific and common names are those accepted by the American Fisheries Society, 1970.

FIELD COLLECTIONS

Collections of coregonines from Bear Lake were made during the period June, 1969-December, 1972. To minimize sampling bias, an 8.2 m (27 ft) semi-balloon otter trawl was utilized, whenever possible, in procuring specimens for the study. The trawl was fished from a 12.2 m (40 ft) barge, specially rigged for trawling and powered by a 210 hp motor. A gasoline powered winch loaded with steel cable was used to set and retrieve the trawl; cable/depth ratio used was 3:1. When in operation, the net had a width of 6.1 m (20 ft), a depth of 2.4 m (8 ft) and speed of approximately 1.5 mph. Samples were usually taken along a specific bottom contour, located with a Bendix depth recorder, and were normally 15-30 minutes duration. Most trawl collections were made during daylight hours.

During periods of ice cover and during spawning runs of the various groups studied, horizontal sinking multi-and monofilament nylon gill-nets were used. Nets varied in length from 13.7-91.4 m (15-100 yds), in bar mesh from 1.9-5.1 cm (3/4-2 in) and in depth from 1.8-2.4 m (6-8 ft). Nets were usually set overnight. Mountain whitefish were collected with electrofishing gear from the Logan River.

Specimens from each trawl haul and gill net set were held separately and taken to the laboratory for processing. Basic data including sex, state of maturation, length, weight, date, time, location, depth and method of capture were recorded for each fish. Length measurements were made to the nearest millimeter and weight to the nearest 0.1 gram. Total length was measured on all fish processed while fork and standard

lengths were taken only during the first year of the study. Specimens to be retained for further study were identified by placing a numbered tag in the mouth, and were preserved in 10 percent formalin. Early in the study all fish were preserved, but due to limited storage facilities, further collections were usually sub-sampled; all specimens of questionable classification were kept.

MORPHOLOGICAL ANALYSIS

Introduction

Morphological characters are often of limited value in coregonine systematics due to extreme phenotypic plasticity among allopatric populations of the same species. In sympatry, however, where environmental conditions are not an influence and where the various groups of coregonines typically have different growth rates, body proportions and meristic counts are often excellent characters (Svardson, 1970).

The endemic nature of the Bear Lake whitefishes eliminates the problem of phenotypic differentiation which might occur in conspecific populations. Select morphometric measurements and meristic counts were therefore examined to provide one line of evidence in evaluating the systematic status of Bear Lake Prosopium.

Methods

A total of 675 specimens was used in the intensive morphological investigation of the endemic species flock of Prosopium inhabiting Bear Lake, Utah-Idaho. Most counts and measurements were made under magnification and, whenever possible, were made on the left side of the body. All measurements were taken in a straight line with dividers and recorded to the nearest 0.5 mm.

To increase efficiency and accuracy of scale counts, a solution of bromocresol green was applied to scales in the area of the count. The temporary stain made individual scales easily discernible. Gill-raker counts were made from the first left gill-arch which was dissected and

stained with alzerine red-s to facilitate accurate enumeration, particularly of rudimentary rakers.

Most characters are defined in accordance with Hubbs and Lagler (1967). The exceptions are given below:

1. Scales below lateral line (suprapelvic scale count) - Starting with the anterior most scale showing, in part or whole, above the dorsal free edge of the pelvic axillary process and proceeding dorso-posteriorly to, but not including, the lateral line (Lindsey, 1962).

2. Scales around body - Number of scale rows crossing a line around the body starting three scales posterior to dorsal fin. An elastic band placed around the body marked this line.

3. Gill-raker count - Identical to the description of Hubbs and Lagler (1967) with the exception that a gill-raker straddling the angle of the arch was included in the count of the upper limb.

4. Gill-raker length - Distance from tip to base of the longest gill-raker.

5. Adipose base length - Distance from the angle between the anterior margin of the adipose fin and the contour of the body, horizontally to the posterior free edge of the base of the fin (Lindsey, 1962).

6. Adipose height - Greatest distance from the angle between the anterior margin of the adipose fin and the contour of body angling upward and backward to the most posterior point.

7. Maxillary length - Distance from the anterior end of the maxilla (recognized by a slight projection) to the posterior most part of the maxilla; does not include the premaxilla.

8. Maxillary width - Maximum width of the maxilla.

9. Pelvic to anal distance - Distance from the anterior insertion of the pelvic fin to the anterior insertion of the anal fin.

10. Peduncle width - Least width of the caudal peduncle.

Early in the study, field collections were made randomly throughout Bear Lake at depths ranging from 3-61 m (10-200 ft). It was assumed these collections would be representative of the whitefish populations.

Attempts at classification proved to be confusing and specimens were retained for later study.

As a baseline for taxonomic decisions concerning P. spilonotus and P. abyssicola, specimens from the spawning populations of these forms were collected. (Only the small form of P. spilonotus which will be defined later, was represented in these early collections.) Fifty morphological characters were examined on 30 fish from each of these populations. Specimens ranged in standard length from 150-212 mm; males and females were equally represented.

Most characters displayed a great deal of variation within species and considerable overlap between species. However, a few characters, along with subtle differences in color, head shape and general body conformation, allowed confident identification of all spawning fish examined. No differences were observed between sexes. Many characters were found to be of little taxonomic value in distinguishing P. spilonotus (small form) from P. abyssicola and were eliminated from further consideration. The study was expanded to the total population using 14 morphometric measurements and 12 meristic counts.

After superficial examination of large numbers of specimens collected throughout Bear Lake, it appeared justifiable to consider several forms in making morphological comparisons. Of the three recognized species, P. abyssicola and P. gemmiferum were treated as originally described (Snyder, 1919). Prosopium spilonotus, however, was partitioned into two groups: P. spilonotus (small form) and P. spilonotus (large form). Two additional forms were also recognized: P. gemmiferum-like hybrids, reported by Sigler and Miller (1963) and a previously unrecognized group hereafter referred to as P. species. Members of the latter

group were not yet mature at sizes larger than the maximum size observed for P. abyssicola or P. spilonotus (small form). This observation, along with certain morphologic considerations, prompted the separate evaluation of this form and the initial hypothesis that these fish were of hybrid origin. Although not collected in the present study, P. williamsoni has been reported to be indigenous to Bear Lake and, for this reason, specimens from the Logan River were included in morphological comparisons. Group assignment of Bear Lake whitefishes was at first based on subjective, qualitative appraisal and then quantitatively assessed.

Results and Discussion

A total of 14 morphometric measurements and 12 meristic counts was used in examination of the six groups of Prosopium. Unlike meristic data, morphometric data must be examined in relative, rather than absolute terms, if "key characters" are being sought, since the dimensions of morphometric characters are continually changing as the fish grows. Standard procedure is to transform body measurements into ratio of one body-part to another. Justification for comparing the average values of transformations can be made only if there is a constant or near constant ratio (isometric growth) between the dimensions of the parts being examined, over the size range of the sample. Differential growth of body parts would cause the value of the ratios to change, thus making such comparisons invalid (Schaefer and Walford, 1950; Schaefer, 1952; Marr, 1955).

To examine the constancy of morphometric ratios, linear regression analysis was applied to non-transformed data. The model for simple

linear regression is expressed by the formula $y = a + bx$ where y = the dependent variable (e.g., length of body part); x = the independent variable (e.g., body length); a (a constant) = the y-intercept or the value of y when x = 0; and b (a constant) = the slope of the line or the constant absolute change in y per unit change of x. If data did not conform to this model ($r^2 \geq .75$) the character was considered inappropriate for comparative purposes; no attempt was made to fit data to non-linear models or to make linear transformations.

Results of linear regression analysis applied to 14 body-part/standard length ratios and five body-part/head length ratios are summarized in Appendix A. An acceptable linear fit was characteristic of most morphometric characters, for all groups, with the exception of P. abyssicola. Within this group, eight of the 19 regressions showed r^2 values less than .75. Only adipose base length and the two gill-raker length ratios were non-linear in two or more groups. P. species and P. williamsoni produced no non-linear relationships.

However, in considering the usefulness of these data, linearity was not the sole consideration. Data may be represented concisely by the linear regression equation, but if the y-intercept differs appreciably from zero, the ratio of one dimension to another will change. Statistically significant differences were found in several instances when the hypothesis $\beta = 0$ was tested (t-test, .05). However, in examining the range of ratios from those of the smallest specimens to those of the largest ones, the change was so slight that it would result in a negligibly small error. Therefore, these comparisons were considered valid.

The mean, standard deviation, standard error and 95 percent confidence interval was calculated for each of 32 comparisons, for the six

groups of fish examined. These data were compared graphically for group differences in a manner similar to that suggested by Hubbs and Perlmutter (1942) and modified by Hubbs and Hubbs (1953) and Simpson, Roe and Lewontin (1960). Such a graphic presentation makes possible a visual pseudo-t-test between the various group means. This type of analysis is common in taxonomic literature but has disadvantages as noted by Rothschild (1963). Most importantly, if all possible pairs of means are compared, the resulting comparisons cannot be totally independent of one another. This results in an unfixed error rate and an unknown level of significance under which the test is being performed. Therefore, visual comparison of population means was augmented by Student-Newman-Keuls' multiple range test (Steel and Torrie, 1960, p. 114) (Table 2).

General description of forms

In the ensuing descriptions, no detailed examination of P. gemmiferum and P. williamsoni is presented. Each of the remaining groups of Bear Lake whitefishes is described in both qualitative and quantitative terms and group distinctions and associations discussed. It must be emphasized that descriptions are based upon specimens within specific size ranges and caution must be used in applying these findings to other size groups, particularly the smaller segment of the populations. Table 3 summarizes the morphologic relationships within the Bear Lake Prosopium complex as determined in this investigation. Distribution of counts and measurements are presented in Appendix B and Tables 10-14. All morphometric data are expressed in thousandths of standard length (SL) unless otherwise noted.

Table 2. Results of Student-Newman-Kuels' multiple range comparison test of morphological differences among members of the Bear Lake Prosopium complex and P. williamsoni, Logan River.[a]

Dorsal base length						
Group[b]	5	2	3	1	4	6
Mean[c]	131	114	111	108	106	96
Adipose base length						
Group	5	4	1	3	2	6
Mean	76	72	64	61	60	50
Adipose height						
Group	5	4	2	1	3	6
Mean	97	92	84	83	81	67
Pelvic base length						
Group	2	3	5	1	4	6
Mean	31	28	27	27	27	24
Maxillary length						
Group	2	6	3	1	4	5
Mean	73	66	63	52	46	45
Maxillary width						
Group	2	3	1	6	4	5
Mean	31	29	29	27	24	24
Eye diameter						
Group	1	3	4	6	2	5
Mean	52	51	51	46	42	40
Interorbital width						
Group	2	3	1	5	4	6
Mean	70	61	57	56	56	53

[a]Lines drawn under the ranked means indicate groups of means not significantly different from one another at the .01 level.

[b]Group designation is as follows: 1 = P. spilonotus (small form) (N = 102), 2 = P. spilonotus (large form) (N = 27), 3 = P. species (N = 108), 4 = P. abyssicola (N = 120), 5 = P. williamsoni (N = 16), 6 = P. gemmiferum (N = 21).

[c]Means of the first 14 body measurements are expressed in thousandths of standard length.

Table 2. Continued

Postorbital head length						
Group	2	6	3	5	4	1
Mean	132	125	124	119	118	113
Head Length						
Group	2	6	3	4	1	5
Mean	261	251	248	233	225	216
Peduncle depth						
Group	5	2	1	4	3	6
Mean	74	72	71	69	68	66
Peduncle width						
Group	5	2	1	3	6	4
Mean	44	39	38	37	36	34
Pelvic to anal distance						
Group	1	4	5	3	2	6
Mean	271	261	253	252	243	228
Gill-raker length						
Group	6	1	2	3	4	5
Mean	35	14	14	14	14	13
Scales in lateral line						
Group	5	3	2	1	6	4
Mean	84.0	83.0	82.9	82.7	76.4	71.0
Scales above lateral line						
Group	5	2	3	1	4	6
Mean	10.1	9.8	9.8	9.5	8.2	8.0
Scales below lateral line						
Group	2	3	5	1	4	6
Mean	7.1	7.1	7.1	7.0	6.3	5.9
Scales around body						
Group	5	3	2	1	4	6
Mean	41.4	40.6	40.6	39.5	35.3	33.8
Scales around peduncle						
Group	2	3	1	5	6	4
Mean	21.8	21.5	20.9	20.6	19.9	18.9

Table 2. Continued

Anterior gill-rakers (upper limb)						
Group	6	4	3	2	5	1
Mean	15.2	9.3	9.0	9.0	8.9	8.7
Anterior gill-rakers (lower limb)						
Group	6	2	3	4	5	1
Mean	26.7	13.7	13.6	13.6	12.8	12.6
Total anterior gill-rakers						
Group	6	4	2	3	5	1
Mean	42.0	22.9	22.7	22.6	21.8	21.3
Posterior gill-rakers (upper limb)						
Group	6	5	4	3	2	1
Mean	15.9	7.9	7.5	7.3	7.1	6.7
Posterior gill-rakers (lower limb)						
Group	6	2	3	4	5	1
Mean	26.9	11.9	11.8	11.7	11.3	10.8
Total posterior gill-rakers						
Group	6	5	4	3	2	1
Mean	42.8	19.2	19.2	19.1	19.0	17.5
Pyloric caeca count						
Group		2	3	1	4	
Mean		136.7	129.4	113.4	77.0	
Maxillary length[d]						
Group	2	6	3	1	5	4
Mean	281	263	256	233	208	198
Maxillary width						
Group	1	2	3	5	4	6
Mean	128	117	117	111	104	101
Eye diameter						
Group	1	4	3	5	6	2
Mean	229	217	207	183	182	160

[d]Remaining morphometric characters expressed in thousandths of head length.

Table 2. Continued

Interorbital width						
Group	2	5	1	3	4	6
Mean	267	262	252	246	239	210
Postorbital head length						
Group	5	2	4	3	1	6
Mean	551	507	506	501	500	498
Gill-raker length						
Group	6	5	4	1	3	2
Mean	139	61	60	60	58	52

Table 3. Summary of morphological relationships of the Bear Lake Prosopium complex and P. williamsoni, Logan River.

Character	P. abyssicola (Mean) Range	SD	P. spilonotus (small form) (Mean) Range	SD	P. spilonotus (large form) (Mean) Range	SD	P. species (Mean) Range	SD	P. gemmiferum (Mean) Range	SD	P. williamsoni (Mean) Range	SD	P. gemmiferum-like (Mean) Range
Dorsal base length[a]	(106) 92-122	.006	(108) 88-122	.007	(114) 101-129	.007	(111) 92-124	.007	(96) 86-106	.005	(131) 116-145	.007	(104) 101-108
Adipose base length	(72) 60-90	.006	(64) 52-80	.006	(60) 52-68	.007	(61) 49-75	.007	(50) 44-58	.003	(76) 68-87	.005	(58) 54-66
Adipose height	(92) 81-110	.006	(83) 71-100	.006	(84) 69-95	.005	(81) 70-95	.006	(67) 60-74	.002	(97) 93-112	.007	(77) 71-85
Pelvic base length	(27) 21-37	.003	(27) 24-33	.002	(31) 27-36	.003	(28) 22-33	.002	(25) 20-28	.002	(27) 25-30	.002	(23) 21-24
Maxillary length	(46) 41-55	.003	(52) 45-64	.003	(73) 66-82	.005	(63) 52-73	.004	(66) 62-72	.002	(45) 38-47	.003	(60) 57-64
Maxillary width	(24) 20-31	.002	(29) 25-33	.002	(31) 25-34	.003	(29) 26-34	.002	(27) 20-29	.001	(24) 22-29	.002	(25) 24-27
Eye diameter	(51) 45-56	.003	(52) 45-57	.003	(42) 35-52	.003	(51) 43-60	.004	(45) 42-49	.003	(40) 34-47	.005	(49) 46-51
Interorbital width	(56) 49-62	.003	(57) 49-64	.003	(70) 61-81	.005	(61) 50-71	.003	(52) 48-59	.002	(56) 52-60	.003	(51) 48-57

[a]First 14 body measurements expressed in thousandths of the standard length.

Table 3. Continued

Character	*P. abyssicola* (Mean) Range	SD	*P. spilonotus* (small form) (Mean) Range	SD	*P. spilonotus* (large form) (Mean) Range	SD	*P.* species (Mean) Range	SD	*P. gemmiferum* (Mean) Range	SD	*P. williamsoni* (Mean) Range	SD	*P. gemmiferum*-like (Mean) Range
Postorbital head length	(118) 109-129	.004	(113) 99-128	.005	(132) 127-141	.003	(124) 114-138	.005	(123) 118-132	.003	(119) 114-128	.005	(121) 116-126
Head length	(233) 214-249	.007	(225) 211-244	.007	(261) 245-279	.008	(248) 223-267	.008	(249) 239-262	.004	(216) 191-233	.011	(240) 234-257
Peduncle depth	(69) 61-76	.003	(70) 62-76	.003	(72) 65-76	.003	(68) 62-76	.003	(65) 61-73	.002	(74) 63-81	.005	(65) 57-73
Peduncle width	(34) 28-42	.003	(38) 29-46	.003	(39) 35-44	.003	(37) 31-44	.003	(35) 30-38	.002	(44) 38-49	.003	(36) 32-43
Pelvic to anal distance	(261) 226-292	.011	(271) 247-296	.009	(243) 214-270	.012	(252) 227-286	.010	(227) 211-258	.009	(253) 231-272	.013	(242) 236-248
Gill-raker length	(14) 11-16	.001	(14) 10-17	.001	(14) 9-16	.001	(14) 10-18	.001	(35) 32-38	.002	(13) 11-16	.001	(26) 23-31
Scales in lateral line	(71.0) 65-79	3.047	(82.7) 76-89	3.345	(82.9) 77-90	3.919	(83.0) 74-93	3.835	(76.4) 71-80	2.501	(84.0) 78-87	2.309	(73.5) 69-80
Scales above lateral line	(8.2) 7-9	.453	(9.5) 9-10	.502	(9.8) 9-11	.483	(9.8) 9-10	.418	(8.0) 7-9	.539	(10.1) 9-11	.574	(7.9) 7-8
Scales below lateral line	(6.3) 6-8	.454	(7.0) 6-8	.219	(7.1) 7-8	.267	(7.1) 6-8	.369	(5.9) 5-6	.302	(7.1) 7-8	.250	(5.9) 5-6

Table 3. Continued

Character	P. abyssicola (Mean) Range	SD	P. spilonotus (small form) (Mean) Range	SD	P. spilonotus (large form) (Mean) Range	SD	P. species (Mean) Range	SD	P. gemmiferum (Mean) Range	SD	P. williamsoni (Mean) Range	SD	P. gemmiferum-like (Mean) Range
Scales around body	(35.3) 32-90	1.575	(39.5) 37-43	1.274	(40.6) 38-45	1.738	(40.6) 38-44	1.264	(33.8) 31-37	1.804	(41.4) 39-43	1.005	(34.5) 32-36
Scales around peduncle	(18.9) 17-21	.647	(20.9) 20-23	.679	(21.8) 20-23	.847	(21.5) 20-23	.826	(19.9) 18-21	.944	(20.6) 20-21	.512	(18.6) 18-19
Anterior gill-rakers (upper limb)	(9.3) 8-11	.678	(8.7) 7-10	.614	(9.0) 8-10	.649	(9.0) 8-11	.563	(15.2) 14-17	.809	(8.9) 8-10	.574	(11.0) 10-12
Anterior gill-rakers (lower limb)	(13.6) 12-16	.827	(12.6) 11-14	.834	(13.7) 13-15	.660	(13.6) 12-16	.883	(26.7) 25-33	2.272	(12.8) 11-14	.911	(18.4) 18-19
Total anterior gill-rakers	(22.9) 20-26	1.184	(21.3) 18-24	1.182	(22.7) 21-25	1.031	(22.6) 20-26	1.207	(42.0) 40-48	2.401	(21.8) 21-24	1.183	(29.0) 28-31
Posterior gill-rakers (upper limb)	(7.5) 6-11	.798	(6.7) 5-9	.7304	(7.1) 6-9	.801	(7.3) 6-9	.711	(15.9) 14-19	1.401	(7.9) 7-9	.443	(10.4) 8-13
Posterior gill-rakers (lower limb)	(11.7) 10-14	.938	(10.8) 9-14	.953	(11.9) 11-13	.675	(11.8) 10-14	.854	(26.9) 22-30	1.265	(11.3) 11-13	.577	(18.0) 16-19
Total posterior gill-rakers	(19.2) 16-22	1.250	(17.5) 15-21	1.282	(19.0) 17-21	1.192	(19.1) 17-21	1.115	(42.8) 36-47	1.834	(19.2) 18-21	.655	(28.4) 26-32

Table 3. Continued

Character	P. abyssicola (Mean) Range	SD	P. spilonotus (small form) (Mean) Range	SD	P. spilonotus (large form) (Mean) Range	SD	P. species (Mean) Range	SD	P. gemmiferum (Mean) Range	SD	P. williamsoni (Mean) Range	SD	P. gemmiferum-like (Mean) Range
Pyloric caeca	(77.0) 53-96	9.519	(113.4) 87-153	13.068	(136.7) 107-174	17.134	(129.4) 83-173	17.707	(65.0)[b] 46-95	---	50-146[c]	---	(72.0) 63-78
Maxillary length[d]	(198) 176-220	.009	(233) 212-250	.009	(281) 254-306	.013	(256) 230-286	.012	(263) 246-274	.008	(208) 194-224	.009	(247) 242-253
Maxillary width	(104) 87-132	.009	(128) 114-143	.007	(117) 105-130	.008	(117) 100-136	.008	(101) 88-117	.006	(111) 90-125	.009	(105) 92-115
Eye diameter	(217) 182-242	.011	(229) 202-272	.012	(160) 134-188	.013	(207) 164-245	.016	(182) 170-196	.008	(183) 160-214	.015	(201) 192-212
Interorbital width	(239) 210-273	.012	(253) 226-283	.013	(267) 238-306	.017	(246) 214-273	.011	(210) 196-225	.008	(262) 224-289	.019	(211) 205-224
Postorbital head length	(506) 460-537	.014	(500) 468-527	.013	(507) 472-533	.014	(501) 472-529	.011	(498) 476-515	.009	(551) 514-579	.019	(500) 487-515
Gill-raker length	(60) 46-71	.005	(60) 47-73	.005	(52) 34-59	.005	(58) 43-72	.005	(139) 125-149	.003	(61) 50-67	.003	(110) 98-128

[b]Counts taken from Perry (1943).

[c]Counts taken from Holt (1960).

[d]Remaining body measurements expressed in thousandths of the head length.

P. abyssicola (91.0-199.0 mm SL). In life, adult P. abyssicola are greenish along the dorsal surface fading to nearly immaculate silver below the lateral line. Scales are marginated and lightly dotted with melanophores which become more accentuated during spawning, especially in the males. The most distinguishing feature of the color pattern is the absence of distinct markings in most specimens over 150 mm SL (Figure 2). Of 221 preserved specimens of this size group, only two (0.9%) showed any evidence of spotting, and in these instances, spots were vague and hardly discernable. Of 56 specimens less than 99 mm SL, only one (1.8%) was without spots while 57 (44.5%) of 128 specimens within the size range 99-150 mm SL showed some spotting. In general, when spotting does occur, spots are larger, fewer in number and less distinct than in other Bear Lake forms.

In comparing specimens of similar size, P. abyssicola has noticeably larger scales than other Bear Lake forms. Head profile is often distinctive, typically sloping gently downward from the occiput to the approximate area of the nostril where declination increases, producing a distinctly decurved snout (Figure 2). Fish belonging to this group are never large; maximum size observed was 224 mm SL.

Characters best typifying P. abyssicola are: adipose height,[1] 81-110 (92); maxillary length, 41-55 (46); head length, 214-249 (233); pelvic to anal distance 226-292 (261); scales in lateral line, 65-79 (71.0); scales above lateral line, 7-9 (8.2); pyloric caeca, 53-96 (77.0); and maxillary length/head length, 176-220 (198) (Table 3).

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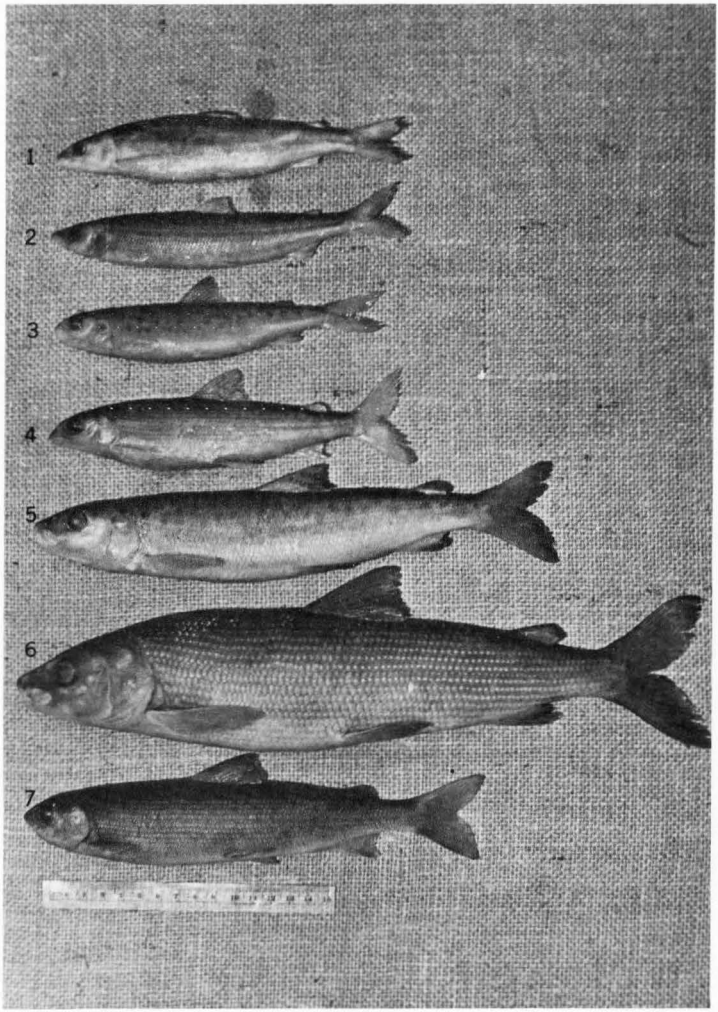
[1] Although adipose height in P. abyssicola had a poor linear fit (r^2 = .71, Appendix A) it was considered a useful character since the mean was larger than in other Bear Lake forms, and the positive curvilinearity produced by larger specimens contributes to the usefulness of the character.



1. P. gemmiferum-like; 2. P. gemmiferum; 3. P. spilonotus (small form); 4. P. abyssicola; 5. P. species; 6. P. spilonotus (large form); 7. P. williamsoni.

Figure 2. General appearance of Bear Lake whitefishes and P. williamsoni (Logan River).

P. spilonotus (small form) (95.5-221.0 mm SL). Prosopium spilonotus (small form) is similar to P. abyssicola in coloration, but is more darkly pigmented along the dorsal surface and is rarely without numerous gray spots extending dorsoventrally to the lateral line and from the occiput to base of caudal. Spots are typically oval with a long vertical axis; intensity, size and position varies conspicuously (Figure 2). Of 445 preserved specimens examined, only seven (1.6%) were lacking this character, and only one of these was under 165 mm SL. Typically, head profile (Figure 2) is symmetrically ovoid, usually lacking the abrupt change in angle of the snout seen in P. abyssicola. These small fish rarely exceed 220 mm SL; maximum size observed was 231 mm SL. Characters best typifying P. spilonotus (small form) are: adipose height, 71-100 (83); maxillary length, 45-64 (52); head length, 211-244 (225); pelvic to anal distance, 247-296 (271); scales in lateral line, 76-89 (82.7); scales above lateral line, 9-10 (9.5); pyloric caeca, 87-153 (113.4); and maxillary length/head length, 212-250 (233) (Table 3).

P. species (108.0-268.0 mm SL). General appearance of P. species is similar to P. spilonotus (small form) except for slight differences in head conformation. The head is elongate, creating a more pointed profile with the maxillaries noticeably longer (Figure 2). Spots are evident on most specimens up to about 210 mm SL but tend to become faint or absent in larger fish. Body profile is often slightly less robust than that of other Bear Lake forms, with the exception of P. gemmiferum. Members of this group grew to a size larger than that observed for P. abyssicola or P. spilonotus (small form) and were always immature (maximum size observed was 285 mm SL). Characters best typifying P. species are: adipose height, 70-95 (81); maxillary length, 52-73

(63); head length, 223-267 (248); pelvic to anal distance, 227-286 (252); scales in lateral line, 74-93 (83.0); scales above lateral line, 9-10 (9.8); pyloric caeca, 83-173 (129.4); and maxillary length/head length, 230-286 (256) (Table 3).

P. spilonotus (large form) (260.0-408.0 mm SL). General appearance of P. spilonotus (large form) is unmistakably distinctive (Figure 2). Fish belonging to this group are large (260-410 mm SL), robust, rarely spotted and always mature. Except when in spawning condition, they are moderately pigmented along the dorsal surface, fading toward the lateral line with only light pigmentation below the lateral line. During spawning they darken dorsally and laterally, with dark pigmentation often extending to the approximate level of the pelvic fins. The head is characteristically large, snout distinctly pointed and maxillaries elongate; head profile is basically triangular. Characters best typifying P. spilonotus (large form) are: adipose height, 69-95 (84); maxillary length, 66-82 (73); head length, 245-279 (261); pelvic to anal distance, 214-270 (243); scales in lateral line, 77-90 (82.9); scales above lateral line, 9-11 (9.8); pyloric caeca, 107-174 (136.7); and maxillary length/head length, 254-306 (281) (Table 3).

P. gemmiferum-like (141.0-175.5 mm SL). Members of the group referred to as P. gemmiferum-like were intermediate in general appearance and morphology to P. gemmiferum and either P. spilonotus (small form) or P. abyssicola. Head profile (Figure 2) resembled P. gemmiferum more than other forms, but the head was less attenuate and larger, maxillaries shorter and wider, and lower jaw terminal. One specimen was darkly pigmented along the dorsal surface down to the lateral line and was distinctly spotted. The others were lightly pigmented along the dorsal

surface with silvery sides, much like P. gemmiferum. Several characters demonstrating the intermediate morphology of this form to that of P. gemmiferum and either P. abyssicola or P. spilonotus (small form) were: adipose height, 71-85 (77); maxillary length, 57-64 (60); postorbital head length, 116-128 (121); gill-raker length, 23-31 (26); total anterior gill-rakers, 28-31 (29.0); and total posterior gill-rakers, 26-32 (28.4) (Table 3).

Comparative morphology of Bear Lake whitefishes

P. abyssicola--P. spilonotus (small form). Although no single character examined is adequate for total separation of P. abyssicola and P. spilonotus (small form), data collected in this study provide evidence that these forms are morphologically distinct. Only 7 of 32 morphological mean comparisons were found to be nonsignificant at the .01 level (Table 2). As is evidenced by closeness of means and large amount of range overlap, several of these characters (e.g., postorbital head length and pelvic width) are of little significance in group separation. These characters do, however, contribute to the totality of evidence supporting group distinction.

Gross morphological features of head make-up and pigmentation (as discussed above) are among the most useful indices for group classification. Quantitatively these forms are best separated by meristic characters (Figures 3-8; Table 3). In every instance, there is some overlap in range, but a combination of these characters allowed confident separation of all fish examined. Scales in the lateral line and pyloric caeca count proved to be the most useful.

