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THE SYSTEMATICS OF THE PRICKLY SCULPIN, COTTUS ASPER,
AN INVESTIGATION OF GENETIC AND NON-GENETIC VARIATION
WITHIN A POLYTYPIC SPECIES.

ABSTRACT

The prickly sculpin, Cottus asper, is a polytypic species characteristically represented by very prickly, fresh-water spawning "inland" forms, and less prickly, brackish-water spawning "coastal" forms. Its wide-spread geographic distribution, pronounced phenotypic variability, and the effects of the contrasting environments in which it occurs are the subject of this investigation. A complete nomenclatural history and synonymy of the species for the period 1836-1936 is presented. Morphological evidence is interpreted in the light of field and laboratory studies of the migration and reproductive behaviour.

Differences found in distribution and intensity of body prickles (modified scales), geographical distribution, and migratory behaviour, support the contention that the polytypy of "coastal" and "inland" forms of Cottus asper has a genetic basis.

Other morphological evidence is equivocal in support of this interpretation. Differences in fin ray counts, e.g. pectoral rays, between "coastal" and "inland" forms are correlated positively with the presence or absence of salinity in the environment. However, it is not known whether such differences are the result of individual modifications induced by the local environment, or due to long term genetic fixation.

Evidence from studies of closely-related species supports the interpretation that Cottus asper is polytypic species which has become, and is in the process of becoming, modified into several characteristic genotypes. Evolution within this "asper species group" probably occurred in three stages, each correlated with past geologic history.

During the first stage, perhaps in the Pliocene or Late Miocene, "coastal" and "inland" forms were derived from an ancestral marine cottid. The second stage, during the Pleistocene, was characterized by fragmentation of the gene pool of the "inland" form into a series of geographically isolated populations which have since evolved into valid species. The third stage, in Recent Time since the retreat of the Cordilleran glaciers, has

occurred primarily within the northern representatives of the "coastal" form. At least two derivatives can now be distinguished within the "coastal" form.

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
ZOOLOGY

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

JUNE, 1965

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Department of Zoology

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Date 8 June 1965

ABSTRACT

The prickly sculpin, Cottus asper, is a polytypic species characteristically represented by very prickly, fresh-water spawning "inland" forms, and less prickly, brackish-water spawning "coastal" forms. Its widespread geographic distribution, pronounced phenotypic variability, and the effects of the contrasting environments in which it occurs are the subject of this investigation. A complete nomenclatural history and synonymy of the species for the period 1836-1936 is presented. Morphological evidence is interpreted in the light of field and laboratory studies of the migration and reproductive behavior.

Differences found in distribution and intensity of body prickles (modified scales), geographical distribution, and migratory behavior, support the contention that the polytypy of "coastal" and "inland" forms of Cottus asper has a genetic basis. Other morphological evidence is equivocal in support of this interpretation. Differences in fin ray counts, e.g., pectoral rays, between "coastal" and "inland" forms are correlated positively with the presence or absence of salinity in the environment. However, it is not known whether such differences are the result of individual modifications induced by the local environment, or due to long term genetic fixation.

Evidence from studies of closely-related species supports the interpretation that Cottus asper is a polytypic species which has become, and is in the process of becoming, modified into several characteristic genotypes. Evolution within this "asper species group" probably occurred in three stages, each correlated with past geologic history.

During the first stage, perhaps in the Pliocene or Late Miocene, "coastal" and "inland" forms were derived from an ancestral marine cottid. The second stage, during the Pleistocene, was characterized by fragmentation of the gene pool of the "inland" form into a series of geographically isolated populations which have since evolved into valid species. The third

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INTRODUCTION

The role of the environment versus the role of heredity in determining the phenotypic variations found among and within natural populations has long been a problem of central interest to students of evolution.

Because fishes apparently undergo modification by their environment, they have proved to be useful in the study of phenotypic variation. For example, several authors have shown that non-genetic morphological or functional variation in fishes can be caused by maternal care and diet prior to egg deposition, and to the effects of environment during fertilization and development, and after hatching. In spite of such documentation many systematic studies tacitly assume that differences discovered between individuals, or within and/or among series of specimens, are genetic.

In some species, breeding experiments have shown that, under controlled conditions, the integrity of the parental phenotype is maintained in the F_1 generation. Such results have been interpreted as being genetically determined. Except for a few notable examples, there have been no studies on fishes which have attempted to correlate the morphological and physiological evidence and to relate both to the life history of the species concerned. Such an approach is attempted in this investigation.

The prickly sculpin ranges geographically over about 3000 miles of Pacific North Temperate coastline and inland as far as 300 miles. Structural modifications correlated with latitudinal changes in temperature or salinity should, if present, be revealed by morphological analysis. Like the stickleback Gasterosteus aculeatus, and the darter Etheostoma (Boleosoma) nigrum, the prickly sculpin exists in two modes of morphological variability: one, a fresh-water spawner, has extensive squamation on certain regions of the body; the other, a brackish-water spawner, has little or none. Since prickly sculpin eggs are spawned naturally in environments which are known to vary in at least one major factor, i.e., salinity, and since, under contrasting

environmental circumstances, it shows so many similarities with the stickleback, the prickly sculpin is an excellent subject for variational studies.

Prior to the present study, regional systematic treatments of this widespread species resulted in a proliferation of generic and specific taxa, all referable to Cottus asper. A complete nomenclatural history and synonymy of the species for the period 1836-1936 is presented. Morphological evidence based on examination of 1604 specimens from 190 collections throughout the range of the species is correlated with that from field and laboratory studies of the migratory and reproductive behavior.

The thesis is presented in two sections corresponding to the morphological and life history approaches followed in this investigation. A general discussion considers the morphological and ecological variation within the species and attempts to reconstruct the phylogeny of Cottus asper and closely-related species.

Literature Review

Hubbs (1943) has listed many reasons why fishes are particularly well-suited for determination of genetic vs. environmental responses. He has also summarized (1926) much of the early work especially in regard to the structural consequences of varying developmental rates. Numerous workers have found that different morphological or meristic series in fishes are "plastic," i.e., sensitive to environmental influence before egg deposition, during fertilization, during development, and after hatching.

Taning (1944) ascribed at least one instance of mass vertebral deformities and low egg survival to an accident befalling the female trout before the eggs were removed from her. Hubbs and Stavenhagen (1958) have shown that low survival of different egg lots was caused by carotenoid deficiency in the maternal diet.

Kinne (1962) reviewed some of the recent literature on structural and functional properties of fish egg membranes and suggested that the spawning

medium affects the physical properties of the immediate environment of the embryo and that these induced properties "tend to persist in later different salinities." On the basis of his own studies, of Cyprinodon macularius, he interprets such conditioning by the spawning medium, leading to irreversible functional or structural adjustment in the embryo, as a special case of imprinting, or "irreversible non-genetic adaptation."

Battle (1929); Mottley (1934); Tåning (1944); Gabriel (1944); Heuts (1949); Lindsey (1954); and Seymour (1959), have demonstrated the effects of environmental influences, especially temperature, during different developmental stages prior to hatching.

Strawn (1961) found that the diet of newly-hatched larvae can affect the morphology, Lindsey (1954) found that certain meristic characters are thermolabile up to 20 days after hatching.

Lagler and Bailey (1947) studied the inheritance of differential morphological characters in two subspecies of Etheostoma (Boleosoma) nigrum, a darter. The main differences between the subspecies lie in the extent of the squamation on the nape, cheek, and breast, one being typically naked or with few scales, and the other being well, if not fully, scaled. Lagler and Bailey found that the F_1 generation of each subspecies, when reared and hatched under uniform environmental conditions in the laboratory, maintained the integrity of the parental phenotype. They concluded that these characters were genetically fixed.

After a vast and careful examination of some 9000 individuals, Bertin (1925) concluded that in populations of the stickleback, Gasterosteus aculeatus, throughout Europe, most of the variable characters, especially the lateral body plates, are direct individual adaptations to environmental influences, especially temperature. He described four forms based primarily on body plate numbers.

Heuts (1947a), however, showed that, at least in Belgian sticklebacks,

only two main modes of variability exist, each correlated with definite ecological characteristics, each with differences in breeding habits and distribution. He also showed (1947b) that certain physiological characters are correlated with morphological ones and he attempted to demonstrate that natural selection favors different complexes of genes in the different ecological niches in which the species occurs. He considers the two types of sticklebacks to be valid genetic races.

Robins and Miller (1957) have called attention to the fact that because variation is so marked and haphazard in the sculpins of the genus Cottus, interpretation of the species limits within the group is frequently difficult. They consider Cottus to be one of the most perplexing groups of North American freshwater fishes. In considering a character such as prickles on the body, they state that so much variation occurs between populations that its geographic consistency in one or two forms is difficult to interpret. They also consider that a character such as "armature, like body prickles, may greatly assist in the identification of a species at any one locality, but is often unreliable for relating or distinguishing allopatric forms."

MORPHOLOGICAL ANALYSIS OF PRICKLY SCULPIN POPULATIONS

Materials and Methods

Museum Collections. - Specimens examined include those in the following institutional collections (abbreviations listed are used in the text):

- AB Bureau of Commercial Fisheries, Biological Laboratory, Auke Bay, Alaska
- BC University of British Columbia, Vancouver, Canada
- CAS California Academy of Sciences, San Francisco
- NMC National Museum of Canada, Ottawa, Ontario
- OSC Oregon State University, Corvallis
- SNHM Natural History Museum, Stanford University, Palo Alto, California (SU)

UMMZ University of Michigan Museum of Zoology, Ann Arbor
 USNM United States National Museum, Washington, D. C.
 UW University of Washington, Seattle

Additional non-catalogued British Columbia material used in this study was made available through the personal field collecting of the following individuals. Abbreviations used are those which preface field collection numbers:

K- R. J. Krejsa: Little Campbell R., and miscellaneous others
 A- G. F. Hartman, D. W. Wilkie, and C. A. Gill: South Alouette R.
 V- " " " " " " " " " : Vedder R.
 SW- " " " R. J. Krejsa, " " " " : Sweltzer Cr.
 S- J. S. Nelson, and P. J. McCart: Peace R. drainage.

Material Examined. - A total of 1604 specimens from 190 collections was utilized in this study. Data for 158 specimens, from 16 collections, was culled from the published accounts of Snyder (1905, 1908b, and 1913), and Rutter (1908). Counts and measurements for 63 specimens, from 6 collections, were taken by Dr. D. E. McAllister of the National Museum of Canada. The remaining 1383 specimens were examined by the author.

A list of collections, together with pertinent data, is presented in Appendix Table 1.

Counts and Measurements. - Measurements were taken to within 0.1 mm using break-arm dividers with one flat point and one needle point, in accordance with the methods of Hubbs and Lagler (1958).

Counts for median fins and pelvic fins follow the methods outlined by Robins and Miller (1957). Other counts were taken as follows.

Pectoral Fin Rays: Counts from both the right and left side were summed by population and then divided by the total number of fins. Pectoral fin asymmetry in Cottus asper was investigated to ascertain the incidence of occurrence, the direction, and the amount of asymmetry in this species, and

to determine whether individual populations, population aggregates, or geographical regions could be characterized by these criteria.

Distribution of Prickles on the Body: The areal distribution of body prickles is defined as the area of skin surface covered, or formerly covered, by prickles. It was recorded as follows. A superficial median incision was made through the dorsum and venter of a single adult specimen of Cottus asper, 80 mm in standard length (S.L.). A transverse incision was made ventrolaterally from the median supratemporal pore to a point medial and posterior to the pelvic fin base. The skin was then peeled off the left side of the body as far posterior as the hypural fold where it was excised.

It was then placed flat on a sheet of paper and a tracing made around the perimeter. The resulting blank outline tracing was then subdivided into 14 lettered sections based on morphological landmarks. The subdivided outline of the original skin hereinafter referred to as the "skin map," was stenciled onto sample work sheets on which all counts and measurements were recorded (Fig. 1B).

To estimate the areal distribution of prickles, a specimen is examined under the binocular dissecting microscope and the perimeter of the prickly area on the left side is outlined by scratching the mucous layer with a sharp needle point. This "apparent" outline is copied onto the work sheet skin map with colored ink. The mucus is then scraped from the entire left side with the aid of a syringe-needle jet of compressed air, exposing those partially-resorbed prickles which do not project through the mucous layer. As will be discussed later, some prickles in Cottus asper are completely resorbed during maturation. Therefore, further treatment is necessary to expose the extent of the prickling in its entirety, i.e., the "virtual" prickling. Vigorous rubbing or massaging of the skin with the air needle will expose the areas formerly covered by prickles. This technique presumably causes the breakdown of the sub-epidermal chromatophores. The

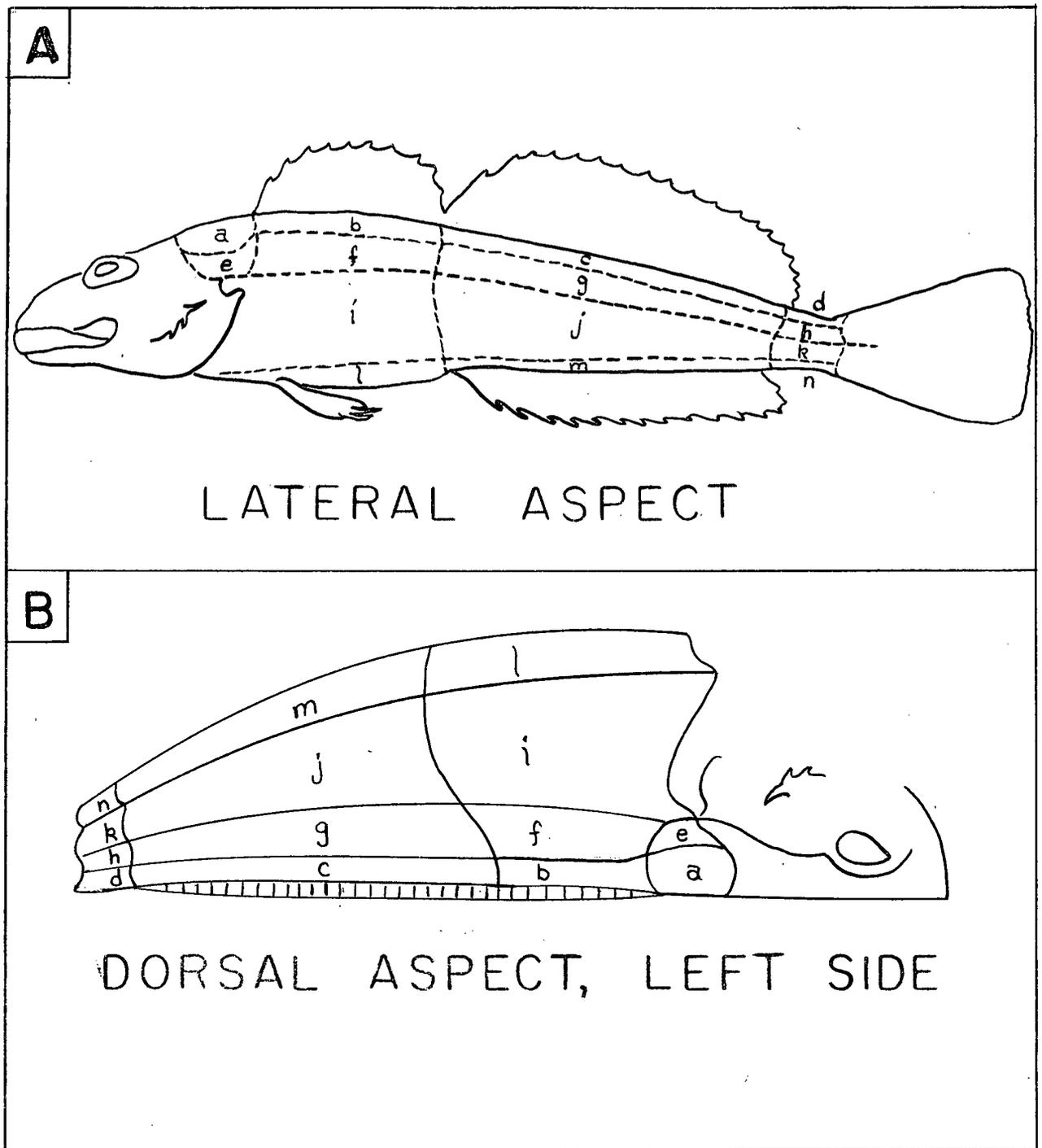


Figure 1.--"Skin Map" Used for Recording Distribution and Intensity of Prickling in *Cottus asper*.

melanin granules thus released become aggregated in the empty dermal prickle pockets and the areas of resorption become visible. Thus resurrected, the original or "virtual" areal distribution of prickling can be recorded in ink of another color over the "apparent" prickling distribution already recorded on the skin map (Fig. 2).

Since each of the 14 lettered sections of the skin map represents a fraction of the total body surface on the left side of the animal, a polar planimeter was used to determine the total area occupied by each section. Sectional areas were then converted into a set of fractional constants, each representing a percentage of the total area of the skin map. These constants were used in calculations of the absolute prickling in each section.

For statistical treatment, the total areal distribution of prickles was tabulated as follows: A copy of the skin map was permanently printed onto a piece of transparent plastic. On this overlay, each of the lettered sections was further partitioned into subdivisions of 5, 10, and 25%. The plastic overlay was matched with the completed skin map on the work sheet and the percentage area covered by prickles in each numbered section was visually estimated to within 5%. The estimates for each section were then transcribed and summed for all specimens in the sample and a mean percentage "apparent" and mean percentage "virtual" prickling was determined. Multiplication of each of these sectional mean percentages by the appropriate fractional constant (previously determined) resulted in a product which is an estimate of the mean percentage absolute prickling ("virtual" and/or "apparent") for each section.

The sum of all 14 sectional products is an estimate of the mean percentage areal prickling ("virtual" or "apparent") for the population sample.

Subtraction of the population mean percentage "apparent" areal prickling from the population mean percentage "virtual" areal prickling results in a remainder which represents the population mean percentage absolute resorption.

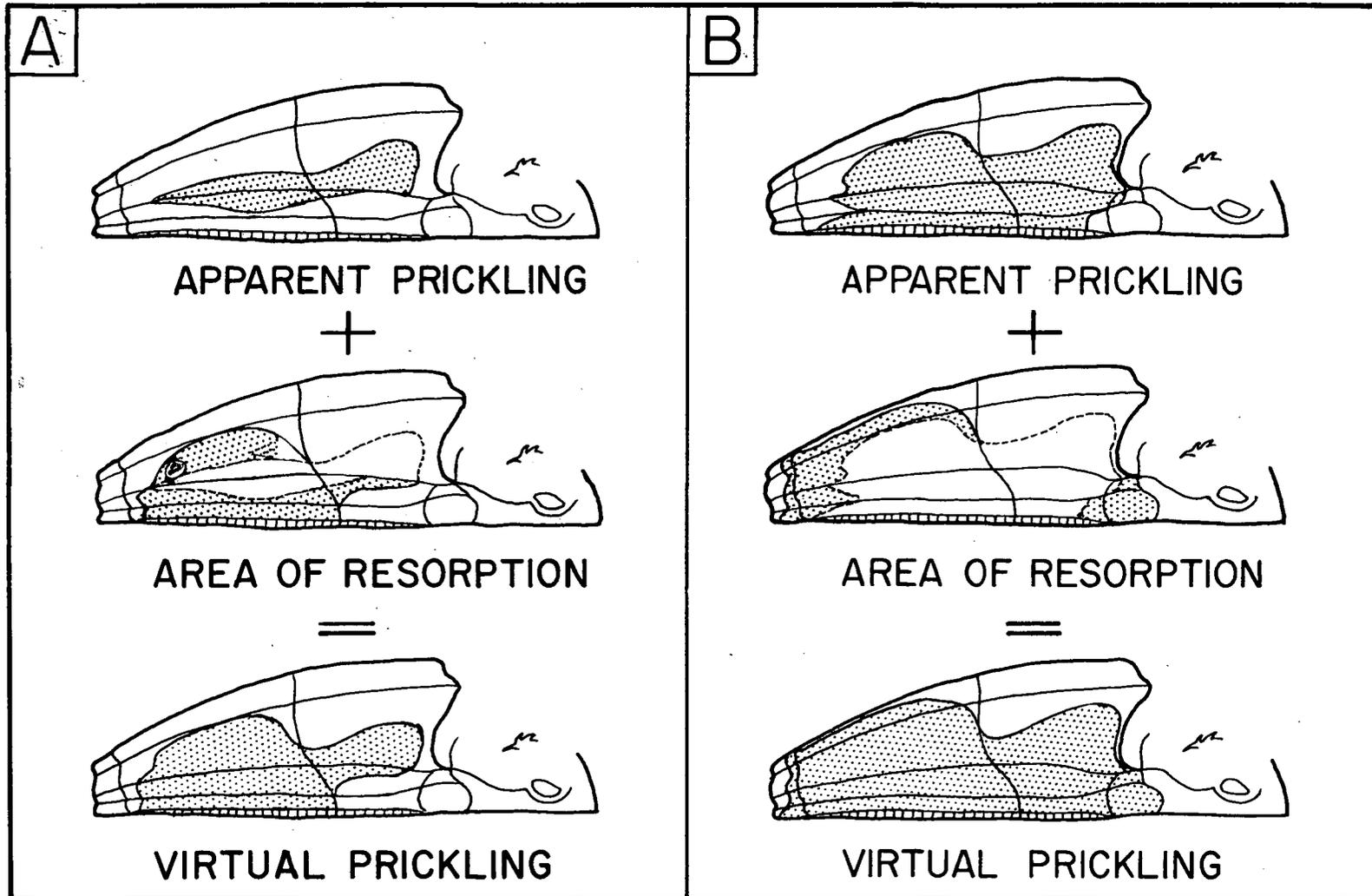


Figure 2.--Areas of Prickling and Areas of Resorption: A. in Coastal *Cottus asper*; B. in Inland *Cottus asper*.

for any given sample.

The mean percentage relative resorption in any given population sample is obtained by the formula:

$$\text{Mean \% relative resorption} = 100\% - 100 \left(\frac{\text{Mean \% "Apparent"}}{\text{Mean \% "Virtual"}} \right)$$

An examination of the condition of the gonads in more than 1000 specimens indicated that Cottus asper usually becomes reproductively mature at a size of 60 mm S.L. On this basis, treatment of all prickling data was divided into groups of specimens smaller than, or equal to and larger than, 60 mm.

Prickling Intensity: The size of prickles in Cottus asper varies directly with the size of the animal. However, the intensity, i.e., the number per unit area, does not appear to be a direct function of size. It varies among individuals of all sizes and even on different sections of the same individual. Because of the impracticality of recording absolute prickle numbers for large numbers of specimens, a relative index of range 0 through 5 was established. In this index zero indicated no prickling, and five indicated the most intense prickling.

When a single prickle was found in an otherwise naked area, it was given an arbitrary value of 0.5. For statistical purposes, a single isolate was considered to have an areal distribution which was proportional to the lettered body section of the skin map in which it was found, i.e., 4% in sections 'a' and 'b'; 10% in sections 'd', 'e', 'h', 'k', and 'n'; and 5.5% in sections 'l' and 'm'. If more than 4 prickles were found in an isolated patch, an index value of "1" was assigned and the areal distribution was estimated to the nearest unit percentage.

To determine the nature of differential mean intensity index values, sample counts of prickles were taken from sq. cm. sections of skin adjudged to have index values of one and five. In rounded numbers, an index value of

"1" is equivalent to 400 prickles per sq. cm., whereas a value of "5" is equivalent to an estimated 2500 prickles per sq. cm. Mean values were interpolated from these counts.

Lateral Line: Previous workers (Robins and Miller, 1957) have considered the lateral line as incomplete if the number of pored-scales did not reach the hypural fold. The number of completely pored lateral line scales varies with size and among populations. Close examination of sculpins reveals that although a specimen may have an "incomplete" lateral line (i.e., pored-scale count), unenclosed neuromast hillocks are present and readily visible. Thus the most reliable measure of serial repetition along the lateral line, for all size categories other than young-of-the-year, is a count of the complete pored-scales plus the partially, or completely unenclosed neuromast hillocks which appear sequentially along the trunk and out onto the caudal fin. In practice, this count was made only to the hypural fold and the mean number of pored-scales plus hillocks was considered to represent a "complete" lateral line count. "Complete" counts were made for less than one half of the specimens examined in this study and, in most small specimens, the count was listed only as "incomplete." The number of collections is few in which all size ranges from juvenile to adult are represented. The number in which "complete" lateral line counts have been taken is even fewer.

Critique of the Methods of Determining Prickling Distribution and Intensity. - The method of determining distribution proved unreliable on extremely old and/or badly preserved specimens. In some the skin was so desiccated that massage was impossible without damage to the specimen. In others, all the pigment had been bleached after years of preservation and no amount of massaging would make the empty prickle pockets appear. In such specimens only the "apparent" prickling distribution was determined and recorded. Estimates of prickling distribution on badly preserved or

desiccated specimens were not used in compiling population means.

Tiny prickles in peripheral areas of immature specimens, and partially resorbed prickles on heavily pigmented mature specimens were difficult to see, even with the aid of the microscope. Therefore the estimates of "apparent" prickling both in mature and immature specimens are less than the "virtual" prickling in immature specimens. The accuracy of the visual estimate in peripheral areas was checked against alizarin-stained specimens, and was found to be within $\pm 10\%$ on specimens ≥ 60 mm, and within $\pm 5\%$ in specimens < 60 mm.

While 60 mm appears to be a valid estimate of the average size at which most Cottus asper attain reproductive maturity, not all spawn at that size. Some populations, e.g., from Queen Charlotte Is., are known to have females which spawn at a size of only 42 mm S.L., while in other populations, a few females do not spawn until a size of 70 mm is attained. The discrepancy in Table I between the mean percentage "virtual" prickling and the slightly lower (from 2-7%) "apparent" prickling in fishes < 60 mm is attributed to this cause.

Another discrepancy in the data reported in Table I is that mean differences of from 4 to 10% occur between the "virtual" prickling percentages in specimens < 60 mm, and those ≥ 60 mm from the same population. These differences are attributed to the inability to "resurrect" all the prickle pockets completely.

Statistical Methods. - Most of the raw data has been converted to means or percentages. Obvious differences were not tested. When a comparison of means was thought necessary, the two most divergent values were examined first. If no significant differences were revealed, the less divergent means were not tested. The single-classification χ^2 test, or the Student t-test, was used at the 5% critical level to determine acceptance or rejection of an hypothesis of equal means. Graphical presentation of certain

meristic characters is according to the format of Hubbs and Hubbs (1953).

Synonymy

It has been almost 130 years since Cottus asper was first described by Sir John Richardson. Early revisionary work by Girard in 1851 and 1852 was incomplete because of lack of specimens. Recent regional works (Robins and Miller, 1957; McAllister, 1957; McAllister and Lindsey, 1959; and Bond, 1963) have included the species as part of a geographical area or river drainage system, but there has never been a comprehensive treatment of the species throughout its entire range. In the period 1836-1936, 38 reports of Cottus asper were cited in the literature. In the same period, 32 additional citations occurred which were either misidentifications or synonyms properly referable to Cottus asper. In none of the systematic treatments published since the original description in 1836 has there been a synonymy containing more than 7 citations. McAllister (1957) listed 15 citations in his unpublished M.A. thesis.