Group overlap was more pronounced among proportional characters. In an effort to find a more useful means of expressing morphometric

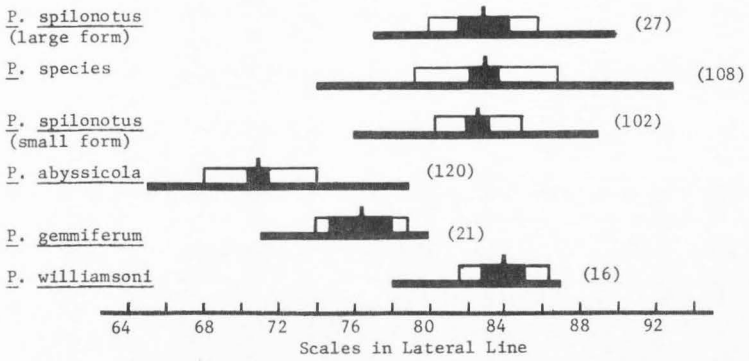


Figure 3. Comparison of scales in lateral line among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

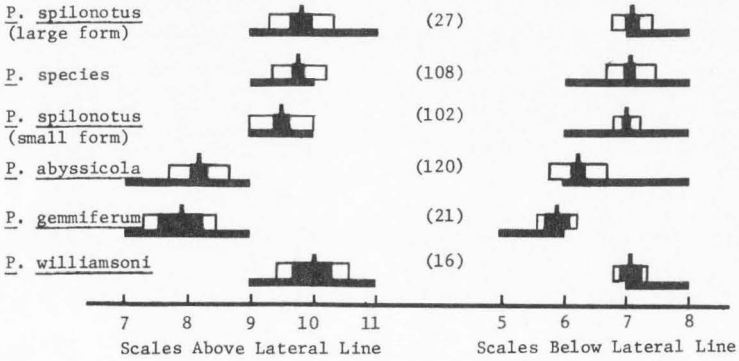


Figure 4. Comparison of scales above and below lateral line among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

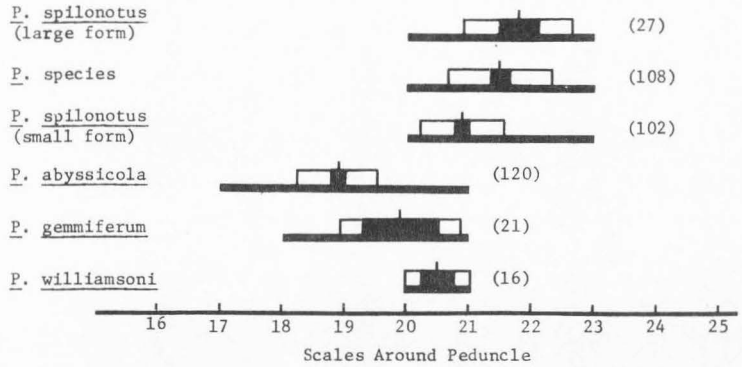


Figure 5. Comparison of scales around peduncle among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

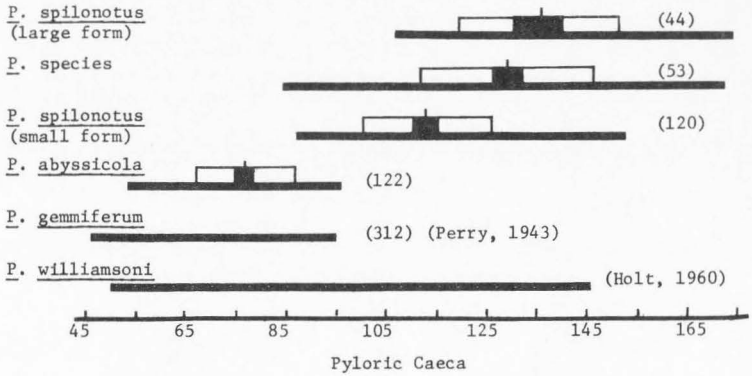


Figure 6. Comparison of pyloric caeca counts among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

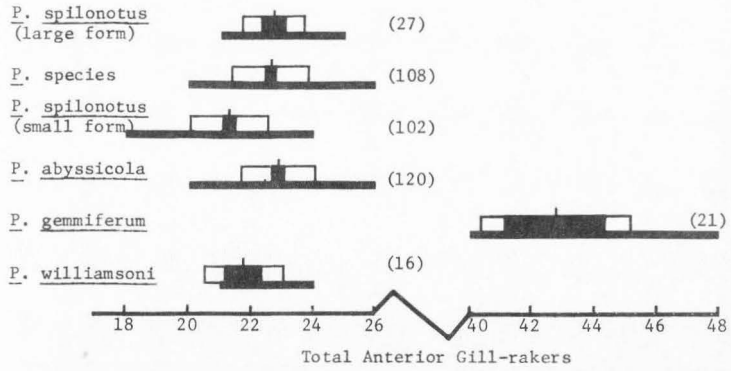


Figure 7. Comparison of total anterior gill-rakers among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

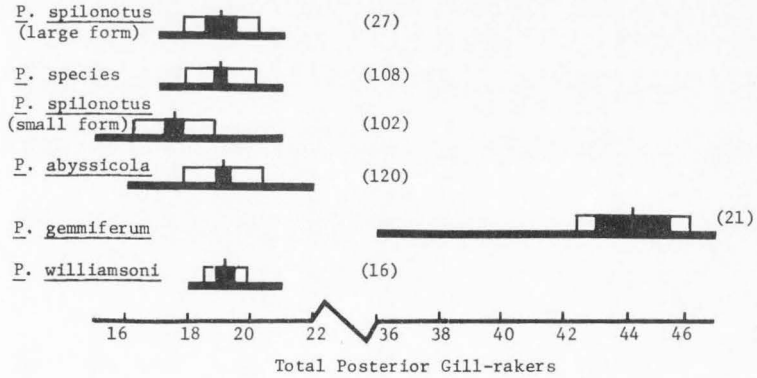


Figure 8. Comparison of total posterior gill-rakers among Bear Lake whitefishes and P. williamsoni, Logan River. Horizontal line = range; vertical line = mean; rectangle = standard deviation; black = 95 percent confidence interval; sample size in parentheses.

differences, pairs of morphometric values were plotted graphically. In determining which characters to use, a character of species A which had a higher mean than species B was plotted on the x axis while a character having a lower mean than species B was plotted on the y axis. Of the characters examined for P. abyssicola and P. spilonotus (small form), comparison of maxillary length to head length (Figure 9) and adipose height to maxillary length (Figure 10) gave the most clear-cut separation. Proportional values of maxillary length plotted against observed head length further supported independent evaluation of these forms (Figure 11).

P. abyssicola--P. species. Morphological parameters provide for virtually complete separation of P. abyssicola and P. species. Pigmentation and head conformation, as discussed above, are extremely valuable in field identification. Meristic counts (Figures 3-8) are of the approximate magnitude of usefulness in distinguishing P. abyssicola from P. species as they were in the above description. Morphometric characters, on the other hand, provide for nearly complete separation. Proportional measurements associated with maxillary length are the most useful with maxillary length/head length ratios versus observed head length providing the widest separation (Figure 12). Proportional comparisons of maxillary length to adipose height (Figure 13) and to pelvic to anal distance (Figure 14) provide further evidence of group distinction.

P. spilonotus (small form)--P. spilonotus (large form)--P. species. Although P. spilonotus (small form), P. spilonotus (large form) and presumably P. species were originally considered as being members of the same group (Snyder, 1919), morphological evidence collected in this

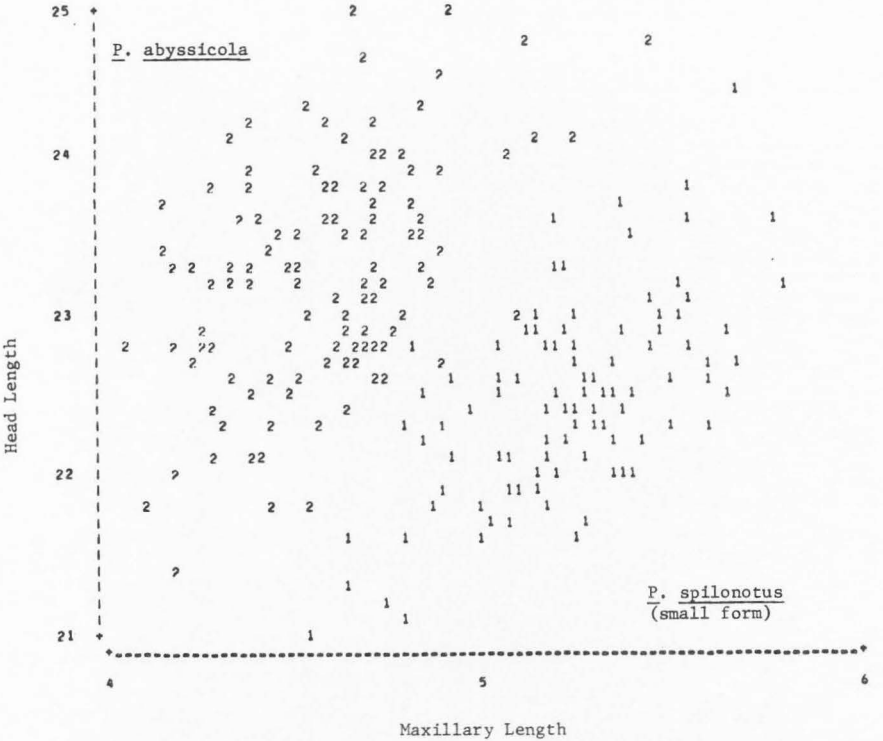


Figure 9. Separation of P. abyssicola and P. spilonotus (small form) on the basis of maxillary length and head length; measurements in thousandths of SL.

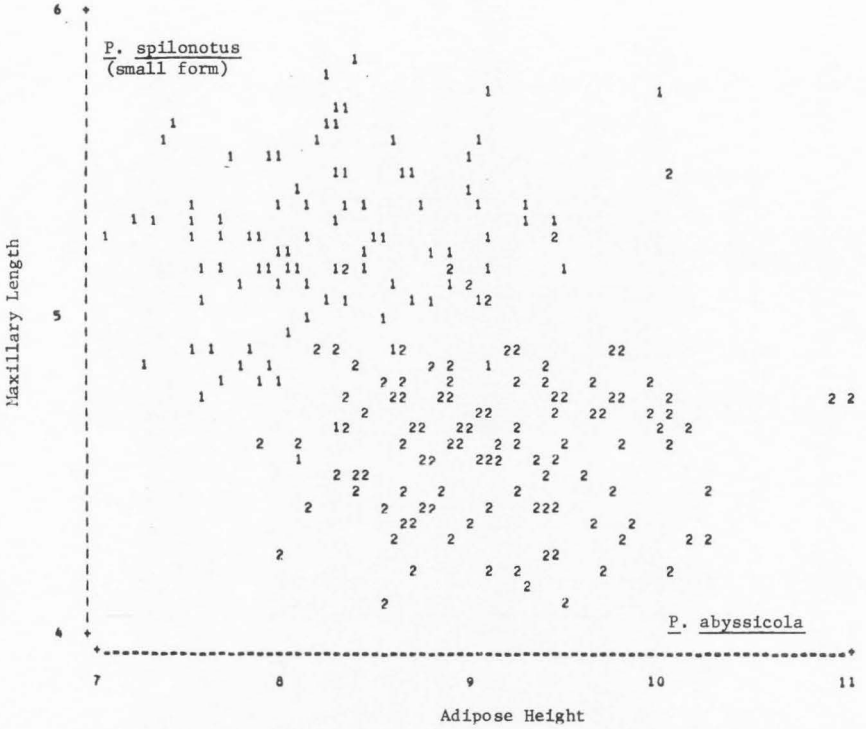


Figure 10. Separation of P. abyssicola and P. spilonotus (small form) on the basis of adipose height and maxillary length; measurements in thousandths of SL.

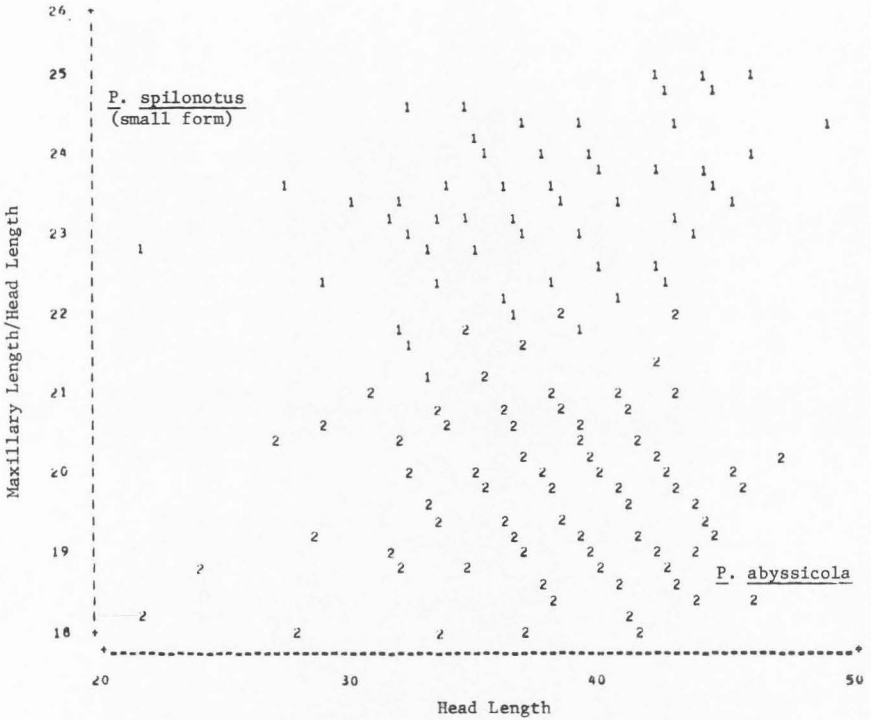


Figure 11. Separation of P. abyssicola from P. spilonotus (small form) on the basis of observed head length and maxillary length/head length ratio; measurements in thousandths of SL or head length.

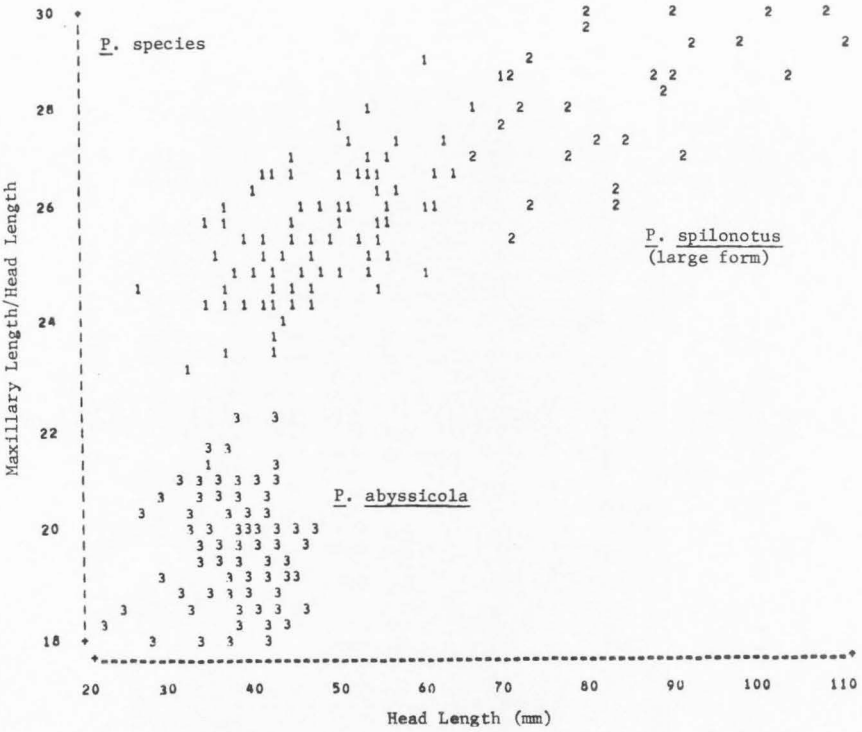


Figure 12. Separation of P. abyssicola from P. species and P. spilonotus (large form) on the basis of observed head length and maxillary length/head length ratio.

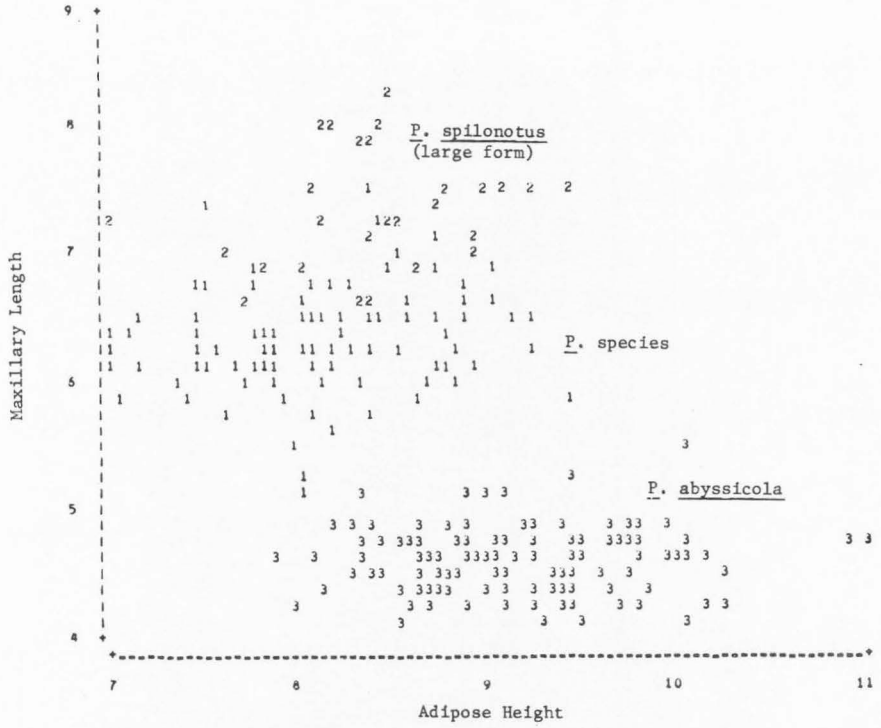


Figure 13. Separation of P. abyssicola from P. species and P. spilonotus (large form) on the basis of proportional values of adipose height and maxillary length; measurements in thousandths of SL.

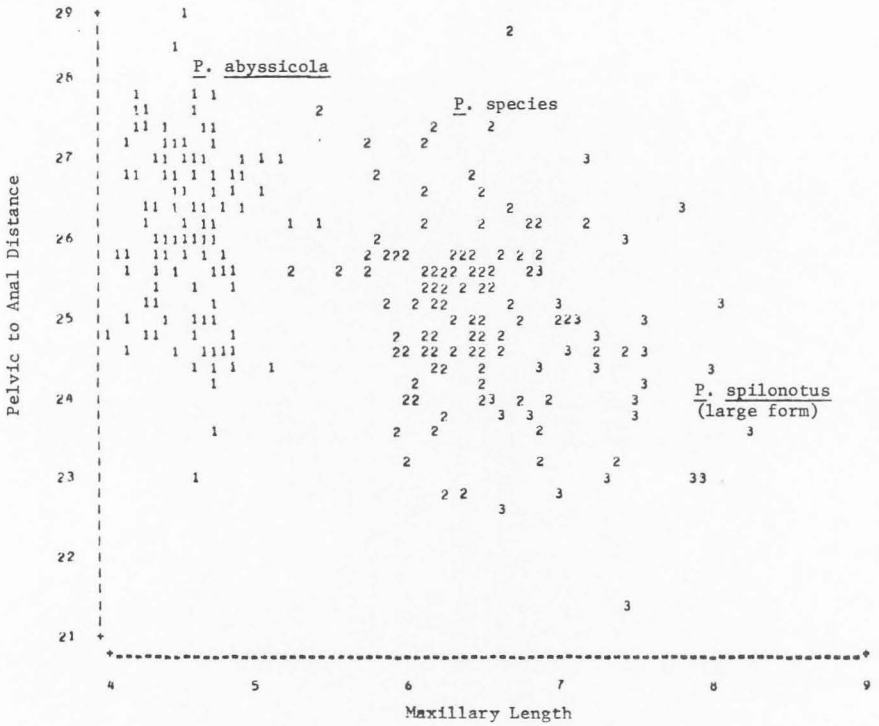


Figure 14. Separation of P. abyssicola from P. species and P. spilonotus (large form) on the basis of proportional values of maxillary length and pelvic to anal distance; measurements in thousandths of SL.

investigation supports the hypothesis that within this complex two discrete groups should be recognized.

In general appearance P. spilonotus (small form) and P. species are extremely similar. Members of both groups usually have numerous spots which become increasingly vague or absent in individuals larger than 210 mm SL. Phenotypic cues useful in field separation of these forms are primarily associated with slight differences in head morphology. Prosopium spilonotus (small form) typically has a relatively small, oval-shaped head with rounded snout and short maxillaries. In contrast, the head of P. species is proportionately larger, the snout more acutely pointed and the maxillaries noticeably elongate. Body profile of P. species is often less robust than that of P. spilonotus (small form) but the magnitude of this difference is so slight that it renders the character ineffectual for use by persons unfamiliar with the group. This appearance probably was a result of all specimens of P. species being immature.

In statistical examination of means, 22 of the 32 comparisons showed significant differences (.01) between P. spilonotus (small form) and P. species (Table 2). No character provided for complete group separation and the magnitude of overlap was usually large (Table 3). Meristic counts contributed little to differentiating these forms, but it is important to note that in every instance P. species had a mean which was larger than that observed for P. spilonotus (small form) (Table 3, Figures 3-8).

The use of morphometric characters was most effective in distinguishing between these forms. Maxillary length in proportion to both standard length and head length were the best characters for separation

(Table 3). Group differences, however, were best illustrated by comparing characters, two at a time, as discussed above. The plot of maxillary length against pelvic to anal distance showed nearly complete group separation (Figure 15). Similar results were obtained when comparing maxillary length/head length ratios with pelvic to anal distance (Figure 16) and head length with pelvic to anal distance (Figure 17). Morphological differences strongly support the contention that these forms are indeed unique and that separate consideration is justified. This leaves the relationship of P. spilonotus (large form) to P. spilonotus (small form) and P. species to be established. Obviously this group was the large segment of one of the above populations. The question then became to which group should they be assigned and upon what basis would this assignment be made.

Prosopium spilonotus (large form) closely resembles P. species in head profile but is without spots and is always mature. This is suggestive of the possible relatedness of these forms since spotting is less prominent or absent in large specimens of P. species and the maximum size of P. species (all immature) overlaps slightly with the minimum size of P. spilonotus (large form) (all mature). It appears that P. spilonotus (large form) is the mature segment of the P. species population.

Mean comparisons among morphological characters of P. spilonotus (large form) and both P. spilonotus (small form) and P. species provide quantitative evidence supporting this relationship. Prosopium spilonotus (large form) and P. spilonotus (small form) were statistically distinct in 26 of the 32 comparisons examined while only 15 comparisons between P. spilonotus (large form) and P. species were shown to be statistically different (Table 2).

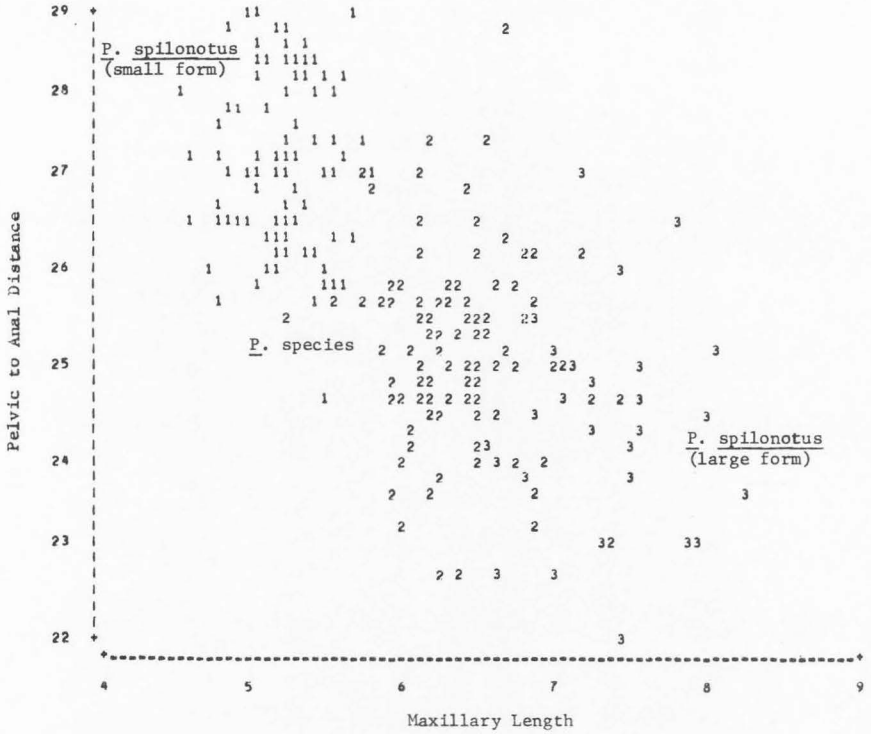


Figure 15. Separation of P. spilonotus (small form) from P. species and P. spilonotus (large form) on the basis of maxillary length and pelvic to anal distance; measurements in thousandths of SL.

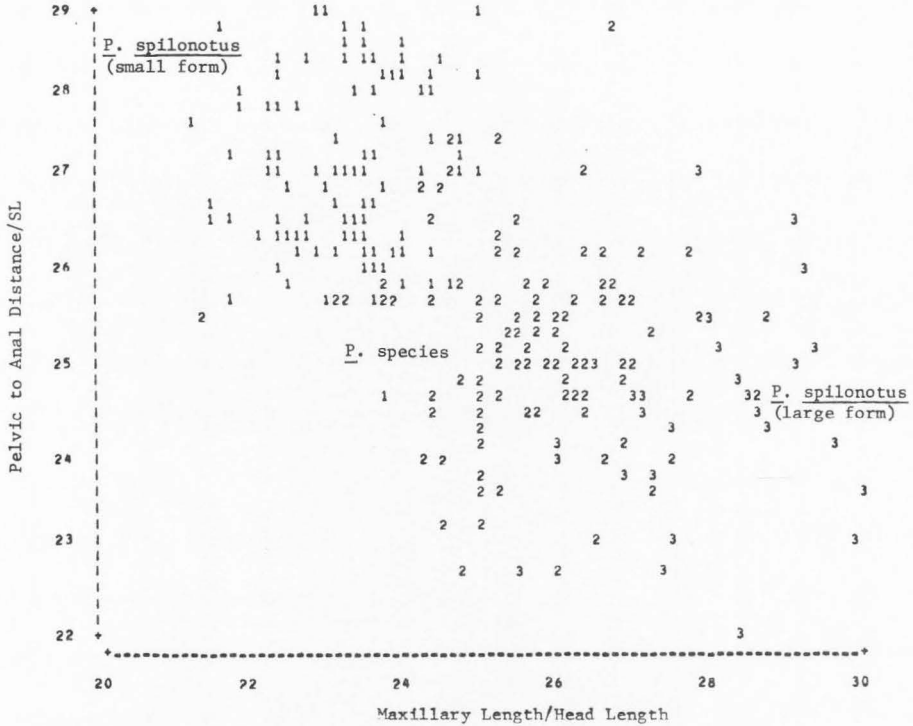


Figure 16. Separation of P. spilonotus (small form) from P. species and P. spilonotus (large form) on the basis of proportional values of maxillary length/head length and pelvic to anal distance/SL.

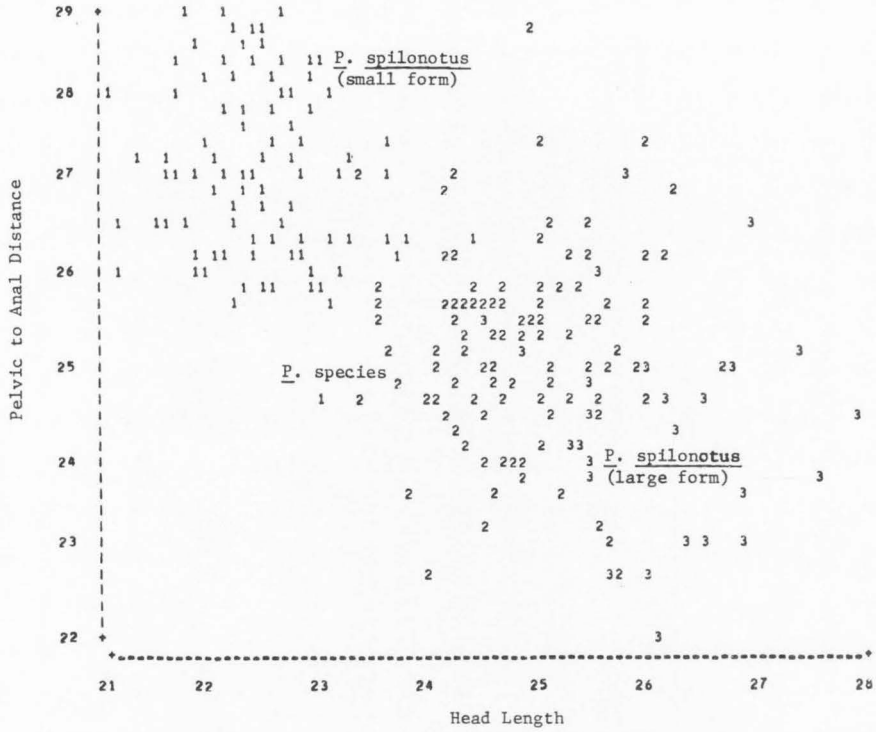


Figure 17. Separation of P. spilonotus (small form) from P. species and P. spilonotus (large form) on the basis of head length and pelvic to anal distance; measurements in thousandths of SL.

Fourteen of these 15 characters were morphometric characters while only one was a meristic count. Meristic characters were always most like P. species and were often identical (Figures 3-8). As noted earlier, proportional characters are often influenced by allometric growth. In general, the larger the size range of the sample, the greater the probability of a change in relative growth rate. When body-part measurements of P. spilonotus (small form), P. spilonotus (large form) and P. species were plotted against standard length for the proportional characters (not shown), the point distribution of P. spilonotus (large form), in every instance, slightly overlapped with that of P. species, forming a continuation of the curve. In evaluating the resultant combined curve, the growth rate of body parts either increases (e.g., maxillary length) or decreases (e.g., eye diameter) relative to standard or head length, establishing a curvilinear relationship. This accounts for the significant differences of morphometric characters between P. species and P. spilonotus (large form) and further supports the contention that these groups are segments of one population. This proposed relationship is well illustrated in Figures 15-17 where P. spilonotus (large form) is always most closely associated with P. species.

P. williamsoni--Bear Lake Prosopium. Although reported to be indigenous to Bear Lake, P. williamsoni was not collected in the present study. Morphological examination of a small sample from the Logan River showed P. williamsoni to be distinct from all Bear Lake whitefishes.

In general appearance, P. williamsoni most closely resembles P. spilonotus (small form) but is more robust than this form and other

Bear Lake forms; the head and eyes are smaller, and the dorsal and adipose fins larger. None of the specimens examined (138.0-285.0 mm SL) had spots.

Meristically, P. williamsoni showed near complete overlap with P. spilonotus (small form), P. spilonotus (large form) and P. species but was well separated from P. abyssicola (Figures 3-8). Morphometric analysis showed P. williamsoni totally separated from P. species and P. spilonotus (small form) by maxillary length/head length ratios. Dorsal base length/standard length ratios provided for nearly complete separation of P. williamsoni from P. spilonotus (small form) and P. abyssicola (Table 3). Bivariant comparison of dorsal base length and maxillary length showed good distinction between P. spilonotus (small form) and P. williamsoni (Figure 18).

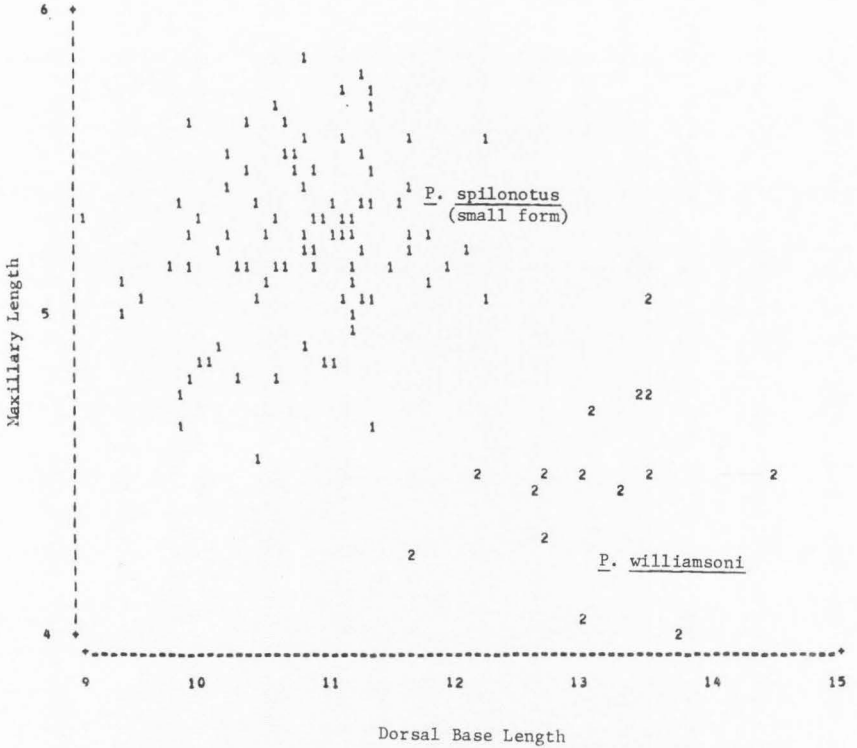


Figure 18. Separation of P. williamsoni and P. spilonotus (small form) on the basis of dorsal base length and maxillary length; measurements in thousandths of SL.

MULTIPLE DISCRIMINANT FUNCTION ANALYSIS

Introduction

In the preceding section, morphologic distinction among members of the Bear Lake Prosopium complex was accomplished by comparing variables, one or two at a time. Good group separation was evidenced by a number of comparisons but varying degrees of group overlap was characteristic and rarely was separation complete. As a means of further substantiating these findings, the procedure of multiple discriminant function analysis was applied. This analysis is a sophisticated statistical tool which discloses the degree of distinctiveness among groups based on a number of variables considered simultaneously. Populations of organisms may be very distinct with respect to several simultaneously considered characters and yet overlap with respect to each of the same characters separately (Jolicoeur, 1959). Much of the usefulness of this analysis lies in the fact that it serves to reduce the dimensions of the multivariant problem without losing a great deal of predictive power, and in addition makes interpretation of the classification procedure more straight-forward (Waite, 1971).

In addition to group separation, multiple discriminant function analysis identifies the group to which each individual in the study is most closely related and ultimately generates a predictive model which can be used in the placement of questionable specimens.

The technique of discriminant function analysis, first introduced by Fisher (1936), has only recently (due to availability of digital computers) come into common usage in various biological fields, especially

systematics (Sokal and Rohlf, 1969). Jolicoeur (1959) gives a good discussion of the usefulness of the technique for multivariant problems.

The extent of application of this analysis by researchers is difficult to determine in that rarely do titles of papers allude to the analysis employed. Recent studies by Atchley (1971), Calhoon and Jameson (1970), Thomas and Jameson (1970), and Ball and Jameson (1966) have successfully applied the technique to problems ranging from geographic variation to premating isolating mechanisms. Lawrence and Bossert (1967) and Rogers (1972) have utilized the technique in examining the taxonomic relationships of three species of Canis and three species of Bufo, respectively.

To the author's knowledge, the first application of discriminant function analysis to problems associated with fish systematics was a study by Stone (1947) who utilized the technique to evaluate the taxonomic status of two species of darters, genus Boleosoma. Hill (1959) used the analysis in classifying races of American shad. Later, McPhail (1961) applied the technique to the differentiation of sympatric populations of Salvelinus malma and S. alpinus and Fenderson (1964) examined the differences between dwarf and normal forms of the whitefish Coregonus clupeaformis. Nelson (1968) reported application of the analysis to evaluate the results obtained from using a character index to distinguish between Catostomus species and their hybrids but gives no detailed account of the analysis. More recently, Menzel and Darnell (1973) compared sympatric populations of Poecilia mexicana, P. formosa and t.iploid hybrids.

The discriminant function analysis in each of the above studies of fish systematics was limited to pair-wise examination of forms. Only

one study using multiple discriminant function analysis as discussed by Rao (1965) and Cooley and Lohnes (1962) was found. In this instance the analysis was used to determine which morphological characters best separate five recognized species of trout (Quellette and Qadri, 1968).

The orthogonal method of calculating discriminant functions was utilized in the present study. In short, discriminant function analysis is a procedure for estimating the position of an individual on a line that best separates groups. Since one "best" line may not exhaust the predictive power of the variables, additional functions are calculated (Cooley and Lohnes, 1962). The number of orthogonal discriminants calculated is equal to the number of groups less one, or the number of variables - whichever is less. In the present study, the initial analysis was based on the comparison of five groups, thus four discriminant functions were computed. The first function is the linear combination of variables which best distinguishes between groups according to the basic principle of maximizing the between-mean variance to the within-group variance. The second function accounts for the second best variance, etc. Each variable is weighted separately for each function, thus each specimen analyzed receives a score on each of the discriminants (Christensen, 1973). Since there were five groups in the present study, all of the information contained in the set of characters examined was condensed into four discriminant scores for each specimen.

For classification purposes, the problem is one of deciding on the membership of a specimen to one of a given set of populations. This decision is founded on the comparison of the individual's profile (based on parameters supplied) with the profile of the various groups. To perform the classification, the discriminant function score computed for

each individual is compared with the profile of the corresponding score of each group centroid (the mean discriminant function score for the group). Classification decisions are based upon testing a group of hypotheses regarding group membership with the hypothesis with the highest probability being selected (Waite, 1971). All computations were performed on a Burrows 6700 digital computer using a series of computer programs developed by Dr. Rex L. Hurst (1972), Utah State University.

Results and Discussion

Discriminant function analysis of five groups of Prosopium

Five groups of Prosopium (P. spilonotus (small form), P. abyssicola, P. species, P. gemmiferum, and P. williamsoni) were subjected to multiple discriminant function analysis using 12 morphological variables (Table 4). Variable selection was based upon results of multiple mean comparison tests (Table 2) with variables contributing the most to pairwise separation being selected.

The discriminating power of these variables was tested using Wilks' lambda criterion which is "a multivariant extension of the F test for equality of group means, to a test for equality of group centroids" (Hurst, 1972). The lambda value for the five groups was .000408 ($F_{48, 1358} = 186.2$), significant at .001 level. Thus the chance of producing group differences of this magnitude or greater by taking a random sample of fish from the natural population would be less than one in one thousand. The null hypothesis that there were no differences among groups was therefore rejected.

Table 4. Scaled vectors showing the relative contribution of the 12 variables to each of the four discriminant functions.

Character	Discriminant Function			
	1	2	3	4
1. Dorsal base length*	0.2644632	0.0172899	-0.3567379	0.3574994
2. Adipose height*	0.1942995	0.1965070	-0.1901893	0.2770379
3. Maxillary length*	-0.7561281	-0.9685053	0.2342485	-0.2026091
4. Interorbital width*	0.5516285	-0.0781740	-0.2970920	0.1828975
5. Postorbital head length	-0.0355479	0.0069139	-0.5030083	0.7613339
6. Head length*	-0.0541711	0.1299031	0.6619883	0.1149898
7. Pelvic to anal distance*	0.1097464	-0.0063934	0.0465878	-0.3578921
8. Scales in lateral line	0.0004799	-0.0005003	-0.0002779	-0.0003260
9. Scales above lateral line	0.0023064	-0.0025062	-0.0035200	0.0012659
10. Scales below lateral line	0.0025731	-0.0015144	0.0005223	0.0003129
11. Total anterior gill-rakers	-0.0034213	0.0001430	-0.0001886	-0.0011522
12. Total posterior gill-rakers	-0.0041090	0.0001475	-0.0010117	0.0006122

*Characters contributing most to group separation; the larger the function value, disregarding sign, the greater the contribution of the character to group separation.

Four functions were necessary to account for 100% of the variance in the data (Table 5). For each function, the variation observed between groups is significantly greater than can be explained by chance ($p < .001$). The first two functions, accounting for 92.5% of the variation, contribute most to group separation. Group separation is well illustrated when the centroids for functions one, two and three are plotted in discriminant space (Figure 19). Further illustration of group separation is seen in the "centours of centroids" matrix (Table 6) which shows the extent of overlap among groups. P. abyssicola, P. gemmiferum and P. williamsoni are each shown to be totally distinct from any other group while only slight overlap (.09%) was apparent between P. spilonotus (small form) and P. species.

Table 5. Summary of discriminatory analysis among five groups of Prosopium based on 12 biometric characters. (Groups included are: P. abyssicola, N = 120; P. spilonotus (small form), N = 102; P. species, N = 108; P. gemmiferum, N = 21; and P. williamsoni, N = 16.)

Discriminant axis	1	2	3	4
Variance component	2635.3	1036.5	204.3	92.4
Percent of total	66.4	26.1	5.1	2.3
Degrees of freedom	15	13	11	9
Probability	< .001	< .001	< .001	< .001

Scaled vectors (Table 4) show the relative contribution of each variable to the four discriminants. The large contributors to group separation along the first function, in order of importance, were maxillary length, interorbital width, dorsal base length, adipose height

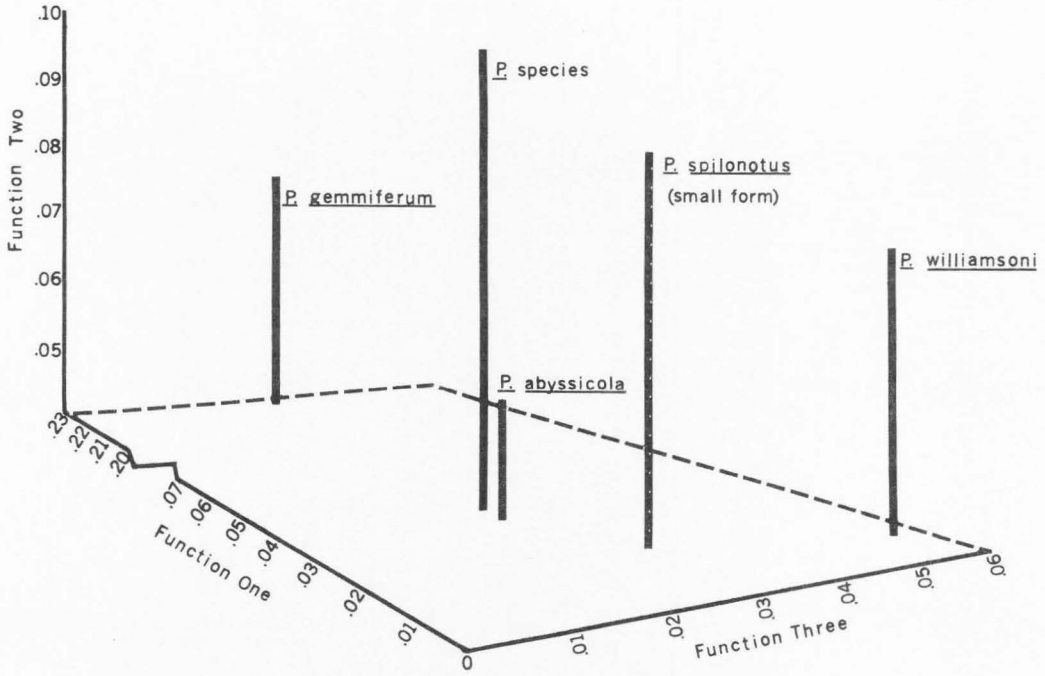


Figure 19. Distribution of the centroids of five species of Prosopium in reduced space formed by functions one, two and three.

and pelvic to anal distance. In the second function the most important contributor to group separation was once again maxillary length, followed by adipose height, head length, interorbital width and dorsal base length. The six characters important in functions one and two also dominate in importance in the remaining functions (Table 4).

Table 6. Centours of centroids matrix showing the amount of overlap between five groups of Prosopium.

	Prosopium abyssicola	Prosopium spilonotus (small form)	Prosopium species	Prosopium gemmiferum	Prosopium williamsoni
Prosopium abyssicola	1.0000	0.0000	0.0000	0.0000	0.0000
Prosopium spilonotus (small form)	0.0000	1.0000	0.0009	0.0000	0.0000
Prosopium species	0.0000	0.0009	1.0000	0.0000	0.0000
Prosopium gemmiferum	0.0000	0.0000	0.0000	1.0000	0.0000
Prosopium williamsoni	0.0000	0.0000	0.0000	0.0000	1.0000

After group analysis was completed, each specimen in the groups studied was re-classified by computing a set of scores for that specimen and comparing these with each of the group centroids. A chi-square value was calculated for each comparison and the specimen re-classified into the group for which it received the lowest chi-square.

Results of this re-classification were identical to those shown in the centours of centroids matrix, with every specimen originally

included in the P. abyssicola, P. gemmiferum and P. williamsoni groups being re-classified accordingly. The importance of the re-classification however lies in the fact that individuals causing the small amount of overlap between P. spilonotus (small form) and P. species were identified. The smallest specimen of P. spilonotus (small form) (86 mm SL) was re-classified as P. species and three specimens of the P. species group were re-classified as P. spilonotus (small form). After re-examining the small specimen of P. spilonotus (small form), along with a number of others of approximate same size, it was judged that identification of fish this small was questionable and that they should be excluded from further consideration.

Of the three specimens originally included in the P. species group, one was an obvious mis-classification while the others were P. species-like in gross appearance. Re-examination of the six characters most important in the discriminant analysis, (Table 4) revealed these two specimens were intermediate in maxillary length, postorbital head length and head length, i.e., proportions for these characters were near the lower range of P. species and near the upper range of P. spilonotus (small form); both fish were immature. Because of the uncertain status of these specimens, they were eliminated from the study.

Relationship of P. spilonotus (large form) to other Bear Lake Prosopium

Univariant and bivariant analysis discussed earlier strongly supported the hypothesis that P. spilonotus (large form) was the mature sector of the P. species population. This hypothesis was further confirmed by multiple discriminant function analysis.

The model generated by the analysis of the previously examined groups was used to predict the group to which P. spilonotus (large form)

was most closely related. Results unanimously supported the hypothesized relationship of P. species and P. spilonotus (large form). A two dimensional plot (functions one and two as coordinates) of these data, combined with data of P. spilonotus (small form) and P. abyssicola obtained in the original analysis, vividly illustrate distinctness of groups (Figure 20). Prosopium spilonotus (large form) is well intergraded with P. species, while P. spilonotus (small form) overlaps only slightly with the above, and P. abyssicola is totally distinct.

Examination of questionable specimens

As mentioned earlier, all specimens of questionable identity were retained throughout the study. Of the several thousand fish examined (>100 mm SL), only 34 were considered to be nontypical of one of the above groups.

Seventeen of these specimens were hypothesized to be P. spilonotus (small form). Although they were distinctly P. abyssicola-like in gross appearance, all were larger than 150 mm SL (163-187 mm) and all possessed vague spots. Means of morphological characters (not shown) were most similar to those of P. spilonotus (small form), alluding to their probable relationship. This hypothesized relationship was confirmed in every instance by the multiple discriminant function analysis.

The remaining 17 specimens were all immature and intermediate in appearance to P. spilonotus (small form) and P. species. They ranged in SL from 110-197 mm. Multiple discriminant function analysis classified six of these specimens as P. spilonotus (small form) and 11 as P. species. It is possible that these specimens, as well as the two intermediate specimens revealed by the discriminant function analysis, are hybrids between P. spilonotus (small form) and P. spilonotus (large form).

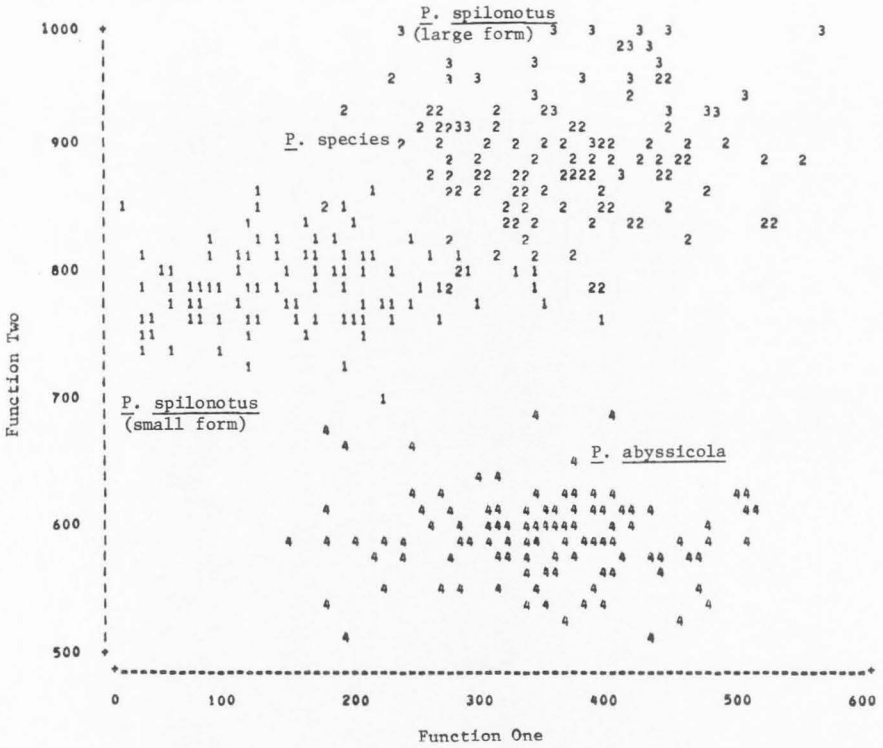


Figure 20. Group dispersion in discriminant functions one and two.

Multiple discriminant function analysis served well in substantiating the findings of univariant and bivariant analysis of members of the Bear Lake Prosopium complex. The efficacy of this statistical tool is demonstrated by the degree of separation among the three most similar forms (Figure 20). In traditional analysis of biometric data, every comparison showed some degree of overlap between P. abyssicola and P. spilonotus (small form). By the simultaneous evaluation of 12 characters, multiple discriminant function analysis showed these forms very distinct. Overlap between P. spilonotus (small form) and P. species was much more pronounced in univariant and bivariant comparisons than in the above forms, but nearly complete group separation was accomplished by use of discriminant functions. The model generated by the comparison of five groups of Prosopium proved useful in analyzing the relationship of P. spilonotus (large form) to other Bear Lake whitefishes. As was hypothesized from morphological comparisons, P. spilonotus (large form) was shown to be a segment of the P. species population.

Of the 12 characters used in the discriminant analysis, six were shown to be important to group separation (Table 4). Interestingly enough, all six were morphometric proportions. None of the meristic characters were found to contribute significantly to the analysis. This is not to say that meristic characters have no value in distinguishing between forms, however. Biological systems are highly integrated, and their information content is often redundant (Quellette and Qadri, 1968). Therefore, among the group of characters analyzed, meristic characters contained little information in addition to that contained in morphometric proportions.

In future investigations of the Bear Lake whitefishes, a new model could be generated from data presented in the present study using only the six most important parameters. By doing this, even persons unfamiliar with these fishes need only make six measurements and feed this information into the prediction model. Because of the small overlap between groups, good reliability could be placed on predictions of group membership.

In summary, morphological analysis of Bear Lake whitefishes provides evidence justifying the recognition of four distinct groups in addition to P. gemmiferum. These groups include P. abyssicola, as described by Snyder (1919) and P. gemmiferum-like hybrids reported by Sigler and Miller (1963). The P. spilonotus group described by Snyder (1919) is shown to consist of two morphologically distinct forms: P. spilonotus (small form) and the P. spilonotus (large form) - P. species group which will now be referred to collectively as P. spilonotus (large form).

EXPERIMENTAL HYBRIDIZATION

Introduction

Hybridization between fish species in nature has long been recognized but only recently has interest in the subject been acute (see Schwartz, 1972). The recent influx of hybrid literature has documented characteristics of natural and experimentally produced interspecific hybrids and has led to a reasonably good understanding of this phenomenon.

Typically, F1 hybrids are intermediate in respect to those characters which differ significantly between parental forms (Hubbs, 1955). Hybrids may, however, be identical to, or closely approach, the phenotype of only one of the parental species (Simon and Noble, 1968), or they may display characteristics entirely outside the range of either parent (Hubbs and Strawn, 1956). Uniformly intermediate characters may be taken as a strong indication of hybrid sterility while wide variation of hybrid offspring suggests at least partial fertility (Lagler, Bardach and Miller, 1962). Most researchers agree that the ability to hybridize is correlated with phylogenetic relatedness (Hubbs, 1955; West and Hester, 1966; Hester, 1970).

Interspecific hybrids among various coregonines are not uncommon. Schwartz (1972) lists 94 references to whitefish hybrids, 74 of which involve members of the genus Coregonus. A prominent portion of this literature is of European origin.

Experimental hybrids among various Coregonus species have been extensively studied by Swedish biologists at the Institute of Freshwater Research at Drottningholm. The primary objectives of these studies have

been to obtain information on gill-raker inheritance and to experimentally test the hypothesis that variation among whitefish populations of Coregonus is mostly caused by introgression (Svardson, 1970). These studies revealed that F2 hybrids were often fertile and consequently introgression was possible. Heterosis and increased survival were evident in all experiments and hybrids possessed intermediate numbers of gill-rakers.

Reports of natural hybridization among North American whitefishes are not prevalent in the literature. This is probably in part a reflection of the lack of in-depth studies concerning the coregonine fishes. The most recent published account was that of Alt (1971) who describes natural hybrids between the inconnu (Stenodus leucichthys) and humpback whitefish (Coregonus pidschian) from Chatanika River, Alaska. Paetz[1] has recently completed a study on natural and experimental hybrids between Coregonus clupeaformis and the C. artedii complex from several Canadian lakes.

Hybrids among Prosopium species are nearly unknown. Gilbert (1895) reported an apparent Prosopium x Coregonus hybrid and McPhail and Lindsey (1970) suggested that Alaskan populations of morphologically intermediate whitefish found sympatrically with P. coulteri and P. cylindraceum could possibly be of hybrid origin. Although P. williamsoni and P. cylindraceum overlap somewhat in distribution, no evidence of interbreeding has been found (McPhail and Lindsey, 1970). Presumed hybrids between P. gemmiferum and P. spilonotus, Bear Lake, Utah-Idaho, were reported by Sigler and Miller (1963). The origin of these and other intermediate Bear Lake forms has been examined in the present study.

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[1]Excerpts from an in-progress Ph.D. Dissertation by Martin J. Paetz, University of Alberta, Edmonton, Alberta, Canada, June, 1972.

Moenkhaus (1910) effected reciprocal crosses between whitefish (Coregonus clupeaformis) and cisco (Leucichthys artedii) and obtained viable progeny from both. Garside and Christie (1962) made experimental crosses between Coregonus clupeaformis, C. artedii and P. cylindraceum. Embryos of the C. clupeaformis x P. cylindraceum cross developed normally. The reciprocal of this cross and reciprocal crosses of P. cylindraceum and C. artedii produced no offspring; other crosses were successful.

Although experimental hybridization has long been practiced by European researchers, little information dealing with whitefish culture is available. Most studies have been conducted by planting hybrid fry in ponds or lakes previously void of whitefishes. Paetz[2] reared experimental hybrids in barrow pits on the advice of Svardson, who suggested that it would be difficult to culture young whitefish in the laboratory. Mellen (1923) presented an account of the culture of C. clupeaformis at the New York Aquarium. Extensive work with artificial hybrids of Great Lakes whitefishes has apparently been done at the Great Lakes Laboratory, but accounts of this research have not been published.

Early in the present study, the taxonomic confusion associated with the Bear Lake whitefishes was postulated to have resulted, in part, from hybridization among the various groups. This hypothesis was prompted by: (1) the presence of P. gemmiferum-like intermediates in the natural population, (2) the occurrence of ripe P. gemmiferum males during the spawning runs of both P. abyssicola and P. spilonotus (small form) and (3) the immaturity of P. spilonotus (large form) at sizes larger than the maximum observed size of P. spilonotus (small form).

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[2]Excerpts from an in-progress Ph.D. Dissertation, Martin J. Paetz, June, 1972.

To examine the validity of the hybridization hypothesis, experiments were conducted to determine the hybridization capacities among combinations of P. abyssicola, P. spilonotus (small form), P. spilonotus (large form), P. gemmiferum and P. williamsoni and to make morphological comparisons between successful hybrids and suspected hybrids from the natural population.

Although representatives of P. williamsoni were not collected in Bear Lake during the present study, this group was not dismissed as a possible source of hybrids. Prosopium williamsoni originating from the Logan River were used in all crosses involving this species. No attempt was made to induce gonad development in any group studied, thus limiting artificial crosses to those in which individuals of two or more groups from the natural population were found ripe at the same time, or to those involving males of early spawning species held over in the laboratory.

Experimental crossing, particularly in environmentally plastic species such as whitefishes, need not and often does not yield offspring similar to those produced under natural conditions. In an attempt to circumvent this difficulty, control crosses of known pure parentage were made.

Difficulty was often experienced in obtaining desired combinations of ripe fish and it was rarely possible to establish ova viability controls by making both homo- and heterospecific crosses from the same female. For this reason, along with improper controls on incubation temperature and crowding, due to limited facilities, success of crosses is reported in relative terms.

During the 1969-1970 and 1970-1971 spawning seasons, no special attempt was made to collect ripe P. spilonotus (large form). At this time, P. spilonotus (large form) was thought to be either of hybrid origin or large individuals of P. spilonotus as described by Snyder (1919). Trawl and gill-net collections indicated that they were not abundant and morphological findings suggested that they were distinct from P. spilonotus (small form). In early December, 1971, preliminary examination of successful crosses revealed that the identity of this group was not elucidated by any known hybrid. A concentrated effort was made at this time to collect spawning fish, but all P. spilonotus (large form) collected were in post-spawning condition. Ripe specimens of P. spilonotus (large form) were not collected until late November, 1972.

Methods

Ripe adult fish for homo- and heterospecific crosses were collected by gill net during their respective spawning runs. Upon removal from the nets, spawners were transferred to a large container of lake water and with few exceptions, transported to the laboratory at Utah State University where the various crosses were attempted.

Water from the transporting containers (≃ 4 C) was used as a temperature bath for shallow metal pans into which eggs and milt were stripped. Pans were gently rotated for approximately one minute before adding a small amount of dechlorinated tap water at 4 C. After 8-10 minutes, eggs were rinsed to remove seminal fluid and transferred to egg trays. Dechlorinated water was used in this operation to prevent sperm of unknown origin from being introduced.

In attempting several hybrid crosses and a few pure crosses, only spawned-out males were available. In such instances, testes of several males were maserated in an attempt to obtain viable sperm. Efforts to alleviate this problem were made by collecting ripe males of early spawning species and maintaining them in the laboratory, at or near 0 C.

Eggs were incubated in floating egg trays made of redwood frames with aluminum screen bottoms. Tray size varied considerably and no specific number of eggs to area of tray ratio was followed. In general, enough eggs were placed in the trays to nearly cover the bottom. Trays were floated in temperature controlled aquaria or min-o-cool units. Recording thermometers were unavailable for most units, thus temperature was taken manually three times daily with a centigrade thermometer. Trays were kept from direct light and were usually covered with black plastic. Dead eggs were picked regularly to avoid spread of fungus; eggs were never chemically treated.

Progeny of artificial crosses were placed into rectangular plastic utility boxes (30 x 17 x 9 cm or 40 x 27 x 15 cm) soon after hatching. Boxes were floated in the water bath in which the eggs were incubated by securing a strip of styrofoam to each end. To allow for water circulation, a 4 x 8 cm hole was cut in each side of the containers, near the top. These openings were covered with small mesh plastic screen. Each container was equipped with an air stone and water from the bath was continually air-lifted into the containers to maintain circulation.

Soon after hatching, a feeding program consisting of a diet of brine shrimp (Artemia sp.) nauplii, fed twice daily, was begun. After 6-8 weeks on this diet, a small amount of commercial trout starter was offered several times daily, in addition to the routine brine shrimp

feedings. The quantity of dry food offered was gradually increased, and after an additional 8 weeks, most fish were readily taking the dry diet. During the fifth month, transfer to a total dry food diet was accomplished by a gradual reduction in the amount of brine shrimp fed. If dry food was not offered within the first three months after hatching, the success of conversion to this diet was poor, usually resulting in 50 percent or greater mortality.

Near the beginning of the diet transformation period, fish were moved to a series of rectangular fiberglass troughs, each divided lengthwise into two sections, with each section divided into one to four compartments. Troughs were supplied with a continuous flow of dechlorinated water at a rate of 1.2 liters per minute, maintaining a temperature of 13.3 C (56 F). Water entered the troughs through vertical pipes and flowed down cylindrical aluminum screens or baffled aluminum pipes. This provided for increased exposure of water to air, thus reducing the concentration of supersaturated gases (primarily nitrogen) in the water and minimizing problems with gas-bubble disease. After approximately one year in the troughs, fish were distributed among 17, 250 liter (66 gal) aquaria, to allow for better growth and to free troughs for the current year's fry. Aquaria were supplied with a continuous flow of aerated dechlorinated tap water.

In response to growth of fish during the first year and subsequent years, food size was increased as appropriate from 595 microns to 2.83 mm (U.S. Series Sieve Opening) as supplied by Moore-Clark Company.

Table 7. Artificial crosses among members of the Bear Lake Prosopium complex and P. williamsoni, Logan River. A: P. abyssicola, S: P. spilonotus (small form), S (lg): P. spilonotus (large form), G: P. gemmiferum, W: P. williamsoni.

Cross[c]	Date	Mean Incubation Temperature (C°)	Duration of Hatching (days)[a]	Relative Fertilization Success[b]
A x A	2-21-70	5.4	60 - 93	Excellent
A x A	3-7-70	5.4	64 - 73	Excellent
A x G	3-7-70	5.4	59 - 73	Excellent
W x W	12-10-70	4.2	76 - 95	Excellent
W x W	12-10-70	4.2	---	None
W x S	12-10-70	4.2	76 - 89	Excellent
W x S	12-10-70	4.2	71 - 92	Excellent
W x G	12-10-70	4.2	90 - 95	Very Poor
S x G	12-22-70	4.0	76 - 88	Excellent
S x G	12-22-70	4.0	---	None
S x S	12-22-70	4.0	---	None
S x S	12-22-70	4.0	---	None
S x S	12-24-70	4.0	74 - 85	Excellent
S x S	12-24-70	4.0	74 - 85	Good
S x S	12-24-70	4.0	76 - 86	Excellent
S x S	12-24-70	4.0	76 - 82	Poor
S x S	12-24-70	4.0	---	None
S x S	12-24-70	4.0	---	None
S x W	12-24-70	4.0	85 - 91	Poor
S x W	12-24-70	4.0	---	None
S x G	12-30-70	4.0	81 - 93	Good
S x G	12-30-70	4.0	---	None
S x S	12-31-70	4.0	---	None
S x S	12-31-70	4.0	---	None
G x G	1-17-71	3.7	79 - 88	Fair

[a] Number of days after fertilization to commencement and terminus of hatching.