The present synonymy, consisting of 70 citations published during the period 1836 to 1936, is thought to be complete. Since 1936, the species has been cited in numerous fishery journals and publications. Therefore, only the major systematic, or otherwise noteworthy, citations occurring in the past 29 years have been recorded.

Cottus asper Richardson, 1836

Cottus asper. - Richardson, 1836:295, pl. 95, Fig. 1 (original description and figure; Columbia R.; collected by Dr. Gairdner (probably near Fort Vancouver, Washington Territory)). Storer, 1846a:260, and 1846b:8 (northwestern coast of N. America). Girard, 1850:409, and 1851a:189 (discusses propriety of present nomenclature). Eigenmann, 1895:118 (abundant in Fraser system from tidewater to 1900 feet; Mission, Sicamous, Kamloops, and Griffin L., British Columbia; and Umatilla, Oregon). Seale, 1896:854 (Lake Washington). Gilbert and

Evermann, 1895:201 (description; comparison to Sacramento R. form; Walla Walla R. at Wallula, and Lake Washington, Washington).

Gilbert, 1896:418 (description; stream entering Departure Bay, Vancouver Island). Jordan and Evermann, 1896:439 (synonymy; streams of the Cascade Range, from Vancouver Island to Oregon). Gilbert, 1898:1 (Columbia R.; notes absence in Klamath R.). Jordan and Evermann, 1898:1944 (description; synonymy; Walla Walla; Departure Bay; about Port Townsend; streams of the Cascade Range, from Vancouver Island to Oregon). Evermann and Meek, 1898:83 (Lake Washington). Meek, 1899:231 (Lake Southerland, Olympic Pen., Washington). Snyder, 1905:337 (description; affinities; habitat preference; San Franciscito, Madera, San Antonio, Guadalupe, Coyote, and Alameda Creeks, all flowing into San Francisco Bay). Evermann and Goldsborough, 1907a:306 (characters; prickling descriptions; Deep Bay, Naha R., and Steelhead Cr., Loring, Alaska; Hunter Bay, Yes Bay, and McDonald L., Alaska). Evermann and Goldsborough, 1907b:110 (Fraser R. at Mission, Shuswap L. at Sicamous, Thompson R. at Kamloops, and Griffin L.). Rutter, 1908:145 (Cottopsis parvus first placed in synonymy with asper; synonymy, in part, except Uranidea semiscaber (sic) centropleura Eigenmann and Eigenmann; summary of 9 localities in Sacramento R. system). Snyder, 1908a:269 (Russian R., California). Snyder, 1908b:184 (characters; prickling description; summary of 41 localities: from Lake Washington, Columbia and Sacramento R., and river basins in between). Nichols, 1909:172 (head of Chilkoot L., Alaska). Evermann and Latimer, 1910:138 (4 localities in Marin Co., and 2 localities in San Francisco Bay, California; 12 localities in Olympic Pen., Washington). Snyder, 1913:72 (characters; Pajaro R., California). Snyder, 1916:381 (Papermill and Walker Creeks, California). Kermode, 1917:20

(Hanceville, British Columbia (Chilcotin R. drainage)). Jordan, 1919:249 (designates Cottus asper Richardson, as the orthotype of Cottopsis Girard). Bean and Weed, 1920:76 (mouth of Fraser R.). Hubbs, 1921:7 (re-identification of San Luis Cr., California, specimens misidentified by Jordan as C. gulosus (1895:141); range extension to Ventura R., California). Crawford, 1927:177 (streams flowing into Puget Sound). Schultz, 1929:48 (listing only). Schultz, 1930:14 (most streams and lakes of western Washington). Jordan, Evermann, and Clark, 1930:383 (synonymy; streams of the Cascade Range, southeastern Alaska to Oregon; south to Sacramento R.). Kermode, 1931:19 (Cowichan L., Vancouver Island). Evermann and Clark, 1931:56 (summary of 32 recorded localities in California). Schultz and DeLacy, 1936a:128 (synonymy; coastal streams from Alaska to Ventura Co., California; freshwater and brackish water; review of most records from Puget Sound to Oregon, and addition of 26 more localities). Schultz and DeLacy, 1936b:213 (additional synonymy; 3 new localities). Schultz, 1936:179 (keys to species of Cottus; coastal streams from Alaska to Ventura Co., California; freshwater and brackish). Dymond, 1936:71 (description; throughout southwestern British Columbia, including southern Vancouver Island; 16 localities listed). Summer, 1942:1-25 (common in tidewater areas along the Oregon coast). Hubbs and Wallis, 1948:141 (identification of "Cottus sp." recorded by Dill, 1946:54). Bailey and Dimick, 1949:14 (comparison with Cottus hubbsi). Shapovalov and Dill, 1950:387 (listing only). Wilimovsky, 1954:285 (southeast Alaska to California). Robeck, et al, 1954:B-65 (Columbia R., above Trinidad, Washington; cited as "prickly sculpins Cottus sp.", these may include Cottus rhotheus in part.) Lindsey, 1956:777 (Pacific Slope of N. America from Alaska to California; British Columbia mainland from

Columbia, Fraser, and Skeena systems, Stikine R. headwaters, and Peace R. (Summit L., Heart L., Angusmac Cr., and McLeod L.)). Robins and Miller, 1957:229 (Cottopsis parvus again removed from synonymy of C. gulosus). Lindsey, 1957:657 (British Columbia: Columbia R.; Fraser R.; Skeena R.; Coast drainages south of Skeena; Nass R.; Stikine R.; Peace R.). Wilimovsky, 1958:62 (key to species in Alaska; southeast Alaska to California). Shapovalov, Dill, and Cordone, 1959 (listing only). Carl, Clemens, and Lindsey, 1959:158 (description; Pacific drainages from Chilkoot L., Alaska to Ventura R., California. In British Columbia: lakes and rivers of the Columbia, Fraser, Dean, Skeena, Nass, and Stikine systems; coastal rivers of the mainland and Vancouver Island, and Queen Charlotte Islands; headwaters of Peace R. system from Summit L. to McLeod L.). McAllister and Lindsey, 1959:70 (description; synonymy; intra-specific variation; localities as in Carl, Clemens, and Lindsey, 1959). McAllister, 1960:42 (collection in salt water, Pt. Atkinson, British Columbia). Bond, 1961:36 (key to species in Oregon; prickling variation; Columbia R. drainage). Bond, 1963:79 (synonymy; life history observations; oxygen, temperature, and salinity tolerance of adults; fish associates; habitat preference; lists 35 new collection localities in Coastal Oregon, 30 localities from Columbia R. drainage in Oregon, and also some lakes in the southwest corner of Rainer National Park, Washington). Bailey and Bond, 1963:19 (recognition of several species groups within Cottus in western N. America; characters and list of species in the "asper species group").

Centridermichthys asper. - Richardson, 1844:76 (River Oregon = Columbia R.). Günther, 1860:170 (description; synonymy; fresh waters of the Oregon and Washington Territories). Lord, 1866a:130 [life history ;

spawning behavior, in part; Puget Sound; "streams flowing through the Sumass and Chilukweyuk prairies" (Sumas R. and Chilliwack R. (?)), British Columbia; in part, all streams east and west of the Cascades].

Cottopsis asper. - Girard, 1851b:303 (introduction of Cottopsis gen. nov.; synonymy; limited to River Oregon (= Columbia R.)). Girard, 1851c:185 (not seen). Girard, 1852:61 (definition of Cottopsis gen. nov., based on Richardson's description of Cottus asper; synonymy; Columbia R.). Girard, 1859:51 (description; synonymy; based on 8 specimens from Astoria and Fort Dalles, Oregon, and Fort Steilacoom, Puget Sound, Washington Territory). Suckley (in Cooper and Suckley, 1859) 1859:351 (description; synonymy; small fresh water streams emptying into Puget Sound; Ft. Steilacoom; and Columbia R. 200 miles above mouth). Suckley, 1860:351 (description; synonymy; small fresh-water streams emptying into Puget Sound; Ft. Steilacoom; and Columbia R. 200 miles above mouth). Jordan and Jouy, 1882:5 (Puget Sound; Columbia R.; Mare Island and Sacramento R., California).

Uranidea aspera. - Jordan and Gilbert, 1883:694 (description; synonymy; streams west of the Sierra Nevada and Cascade Mountains). Jordan, 1885:110 (sub-genus Cottopsis and a list of species therein).

Trachidermus richardsoni. - Heckel, 1840:162 (synonymy; Columbia R.), (not Cottus richardsoni of Agassiz, 1850).

Cottopsis parvus. - Girard, 1856b:144 (original description; Presidio (on San Francisco Bay), California). Girard, 1857:11 (description; Presidio, and Monterey, California). Girard, 1859:54 (description; synonymy; Monterey, Presidio, Fort Reading, and Petaluma, California). Cooper, 1868:492 (listing only). Jordan, 1877:5 (as the young of Cottopsis asper).

Centridermichthys parvus. - Günther, 1860:170 (description; synonymy; fresh waters of California). Lord, 1866b:352 (listing; "frequenting the same localities as..." Centridermichthys asper).

Uranidea aspera var. parvus. - Jordan and Gilbert, 1883:694 (Sacramento R. forms).

Cottus gulosus parvus. - Jordan and Evermann, 1898:1945, and Jordan, Evermann, and Clark, 1930:383 (Cottopsis parvus: Monterey, Presidio, Fort Reading, and Petaluma, California).

Uranidea gulosus, in part. - Jordan and Gilbert, 1883:695 (misidentifications: all specimens from "Vancouver's Island" and probably those from "about Port Townsend," cf. Jordan and Evermann, 1898:1944). Kermode, 1909:87 (listing only; probable misidentification: Shawnigan L., Vancouver Island).

Cottus gulosus, in part. - Jordan, 1895:141 (misidentification: San Luis Cr., near Avila, California. cf. Hubbs, 1921:7). Jordan and Evermann, 1898:1945 (misidentification: all specimens from San Franciscito Cr., Santa Clara Co., California). Jordan, Evermann, and Clark, 1930:383 (probable misidentifications: specimens from Loring and Boca de Quadra, Alaska). Evermann and Clark, 1931:57 (misidentifications: Presidio, Monterey, Fort Reading, Petaluma, and San Luis Cr., California). Evermann and Clark, 1931:12, 13 (misidentifications: Monterey, Presidio, Fort Reading, and Petaluma). Bean and Weed, 1920:76 (questionable identification: 4 specimens from Victoria, Vancouver Island, British Columbia). Wilimovsky, 1954:285 (doubts validity of southeast Alaska record).

Centridermichthys gulosus. - Lord, 1866b:352 (listing; "frequenting the same localities as..." Centridermichthys asper).

Cottus sp. - Dill, 1946:54 (San Joaquin R. near Friant, California: identification as asper by Hubbs and Wallis, 1948:141).

Nomenclatural History

The specific name asper is currently well founded in the genus Cottus, to which it was originally designated by Richardson in 1836. But, as shown in the preceding synonymy, the binomen was extremely unstable for the first 100 years after its introduction. After an initial period of uncertainty regarding its affinity to marine or to freshwater Cottoids, three main nomenclatural difficulties are encountered: the often-repeated misidentification as Cottus gulosus (Girard); the failure to recognize that Cottopsis parvus and Cottus asper are conspecific; and the failure to recognize the specific relationship of asper to other species in the genus Cottus.

The almost immediate placement of asper into Trachidermus by Heckel (1840), and then into Centridermichthys by Richardson (1844), reflects the early opinion that asper was more closely allied to the marine Cottoids. Girard (1851b; 1852) recognized its affinities with the freshwater genus Cottus, but distinguished it from that genus by erecting the genus Cottopsis, based on the presence of palatine teeth and the "skin beset with prickles, instead of being smooth and scaleless." Lacking any specimens, Girard defined Cottopsis on the basis of Richardson's original description but, on p. 63, he misquoted Richardson especially in regard to the absence of scales. Girard's lack of specimens proved unfortunate since soon thereafter (1856b) he named and described Cottopsis parvus, from the Presidio (in San Francisco), California, comparing it not with C. asper, but with Cottopsis gulosus Girard, also newly described (1856a), from the San Joaquin R., California. In his later report (1859), Girard had 8 specimens of C. asper in his possession, from the Columbia R. and Puget Sound. Obviously he again failed to recognize the conspecificity of asper and parvus and he followed Richardson's original description rather than compare them with specimens of parvus, which he seems to have reserved for comparison with gulosus.

Jordan (1877) referred, in passing, to Cottopsis parvus as the young of

C. asper. Jordan and Jouy (1882) however, listed specimens of Cottopsis asper from Mare Island and Sacramento R., California, and from Puget Sound and the Columbia R. Less than a year later, Jordan and Gilbert (1883) placed asper into the genus Uranidea DeKay, subgenus Cottopsis, based on the presence of palatime teeth, and the gill membranes being broadly united to the isthmus. In the same report, they refer to the Sacramento R. form of U. aspera as "var. parvus, smaller in size, paler in color and with the inter-orbital space concave, narrower than eye."

Eigenmann (1895) used the valid name to describe specimens from the Fraser and Columbia R., as also did Gilbert and Evermann (1895), who suggested that the nominal species was separable "at least subspecifically from the Sacramento River form." Seale (1896), and Gilbert (1896), used the valid name for northern specimens. But obviously, Jordan (1895), and Jordan and Evermann (1896), still thought in terms of a distinct Californian species (gulosus), and a distinct northern species (asper). Jordan misidentified a specimen of asper from San Luis Cr. near Avila, California, as gulosus. Jordan and Evermann listed the range of the nominal species from Vancouver Island to Oregon, and of gulosus, from California Coast Range streams and inland in the San Joaquin R. Gilbert (1896) referred to Cottus asper of the Columbia and Cottus gulosus of the Sacramento as "two species so extremely similar that it is difficult to distinguish them." Jordan and Evermann (1898) repeated the suggestion of Gilbert and Evermann that the nominal species is separable, at least subspecifically, from the Sacramento R. form "Cottus gulosus."

That Jordan and Evermann perceived neither the conspecific relationship of parvus to asper, nor the limits of the valid species Cottus gulosus, becomes more fully evident on the next page (p. 1945) of the 1898 report. Their description of Cottus gulosus (Girard) is taken from misidentified specimens of C. asper collected in San Franciscito Cr., Santa Clara Co.,

California. These were large specimens "3 to 7 inches in length" and, most significantly, the count for anal rays is given as "A. 16 to 18." Both of these characters separate asper from gulosus. Furthermore, they include Cottopsis parvus Girard, from Monterey, the Presidio, Fort Reading, and Petaluma, California, in the synonymy of gulosus.

Snyder (1905) collected and correctly identified Cottus asper from the same locality, San Franciscito Cr. He was probably the only one of his time to understand and explain the true relationships of asper, parvus, and gulosus. On p. 337, he states:

Recent authors have identified the common Sacramento form which represents the Cottus asper of the Columbia River with the Cottopsis gulosus of Girard. They have sometimes considered the Sacramento form as identical with C. asper and have placed the name gulosus in the synonymy of the latter. At other times they have considered the species as a slightly differentiated form worthy of recognition in nomenclature, and have used the name gulosus to designate it. The former view concerning the species is probably correct. The association of the name gulosus with it, however, is without warrant. The latter belongs to a species easily distinguished from C. asper, differing notably in having a much shorter anal fin. There are usually fewer dorsal spines and rays, a more limited distribution of prickles, and an almost uniform absence of palatine teeth. In C. asper the dorsal has 8 to 10 spines and 19 to 22 articulated rays, the anal 16 to 18 rays, while in C. gulosus the dorsal has 7 to 9 spines, 17 to 18 rays, the anal 12 to 14 rays.

Snyder then continues with a note on habitat preference:

In its distribution C. asper appears to be largely confined to the lower courses of the streams, being especially abundant near tide water, while C. gulosus is found further up, where the water is clear and the current rapid.

Rutter (1908) correctly placed Cottopsis parvus into the synonymy of Cottus asper, presumably recognizing that the two were conspecific. However, he incorrectly synonymized Uranidea semiscabra centropleura Eigenmann and Eigenmann, which is properly referable to Cottus gulosus.

Snyder was the first to consider a series of specimens of the nominal species throughout its entire range, as then known, and, in the same issue of the Bull. Bur. Fisheries in which Rutter had correctly synonymized parvus, he noted the extreme variation of prickling investment. While recognizing

the variation between streams, he also noted that the prickling variation is common among individuals from the same stream.

Although explicitly aware of Snyder's comments on asper and gulosus, Evermann and Goldsborough (1907a) identified 16 specimens of gulosus from Loring and Boca de Quadra, Alaska. The reliability of these identifications is questionable. Kermode's listing (1909) of Uranidea gulosa from Shawnigan L., Vancouver Island, is probably a misidentification of C. asper.

Snyder (1913; 1916) again recorded the occurrence of C. asper and gulosus in differing habitats of the same stream. Hubbs (1921) recognized Jordan's earlier misidentification of gulosus from San Luis Cr., California. He also commented on the variability of prickling in C. asper from several streams.

It would seem that with the accession of Snyder's insight into the problem, the valid name was destined for stability. However, Jordan, Evermann, and Clark (1930) repeated the earlier error of Jordan and Evermann (1898) by including Cottopsis parvus as a synonym of Cottus gulosus. In a similar manner, they also incorporated the error of Evermann and Goldsborough (1907a), previously cited, by including the misidentified specimens of asper from Loring and Boca de Quadra, Alaska in the list of records for gulosus. In the same work, Jordan and Evermann extended the range of asper (cited in 1898 as "streams of the Cascade Range, from Vancouver Island to Oregon") by appending the phrase "south to Sacramento River." Evermann and Clark (1931) also retained Cottopsis parvus in the synonymy of C. gulosus and perpetuated Jordan's misidentification of the San Luis Cr. gulosus, which Hubbs had correctly re-identified as asper ten years before (1921).

Schultz and DeLacy's catalogue (1936) included a comprehensive listing of Washington and Oregon localities for C. asper. However, some of the localities are doubtful since they frequently misidentified C. asper as gulosus and/or perplexus. They also incorrectly maintained the presence of

C. gulosus in Alaska.

Robins and Miller (1957) presumably overlooked the earlier citation of Rutter (1908) and removed Cottopsis parvus from the synonymy of gulosus, placing it in synonymy with asper, supposedly for the first time.

McAllister and Lindsey (1959) first suggested the probable existence of "coastal" and "non-coastal" populations of Cottus asper on the basis of morphological and, perhaps, behavioral differences.

Bond (1961) hinted at the possibility of polytypy in Cottus asper when he stated in his key that the body is "well covered with prickles, especially in inland waters and in young individuals from coastal waters. Bond (1963) gives the most comprehensive treatment yet recorded for Cottus asper and 12 other species in the genus. His study, however, is more concerned with interspecific rather than intraspecific relationships within the genus. Bailey and Bond (1963) have indicated their concern for the supraspecific relationships within the genus Cottus by their recognition of several species groups, one of which is the "asper species group."

Distribution

Range. - Pacific Slope Drainage of North America: Coastal streams from Seward, Alaska, to Ventura R., California; lakes and streams of the Queen Charlotte Islands and Vancouver Island; and all major Pacific drainages from the headwaters of the Stikine R. in British Columbia, to the Kern R., San Joaquin R. drainage, California. The following are exceptions: Fraser R. in the area of the Rocky Mountain Trench, east of Prince George, British Columbia (area not yet collected); Kootenay Lake drainage of the Columbia R. in British Columbia; Upper Snake R. of the Columbia R. drainage in Washington and Oregon; Middle Fork of the Willamette R. in Oregon, above Oakridge; Klamath R. Basin in Oregon; and Sacramento R. drainages above Lake Shasta, California. Arctic Slope Drainage of North America: Headwaters of the Peace R. in British Columbia: from Summit L. to McLeod L., Crooked R. drainage; from Tacheeda L.,

Parsnip R. drainage; from Tchentlo L., Nation R. drainage.

The present distributional range of Cottus asper is illustrated in Fig. 3.

Results: Analysis of Geographic Variation

Prickling Distribution. - As previously defined (p. 7), the "virtual" prickling represents the sum of two component percentages, i.e., the "apparent" prickling and the resorbed prickling. Fig. 4 illustrates graphically that mature specimens from populations of C. asper from coastal localities are considerably less prickled, both apparently and virtually, than inland localities. However, most inland populations from the Peace, Nass, Stikine, and parts of the Skeena R. drainage systems are coastal in their prickling affinities. Hereafter, these populations will be referred to as "coastal derivative." Likewise, certain populations from lakes on Vancouver Id. and the Queen Charlotte Islands (Q.C.I.) are also coastal in their prickling affinities. Fig. 4 also indicates that the population from Carquinez Strait, at the mouth of the Sacramento R. in San Pable Bay, California, has a mean "virtual" prickling percentage greater than that of any coastal population, and lower than all but one of the inland populations. For comparative purposes, the Carquinez Strait population will hereafter be referred to as the "intergrade" population.

Table I summarizes the mean percentage areal prickling and resorption for all populations grouped into aggregates according to locality and prickling affinity.

If the data for specimens under 60 mm S.L. are considered separately, there is a significant difference in mean percentage prickling, both "apparent" and "virtual," between the coastal and inland populations. Expressed in terms of a ratio between coastal-inland populations, a ratio of "apparent" prickling 1 : 1.8, and "virtual" prickling 1 : 1.5, is obtained. The aggregate means for the "coastal derivative" populations are essentially

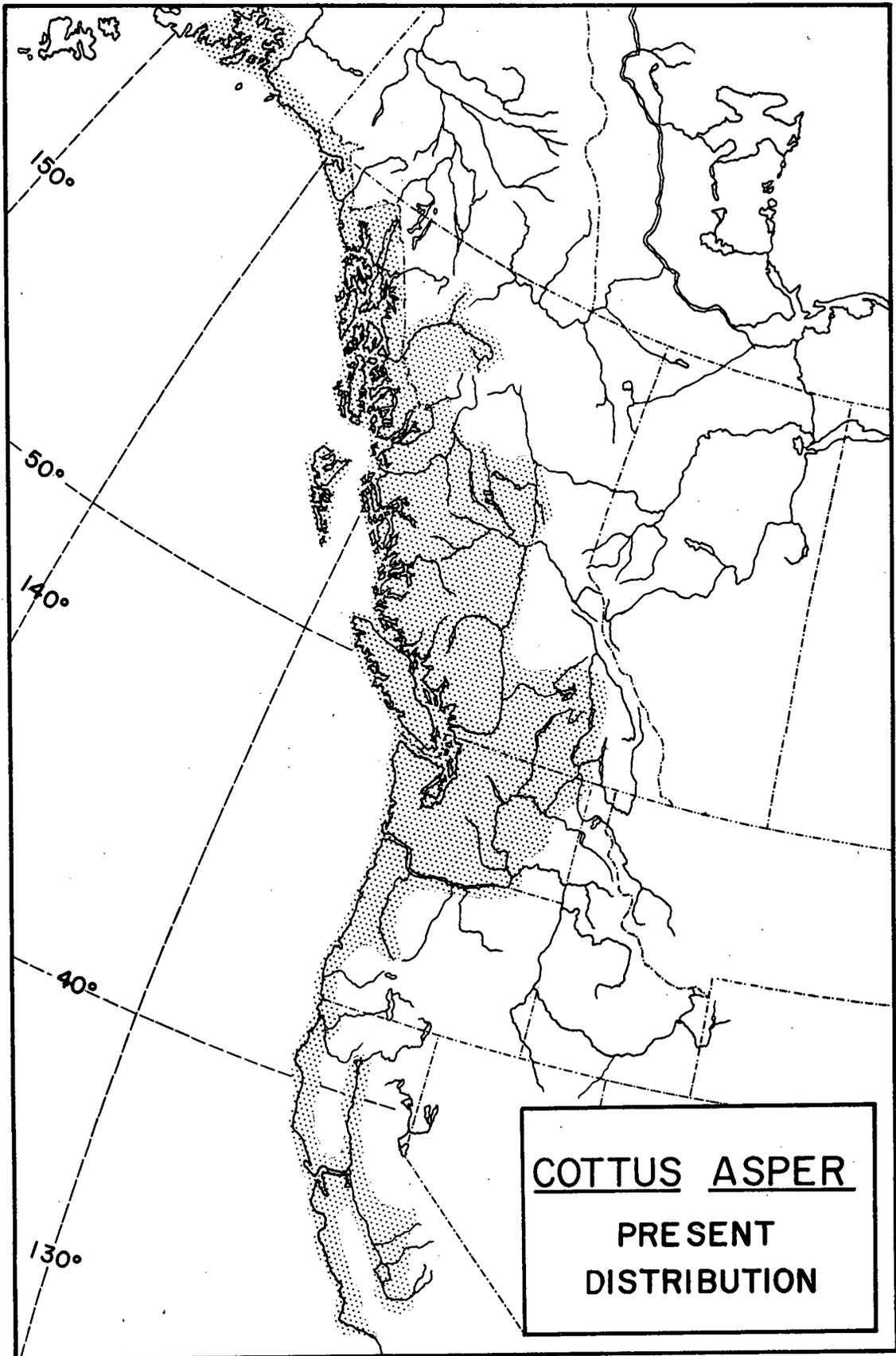


Figure 3.--Distributional Range of Cottus asper.

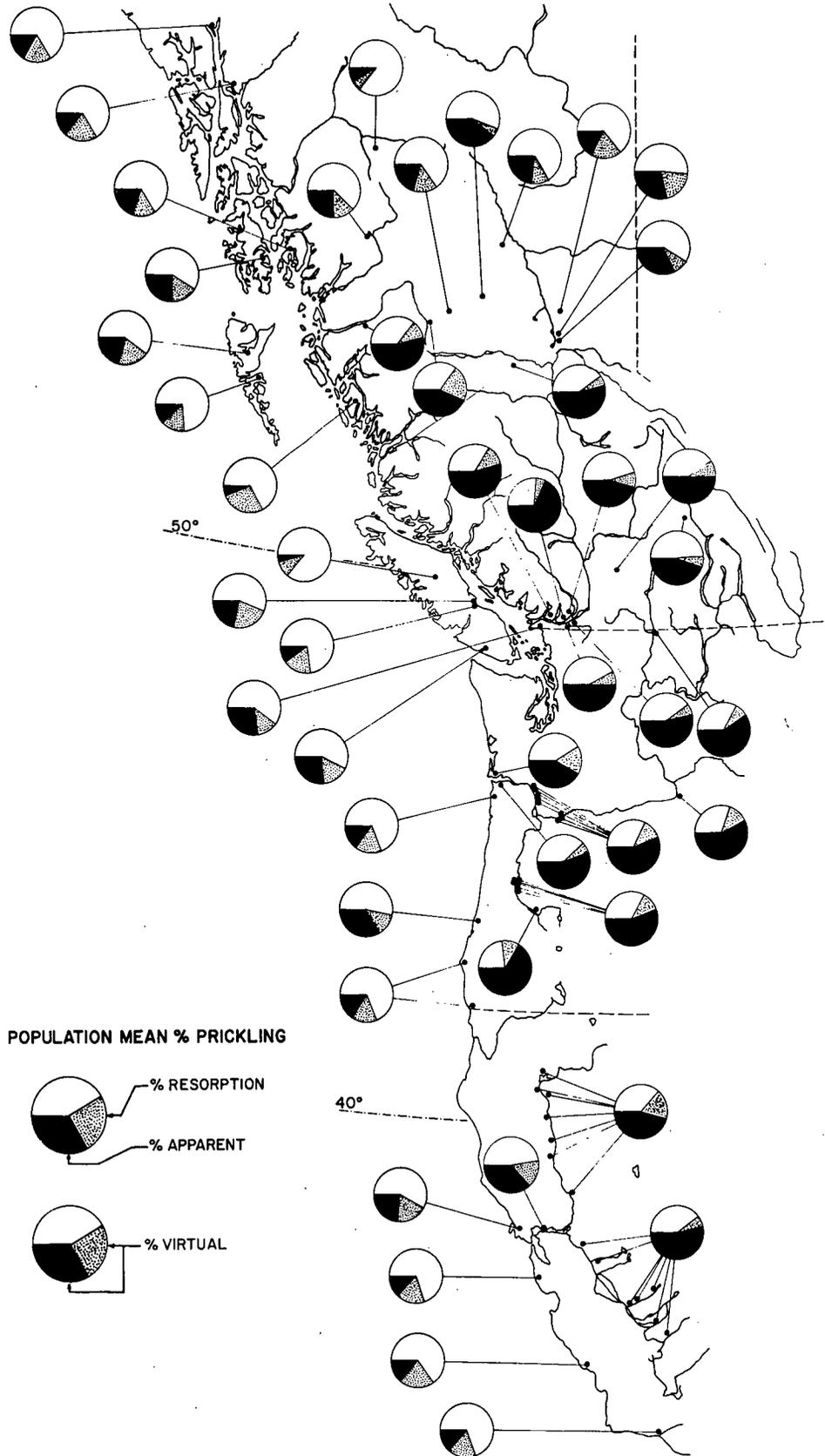


Figure 4.--Virtual, Resorbed, and Apparent Prickling in Cottus asper.

TABLE I. Mean Percentage Prickling and Resorption Among Aggregate Populations of Cottus asper.

Aggregate Population Designation	Specimens <60 mm S.L.		Specimens ≥60 mm S.L.			
	Virtual	Apparent	Virtual	Apparent	% Resorption	
					Relative	Absolute
Coastal ¹	43.5 (9) *	36.0 (12)	35.0 (16)	17.8 (19)	48.9	17.2
Coastal Derivative ²	44.8 (6)	41.8 (6)	34.7 (6)	24.2 (6)	32.0	10.5
Intergrade ³	60.1 (1)	57.1 (1)	52.9 (1)	35.6 (1)	32.8	17.3
Inland ⁴	67.2 (16)	65.3 (18)	63.2 (18)	53.2 (19)	16.1	10.0

* Brackets enclose numbers of population means in determination of aggregate mean percentages.

1 Populations 1-31, listed in Appendix Table 1

2 Populations 32-43, listed in Appendix Table 1

3 Population 73, listed in Appendix Table 1

4 Populations 44-72, listed in Appendix Table 1

the same as those for the coastal, and they differ significantly from the aggregate means for the inland populations. The mean for the intergrade population lies closer to the inland aggregate.

When specimens larger than 60 mm S.L. are considered, the same magnitude of difference is noted between the coastal and inland "virtual" percentages, i.e., a ratio of 1 : 1.8, but the "apparent" prickling percentages are even more divergent, having a ratio of 1 : 3. Since the "virtual" ratio remains constant, the divergent "apparent" ratios indicate a differential percentage resorption between mature specimens from coastal and inland populations. This differential is further suggested by the inverse relationship which exists between the mean percentage "apparent" prickling and the mean percentage relative resorption. It indicates that in coastal populations a greater percentage of the "virtual" prickling area is being resorbed than in inland populations. The reality of this differential resorption is shown in the figures for mean percentage absolute resorption which indicate that, in coastal forms, resorption occurs over almost twice as much area as in inland forms. The differential can be expressed in terms of a coastal-inland ratio, i.e., 1.7 : 1.

Prickling and resorption percentages on which Table I is based are given for all populations in Appendix Table 2.

Population analysis of the non-weighted mean percentage "virtual" prickling in each of the 14 body sections, of specimens > 60 mm S.L., indicates that in coastal and "coastal derivative" populations, body sections 'a', 'k', 'l', and 'n' are completely naked except for the rare occurrence of an isolated prickle. Similarly, in coastal and "coastal derivative" populations, only small portions of sections 'b', 'd', 'e', 'h', and 'm' are prickled. When compared to the mean percentage "virtual" prickling of inland populations, all nine of these sections are significantly different. Furthermore, in the remaining five sections ('c', 'f', 'g', 'i', and 'j'), the mean

percentage "virtual" prickling is always higher in the inland populations. These results corroborate the suggestion, made for the aggregate population means, that the areal distribution of prickling in coastal and inland populations of C. asper is different. Data for this analysis are presented in Appendix Table 3.

Prickling Intensity. - In general, the intensity of prickling, i.e., the number of prickles per unit area, is greater in inland fish than in coastal fish. In coastal populations, where prickles are almost never present in sections 'a', 'k', 'l', and 'n', no comparison of intensity can be made. Rarely, however, when an isolated prickle or group of prickles occurs in one of these sections, the intensity is always less than that of the corresponding section in an inland population. The same holds true for sections 'b', 'd', 'e', 'h', and 'm'. The comparison of intensity must therefore be made in one of the sections in which prickles are always present on both inland and coastal specimens. Section 'j' was chosen as representative. Table II shows that the mean relative intensity is greater in the inland populations than in coastal or "coastal derivatives." Interpolation of mean intensity values given in Table II into approximate number of prickles per sq. cm. (cf. Methods) yields counts of ca. 1325 prickles per sq. cm. in coastal forms (2.94), and ca. 1820 per sq. cm. in inland forms (3.86). Expressed in terms of differences between coastal and inland intensities, a ratio of 1 : 1.4 is obtained. Comparison to the ratio obtained for area prickling resorption, i.e., 1.7 : 1, indicates that even though inland fish have more prickles per unit area, more resorption (on a prickle for prickle basis) occurs in coastal fish. Mean relative intensity values for individual populations of Cottus asper are given in Appendix Table 4.

Table II also shows that in mean intensity of prickling, the "coastal derivative" populations aggregate is near the coastal mean whereas the "intergrade" population is closest to the inland mean. If the mean intensity

TABLE II. Mean Relative Prickling Intensity for Populations of Cottus asper
 Aggregated by Locality and Prickling Affinity. Skin Section 'j'.

Aggregate Population Designation	Specimens <60 mm S.L.		Specimens ≥60 mm S.L.	
	Sample Size	Intensity Mean (Range)	Sample Size	Intensity Mean (Range)
1 Coastal	136 (13) *	2.94 (1-5)	235 (18) *	2.64 (1-5)
2 Coastal Derivative	103 (11)	2.74 (1-4)	43 (7)	2.95 (1-5)
3 Intergrade	8 (1)	3.75 (3-5)	20 (1)	3.45 (2-4)
4 Inland	238 (21)	3.86 (2-5)	265 (19)	4.20 (3-5)

* Brackets enclose numbers of populations included in aggregate sample.

- 1 Populations 1-31, listed in Appendix Table 1
- 2 Populations 32-43, listed in Appendix Table 1
- 3 Population 73 only, listed in Appendix Table 1
- 4 Populations 44-72, listed in Appendix Table 1

values of certain coastal lake forms, i.e., Horne L., Buttle L., Skidegate L., and Chilkoot L., are considered (Appendix Table 4), they are found to be slightly lower than the coastal means. These data corroborate the differences already shown to exist in mean areal distribution of prickling between coastal and inland populations.

Pectoral Fin Asymmetry. - Of 59 populations investigated for pectoral fin asymmetry, 56 had some specimens with asymmetrical pectoral fin element counts. Of 1163 paired counts, from 59 populations, 23.6% (275 pairs) were asymmetrical (Table III). This percentage incidence of occurrence is similar to the percentages reported for other cottids by Hubbs and Hubbs (1945).

Of the 56 populations of Cottus asper exhibiting asymmetry, 39 (69.6%) were sinistral, 11 (19.6%) were dextral, and 6 (10.7%) had equal numbers of right and left asymmetrical fins. This apparent direction of asymmetry within populations is not statistically significant since the sample sizes of asymmetrical fins within each population were very small. However, if the asymmetrical fins are grouped according to locality and supposed derivation (based on prickling), or pooled for all populations (Table III, columns 5 & 6), the overall direction of asymmetry in Cottus asper is significantly sinistral ($\chi^2 = 21.56$, $\alpha = .05$, 1 d.f., for the pooled sample).

While Cottus asper is significantly sinistral in the overall direction of its asymmetry, the amount of sinistrality within populations varies from 0 to 100%. When the populations are grouped according to locality and supposed derivation (Table III, col. 5), the amount of sinistrality for 24 coastal populations is 66.7%; for 12 coastal derivative populations, 69.2%; and for 23 inland populations, 60.8%. These differences among aggregate populations are not significant. Additional analysis of data on a north-south basis revealed no significant differences in direction or amount of asymmetry.

Total pectoral fin counts on which Table III is based are given for all

TABLE III. Incidence of Occurrence, Direction, and Amount of Pectoral Fin Asymmetry Within and Among Aggregated Populations of Cottus asper.

Locality	No. Pairs	Symmetrical	Asymmetrical	Sinistral	Dextral
Coastal*	460	367 (79.8)**	93 (20.2)	62 (66.7)	31 (33.3)
Coastal Derivative	152	113 (74.4)	39 (25.6)	27 (69.2)	12 (30.8)
Inland	551	408 (74.0)	143 (26.0)	87 (60.8)	56 (39.2)
Pooled Total	1163	888 (76.4)	275 (23.6)	176 (64.0)	99 (36.0)

* Includes three coastal island lake populations

** Brackets enclose aggregate mean percentages

populations in Appendix Table 5.

It has been shown for several species of fish that the lowermost pectoral ray is shorter on the side which has the higher count (Hubbs and Hubbs, 1945; Hubbs, 1963). Cottus asper appears to follow this rule. Of 69 specimens, from 17 populations having asymmetrical pectoral fin counts, 66 had a shorter lowermost ray on the side with the higher count, and only 3 had the lowermost rays equal on each side.

While Cottus asper demonstrates a significant sinistrality in the direction of its pectoral fin asymmetry, the amount of this sinistrality within and among populations cannot be used to separate individual populations or geographically aggregated groups of populations.

Pectoral Fin Ray Count. - The mean number of pectoral fin rays increases progressively from south to north in the inland populations (Figs. 5 & 11). Coastal populations show a similar increase northward only to about 42-44° N. Latitude where the mean pectoral fin ray counts diverge from the inland counts and decrease toward the north. Mean counts for the "coastal derivative" population are found to be equal to or less than inland population means, but always higher than those of the coastal means, at the same latitudes. The means of certain coastal island lake and coastal mainland lake populations (Buttle, Horne, Skidegate, and Owikeno L., cf. Appendix Table 1) are almost a full count higher than the means of nearby stream populations from which they probably were derived. Data from Carquinez Strait "intergrade" population and two additional populations from the San Francisco-San Pablo Bay area, thought to be intergrades, (cf. Appendix Table 1, population numbers 74 & 76) were compared. At the low latitudes in which they occur, their mean pectoral ray counts were indistinguishable from either coastal or inland means.

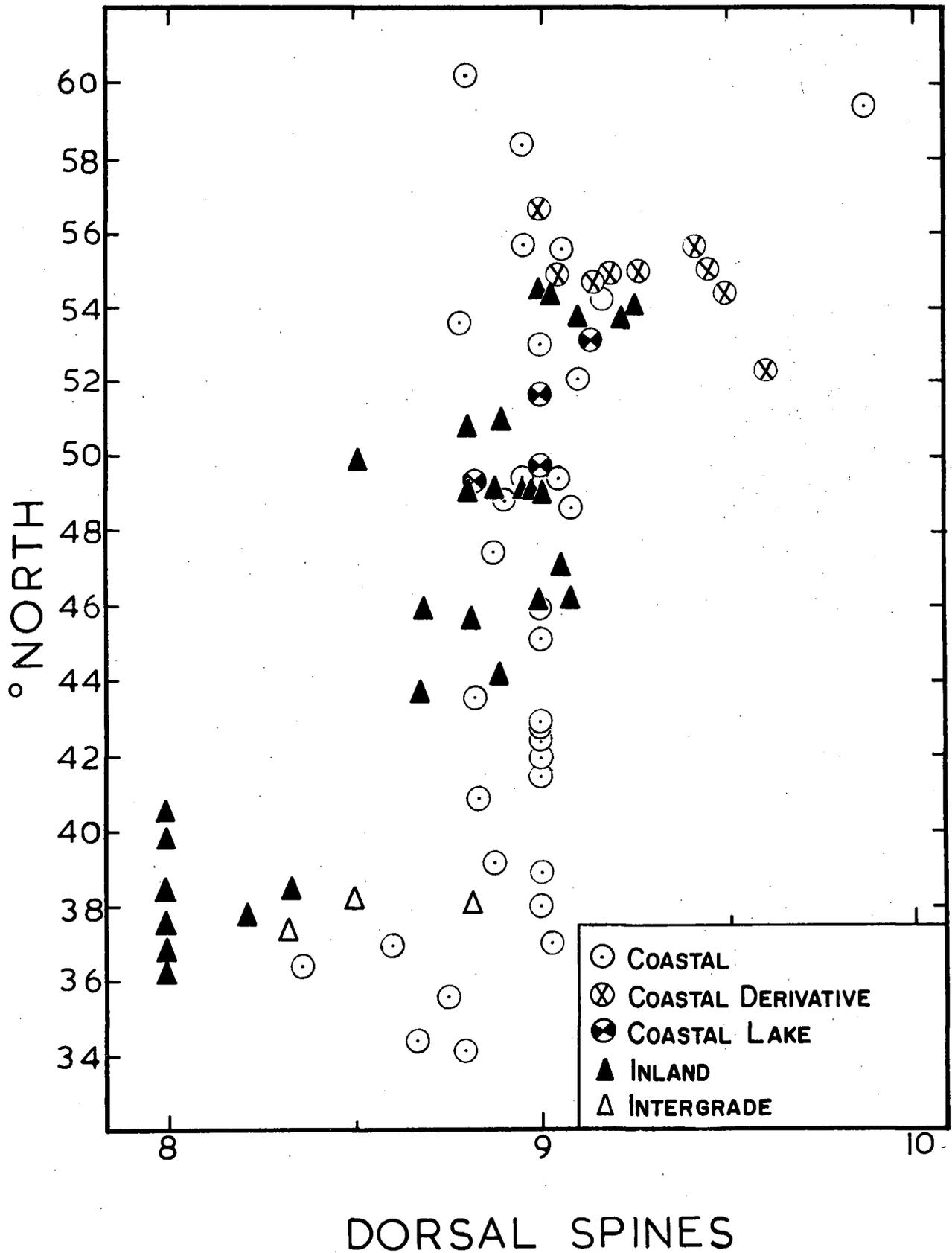
Spiny Dorsal Fin. - The average spine number is clustered about nine for all coastal populations except the southernmost California populations

which are slightly lower (Fig. 6). The San Joaquin-Sacramento R. inland populations have a mean count of eight or slightly higher. This wide divergence tends to accentuate a slight, but discernible, geographic cline for the inland populations as a whole. The mean counts are slightly higher than nine in the high latitudes, slightly lower in the mid-latitudes, and much lower in the low latitudes (cf. Fig. 11). A comparison of the ranges (Appendix Table 6) indicates high counts of nine to eleven in the north, and low counts of seven to nine in the south of the distributional range of the species. The intermediate positions of the three "intergrade" populations within the San Francisco-San Pablo Bay area should be noted. The means of the "coastal derivative" populations tend to be closer to those of the inland populations.

Soft. Dorsal Fin. - The mean soft-ray number varies considerably with latitude. Counts are slightly higher than 20 in the high latitudes, closer to 21 in the mid-latitudes, and between 19 and 20 in the low latitudes. As can be seen in Fig. 7, the inland Sacramento and, especially, the San Joaquin R. populations have considerably lower mean counts than their coastal counterparts at the same latitudes. If the soft-ray counts for all inland populations are summed into aggregates of 2-degree latitude and plotted according to the Hubbs-Hubbs format (Fig. 8), the V-shaped geographic cline within the means and the ranges becomes immediately apparent (cf. Fig. 11).

Combined Dorsal Fin Elements. - Combining the spiny and soft dorsal elements tends to minimize the variation in means at the middle of the range, while accentuating the divergence between coastal and inland populations in the high and, especially, the low latitudes (Fig. 9). The divergence between the San Joaquin-Sacramento populations and their coastal counterparts at the same latitude is especially enhanced (cf. Fig. 11). The intermediate position of the intergrade population means and the position of the "coastal derivative" means will be discussed later.

Anal Fin. - The mean number of anal rays varies around 17 for all



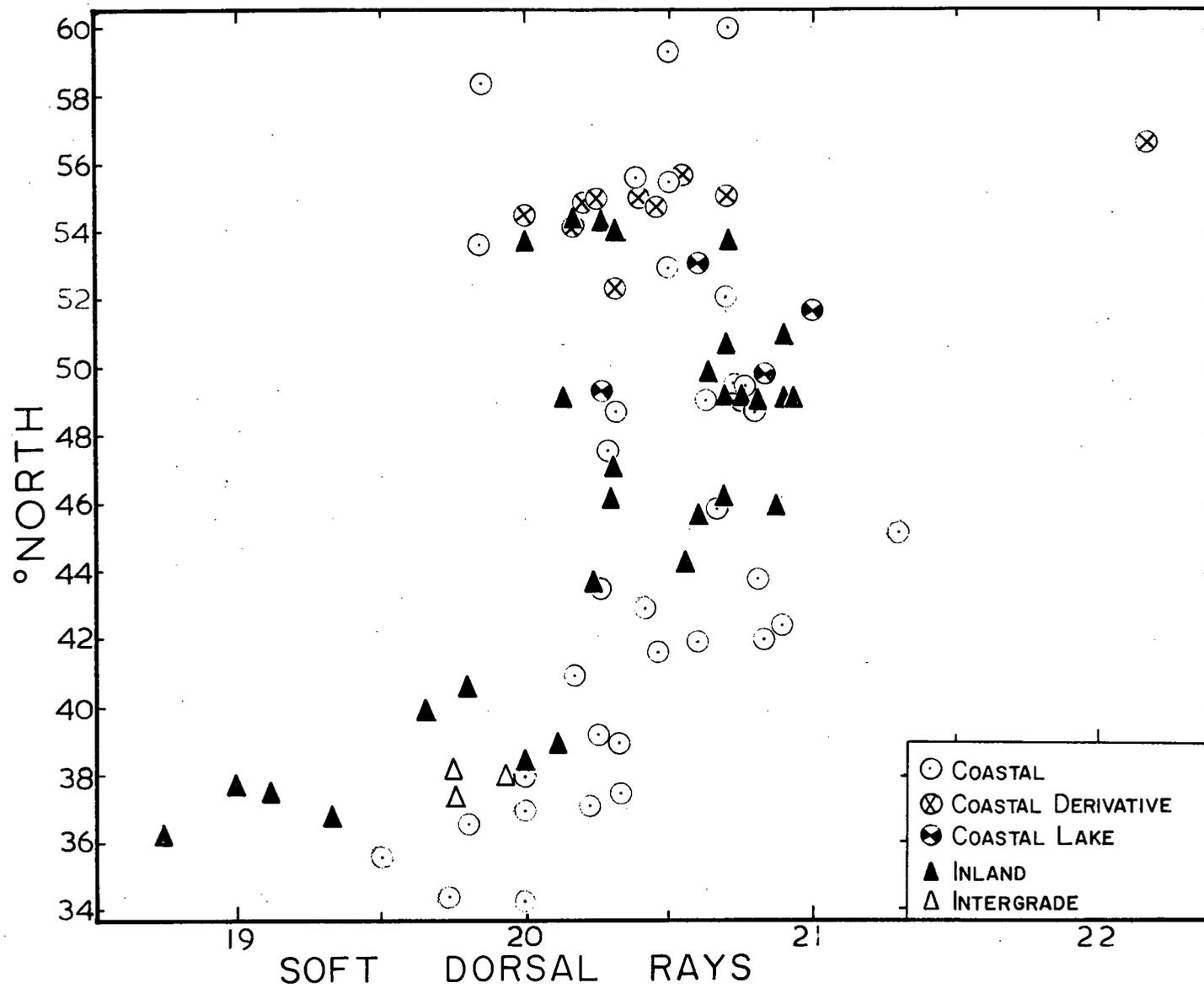


Figure 7.--Mean Soft Dorsal Fin Ray Count by Latitude.

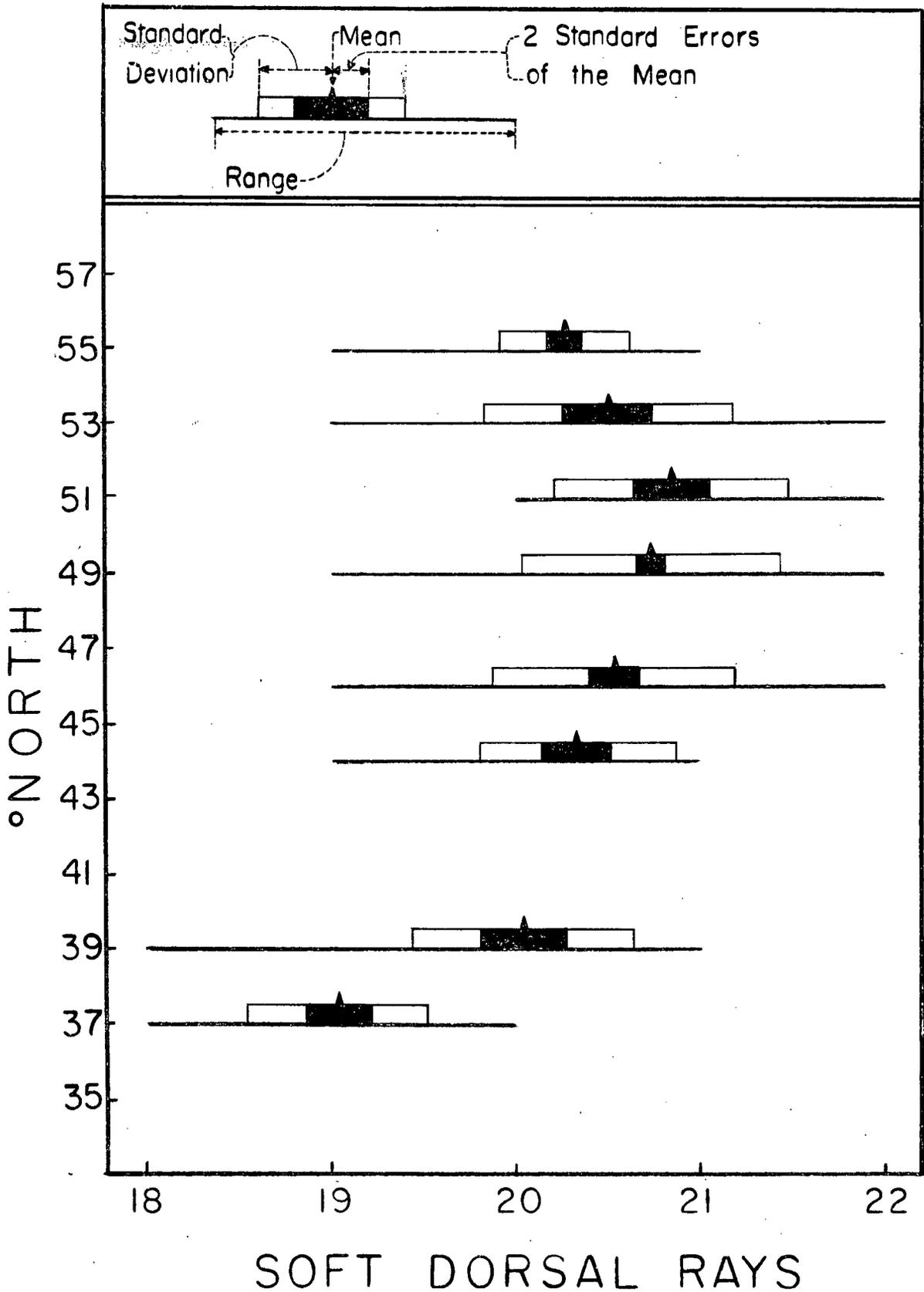


Figure 8.--Hubbs-Hubbs Plot of Soft Dorsal Fin Ray Counts for Inland Population; Samples Pooled into Aggregates of Two Degrees Latitude.