[b] Excellent > 80%; Good, 60-80%; Fair, 30-60%; Poor < 30%.

[c] Female listed first.

Table 7. Continued

Cross	Date	Mean Incubation Temperature (C°)	Duration of Hatching (days)[a]	Relative Fertilization Success[b]
G x S	1-17-71	3.7	---	None
G x W	1-17-71	3.7	---	None
A x G	2-11-71	3.7	---	None
A x G	3-5-71	3.7	---	None
A x A	3-5-71	3.7	67 - 75	Excellent
A x S	3-5-71	3.7	---	None
A x A	3-9-71	4.0	65 - 71	Good
A x G	3-9-71	4.0	62 - 70	Poor
A x A	3-18-71	4.0	63 - 68	Fair
A x G	3-18-71	4.0	64 - 79	Excellent
A x A	3-22-71	4.0	58 - 76	Good
S x S	12-17-71	4.4	88 - 125	Excellent
S x S	12-17-71	4.4	93 - 126	Good
S x W	12-17-71	4.4	93 - 134	Excellent
S x G	12-17-71	4.4	94 - 105	Excellent
S x A	12-17-71	4.4	---	None
S x S (lg)	12-17-71	4.4	102 - 105	Very Poor
S (lg) x S (lg)	11-24-72	3.9	76 - 94	Good
S (lg) x S	11-24-72	3.9	80 - 95	Excellent
S (lg) x S (lg)	11-26-72	3.9	---	Good
S (lg) x W	11-28-72	3.9	76 - 104	Excellent
S (lg) x S (lg)	12-6-72	3.9	79 - 98	Excellent
S (lg) x S	12-6-72	3.9	82 - 99	Good
S x S	12-6-72	3.9	79 - 90	Excellent
S x S (lg)	12-6-72	3.9	82 - 98	Excellent

[a]Number of days after fertilization to commencement and terminus of hatching.

[b]Excellent > 80%; Good, 60-80%; Fair, 30-60%; Poor < 30%.

Results and Discussion

Hybridization success

A total of 50 artificial crosses was made during the period February, 1970 through December, 1972. Crosses attempted and their relative success are summarized in Table 7. Unless otherwise noted, the female is listed first in all crosses.

During the 1969-1970 season, artificial crosses were limited to those involving P. abyssicola females. Ripe P. abyssicola were never abundant in collections but a sufficient number of ripe specimens was obtained to make three crosses. Two crosses were homospecific matings and the third was a cross with a ripe male P. gemmiferum (Table 7). No ripe P. spilonotus (small or large form) were found. Females used in these crosses had freely running ova and fertilization in each instance was high (estimated greater than 90%); mortality to hatching was negligible. A portion of the progeny from these crosses was used in morphological comparisons and the remainder, three years old at this writing, were maintained in the laboratory for further examination.

During the 1970-1971 spawning season, 33 artificial crosses were made (Table 7). Slight temporal overlap of ripe male P. spilonotus (small form) and ripe male P. gemmiferum with the spawning of P. williamsoni in the Logan River made interspecific crosses possible. Female P. williamsoni were crossed with male P. williamsoni, P. spilonotus (small form), and P. gemmiferum. Fertilization success of P. williamsoni x P. williamsoni and P. williamsoni x P. spilonotus (small form) crosses was quite high (approximately 80%). However, the P. williamsoni x

P. gemmiferum cross showed nearly total inviability. After 10 days only two eggs of approximately 1500 showed evidence of development. Eggs used in this cross were from the female used in the successful pure parental cross. Therefore, the poor fertilization success was attributed to either the quality of sperm or to genetic incompatibility. Although the male P. gemmiferum used in this cross was not "running" ripe, milt was extruded when pressure was applied to the abdomen. Each of the two P. williamsoni x P. gemmiferum hybrids hatched but neither survived beyond the larval stage.

High embryo mortality was experienced in all P. williamsoni crosses and all eggs of one pure cross died. Mortality apparently resulted from insufficient oxygen due to crowding, and subsequent infestation of fungus. No treatment was attempted and despite high mortality, sufficient numbers of eggs successfully hatched and progeny were cultured. Some were used in morphological comparisons and a portion were maintained in the laboratory for further study.

Crosses involving female P. spilonotus (small form) consisted of 10 matings with male P. spilonotus (small form), three with male P. gemmiferum, and two with male P. williamsoni. Success of crosses varied from zero to excellent. Total inviability of four pure P. spilonotus (small form) crosses points to the fact that one must be careful in judging the results of crosses (when no control crosses are possible) in that reduced fertility may well be a function of the quality of the ova or sperm rather than genetic incompatibility. In each case of reduced or zero fertilization the female donor was not fully ripe and an abnormally large amount of pressure was necessary to extrude eggs. The remaining pure parental crosses and three of the four P. spilonotus

(small form) x P. gemmiferum crosses were successful. Maximum fertilization success between P. spilonotus (small form) and P. gemmiferum was comparable to that observed between P. abyssicola and P. gemmiferum.

One P. spilonotus (small form) x P. williamsoni cross was totally unsuccessful while a second cross was of marginal success. The male P. williamsoni used in these matings were held in the laboratory for several weeks prior to making the crosses, and only a small amount of milt was extruded by applying abdominal pressure. Testes were therefore dissected out and maserated to release sperm; microscopic examination revealed good sperm motility. None of the progeny of this parentage survived to a size large enough for morphological comparison.

Three crosses with female P. gemmiferum were attempted. The pure cross was of fair success while the hybrid crosses with male P. spilonotus (small form) and P. williamsoni were totally unsuccessful. In each of the latter two crosses the males, which had been held in the laboratory, were spawned out and the testes were dissected out and maserated in an attempt to release viable sperm. Prosopium gemmiferum progeny were successfully cultured in the laboratory for about six months but were all lost due to a gill fungus infestation.

A total of nine crosses involving female P. abyssicola were made in 1971. Eight of these were the same as those made during the 1970 spawning period and similar results were obtained. In addition, one P. abyssicola x P. spilonotus (small form) cross was attempted. The testes of four spawned out P. spilonotus (small form) males were maserated to provide sperm; no eggs were fertilized.

During the 1971-1972 spawning seasons, crosses were confined to various combinations with P. spilonotus (small form) females (Table 7).

Of the six crosses attempted, two pure P. spilonotus (small form) matings and a P. spilonotus (small form) x P. gemmiferum mating resulted in similar degrees of success to those reported earlier.

A P. spilonotus (small form) x P. williamsoni cross, however, produced strikingly different results from those obtained in previous attempts. This cross proved to be highly viable and fertilization was in excess of 80 percent. This is in contrast to approximately 10 percent fertilization in an earlier cross. The male P. williamsoni which had been held in the laboratory for several weeks, was in prime spawning condition and milt freely flowed when a small amount of abdominal pressure was applied.

The two remaining crosses had not previously been attempted. No viable ova resulted from a P. spilonotus (small form) x P. abyssicola cross. The male P. abyssicola was not yet in spawning condition, and no milt was extruded when pressure was applied to the abdomen. The testes were dissected out and maserated to make the cross; microscopic examination of sperm revealed good motility. Results of a P. spilonotus (small form) x P. spilonotus (large form) cross were extremely poor. Of approximately 800 eggs, only 12 were fertilized. The male used in this cross was in post-spawning condition, but sperm extruded from maserated testes were motile.

Artificial crosses made in November and December, 1972 were comprised of three pure P. spilonotus (large form) matings, one P. spilonotus (large form) x P. williamsoni mating, two P. spilonotus (large form) x P. spilonotus (small form) matings and one reciprocal of this cross, and one pure P. spilonotus (small form) mating (Table 7). Success was high in all crosses, and fertilization was usually in excess of 80

percent. Virtually no embryo mortality occurred after the initial unfertilized eggs were removed. One exception to this was a pure P. spilonotus (large form) cross which developed normally until hatching commenced, after which all embryos died within two days. Oxygen deficiency due to crowding of embryos in egg trays (2-3 deep) was probably responsible for this large mortality. Progeny of these crosses were too small to use in morphological comparisons at this writing.

Of the hybrid crosses attempted, no indication of genetic incompatibility was observed with the possible exception of P. williamsoni x P. gemmiferum (Table 8). Lack of success of this cross could as well have been due to condition of the sex products of the male P. gemmiferum donors. All experimental hybridization attempts involving simultaneously ripe specimens of two groups showed maximum fertilization success equaling that of pure crosses.

Morphological comparisons

Nineteen morphological characters were used in the biometric examination of artificially produced progeny of inter- and intraspecific crosses (Table 9). Characters were selected on the basis of their utility in separating two or more parental forms.

Natural and cultured pure forms.[3] Koelz (1929) described the morphology of known C. clupeaformis which were cultured and reared at the New York Aquarium. Body parts showed great modification in all specimens and no cultured fish closely resembled any whitefish taken in the Great Lakes. The aberrant morphology of these specimens was no doubt a manifestation of physiological responses to different evironmental conditions.

[3]Size range of cultured fish: P. spilonotus (small form), 90.0-123.5 mm SL; P. abyssicola, 94.0-149.0 mm SL.

Table 8. Attempted hybrid crosses and maximum relative success.

Female		Male	Success
P. williamsoni	X	P. spilonotus (small form)	Excellent*
P. williamsoni	X	P. gemmiferum	Very poor
P. spilonotus (small form)	X	P. gemmiferum	Excellent
P. spilonotus (small form)	X	P. williamsoni	Excellent
P. spilonotus (small form)	X	P. abyssicola	None
P. spilonotus (small form)	X	P. spilonotus (large form)	Excellent
P. spilonotus (large form)	X	P. spilonotus (small form)	Excellent
P. spilonotus (large form)	X	P. williamsoni	Excellent
P. gemmiferum	X	P. spilonotus (small form)	None
P. gemmiferum	X	P. williamsoni	None
P. abyssicola	X	P. gemmiferum	Excellent
P. abyssicola	X	P. spilonotus (small form)	None

*Excellent = > 80%; Very poor <1%.

To examine the effect of laboratory rearing and/or size upon morphology, progeny of pure control crosses were compared with their respective group from the lake population. As noted earlier, growth rate of body parts changes with increased size, often negating reliability of making comparisons among different size groups of fish. This is well evidenced when one compares means of proportional data of the small-sized, cultured P. spilonotus (small form) and P. abyssicola with their larger-sized counterparts (See Appendix B and Tables 10-14).

Table 9. Summary of morphological relationships of cultured homo - and heterospecific crosses.

Character	*P. abyssicola* (Mean) Range	SD	*P. abyssicola* X *P. gemmiferum* (Mean) Range	SD	*P. spilonotus* (small form) X *P. gemmiferum* (Mean) Range	SD	*P. spilonotus* (small form) (Mean) Range	SD	*P. williamsoni* X *P. spilonotus* (small form) (Mean) Range	SD	*P. williamsoni* (Mean) Range	SD
Dorsal base length	(111) 98-122	.006	(102) 92-115	.006	(101) 88-110	.005	(102) 96-111	.004	(113) 102-124	.005	(126) 116-134	.006
Adipose base length	(84) 68-93	.006	(80) 69-94	.005	(53) 46-61	.004	(74) 65-84	.006	(79) 71-97	.005	(91) 75-100	.007
Adipose height	(101) 86-116	.007	(98) 83-110	.005	(72) 64-82	.004	(92) 74-102	.006	(100) 90-128	.007	(109) 88-121	.010
Pelvic to anal distance	(254) 233-266	.008	(233) 209-254	.010	(237) 215-261	.011	(251) 231-267	.009	(246) 233-280	.010	(250) 240-260	.006
Head length	(253) 220-278	.012	(237) 220-267	.011	(260) 239-286	.009	(250) 232-264	.008	(252) 241-265	.006	(244) 226-260	.010
Postorbital head length	(125) 99-140	.008	(119) 107-134	.006	(133) 120-147	.005	(125) 116-134	.004	(129) 121-139	.005	(129) 118-144	.009
Maxillary length	(53) 42-60	.005	(51) 36-63	.006	(67) 57-72	.003	(59) 54-63	.003	(59) 51-65	.003	(53) 47-58	.004
Interorbital width	(55) 47-63	.003	(54) 48-58	.003	(58) 52-62	.003	(58) 52-65	.003	(63) 51-68	.004	(60) 50-66	.005
Eye diameter	(57) 47-69	.005	(53) 45-63	.004	(55) 49-65	.003	(60) 52-67	.004	(60) 53-67	.003	(53) 46-59	.004
Gill-raker length	(17) 14-20	.002	(25) 20-29	.002	(26) 23-29	.001	(17) 13-19	.002	(15) 13-19	.002	(14) 12-17	.002
Scales in lateral line	(74.5) 69-82	3.467	(78.4) 73-83	2.167	(84.6) 80-91	2.700	(86.7) 79-92	3.118	(85.1) 78-90	2.963	(84.8) 80-91	3.539

Table 9. Continued

Character	*P. abyssicola* (Mean) Range	SD	*P. abyssicola* X *P. gemmiferum* (Mean) Range	SD	*P. spilonotus* (small form) X *P. gemmiferum* (Mean) Range	SD	*P. spilonotus* (small form) (Mean) Range	SD	*P. williamsoni* X *P. spilonotus* (small form) (Mean) Range	SD	*P. williamsoni* (Mean) Range	SD
Scales above lateral line	(8.6) 7-10	.651	(8.6) 8-9	.490	(8.7) 8-9	.449	(9.1) 8-10	.403	(9.1) 9-10	.307	(9.6) 9-11	.650
Scales below lateral line	(6.5) 5-8	.853	(6.6) 6-7	.490	(6.4) 6-7	.502	(6.8) 6-8	.461	(7.0) 6-8	.280	(7.2) 7-8	.376
Anterior gill-rakers (upper limb)	(8.3) 7-10	.684	(11.9) 10-14	.834	(12.0) 10-13	.851	(8.1) 7-9	.571	(8.3) 7-10	.686	(8.5) 7-9	.660
Anterior gill-rakers (lower limb)	(13.1) 12-14	.718	(18.9) 17-21	.982	(18.8) 17.22	1.100	(12.7) 10-14	.952	(12.7) 11-15	.898	(13.2) 12-14	.599
Total anterior gill-rakers	(21.5) 20-24	1.010	(30.8) 28-33	1.391	(30.8) 28-34	1.358	(20.8) 17-23	1.262	(20.9) 19-24	1.213	(21.7) 19-23	1.109
Posterior gill-rakers (upper limb)	(6.9) 5-8	.802	(9.7) 8-12	.736	(10.6) 9-13	.808	(6.2) 5-7	.484	(6.1) 5-7	.641	(6.5) 6-8	.660
Posterior gill-rakers (lower limb)	(11.3) 10-14	.968	(17.2) 15-20	1.104	(17.5) 16-20	1.002	(10.7) 9-13	.952	(10.9) 10-12	.788	(10.9) 10-13	.862
Total posterior gill-rakers	(18.3) 16-21	1.152	(26.9) 24-30	1.392	(28.1) 26-32	1.300	(16.9) 15-19	1.062	(17.0) 15-19	1.100	(17.5) 16-19	.877

Means of cultured specimens were higher in seven of 10 morphometric comparisons between the two groups of P. spilonotus (small form) and eight of 10 comparisons between the two groups of P. abyssicola. Both groups of cultured fish had lower pelvic to anal distance ratios than larger sized natural specimens and cultured P. spilonotus (small form) had a lower mean for dorsal base length. Statistical comparison (t-test, .05) between natural and cultured specimens of P. spilonotus (small form) and of P. abyssicola showed them to be significantly different in all morphometric comparisons except interorbital width.

Meristic characters, for the most part, are independent of the influence of growth. However, they are often influenced by environmental factors. Taning (1952), Hempel and Blaxter (1961), and Wallace (1973) have shown that temperature differences during embryonic development may significantly alter meristic characters. Fingerlings of Coregonus, artificially hatched, and reared in a pond, showed such marked differences in scale number from the natural population that Svardson (1952, 1970) suggested this as a method of mass-marking small fish.

Contrary to most morphological characters of coregonines, gill-rakers tend to be genetically stable (Svardson, 1965, 1970) and have thus been of traditional importance in whitefish taxonomy. Gill-raker number does, however, gradually increase between fry and adult stages of development (Svardson, 1950, 1952, 1965; Lindroth, 1957; Lindstrom, 1962) with the age at which full adult number is achieved, differing among species.

Statistical comparison (t-test, .05) of meristic characters between cultured and natural specimens of both P. spilonotus (small form) and P. abyssicola revealed no significant differences between groups in

four of nine comparisons: scales below lateral line, anterior gill-rakers (lower limb), total anterior gill-rakers and posterior gill-rakers (lower limb). Difference in scales below lateral line and in posterior gill-rakers (lower limb) was non-significant between the two groups of P. abyssicola.

Of the meristic characters examined, lateral line scales showed the most pronounced difference between natural and cultured specimens. Prosopium abyssicola and P. spilonotus (small form) from the natural population had means and ranges of 71.0 (65-79) and 82.7 (76-89) respectively as compared to means and ranges of 74.5 (69-82) and 86.7 (79-92) for cultured specimens of these groups. Number of gill-rakers was essentially unchanged or slightly lower in cultured specimens of both groups.

Unlike the findings of Koelz (1929), artificially reared progeny of pure crosses of P. spilonotus (small form) and P. abyssicola did not markedly differ in general appearance from their respective counterparts in the natural population.

Known and suspected P. gemmiferum hybrids. In general appearance, known hybrids of P. abyssicola x P. gemmiferum (A x G) origin were intermediate between parental forms while P. spilonotus (small form) x P. gemmiferum (S x G) hybrids[4] more closely resembled P. gemmiferum (Figure 21). Qualitatively, adipose fins were markedly different in size between the two groups with A x G hybrids having a long fleshy adipose compared to the much smaller, fragile appearing adipose of S x G hybrids. Head morphology varied considerably but characteristically S x G hybrids

[4]Size range of cultured hybrids: A x G, 95.5-176.0 mm SL; S x G, 101.0-143.5 mm SL.

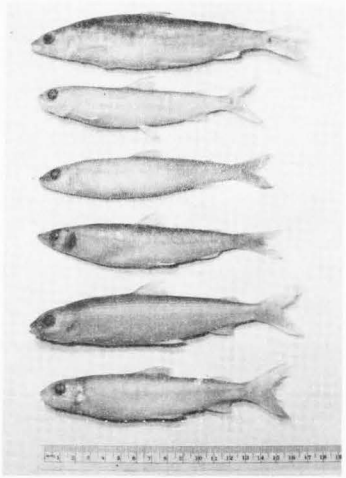

Figure 21. Comparison of P. gemmiferum hybrids with parental forms.

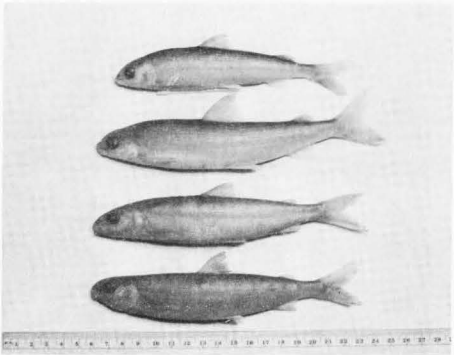

Figure 22. Comparison of cultured P. williamsoni and W x S hybrids with P. spilonotus (small form) and P. spilonotus (large form) from the natural population.

had a more pointed, cisco-like head profile while the head profile of A x G hybrids was more curved.

The most consistent distinction between head characteristics was the position of the lower jaw. All A x G hybrids examined had a superior lower jaw compared to the terminal or slightly subterminal jaw of S x G hybrids. The degree of projection of the lower jaw among A x G hybrids varied from being slightly superior to protruding as much as 2.5 mm in one specimen (157 mm SL).

Jaw deformaties were present in 52.7 percent of 74 A x G hybrids as opposed to 8.5 percent of 82 S x G hybrids examined. Deformaties among A x G hybrids appeared to be genetically induced as evidenced by the occurrence of only one (.95 percent) jaw malformation among 105 pure P. abyssicola progeny originating from the same female used in the A x G cross. Each group was cultured under similar conditions and neither group was treated chemically. No jaw deformations were observed in cultured P. spilonotus (small form).

When small, both groups were silvery in appearance with darker pigmentation and distinct spotting along the dorsal surface, extending dorsoventrally to the lateral line. Spots were absent in A x G hybrids by the time they reached 150 mm SL but specimens of S x G hybrids of similar size retained some spotting, particularly along the dorsal surface. Both groups were intermediate in robustness between parental forms.

Based on general appearance, the five presumed P. gemmiferum-like hybrids collected from the natural population most closely resembled S x G hybrids. This was also true of the three presumed hybrids reported by Sigler and Miller (1963) (UMMZ 179265). All natural hybrids

had terminal or slightly subterminal lower jaws, small adipose fins and head profiles distinctly P. gemmiferum-like. Morphological data including maxillary length, scales along lateral line, scales above and below lateral line, scales around peduncle and scales around body from the three museum specimens were combined and reported with presumed hybrid data collected in the present study.

Reliable biometric comparisons between parental forms from the natural population and known hybrids cultured in the laboratory were difficult. Ideally, comparisons between P. gemmiferum-like hybrids and presumed parental forms from the lake population could be related to similar comparisons among known pure and hybrid crosses cultured in the laboratory. In this way obvious differences (Appendix B and Tables 10-14) associated with allometry and/or environmental phenoplasticity related to size differences and laboratory culture could be segregated and placed in proper perspective. In the present study, however, such comparisons were not possible in evaluating P. gemmiferum hybrids, since no cultured P. gemmiferum survived to a large enough size to be included in morphological studies.

Assuming that most morphologic characters would be intermediate in hybrids, a predicted value, midway between means of natural P. gemmiferum--P. spilonotus (small form) and P. gemmiferum--P. abyssicola, was calculated for each character and compared with mean values of P. gemmiferum-like hybrids. Most predicted values were found to be similar between the two groups of presumed parents. Six of nine morphometric comparisons were either identical to presumed hybrids or the means of presumed hybrids were intermediate between those of the two sets of suspected parents. Mean head length and pelvic to anal distance between

P. abyssicola and P. gemmiferum were more like presumed P. gemmiferum hybrids while lake hybrid maxillary length was closer to predicted mean maxillary length of P. spilonotus (small form)--P. gemmiferum. Scale characters and gill-raker characters were most closely associated with predicted A x G hybrids and S x G hybrids respectively. Such comparisons were of little value in predicting parental origin of P. gemmiferum-like lake hybrids.

Comparisons between the two groups of known P. gemmiferum hybrids show important distinctions (Table 9). Adipose dimensions were markedly smaller in S x G hybrids (Tables 10 and 11) while dimensions of maxillary length, head length and postorbital head length had higher means than A x G hybrids (Tables 12-14). P. gemmiferum-like fish from the natural population were intermediate between P. gemmiferum and either P. spilonotus (small form) or P. abyssicola concerning these characters.

If the assumption is made that relative growth relationships between natural and cultured forms remain reasonably constant (i.e., higher or lower mean for a character of a group from the natural population would also be higher or lower for cultured specimens of the same form) some speculation can be made concerning possible relatedness. Adipose base length and adipose height of presumed P. gemmiferum hybrids had lower means than natural P. spilonotus (small form) or P. abyssicola, while mean maxillary length, head length and postorbital head length was higher than in either of these forms (Tables 10-14). Among cultured specimens, S x G hybrids adhered to this pattern while A x G hybrids did not. S x G hybrids had much smaller adipose dimensions and somewhat larger maxillary length, head length and postorbital head length than cultured P. spilonotus (small form) or P. abyssicola while A x G hybrids

Table 10. Comparison of adipose base lengths among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	44-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-100	Mean
P. spilonotus (small form)	102		3	18	35	28	13	4	1				64
P. spilonotus (large form)	27		4	7	11	5							60
P. species	108	2	11	27	44	17	7						61
P. abyssicola					9	32	45	23	8	2	1		72
P. gemmiferum	21	11	8	2									49
P. williamsoni	16					2	6	5	1	2			76
P. gemmiferum-like	5		1	3		1							58
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30					4	12	10	4				74
P. spilonotus (small form) X P. gemmiferum	41	10	18	9	4								53
P. abyssicola X P. gemmiferum	40					1	4	12	17	5	1		80
P. abyssicola	35							7	9	9	9		84
P. williamsoni	13							1	1	3	2	6	91
P. williamsoni X P. spilonotus (small form)	39						7	15	13	3		1	79

Table 11. Comparison of adipose heights among members of the Bear Lake *Prosopium* complex, *P. williamsoni* and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-111	111-114	115-119	Mean
P. spilonotus (small form)	102			5	26	36	19	14	1	1				83
P. spilonotus (large form)	27		1		3	10	8	5						84
P. species	108			7	34	36	24	6	1					81
P. abyssicola	120				1	13	33	37	24	10	1	1		92
P. gemmiferum	21	4	11	6										67
P. williamsoni	16						1	7	4	2		2		97
P. gemmiferum-like	5			2	2		1							77
Homo - and Heterospecific Crosses														
P. spilonotus (small form)	30			1		1	6	12	9	1				92
P. spilonotus (small form) X *P. gemmiferum*	41	1	8	24	7	1								72
P. abyssicola X *P. gemmiferum*	40					1	1	7	13	13	4	1		98
P. abyssicola	35						1	5	9	7	10	2	1	101
P. williamsoni							1		2	1	2	3	4	109
P. williamsoni X *P. spilonotus* (small form)	39							6	12	14	6	1		100

Table 12. Comparison of maxillary lengths among members of the Bear Lake *Prosopium* complex, *P. williamsoni* and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	75-80	81-85	Mean
P. spilonotus (small form)	102			19	73	10						52
P. spilonotus (large form)	27							8	12	5	2	73
P. species	108				2	19	61	21	5			63
P. abyssicola	120		47	67	6							46
P. gemmiferum	21						8	12	1			66
P. williamsoni	16	1	10	5								45
P. gemmiferum-like	8					5	3					60
Homo - and Heterospecific Crosses												
P. spilonotus (small form)	30				2	19	9					59
P. spilonotus (small form) X *P. gemmiferum*	41					3	10	21	7			67
P. abyssicola X *P. gemmiferum*	40	3	4	10	18	4	1					51
P. abyssicola	35		2	9	11	13						53
P. williamsoni	13			4	6	3						53
P. williamsoni X *P. spilonotus* (small form)	39				4	24	11					59

Table 13. Comparison of head lengths among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	191-200	201-210	211-220	221-230	231-240	241-250	251-260	261-270	271-280	281-290	Mean
P. spilonotus (small form)	102		1	23	64	13	1					225
P. spilonotus (large form)	27						2	11	11	3		261
P. species	108				2	12	58	31	5			248
P. abyssicola	120			5	39	61	14	1				233
P. gemmiferum	21					1	8	10	2			249
P. williamsoni	16	1	3	6	4	2						216
P. gemmiferum-like	5					4		1				240
Homo - and Heterospecific Crosses												
P. spilonotus (small form)	30					3	12	11	4			250
P. spilonotus (small form) X P. gemmiferum	41					1	5	15	17	2	1	260
P. abyssicola X P. gemmiferum	40			1	11	14	10	3	1			237
P. abyssicola	35			1	1	2	11	11	6	3		253
P. williamsoni	13				1	2	8	2				244
P. williamsoni X P. spilonotus (small form)	39						17	18	4			252

Table 14. Comparison of postorbital head lengths among members of the Bear Lake *Prosopium* complex, *P. williamsoni* and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	99-104	105-110	111-116	117-122	123-128	129-134	135-140	141-146	147-152	Mean
P. spilonotus (small form)	102	2	21	60	17	2					113
P. spilonotus (large form)	27					3	17	6	1		132
P. species	108			7	29	53	17	2			124
P. abyssicola	120	1	4	41	53	21					118
P. gemmiferum	21				5	11	5				123
P. williamsoni	16			5	6	5					119
P. gemmiferum-like	5			1	3	1					121
Homo - and Heterospecific Crosses											
P. spilonotus (small form)	30			1	6	19	4				125
P. spilonotus (small form) X *P. gemmiferum*	41				2	4	21	12	1	1	133
P. abyssicola X *P. gemmiferum*	40		2	9	17	9	3				119
P. abyssicola	35	1		3	8	10	10	3			125
P. williamsoni	13				3	5	1	2	2		129
P. williamsoni X *P. spilonotus* (small form)	39				6	13	17	3			129

had larger and smaller means for these characters, respectively. With respect to these characters, known S x G hybrids have attributes most closely associated with P. gemmiferum-like hybrids from the lake population.

As previously noted, meristic characters may be altered by environmental influences, particularly temperature. Such influence was indicated in scale counts of cultured specimens by the fact that the means and ranges of cultured P. spilonotus (small form) and P. abyssicola were higher than their counterparts in the lake population (Tables 3 and 9). The degree of difference between natural and cultured specimens of these forms is approximately equal, however. Since A x G and S x G hybrids were incubated in the same water baths as pure crosses of P. abyssicola and P. spilonotus (small form), environmental influence is assumed to be equivalent.

Scales above and below lateral line showed total overlap between cultured hybrids (Table 9). Scales along the lateral line, however, were quite divergent between known P. gemmiferum hybrids with a mean of 84.6 for S x G and 78.4 for A x G. Comparing these means with mean number of scales in the lateral line of natural P. gemmiferum-like hybrids (73.5) (mentally adjusting for assumed environmental influence) showed known A x G hybrids to be similar to presumed hybrids with respect to this character.

Number of gill-rakers provided the most conclusive evidence that presumed P. gemmiferum hybrids were indeed hybrids and originate from hybridization between P. gemmiferum and either P. spilonotus (small form) or P. abyssicola. Unfortunately, however, gill-raker structure and number is so similar between P. abyssicola and P. spilonotus (small

form) that the intermediacy produced in hybrids resulting from crosses with P. gemmiferum is virtually the same and therefore of little use in relating known hybrids to presumed P. gemmiferum hybrids from the natural population.

Pyloric caeca count was shown to be one of the more important characters in separating P. spilonotus (small form) and P. abyssicola (Table 3). Most cultured specimens, however, were too small for making accurate caeca counts and this character was not included in the general morphological analysis.

Caeca counts on samples of four each of A x G and S x G hybrids had means and ranges of 77.8 (67-87) and 94.7 (87-99) respectively. Three P. gemmiferum-like hybrids had a mean of 72.0 and range of 63-78. As with lateral line scales, known A x G hybrids appear most closely allied to P. gemmiferum-like hybrids from the natural population. In examining the range of caeca counts for P. abyssicola (53-96), P. spilonotus (small form) (87-153) and P. gemmiferum (46-95) it is noted that ranges of all three groups are somewhat overlapping. If parents of crosses were extreme in caeca number, hybrids of S x G origin could possibly be within the range observed for P. gemmiferum-like hybrids.

The predictive model generated by discriminant function analysis of P. abyssicola, P. gemmiferum, P. spilonotus (small form), P. species and P. williamsoni (based on 12 morphological characters, Table 4) was used in predicting the group to which presumed P. gemmiferum hybrids were most closely related. Results of the analysis showed each of the presumed hybrids to be morphologically most closely allied to P. abyssicola. High chi-square values, however, indicated that hybrids were not closely related to any of the above groups.

In examining means of the 12 characters used in the analysis, P. gemmiferum-like hybrids were most like P. abyssicola in five comparisons, P. gemmiferum in six comparisons and P. spilonotus (small form) in one comparison. These data strongly suggest that P. gemmiferum-like hybrids originate from A x G parentage.

Known hybrids were not analyzed by discriminant function analysis because of allometric and/or environmentally induced differences between cultured specimens and specimens from the lake population. A cluster analysis based on 21 characters, not reported in detail here, was used for predicting group membership of spawning P. spilonotus (small form) and P. abyssicola and to examine the relationship of two P. gemmiferum-like hybrids to these groups. Results of this analysis showed P. gemmiferum-like hybrids clustering with P. abyssicola, thus further supporting an A x G origin.

Biometric comparisons among known and presumed P. gemmiferum hybrids were not consistent in relating either of the known P. gemmiferum hybrids to the P. gemmiferum-like hybrids from the lake population. From the data available, no definitive statement can be made concerning the origin of P. gemmiferum-like hybrids except that they undoubtably are hybrids between P. gemmiferum and either P. spilonotus (small form) or P. abyssicola.

General appearance and morphometric characteristics indicate that P. gemmiferum-like hybrids are most closely related to S x G as was hypothesized by Sigler and Miller (1963). Meristic evidence and results of discriminant function and cluster analyses, however, were not consistent with this observation.

The possibility of representatives of both S x G and A x G hybrids being present in the sample cannot be eliminated, although individual comparisons of the five presumed hybrids with known hybrids showed no consistent relationship of any one fish to one or the other group of known hybrids. An alternative hypothesis is that presumed hybrids have their origin from one or both reciprocal crosses (G x S or G x A) which were not successful in the laboratory. Although no ripe male P. spilonotus (small form) or P. abyssicola were collected during the spawning period of P. gemmiferum, it seems highly probably that some ripe male P. spilonotus (small form) would be available for crossing. The chance of hybridization between female P. gemmiferum and male P. abyssicola is considered less since spawning activity of P. abyssicola is restricted to deep water (> 15 m; > 50 ft) while P. gemmiferum appears to spawn primarily (although not exclusively) over rocky shallows.

P. williamsoni x P. spilonotus (small form)--Parental forms. When small (< 120 mm SL) P. spilonotus (small form), P. williamsoni and their hybrids (W x S) were much alike in outward appearance (Figure 22). P. williamsoni had a somewhat more elongate adipose fin, proportionately smaller, more rounded and less deeply forked caudal fin and the body was more cylindrical than in P. spilonotus (small form). P. williamsoni often had a somewhat distinct hump immediately posterior to the head which was always absent in P. spilonotus (small form). W x S hybrids were intermediate in each of these characteristics. Spots along the dorsal surface, extending downward to the lateral line, were characteristic of each group although they were less distinct in P. williamsoni and occasionally absent by the time they were 120 mm SL. In life the pectoral and pelvic fins of W x S hybrids and P. williamsoni fingerlings

had a distinct golden-bronze cast. (This coloration was observed to be even more brightly displayed among natural P. williamsoni of similar size in the Logan River.) The head of P. williamsoni appeared smaller and more rounded while head profile of P. spilonotus (small form) presented a somewhat more pointed appearance. Hybrids were intermediate in head profile.

With further growth, the snout of W x S hybrids typically increased in length and became fleshy, presenting the "pug-nosed" appearance common to P. williamsoni. Spots were normally lost before hybrids reached 150 mm SL. The mouth, like that of parental forms, was subterminal in hybrids and no jaw deformaties were observed.

Morphometrically (Table 9), W x S hybrids (98.0-124.0 mm SL) were intermediate in dorsal base length, adipose base length, adipose height and gill-raker length when compared with pure parental crosses of P. spilonotus (small form) (90.0-123.4 mm SL) and P. williamsoni (102.0-147.0 mm SL). In contrast to these intermediate traits, however, other measured characters were more like one of the pure crosses or were higher or lower than either of these. In eye diameter, maxillary length and head length, hybrids were more like P. spilonotus (small form) while postorbital head length was like P. williamsoni. Interorbital width was larger in hybrids than in either pure cross while pelvic to anal distance was smaller.

Meristic characters of parental species showed extensive overlap and therefore were of little value in morphological comparisons of either pure or hybrid crosses (Table 3). Although the reciprocal of the W x S cross was highly successful, all but three progeny were lost, and these fish were too small to use in morphological comparisons.

P. williamsoni x P. spilonotus (small form)--P. spilonotus (large form). The major objective of making the W x S cross was to determine if these hybrids could explain the origin of the P. spilonotus (large form) group. The approach used in relating W x S hybrids to the P. spilonotus (large form) group was to compare pure crosses of P. spilonotus (small form) and P. williamsoni with W x S hybrids and relate these comparisons to morphological comparisons among P. spilonotus (small form), P. williamsoni and the immature segment of the P. spilonotus (large form) group, previously referred to as P. species (Table 15).

As discussed earlier, morphometric characters were most important in distinguishing between P. spilonotus (small form), P. williamsoni and P. spilonotus (large form). Of these forms, P. williamsoni was most distinctive having much larger adipose and dorsal fins and small maxillaries (Table 3). Dorsal base length, adipose base length and adipose height in hybrid W x S were intermediate between cultured P. spilonotus (small form) and cultured P. williamsoni (Table 15). In contrast, immature P. spilonotus (large form) were more like natural P. spilonotus (small form) in dorsal base length and adipose height and had a lower mean adipose base length than either P. spilonotus (small form) or P. williamsoni from the natural population. Mean maxillary length (a distinctive attribute of P. spilonotus (large form)) of W x S hybrids was identical to that of cultured P. spilonotus (small form) (Table 15) while mean maxillary length of P. spilonotus (large form) was much higher than in natural P. spilonotus (small form) or natural P. williamsoni. P. spilonotus (large form) also had higher mean head length, postorbital head length, and interorbital width than observed for natural occurring P. spilonotus (small form) or P. williamsoni. W x S

Table 15. Morphologic comparisons of means of cultured P. williamsoni x P. spilonotus (small form) hybrids with pure crosses of parental forms and with naturally occurring P. williamsoni, P. spilonotus (small form) and immature P. spilonotus (large form). S: P. spilonotus (small form), W: P. williamsoni, S(lg): P. spilonotus (large form).

	Cultured			Natural		
Character	S	W X S	W	S	S(lg) (P. species)	W
Dorsal base length	102	113	126	108	111	131
Adipose base length	74	79	91	64	61	76
Adipose height	92	100	109	83	81	97
Eye diameter	60	60	53	52	51	40
Maxillary length	59	59	53	52	63	45
Interorbital width	58	63	60	57	61	56
Postorbital head length	125	129	129	113	124	121
Head length	250	252	244	225	248	240
Gill-raker length	17	15	14	14	14	13
Pelvic to anal distance	251	246	250	271	252	253

Table 15. Continued

Character	Cultured S	Cultured W X S	Cultured W	Natural S	Natural S(lg) (P. species)	Natural W
Scales in lateral line	86.7	85.1	84.6	82.7	83.0	84.0
Scales above lateral line	9.1	9.1	9.6	9.5	9.8	10.1
Scales below lateral line	6.8	7.0	7.2	7.0	7.1	7.1
Anterior gill-rakers (upper limb)	8.1	8.3	8.5	8.7	9.0	8.9
Anterior gill-rakers (lower limb)	12.7	12.7	13.2	12.6	13.6	12.8
Total anterior gill-rakers	20.8	20.9	21.7	21.3	22.6	21.8
Posterior gill-rakers (upper limb)	6.2	6.1	6.5	6.7	7.3	7.9
Posterior gill-rakers (lower limb)	10.7	10.9	10.9	10.8	11.8	11.3
Total posterior gill-rakers	16.9	17.0	17.5	17.5	19.1	19.2

hybrids were more like cultured P. williamsoni in postorbital head length, more like cultured P. spilonotus (small form) in head length and had a slightly higher mean interorbital width than either of the cultured parental forms (Table 15). Eye diameter was like P. spilonotus (small form) in both W x S hybrids and P. spilonotus (large form). Meristic characters showed near total overlap between groups and therefore were of no utility in making comparisons (Table 15).

If the above comparisons are valid, morphological evidence strongly supports the rejection of the hypothesis that P. spilonotus (large form) have their origin from hybridization between P. williamsoni and P. spilonotus (small form). This conclusion is strengthened by circumstantial evidence concerning the possibilities of such a cross in Bear Lake.

As previously noted, no P. williamsoni were observed in the four years of field work associated with the present study. Furthermore, to the author's knowledge, no verification of the presence of this species in Bear Lake exists.

In Snyder's original description of the Bear Lake whitefishes (1919, p. 3) he stated that, with the exception of the Bonneville cisco, "the others are species of Coregonus, which is represented also by C. williamsoni, a common fish of the streams." It is not entirely clear if Snyder was referring to the presence of the mountain whitefish in Bear Lake or to the Bear River system. The next mention in the literature of this species in Bear Lake was that of McConnell et al. (1957, p. 53) who reported that the "Rocky Mountain whitefish is considered a rare migrant from Bear River." Sigler and Miller (1963, p. 162) described the mountain whitefish as being "scarce in the lake, only 7 specimens having been taken during the Bear Lake studies (5 years) by

McConnell, Clark and Sigler (1957), and it was unknown to the lake previously."

The identification of mountain whitefish reported by McConnell et al. (1957) was possibly in error. This is partially supported by the fact that Holt (1960) reported the omission from her study of a collection of presumed mountain whitefish from Bear Lake (supplied by McConnell) due to confusion with other species.

All evidence available casts considerable doubt on the presence of P. williamsoni in Bear Lake. If they do occur or have occurred there in the recent past, their numbers are/were apparently so small that it is virtually inconceivable that their hybrids could be the source of the P. spilonotus (large form) group.

In summary, hybridization studies among Bear Lake Prosopium and P. williamsoni from the Logan River provide no evidence that interspecific crosses are less successful than conspecific crosses, with the possible exception of P. williamsoni x P. gemmiferum. The origin of P. gemmiferum-like hybrids in the lake population was not consistently explained by morphological comparisons of known A x G and S x G hybrids; morphometric characters were more like S x G hybrids while meristic characters were more closely associated with A x G hybrids. Discriminant function and cluster analyses showed presumed hybrids to be morphologically most closely related to P. abyssicola from the natural population. Based on evidence available, no definitive statement can be made concerning the origin of P. gemmiferum-like hybrids except that they are hybrids among combinations of P. gemmiferum and either P. spilonotus (small form) or P. abyssicola. W x S hybrids were either intermediate between parental forms or were more like one or the other parent in morphology. Their

morphology does not explain the origin of the P. spilonotus (large form) group. It is unlikely that P. williamsoni is present in Bear Lake and therefore that such a cross could be possible.

ELECTROPHORETIC STUDIES

Introduction

Systematic evaluation based upon traditional morphological analysis has often fallen short of providing unequivocal evidence of relatedness among groups of organisms. In recent years, the need for diagnostic characters to supplement existing ones has provided stimulus for numerous studies involving "protein taxonomy."

Much genetic information is contained within the structure of the protein molecule (Tsuyuki and Roberts, 1965). The physical properties of proteins are eminently suited to provide diagnostic information at the molecular level since their structure is a direct translation of the genetic code of nucleic acids (Tsuyuki, Roberts, Lowes and Hadaway, 1968). Structural dismemberment of protein molecules to derive the amino acid sequence should yield the most useful information (Behnke, 1970). Methodology of structural analysis, however, is as yet laborious and not adaptable for rapid comparisons of large numbers of proteins on a wide scale (Tsuyuki et al., 1968). For this reason, the well established techniques of electrophoretic analysis, which take advantage of differing molecular charges among protein constituents, have been widely used and found to be of much value.

Numerous protein systems have been investigated in examining phylogenetic relationships of various groups of fishes. Serum proteins have been the most widely studied of the protein complexes (Chellevold, 1970). Their usefulness in establishing genetic relationships has been generally condemned because of pattern variability associated with the

physiological state of the organism (for review see Booke, 1964). Chellevold (1970), however, maintained that serum proteins are very reliable means of establishing genetic relationships when examined with high resolution techniques under carefully controlled laboratory conditions.

Skeletal muscle proteins have also been intensively examined and are found to provide information useful in classification at generic and higher taxonomic levels (Tsuyuki, Roberts, Vanstone and Markert, 1965; Tsuyuki and Roberts, 1966; Tsuyuki et al., 1968) and in most cases at the species level (Huntsman, 1966; Tsuyuki et al., 1968). In addition to often being species specific, muscle proteins are virtually unaffected by factors other than genetic (Tsuyuki and Roberts, 1965; Tsuyuki, Roberts and Vanstone, 1965). These proteins have also been useful in the diagnosis and genetic interpretation of hybrids (Aspinwall and Tsuyuki, 1968; Tsuyuki and Roberts, 1965; Paetz, 1972[1]). Intraspecies polymorphisms in muscle proteins have been reported (Tsuyuki et al., 1965).

Electrophoretic studies of various enzyme systems have also been prominent in the literature. Among these, the dehydrogenases are especially good markers for gene activity and most organisms show both species and tissue specific differences. These systems also often display intraspecific polymorphisms (Massaro, 1972; Johnson, Utter and Hodgins, 1972; Goldberg, 1969; Markert and Faulhaber, 1965).

In the present study, electrophoretic examination of P. abyssicola, P. gemmiferum, P. spilonotus (small form), P. spilonotus (large form) and P. williamsoni was undertaken to determine if species differences could be detected. Analyses were limited to a survey of general

[1]Excerpts from an in-progress Ph.D. Dissertation, Martin J. Paetz, June, 1972.

proteins, lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and glutamate dehydrogenase (GDH) associated with five tissues: blood serum, liver, white muscle, whole eye (except eye lens) and brain. It was beyond the scope of this investigation to perform exhaustive examination of these systems since this would be a study in itself. Cursory examination, however, was considered desirable to determine if species specific patterns were present and to relate these data to morphological and ecological findings.

Methods

Fishblood samples were taken in the field by cardiac puncture, using a 1 cc disposable syringe with a 22 gauge needle. Samples were placed on ice and transported to the laboratory. Four to six hours after collection, serum was drawn off, centrifuged for 30 minutes at 30 X g in a refrigerated centrifuge and frozen at -20 C for later analysis. Specimens to be used for tissue analysis were placed on ice in the field and upon returning to the laboratory were frozen as above. Most samples analyzed were frozen for no more than six weeks.

In final preparation for electrophoresis, serum samples were thawed and centrifuged for 30 minutes at 30 X g. Tissue samples were excised from frozen fish so as to prevent thawing of remaining tissues which would be used in later analyses. Tris-glycine buffer, pH 9.3, was added to tissue samples in a ratio of 2:1 and the sample was homogenized in a Virtis Model 23 tissue grinder. The homogenate was centrifuged 15 minutes at 5,000 rpm, drawn off, and centrifuged two or three additional times, for one hour each, at 30 X g. A density solution, containing bromphenol blue as a marker, was added to serum or supernatant

in a 1:4 ratio. Samples were refrigerated at 4 C for one to six days while various biochemical systems were being analyzed.

The technique of vertical acrylamide gel electrophoresis utilizing a continuous buffer system (tris-glycine, pH 9.3) was employed in electrophoretic examination of serum and tissues. The electrophoresis chambers used were those supplied by E-C Apparatus Corporation (model EC 49); the power supply was a Sylvania Electric. Techniques, buffer systems and stains were those being utilized by students of the Utah Cooperative Fishery Unit in genetic studies of Salmo. Components of the gel, buffers and stains are listed in Appendix C.

Gels were allowed to polymerize for 30-45 minutes and then pre-run for 20 minutes at 200 milliamps before samples were applied. A micropipet was used to introduce 5 to 40 microliters of sample, depending on the tissue, to each of 16 slots located along the top of the gel. Two chambers were operated simultaneously and samples from each of the six groups of Prosopium were included in each chamber to augment ease and reliability of comparisons. After samples settled evenly within slots, the run was started by applying 50 milliamps of current to the chambers. When the sample had migrated into the gel (10-15 minutes), the current was increased to the desired amperage and maintained at this point for the duration of the run. A continuous flow of cooling water at 13 C maintained a constant buffer temperature. Upon completion of electrophoresis, gels were placed in staining boxes and the desired staining solution added. Poloroid photographs were taken of gels for permanent record and bands not visible on photos were noted.

Results and Discussion

Electrophoretic data are based on analyses of 6-16 specimens (except where noted otherwise) of each group of Prosopium studied. Since the analyses were for the purpose of examining species specific differences, no attempt was made to determine tissue specific dissimilarities.

Enzyme systems

LDH isozyme patterns of white muscle, liver and blood sera of all groups studied consisted of five bands and were remarkably uniform, with no species specific differences. Brain LDH patterns were likewise identical between species, but each contained eight, rather than five bands. Numerous LDH isozymes were characteristic of whole eye preparations. Although some difficulty was encountered in counting bands, specific patterns were similar and contained either 15 or 16 bands with the exception of P. spilonotus (small form). In this group, LDH was found to be polymorphic with 14 of 16 specimens examined exhibiting the typical 15 or 16 band pattern while two showed a distinctly different pattern containing a minimum of 20 bands; each of these fish were males.

The five banded LDH isozyme pattern found in blood sera of Bear Lake Prosopium and P. williamsoni was similar to that described by Chellevold (1970) for P. coulteri and P. cylindraceum. Unlike the findings of the present study, Massaro (1972), using starch gel electrophoresis found species specific LDH patterns in liver, brain and eye tissues of P. coulteri and P. cylindraceum.

The lack of species specificity was also characteristic of most MDH isozymes. Liver, brain and eye MDH revealed identical patterns among species, within each tissue. Blood serum MDH patterns, although

somewhat indistinct, appeared polymorphic with no species specific differences observed. Contrary to other tissues, white muscle MDH, although polymorphic, showed some species specific differences (Figure 23). MDH pattern of both P. gemmiferum and P. williamsoni differed from other Prosopium examined by having a single cathodal band above the three to six banded polymorphic pattern typical of all groups. No consistent differences were found among P. abyssicola, P. spilonotus (small form) or P. spilonotus (large form).

Electrophoretic technique used in examining GDH isozymes was not well adapted for whitefishes. Patterns were usually indistinct and difficult to interpret. Eye and brain GDH appeared homogenous between all groups examined while other tissues displayed polymorphic patterns with no consistent species differences discernible.

General proteins

Although general proteins contained in muscle tissue have often been found to be species specific, no consistent differences were observed in muscle protein patterns of Prosopium examined in the present study. This was also true of brain and liver general proteins; eye patterns were indistinguishable.

Despite the often reported variations in general serum proteins, these proteins provided the only evidence of species specific patterns among tissues examined. Three basic groups of species patterns were apparent: (1) P. williamsoni; (2) P. abyssicola--P. gemmiferum; and (3) P. spilonotus (small form)--P. spilonotus (large form) (Figure 23). Serum protein patterns of P. williamsoni were totally uniform among six specimens (three male and three female) examined, with the exception of the second, very thin cathodal band which was present in one male and

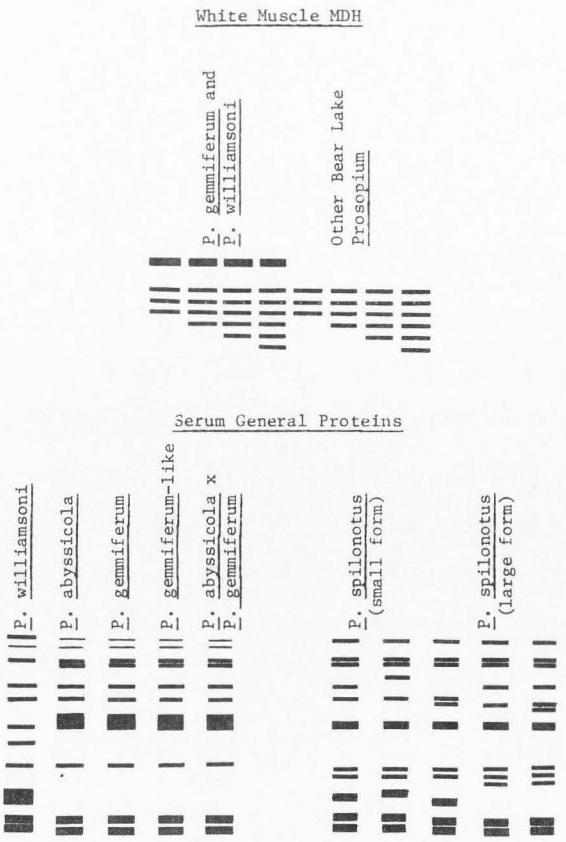

Figure 23. Diagrammatic representation of electrophoretic analyses of white muscle MDH and serum general proteins.

one female. Hansen (1970) using disc polyacrylamide electrophoresis techniques showed sex specific serum protein patterns in P. williamsoni. Further, he reported banding patterns markedly different from those observed in the present study.

All specimens of P. abyssicola (6) and P. gemmiferum (2) had identical serum protein patterns (Figure 23). Patterns among six P. spilonotus (small form) and 12 P. spilonotus (large form) showed some variation, but variations were not confined to one or the other group. One specimen of P. spilonotus (small form) had a markedly unique pattern (Figure 23).

One P. gemmiferum-like hybrid from the lake population and a known P. abyssicola x P. gemmiferum hybrid were included in the analysis of serum proteins. Patterns (although somewhat blurred) appeared identical to those of P. gemmiferum and P. abyssicola (Figure 23) providing evidence that P. gemmiferum-like hybrids originate from P. abyssicola--P. gemmiferum parentage. Known hybrids of P. spilonotus x P. gemmiferum were too small to obtain adequate serum samples for analysis.

Patterns of P. spilonotus (small form) and P. spilonotus (large form) were most closely associated with those of P. williamsoni. This, along with the similarity of P. gemmiferum and P. abyssicola lends support to a proposed phylogeny of these species based on karyotype data (Booke, 1974) which will be discussed more fully later. However, since sample sizes were small, not a great deal of credence can be placed on these findings. Their usefulness, rather, should be to serve as a guide for future work. Improved techniques of starch gel electrophoresis appear promising in that they provide equally good resolution and

are much less time demanding; the several months of work upon which this study is based could easily be done in one week using starch gel techniques.

In summary, species specific differences were rare among protein systems examined. Only white muscle MDH and blood serum general proteins showed specific differences and then, only P. williamsoni was totally unique. If these data are reliable, their most significant contribution to the study is to show P. williamsoni distinct from all Bear Lake Prosopium examined. The similarity between P. spilonotus (small form) and P. spilonotus (large form) in serum proteins neither supports or refutes the proposed distinctions between these forms. The observation that two species, as morphologically distinct as P. gemmiferum and P. abyssicola, can have appearingly identical protein patterns, points out that only when patterns differ are they useful in distinguishing between forms. Utter, Hodgins and Allendorf (1973) emphasize that non-significant differences between groups should be regarded only as an indication that these groups are not necessarily different, but not as strong evidence that they are the same. Similarity of protein patterns among P. gemmiferum-like hybrids, known P. abyssicola x P. gemmiferum hybrids and both P. gemmiferum and P. abyssicola lends support to a P. gemmiferum--P. abyssicola parentage of natural hybrids.

ECOLOGICAL LIFE HISTORY CHARACTERISTICS OF BEAR LAKE *PROSOPIUM*

It is useful to examine biological features as well as morphophysiological characters in evaluating the systematic status of fishes (McAllister, Jolicoeur and Tsuyuki, 1972). The importance of ecological differences in maintaining reproductive isolation among sympatric whitefishes has often been stressed (Svardson, 1958, 1959, 1961, 1970; Lindstrom and Nilsson, 1962; Lindstrom, 1967). Species-characteristic ecological differences are typically manifested by differing growth rates, size and age at maturity, time and/or location of spawning and habitat preference. To further assess group relationships among Bear Lake whitefishes, the above life history characteristics were examined.

Age and Growth

Methods

The scale method was used to determine age and growth characteristics of Bear Lake *Prosopium*. Scale samples were removed from the left side of the fish, midway between the dorsal fin and lateral line and were stored in labeled scale envelopes. Impressions of 8-10 scales from each fish were made on cellulose acetate strips using a Carver Laboratory hydraulic heat press. Twenty-thousand pounds of pressure were applied for a period of 1.5-2 minutes. Scale images were magnified 90 X and projected for study with a microprojector similar to that described by Van Oosten, Deason, and Jobes (1934). No regenerated scales were used.

For purposes of back-calculation, average sized scales in the sample were selected. Scale proportions (i.e., distance from focus to annuli and central anterior margin of magnified scale image) were measured with a transparent plastic rule to the nearest millimeter. Before making final judgement on the age of a fish, three or more scales in the sample were examined. Sexes were not considered separately.

Results and discussion

Identification of annuli

Annulus identification was based upon crowding and discontinuity of two or more circuli in the posterior-lateral fields, followed by one or more complete circuli. The first four or five annuli were usually distinct while erosion of circuli in the posterior field and crowding of annual marks often made age evaluation difficult in older age groups.

False annuli, hypothesized to be spawning checks, often occurred immediately preceding an annulus. These checks were characterized by close proximity to true annuli, few crossovers, and no circuli continuing entirely around the scale. False annuli were most commonly associated with annuli III and IV. The interpretation of these marks as being accessory checks was also based upon the observation that what appeared to be a completed annulus at the anterior margin of the scale was often present in specimens collected during the various spawning periods (December-March); checks were never observed in immature specimens. Observations of scales from fishes taken in June and July showed these to be false checks. Similar accessory checks were reported by Perry (1943) for P. gemmiferum. Although these marks were considered in some detail, Perry offered no explanation for their formation.

Annulus formation

Annulus formation in one year old P. abyssicola and P. spilonotus (small form) occurred in early June while most fish of older age groups formed an annulus during the period mid-June to mid-July; annulus formation only rarely extended into early August for individuals six years of age or older. Although few P. spilonotus (large form) were collected during the above time period, it appeared that time of annulus formation in this group was similar to that of P. abyssicola and P. spilonotus (small form).

Earlier annulus formation in the younger age groups has been reported by Hile (1941) and others. Most reports of annulus formation in coregonines are similar to those observed in the present study (for summary see Carlander, 1969). Both Edsall (1960) and Bailey (1963) report annulus formation extending into August for older age groups of lake whitefish and round whitefish, respectively.

Validation of the scale method for aging

The validity of the annulus as a true year mark has been documented for numerous species of fish. Van Oosten (1923, 1929) pioneered validation techniques in his studies of lake whitefish, Coregonus clupeaformis. Four validation criteria established by Van Oosten (1929) were examined for P. abyssicola, P. spilonotus (small form) and P. spilonotus (large form).

1. Correlation between age and size: Each group of Prosopium examined showed a regular increase in number of annuli accompanying increased length of fish (Tables 16-18). Among younger age groups (0, I, II) length frequency distributions coincide with lengths of age groups based on scale readings (Tables 16-20). All P. abyssicola

Table 16. Mean calculated total lengths and increments, Prosopium abyssicola, Bear Lake, Utah-Idaho (1969-1971).

Age Group	Number of Fish	Mean Observed Length (mm)	Mean Calculated Total Length at Annulus (mm)										
			1	2	3	4	5	6	7	8	9	10	11
I	43	107	90										
II	40	149	91	139									
III	26	168	78	132	160								
IV	19	184	81	132	162	180							
V	31	198	77	128	155	173	186						
VI	42	207	83	131	157	176	188	198					
VII	53	213	84	132	157	175	188	199	208				
VIII	46	218	80	129	153	170	183	194	204	212			
IX	12	224	83	138	161	176	186	197	206	214	220		
X	3	243	76	131	156	170	183	195	205	213	220	226	
XI	3	243	80	127	155	172	182	192	202	211	217	224	229
Grand average calculated length			84	132	157	174	186	197	206	212	220	225	229
Growth increments			84	49	25	17	12	11	9	6	8	5	4
Number of fish reaching age			318	275	235	209	190	159	117	64	18	6	3

Table 17. Mean calculated total lengths and increments, Prosopium spilonotus (large form), Bear Lake, Utah-Idaho (1969-1971).

Age Group	Number of Fish	Mean Observed Length (mm)	Mean Calculated Total Length at Annulus (mm)								
			1	2	3	4	5	6	7	8	9
I	7	185	118								
II	54	202	116	173							
III	95	230	116	178	212						
IV	72	261	113	177	213	243					
V	29	294	116	178	218	251	279				
VI	19	346	111	178	224	257	294	323			
VII	28	366	118	176	215	251	283	312	336		
VIII	28	400	124	185	226	264	295	324	358	383	
IX	8	407	118	174	219	253	289	319	347	370	393
Grand average calculated length			116	178	216	251	287	319	347	380	393
Growth increments			116	61	38	35	37	32	28	33	13
Number of fish reaching age			340	333	279	184	112	83	64	36	8

Table 18. Mean calculated total lengths and increments, Prosopium spilonotus (small form), Bear Lake, Utah-Idaho (1969-1971).

Age Group	Number of Fish	Mean Observed Length (mm)	Mean Calculated Total Length at Annulus (mm)					
			1	2	3	4	5	6
I	43	127	102					
II	67	175	105	163				
III	92	195	99	162	187			
IV	69	215	102	159	186	203		
V	46	226	99	153	180	196	209	
VI	9	240	102	156	181	197	229	220
Grand average calculated length			101	160	185	200	209	221
Growth increments			101	59	25	15	9	11
Number of fish reaching age			326	283	216	124	55	9

Table 19. Length frequency distribution of young age groups of P. abyssicola on specific collection dates.

Age Group	0		I			II		III		
Collection Date	Aug. 28	Sept. 9-25	June 18	July 8-17	Sept. 3-17	July 8-17	Sept. 3-17	June 18	July 8-17	Sept. 3-17
Total Length (mm)										
0-9										
10-19										
20-29	2									
30-39	1									
40-49		8								
50-59		4								
60-69		1								
70-79										
80-89										
90-99			1	11						
100-109				13	2					
110-119			1	7	6					
120-129					8					
130-139						4				
140-149						9	3			
150-159						2	3	2	3	
160-169							1		7	2
170-179									1	7
180-189										
Number of Fish	3	13	2	31	16	15	7	2	11	9
Mean Length	37.7	50.3	104.5	103.1	118.8	143.3	151.4	152.5	162.3	171.1
Grand Mean	47.7			108.4			145.9		165.0	

Table 20. Length frequency distribution of young age groups of P. spilonotus (small form) on specific collection dates.

Age Group	0*			I				II			III		
Collection Date	July 14	Aug. 27-28	Sept. 25	Oct. 10	June 18-23	July 8-17	Sept. 3-17	Dec. 4	June 18	July 8-17	Sept. 3-17	June 18-23	July 8-17	Sept. 3-17
Total Length (mm)														
0-9														
10-19														
20-29														
30-39	5													
40-49	15													
50-59	2													
60-69		7												
70-79		5	2											
80-89		2	10											
90-99			1	6										
100-109					1									
110-119					4	12								
120-129						7	2							
130-139						2	2	3						
140-149						2	1	4	2					
150-159								1		2				
160-169										14	2			
170-179										7	2	1	2	
180-189										2	5	6	16	
190-199												2	6	3
200-209												1	2	4
Number of Fish	22	14	13	6	5	23	5	8	2	25	9	10	26	7
Mean Length	42.2	70.6	83.5	95.3	113.0	121.3	132.2	137.0	142.5	167.1	178.	186.1	188.0	200.0
Grand Mean		65.0				123.7				168.5			189.5	

*Age 0 and small individuals of age "I" P. spilonotus (small form) and P. spilonotus (large form) are not separable, therefore both groups may be included in these data.

collected in 1970 <70 mm total length, had no annuli and all between 90 and 129 mm total length had one annulus. Although some overlap existed between age groups II and III, modes of length frequency for any one collection period were distinct for each of these age groups (Table 19). Similar results were observed for P. spilonotus (small form) (Table 20).