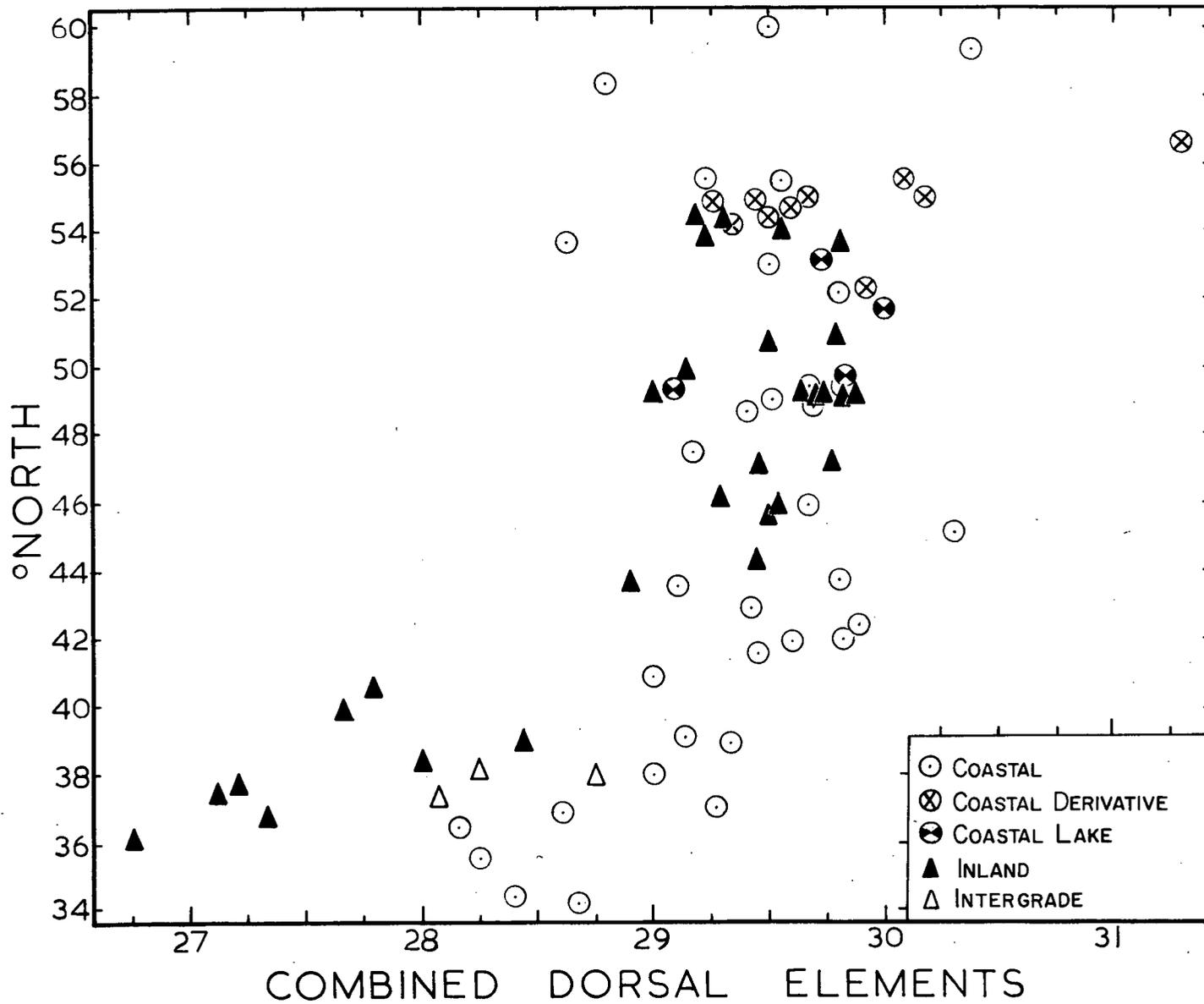


Figure 9.--Mean Combined Dorsal Fin Ray Count by Latitude.

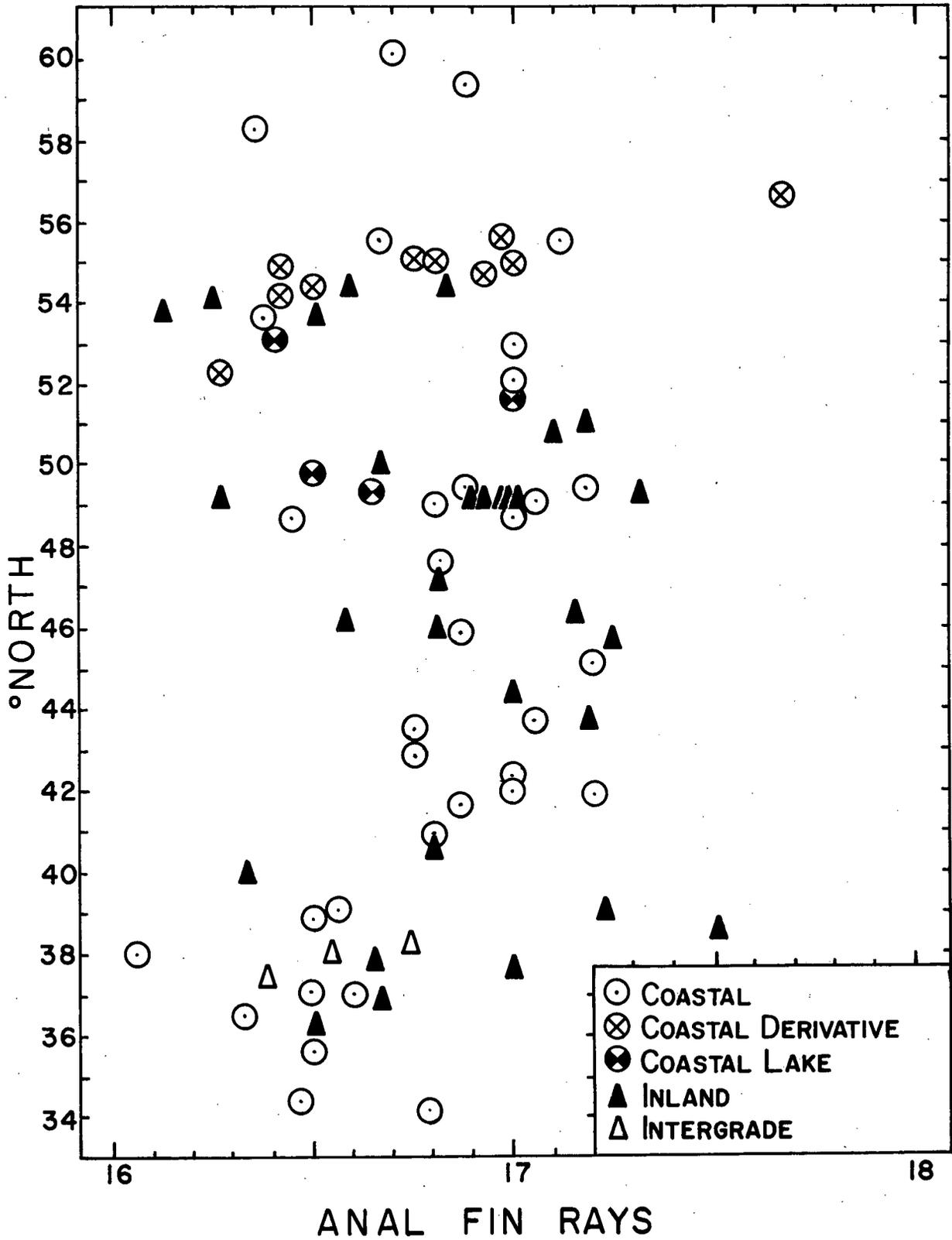
populations (Fig. 10). There is a tendency for the mean to be slightly lower in the northern and southern ends of the distributional range, whereas in the mid-latitudes the means are clustered about 17. This pattern tends loosely to follow the V-shaped curve observed in the number of soft dorsal rays (cf. Fig. 11).

Pelvic Fin. - The pelvic fin almost invariably consists of 1 spiny plus 4 segmented rays. Among more than 1000 specimens examined for this character, there were only 20 deviants from the usual left-right count of 4-4. In one specimen both fins, and another specimen, the left fin was missing. In neither specimen was there any apparent injury. Of the remaining 18, 7 deviants (4 damaged) were on the left side, and 11 (4 damaged) on the right. Thus even in the most stable meristic character, rare deviations occur.

A summary of meristic counts for all populations is given in Appendix Table 6.

Latitudinal Variation in Ranges of Mean Fin Ray Counts. - Figure 11 is derived from each of the Figures: 5, 6, 7, 9, and 10. When the means of the inland and the coastal populations are enclosed by sets of lines approximating the range of means, a family of curves representing all the meristic data for all latitudes is generated. Several trends are apparent in Figure 11:

- 1) The curves for inland and coastal population means, though overlapping in some areas, are widely divergent in others;
- 2) All curves, except for the spiny dorsal and the inland pectoral means, demonstrate a characteristic V-shaped pattern with an inflection occurring at about 42-44° N. Latitude;
- 3) For pectoral fins, the greatest amount of divergence between coastal and inland means exists in the high latitudes. The opposite is true for the dorsal fin elements; and
- 4) In areas where coastal and inland curves are divergent, the means



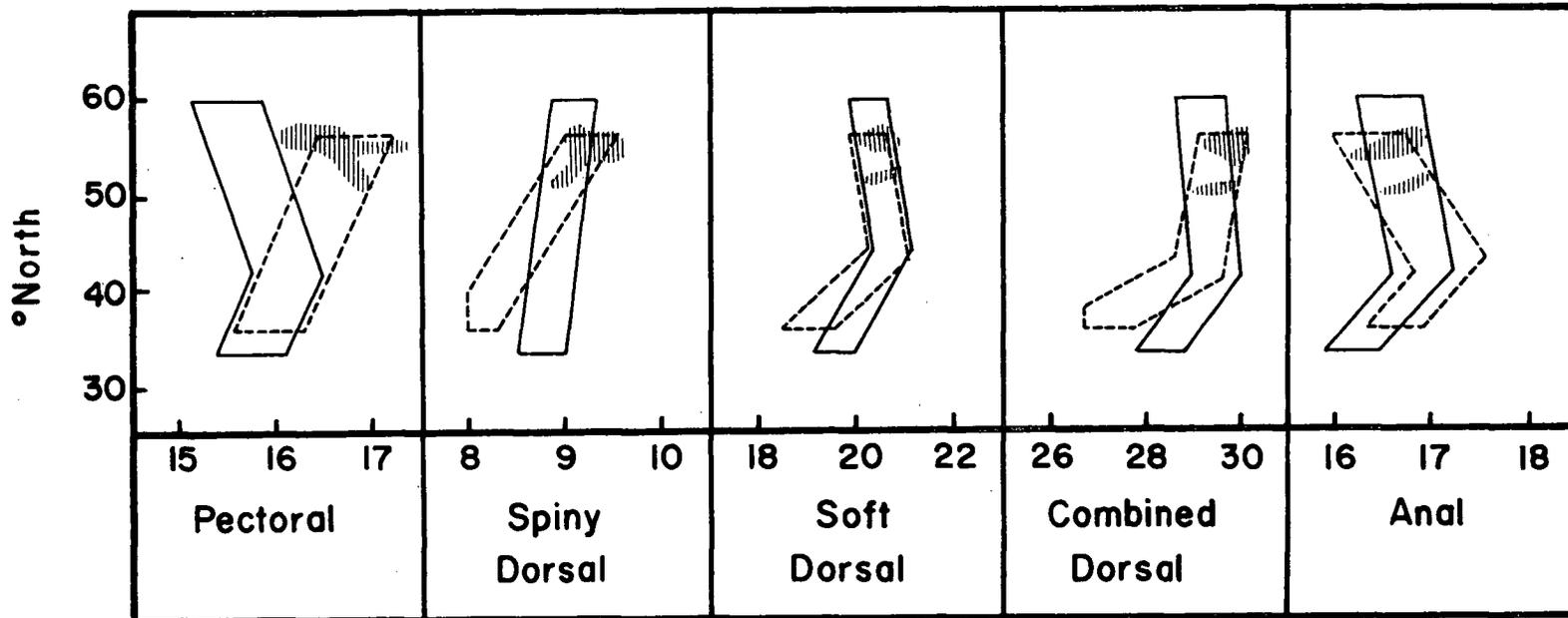


Figure 11.--Approximate Ranges of Mean Fin Ray Counts Plotted Against Latitude for Inland (---), Coastal (—), and Coastal Lake and Coastal Derivative (hatched) Populations. Curves fitted by eye from Figures 5, 6, 7, 9, and 10.

for coastal lake and "coastal derivative" populations always approximate the inland rather than the coastal curve.

The interpretation of these curves and the similarity of their characteristic V-shape to curves generated from laboratory rearing experiments under controlled temperatures will be considered in the discussion on meristic variation within Cottus asper (below).

Lateral Line. - The number of lateral line pored-scales varies directly with size up to about 60 mm S.L., the average size at which most Cottus asper first become reproductively mature (Table IV). In most specimens larger than 60 mm, the pored-scale count approaches, or equals, the "complete" lateral line count. One obvious exception is in a spawning population collected from the estuary of a small stream in Juskatla Inlet, Queen Charlotte Islands, in which many of the small specimens 40-49 mm S.L. were in spawning condition. Their pored-scale counts approached or equalled the mean "complete" lateral line count (Table IV). Another exception to the generalization is that afforded by specimens from the coastal lake populations found on the British Columbia or Alaska mainland, or on the offshore islands. Most mature specimens are characterized by their low pored-scale counts (Table IV). Of the coastal lake populations, small specimens were available only from Skidegate L. All of these were immature and all had low pored-scale counts, but the "complete" counts of this, and other coastal lake populations, were equivalent to the mean counts for other coastal and inland populations.

Tentative analysis of mean "complete" lateral line counts indicates a tendency toward higher counts in the north. Paucity of counts throughout the entire range of Cottus asper precludes any further comparisons at this time.

Discussion of Meristic Variation Within Cottus asper

Lindsey (1961; 1962) has reviewed literature which demonstrates that

TABLE IV. Lateral Line Pored-Scale Counts by Size Groups for Selected Representative** Populations of *C. asper*

Population	Size	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	
Saltery Cr. Alaska **"complete" $\bar{X}=40.06$	≥ 60	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	3	9	3	--	--	4
Cultus L. B.C. "complete" $\bar{X}=40.27$	≥ 60	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	1	1	3	3	2	2	--	4
	50-60	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--
	40-49	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	1	--	--	--	--	--	--	--	--	--	--	--	--
	30-39	--	--	--	--	--	--	--	--	--	--	1	--	1	2	1	1	--	--	--	--	--	--	--	--	--	--	--	--
20-29	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
Graham Id., QCI Juskatla Inlet "complete" $\bar{X}=39.33$	≥ 60	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	4	13	3	1	--	--	
	50-59	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	2	34	--	--	--	--	
	40-49	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	1	--	2	3	19	5	15	--	--	--	--	
	30-39	--	--	--	--	--	--	--	--	1	--	1	2	2	--	--	--	--	1	--	3	2	--	--	--	--	--	--	
20-29	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
Moresby Id., QCI Skidgate L. "complete" $\bar{X}=39.70$	≥ 60	--	--	--	--	--	--	--	--	--	--	--	2	1	2	1	--	--	3	--	2	4	2	3	--	--	--	--	
	50-59	--	--	--	--	--	--	--	--	1	--	--	1	2	--	--	--	--	--	--	--	--	1	--	--	--	--	--	
	40-49	--	--	--	--	--	--	--	1	--	1	1	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
	30-39	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
Buttle L. Van. Id. "complete" $\bar{X}=39.71$	≥ 60	--	--	--	1	--	1	--	--	--	1	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	
	40-49	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
Horne L., Van. Id. "complete" $\bar{X}=39.45$	≥ 60	--	--	--	--	--	--	--	--	--	1	1	2	2	2	2	--	--	--	--	--	--	1	--	--	--	--	--	

* "complete" counts are mean counts of lateral line pored-scales plus unenclosed neuromast hillocks.
 ** Saltery Cr. represents a typical coastal population; Cultus L. represents a typical inland population; Juskatla Inlet represents a coastal island stream population; Skidgate, Buttle, and Horne L. represent coastal lake populations

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in fishes reared experimentally over a wide range of temperatures, a V-shaped, or inverted V-shaped, curve is typical for meristic series, especially vertebrae. Generally, an intermediate temperature produces the minimum count, but sometimes, a maximum count. Lindsey (1962) states that the inflection in the curve might not be discovered if a narrow range of temperature were used and that demonstration of a V-shaped, rather than a simple direct or inverse, relationship between meristic counts and temperatures sometimes requires rearing at extremes close to the upper or lower level of temperature tolerance of the species.

Such V-shaped curves have seldom been shown to exist in natural fish populations. That they exist in Cottus asper, a latitudinally wide-ranging species, might be interpreted to indicate that, at the ends of its distributional range, the prickly sculpin's eggs are subjected to developmental temperatures close to the upper and lower levels of tolerance. However, we have elsewhere indicated (p. 53) that the usual spawning range for Cottus asper is from 8 to 13° C. It is assumed that in all populations spawning is initiated within this 5° range of temperature which proceeds in somewhat of a thermal "wave" from south to north in both inland and coastal localities (Fig. 5). This is not to say that they all spawn at the same temperature within that range. Furthermore, because the monthly rate of increase of ambient temperature is greater in the north (Fig. 12, and Appendix Table 7), the duration of exposure to any given temperature within the 5° temperature range may be shorter. Eggs subjected to these conditions would presumably have a faster development than eggs which developed under relatively more thermostable conditions such as occur in the south. Low meristic counts are generally (although not invariably) associated with faster rates of development. Based on the information given above, northern eggs should produce offspring with low meristic counts. But when plotted against latitude, the mean pectoral fin ray counts of inland Cottus asper populations

produce a linear curve which is typically clinal, i.e., with more rays in the high latitudes, fewer in the low latitudes. The coastal population means demonstrate a V-shaped curve with low counts in the high and low latitudes, and higher counts in the mid latitudes. Such results are enigmatic.

Whether a temperature range of only 5° C. is enough to elicit a V-shaped response has not been experimentally confirmed for Cottus asper, but Lindsey (1962) obtained such a curve in the mean counts of pectoral fin rays in the stickleback, Gasterosteus aculeatus, over a developmental range of 15 to 20° C.

It is apparent from Fig. 11 that V-shaped curves are characteristic for the median soft fin ray counts of Cottus asper whereas for the paired pectoral fins, only the coastal populations show a V-shaped curve. The inland means appear to be the only exception, at least in the high latitudes. The existence of such a divergence between coastal and inland means indicates that temperature alone is not the determining factor.

Interpretation of the divergent results between coastal and inland means is facilitated by an analysis of mean pectoral fin ray counts for coastal lake and coastal derivative populations. In the former, the mean counts do not fall, as would be expected, on the curve for coastal populations but they are directly in line with, and indistinguishable from, the higher means of inland populations. In the derivative populations, the means are found to be equal to, or slightly less than, the inland means but always greater than the coastal means at the same latitude (Fig. 5). This further suggests that temperature alone cannot be the determining factor.

There is only one universal factor which, at any given latitude, varies between coastal populations and all others. This factor is salinity and/or the lack of access to it in the spawning population. At least two of the four coastal lake populations are restricted to spawning in fresh water

because of man-made or natural barriers, i.e., Horne L. and Buttle L. on Vancouver Island. Even though the mouth of Skidegate L. on Moresby Island, QCI, is only about 10 miles from the sea, the population of Cottus asper from which the meristic data were sampled, is known to spawn in fresh water inlet streams. The spawning locality of the Owikeno L., B. C., population is unknown. That of the Chilkoot L., Alaska, population is also unknown but the fin ray counts are typically inland whereas the prickling pattern is definitely coastal in its affinity. It may therefore be supposed that spawning occurs in fresh water.

It may also be presumed that all the coastal derivative forms now spawn in fresh water. Therefore, in the high latitudes, increased mean pectoral fin ray counts in coastal lake or "coastal derivative" populations, and in inland populations, is correlated with the lack of salinity in the environment.

Any discussion of the nature of the differences between coastal and all other populations is a matter of conjecture with the evidence now at hand. Two opposing hypothesis can be postulated:

- 1) The observed differences reflect environmentally induced changes of the individual phenotypes within each population; or
- 2) The differences have become genetically fixed in the populations over a long period of time.

Consideration of these alternatives rests on an interpretation of the relationship of the coastal lake and "coastal derivative" populations to the main coastal population. In the areal distribution and intensity of their prickling, the coastal lake and "coastal derivative" forms show very close affinity with the coastal populations. Furthermore, because of the glacial history of the coastal islands on which they are found, the near-naked forms from Buttle L., Horne L., and Skidegate L., can be assumed to have been derived from coastal stream forms which colonized the island after the retreat

of the Cordilleran ice sheet which covered the area during the late Wisconsin Glaciation. The probability that they were colonized by inland forms is remote since the nearest inland forms would presumably have been found in unglaciated areas of the lower Columbia R. basin (cf. Fig. 20).

In similar manner, the occurrence of the "coastal derivative" populations only in parts of northern British Columbia relatively recently exposed by the retreating glaciers argues that these populations are probably derived from coastal ancestors which followed the retreat of the glaciers northward and then inland. It can be assumed that they are more recent than their coastal lake counterparts, and perhaps even more recent than those inland forms which followed the retreat of the ice in the Fraser R. drainage (cf. final discussion, p. 79).

As was previously stated, the increased mean pectoral fin ray counts in coastal lake and "coastal derivative" populations is correlated with a lack of salinity. One can explain the phenotypic changes in pectoral fin ray counts by postulating an environmental inhibition or alteration of the metabolic pathway usually traversed by the gene which controls the phenotypic expression. The lack of salinity in the environment might produce such an alteration. But, since not all of the "coastal derivative" means are equal to those of the inland populations, it can also be argued that, because of a selective pressure caused by the absence of salinity in the environment, the coastal lake populations have become, and the "coastal derivative" populations are becoming, genotypically modified toward the means characteristic of the inland forms of Cottus asper. Such modification might be envisioned in terms of a mutation in one of the steps in the metabolic pathway of the controlling gene.

Whatever the cause of the differences, the evidence at hand is not now sufficient to determine its nature. A definitive experiment regarding the nature of the differences would consist of taking the eggs of coastal lake

or "coastal derivative" forms and rearing them in brackish water using fresh water reared eggs as a control. If the mean fin ray counts of the F_1 generation were significantly lower than the control means, the result could be interpreted as being due to environmental induction rather than to long term genetic fixation. In either event, the mechanisms involved in the actual modification of the phenotype and/or genotype would still remain a matter for more refined genetic experiment.

Summary of Morphological Analysis

1. Cottus asper is found in all major Pacific Slope drainages from Seward, Alaska, to Ventura, California. On the Arctic Slope drainage its distribution is limited to the Upper MacKenzie R. drainage only in the headwaters of the Peace R. in British Columbia.

2. Some of the prickles found in the skin of Cottus asper are resorbed during reproductive maturation which occurs at about 60 mm S.L. Because of this, all population means were calculated for groups of specimens less than or greater than 60 mm S.L.

3. Estimates of the percentage of total body surface covered with prickles are calculated from the formula:

$$\% \text{ "virtual" prickling} = \% \text{ "apparent" prickling} + \% \text{ area of resorbed prickling.}$$

4. Coastal populations of Cottus asper are, "apparently" and "virtually," less prickled than inland populations. Differences in "apparent" prickling between coastal and inland populations are more pronounced in specimens \geq 60 mm S.L., i.e., a coastal-inland ratio of 1 : 3 exists.

5. Inland populations of C. asper from the headwaters of the Peace, Ness, Stikine, and Skeena R. systems in northern British Columbia, are coastal in their prickling affinities and are referred to as "coastal derivative" populations.

6. A population of C. asper from the mouth of the Sacramento R. in

California is intermediate in its prickling affinities and it is designated as an "intergrade" population.

7. Asymmetrical pectoral fin element counts were found in 56 of 59 populations of C. asper. Of 1163 paired counts, from 59 populations, 23.6% were asymmetrical. When the asymmetrical fins from all populations were pooled, the overall direction of asymmetry was significantly sinistral (64% sinistral, 36% dextral).

8. Differences in amount of sinistrality within and among aggregate populations are not significant. No clinal trends are evident.

9. Mean pectoral fin ray counts for all populations are similar in the low and mid-latitudes of the distributional range, but are widely divergent between coastal and inland populations in the high latitudes.

10. Means of "coastal derivative" populations are equal to or less than those of inland population means but always higher than those of coastal means at the same latitude.

11. Means of coastal lake forms are a full count higher than the means of coastal stream populations from which they were probably derived. They are indistinguishable from inland means at the same latitude.

12. When plotted against latitude, mean fin ray counts produce curves which are different for inland and coastal populations.

13. For pectoral fins, the greatest amount of divergence between inland and coastal means exists in the high latitudes. The opposite is true for the dorsal fin elements.

14. Except for the spiny dorsal and the inland pectoral means, all meristic curves demonstrate a characteristic V-shaped pattern with the inflection occurring at about 42 to 44° N. Latitude.

15. The pelvic fin almost invariably consists of 1 spiny plus 4 segmented rays.

16. Counts of the lateral line pored-scales are extremely variable.

with size up to about 60 mm S.L. In Cottus asper, a "complete" lateral line count cannot be considered reliable unless a count is made of the number of pored-scales plus the number of unenclosed neuromast hillocks.

STUDIES ON THE LIFE HISTORY OF THE PRICKLY SCULPIN

Present Knowledge of Spawning Migration in Cottus asper

The existence of a seaward spawning migration of prickly sculpins in coastal streams has been suggested, or implied, for at least 30 years (Taft, 1934; Pritchard, 1936; Sumner, 1953; Shapovalov and Taft, 1954; Hunter, 1959; and McAllister and Lindsey, 1959). Although some of these authors have observed the presence of reproductively mature Cottus asper in the intertidal areas of coastal streams, none has demonstrated that intertidal spawning actually occurs.

Populations of Cottus asper occurring in lakes and streams far enough inland to preclude the possibility of an annual seaward spawning migration are presumed to spawn in fresh water. The approximate or exact spawning sites of some of these populations have now been determined from the presence of larvae (Nicola L., B. C.), and egg clusters or gravid females (Pothole L., near Merritt, B.C.). Other localities are close enough to the sea to imply the existence of a short seaward migration on the part of the Cottus asper populations living therein, but access to the sea is prevented by natural or manmade barriers, e.g., Buttle L. and Horne L. on Vancouver Island, B.C. Spawning of prickly sculpins in these areas is necessarily restricted to fresh water.

Still other localities, frequented by migratory salmonids, are close enough to the sea to imply a seaward migration on the part of Cottus asper, but it does not occur. For example, the spawning sites of the following prickly sculpin populations in the lower Fraser Valley in British Columbia

are known from capture of gravid fish and/or egg masses: South Alouette R.; Kenworthy Cr. and Chilqua Slough (both are inlet streams to Hatzic L.); Squakum L.; and Cultus L. In addition, spawning fish have been captured in inlet streams of Skidegate L., in the Queen Charlotte Islands, along with migratory juvenile salmonids. The outlet of Skidegate L. is only about 13 miles from the sea. A newly-hatched larva of Cottus asper (?) has been taken in a plankton net in the Second Narrows region of Owikeno L. (about 30 miles from the sea), on the coast of central British Columbia. It is presumed that the parents spawned in fresh water.

Spawning Period and Temperature Relationships. - Egg clusters were collected from several localities in the lower Fraser valley and in the Little Campbell R. Gonads were examined in over 1100 of the preserved specimens from all latitudes. These data indicate that egg deposition begins in the south of the distribution range (low latitudes) in February, and progresses northward until late July. Males usually attain full reproductive maturity about a month before, and remain in spawning condition for almost a month after, the period of oviposition in females. Gravid females have been found over a 4-week period in Squakum L., and 6 weeks in the Little Campbell R. Ripe males have been taken over an 8 to 12 week period, respectively, in these same localities.

The earliest date on which a ripe male, in nuptial dress and with flowing sperm, was collected is February 6th, in San Francisco Bay. The earliest collection of gravid females was in Waddell Cr., California, on February 24th. In the north end of the range, gravid females were taken as late as June 20th in Petersen Cr., near Juneau, Alaska, and on July 22nd in streams entering Juskatla Inlet, Queen Charlotte Islands. Gravid females have also been collected from Middle R., near Takla L., on June 28th, and from Meziadin L., B.C., on July 25th.