2. Determination of only one annulus being deposited each year over a period of years: Periodic samples of each group of Prosopium were collected between June and the following March of 1969-1970 and 1970-1971. In young age groups, one annulus was formed per year as discussed above. In older age groups, some individuals laid down an accessory check which had characteristic features enabling reliable recognition.

3. Agreement among calculated growth histories: Lengths of older age groups at the end of various years of life as determined by back-calculation, showed generally good agreement with empirical lengths of younger age groups (Tables 16, 17 and 18). Empirical lengths were invariably larger than back calculated lengths because empirical lengths were based upon fish collected throughout the growing season, while back-calculated lengths represent the size of the fish at annulus formation.

4. Agreement on length at age of fish from the same age group collected in different years and agreement of calculated growth among different year classes: Good agreement between mean observed lengths of the same age group collected in different years (between October and February) was observed for each of three groups of Prosopium examined (Table 21). Comparison of calculated growth histories of several year

Table 21. Comparison of mean observed lengths of whitefishes from the same age group collected in different years from Bear Lake, Utah-Idaho.

		P. spilonotus (small form)		*P. spilonotus* (large form)		*P. abyssicola*	
Age group	Year caught	N	mean length	N	mean length	N	mean length
1	1969	43	127	5	182.2	43	107.0
	1970	--	--	2	192.0	--	--
2	1969	9	183.7	11	200.4	36	148.6
	1970	18	182.9	11	207.6	3	155.6
	1971	--	--	26	204.3	--	--
3	1969	18	194.9	8	239.5	21	168.6
	1970	24	196.9	11	237.2	5	167.2
	1971	--	--	49	223.7	--	--
4	1969	11	213.4	--	--	9	181.2
	1970	11	217.5	18	261.8	5	182.8
	1971	--	--	16	255.1	5	191.6
5	1969	9	222.0	5	288.4	12	195.9
	1970	13	225.8	4	287.3	15	199.3
	1971	--	--	5	287.4	4	198.5
6	1969	--	--	2	327.5	17	209.0
	1970	3	241.0	2	322.0	23	203.9
	1971	2	246.0	2	336.5	--	--
7	1969	--	--	4	371.3	15	210.6
	1970	--	--	4	378.0	22	209.6
	1971	--	--	5	370.0	--	--

classes also showed close agreement in yearly growth (Table 22). These data, in conjunction with those presented above, provide evidence supporting the use of scales for validly determining the age and past growth history of Bear Lake Prosopium.

Body-scale relationship

When the body-scale relationship of a fish population is understood it is possible to calculate previous yearly growth for individual fish from that population (Sigler, 1951). Body-scale relationships of coregonines have usually been described as linear. This is probably due to inadequate sampling of young and/or old age groups. Heard and Hartman (1966) found that a fourth degree polynomial gave the most realistic mathematical fit for describing the body-scale relationship of P. coulteri in the Nadnek River system, Alaska, and Sigler (1951) used a third degree polynomial in describing the relationship for P. williamsoni, Logan River.

An empirical plot of fish length against scale radius suggested a curvilinear body-scale relationship for each group of Bear Lake Prosopium examined in the present investigation. Computer analyses employing Carlander's third degree polynomial model was utilized. Components of the model are:

$$L = b_o + b_1 S + b_2 S^2 + b_3 S^3$$

where L = total body length (mm)

S = anterior scale radius X 90

b_o, b_1, b_2, b_3 = empirical constants

Body-scale relationships based upon 318 P. abyssicola, 326 P. spilonotus (small form) and 340 P. spilonotus (large form) were described by the following formulae (Figure 24).

Table 22. Comparison of calculated growth among different year classes of Bear Lake Prosopium.

Prosopium abyssicola

Number of annuli		1	2	3	4	5	6	7	8
Year class	N								
1968	43	90.0							
1967	40	91.3	139.5						
1966	21	78.5	132.6	159.8					
1965	9	84.0	135.3	160.7	178.3				
1964	12	81.9	127.6	152.8	170.4	183.5			
1963	15	80.9	133.0	160.0	178.1	192.0	202.3		
1962	16	89.0	133.0	157.6	174.4	186.8	197.4	206.2	
1961	20	87.0	137.4	155.4	171.8	184.9	195.7	205.6	214.4

Prosopium spilonotus (large form)

Number of annuli		1	2	3	4	5	6
Year class	N						
1969	5	114.9					
1968	12	112.3	177.5				
1967	10	116.1	183.5	214.2			
1966	18	109.2	173.9	207.4	230.7		
1965	5	108.7	173.5	213.6	248.7	274.8	
1963	3	113.0	164.1	195.3	232.0	260.7	290.8

Prosopium spilonotus (small form)

Number of annuli		1	2	3	4	5
Year class	N					
1968	43	102.5				
1967	34	103.5	161.1			
1966	17	101.8	166.4	189.3		
1965	20	102.9	160.4	185.5	203.3	
1964	19	100.7	152.5	176.0	192.2	205.1

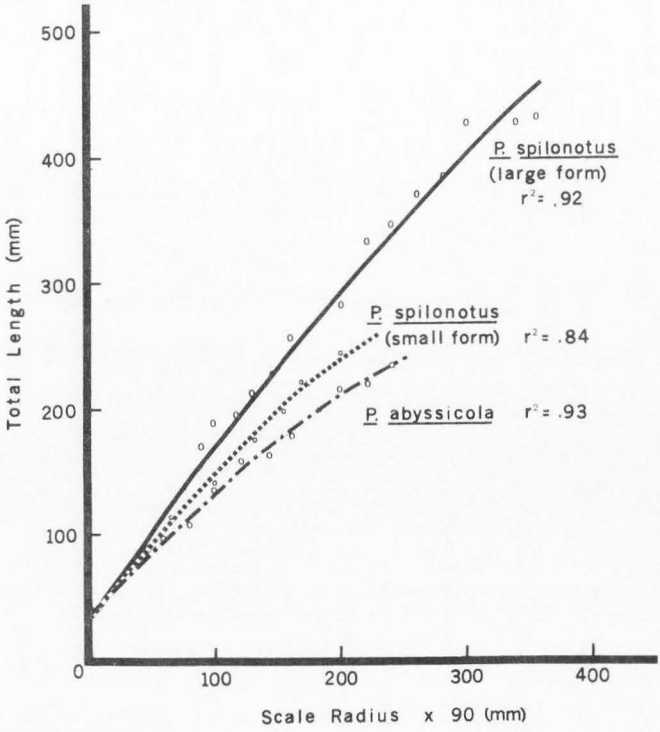

Figure 24. Body-scale relationships of three groups of Bear Lake whitefishes. Circles represent mean observed length.

P. abyssicola: $L = 33.9846 + 1.0297S - .0001S^2 - .0000039S^3$

P. spilonotus (small form): $L = 25.0490 + 1.4490S - .0017S^2 - .00000086S^3$

P. spilonotus (large form): $L = 35.0000 + 1.4205S - .0006S^2 + .000000025S^3$

Scale formation of both natural and cultured specimens of *P. abyssicola* and cultured specimens of *P. spilonotus* (small form) was complete (in the area sampled for aging) in all specimens examined > 35 mm total length. This was also true of all young-of-the-year *P. spilonotus* (small form and/or large form) taken from the lake population. These observations are in accordance with those reported for other whitefish species. Van Oosten (1929) reported scale formation at 35-40 mm total length for *C. clupeaformis* and Brown (1972) and Hagen (1956) report full scalation between 40 and 50 mm total length for *P. williamsoni*.

Calculated intercepts ($b_o \cong$ size of fish at scale formation) for *P. abyssicola* and *P. spilonotus* (small form) were reasonably close to observed size of fish at scale formation. Few age I specimens of *P. spilonotus* (large form) were identified and therefore an intercept at 35 millimeters was specified in calculating the body-scale relationship. Specifying the intercept had virtually no effect on predicted lengths of specimens belonging to age groups III and older but provided far more realistic results for age groups I and II. Empirical observations of body-scale relationships fit calculated curves well (Figure 24).

Comparison of growth histories

Pronounced differences between growth histories of *P. abyssicola*, *P. spilonotus* (small form) and *P. spilonotus* (large form) were observed (Figure 25). Growth of *P. spilonotus* (small form) and *P. spilonotus*

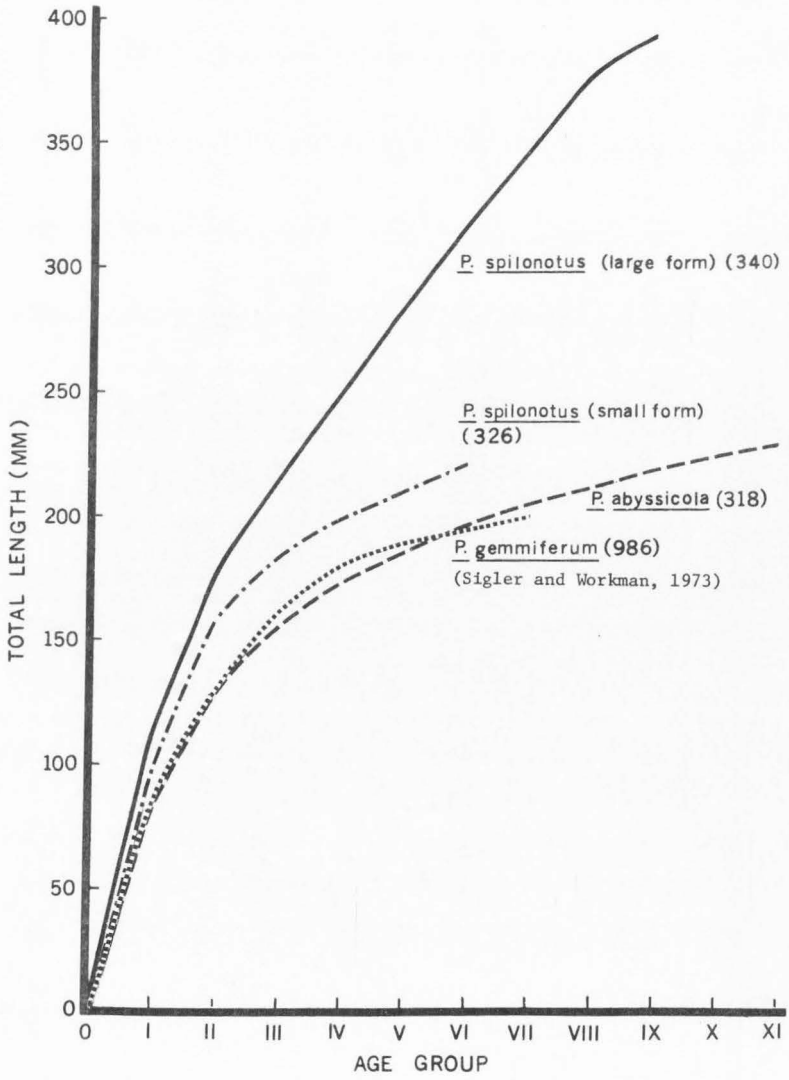

Figure 25. Calculated growth histories of four groups of Bear Lake whitefishes.

(large form) was somewhat similar during the first two years of life with P. spilonotus (large form) being 15-18 mm larger in total length each year. After year two growth became markedly divergent between the two forms. Prosopium spilonotus (large form) continued to grow rapidly while growth rate of P. spilonotus (small form) decreased. Growth of P. spilonotus (large form) was found to be similar to that reported for mountain whitefish in the Logan River (Sigler, 1951).

Prosopium abyssicola was considerably smaller than either P. spilonotus (small form) or P. spilonotus (large form) at first annulus formation. Later spawning period and therefore shorter first year growing season may, in part, account for this slower growth. Subsequent growth increments closely parallel those of P. spilonotus (small form) (Figure 25).

Maximum observed age was 11 years for P. abyssicola, 9 years for P. spilonotus (small form) and 13 years for P. spilonotus (large form). Older age groups of P. spilonotus (small form) and P. spilonotus (large form) were excluded from age and growth analyses due to insufficient numbers. Specimens excluded include: P. spilonotus (small form) age group VII, one specimen; age group VIII, two specimens; and age group IX one specimen; P. spilonotus (large form) age group XI, two specimens; age group XII, two specimens and age group XIII, two specimens. No ten year old P. spilonotus (large form) were observed.

Age and growth studies were important in providing further evidence supporting separate consideration of P. spilonotus (small form) and P. spilonotus (large form). Little doubt remains that these two groups represent distinct populations.

Length-weight relationships

Length-weight relationships were described for combined sexes of 687 P. abyssicola, 647 P. spilonotus (small form) and 312 P. spilonotus

(large form), for the purpose of determining species-specific relationships. To limit influence of increased weight due to gonad development, only collections taken during the period May to August were utilized in examining the length-weight relationships of P. abyssicola and P. spilonotus (small form). Because of limited numbers of P. spilonotus (large form) collected in the above time period, specimens collected throughout the year were used in length-weight analysis. All mature specimens of this group used in the analysis were collected either during this period or after having spawned, thus the effect of year around collections was presumed unimportant.

A linear regression was fitted to each group of length-weight data by the method of least squares. This relationship is described mathematically as follows:

$$\text{Log } W = \log a + b \ (\log L)$$

where W = weight in grams

L = total body length in millimeters

b = regression coefficient

a = Y-intercept

The calculated length-weight relationships of Bear Lake Prosopium are summarized in Figure 26 and Table 23. As one would expect from species with similar body form, length-weight relationships were decidedly analogous. P. spilonotus (small form) and P. abyssicola occupied nearly overlapping positions when length-weight relationships were plotted. Within comparable size ranges, P. spilonotus (large form) was slightly lighter in weight at a specified length than was P. spilonotus (small form) or P. abyssicola. This illustrates the slight difference in robustness of immature P. spilonotus (large form) noted earlier.

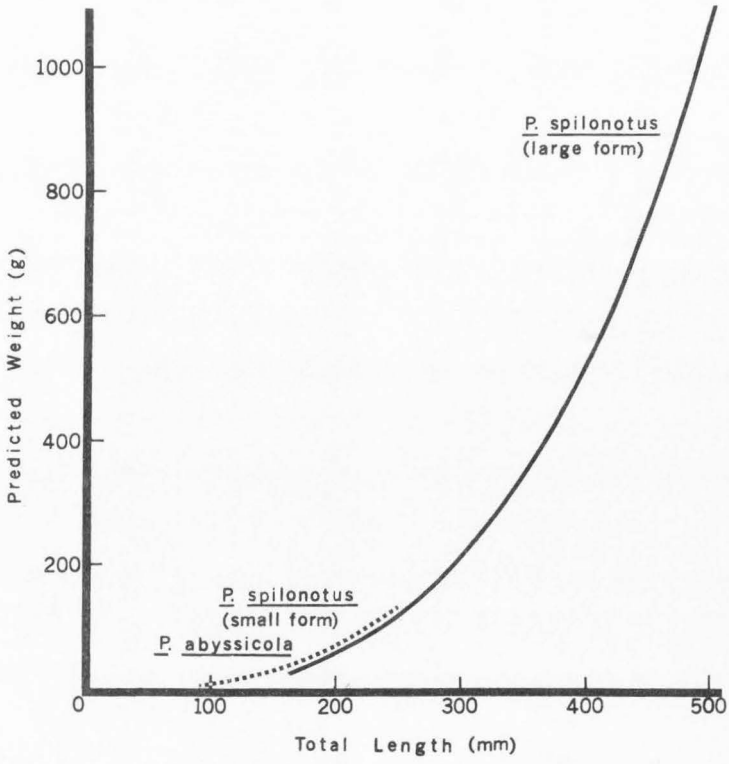

Figure 26. Length-weight relationship of three groups of Bear Lake whitefishes.

Table 23. Length-weight relationships of Bear Lake Prosopium.

Species	Number	R^2	Length-weight relationship
P. abyssicola	687	.99	Log W = -5.3775 + 3.1190 Log L
P. spilonotus (small form)	647	.99	Log W = -5.2999 + 3.0967 Log L
P. spilonotus (large form)	312	.98	Log W = -5.5199 + 3.1699 Log L

Reproduction

Methods

Gill-nets were utilized in sampling spawning populations of all forms of Bear Lake whitefishes. Supplementary collections of P. spilonotus (large form) were made by angling. Data presented are based upon extensive collections made during the following time periods: P. spilonotus (large form)--early December, 1971, mid-November-mid-December, 1972; P. spilonotus (small form)--late November and/or December, 1969-1972; P. abyssicola--late January, February and March, 1970, 1971.

Results and discussion

Characteristics common to each group

Males of each group of Bear Lake Prosopium ripened earlier and remained ripe longer than females. Males characteristically moved into presumed spawning areas several weeks prior to females and were abundant there throughout the spawning season. Ripe females migrated into spawning areas and spawned, after which they moved into deeper water.

Collections made during respective spawning runs in areas not thought to be utilized for spawning typically contained spent or

ripening fish (predominately females) and those fish captured were located throughout the vertical axis of the gill-nets. This is in contrast to collections made in presumed spawning areas which were characterized by a predominance of ripe fish, a male to female sex ratio ranging from 2:1 to > 10:1 and most fish being captured in the lower one-third of the gill-net (often in the lower 10-20 cm). The frequent observation of several ripe males positioned near the bottom of the gill-net in close proximity to a gravid female suggested that the spawning act involves one female and several males and that eggs are broadcast on or near the bottom. No direct observations of spawning behavior were made and identity of spawning areas was based upon the presence of running-ripe males and females, as described above.

Daily spawning pattern was not specifically investigated. Gill-nets were usually set in mid- to late-afternoon and retrieved the following morning. In one instance during the spawning period of P. spilonotus (small form), gill-nets set in mid-morning contained no fish when checked and reset in mid-afternoon. By the following morning, however, large numbers of ripe fish had been captured. Fishermen reported taking P. spilonotus (large form) most readily during early morning and late evening hours except on cloudy days when fish were taken throughout the day. Similar observations have been made concerning the dip-net fishery for P. gemmiferum.

P. spilonotus (large form). P. spilonotus (large form) spawned during late November and early December at water temperatures ranging from 2.2 to 4.4 C (36-40 F). No ripe specimens were collected after the first week of December. Spawning appeared to be confined to rocky shallows at depths ranging from 1 to 7 m (3-23 ft). Although extensive

collections over other bottom types were not made, neither angling or gill-nets took ripe specimens of this form in potential spawning areas over sand bottom. Rocky points appeared to be preferred; man-made breakwaters also attracted spawning P. spilonotus (large form).

Although these findings are based on only one year's sampling (except for December collections), they are in agreement with observations related to the author by Mr. LaVon Thomas.[1] According to Mr. Thomas, peak spawning usually occurs around Thanksgiving weekend with the entire spawning run lasting for two to three weeks. Limited creel census data for 1968, 1969 and 1971 (Utah Division of Wildlife Resources), obtained during the spawning period, also support these findings.

Only one mature specimen of P. spilonotus (large form) less than five years of age (sixth year of life) was taken in four years of collections. This individual was a male in its fourth year of life (age group III). Normally, sexual maturity of P. spilonotus (large form) was attained during the sixth or seventh year of life (age groups V or VI).

Fecundity, determined by the gravimetric method, was examined in two females. A seven year old female (343 mm TL) contained an estimated 6,641 eggs while a nine year old female (410 mm TL) had an estimated 13,061 eggs. Water hardened eggs (from hybridization experiments) had a mean diameter of 2.95 mm. The method of vonBayer (1910) was used in determining egg diameter.

Tubercles were profuse on spawning individuals of both sexes of P. spilonotus (large form) but were generally better developed in males.

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[1]Personal communication with Mr. LaVon Thomas, Utah Division of Wildlife Resources, Northern Region, Randolph, Utah, November, 1972.

Degree of tubercle development varied markedly from sparse development in the area of the lateral line to the presence of a tubercle on every body scale except the area of small crowded scales in the anterior abdominal region extending from the ismus to approximately one-half way to the origin of the pelvic fins. Tubercles were developed to a lesser degree on lateral line scales; two, rather than the characteristic one tubercle per scale were often present on some lateral line scales. No tubercles were observed on the fins, but a small number were often found on the opercle. All mature, prespawning specimens (taken during the spawning period) showed some degree of tubercle development. Spawning coloration was conservative and consisted of a general darkening in some fish. No sexual dimorphism was apparent.

P. spilonotus (small form). Although temporal initiation of spawning varied from year to year, spawning of P. spilonotus (small form) commenced during the first two weeks of December and continued for about 14 days with peak spawning occurring between December 15 and December 24 in each of four years studied. Ripe males were observed as early as the last week of November. Water temperature at peak spawning ranged from 2-4 C (35.6-39.2 F). A few ripe individuals of P. spilonotus (small form) were observed as late as December 31, but by mid-January all specimens examined were spent.

Spawning appeared to be confined to depths ranging from 3-14 m (10-45 ft) with the greatest concentration of ripe fish being collected between the 5 and 9 m (16-30 ft) contours. Although rocky areas appeared to be preferred spawning sites, spawning of P. spilonotus (small form) was apparently not confined to such areas since ripe individuals of both sexes were taken over sand substrate. Condition of gonads and

position of males and females in gill-nets formed the basis for this assumption.

Prosopium spilonotus (small form) matured during the third or fourth year of life. Estimated fecundity of 23 females collected December 7, 1970, ranged from 911 in a 191 mm TL fish to 2,635 in a 227 mm TL specimen. Variation of fecundity with total length is presented in Figure 27. Mean size of water hardened eggs was 2.84 mm.

Distribution of nuptial tubercles in P. spilonotus (small form) was similar to that described for P. spilonotus (large form). Both males and females had well developed tubercles with the more profuse development in males. Rarely, two or three tubercles were observed on the opercle; tubercles were usually absent on the lateral line and no tubercles were observed on the fins. General darkening, confined primarily to the area above the lateral line, was the only noticeable color change associated with spawning.

P. abyssicola. Spawning period was more protracted in P. abyssicola than observed in other Bear Lake Prosopium. Ripe specimens were obtained from early February to late March at water temperatures ranging from 2.2-3.9 C (36-39 F). Although collections at 28 m (90 ft) or deeper usually produced the largest number of P. abyssicola, ripe specimens were rarely taken at these depths. Maturing and spent females dominated these collections with males being rare or absent. No adult P. abyssicola were collected at depths < 15 m (50 ft). Large concentrations of spawning P. abyssicola were never located, thus peak spawning time was not determined.

Although ripe P. abyssicola were never abundant in collections, a few ripe specimens were taken at depths between 15-28 m (50-90 ft) with

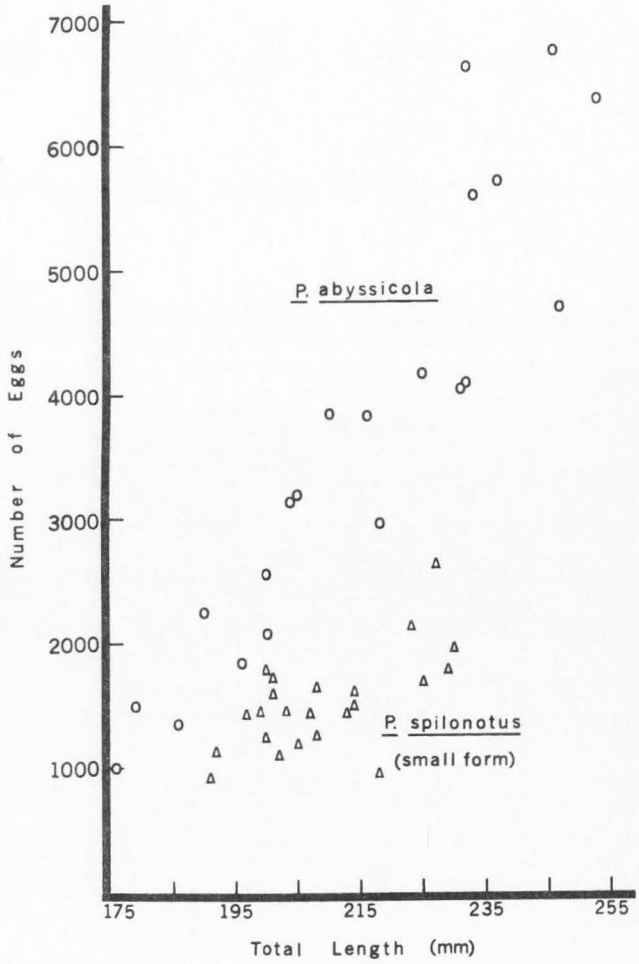

Figure 27. Comparison of change in fecundity with increased length for P. abyssicola and P. spilonotus (small form), Bear Lake, Utah-Idaho.

the largest numbers being collected at 18-20 m (59-66 ft). Bottom substrate at presumed spawning depths was remarkably uniform throughout the lake and was composed predominantly of silt and marl with the exception of a few areas on the east shore where rock rubble extended into these depths. No spawning collections were typical of what might be expected of collections taken on the spawning grounds if characteristics of sex ratios, state of maturation, etc., could be expected to be comparable to those observed for other Bear Lake whitefishes.

Sexual maturity was attained during the third or fourth year of life (age group II or III). Estimated fecundity of 21 P. abyssicola females ranged from 1,090 in a 176 mm TL specimen to 6,748 in a fish 246 mm TL (Figure 27). Water hardened eggs had a mean diameter of 2.58 mm.

Tubercle development was, in general, similar in P. abyssicola to that of the two forms of P. spilonotus. No tubercles were observed on the opercle and tubercles were poorly developed or absent on lateral line scales. Both sexes had well developed tubercles, and as in other Bear Lake whitefishes, tubercles were most pronounced in males.

Spawning coloration of P. abyssicola, although conservative, was more dramatic than in P. spilonotus (small form) or P. spilonotus (large form). Specimens of spawning P. abyssicola were typically much darker, especially the males. The darker appearance of males was often sufficient to separate sexes with good reliability.

P. gemmiferum. Characteristics of the reproductive biology of P. gemmiferum have been previously described and therefore were not rigorously examined in the present study. A recent contribution by Sigler and Workman (1973) provides an updated account of the biology

of this species. Much of the following information concerning the reproductive biology of P. gemmiferum was taken from this report.

Prosopium gemmiferum reach sexual maturity during the second or third year of life. Males ripen several weeks earlier than females and move inshore into spawning areas where they remain throughout the spawning period. The observation that 66 to 80 percent of dip-netting catch consists of males suggests that females apparently move inshore when ripe, spawn, and then move back into deeper water.

Prosopium gemmiferum shoal in large numbers during the spawning season. Spawning occurs at or near the bottom with one female and four or five males taking part in the spawning act. Greatest concentrations of spawners are found in the rocky area between North Eden and South Eden canyons, but spawning is believed to occur in other areas of the lake. Spawning takes place in water as shallow as 15 cm (6 in) and may extend into water 12 or more meters deep (40 ft). Commencement of spawning occurs between January 10 and 19 and rarely lasts more than 12 days. Water temperatures at time of spawning range from 0.6 to 4.0 C (33-39.2 F).

Fecundity of P. gemmiferum is relatively low. In eight females examined by Perry (1943) the total number of eggs ranged from 822 in a 122 mm SL specimen to 2,657 in a 157 mm SL specimen. The mean number of eggs per female has been reported to be 1,301. In the present study, mean water-hardened egg diameter was found to be 2.19 mm.

Spawning coloration of P. gemmiferum is unique among Bear Lake whitefishes and consists of a bright orange-yellow streak extending from the region of the pectoral fins, backward to the area of the anus. Females are usually lighter dorsally than males. As with other Bear

Lake whitefishes, breeding tubercles are usually well developed in both sexes.

Temporal and spatial spawning relationships

Spawning activities of Bear Lake coregonines showed varying degrees of overlap, both spatially and temporally (Table 24). Earliest to spawn was P. spilonotus (large form) which spawned in rocky shallows (< 7 m; 23 ft) during late November and early December at temperatures ranging from approximately 2.2-5.0 C (36-41 F). Male P. spilonotus (small form) began ripening in late November and were taken in small numbers in the same gill-nets used for collecting P. spilonotus (large form). As the number of ripe P. spilonotus (large form) decreased, numbers of ripe male P. spilonotus (small form) increased. Near the termination of spawning activity of P. spilonotus (large form) a few ripe female P. spilonotus (small form) were collected over the same spawning grounds.

Spawning activity of P. spilonotus (small form) usually peaked during the third week of December, at water temperatures ranging from 2-4 C (35.6-39.2 F). Spawning of this group was apparently not entirely confined to rocky areas and major spawning activity appeared to be in somewhat deeper water (5-9 m; 15-30 ft) than that observed for P. spilonotus (large form). By peak spawning time of P. spilonotus (small form) relatively large numbers of ripening male P. gemmiferum were taken in the same area; a few of these fish were ripe. By the end of December, spawning activity of P. spilonotus (small form) had essentially ceased and the number of ripe male P. gemmiferum had increased markedly. No ripe male or female P. spilonotus (small form) were observed during the mid-January spawning period of P. gemmiferum. Spatial spawning activities of P. gemmiferum overlapped with both forms of

Table 24. Comparison of the reproductive biology of four forms of Bear Lake whitefishes.

	Age at Maturity	Spawning Duration	Temperature	Depth	Bottom Substrate
P. spilonotus (large form)	5 - 6	Late Nov.- Early Dec.	2.2 - 5.0 C. (36 - 41 F)	1 - 7 M. (3 - 23 ft.)	Rock
P. spilonotus (small form)	2 - 3	Early Dec.- Late Dec.	2.0 - 4.0 C. (35.6 - 39.2 F)	3 - 14 M. (10 - 45 ft.)	Rock or Sand
P. gemmiferum	1 - 2	Mid-Jan.- Late Jan.	0.6 - 4.0 C. (33 - 39.2 F)	0.15 - > 12 M. (.5 - > 40 ft.)	Rock
P. abyssicola	2 - 3	Early Feb.- Late March	2.2 - 4.0 C. (36 - 39 F)	15 - 28 M. (50 - 90 ft.)	Silt - Marl

P. spilonotus with eggs being deposited primarily over rocky substrate, from near shore to a depth of 12 m (40 ft) or more. Water temperatures ranged from 0.6-4 C (33-39.2 F).

Initiation of spawning in P. abyssicola occurred in early February and extended into late March at water temperatures of 2.2-3.9 C (36-39 F) and at depths of 15-28 m (50-90 ft). Spatially, P. abyssicola were well segregated from other Bear Lake whitefishes with respect to spawning activities. No ripe male or female P. abyssicola were observed during the January spawning run of P. gemmiferum. Ripe male P. gemmiferum, however, were found in small numbers throughout the spawning period of P. abyssicola.

Distribution

It was beyond the scope of the present investigation to thoroughly examine distributional patterns of Bear Lake coregonines. However, during the summers, 1969-1970, 59 and 41 trawl collections, respectively, were made at locations throughout much of Bear Lake at depths ranging from 3 to 61 m (10-200 ft). Although incomplete, these data provide insight into gross patterns of summer distribution and degree of spatial isolation of P. abyssicola, P. spilonotus (small form) and P. spilonotus (large form) and therefore provide additional evidence useful in evaluating the status of these forms.

Results and discussion

Distributional patterns of whitefishes collected during the interum, June 18 to September 17, 1969 (Figure 28) were similar to collections made during the same time period in 1970. At any particular depth, during this period, percent of total whitefish catch for each group of Bear

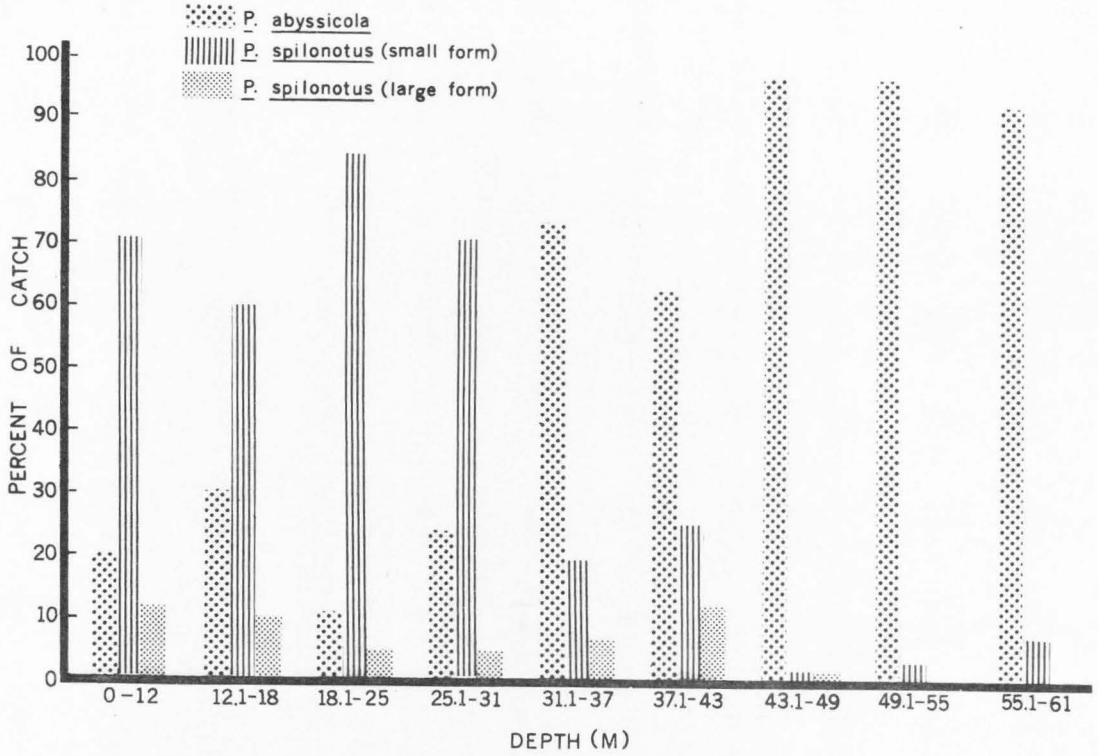

Figure 28. Distribution of three forms of Bear Lake whitefishes based upon 59 trawl collections, June 18 - September 17, 1969.

Lake Prosopium remained surprisingly uniform regardless of location within the lake.

P. abyssicola

Specimens of P. abyssicola were collected at depths as shallow as three meters (10 ft) and made up 10-30 percent of the total whitefish catch at depths < 31 m (102 ft) (Figure 28). No mature P. abyssicola were collected in water < 15 m (50 ft) deep while a mixture of mature and immature specimens were found between 15 and 31 m (50-102 ft). At depths > 31 m (102 ft), P. abyssicola dominated, making up 62-100 percent of the total whitefish catch.

P. spilonotus (small form)

Prosopium spilonotus (small form) dominated catches at all depths < 31 m (102 ft) with percentage composition ranging from 60-85 percent of the total number of whitefish collected at these depths (Figure 28). Between 31 and 43 m (102-141 ft), P. spilonotus (small form) made up 25 percent or less of the total whitefish catch and were rarely taken at greater depths. Both immature and mature specimens were common in shallow water trawls (< 31 m; 102 ft) with most individuals collected in deeper water being sexually mature.

P. spilonotus (large form)

Prosopium spilonotus (large form) were never abundant in trawl collections, making up an average of 4.5-12.5 percent of whitefish catches at water depths < 43 m (141 ft); at greater depths specimens of this form were rare or absent (Figure 28).

These data provide evidence that distributional patterns of P. abyssicola and P. spilonotus (small form), during the period of sampling, are distinct. P. abyssicola was found to be basically a deep water form

(> 31 m; 102 ft) when sexually mature while P. spilonotus (small form) was primarily confined to shallower depths (< 31 m; 102 ft) at all stages of maturation. Adults of both groups were found between 24 and 43 m (80-140 ft) but the break in distributional pattern at 31 m (102 ft) was of conspicuous magnitude (Figure 28). A large portion of the P. abyssicola collected at depths < 31 m (102 ft) were immature.

Immature developmental stages of P. abyssicola, P. spilonotus (small form) and/or P. spilonotus (large form) were largely confined to depths between 6 and 18 m (20-92 ft); young-of-the-year specimens of all forms were most common in trawl catches made between 6 and 14 m (20-45 ft).

Few specimens of P. spilonotus (large form) were collected by trawl, but data available showed them to be fairly evenly distributed to a depth of 43 m (140 ft) (Figure 28). These data, however, are perhaps not representative of the P. spilonotus (large form) population.

Specimens of P. spilonotus (large form) were observed in relatively large concentrations along the rocky, eastern shoreline of Bear Lake on June 1, 1972. Concentrations were apparently associated with spawning activities of Utah Sucker (Catostomus ardens). While observing sucker spawning behavior, it was noted that after a spawning frenzy, whitefishes would dart into the area to presumably feed upon the newly deposited eggs. Mid-morning gill-net collections at depths of one-seven meters (3-25 ft) took considerable numbers of whitefishes with a breakdown of 70 percent P. spilonotus (large form) and 30 percent of P. spilonotus (small form). Subsequent collections (June 8 and 9) contained as high as 90 percent P. spilonotus (large form). Perhaps P. spilonotus (large form) is more dependent upon shallow rocky areas than are other Bear Lake whitefishes and thus are not adequately represented in trawl collection.

In summary, ecological characteristics of Bear Lake Prosopium have revealed important distinctions between forms. Age and growth studies revealed pronounced differences between growth histories of P. abyssicola, P. spilonotus (small form) and P. spilonotus (large form). Distinct growth differences between forms of P. spilonotus provide further evidence supporting their separate consideration. Length-weight relationships showed no specific differences. Spatial overlap of spawning activities was marked between P. spilonotus (large form), P. spilonotus (small form) and P. gemmiferum. P. abyssicola was well separated spatially from other Bear Lake forms. Temporally, slight overlap was observed between ripe females of one group and ripe males of the succeeding group to spawn, with the exception of P. gemmiferum and P. abyssicola; no ripe P. abyssicola males were observed during the spawning period of P. gemmiferum. Only P. gemmiferum males were observed in ripe condition after cessation of normal spawning activity of a group and thus overlapped with P. abyssicola. The only observation of the simultaneous occurrence of ripe females of two forms was between P. spilonotus (large form) and P. spilonotus (small form); in this instance, the number of ripe females of each form was extremely small. Summer distributional data revealed markedly different distribution patterns of P. abyssicola and the two forms of P. spilonotus.

SYSTEMATIC EVALUATION

Voluminous literature has been devoted to defining species. Mayr (1957, 1969) has presented comprehensive reviews of species concepts, their history and their application. Currently, the most widely adopted of these is the "biological species concept." Based on this concept, Mayr (1969, p. 19) defines a species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups."

Despite more than 200 years of study, the species question within the coregonine fishes remains unsolved. Behnke (1970, 1972) has presented a lucid assessment of some of the problems associated with coregonine systematics along with a historical review. He noted that the problems are characterized by a genuine lack of agreement regarding the species concept, evolutionary affinities, mode of speciation and classification.

The most studied and least understood of coregonine fishes are members of the genus Coregonus. Basis of much of the existing confusion is extreme phenotypic plasticity and schooling and reproductive homing behavior which allows closely related populations to exist in sympatry and remain reproductively isolated (Behnke, 1970, 1972). Polytypic species and/or "ecotypes" among Coregonus populations have resulted in a proliferation of scientific names including tri-and quadranomials (Booke, 1968; Nikolsky and Reshetnikov, 1970). For a period of over 25 years Svardson and co-workers at the Institute of Freshwater Research, Drottningholm, have studied Coregonus complexes by applying

modern systematic principles with emphasis on ecological differentiation (see Svardson, 1949 through 1970). This work has been of major importance toward a better understanding of coregonine systematics. Svardson's (1970) contention that introgression is primarily responsible for the bewildering number of Coregonus forms appears well founded.

Members of the genus Prosopium have had a longer evolutionary history than those of Coregonus and have become more stabilized with regards to their expression of varied phenotypes (Booke, 1968). Problems in Prosopium systematics have been fewer but do exist.

The study of McCart (1970) concerning sibling species of pygmy whitefish (P. coulteri) in three Alaskan lakes illustrates the type of "species" problems confronting coregonine systematists. This study demonstrated that two morphologically and to some extent, ecologically distinct forms of pygmy whitefish occurred sympatrically in Aleknagik, Naknek and Chignik lakes. Furthermore, in Chignik lake, one form was subdivided into shallow and deep-water populations. McCart postulated that these forms differentiated in separate refugia during Pleistocene glaciation to the extent that upon secondary contact they maintained reproductive isolation. McCart suggested that introgression between the two populations may have produced the third population in Chignik lake. More recent work on systematics and distribution of pygmy whitefish (Lindsey and Franzin, 1972) has suggested that this species probably survived Wisconsin glaciation in several refugia, each containing one or more forms with morphological distinctions.

Behnke (1972, p. 657) has presented his views concerning the nomenclature of the sympatric sibling populations of P. coulteri reported by McCart and similar populations of Coregonus species.

> A strict adherence to the biological species concept, emphasizing sympatry with reproductive isolation as a major criterion for species recognition would result in a new species described for the three lakes in addition to a second new species for the third population in Chignik lake.
>
> If further evidence could be developed supporting McCarts' theory of two slightly differentiated stocks invading the three lakes and maintaining their genetic differentiation in sympatry, I (Behnke) would have no objections to the description of new species...For any other than salmonid fishes, full species recognition would be advised in such situations. However, ... species recognition solely on the basis of sympatric occurrence can get out of hand. Until strong evidence is developed demonstrating that all sympatric populations of a species complex can be segregated into monophyletic clusters, the arbitrary relegation of these populations to one species or another based on such labile traits as gillraker number should be avoided because the "species," if inclusive of several populations, is likely to be polyphyletic. An example of such a situation is found in Lindsey et al. (1970). If all sympatric populations of C. clupeaformis investigated by Lindsey were separated into two species based on gillraker number, the newly described species would by polyphyletic; that is, they have almost certainly been derived independently from C. clupeaformis in each geographical area. The alternative course, describing new species for each sympatric population of each lake or drainage basin, would reduce the meaning and evolutionary significance of the species category for some salmonid fishes to be more comparable to that of the local population or deme of other animals.

Behnke (1972) suggests that critical evaluation and comparison of specific proteins of proper evolutionary stability and identification of "marker" chromosomes demonstrating affinities of diverse populations derived from a common ancestor are promising approaches to the problem. If affinities are determined, there remains the problem of how to classify the many sympatric, reproductively isolated populations of independent origin which have initiated genetic separation from a common ancestor in postglacial times (Behnke, 1972).

Nikolsky and Reshnikov (1970) have urged the recognition of sub-subspecific categories while Behnke (1972) suggests the adoption of Mayr's (1969) polytopic subspecies. This

> is a practical device for grouping populations of independent origin but with convergent traits. The major difference from previous usage would be that polytopic subspecies...could be sympatric (Behnke, 1972, p. 663).

It is evident that coregonine systematics is problematic and that there is no general agreement concerning the species question. The magnitude of the taxonomic problem among Bear Lake Prosopium is less, however, since there are no conspecific populations.

Both sympatric and allopatric speciation have been advocated in the interpretation of the high variability and abundance of coregonine sibling species (Kosswig, 1963; Behnke, 1972). The formerly widely accepted theory of sympatric speciation asserts that one population can fragment into two or more reproductively isolated populations in the absence of geographic barriors. Currently, the more accepted view is allopatric speciation requiring geographic isolation for a sufficient time period to allow genetic differentiation to proceed to a degree that reproductive isolation is maintained upon secondary contact (Behnke, 1972). Mayr (1969) presents a lengthy discussion of these modes of speciation and very dogmatically refutes the possibility of sympatric speciation.

Sympatric speciation was proposed by Myers (1960) as the mode of speciation of Bear Lake endemics. Both Miller (1965) and Behnke (1972) have hypothesized that Bear Lake coregonines evolved in geographic isolation during the lacustrine history of the Bonneville basin. Allopatric speciation appears to be the more probably explanation in light of geologic history and available fossil evidence. The geologic history of the Bear River and associated lakes was reported by Bright (1963) and has been summarized by Miller (1965) and Malde (1968).

Prior to 34,000 years ago, the Bear River flowed from Bear Lake northwestward into the Snake River near the present city of Pocatello, Idaho. The river followed the present route of the lower Portneuf River. Subsequently, but still prior to 34,000 years ago, the ancestral Portneuf was damned by basaltic lava flows and the Portneuf and Bear Rivers were impounded to form Lake Thatcher. Further lava flows returned the Portneuf River to its former route and at various intervals may have permitted the Bear River to discharge westward via Lake Thatcher (Malde, 1968). Eventually, successive lava flow between the Bear and Portneuf Rivers built a barrier higher than the lowest rim at the southern end of the lake (elevation 5,445 ft) causing an overflow of Lake Thatcher southward into the Bonneville basin. Timing of this event is estimated to be 27,000 to 30,000 years ago by Bright (1963) and Malde (1968), respectively. Downcutting at the spillway ultimately formed the Oneida Narrows with a floor at an altitude of 4,600 ft.

According to Malde (1968) the rapid addition of water to Lake Bonneville from Lake Thatcher raised the level of the lake above its natural confinement at Red Rock Pass resulting in a catrostrophic flood into the Snake River Valley (30,000 years ago). The water level of Lake Bonneville then rapidly subsided, allowing for the downcutting of the Oneida Narrows and draining of Lake Thatcher. These findings are at odds with those of Bright (1963) who reported that Lake Bonneville rose to its highest level (5,100 ft) approximately 18,000 years ago at which time it overflowed its barrier at Red Rock Pass.

Regardless of the timing of these events, the hydrographic history of Lake Bonneville and associated lakes has been characterized by fluctuating water levels; Bear Lake is no exception. Three former levels

of Bear Lake were reported by Mansfield (1927), Hubbs and Miller (1948) and later described in detail by Williams, Willard and Parker (1962). The valleys occupied by Pleistocene Lake Bonneville lie only 30 miles to the west and the expanded stages of Bear Lake are thought to have an origin similar to those of Lake Bonneville (Williams et al., 1962). Former Bear Lake levels recognized, from oldest to youngest, are: (1) Willis Ranch (5,948 ft); (2) Garden City (5,938 ft); and (3) Liften (5,929 ft). Radiocarbon dating of shells from Willis Ranch and Lifton beach deposits gave respective ages of approximately 8,270 and 7,800 years before present, indicating a probably late-glacial or early post-glacial age (Williams et al., 1962). Drilling samples on the Lifton bar recovered shells at depths of 92 to 95 feet which dated approximately 28,000 years (Williams et al., 1962). From these data it is apparent that Bear Lake has had a history of fluctuating lake stages and further study may reveal levels not yet discovered.

Snyder (1919) hypothesized that Bear Lake coregonines were once numerous in Lake Bonneville, and their range possibly extended to other mountain lakes of the Columbia system and perhaps to Lake Lahontan and quaternary lakes of Oregon. Miller (1965, p. 578) relates the geologic history of Bear River and associated lakes to the probably origin of the endemic species flock of Bear Lake Prosopium as follows:

> ...there were three opportunities for fishes to enter Bear Lake: (1) early in the history of the Bear Valley when Bear River was a direct tributary of the early Snake River; (2) when the connection was first established with Lake Bonneville; and (3) after Lake Bonneville had overflowed into the Snake River. There were also at least three distinct lakes in which ancestral whitefishes could have developed in geographic isolation and later come to coexist in Bear Lake: (1) Bear Lake, (2) Lake Thatcher, and (3) Lake Bonneville. With the exception of Lake Thatcher, these lake basins probably had a long (Pleistocene or earlier) history of successive lake stages.

Recent fossil evidence (Stokes, Smith and Horn, 1964; Smith, Stokes and Horn, 1968) substantiates the hypothesis that Bear Lake endemics were at one time more widely distributed. Cottus extensus, P. gemmiferum and P. spilonotus or P. abyssicola were identified from fossil remains contained in deposits laid down during late stages of Lake Bonneville (11,000-13,000 years before present) and it appears probable that P. spilonotus or P. abyssicola (whichever is not represented) was also a part of this fauna.

How long these fishes have sympatrically occupied Bear Lake is not known, but it has been for a minimum of 7800 years (assuming allopatric speciation). At this time Bear Lake was isolated from the Bear River by deposition of an alluvial fan at the entry of Bear River into the valley. Bear River was not again joined to Bear Lake until 1912 when an artificial canal was constructed.

The age of the Bear Lake endemics is unknown. The above discussion relates the evolution of these fishes to the known hydrographic history of Bear River and associated lakes. Smith et al. (1968) point out that it is tempting to explain Bear Lake Prosopium evolution and distribution in terms of the Pleistocene hydrographic history of the area, but the broad zoogeographical pattern of species distribution was possibly determined earlier than late Pleistocene. This hypothesis remains to be confirmed.

Booke (1968, 1970), using cytotaxonomic parameters, concluded that members of the genus Prosopium were representatives of the earliest derivatives within the phylogeny of Coregoninae. Norden (1970) presented a hypothetical phylogeny of the genus Prosopium (Figure 29) based upon morphological characters and concluded that an ancestoral form of P.

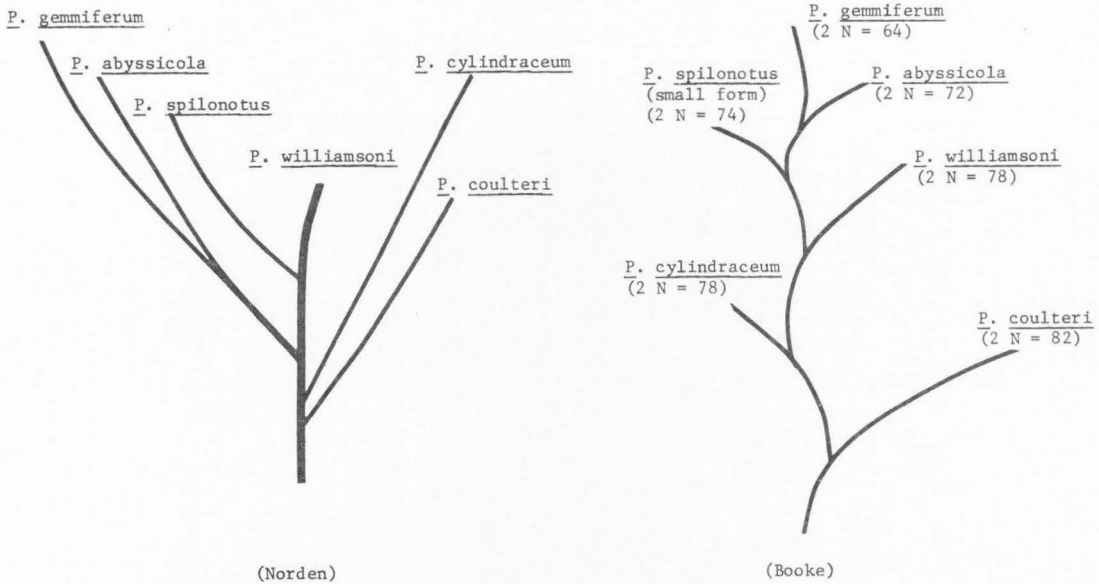

Figure 29. Possible phylogeny of the genus Prosopium as proposed by Norden (1970) and Booke (1974).

williamsoni independently gave rise to all other species of the group. The more recent findings of Booke (1974), based upon karyotype and morphology (Figure 29), appear more realistic. Diploid chromosome numbers range from 82 in P. coulteri to 64 in P. gemmiferum. During speciation diploid numbers tend to decrease with the most recent member having the lowest diploid number (White, 1954). These findings are supported by a re-evaluation of the morphological parameters discussed by Norden (1970).

The presence of parr marks in juveniles of Prosopium is considered a primative characteristic of Coregoninae (Norden, 1963; Behnke, 1970). Of the several thousand juvenile P. gemmiferum examined in the present study, none were observed to have parr marks. Apparent loss of this primative characteristic supports Booke's contention that P. gemmiferum is the most recently evolved Prosopium. (Parr marks were observed on one adult P. gemmiferum.) Booke's proposed phylogeny is also supported by discriminant function analysis of morphological characters which showed P. spilonotus (small form) to be most closely related to P. williamsoni.

Studies of Bear Lake whitefishes revealed no evidence of mass hybridization among forms. Reproductive isolating mechanisms, therefore, must be well established and a brief consideration of possible mechanisms is appropriate.

Mayr (1969) divides isolating mechanisms into two categories: premating and postmating. Premating isolating mechanisms prevent interspecific mating and include temporal, habitat, mechanical and ethological mechanisms. Postmating mechanisms are those that reduce full success of interspecific crosses and serve to maintain the integrity of the

species even though mating may occur. These mechanisms include gamete mortality, zygote mortality, hybrid inviability and hybrid sterility.

Temporal and spatial (habitat) spawning relationships of Bear Lake whitefishes were discussed above. Spawning times of adjacent spawning populations overlapped due to early ripening of males of each succeeding group to spawn (Table 24). The one exception was between P. gemmiferum and P. abyssicola in which no ripe male P. abyssicola were observed during the earlier spawning period of P. gemmiferum. The only observation of ripe females occurring simultaneously was P. spilonotus (large form) and P. spilonotus (small form), and in this instance the number of females of both forms was small. No ripe P. spilonotus (large form) were observed during or after peak spawning of P. spilonotus (small form). Spatial overlap of spawning was observed between P. spilonotus (large form), P. spilonotus (small form) and P. gemmiferum. Important differences in spatial segregation between overlapping forms might be revealed by detailed analysis. Slight differences in depth and substrate preference were noted between P. spilonotus (large form) and P. spilonotus (small form). Ripe P. abyssicola were not observed to overlap spatially or temporally with other spawning forms. From these observations, it is evident that temporal and spatial isolating mechanisms are incomplete among Bear Lake whitefishes and are therefore not fully responsible for reproductive isolation between forms.

Mechanical isolation, referring to copulation attempts with no transfer of sperm (Mayr, 1969) does not exist among whitefishes (Svardson, 1965). Since mechanical isolation does not exist and seasonal and habitat isolation are incomplete among Bear Lake whitefishes, ethological isolation is perhaps important. Of the several mechanisms

preventing interbreeding of animals, Mayr (1969) points out that ethological isolation is often the singly most important. Many studies invoke ethological isolation to be of major importance, but relatively few actually demonstrate the mechanism (Nelson, 1968).

In describing the spawning act of C. lavaretus, Fabricius and Lindroth (1954) report complete promiscuity with no fighting, nipping, chasing or other aggressive behavior. Smith[1] made similar observations regarding spawning behavior of P. williamsoni. No description of spawning behavior of spatially and temporally overlapping sympatric whitefishes has been reported.

Mate selection, based upon optical stimuli has been reported to be important in keeping some species of fish genetically isolated. Nelson (1968) comments on Hanson's evidence that sockeye salmon (Oncorhynchus nerka) tend to select mates of about their own size. Nelson (1968), however, was unable to demonstrate that physical differences of size, morphology or color were important in mate selection and therefore the reproductive isolation of two promiscuous species of suckers. Paetz[2] suggests that size differences may be important in the reproductive isolation of lake whitefish (C. clupeaformis) and cisco (C. artedii) where one of the species is dwarfed. This is based upon the observation that in lakes where adult cisco were very small in relation to adult lake whitefish no evidence of hybridization was found, but in lakes where mature cisco approach adult whitefish in size, hybridization occurred.

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[1]Personal communication with Ross A. Smith, Research Assistant, Utah Cooperative Fishery Unit, Utah State University, Logan, Utah, December, 1973.

[2]Excerpts from an in-progress Ph.D. Dissertation, Martin J. Paetz, June, 1972.

Size differences could be important in the reproductive isolation of P. spilonotus (large form) and P. spilonotus (small form) since the latter form rarely (if ever) reaches the size at which P. spilonotus (large form) matures. In gill-net collections females of neither group were found in close proximity to males of the other form as one would expect if fishes were captured during the spawning act. Monospecific groups of one female and several males were often found in this relationship. Size differences among other Bear Lake forms are similar and would not be expected to be the basis of ethological reproductive isolation--if such a mechanism is operable.

Gametic mortality and zygote mortality were shown by hybridization experiments to be ineffective postmating isolating mechanisms among Prosopium crosses. Hybrid crosses between simultaneously ripe species were found to be no less successful than conspecific crosses. A P. williamsoni x P. gemmiferum cross was the only mating between species not found ripe at the same time, which produced living embryos. Poor success of this cross could be attributed to genetic incompatibility or to condition of the sex products of parent fish. Success of crosses between groups not found ripe simultaneously are of purely academic interest since they could not occur under natural conditions. Compatibility of these crosses could, however, provide evidence useful in interpreting the phylogeny of the group.

Viability of successful hybrid crosses, based upon laboratory culture, equalled that of monospecific crosses and hybrids appeared to display heterosis. It is suggested, however, that under natural conditions, progeny of the P. abyssicola x P. gemmiferum cross would be at a selective disadvantage due to the large percentage of observed jaw

deformities. In general, it appears that hybrid viability is not an important postmating mechanism, with the possible exception of the P. abyssicola x P. gemmiferum cross.

Svardson (1965) reported that viability of Coregonus F1 hybrids was increased by 10-20 percent compared to parent species and that heterosis (Svardson, 1970) probably accounted for superior survival during their first year of life. He concluded that if spontaneous hybridization occurs among sympatric whitefish populations, the hybrids are favored by natural selection at least during their first summer.

Hybrid sterility in whitefishes has been experimentally studied by Swedish scientists. Fertility of F1 hybrids of Coregonus species was reported to be good in all cases while varying degrees of fertility were observed for F2 and later generations (Svardson, 1965, 1970). Paetz[3] found that eggs of natural hybrids of C. clupeaformis and C. artedii were over 99 percent inviable, indicating near total sterility. Some male hybrids, however, produced functional sperm. The degree of hybrid sterility is probably a function of the closeness of relationship of hybridized forms. Even though F1 hybrids may be fully fertile, reproductive success may be reduced by intermediate ecological and behavioral characteristics (Mayr, 1969; Lindsey, 1963).

Little evidence concerning sterility of Bear Lake hybrids was collected in the present study. The three male and two female P. gemmiferum-like hybrids collected from the natural population appeared to have normal gonad development. One male (collected during the spawning run of P. gemmiferum) had well developed tubercles and the testes filled

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[3]Excerpts from an in-progress Ph.D. Dissertation, Martin J. Paetz, June, 1972.

the body cavity. Viability of the sperm, however, was not determined. Sigler and Miller (1963) report that one P. gemmiferum hybrid examined by them had no trace of a gonad.

Neither time nor facilities permitted experimental examination of sterility of known hybrids and only one observation relating to this mechanism was made. Examination of a group of two and one-half year old P. abyssicola x P. gemmiferum hybrids revealed good gonad development in both sexes. Male gonads filled the body cavity and microscopic examination revealed good sperm motility. Females were not as well developed but were obviously maturing. Variation in egg size within ovaries of some females suggested that gonad development was possibly abnormal; other females appeared normal.

Reproductive isolation between Bear Lake whitefishes is thought to be maintained by a combination of temporal, spatial and ethological premating isolating mechanisms; postmating mechanisms are nonfunctional with the possible exception of hybrid sterility.

The taxonomic status of Bear Lake endemic whitefishes has remained tenuous since their original description. Clarification of this problem was the major objective of the present work.

Morphological analysis revealed five forms of Bear Lake whitefishes. Prosopium gemmiferum and P. abyssicola were well differentiated from other forms and were treated as originally described (Snyder, 1919). The P. spilonotus group, however, was found to be made up of two morphologically distinct populations which were referred to as P. spilonotus (small form) and P. spilonotus (large form). The fifth group, represented by only five specimens, was intermediate between P. gemmiferum and either P. spilonotus (small form) or P. abyssicola and was

hypothesized to be of hybrid origin. Discriminant function analysis of the four major groups and P. williamsoni (Logan River) confirmed morphological differentiation between all forms.

Elucidation of the origin of the two groups of P. spilonotus and the P. gemmiferum-like hybrids became the central theme of the study. Experimental hybridization among forms of Bear Lake Prosopium and P. williamsoni revealed that P. gemmiferum-like specimens originate from hybridization between P. gemmiferum and P. spilonotus (small form) and/or P. abyssicola.

Spawning relationships among species dictated that if either form of P. spilonotus was of hybrid origin, parental forms of the hybrid would have to be P. williamsoni and the other form of P. spilonotus. Known hybrids between P. williamsoni and P. spilonotus (small form) did not indicate hybrid origin of the P. spilonotus (large form) group; hybrids between P. williamsoni and P. spilonotus (large form) were too small at this writing to be examined morphologically. It is doubtful that either of these crosses would occur in Bear Lake since P. williamsoni is rare or absent; no specimens of this species were collected in four years of field work associated with the present study. Further, the following circumstantial evidence appears to refute the possibility of P. spilonotus (small form) originating from a P. williamsoni-P. spilonotus (large form) parentage. Maximum size of P. spilonotus (small form) is much smaller than either possible parent; P. spilonotus (small form) spawns later than either P. williamsoni or P. spilonotus (large form). Hybrids are usually intermediate or like one parent.

Assuming neither form of P. spilonotus is of hybrid origin, the systematic status of these fishes was examined. Electrophoretic analysis

of general proteins and several enzyme systems of various tissues showed much similarity between all Bear Lake Prosopium. In only two instances were there species differences and in those cases both forms of P. spilonotus were similar.

Highly significant in evaluation of these forms were ecological differences manifested in growth histories and reproductive cycles. Prosopium spilonotus (large form) was found to grow more rapidly, obtain a much larger maximum size and live longer than P. spilonotus (small form). This size relationship is typical among closely related sympatric coregonines and Svardson (1954) hypothesized that it results from interspecific competition. He suggested that, because of pressures of competition, there is a tendency for different species to consume different sized food particles, thus resulting in different growth rates, which in turn serve as isolating mechanisms keeping species in different ecological niches. Only cursory observations of food habits of P. spilonotus (large form) and P. spilonotus (small form) were made but these observations lend support to this hypothesis. P. spilonotus (large form) appeared to be highly piscivorous after age five while P. spilonotus (small form) fed predominately upon benthic invertebrates; fish were never observed in stomach contents of P. spilonotus (small form).

Reproductive characteristics of these forms (Table 24) were discussed above. Age and size at maturity differ markedly between P. spilonotus (small form) and P. spilonotus (large form). Although both spatial and temporal overlap of spawning was observed, there was no indication of mass hybridization. Hybrids between these forms, however, would be difficult to detect since morphological composition of P. spilonotus (small form) and P. spilonotus (large form) is very similar. Only 17

of over 1,500 specimens examined were considered as intermediates between the two forms. The predictive model formulated by discriminant function analysis of morphological characters classified six of these as P. spilonotus (small form) and 11 as P. spilonotus (large form). In addition, two of 138 specimens originally classified as P. spilonotus (large form) were reclassified by discriminant analysis as P. spilonotus (small form). Re-examination of these two specimens revealed they were intermediate in those characters important in the discriminant analysis. These 19 specimens are possibly of hybrid origin but could just as well be morphological variants. If hybridization is occurring between the two forms of P. spilonotus, it is not thought to be of significant magnitude.