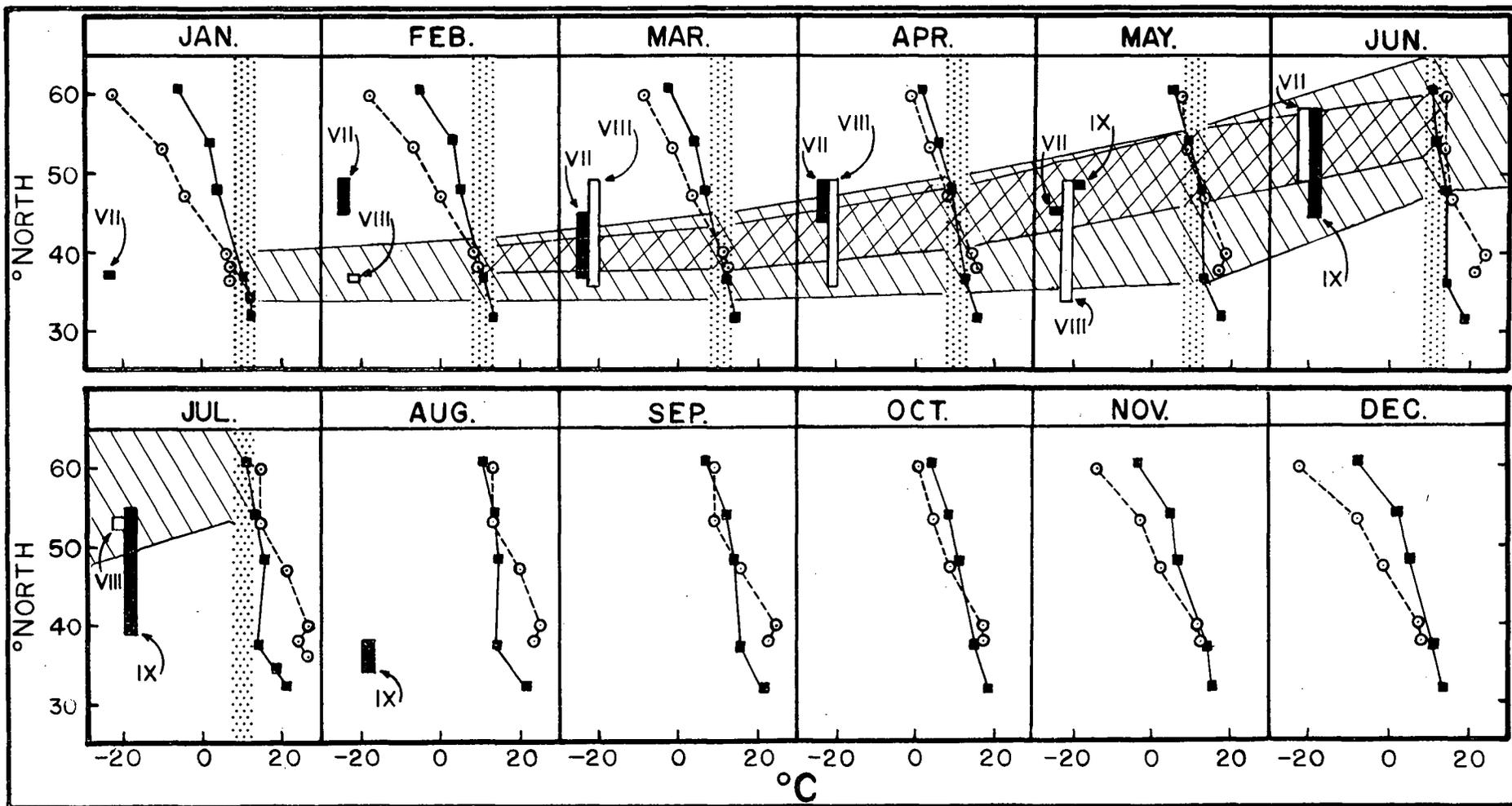
Field records and personal observation indicate that natural spawning

temperature range from 8 to 13° C. Egg rearing experiments at various temperatures resulted in complete mortality in 18° C., and less than 50% survival at 15° C.

The annual mean range of temperatures experienced by inland populations of Cottus asper is twice as great as that experienced by coastal populations at the same latitude (Appendix Table 7). The monthly mean temperature range between northern and southern localities is from 8.8 to 19.5° C. on the coast, and from 9.6 to 29.6° C. inland (Appendix Table 7). A priori, one might expect that inland populations would experience a greater range of developmental temperatures than do coastal populations. Apparently, however, they do not. When monthly mean temperatures, representing inland and coastal localities encompassing the distributional range of Cottus asper, are plotted against latitude, the mean temperature differences between inland and coastal localities during the spawning period are almost negligible (Fig. 12). In fact, the common temperature range of 8 to 13° C. (shaded bar, Fig. 12) can be followed as a thermal "wave" progressing from the south in February, to the north in June. Approximate spawning times, determined from examinations of gonadal condition in over a thousand specimens in all latitudes, are in general agreement with this south-north progression although the latitudinal range over which spawning occurs in March, April, and May is remarkably consistent (Fig. 12).

Theoretically, inland forms have a shorter period of exposure to spawning temperature of 8 to 13° C., than do coastal forms (Fig. 12). This has been born out by field data from the two most frequently collected spawning sites, i.e., Squakum L., and Little Campbell R.

According to Fig. 12, the inception of spawning in inland streams should lag behind that of coastal streams at similar latitudes. This is because upstream or inland areas remain colder for a longer period than coastal areas. This is apparently true in the lower Fraser valley. For example,



LEGEND: Coastal (■—■); Inland (○---○); Empirical Spawning Temperature Range (8-13°C.) [Dotted Box]
 Latitudinal Range of Probable Spawning in: Coastal [Diagonal Lines Box]; Inland [Cross-hatch Box]; and Both [X-hatch Box] Forms.
 State of Maturation: VII = Near Spawning; VIII = Spawning Imminent, Eggs and Sperm Flowing; IX = Spent.

Figure 12. -Monthly Mean Temperatures in °C. Arranged by Latitude for Coastal and Inland Localities Encompassing the Distributional Range of *Cottus asper*. Values obtained from Appendix Table 7. Solid or filled vertical bars, left side of graph, indicate actual ranges of latitude over which specimens have been found in given state of maturity.

the following localities are all within 15' of 49° N. Latitude, and gravid females and/or eggs have been collected from them during the following dates: March 7th to May 10th in Little Campbell R. (122° 46' W. Long.); March 25th to April 15th in S. Alouette R. (122° 35' W. Long.); and April 30th to May 27th in Squakum L. (122° 00' W. Long.).

Some of the implications of these temperature and spawning data have already been discussed, (p. 45).

Materials and Methods

To document the supposed occurrence and to determine the success of intertidal spawning of prickly sculpins in the coastal streams, the Little Campbell R. was chosen as a study stream. In 1960-1961, a series of 18 permanent collecting sites (Fig. 14) was sampled at bi-weekly intervals for a period of one year, and at monthly intervals for an additional six months. The lower reaches of the river, stations C-1 to C-3, were also sampled several times in late Winter and early Spring of 1962 and 1963, to obtain live specimens for experimental studies.

A 3 mm mesh woven nylon seine, 3 meters wide x 2 meters deep, was mounted on collapsible telescoping aluminum poles and used for all field collections. Salinities were measured with three salinity hydrometers, densities: 1.000 to 1.011; 1.010 to 1.021; and 1.020 to 1.031 sp. gr. of NaCl.

Sampling Localities and Study Streams

The primary study area was the Little Campbell R. (Campbell Cr.), which is approximately 15 miles long and empties into Semiahmoo Bay between White Rock, British Columbia, and Blaine, Washington (inset of Fig. 13). The stream drainage consists of an area of approximately 28 square miles.

Collection sites are shown in Fig. 14. Station O-1 is located on a sand-mud flat outside the main river channel. Station C-0 is located at the mouth, in the main channel. Station C-1 is located about 50 yds. inside the

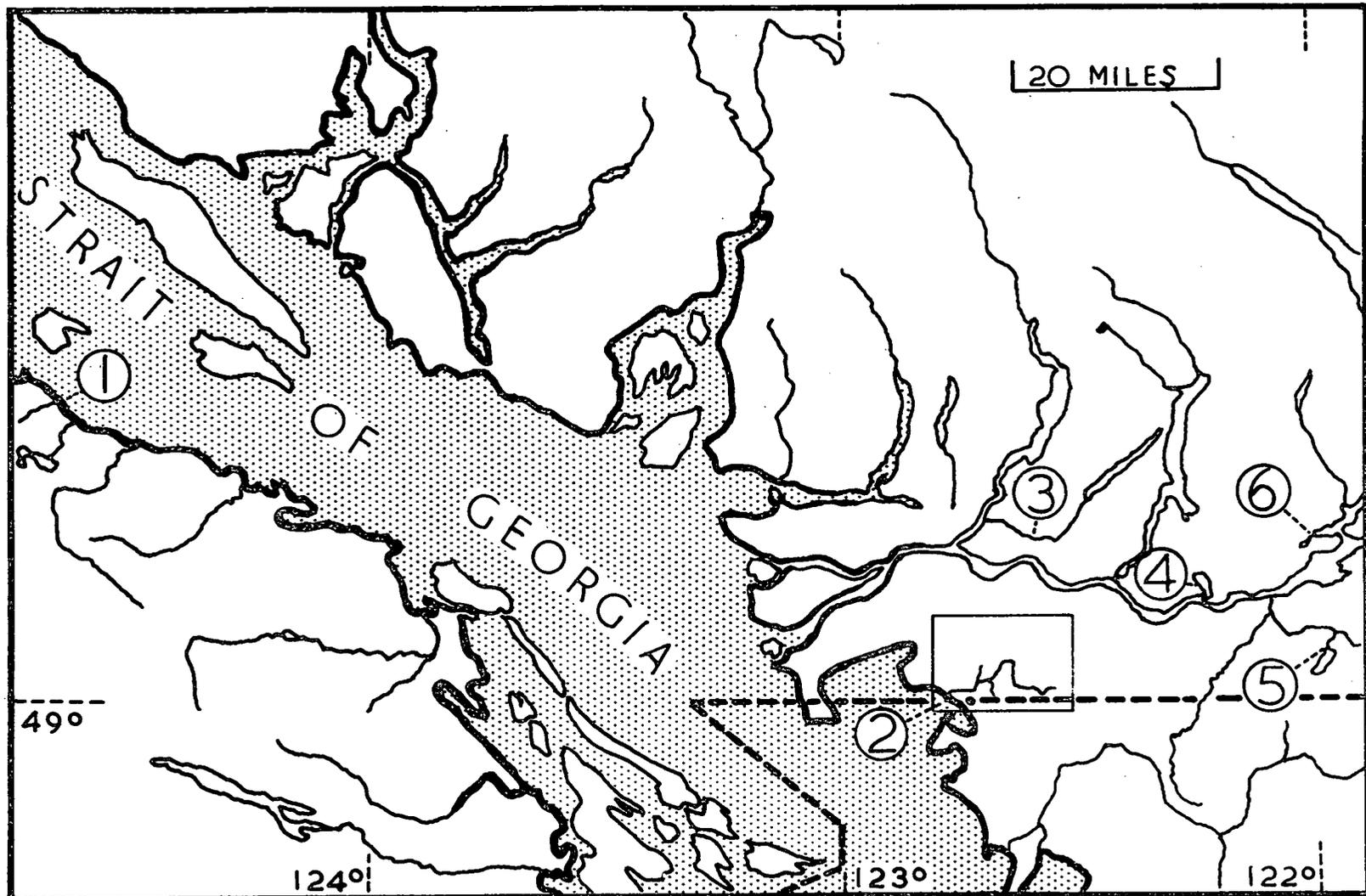


Figure 13.--Collection Localities for Spawning Populations of *Cottus asper* Used in Life History Studies.

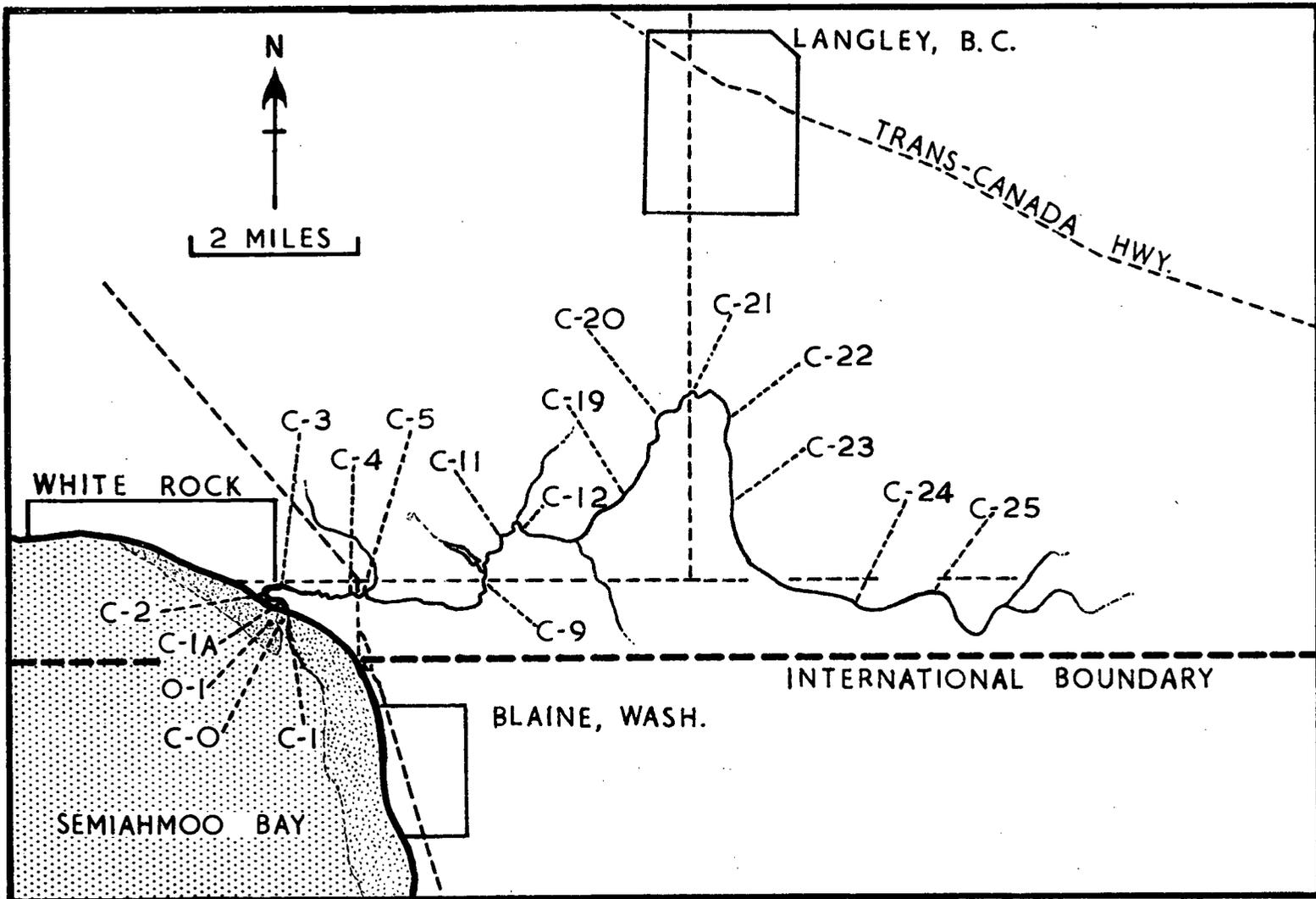


Figure 14.--Collection Localities Within Little Campbell R.

mouth and Station C-1A about 75 yds. inside the mouth. Station C-2 is located 1/4 mile, and C-3 is 1/3 mile, from the mouth. Fig. 15 shows collection sites in relation to salinity gradients and elevation.

Stations C-0 through C-9 are all subject to tidal fluctuations in depth, whereas stations C-0 through C-3 are tidally inundated with mixo-haline waters. Barnacles (Balanus sp.) are found at stations C-0 through C-3, and permanent beds of the oyster, Crassostrea gigas, are located between Stations C-1 and C-1A, and at C-2. Typical fish associates in areas C-0 through C-3 are Leptocottus armatus and Platichthys stellatus; Oligocottus maculosus and Clinocottus acuticeps are commonly found up to Station C-2.

Additional live specimens for use in the experimental studies were collected from the following localities (Fig. 13): Nile Cr. and Big Qualicum R., Vancouver Island; South Alouette R.; Kenworthy and Edwards Cr. (Hatzic L.); Squakum L. (Lake Erroch); and Sweltzer Cr. (outlet of Cultus L.)

Results of Field Studies

The prickly sculpin is distributed primarily in the lower four miles of the Little Campbell R. (Fig. 17). From late February to early March, the prickly sculpin undertakes a migration downstream to the estuary. The only area in the lower four miles of stream in which a suitable spawning substrate (large cobbles, flat rocks) occurs is a stretch about 100 yards long lying one quarter mile upstream from the mouth (Station C-2, Figs. 14 & 15). The males, which come into spawning condition earlier in the season than the females, select nesting sites under large cobbles or flat rocks in areas of the stream bed with current velocities equal to or less than one cubic foot/second (at low tide). It is apparently important that the substrate surface be relatively rough in texture since the adhesive eggs adhere only temporarily to a smooth surface. Old automobile exhaust pipes, or muffler tubes,

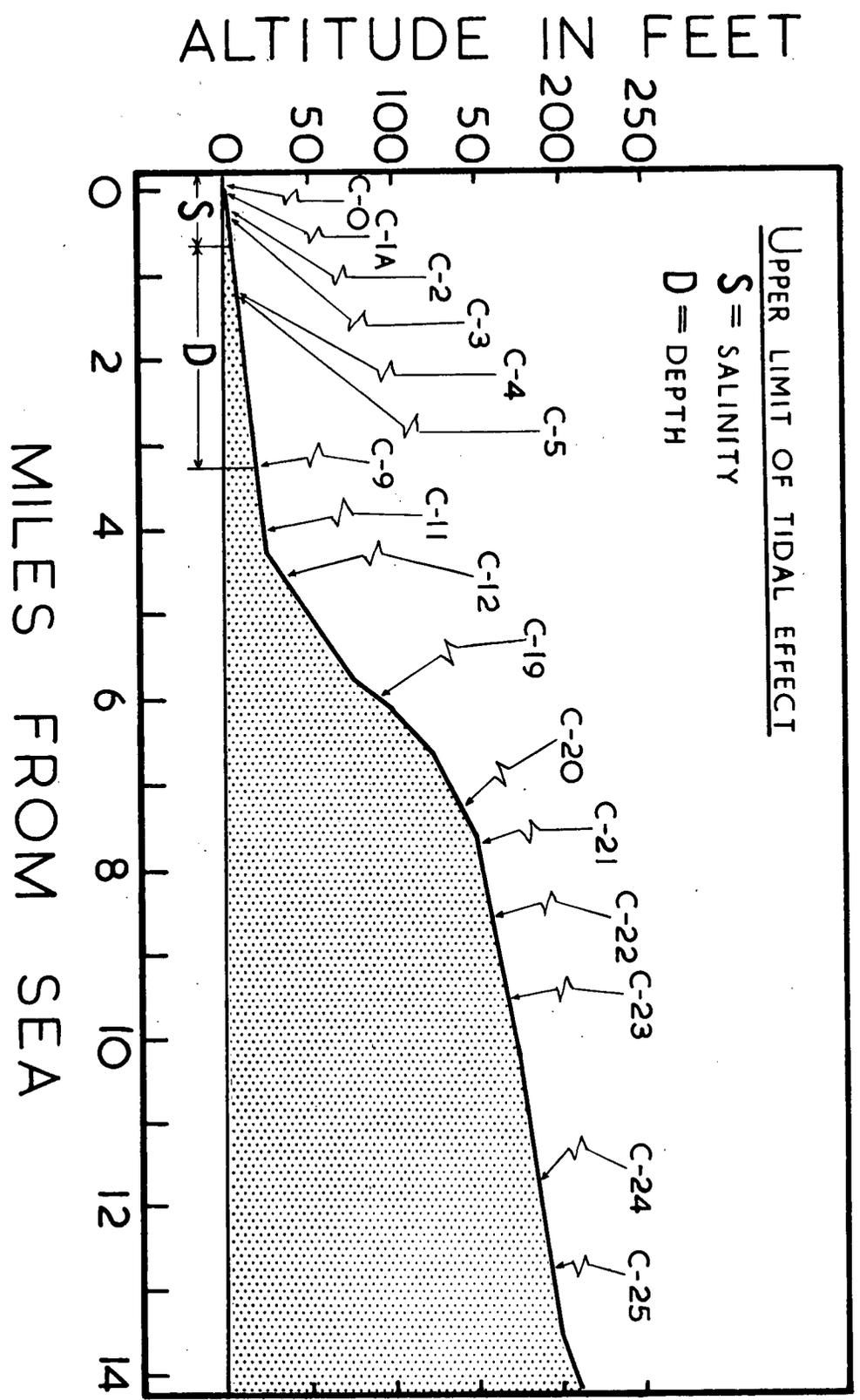


Figure 15.--Collection Sites, Tidal Influence, and Stream Gradients in the Little Campbell R.

are preferred nesting sites when available in the environment (as they are in the Little Campbell R.).

Females aggregate upstream (about Station C-3) above the main spawning area and then move individually onto the spawning beds where they are courted by the males both outside and inside the nest. After the male selects a female to occupy his nest, further courtship and pre-spawning behavior occurs within the nest. The adhesive eggs are laid in a jelly-enclosed cluster on the ceiling of the spawning chamber. Ovariectomy of preserved gravid females from throughout the range of C. asper yielded counts of 336 mature ova in a 49.5 mm S.L. female to 5,652 mature ova in a female 119.5 mm S.L. The largest female examined was 192 mm S.L., but she was spent. A conservative estimate would be about 10,000 eggs for this female. Egg numbers, in masses collected in the field, varied from 700 to 4000. However, one male may court and successfully mate with as many as 10 different females. As many as 10 egg masses, in varying stages of development from newly-fertilized to near-hatching, have been found in the nest of a single brooding male. An estimated 25,000-30,000 eggs were present in this one nest.

After spawning, the spent females leave, or are chased from, the nests and they again aggregate above the spawning areas and begin feeding. The males remain in the nests, fanning and protecting the eggs, and do not eat until hatching is completed. Much of the courtship and pre-spawning behavior, as well as most of the paternal brooding behavior, has been documented but will not be reported here.

Fig. 16 illustrates numbers and distribution of Cottus asper young-of-the-year, 12-25 mm S.L., taken in a total of 700 seine hauls. In late Spring and throughout the Summer, the young-of-the-year are found in great numbers around and below the spawning site. The concentration is greatest around Station C-1A where there is a bed of fine, pea-size gravel adjacent

to a large oyster bed.

In mid-Summer, there is a definite upstream migration of the young-of-the-year. In both 1960 and 1961, the increasing abundance of young-of-the-year at Stations C-4 and C-5 was correlated with the decreasing abundance of specimens in the estuarine areas of the river (Fig. 16).

Fig. 17 illustrates the disjunct distribution of yearlings, sub-adult, and adult prickly sculpins in the Little Campbell R. Especially in Spring, 1961, an increased number of Cottus asper were present in the lower reaches of the river, around the spawning site. Over the 18-month sampling period, no Cottus asper were captured in stations upstream of C-22. With three exceptions, none was taken in the fast flowing, high gradient area of the stream below C-20 and above C-11 (Fig. 15). This area is densely populated with the coastrange sculpin, Cottus aleuticus.

Newly metamorphosed young-of-the-year are found in abundance around and especially below the main spawning beds. Laboratory studies on the behavior of Cottus asper larvae, done in extension of the experimental salinity tolerance experiments, indicate that, at 12° C., the larvae 5 to 7 mm in total length begin swimming immediately upon hatching. They remain pelagic, as lightly-pigmented, transparent larvae, for a period of 30 to 35 days before metamorphosing and settling to the bottom.

Salinity Tolerance in Prickly Sculpin Eggs

Attempts to rear artificially fertilized eggs beyond the critical yolk-sac resorption stage were unsuccessful. Although a few sculpins were reared to a point where meristic series and prickling patterns were fixed, sample sizes were too small to determine whether the salinity of the fertilization and incubation medium was correlated with fin ray numbers, or the intensity and distribution of prickles.

Alternate criteria, based on the percentage hatching success of "in-land" and "coastal" eggs in brackish and fresh water, indicated a phenomenon

of non-genetic adaptation on the part of the "inland" eggs. The low hatching success of "inland" eggs which had been fertilized and incubated in brackish water could be significantly increased by first fertilizing them in brackish water. It was also found that acclimation of "inland" parents to brackish water at least three days prior to fertilization significantly increased the percentage hatching success of their eggs over those eggs from parents which had been maintained in fresh water prior to fertilization. Data for these egg salinity tolerance experiments is on file in the Institute of Fisheries, Department of Zoology, University of British Columbia.

Discussion

This study confirms the existence of a downstream spawning migration of the prickly sculpins in the Little Campbell R. It not only documents the occurrence of intertidal spawning in Cottus asper, but indicates that this spawning is successful.

Figure 16 shows a lag of about two months in the appearance of young-of-the-year C. asper, 12 to 25 mm S.L., after the first recorded spawning in March. Water temperatures in March are normally from 8 to 10° C. Eggs spawned early in March probably have an incubation period several days longer than the 15-16 day period found to be typical at 12° C. in the laboratory. The lag shown in Figure 16 is probably due to an incubation period of three weeks followed by a pelagic larval stage of 4 to 5 weeks. Plankton tows taken during late April in the shallow back-eddies of the stream have captured a few larvae 9 to 10 mm S.L. (not recorded in Fig. 16).

An upstream migration of adults precedes that of the young-of-the-year in late Summer. This is probably related to the food habits of the two groups and also to the fact that a later return of the young-of-the-year coincides with lower water levels in the stream, when reduced velocity facilitates easier access upstream.

Summary of Life History Studies

1. The study stream, the Little Campbell R., is a small coastal stream, the lower one half mile of which is subject to tidal inundation of mixohaline waters.
2. In late Winter and early Spring, the adults and juvenile prickly sculpins migrate downstream to the estuarine region of the Little Campbell R., the only region in the lower four miles in which suitable spawning substrate is available.
3. Males set up nesting sites under large cobbles and rocks and courtship occurs both outside and within the nest.
4. Spawning occurs from March throughout early May.
5. Newly-hatched larvae begin swimming immediately and remain pelagic for a period of 30 to 35 days before metamorphosing and settling to the bottom.
6. In May, metamorphosed young-of-the-year (approximately 12 mm S.L.) begin appearing only in those collections taken in the estuarine portion of the river. They occur in great abundance until September when the numbers decrease in the estuary and increase in upstream, non-estuarine waters.
7. During the non-migratory phase of its life history, the Cottus asper population in the Little Campbell R. is distributed disjunctly in the low gradient, low velocity, portions of the stream.

DISCUSSION

The purpose of this investigation was to determine which characters in Cottus asper were genetically determined and which were due to non-genetic modification. Properly answered, these questions could help the systematist to a better understanding of the selective forces that produce variations within a species. This knowledge would, in turn, facilitate a

more stable classification of taxa.