The hydrographic history of Bear Lake is also important in evaluating P. spilonotus (small form) and P. spilonotus (large form). Radiocarbon dating has provided evidence that Bear Lake has been isolated from the Bear River for a minimum of 7,800 years (Williams et al., 1962). Assuming allopatric speciation, P. spilonotus (small form) and P. spilonotus (large form) have lived sympatrically for at least this length of time. Had reproductive isolating mechanisms not been well developed in these forms, fusion would have occurred. Sympatric speciation in Bear Lake is improbable based upon low niche diversity and known fossil evidence.

Morphological and ecological analyses, combined with results of experimental hybridization, have provided abundant evidence supporting separate recognition of the two forms of P. spilonotus. Karyotypes of P. gemmiferum, P. abyssicola and P. spilonotus (small form) have been determined (Figure 29) and are unique for each species (Booke, 1974).

If the karyotype of P. spilonotus (large form) is found to also be unique, there should be no question that the two forms of P. spilonotus represent distinct species. Booke (1968) points out that if sympatric species are isolated reproductively and have different karyotypes, then speciation is complete since these differences would not be maintained in a freely interbreeding population.

Final clarification of the taxonomic status of P. spilonotus (small form) and P. spilonotus (large form) will not come until the karyotype of P. spilonotus (large form) is determined. However, based upon (1) morphological distinctions supported by multiple discriminant function analysis, (2) failure of hybridization experiments to explain the origin of either of these forms, and (3) ecological differences manifested in distinctly different growth patterns, temporal distinctions in spawning, and marked differences in age and size at maturity, it appears warrented to tentatively recognize these forms as distinct species.

The type specimen of P. spilonotus designated by Snyder (1919) in the original description was 425 mm in length and therefore is synonymous with P. spilonotus (large form) as treated here. It is recommended that this species retain the original name. Prosopium spilonotus (small form), as discussed in the present study, is tentatively designated as a new species, Prosopium nannomaculatum (manuscript), meaning spotted dwarf; the suggested common name is spotted whitefish.

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APPENDIXES

Appendix A

Linear Regression Analysis

Table 25. Results of linear regression analysis of body proportions of *P. abyssicola*, Bear Lake, Utah-Idaho. (N=120; standard length, 91-199 millimeters)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	-1.477	.115	.82
Standard length	Adipose base length	1.001	.066	.60
Standard length	Adipose height	.601	.088	.71
Standard length	Pelvic base length	- .177	.028	.54
Standard length	Maxillary length	- .139	.047	.81
Standard length	Maxillary width	.293	.022	.57
Standard length	Eye diameter	.955	.045	.77
Standard length	Interorbital width	- .967	.062	.83
Standard length	Postorbital head length	- .469	.121	.90
Standard length	Head length	- .979	.239	.93
Standard length	Peduncle depth	-1.354	.077	.88
Standard length	Peduncle width	- .572	.037	.70
Standard length	Pelvic to Anal distance	.372	.259	.87
Standard length	Gill raker length	.271	.012	.58
Head length	Maxillary length	.149	.194	.85
Head length	Maxillary width	.411	.093	.62
Head length	Eye diameter	1.220	.185	.81
Head length	Interorbital width	- .554	.254	.87
Head length	Postorbital head length	.272	.499	.94
Head length	Gill raker length	.411	.049	.57

Table 26. Results of linear regression analysis of body proportions of P. spilonotus (small form), Bear Lake, Utah-Idaho. (N=102; standard length, 95.5-221 millimeters)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	- .257		.82
Standard length	Adipose base length	- .396	.062	.65
Standard length	Adipose height	- .456	.086	.78
Standard length	Pelvic base length	- .174	.028	.82
Standard length	Maxillary length	- .662	.056	.88
Standard length	Maxillary width	- .214	.030	.83
Standard length	Eye diameter	2.002	.039	.84
Standard length	Interorbital width	- .557	.060	.89
Standard length	Postorbital head length	- .169	.114	.91
Standard length	Head length	.321	.223	.95
Standard length	Peduncle depth	-1.137	.077	.92
Standard length	Peduncle width	-1.161	.045	.83
Standard length	Pelvic to Anal distance	- .897	.276	.93
Standard length	Gill raker length	.183	.012	.69
Head length	Maxillary length	- .779	.254	.93
Head length	Maxillary width	- .235	.134	.87
Head length	Eye diameter	2.051	.173	.85
Head length	Interorbital width	- .568	.269	.92
Head length	Postorbital head length	- .394	.514	.97
Head length	Gill raker length	.223	.054	.69

Table 27. Results of linear regression analysis of body proportions of P. spilonotus (large form), Bear Lake, Utah-Idaho. (N=27; standard length, 260-408 millimeters)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	-4.652	.129	.85
Standard length	Adipose base length	-2.767	.069	.82
Standard length	Adipose height	-3.574	.096	.88
Standard length	Pelvic base length	-2.947	.041	.88
Standard length	Maxillary length	-5.575	.090	.90
Standard length	Maxillary width	- .321	.032	.75
Standard length	Eye diameter	6.363	.022	.72
Standard length	Interorbital width	-4.234	.083	.88
Standard length	Postorbital head length	-1.579	.137	.97
Standard length	Head length	-3.371	.272	.95
Standard length	Peduncle depth	-2.785	.081	.94
Standard length	Peduncle width	-2.802	.048	.86
Standard length	Pelvic to Anal distance	-3.727	.255	.89
Standard length	Gill raker length	1.627	.009	.42
Head length	Maxillary length	-4.597	.337	.96
Head length	Maxillary width	- .153	.119	.82
Head length	Eye diameter	6.743	.078	.73
Head length	Interorbital width	-2.578	.298	.88
Head length	Postorbital head length	1.213	.492	.96
Head length	Gill raker length	1.771	.031	.43

Table 28. Results of linear regression analysis of body proportions of P. species, Bear Lake, Utah-Idaho. (N=108; standard length, 108-268 millimeters)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	-1.192	.117	.87
Standard length	Adipose base length	.366	.059	.75
Standard length	Adipose height	- .054	.082	.80
Standard length	Pelvic base length	- .750	.032	.90
Standard length	Maxillary length	-2.957	.079	.93
Standard length	Maxillary width	- .636	.033	.88
Standard length	Eye diameter	3.527	.032	.86
Standard length	Interorbital width	-1.632	.070	.92
Standard length	Postorbital head length	-2.222	.136	.96
Standard length	Head length	-3.289	.265	.97
Standard length	Peduncle depth	-1.604	.077	.95
Standard length	Peduncle width	- .419	.039	.84
Standard length	Pelvic to Anal distance	1.286	.245	.93
Standard length	Gill raker length	- .102	.015	.81
Head length	Maxillary length	-2.022	.299	.97
Head length	Maxillary width	- .187	.122	.90
Head length	Eye diameter	3.966	.120	.88
Head length	Interorbital width	.669	.260	.94
Head length	Postorbital head length	- .463	.511	.98
Head length	Gill raker length	.127	.055	.80

Table 29. Results of linear regression analysis of body proportions of *P. gemmiferum*, Bear Lake, Utah-Idaho. (N=21; standard length, 111.5-177.0)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	- .947	.102	.88
Standard length	Adipose base length	1.743	.038	.70
Standard length	Adipose height	.167	.066	.83
Standard length	Pelvic base length	- .993	.030	.84
Standard length	Maxillary length	1.133	.059	.91
Standard length	Maxillary width	.445	.022	.81
Standard length	Eye diameter	.953	.040	.82
Standard length	Interorbital width	- .302	.055	.84
Standard length	Postorbital head length	1.383	.116	.94
Standard length	Head length	1.047	.244	.96
Standard length	Peduncle depth	-1.136	.073	.90
Standard length	Peduncle width	- .722	.040	.85
Standard length	Pelvic to Anal distance	-3.331	.249	.89
Standard length	Gill raker length	- .284	.037	.86
Head length	Maxillary length	.799	.243	.94
Head length	Maxillary width	.454	.089	.77
Head length	Eye diameter	.626	.166	.88
Head length	Interorbital width	.907	.233	.93
Head length	Postorbital head length	.703	.479	.98
Head length	Gill raker length	- .515	.152	.90

Table 30. Results of linear regression analysis of body proportions of *P. williamsoni*, Logan River, Utah. (N=16; standard length, 138-285 millimeters)

Independent Variable X	Dependent Variable Y	a	b	r^2
Standard length	Dorsal base length	-2.146	.141	.96
Standard length	Adipose base length	- .341	.077	.91
Standard length	Adipose height	-1.473	.104	.91
Standard length	Pelvic base length	-1.186	.033	.98
Standard length	Maxillary length	- .282	.046	.92
Standard length	Maxillary width	.880	.020	.83
Standard length	Eye diameter	3.250	.024	.91
Standard length	Interorbital width	-1.511	.064	.97
Standard length	Postorbital head length	- .063	.119	.97
Standard length	Head length	4.392	.195	.96
Standard length	Peduncle depth	-3.008	.088	.97
Standard length	Peduncle width	-1.638	.052	.94
Standard length	Pelvic to Anal distance	-2.541	.265	.95
Standard length	Gill raker length	.324	.012	.81
Head length	Maxillary length	-1.428	.239	.98
Head length	Maxillary width	.377	.103	.89
Head length	Eye diameter	2.750	.122	.93
Head length	Interorbital width			
Head length	Postorbital head length	-2.354	.603	.99
Head length	Gill raker length	- .010	.061	.89

Appendix B

Distribution of Morphological Characters

Table 31. Comparison of dorsal base lengths among members of the Bear Lake *Prosopium* complex, *P. williamsoni* and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	130-134	135-139	140-144	Mean
P. spilonotus (small form)	102	1	2	10	15	28	33	9	4					108
P. spilonotus (large form)	27				3	4	7	9	2	2				114
P. species	108		1	4	16	25	27	23	11	1				111
P. abyssicola	120		3	14	31	40	22	8	2					106
P. gemmiferum	21	3	5	9	3	1								96
P. williamsoni	16							1	1	4	5	4	1	131
P. gemmiferum-like	5				3	2								104
Homo - and Heterospecific Crosses														
P. spilonotus (small form)	30			7	15	6	2							102
P. spilonotus (small form) X *P. gemmiferum*	41	1	4	10	17	7	2							101
P. abyssicola X *P. gemmiferum*	40		3	9	14	10	3	1						102
P. abyssicola	35			2	3	7	12	9	2					111
P. williamsoni	13							3	1	4	5			126
P. williamsoni X *P. spilonotus* (small form)	39				2	10	13	11	3					113

Table 32. Comparison of pelvic base lengths among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	Mean
P. spilonotus (small form)	102			16	43	34	9				27
P. spilonotus (large form)	27				1	8	4	6	8		31
P. species	108		4	8	45	38	10	3			27
P. abyssicola	120	1	3	35	42	18	10	8	2	1	27
P. gemmiferum	21	1	7	10	1	2					25
P. williamsoni	16			5	3	6	2				27
P. gemmiferum-like	5	1	2	2							23

[a]Measurements expressed in thousandths of standard length.

Table 33. Comparison of maxillary widths among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	Mean
P. spilonotus (small form)	102			2	20	47	27	6			29
P. spilonotus (large form)	27			1	1	8	7	6	4		30
P. species	108			1	21	41	34	8	3		29
P. abyssicola	120	10	31	52	15	9	2	1			24
P. gemmiferum	21		1	11	7	2					25
P. williamsoni	16	3	5	6	2						24
P. gemmiferum-like	5			3	2						25

[a]Measurements expressed in thousandths of standard length.

Table 34. Comparison of eye diameters among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	34-37	38-41	42-45	46-49	50-53	54-57	58-61	62-65	66-69	Mean
P. spilonotus (small form)	102			2	23	57	20				52
P. spilonotus (large form)	27	4	6	14	2	1					42
P. species	108			4	31	47	18	8			51
P. abyssicola	120			1	44	56	17	2			51
P. gemmiferum	21			10	11						45
P. williamsoni	16	8	4	2	2						40
P. gemmiferum-like	5				3	2					49
Homo - and Heterospecific Crosses											
P. spilonotus (small form)	30					1	7	13	7	2	60
P. spilonotus (small form) X P. gemmiferum	41				2	12	19	6	2		55
P. abyssicola X P. gemmiferum	40			1	7	20	8	3	1		53
P. abyssicola	35				2	5	11	10	6	1	57
P. williamsoni	13				2	6	3	2			53
P. williamsoni X P. spilonotus (small form)	39						7	22	9	1	60

Table 35. Comparison of interorbital widths among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	47-51	52-56	57-61	62-66	67-71	72-76	77-81	Mean
P. spilonotus (small form)	102	1	47	51	3				57
P. spilonotus (large form)	27				7	11	8	1	70
P. species	108		12	51	38	7			61
P. abyssicola	120	9	63	45	3				56
P. gemmiferum	21	8	10	3					52
P. williamsoni	16		7	8	1				56
P. gemmiferum-like	5	4		1					51
Homo - and Heterospecific Crosses									
P. spilonotus (small form)	30		11	15	4				58
P. spilonotus (small form) X P. gemmiferum	41		13	26	2				58
P. abyssicola X P. gemmiferum	40	9	24	7					54
P. abyssicola	35	4	19	10	2				55
P. williamsoni	13	2	1	5	5				60
P. williamsoni X P. spilonotus (small form)	39	1	1	9	25	3			63

Table 36. Comparison of peduncle widths among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	28-29	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-47	48-49	Mean
P. spilonotus (small form)	102	1		1	9	31	30	18	9	2	1		38
P. spilonotus (large form)	27				2	5	8	6	5	1			39
P. species	108			9	20	36	21	18	2	2			37
P. abyssicola	120	5	13	41	36	13	8	3	1				34
P. gemmiferum	21		2	2	4	9	4						35
P. williamsoni	16						1	3	2	3	4	3	44
P. gemmiferum-like	5			1	2	1			1				36

[a]Measurements expressed in thousandths of head length.

Table 37. Comparison of peduncle depths among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	61-62	63-64	65-66	67-68	69-70	71-72	73-74	75-76	77-78	79-80	81-82	Mean
P. spilonotus (small form)	102	3	2	4	21	26	27	11	5	2	1		70
P. spilonotus (large form)	27			2	1	3	6	8	6	1			72
P. species	108	5	8	20	24	28	17	3	2	1			68
P. abyssicola	120	4	5	15	33	28	17	12	6				69
P. gemmiferum	21	2	4	6	6	2		1					65
P. williamsoni	16		1		1	2	2	3	1	4	1	1	74
P. gemmiferum-like	5	1	2	1				1					65

[a]Measurements expressed in thousandths of head length.

Table 38. Comparison of pelvic to anal distances among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	208-215	216-223	224-231	232-239	240-247	248-255	256-263	264-271	272-279	280-287	288-295	Mean
P. spilonotus (small form)	102					1		24	32	21	21	3	271
P. spilonotus (large form)	27	1		5	4	9	4	2	2				243
P. species	108			3	8	24	34	27	6	5	1		252
P. abyssicola	120			1	1	14	18	35	32	17	1	1	261
P. gemmiferum	21	3	3	8	6			1					227
P. williamsoni	16			1	2	2	4	2	4	1			253
P. gemmiferum-like	5				1	3	1						242
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30			1	2	8	11	5	3				251
P. spilonotus (small form) X P. gemmiferum	41	1	4	7	12	9	7	1					237
P. abyssicola X P. gemmiferum	40	1	5	11	14	7	2						233
P. abyssicola	35				2	5	12	11	5				254
P. williamsoni	13					5	6	2					250
P. williamsoni X P. spilonotus (small form)	39				13	8	13	3	1		1		246

Table 39. Comparison of gill-raker lengths among members of the Bear Lake *Prosopium* complex, *P. williamsoni* and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	8-10	11-13	14-16	17-19	20-22	23-25	26-28	29-31	32-34	35-37	38-40	Mean
P. spilonotus (small form)	102		52	50									14
P. spilonotus (large form)	27	1	9	17									14
P. species	108		20	83	5								14
P. abyssicola	120		39	81									14
P. gemmiferum	21									9	9	3	35
P. williamsoni	16		9	7									13
P. gemmiferum-like	5						3	1	1				26
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30		1	12	17								17
P. spilonotus (small form) X *P. gemmiferum*	41						13	27	1				26
P. abyssicola X *P. gemmiferum*	40					7	15	17	1				25
P. abyssicola	35			10	24	1							17
P. williamsoni	13		5	7	1								14
P. williamsoni X *P. spilonotus* (small form)	39		10	16	13								15

Table 40. Comparison of scales in lateral line among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	64-66	67-69	70-72	73-75	76-78	79-81	82-84	85-87	88-90	91-93	Mean
P. spilonotus (small form)	102					9	31	28	22	12		82.7
P. spilonotus (large form)	27					4	8	7	4	4		82.9
P. species	108				1	17	19	32	29	7	3	83.0
P. abyssicola	120	9	33	39	28	10	1					71.0
P. gemmiferum	21			2	5	9	5					76.4
P. williamsoni	16					1		8	7			84.0
P. gemmiferum-like	8		1	2	3	1	1					73.5
Homo - and Heterospecific Crosses												
P. spilonotus (small form)	30						2	4	10	12	2	86.7
P. spilonotus (small form) X P. gemmiferum	41						5	16	13	6	1	84.6
P. abyssicola X P. gemmiferum	40				3	20	14	3				78.4
P. abyssicola	35		3	8	11	8	4	1				74.5
P. williamsoni	13						3	3	3	3	1	84.6
P. williamsoni X P. spilonotus (small form)	39					1	3	11	17	7		85.1

Table 41. Comparison of scales above and below lateral line among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	Scales above Lateral Line						Scales below Lateral Line				
		7	8	9	10	11	Mean	5	6	7	8	Mean
P. spilonotus (small form)	102			50	52		9.5		4	97	1	7.0
P. spilonotus (large form)	27			6	20	1	9.8			25	2	7.1
P. species	108			24	84		9.8		4	93	11	7.1
P. abyssicola	120	2	90	28			8.2		91	28	1	6.3
P. gemmiferum	21	2	17	2			7.9	2	19			5.9
P. williamsoni	16			2	11	3	10.1			15	1	7.1
P. gemmiferum-like	8	1	7				7.9	1	7			5.9
Homo - and Heterospecific Crosses												
P. spilonotus (small form)	30		1	25	4		9.1		6	23	1	6.8
P. spilonotus (small form) X P. gemmiferum	41		12	30			8.7		23	18		6.4
P. abyssicola X P. gemmiferum	40		15	25			8.6		15	25		6.6
P. abyssicola	35	1	14	18	2		8.6	5	11	16	3	6.5
P. williamsoni	13			6	6	1	9.6			11	2	7.2
P. williamsoni X P. spilonotus (small form)	39			35	4		9.1		1	36	2	7.0

Table 42. Comparison of scales around body among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.

Form	N	30–31	32–33	34–35	36–37	38–39	40–41	42–43	44–45	Mean
P. spilonotus (small form)	102				7	38	51	6		39.5
P. spilonotus (large form)	27					6	13	6	2	40.6
P. species	108					17	65	25	1	40.6
P. abyssicola	120		10	60	40	8	2			35.3
P. gemmiferum	21	1	8	9	3					33.6
P. williamsoni	16					1	8	7		41.4
P. gemmiferum-like	8		2	3	3					34.5

Table 43. Comparison of scales around peduncle among members of the Bear Lake Prosopium complex and P. williamsoni.

Form	N	17	18	19	20	21	22	23	Mean
P. spilonotus (small form)	102				26	61	13	2	20.9
P. spilonotus (large form)	27				1	10	10	6	21.8
P. species	108				9	50	35	14	21.5
P. abyssicola	120	2	26	80	10	2			18.9
P. gemmiferum	21		1	5	10	5			19.9
P. williamsoni	16				7	9			20.6
P. gemmiferum-like	8		3	5					18.6

Table 44. Comparison of anterior gill-rakers (upper limb) among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	7	8	9	10	11	12	13	14	15	16	17	Mean
P. spilonotus (small form)	102	2	30	63	7								8.7
P. spilonotus (large form)	27		5	17	5								9.0
P. species	108		17	76	14	1							9.0
P. abyssicola	120		10	65	41	4							9.3
P. gemmiferum	21								6	6	7	2	15.6
P. williamsoni	16		3	11	2								8.9
P. gemmiferum-like	5				1	3	1						11.0
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30	3	20	7									8.1
P. spilonotus (small form) X P. gemmiferum	41				2	8	18	13					12.0
P. abyssicola X P. gemmiferum	40				2	10	21	6	1				11.9
P. abyssicola	35	3	18	13	1								8.3
P. williamsoni	13	1	5	7									8.5
P. williamsoni X P. spilonotus (small form)	39	3	24	10	2								8.3

Table 45. Comparison of anterior gill-rakers (lower limb) among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific crosses. (Measurements expressed in thousandths of standard length.)

Form	N	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26	27-28	29-30	31-32	33-34	Mean
P. spilonotus (small form)	102	49	53											12.6
P. spilonotus (large form)	27		54	3										13.7
P. species	108	11	79	18										13.6
P. abyssicola	120	13	96	11										13.6
P. gemmiferum	21								12	7	1		1	27.2
P. williamsoni	16	6	10											12.8
P. gemmiferum-like	5				3	2								18.4
Homo - and Heterospecific Crosses														
P. spilonotus (small form)	30	12	18											12.7
P. spilonotus (small form) X P. gemmiferum	41				15	24	2							18.8
P. abyssicola X P. gemmiferum	40				16	23	1							18.9
P. abyssicola	35	7	28											13.1
P. williamsoni	13	1	12											13.2
P. williamsoni X P. spilonotus (small form)	39	20	17	1										12.7

Table 46. Comparison of total anterior gill-rakers among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	17-19	20-22	23-25	26-28	29-31	32-34	35-37	38-40	41-43	44-46	47-49	Mean
P. spilonotus (small form)	102	5	80	17									21.3
P. spilonotus (large form)	27		10	17									22.7
P. species	108		49	58	1								22.6
P. abyssicola	120		44	74	2								22.9
P. gemmiferum	21								7	11	2	1	42.8
P. williamsoni	16		11	5									21.8
P. gemmiferum-like	8				2	6							29.0
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30	3	26	1									20.8
P. spilonotus (small form) X P. gemmiferum	41				3	27	11						30.8
P. abyssicola X P. gemmiferum	40				2	22	16						30.8
P. abyssicola	35		30	5									21.5
P. williamsoni	13	1	9	3									21.7
P. williamsoni X P. spilonotus (small form)	39	2	32	5									20.9

Table 47. Comparison of posterior gill-rakers (upper limb) among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Mean
P. spilonotus (small form)	102	2	40	50	8	2											6.7
P. spilonotus (large form)	27		6	13	7	1											7.1
P. species	108		14	51	41	2											7.3
P. abyssicola	120		10	49	45	13	2	1									7.5
P. gemmiferum	21										2	5	10	2	1	1	16.2
P. williamsoni	16			2	13	1											7.9
P. gemmiferum-like	5				1		2	1		1							10.4
Homo - and Heterospecific Crosses																	
P. spilonotus (small form)	30	1	21	7													16.2
P. spilonotus (small form) X P. gemmiferum	41					2	19	16	3	1							10.6
P. abyssicola X P. gemmiferum	40				1	16	20	2	1								9.7
P. abyssicola	35	1	9	16	9												6.9
P. williamsoni	13		7	5	1												6.5
P. williamsoni X P. spilonotus (small form)	39	6	23	10													6.1

Table 48. Comparison of posterior gill-rakers (lower limb) among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26	27-28	29-30	Mean
P. spilonotus (small form)	102	45	54	3									10.8
P. spilonotus (large form)	27		22	5									11.9
P. species	108	6	84	18									11.8
P. abyssicola	120	12	81	27									11.7
P. gemmiferum	21							1	2	5	8	5	28.0
P. williamsoni	16		15	1									11.3
P. gemmiferum-like	5				1	2	2						18.0
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30	14	15	1									10.7
P. spilonotus (small form) X P. gemmiferum	41				6	28	7						17.5
P. abyssicola X P. gemmiferum	40				7	28	5						17.3
P. abyssicola	35	6	25	4									11.3
P. williamsoni	13	4	8	1									10.9
P. williamsoni X P. spilonotus (small form)	39	14	25										10.9

Table 49. Comparison of total posterior gill-rakers among members of the Bear Lake Prosopium complex, P. williamsoni and homo - and heterospecific laboratory crosses. (Measurements expressed in thousandths of standard length.)

Form	N	15-17	18-20	21-23	24-26	27-29	30-32	33-35	36-38	39-41	42-44	45-47	Mean
P. spilonotus (small form)	102	58	41	3									17.5
P. spilonotus (large form)	27	4	21	2									19.0
P. species	108	10	87	11									19.1
P. abyssicola	120	11	95	14									19.2
P. gemmiferum	21								2	4	8	7	44.2
P. williamsoni	16		15	1									19.2
P. gemmiferum-like	5				1	3	1						28.4
Homo - and Heterospecific Crosses													
P. spilonotus (small form)	30	23	7										16.9
P. spilonotus (small form) X P. gemmiferum	41				5	31	5						28.1
P. abyssicola X P. gemmiferum	40				17	22	1						26.9
P. abyssicola	35	9	25	1									18.3
P. williamsoni	13	6	7										17.5
P. williamsoni X P. spilonotus (small form)	39	28	11										17.0

Table 50. Comparison of number of pyloric caeca among members of the Bear Lake Prosopium complex and P. williamsoni.

Form	N	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150-159	160-169	170-179	Mean
P. spilonotus (small form)	120					2	20	29	32	25	9	2	1			113.4
P. spilonotus (large form)	44							2	6	8	11	6	7	2	2	136.7
P. species	53					3	1		12	7	17	7	4	1	1	129.4
P. abyssicola	122		7	17	53	33	11	1								77.0
P. gemmiferum[a]	312	├	─	─	─	─	┤									65.0
P. williamsoni[b]	357		├	─	─	─	─	─	─	─	─	┤				110.4
P. gemmiferum-like	3			1	2											72.0

[a]Counts taken from Perry (1943).

[b]Counts taken from Holt (1960).

Table 51. Comparison of maxillary length/head length ratios among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	176-185	186-195	196-205	206-215	216-225	226-235	236-245	246-255	256-265	266-275	276-285	286-295	296-306	Mean
P. spilonotus (small form)	102				2	23	38	29	10						233
P. spilonotus (large form)	27								2	2	7	6	6	4	281
P. species	108				1		3	13	41	28	17	3	2		256
P. abyssicola	120	15	36	44	21	4									198
P. gemmiferum	21								2	11	7		1		263
P. williamsoni	16		1	6	6	3									208
P. gemmiferum-like	5							2	3						247

[a]Measurements expressed in thousandths of head length.

Table 52. Comparison of maxillary width/head length ratios among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	82-87	88-93	94-99	100-105	106-111	112-117	118-123	124-129	130-135	136-141	142-147	Mean
P. spilonotus (small form)	102						7	17	37	28	10	3	128
P. spilonotus (large form)	27			1	2	4	6	9	4	1			117
P. species	108				2	17	31	39	15	3	1		117
P. abyssicola	120	1	12	24	41	24	10	5	1	2			104
P. gemmiferum	21		1	9	5	5	1						101
P. williamsoni	16		1		3	2	8	1	1				111
P. gemmiferum-like	5		1		1	2	1						105

[a]Measurements expressed in thousandths of head length.

Table 53. Comparison of eye diameter/head length ratios among members of the Bear Lake Prosopium complex and P. williamsoni.[a]

Form	N	134-143	144-153	154-163	164-173	174-183	184-193	194-203	204-213	214-223	224-233	234-243	244-253	254-263	264-273	Mean
P. spilonotus (small form)	102							1	9	22	35	25	7	1	2	229
P. spilonotus (large form)	27	4	2	11	6	3	1									160
P. species	108				2	4	17	23	28	14	16	3	1			207
P. abyssicola	120					1	1	8	35	42	21	12				217
P. gemmiferum	21				2	12	5	2								182
P. williamsoni	16			1	4	5	1	4		1						183
P. gemmiferum-like	5						1	2	2							201

[a]Measurements expressed in thousandths of head length.

Table 54. Comparison of interorbital width/head length ratios among members of the Bear Lake Prosopium complex and P. williamsoni.[a]

Form	N	196-205	206-215	216-225	226-235	236-245	246-255	256-265	266-275	276-285	286-295	296-306	Mean
P. spilonotus (small form)	102				4	14	42	30	11	1			253
P. spilonotus (large form)	27					2	6	8	4	3	2	2	267
P. species	108		1	5	7	37	36	17	5				246
P. abyssicola	120		2	11	36	35	26	7	3				239
P. gemmiferum	21	6	10	5									210
P. williamsoni	16			1		2	4	1	4	2	2		262
P. gemmiferum-like	5	2	2	1									211

[a]Measurements expressed in thousandths of head length.

Table 55. Comparison of postorbital head length/head length ratios among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	460-469	470-479	480-489	490-499	500-509	510-519	520-529	530-539	540-549	550-559	560-569	570-579	Mean
P. spilonotus (small form)	102	1	4	8	12	45	22	10						504
P. spilonotus (large form)	27		2	1	2	11	5	5	1					507
P. species	108		5	13	15	53	15	7						501
P. abyssicola	120	2	2	9	18	34	34	17	4					506
P. gemmiferum	21		1	4	3	11	2							498
P. williamsoni	16						1	2		6	1	4	2	551
P. gemmiferum-like	5			1	1	2	1							500

[a]Measurements expressed in thousandths of head length.

Table 56. Comparison of gill-raker length/head length ratios among members of the Bear Lake *Prosopium* complex and *P. williamsoni*.[a]

Form	N	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140	141-150	Mean
P. spilonotus (small form)	102		2	58	41	1								60
P. spilonotus (large form)	27	1	7	19										52
P. species	108		5	74	28	1								58
P. abyssicola	120		7	61	51	1								60
P. gemmiferum	21											12	9	139
P. williamsoni	16		1	7	8									61
P. gemmiferum-like	5							1	3	1				110

[a]Measurements expressed in thousandths of head length.

Appendix C

Components of Gel, Stains and Buffers

5% Polyacrylamide Gel

Cyanogum	15 g
Tris Glycine pH 9.3	300 ml
TMED	.3 ml
Ammonium Persulfate	.3 g

Tris Glycine Buffer pH 913

Tris	138.2 g
Glycine	21.0 g
Water to 4 liters	
Adjust pH with glycine	

Tris-HCl Buffer pH 8.5

Tris	60 g
HCl	12.5-14 ml
Water to 1 liter	
Adjust pH with CHl	

Dye Solvent

Methanol	500 ml
Water	500 ml
Glacial Acetic Acid	100 ml

General Protein (Amido Black Stain)

Amido Black	2 g
Dye Solvent	1 liter

Lactate Dehydrogenase Stain

Tris-HCl Buffer pH 8.5	100.0 ml
Sodium Lactate	1.8 ml
Diphosphopyridine Nucleotide (DPN)	30.0 mg
Nitro Blue Tetrazolium Chloride (NBT)	50.0 mg
Phenazine Methosulfate	10.0 mg

Malate Dehydrogenase Stain

Tris-HCl Buffer pH 8.5	100.0 ml
Sodium Malate	500.0 mg
DPN	30.0 mg
NBT	20.0 mg
PMS	10.0 mg

Glutamate Dehydrogenase Stain

Tris-HCl Buffer pH 8.5	100 ml
L-(2)-Glutamic Acid	600 mg
DPN	30 mg
NBT	20 mg
PMS	10 mg

VITA

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