Morphological Variation Within Cottus asper

The interpretation of the morphological variation will be considered in the light of experimental and life history data obtained in this investigation. Table V summarizes several of the variable characteristics for aggregate populations of Cottus asper.

Coastal vs. Inland Populations. - The data presented in Tables I and V, and in Figure 4, reveal consistent differences in prickling patterns which coincide exactly with the geographic locality of collections. Coastal fish have less area of the body covered by prickles (ratio 1 : 1.8), and less prickles per unit area (ratio 1 : 1.4) than inland fish. The existence and maintenance of such a remarkable discontinuity of characters between closely related but geographically distinct populations, distributed over a wide range of latitudes, must be interpreted as being genetically determined. Furthermore, these populations, which can be separated on the basis of prickling patterns and geographic distribution, can also be separated by other characters. For example, consider the migratory behavior.

Weakly-prickled Cottus asper living in coastal streams having open access to the sea undertake a downstream migration to the estuarine regions where they spawn. Densely-prickled Cottus asper living in distant inland streams, where access to the sea is almost impossible, undertake only local migratory movements. But densely-prickled forms living in some inland lakes and streams relatively close to the sea, where access to the sea is open and relatively easy, do not migrate seaward. They also undertake only local movements and spawn within the fresh water system in which they are found. These primary differences in behavior patterns correlated with distinct prickling patterns further corroborate the contention that coastal and inland forms of Cottus asper are genetically distinct.

The evidence based on meristic counts is equivocal. When plotted

TABLE V. Summary of Variable Characteristics for Selected Phenotypes of Cottus asper.

Phenotype Description:	COASTAL	Northern COASTAL DERIVATIVE	Northern COASTAL LAKE	Southern INTERGRADE	INLAND
Distribution:	Streams of Pacific Coast from Alaska to California	River drainages north of Fraser R. drainage in British Columbia	Island and mainland lakes close to sea in British Columbia and Alaska	Mouth of Sacramento R. in San Pablo and San Francisco Bays	All major inland drainage systems on Pacific Slope except drainages north of Fraser River.
<u>Prickling</u>					
Virtual Area:	Low	Low	Lowest	Higher	Highest
Intensity:	Low	Low	Lowest	Higher	Highest
% Resorption:	High	Lower	Lower	High	Lowest
<u>Meristics</u>					
Pectoral Ray Numbers @ High Latitude	Low	Higher	Highest	---	Highest
Combined Dorsals at Low Latitudes	Highest	---	---	Higher	Low

TABLE V (cont'd). Summary of Variable Characteristics for Selected Phenotypes of Cottus asper.

Phenotype Description:	COASTAL	Northern COASTAL DERIVATIVE	Northern COASTAL LAKE	Southern INTERGRADE	INLAND
Migratory Behavior:	Seaward Migration	?	?	?	Local Migratory movement
Natural Spawning Environment:	Brackish	Presumably Fresh	Presumably Fresh	Presumably Brackish	Fresh
Egg Survival in other than natural media:	Excellent; as in natural medium	?	?	?	Poor; significantly less except if parents or eggs pre-acclimated

against latitude, the means for inland and coastal populations form V-shaped curves which, though overlapping in certain areas, are widely divergent in others (Fig. 11). For example, the pectoral rays of inland and coastal populations are similar in the low latitudes but at a point about 42-44° N. Lat., the coastal means begin to decrease, whereas the inland means continue to increase, in fin ray numbers. Such divergence in mean counts between coastal and inland populations can not be explained on the basis of temperature alone. Salinity in the spawning environment is the only factor which, at any given latitude, can be shown to vary directly between inland and coastal populations.

The nature of the differences between coastal forms and all the populations probably derived from them, or between coastal and inland forms, is a matter of conjecture. Phenotypic modifications now shown to exist can, on the basis of present evidence, be interpreted either as being individual changes induced by the local environment, or, as having become genetically fixed in the populations over long periods of time. Theoretical arguments for each interpretation have been presented (p. 48), but the final determination of the underlying nature of existing differences in fin ray counts awaits the test of successful rearing, under controlled conditions, to a stage where fin ray numbers are fixed.

Derivative and Intergrade Populations. - Certain sub-groups of prickly sculpins have been found which are morphologically distinctive but which have close affinity to either the coastal or inland forms. An analysis of these populations corroborates the contention that, at least in prickling pattern and migratory behavior, coastal and inland forms of Cottus asper are genetically discrete.

Even though the coastal lake and "coastal derivative" populations have prickling patterns similar or identical to coastal forms, the absolute percentage resorption is more like that of the inland forms (Tables I and V).

This might be expected since presumably they no longer spawn in brackish water and the osmotic stresses experienced while spawning in fresh water must be different.

The prickling pattern of the southern "intergrade" population (Carquinez Str., Calif.) is similar to that of the densely prickled inland population forms from which it may have been derived. The amount of prickling resorption, however, approaches that of the coastal percentage. If we assume, as we have above, that the percentage resorption is greater in brackish water, this would indicate that they spawn in estuarine conditions. In their mean fin ray counts, other populations from the San Pablo-San Francisco Bay area are intermediate between the coastal and inland populations. With the information now available, it would be difficult to determine whether these are true inland derivatives which have colonized the streams of the Bay region or whether they are intergrades between inland and coastal forms.

The Phylogeny of *Cottus asper* and Closely-Related Species

The prickly sculpin, *Cottus asper*, is a polytypic species. Figure 18 shows the known range of various phenotypes of *Cottus asper*, determined in this study, plotted against the distributional ranges of closely-related species which comprise the "asper species group" proposed by Bailey and Bond (1963). From a taxonomic viewpoint several interpretations of this polytypy can be made:

- 1) *Cottus asper* is a phenotypically variable species within which can be recognized 4 or 5 races; or
- 2) *Cottus asper* represents a species complex comprised of at least two sibling species, each with one or more derivative subspecies (or races if the phenotypic differences can be shown to be environmentally induced).
- 3) *Cottus asper* represents a polytypic species complex in which a spectrum of evolutionary grades, from incipient subspecies through

Figure 18.--Known Ranges of Various Phenotypes of Cottus asper Plotted Against the Distributional Ranges of Closely-Related Species in the "asper species group".

full species, can be traced.

Evidence presented in this study favors the latter interpretation.

The genus Cottus is a fresh water derivative of the predominantly marine family Cottidae. The genus Cottus is most closely related to the Asiatic marine genus Trachidermus, represented on the Pacific Coast of N. America by Leptocottus, a closely-allied genus. Although their interpretations of relationships within the genus Cottus were not always accurate, I concur with the earlier opinion of Jordan and Evermann (1898, p. 1942) that, of the species of Cottus occupying the Pacific Slope, Cottus asper appears to be more closely allied to Trachidermus.

It has been concluded that differences in prickling patterns and migratory behavior between the geographically separated coastal and inland populations of Cottus asper are genetic (p.66). The discontinuity in such conservative characteristics indicates that the isolation of the inland populations from the coastal gene pool has been of long standing, perhaps since the Pliocene or late Miocene. Evidence to support this speculation is based on the geologic history of the area now occupied by Cottus asper and closely-related species in the "asper species group" discussed below.

Stage I. - It must be assumed that at sometime in the distant past, i.e., perhaps Pliocene or earlier, the ancestral form of Cottus asper was derived from a marine ancestor similar to Trachidermus. After this initial separation, some of the ancestral Cottus asper penetrated inland and, through geological agencies and/or biological processes, became isolated from the coastal gene pool. Such an isolation is represented schematically as Stage I in the evolution of Cottus asper (Fig. 19). The dashed arrows indicate probable routes of invasion of coastal types inland via either the Columbia R. or the Sacramento R. system. During the Pleistocene, access to the north was blocked by the Cordilleran ice sheet, lobes of which advanced and retreated several times. The limits shown in Fig. 18 indicates the maximum

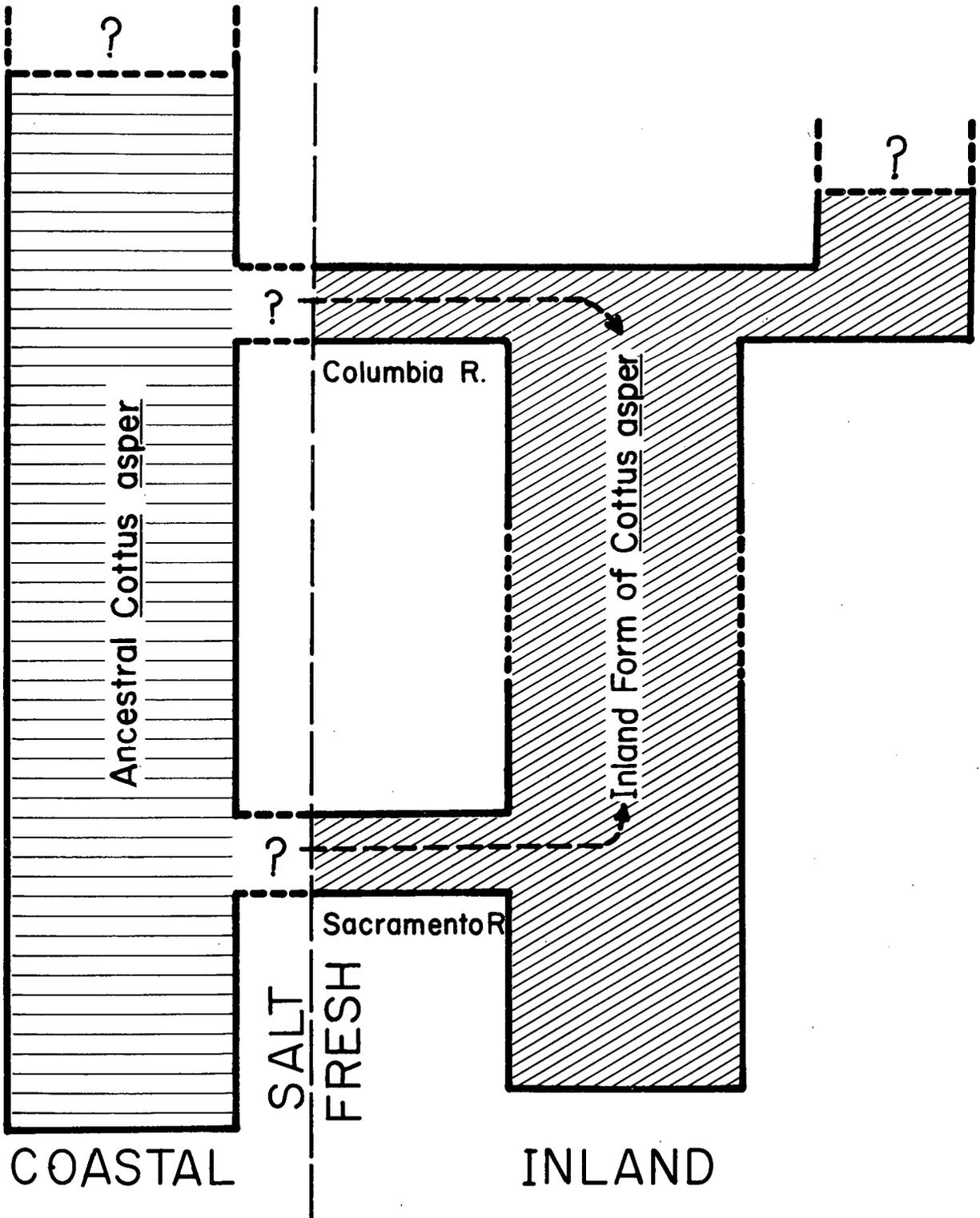


Figure 19.--Phylogeny of *Cottus asper*. Stage I. Evolution in the Pliocene (?). Similar pattern of background indicates continuous range.

southward extent of ice cover during the late Pleistocene; earlier advances were somewhat further southward.

Zoogeographically, the disjunct populations of Cottus asper and "asper species group" represented in Fig. 18 are members of one of three great Pacific Slope fresh water ichthyofaunae, i.e., the Columbia; the Klamath; and the Sacramento. It is here proposed that at some time or times before the basins, especially the Klamath, became completely isolated from one another by alternate periods of floods and desiccation, lava flows, and mountain building, a continuous exchange of fauna was possible. The geological evidence of contemporaneous connections between the (Pleistocene) pluvial lake basins is wanting, but the ichthyological evidence calls for such a connection some time in the past (Hubbs and Miller, 1948). For example, the cyprinid genus Ptychocheilus is absent from the Klamath system but closely related species are present in the Columbia system to the north, and in the Sacramento system to the south. The sucker, Catostomus snyderi, and local representatives of the dace Rhinichthys occurring in the Klamath basin may be related to the forms in the Columbia and the Sacramento (Hubbs and Miller, 1948).

Stage II. - The fluctuating regimen of the pluvial lakes in the Great Basin has been correlated approximately with the advances and retreats of the Cordilleran glaciers (Flint, 1957; Hubbs and Miller, 1948). It is here suggested that during this period of extensive flooding and desiccation, the gene pool of the previously continuous inland population of Cottus asper was divided up into a series of geographically isolated populations, some in the Klamath basin, some in the upper Sacramento, and some in the Deschutes R. drainage of the Columbia. To the south of Klamath, Cottus gulosus evolved as a fast water, upstream derivative of inland Cottus asper and spread southward and out to the Pacific Coast. Among other differences, the fecundity of gulosus is intermediate between the high egg complement of

asper and the low complements of non-related species of Cottus (Bond, 1963). Perhaps one of the most intensive selective factors impinging on the incipient gulosus was that favoring a large egg which would produce a non-pelagic larva in the fast water environment (Cottus asper has pelagic larvae).

Cottus pitensis, a disjunct relict form from the upper Sacramento R. above Lake Shasta, and from the upper Pit R. and Goose L. drainage, is thought to be derived from gulosus (Bailey and Bond, 1963; Bond, 1963).

To the north of Klamath, Cottus perplexus was probably derived from inland asper as the northern ecotypic counterpart of gulosus, in so far as it also prefers upstream areas and has an intermediate egg complement. By an unknown connection, perhaps through the outlet of Pluvial Fort Rock L. which contains fossils of possible faunal relationship with the Klamath Lakes, Lake Lahontan, Lake Bonneville, and the Columbia River (Hubbs and Miller, 1948), perplexus worked its way into the Deschutes R. and down to the Columbia R. where it spread both upstream and downstream (Fig. 20). Cottus marginatus is probably a relict form of a formerly more widespread distribution of perplexus (Bond, 1963).

Ecologically variable, and closely related to perplexus, is Cottus klamathensis, a disjunct relict found in Klamath L., Oregon and Pit R. California (Gilbert, 1898; Bailey and Dimick, 1949; Robins and Miller, 1957; Bailey and Bond, 1963; and Bond, 1963). A Pleistocene connection between the Klamath, Goose L., and Pit R. basins has been suggested by Hubbs and Miller (1948), and Robins and Miller (1957). The fecundity of klamathensis is as high as in asper, and other characters suggest a close relationship with, and an early derivation from, the ancestral asper or perplexus. For example, Gilbert (1898, p. 11) commented on the resorption of body prickles occurring in klamathensis: "These [the prickles of the young] become gradually absorbed with age, adults being nearly or quite naked." This is the

first recorded observation on prickling resorption and it had been completely overlooked by later authors.

The suggestion of Robins and Miller (1957) that Cottus princeps is a long-standing derivative of asper is probably correct. The relationship is probably closest to the ancestral inland asper.

Meristic evidence that the "asper species group" could have been derived from an ancestral inland form of Cottus asper is presented in Table VI. With few exceptions, the ranges of counts for all fin rays for all of the species fall within the range of counts typical of the present populations of inland Cottus asper. Such a correlation may be interpreted to indicate that the genotype of the inland asper has a wide reaction range.

A schematic representing the proposed second stage of the phylogeny of Cottus asper is presented in Fig. 20.

Additional consideration of Cottus perplexus and C. gulosus will now be given. In its coastal distribution, Cottus perplexus is widespread in drainages of Washington and Oregon but does not cross the California border (Fig. 18). On the other hand, Cottus gulosus is found somewhat north and south of San Francisco, but only disjunctly in northern California and parts of the Oregon coast. When they occur in the same stream, perplexus is generally, though not always, found in faster water, whereas gulosus occurs somewhat downstream in slightly slower velocity waters (Bond, 1963). Bond (personal communication) has stated that in areas where asper, gulosus, and perplexus occur in the same stream, a very thin slice of allopatry is cut! However, where upstream migration to the upper portion of streams has been blocked by impassable falls, perplexus is often found above the falls whereas gulosus is always found below (Bond, 1963). This indicates, perhaps, that in streams where both species are present, gulosus is the most recent arrival. Both species have been found to be salt tolerant of at least 24 ‰ S. (Bond, 1963). Cottus asper is tolerant of long periods of

TABLE VI. Summary of Meristic Data for Cottus asper and Other Species in the "asper species group."

Species	D ₁	D ₂	D ₁ + D ₂	A	P ₁	P ₂
<u>asper</u> (coastal)	8-10 (11)	19-22 (23)	(26) 27-32	15-18	14-18	(3) 4
<u>marginatus</u>		17-19 ⁴	---	14-16 ⁴		3 (4) ³
<u>perplexus</u>	7-8 ²	18-20 ²	---	13-16 ²	(13) 14-15 (16) ¹ 14-16	4 ²
<u>klamathansis</u>	(6) 7-8 ²	18-20 ²	---	13-15 ²	14-16	4 ²
<u>asper</u> (inland)	7-10	(16) 18-22 (23)	26-32	15-18 (20)	(13) 14-19 (19)	(3) 4
<u>princeps</u>	6-8 ²	19-23 ²	26-30 ²	15-18 ²	14-16 ²	4 ²
<u>qulosus</u>	7-9 ^{5,6}	16-19 ³ 17-19 ⁶	---	14-16 ³ 13-15 ⁶ 12-14 ⁵	(14) 15-16 (17) ¹ 14-16 ⁶	-
<u>pitensis</u>	(6) 8-9 (10) ¹	(16) 17-18 (19) ¹	---	(12) 13-15 ¹	(12) 13-15 (16) ¹	(3) 4 ¹

Superscript Notation: 1) Bailey and Bond, 1963; 2) Robins and Miller, 1957; 3) Bond, 1961; 4) Schultz, 1936; 5) Snyder, 1905; 6) Snyder, 1913. All data on asper from this study.

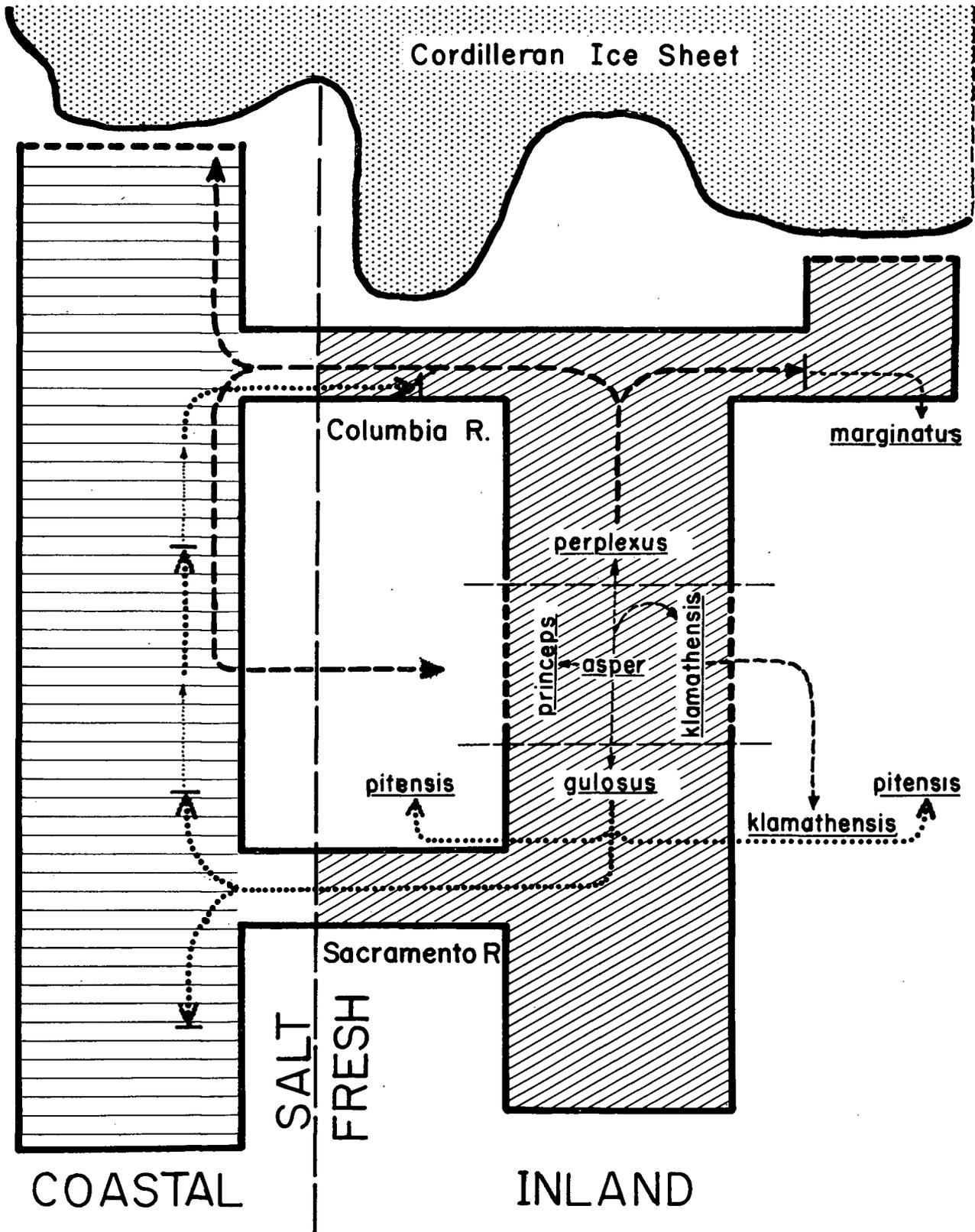


Figure 20.--Phylogeny of *Cottus asper*. Stage II. Evolution of "*asper* species group" During the Pleistocene.

immersion in higher salinities, i.e., greater than 31 ‰ S. (personal observation; and Bond, 1963). The salt tolerance of other "asper complex" species is unknown.

Stage III. - By late Pleistocene, most of the speciation within the inland Cottus asper complex probably had occurred. But another surge of evolutionary activity was yet to occur, primarily within the coastal population (Fig. 21).

With the final retreat of the Puget and Juan de Fuca lobes of the Cordilleran ice sheet (late Vashon Stage) about 13,500 years before present (Armstrong, et al, 1965), coastal Cottus asper began to move northward along the newly exposed coastline of British Columbia. With the more or less contemporaneous retreat of the Okanagan and Spokane lobes from the Columbia R. basin, inland Cottus asper from the lower Columbia advanced northward into Canada and, perhaps at that time, colonized the interior Fraser R. system through meltwater channels then in existence.

Coastal Cottus asper now exists in three phenotypic forms in areas of the Pacific Slope formerly covered by the Cordilleran ice sheet:

- 1) The typically prickled, estuarine spawning, coastal form with lower pectoral fin ray counts;
- 2) a typically prickled, fresh water spawning derivative form with high pectoral fin ray counts, found far inland in the Stikine, Nass, Peace, and parts of the Skeena R. drainages; and
- 3) a very weakly-prickled, fresh water spawning derivative form with high pectoral fin ray counts, found in certain mainland and island lakes.

These "coastal derivative" forms probably followed the recent retreat of glacial lobes up narrow valleys in northern British Columbia. These forms are necessarily the most recent invaders, arriving, perhaps, even later than the upper Fraser R. forms of the inland Cottus asper from which

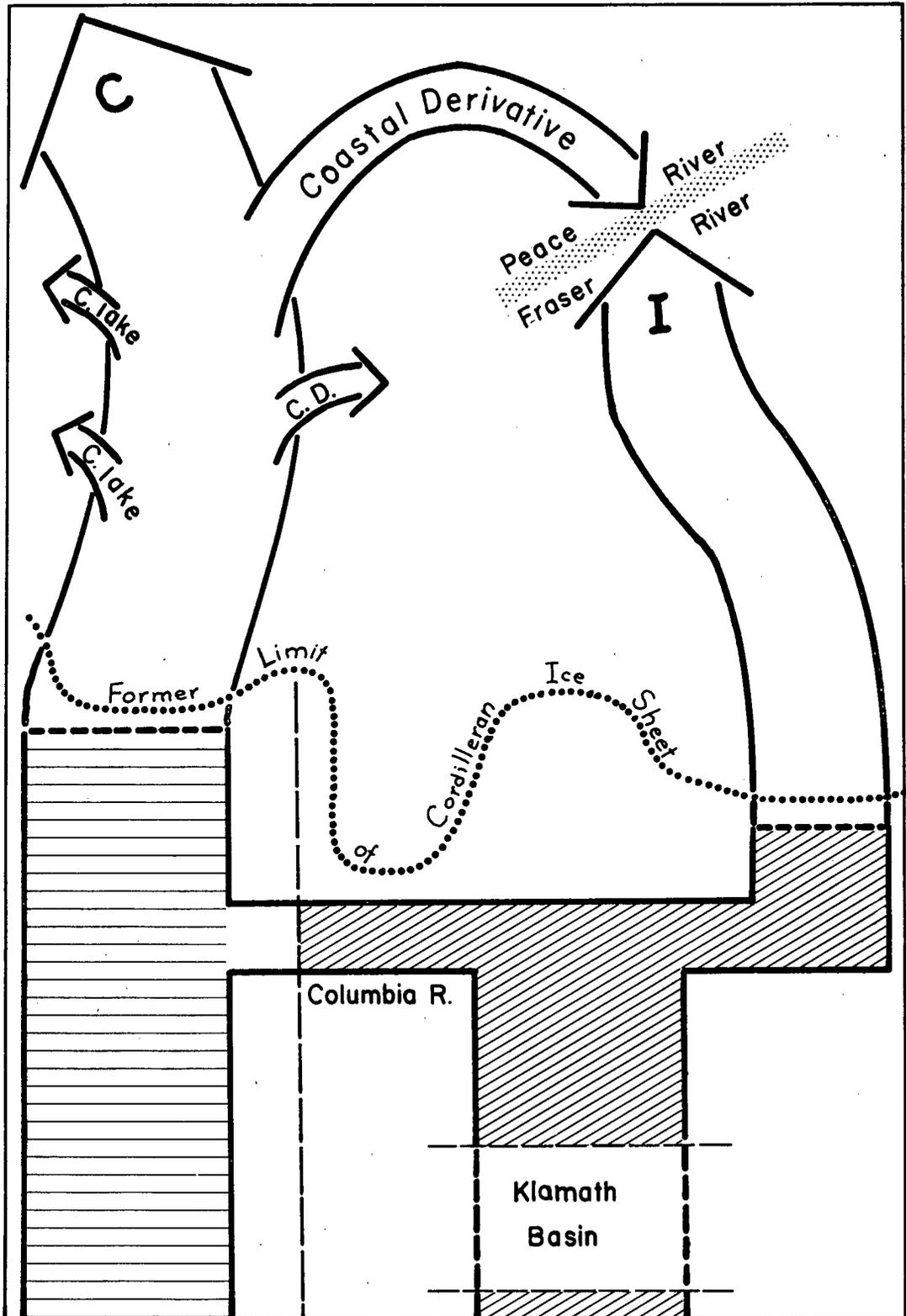


Figure 21.--Phylogeny of *Cottus asper*. Stage III. Evolution of Coastal Form Following Retreat of Cordilleran Glaciers During Recent Time.

they are distinct.

Lindsey (1956) presented distributional evidence that the following primary fresh water species: Catostomus macrocheilus; Mylocheilus caurinum; Ptychocheilus oregonense; and Richardsonius balteatus; plus Cottus asper, a euryhaline species, had penetrated into the Peace R. system from the Skeena or Fraser R. system. "All are present in the Columbia, Fraser, and Skeena systems, all are absent from the Yukon, and all have been taken in the Mackenzie system only from the upper portion of the Peace drainage." The restricted range of these species in the Peace R. system indicates their relatively recent arrival.

The present study indicates that the Peace R. representatives of Cottus asper are coastal derivatives which must have penetrated inland via the Stikine, Nass, or upper Skeena R. The inland form of Cottus asper has apparently failed to penetrate northward beyond the limits of the upper Fraser R. drainage. The exchange probably occurred and the connection became closed before the inland Cottus asper arrived on the scene. Evidence from the distribution of other primary freshwater fishes bears this out. Several species got only as far north as the inland asper. For example, the leopard dace, Rhinichthys falcatus, is a Columbia R. form which has penetrated northward (presumably following the same routes as inland asper) as far as Middle River near Takla L., about 120 miles northwest of Prince George, B.C. The bridgelip sucker, Catostomus columbianus, another Columbia R. form, has been taken in the Salmon R. system just north of Prince George. Extensive collecting in the areas north of Prince George indicates that both species have failed to penetrate into the Peace or the Skeena R. systems.

The prickly sculpin, Cottus asper, is interpreted as being a polytypic species which has become, and is in the process of becoming, modified into several characteristic genotypes. The dichotomy between "inland" and "coastal" forms is basically subspecific in nature. Classification of the

"asper species group" is beyond the limits of a system of binomial nomenclature. Modifications in some of the earlier derivatives of the inland form have presumably become genetically fixed, and various authorities have assigned them full specific rank. More recently derived forms of the coastal Cottus asper, such as occur in the coastal lakes of British Columbia and Alaska, or in the British Columbia river drainage systems north of the Fraser R., are modified sufficiently to perhaps warrant classification as subspecies, but the genetic nature of the modification has not been determined. It is not known whether the marked differences in phenotype of the "coastal derivative" or coastal lake forms are results of a phenomenon which occurs in one generation, or over a long period of time. If the changes are not environmentally induced, then genetic fixation can be assumed to have occurred within the past 10,000 years or less.

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Appendix Table 1. List of Collections, Localities, and Other Pertinent Information.

Pop. No.	General Locale Collection No.	Specific Locality	< 60 mm S.L.	≥ 60 mm S.L.	N. Lat.	W. Long.
<u>COASTAL POPULATIONS</u>						
<u>Alaska</u>						
1.	Seward area:				60°07'	149°24'
	BC 64-311	"ditch at airport"	1(56.0)			
	NMC 61-133	"lagoon at north edge of Seward"	9(28.2-38.6)			
2.	Haines area:				59°23'	135°35'
	USNM 76408	"head of Chilkoot L."		8(62.9-125.0)		
3.	Juneau area, Lynn Canal, Favorite Channel:				58°22'	134°36'
	AB 61-100	Petersen Creek, 12 mi. N. of Juneau	2(53.9-59.5)	8(73.2-119.2)		
	AB 61-489	" "		2(70.1- 77.8)		
	AB 61-490	" "		8(78.0-142.1)		
4.	Loring area, Revillagigedo Id.:				55°35'	131°40'
	USNM 64130-49	Loring		14(112.8-166.2)		
	USNM 60801	Deep Bay		2(87.5-94.0)		
	USNM 60371	Mouth of River		3(115.4-135.0)		
	USNM 60316	Naha River		2(68.9- 76.0)		
5.	Kasaan Bay, Prince of Wales Id.:				55°00'	132°00'
	SU 23989	Stream of Karta Bay		2(111.6-116.7)	35'	35'
	AB 62-76	Saltery Cr., Paul's Bight, Skowl Arm		11(83.9-139.0)	25'	30'
	AB 62-77	Saltery Cr.		2(149.5-154.5)		
	AB 63-167	Saltery Cr., 100 yds. up from mouth		3(94.3-112.1)		
<u>British Columbia</u>						
6.	Queen Charlotte Is., Graham Id., Juskatla Inlet				53°00'	132°00'
	BC 60-437	Small stream about 2 mi. W. of Juskatla	10(28.5-56.6)	9(60.2- 90.2)	37'	23'
	BC 60-439	Mouth of stream 3 mi. W. of Juskatla	59(26.4-59.6)	11(62.2-136.2)	36'	25'
	BC 60-440	" " " " " "	38(32.7-59.5)	6(61.5- 83.3)		
7.	Queen Charlotte Is., Moresby Id.:				53°06'	132°00'
	BC 60-420	Creek entering Skidegate L.	23(25.0-57.4)	20(61.0-132.2)		
	BC 60-424	Shore of Skidegate L.	12(25.3-59.1)	6(62.3- 98.5)		
8.	Princess Royal Id.:				52°57'	128°50'
	BC 53-214	Bloomfield L., N.E. side, Laredo Inlet		2(122.0-123.5)		
9.	King Id., Ocean Falls area:				52°06'	127°45'
	BC 54-434*	Port John L.	4(63.1-70.8)**	16(72.4- 85.7)**		
10.	Rivers Inlet area:				51°40'	126°40'
	BC 56-629	Owikeno L., 2nd Narrows*		10(none listed)		

*Counts taken by D.E. McAllister; **Lengths given are Total Lengths.

Appendix Table 1. List of Collections, etc. (cont'd).

11.	Vancouver Id., Campbell R. area:			
	BC 54-114	Buttle L.	1(42.5)	1(106.5) 49°47' 125°40'
	BC 64-312	Buttle L.		2(71.0- 76.0)
	BC 64-313	Buttle L.		2(ca75-117.5)
	BC 64-314	Upper Campbell L.		1(132.7) 49°55' 125°40'
12.	Vancouver Id., Qualicum area:			49°20' 124°40'
	BC 54-39	Horne L.		11(108.1-132.0)
13.	Vancouver Id., Qualicum area:			49°25' 124°40'
	K61-13	Nile Cr., 100 paces from mouth	5(49.4-59.6)	17(61.5- 91.0)
14.	Vancouver Id., South end:			48°40' 124°50'
	BC 63-1462	Nitinat L.	14(39.9-59.5)	11(63.0- 89.2)
15.	Gambier Id., Howe Sound:			49°25' 123°23'
	BC 58-410	Outlet Cr., 100 ft. from mouth	17(23.0-59.9)	16(60.5-129.3)
16.	White Rock area, Little Campbell R.			49°-- 122°--
	K 60-52	Stn. C-22		2(89.7- 90.2) " 04' " 40'
	K 60-40	" "		10(77.5-107.7)
	K 60-71	" "		2(92.8-127.5)
	K 60-88	" "		3(93.0-102.4)
	K 60-128	" "		2(80.7-111.0)
	K 60-169	" "		2(80.0- 89.5)
	K 60-27	" C-2		9(60.6- 71.8) " 00' " 46'
	K 60-12	" "	1(39.5)	3(64.0- 88.5)
	K 63-6	" "		6(81.5-118.5)
	K 60-80	" C-3	33(13.0-58.5)	2(70.1- 71.6) " 01' " 46'
	K 60-101	" "	5(55.0-58.6)	9(60.5- 97.3)
	K 60-116	" "	5(51.6-59.5)	7(60.4- 73.3)
	K 60-139	" "	2(57.5-58.5)	9(63.5- 83.2)
17.	Saturna Id., Strait of Georgia:			48°48' 123°10'
	BC 56-81	Lyell Harbor Cr.	10(28.4-39.8)**	
<u>Oregon</u>				
18.	Clatsop Co., Cannon Beach area:			45°54' 123°58'
	UMMZ 93427	Mouth of Elk Cr.	10(21.7-59.4)	5(68.4-100.2)
19.	Coos Co., Lakeside, Ten Mile Lake			43°35' 123°10'
	BC 63-1089	Ten Mile L. outlet wier		33(60.3-114.1)
20.	Curry Co., Sixes area:			42°55' 124°30'
	SU 9270	Flores R.	3(44.2-55.3)	9(77.0-154.0)
21.	Curry Co., Winchuck Area, Winchuck R.:			42°00' 124°15'
	OSC 198	2 mi. upstream from U.S. Hwy 101	6(36.3-50.9)	

Appendix Table 1. List of Collections, etc. (cont'd).

California

22.	Del Norte Co., Crescent City area:			41°50' 124°15'
	SU 23598	Point St. George	1(62.3)	" " " "
	CAS 18026	Wilson Cr., at bridge 1-05, U.S. 101	1(84.7)	" 55' " "
	CAS 18028	Smith R., at bridge on U.S. 199	3(31.7-397)	
23.	Del Norte Co.:			41°34' 124°10'
	SU 9272	Mouth of Klamath R., at Requa	14(33.3-59.8) 16(62.0-115.0)	
24a.	Mendocino Co., Navarro area, Navarro R.:			39°09' 123°34'
	CAS 19066	Indian Cr., bridge on Hwy. 128, Philo	1(63.0)	
	SU 35131-3	N. fork, 0.2 mi. E. of Flynn Cr.	3(71.6-106.5)	
	SU 38016	Albion R., 2 mi. below Comptche	1(49.6)	
25a.	Marin Co., Tomales Bay drain., Lagunitas (Papermill) Cr.:			38°00' 122°45'
	CAS 18616	S.P. Taylor St. Park, at Camp Taylor	1(93.0)	
	SU 40849	Near Point Reyes Station	6(22.7-44.4)	
26.	Santa Cruz Co., Waddell Cr.:			37°06' 122°17'
	CAS 20857	3 mi. S.W. of Ano Nuevo Point	24(96.0-143.2)	
	CAS 20862	" " " " " " "	14(95.8-143.1)	
27.	Santa Cruz Co., Soquel area:			36°57' 121°55'
	CAS 19086	Soquel Cr., at Soquel	1(54.7)	
	SU 4816	Soquel Cr.	4(64.9-105.2)	
28.	San Luis Obispo Co., San Simeon area:			35°35' 121°12'
	SU 15183	San Simeon Cr.	4(22.9-42.5) 2(124.9-127.2)	
29.	Santa Barbara Co., Lompoc area:			34°41' 120°35'
	SU 40323	Santa Ynez R.	2(76.8- 86.3)	
30.	Santa Barbara Co., Gaviota:			34°24' 120°15'
	UMMZ 131728	Gaviota Cr., at mouth	15(21.7-47.4)	
31.	Ventura Co., Ventura R.:			34°10' 119°20'
	UMMZ 131734	6.4 mi. N.E. of Ventura	1(113.5)	
	UMMZ 132891	1/2 mi. from Foster Park, towards Ventura	2(119.0-151.1)	

Appendix Table 1. List of Collections, etc. (cont'd).

COASTAL DERIVATIVE
POPULATIONS
British Columbia

32.	Stikine R. drainage:			56°40' 128°40'
	BC 54-485	Cold Fish Lake	2(77.7-82.5)	
	BC 54-485	Cold Fish Lake*	3(48.6-66.7)	1(81.7)
33.	Nass R. drainage, Meziadin Lake:			55°03' 129°10'
	BC 55-221	At outlet	8(81.0-109.1)	
	BC 55-221-A	At outlet	5(66.2-82.0)	
	BC 56-536	Off McLeod Creek	11(73.2-87.2)	
34.	Skeena R. drainage, Babine Lake:			54°50' 126°0-05'
	BC 55-452	Wright Bay	1(60.6)	
	BC 55-453	Opposite Donald's Landing	9(15.8-34.4)	
	BC 56-455	At Topley Landing	6(34.2-54.3)	3(61.1-96.9)
35.	Fraser R. drainage, Takla Lake outlet:			54°55' 125°05'
	BC 54-249	Middle R.	12(27.4-35.2)	4(65.5-83.5)
36.	Mackenzie R. drainage, Nation Lakes area:			55°12' 125°00'
	BC 64-102	Tchentlo L. inlet stream mouth	3(41.2-54.7)	
	BC 64-101	Tchentlo L. inlet end	3(33.1-47.0)	
37.	Mackenzie R. drainage, Manson Creek area:			55°37' 124°25'
	BC-56-458	Outlet of Wolverine L.	13(31.0-58.0)	11(65.0-133.3)
38.	Mackenzie R. drainage, Parsnip R. watershed:			54°42' 122°30'
	BC-61-464	Tacheeda Lake	13(34.0-58.5)	2(65.6-666.2)
39.	Mackenzie R., Crooked R. watershed:			55°00' 123°00'
	BC 54-477	McLeod Lake	15(13.8-23.0)	
40.	Mackenzie R., Crooked R. watershed:			54°28' 122°47'
	S-98	Bear L. N. of Summit L.	3(48.5-59.9)	4(61.5-141.0)
41.	Mackenzie R., Crooked R. watershed:			54°15' 122°40'
	BC 61-463	Hart L. off Hart Highway	2(79.5-80.1)	
42.	Mackenzie R., Crooked R. watershed:			52°20' 125°10'
	BC 56-362	Summit L., N. of Prince George	1(25.9)	
	BC 54-459	Summit L., N. of Prince George	11(10.7-50.8)	
43.	Dean R. drainage, Chilcotin area:			
	BC 56-483	Nimpo L.	15(12.5-34.4)	

Appendix Table 1. List of Collections, etc. (cont'd).

INLAND POPULATIONS

British Columbia

Skeena R. Drainage:

44.	BC 56-411	Lakelse R., at Terrace	14(40.8-55.9)	15(60.5-153.6)	54°21'	128°35'
45.	BC 56-453	Bulkley R., 1 mi. below Bulkley	3(34.4-50.4)	9(67.1-130.7)	54°28'	126°30'
Fraser R., Nechako R. drainage:						
46.	BC 55-10	Fraser L., 2 mi. from West end	15(16.8-55.6)	1(68.1)	54°05'	124°50'
47.	BC 54-162	Eulatazella L., Deep Cr.	6(43.5-57.9)	15(62.2-105.5)	53°42'	123°40'
48.	BC 54-367	Nadšilnich L., St. Joseph's Cr.*	9(53.6-67.0)**		53°45'	122°50'
Fraser R., Thompson R. drainage:						
49.	BC 54-242	Kamloops L.*	10(14.6-25.7)**		50°45'	120°40'
50.	BC 55-139	Pothole L. outlet (Quilchena Cr.)	12(25.3-58.0)	10(60.0- 88.7)	49°55'	120°30'
Fraser R., Fraser Valley drainage:						
51.	K misc.	Squakum L. outlet stream	11(35.0-59.0)	7(73.8-104.8)	49°14'	122°00'
	"	" " " "		9(68.4-111.9)		
	"	" " " "	1(47.6)	1(68.8)		
	K 62-19	" " " "		7(73.9-119.0)		
	BC 54-197	Squakum L.	2(33.5-43.0)			
	BC 54-196	" "		5(103.0-118.5)		
	BC 54-195	" "		3(113.0-143.8)		
52.	V-100	Vedder R. Stn. V-6, at end of Ford Rd.	15(37.6-58.6)	13(61.0-100.1)	49°06'	122°00'
	V-150	" " " " " " " "		1(97.2)		
	V-203	" " " V-4, Vedder R. Canal		2(116.7-129.0)		
	BC 59-612	Vedder Canal, above highway bridge		3(113.1-148.2)		
	BC 54-43	Vedder R.		3(109.5-128.1)		
	BC 54-427	"		2(106.6-140.0)		
	BC 59-504	"		1(104.3)		
53.	BC 62-70	Cultus L.		5(62.8-105.7)	49°04'	121°59'
	K misc.	Cultus L., outlet wier in Sweltzer Cr.		5(74.6- 96.5)		
	K 63-16	" " " " " " "		3(72.0- 77.0)		
	K 63-17	" " " " " " "		2(74.2- 94.3)		
	SW-1	Sweltzer Cr., 1/4 mi. below Cultus L.	13(17.6-51.0)	2(70.8-116.0)		
54.	BC 56-564	Hatzic L., Hatzic Slough		4(64.5- 70.1)	49°10'	122°14'
	BC 54-212	" " Swan Point	6(24.2-32.2)	9(75.4-112.9)		
	BC 54-209	" "	1(20.9)	3(104.5-130.2)		
	BC 56-120	" " Edwards Cr.	13(32.2-50.5)			
	BC 55-313	" " " " mouth		1(138.2)		
	K misc.	" " " " "		2(66.7- 68.0)		

Appendix Table 1. List of Collections, etc. (cont'd).

55.	A-51	S. Alouette R.,	Stn. A-8,	14th Ave.	3(73.5- 82.6)	49°14'	122°35'
	A-122	"	"	"	2(95.4-103.4)		
	A-153	"	"	"	3(30.0-54.2)		
	A-220	"	"	"	13(15.0-59.6)		
	K 63-12	"	"	A-7,	8(65.5- 97.0)		
				8th Ave.			
	Columbia R. drainage, Revelstoke area:					50°59'	118°11'
56.	BC 54-369	Williamson L.			13(86.0-123.6)		
	BC 59-424	"	"	, off diving float	14(27.8-39.8)		
	Columbia R. drainage, Grand Forks area:					49°09'	118°11'
57.	BC 54-124	Christina L.			3(34.4-42.6)		
	BC 56-534	"	"	, 1 mi. from S. end	11(19.8-34.4)	1(73.3)
	Columbia R., Okanagan R. drainage:					49°11'	119°30'
58.	BC 53-187	Osoyoos L.			23(36.3-59.9)	6(60.5-	79.8)
	<u>Washington-Oregon</u>						
	Columbia R. drainage:						
59.	USNM 104608	Moses L.,	Grant Co.,	Wash.	20(18.8-26.6)	47°06'	119°19'
	UW 14614	McNary Dam,	Benton Co.,	Wash.	1(59.5)	3(70.4-161.5)
	UW 14747	"	"	"	1(58.9)	4(76.8-100.3)
	OSC misc.	Umatilla R. mouth,	Umatilla Co.,	Ore.			2(125.4-169.2)
	OSC "	"	"	"			1(149.5
	OSC "	"	"	"			3(93.8-186.0)
	CAS (I.U.M.4444)	"	"	"			1(62.2
	Columbia R. drainage, Portland and Vicinity:					45°20'	-122°10'
61.	OSC misc.	Abernathy Cr.,	at mouth,	Cowlitz Co.	2(118.8-119.5)	46°02'	122°52'
	"	Kalama R.,	1/4 mi. above	mouth	1(113.5)	
	"	Coweman R.,	at mouth	"	1(105.6)	
	"	"	"	, 100 yds. upstream	3(88.0-172.0)		
	"	Lewis R.,	E. fork at	U.S. 99,	Clark Co.	4(112.5-164.5)	
	"	"	"	, below U.S. 99 bridge	1(121.7)	
	"	Washougal R.,	1 mi. above	mouth	3(94.6-106.0)		
	"	"	"	, below old Hwy 30 bridge	1(146.5)	
	"	Vista Slough,	Big Rock,	Multnomah Co.	1(97.2)	
	"	Sandy R. below	old Hwy 30	bridge	2(110.9-121.5)		
	"	Sandy R.			1(91.4)	
	"	Clackamas R.,	near mouth,	Clackamas Co.	1(175.0)	

Appendix Table 1. List of Collections, etc. (cont'd).

Columbia R. mouth, Washington Shore, Pacific Co.:				46°17' 123°57'
62.	UMMZ 93425	Columbia R. at end of Chinook Pier	6(97.5-150.6)	
	OSC misc.	Chinook R.	2(116.5-118.0)	
	OSC misc.	Chinook R., above tide gate	2(86.5-128.2)	
	SU 38019	Columbia R., 1/2 mi. W. of Megler Ferry	1(24.6)	2(60.1-112.7)
Columbia R. mouth, Oregon Shore, Clatsop Co.:				46°11' 123°50'
63.	SU 38018	Columbia R. at Astoria	7(127.5-154.0)	
	SU 38017	" " " "	11(100.8-131.5)	
	OSC 762	Walluski R., 6 mi. S.E. of Astoria	2(87.8- 89.8)	
	OSC misc.	Big Creek, at mouth	4(119.3-134.5)	
Willamette R. drainage, Corvallis area:				44°15' 123°10'
64.	OSC 189	Overflow slough at Corvallis	2(150.3-150.7)	30' 15'
	OSC misc.	Corvallis Sand & Gravel Pits, along R.	2(123.5-133.5)	
	OSC 402	Pothole, Willamette R. at Corvallis	1(53.4)	
	OSC #702	Stn. 5, above Corvallis	1(34.5)	
	OSC misc.	Stn. 6, Harrisburg	1(73.3)	
	OSC misc.	Stn. 7, Peoria	2(66.8- 74.6)	
Willamette R. drainage, S.E. of Eugene, Lane Co.:				43°45' 122°40'
65.	OSC 744	Lookout Point Reservoir, Landax	11(17.5-56.1)	10(65.0- 84.9)
<u>California</u>				
Sacramento R. drainage, Shasta Co.:				
66a.	CAS 18081	O'Brien Cr., emptying in Shasta L.	2(28.5-31.0)	40°48' 122°16'
	UMMZ 93428	Clear Cr., a few mi. S. of Redding	1(78.4)	" 30' " "
66b.	USNM 295	Fort Reading (on Cow Cr.)	3(86.7-105.2)	" 28' " 11"
Sacramento R. drainage, Tehama and Glenn Co.:				
67.	UMMZ 93429	Sacramento R., a little below Red Bluff	1(69.7)	40°09' 122°13'
	UMMZ 93430	Thomas Cr., at Richfield	1(99.0)	39°56' 122°13'
	UMMZ 93431	Stony Cr., near Orland	1(71.8)	39°45' 122°13'
Sacramento R. drainage, Sacramento area:				
68.	OSC misc.	Sacramento Brickyard Pond. S. of city	2(65.5-100.7)	38°30' 121°30'
San Joaquin R. drainage, San Joaquin Co.:				
69.	CAS 20887	San Joaquin R. (exact locality unknown)	10(31.5-56.5)	4(61.0- 84.0) ca37°45' 121°20'
San Joaquin R. drainage, Stanislaus Co.:				
70.	CAS 17966	Irrigation ditch on Hwy 132, 1 mi. E.	4(27.5-44.9)	37°35' 120°55'
	CAS 19098	of Empire. " " " " " " " "	3(25.0-50.5)	
San Joaquin R. drainage, Madera and Fresno Co.:				
71.	CAS 20252	Madera Canal, presumably from Millerton L.	1(120.9)	ca37°00' 119°50'
	OSC misc.	San Joaquin R. at Mendota	1(30.0)	1(72.1) 37°40' 120°20'

Appendix Table 1. List of Collections, etc. (cont'd).

San Joaquin R. drainage, Fresno and Tulare Co.:					
72.	CAS 25541	Kings R., at Dutch John Cut	1(46.5)	?	?
	CAS 20904	Kaweah R., near Visalia	3(34.5-58.3)	36°15'	119°16'
<u>INTERGRADE POPULATIONS</u>					
Sacramento R. drainage, Contra Costa Co., Carquinez Strait:					38°00' 122°10'
73.	UMMZ 142373	ca 1/2 mi.E. of Eckley, S. of Dillon Pt.	8(35.0-57.5) 20(60.0-183.4)		
San Pablo Bay area, Sonoma Co., California:					38°11' 122°40'
74.	USNM 296	Petaluma	2(30.9-39.5) 2(71.8-109.5)		
Additional Material From the Literature, Used Separately, or in Combination, with Populations Listed Above.					
Sacramento R. drainage:					
75.	Rutter, 1908:145	Sacramento R. at Redding	2 specimens	40°30'	122°10'
	" "	" " " " mouth of Battle Cr.	1 "	40°21'	122°09'
	" "	" " " " at Red Bluff	1 "	40°09'	122°13'
	" "	" " " " at Jacinto	1 "		
	" "	" " " " Arcade Cr., at Arcade	9 "		
	" "	" " " " Feather R. at Marysville	1 "	39°05'	121°35'
San Francisco Bay, San Mateo Co.:					
76.	Snyder, 1905:338	San Francisquito Cr.	34 specimens	37°24'	122°09'
Santa Cruz Co., Watsonville area:					
77.	Snyder, 1913:72	Pajaro R.	25 specimens	36°50'	121°50'
Marin Co., Tomales Bay area:					
25b.	Snyder, 1908b:185	Papermill Cr.	10 specimens	38°00'	122°45'
Mendocino Co., Point Arena area:					
78.	Snyder, 1908b:185	Garcia R.	6 specimens	38°55'	123°45'
Mendocino Co., Navarro area:					
24b.	Snyder, 1908b:185	Navarro R.	11 specimens	39°09'	123°34'
Humboldt Co., Arcata area:					
79.	Snyder, 1908b:185	Mad R.	6 specimens	40°55'	124°08'
Curry Co. Oregon, Gold Beach area:					
80.	Snyder, 1908b:185	Rogue R., near mouth	8 specimens	42°26'	124°23'
Douglas Co., Reedsport area:					
81.	Snyder, 1908b:185	Takenitch R.	16 specimens	43°45'	124°07'
Tillamook Co., Nestucca Bay area:					
82.	Snyder, 1908b:185	Nestucca R.	10 specimens	45°10'	123°57'
King Co., Washington, Seattle area:					
83.	Snyder, 1908b:185	Lake Washington	17 specimens	47°30'	122°15'
Additional Material: UMMZ 131771, Kern R., California				1 specimen (not used)	35°-- 119°--

Appendix Table 2. Weighted Mean Percentage Prickling and Resorption for Individual Populations of *Cottus asper* Used in Compiling Table I and Figure 4.

Population No.	Specimens ≤ 60 mm S.L.			Specimens ≥ 60 mm S.L.					
	Coastal	n	Virtual	Apparent	n	Virtual	Apparent	% Resorption	
							Relative	Absolute	
1		1*	37.9	34.2	--	--	--	--	--
2		--	--	--	8	34.1	17.1	49.9	17.0
3		2	34.6	17.8	18	33.6	14.0	58.2	19.6
4		--	--	--	9	34.3	20.2	41.1	14.1
5		--	--	--	16	40.8	24.7	39.5	16.1
6		11	42.0	40.3	9	40.5	21.1	48.0	19.4
7		12	32.1	20.5	18	26.2	11.7	55.3	14.5
11		--	--	--	5	13.7	3.5	74.6	10.2
12		--	--	--	11	27.1	10.3	62.1	16.8
13		5	41.1	24.4	17	44.5	21.8	51.1	22.7
14		14	49.3	42.9	11	43.4	27.3	37.0	16.1
15		17	54.0	51.0	16	43.0	24.8	42.3	18.2
16		16	44.2	41.4	29	40.3	27.5	31.8	12.8
18		10	49.7	41.6	5	31.0	15.4	50.1	15.6
19		--	--	--	33	47.0	34.0	27.7	13.0
20-21		9	--	30.6	9	--	16.5	--	--
25a		6	--	41.7	1*	--	24.2	--	--
26		--	--	--	24	30.4	12.9	57.5	17.5
28		6	--	35.4	2	--	14.4	--	--
29		--	--	--	2	--	7.6	--	--
30		15	44.8	43.8	--	--	--	--	--
31		--	--	--	3	29.5	13.0	55.8	16.5
\bar{X}		--	43.5	36.0	--	35.0	17.8	48.9	17.2
Coastal Derivative									
32		--	--	--	2	15.0	8.9	40.3	6.1
33		--	--	--	19*	37.8	25.4	32.9	12.4
34		5	49.5	48.6	1	35.4	22.3	37.0	13.1
35		12	49.0	46.2	4	43.8	38.6	11.8	5.2
36		6	42.4	38.4	--	--	--	--	--
37		13	42.9	40.5	11	34.8	23.4	32.8	11.4
38		13	34.5	29.1	2*	36.1	17.2	52.4	18.9
40		6	50.8	48.3	1	49.3	27.7	43.8	21.6
41		--	--	--	2	40.5	31.6	21.8	8.9
\bar{X}		--	44.8	41.8	--	34.7	24.2	32.0	10.5

Appendix Table 2 (cont'd). Weighted Mean Percentage Prickling and Resorption for Individual Populations of Cottus asper Used in Compiling Table I and Figure 4.

Population No.	Specimens < 60 mm S.L.			Specimens ≥ 60 mm S.L.			% Resorption		
	Inland	n	Virtual	Apparent	n	Virtual	Apparent	Relative	Absolute
44		15	67.7	64.8	14	64.1	53.9	16.0	10.2
45		3	69.3	65.8	9	65.0	44.2	32.0	20.8
46		4	65.1	61.6	1*	62.6	60.4	3.6	2.2
47		6	65.4	60.7	15	59.9	54.3	9.4	5.2
50		12	61.4	56.4	10	59.6	49.9	16.3	9.7
51		11	65.4	60.6	31	55.3	46.1	16.6	9.2
52		15	56.4	53.5	25	59.9	52.6	12.1	7.3
53		13	63.1	61.0	15	58.3	49.7	14.7	8.6
54		20	77.6	73.3	21	73.5	68.0	7.5	5.5
55		12	69.8	67.0	20	67.4	53.5	20.7	13.9
56		14	52.3	51.1	13	51.0	45.0	11.8	6.0
57		8	66.9	66.3	1*	61.3	60.3	1.7	1.0
58		24	66.5	65.1	6	67.1	60.3	10.1	6.8
60		1*	84.2	81.2	7	69.5	57.8	16.9	11.7
61		--	--	--	15	67.3	55.8	17.1	11.5
62		2	--	67.0	6	58.8	42.1	28.4	16.7
63		--	--	--	11	60.7	56.4	7.1	4.3
64		2	--	77.4	7	--	57.0	--	--
65		11	81.9	80.6	10	76.7	65.8	14.2	10.9
66-68		2	74.5	74.5	6	63.3	46.2	26.9	17.1
69-72		23	71.5	68.0	7	63.3	52.6	12.7	7.7
\bar{X}		--	67.2	65.3	--	63.2	53.2	16.1	10.0
Intergrade									
73		8	60.1	57.1	20	52.9	35.6	32.8	17.3

* Single specimens not included in means (\bar{X})

Appendix Table 3. Non-weighted Mean¹ % Virtual Prickling in Each of 14 Body Sections
(Specimens \geq 60 mm S.L.)

Population No.	Sample Size	Lettered Body Sections (from Skin Map, Fig. 1)													
		a	b	c	d	e	f	g	h	i	j	k	l	m	n
Coastal															
2	8	--	--	70.6	--	--	35.6	72.5	--	32.5	55.6	--	--	--	--
3	18	--	1.4	65.9	1.1	2.8	31.1	60.3	--	42.8	53.6	--	--	--	--
4	8	--	--	65.6	--	--	25.6	72.8	--	41.1	51.1	--	--	--	--
5	16	--	0.9	78.8	3.1	7.8	41.2	75.9	--	44.7	66.6	--	--	2.2	--
6	9	--	0.9	86.7	10.6	3.3	28.3	85.6	--	41.1	66.1	--	--	1.1	--
7	18	--	--	56.9	--	4.7	26.1	48.9	--	32.2	37.5	--	--	--	--
11	5	--	--	2.4	--	--	18.0	25.0	--	25.0	17.0	--	--	--	--
12	11	--	--	32.7	--	--	14.1	47.7	--	30.9	41.4	--	--	--	--
13	17	--	6.9	90.9	20.6	12.0	53.2	88.8	11.8	43.5	69.7	1.2*	--	--	--
14	11	0.7*	8.9	90.0	9.1	9.5	56.8	84.5	2.3	42.3	67.3	--	--	--	--
15	16	--	4.7	90.3	20.0	14.7	50.3	86.6	2.1	43.4	64.4	--	--	1.9	--
16	6	--	--	85.8	--	5.8	40.8	80.0	--	38.3	67.5	--	--	5.8	--
18	5	--	4.0**	26.0	--	4.0	46.0	50.0	--	41.0	47.0	--	--	10.0	--
19	33	3.0**	16.5	92.3	8.9	27.4	65.9	87.0	3.5	43.2	74.1	--	--	5.3	--
20-21	9	--	--	(6.7) ⁺	--	(10.0)	(39.4)	(21.1)	--	(35.6)	(11.1)	--	--	--	--
25a	1	--	--	--	--	--	15.0	50.0	--	35.0	50.0	--	--	--	--
26	24	--	1.9	50.4	--	--	20.6	57.9	--	36.2	52.3	--	--	--	--
28	2	--	--	--	--	--	--	17.5	--	35.0	20.0	--	--	--	--
29	2	--	--	--	--	--	5.0	--	--	30.0	--	--	--	--	--
31	3	--	--	53.3	--	--	5.0	56.7	--	43.3	61.7	--	--	--	--
Coastal Derivative															
32	2	--	--	32.5	--	--	15.0	25.0	--	25.0	15.0	--	--	--	--
33	19	--	2.6	87.9	2.6	6.8	46.1	83.4	--	32.6	57.6	--	--	--	--
34	1	--	--	80.0	--	--	65.0	65.0	--	35.0	50.0	--	--	--	--
35	4	1.0*	2.2	97.5	23.8	18.8	56.2	93.8	15.0	38.8	62.5	2.5*	--	5.0	--
37	11	--	5.4	83.6	--	0.4	44.5	76.8	--	32.3	48.2	--	--	--	--
38	2	--	--	90.0	--	20.0	37.5	80.0	--	30.0	55.0	--	--	2.5	--
41	2	--	7.0	90.0	--	--	52.5	82.5	--	37.5	62.5	--	--	--	--

Appendix Table 3 (cont'd). Non-weighted Mean % Virtual Prickling in Each of 14 Body Sections
(Specimens ≥ 60 mm S.L.)

Population No.	Sample Size	Lettered Body Sections (from Skin Map, Fig. 1)													
		a	b	c	d	e	f	g	h	i	j	k	l	m	n
Inland															
44	14	33.3	68.9	99.6	56.8	100.0	98.6	98.9	37.5	57.5	91.8	10.7	--	21.8	3.6
45	9	31.6	52.8	100.0	68.3	60.6	86.1	100.0	60.6	56.7	97.2	22.8	1.2	32.2	19.4
46	1	75.0	70.0	100.0	65.0	100.0	100.0	100.0	25.0	55.0	85.0	--	--	10.0	--
47	15	23.7	51.0	99.0	59.3	57.3	89.0	99.0	53.0	50.3	90.7	25.3	--	17.3	--
50	10	40.0	65.0	100.0	46.5	99.0	92.5	100.0	35.5	47.0	88.0	6.0	--	13.0	--
51	31	26.3	28.0	97.7	31.6	82.3	84.0	95.5	12.6	53.5	83.1	--	--	15.2	--
52	25	45.8	65.6	99.0	44.0	91.4	91.8	97.2	29.8	55.0	87.2	6.6	--	1.4	--
53	15	11.3	43.5	98.7	29.3	74.3	85.7	95.3	13.7	55.7	87.0	1.0	--	15.7	--
54	21	82.6	93.8	100.0	65.0	100.0	99.5	99.5	61.7	69.5	96.4	31.4	2.8	42.9	5.0
55	20	75.7	91.8	100.0	64.5	95.2	99.2	100.0	57.0	57.0	95.2	20.2	--	21.8	5.5
56	13	6.3	15.3	98.8	38.8	62.3	72.7	91.9	69.6	45.8	80.0	0.8	--	2.8	--
57	1	60.0	75.0	100.0	70.0	100.0	100.0	100.0	35.0	50.0	85.0	10.0	--	10.0	--
58	6	77.5	94.2	100.0	72.5	100.0	100.0	99.2	53.3	54.2	93.3	20.8	--	27.2	5.0
60	7	68.3	92.1	99.3	50.7	97.1	100.0	98.6	35.0	60.7	91.4	20.0	--	47.1	15.7
61	15	87.0	95.3	98.7	37.3	93.3	100.0	96.0	33.0	60.3	88.7	10.0	0.7	30.3	4.7
62	6	26.7	43.3	100.0	45.0	75.0	89.2	98.3	26.7	52.5	83.3	1.7	--	20.8	--
63	11	51.8	89.5	94.1	27.7	95.4	96.8	90.9	22.7	60.0	78.6	1.4	1.4	11.8	--
64	7	(44.3)	(78.6)	(93.6)	(25.7)	(97.9)	(95.0)	(79.3)	(7.1)	(60.0)	(73.6)	(2.8)	(0.7)	(9.3)	--
65	10	94.5	100.0	100.0	69.5	100.0	100.0	100.0	49.5	72.0	96.0	30.5	7.0	59.0	8.0
66-68	6	64.0	94.2	100.0	57.5	97.5	100.0	100.0	49.2	50.8	89.2	11.7	--	11.7	--
69-72	7	17.1	82.8	95.0	31.4	80.0	98.6	93.3	33.6	57.1	90.0	11.4	--	3.6	--
Intergrade															
73	20	25.2	50.0	96.5	38.0	55.2	84.2	93.5	17.5	46.5	77.8	2.0	--	8.8	--

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* Represents only 1 or 2 prickles in this body section.
 ** One specimen in this sample was in all respects typically "inland" in its prickling.
 + Data enclosed by brackets indicate mean % "apparent" prickling only.
 1 These mean percentages have not been weighted by multiplication of fractional constants appropriate to each body section.

Appendix Table 4. Mean Relative Prickling Intensity Index Values For All Populations of Cottus asper.

Population No.	Standard Length < 60 mm			Standard Length ≥ 60 mm		
	Sample Size	Intensity		Sample Size	Intensity	
		Mean	Range		Mean	Range
Coastal						
1	2	1.0	--	---	-----
2	--	---	-----	8	2.9	(2-3)
3	2	2.0	18	2.3	(1-3)
4	--	---	-----	10	2.4	(1-3)
5	--	---	-----	16	3.1	(2-4)
6	10	2.7	(2-3)	9	2.9	(2-4)
7	12	1.6	(1-2)	18	1.2	(1-2)
8	--	---	-----	2	3.0
11	--	---	-----	2	1.0
12	--	---	-----	11	1.5	(1-3)
13	5	3.0	(2-4)	17	2.6	(1-5)
14	14	2.8	(2-4)	11	2.6	(1-4)
15	17	3.8	(3-5)	16	3.8	(2-5)
16	28	3.6	(1-5)	26	3.2	(2-5)
18	10	2.7	(1-4)	5	1.6	(1-3)
19	--	---	-----	33	3.4	(1-5)
20-21	9	1.9	(1-5)	6	3.2	(2-4)
25a	6	3.8	(3-5)	1*	4
26	--	---	-----	24*	2.0	(1-3)
28	6	2.8	(2-3)	1	3
30	15	2.9	(2-3)	--	---	-----
31	--	---	-----	3	2.3	(2-3)
	Range	(1.0-3.8)			(1.0-3.8)	
Coastal Derivative						
32	--	---	-----	2	1.5	(1-2)
33	--	---	-----	19	3.0	(2-3)
34	15	3.3	(2-4)	3	3.0
35	12	3.0	4	4.0	(3-5)
36	6	3.0	--	---	-----
37	13	3.2	(2-4)	11	2.9	(2-3)
38	13	2.1	(1-3)	2	2.5	(2-3)
39	14	1.9	(1-2)	--	---	-----
40	6	3.0	1*	3
41	--	---	-----	2	3.0
42	11	2.9	(2-4)	--	---	-----
43	13	2.6	(1-4)	--	---	-----
	Range	(1.9-3.3)			(2.5-4.0)	

Appendix Table 4 (cont'd). Mean Relative Prickling Intensity Index Values For All Populations of Cottus asper.

Population No.	Standard Length <60 mm			Standard Length ≥60 mm		
	Sample Size	Intensity		Sample Size	Intensity	
		Mean	Range		Mean	Range
Inland						
44	15	3.7	(3-4)	14	3.9	(3-5)
45	3	3.7	(3-4)	9	4.0
46	15	3.0	(2-4)	1*	4
47	6	3.7	(3-4)	15	3.7	(3-4)
50	12	3.3	(2-4)	10	3.4	(3-4)
51	11	5.0	31	4.6	(4-5)
52	15	3.1	(3-4)	25	4.2	(3-5)
53	13	3.8	(2-4)	15	4.3	(4-5)
54	20	4.3	(4-5)	21	4.9	(4-5)
55	16	3.9	(2-5)	20	3.9	(3-4)
56	14	3.2	(2-4)	13	3.3	(3-4)
57	14	3.6	(2-5)	1*	4
58	24	4.5	(3-5)	6	4.7	(4-5)
59	20*	3.6	(3-4)	--	---	-----
60	1	5	7	4.3	(4-5)
61	--	---	-----	21	4.3	(3-5)
62	2	4.5	(4-5)	9	4.0	(3-5)
63	--	---	-----	18	4.5	(4-5)
64	2	4.5	(4-5)	7	4.9	(4-5)
65	11	4.2	(4-5)	10	4.2	(4-5)
66-68	2	4.5	(4-5)	7	4.0	(3-5)
69-72	23	4.2	(4-5)	6	3.6	(3-4)
Range		(3.0-5.0)			(3.3-4.9)	
Intergrade						
73	8	3.8	(3-5)	20	3.4	(2-4)

* Single specimens not used in computing means

Appendix Table 5. Pectoral Fin Asymmetry in Cottus asper, by Population.

Population No.	Sample Size (Pairs)	Symmetrical		Asymmetrical		Total Ray Count		Direction of Asymmetry Within Population		
		No. Pairs	%	No. Pairs	%	Greater on Left	Greater on Right	Sinistral	Dextral	Equal
Coastal										
1	10	9	90.0	1	10.0	1	-	+	-	-
2	8	7	87.5	1	12.5	-	1	-	+	-
3	20	14	70.0	6	30.0	5	1	+	-	-
4	21	18	85.7	3	14.3	3	-	+	-	-
5	18	16	88.9	2	11.1	1	1	-	-	+
6	19	15	78.9	4	21.1	2	2	-	-	+
7	30	20	66.7	10	33.3	9	1	+	-	-
8	2	2	100.0	0	-	-	-	-	-	-
11	5	3	60.0	2	40.0	-	2	-	+	-
12	11	9	81.8	2	18.2	1	1	-	-	+
13	22	15	68.2	7	31.8	5	2	+	-	-
14	24	17	70.8	7	29.2	5	2	+	-	-
15	33	29	87.8	4	12.2	3	1	+	-	-
16	72	60	83.3	12	16.7	7	5	+	-	-
18	15	13	86.7	2	13.3	-	2	-	+	-
19	33	30	90.9	3	9.1	2	1	+	-	-
20	12	8	67.7	4	33.3	3	1	+	-	-
21	5	4	80.0	1	20.0	1	-	+	-	-
23	30	26	86.7	4	13.3	3	1	+	-	-
25a	7	4	57.1	3	42.9	1	2	-	+	-
26	35	28	80.0	7	20.0	5	2	+	-	-
28	8	4	50.0	4	50.0	3	1	+	-	-
29,31	5	2	40.0	3	60.0	2	1	+	-	-
30	15	14	93.3	1	6.7	-	1	-	+	-
Totals	460	367	79.8	93	20.2	62	31	15(65.2)	5(21.7)	3(13.1)

Appendix Table 5 (cont'd). Pectoral Fin Asymmetry in Cottus asper, by Population

Population No.	Sample Size (Pairs)	Symmetrical		Asymmetrical		Total Ray Count		Direction of Asymmetry Within Population ^a		
		No. Pairs	%	No. Pairs	%	Greater on Left	Greater on Right	Sinistral	Dextral	Equal
Inland										
44	26	26	89.6	3	10.4	2	1	+	-	-
45	12	9	75.0	3	25.0	3	-	+	-	-
46	16	10	62.5	6	37.5	4	2	+	-	-
47	21	17	81.0	4	19.0	-	4	-	+	-
50	22	9	40.9	13	59.1	5	8	-	+	-
51	42	32	76.2	10	23.8	6	4	+	-	-
52	40	34	85.0	6	15.0	5	1	+	-	-
53	27	20	74.1	7	25.1	6	1	+	-	-
54	41	30	73.2	11	26.8	6	5	+	-	-
55	37	29	78.4	8	21.6	6	2	+	-	-
56	27	17	63.0	10	37.0	4	6	-	+	-
57	15	7	46.7	8	53.3	5	3	+	-	-
58	30	22	73.3	8	26.7	3	5	-	+	-
59	18	9	50.0	9	50.0	6	3	+	-	-
60	16	11	68.8	5	21.2	3	2	+	-	-
61	21	15	71.4	6	28.6	6	-	+	-	-
62	19	19	100.0	0	--	-	-	-	-	-
63	19	14	73.7	5	26.3	3	2	+	-	-
64	8	7	87.5	1	12.5	1	-	+	-	-
65	22	17	77.3	5	22.7	2	3	-	+	-
66-68	11	7	63.6	4	36.4	2	2	-	-	+
69-72	30	26	86.6	4	13.4	4	-	+	-	-
73	28	21	75.0	7	25.0	5	2	+	-	-
Totals	551	408	74.0	143	26.0	87	56	16(72.7)	5(22.7)	1(4.6)

Appendix Table 5 (cont'd). Pectoral Fin Asymmetry in Cottus asper, by Population.

Population No.	Sample Size (Pairs)	Symmetrical		Asymmetrical		Total Ray Count		Direction of Asymmetry Within Population		
		No. Pairs	%	No. Pairs	%	Greater on Left	Greater on Right	Sinistral	Dextral	Equal
Coastal Derivative										
32	2	0	--	2	100.0	2	-	+	--	-
33	22	18	81.8	4	18.2	4	-	+	-	-
34	19	14	73.7	5	26.3	2	3	-	+	-
35	16	11	68.8	5	21.2	3	2	+	-	-
36	6	4	66.7	2	33.0	1	1	-	-	+
37	23	16	69.6	7	30.4	4	3	+	-	-
38	15	11	73.3	4	26.7	3	1	+	-	-
39	15	12	80.0	3	20.0	3	-	+	-	-
40	7	5	71.4	2	28.6	2	-	+	-	-
41	2	2	100.0	0	--	-	-	-	-	-
42	11	10	90.9	1	9.1	1	-	+	-	-
43	14	10	71.4	4	28.6	2	2	-	-	+
Totals	152	113	74.4	39	25.6	27	12	8(72.7)	1(9.1)	2(18.2)
Grand Totals	1163	888	76.4	275	23.6	176	99	39(69.6)	11(19.6)	6(10.7)

Appendix Table 6. Summary of Meristic Counts (Means and Ranges) for all Populations of *Cottus asper*.

Pop. No.	No. Specs.	D ₁	D ₂	A	P ₁ left	P ₁ right	D ₁ + D ₂
1.	10	8.80 (8-9)	20.70 (20-22)	16.70 (16-18)	15.30 (15-16)	15.20 (15-16)	29.50 (29-31)
2.	8	9.88 (9-11)	20.50 (20-21)	16.88 (16-17)	15.75 (15-16)	15.88 (15-16)	30.38 (29-32)
3.	20	8.95 (9-10)	19.85 (19-21)	16.35 (16-17)	15.50 (15-16)	15.30 (15-16)	28.80 (28-30)
4.	21	8.95 (8-10)	20.38 (20-21)	16.67 (15-18)	15.95 (15-17)	15.81 (15-16)	29.33 (28-30)
5.	18	9.06 (9-10)	20.50 (20-21)	17.11 (16-18)	15.22 (15-16)	15.22 (15-16)	29.56 (29-30)
6.	19	8.79 (8-9)	19.84 (19-21)	16.37 (16-17)	15.63 (15-16)	15.63 (15-16)	28.63 (28-30)
7.	30	9.13 (9-10)	20.60 (20-21)	16.40 (15-17)	16.63 (16-17)	16.37 (16-17)	29.73 (29-31)
8.	2	9.00 (9)	20.50 (20-21)	17.00 (17)	16.00 (16)	16.00 (16)	29.50 (29-30)
9.	20	9.10 (9-10)	20.70 (20-22)	17.00 (16-18)	15.84 (15-17)	---	29.80 (29-32)
10.	10	9.00 (9)	21.00 (20-22)	17.00 (16-18)	16.60 (16-18)	---	30.00 (29-31)
11.	6	9.00 (9)	20.83 (20-21)	16.50 (16-17)	16.50 (16-17)	16.83 (16-17)	29.83 (29-30)
12.	11	8.82 (8-9)	20.27 (20-21)	16.64 (16-17)	17.00 (16-18)	17.00 (17)	29.09 (28-30)
13.	22	8.95 (8-9)	20.73 (20-22)	17.18 (16-18)	15.95 (15-17)	15.82 (14-16)	29.68 (29-31)
14.	25	9.08 (8-10)	20.32 (19-21)	16.44 (15-18)	15.38 (15-16)	15.24 (15-16)	29.40 (28-31)
15.	33	9.06 (8-10)	20.76 (20-21)	16.88 (16-18)	15.55 (15-16)	15.48 (15-16)	29.82 (29-31)
16.	72	8.99 (8-10)	20.53 (19-21)	16.80 (16-18)	15.89 (15-17)	15.86 (15-17)	29.52 (28-31)
17.	10	8.90 (8-9)	20.80 (20-21)	17.00 (16-18)	16.20 (16-17)	---	29.70 (29-30)
18.	15	9.00 (9)	20.67 (20-21)	16.87 (16-18)	15.93 (15-16)	16.07 (16-17)	29.67 (29-30)
19.	33	8.82 (8-10)	20.27 (18-21)	16.76 (16-18)	16.45 (16-17)	16.42 (16-17)	29.09 (26-30)
20.	12	9.00 (9)	20.42 (20-21)	16.75 (16-18)	16.75 (16-18)	16.58 (16-18)	29.42 (29-30)
21.	6	9.00 (9)	20.83 (20-21)	17.00 (16-18)	16.20 (16-17)	16.00 (16)	29.83 (29-30)
22.	30	9.00 (9)	20.47 (20-21)	16.87 (16-18)	16.10 (15-17)	16.00 (14-17)	29.45 (29-30)
23.	5	9.00 (9)	20.60 (20-21)	17.20 (17-18)	16.40 (16-17)	16.20 (16-17)	29.60 (29-30)
24a.	5	9.00 (9)	20.80 (20-22)	16.80 (16-18)	15.60 (15-16)	15.60 (15-16)	29.80 (29-31)
25a & b.	17	9.00 (9)	20.14 (20-21)	16.00 (15-17)	16.14 (15-17)	16.29 (16-17)	29.14 (29-30)
26.	35	9.03 (8-10)	20.23 (19-21)	16.49 (15-18)	16.46 (16-17)	16.37 (15-17)	29.26 (28-30)
27.	5	8.60 (8-9)	20.00 (20)	16.60 (16-17)	16.20 (16-17)	16.00 (15-17)	28.60 (28-29)
28.	8	8.75 (8-9)	19.50 (19-20)	16.50 (16-17)	16.38 (15-17)	16.12 (15-17)	28.25 (27-29)
29,31.	5	8.80 (8-10)	20.00 (20)	16.80 (16-17)	15.60 (15-16)	15.40 (15-16)	28.67 (28-30)
30.	15	8.67 (8-9)	19.73 (19-20)	16.47 (15-17)	16.00 (15-17)	16.07 (15-17)	28.40 (27-29)
32.	6	9.00 (8-10)	22.17 (22-23)	17.67 (17-18)	16.67 (16-17)	---	31.17 (30-32)
33.	24	9.46 (9-11)	20.70 (20-21)	16.75 (16-18)	16.09 (16-17)	15.91 (15-17)	30.17 (29-31)
34.	19	9.05 (9-10)	20.21 (20-21)	16.42 (15-17)	16.53 (16-17)	16.58 (16-18)	29.26 (29-31)
35.	16	9.19 (9-10)	20.25 (20-21)	17.00 (16-18)	16.25 (16-17)	16.19 (16-17)	29.44 (29-31)
36.	6	--	---	---	16.50 (16-17)	16.50 (16-17)	---
37.	24	9.42 (9-10)	20.54 (20-22)	16.96 (16-18)	16.39 (15-17)	16.38 (15-17)	29.96 (29-32)

Appendix Table 6. Summary of Meristic Counts (Means and Ranges) for all Populations of *Cottus asper*, (cont'd).

Pop. No.	No. Specs.	D ₁	D ₂	A	P ₁ left	P ₁ right	D ₁ + D ₂
38.	15	9.13 (9-10)	20.47 (20-21)	16.93 (16-18)	16.73 (16-17)	16.67 (16-18)	29.60 (29-31)
39.	15	9.27 (9-10)	20.40 (20-21)	16.80 (16-18)	16.27 (15-17)	16.07 (15-17)	29.67 (29-31)
40.	7	-- --	--- ---	--- ---	17.43 (17-18)	17.14 (17-18)	---
41.	2	9.50 (9-10)	20.00 (20)	16.50 (16-17)	17.50 (17-18)	17.50 (17-18)	29.50 (29-30)
42.	12	9.17 (9-10)	20.17 (20-21)	16.42 (15-18)	16.17 (16-17)	16.00 (16)	29.34 (29-31)
43.	15	9.61 (8-10)	20.31 (20-21)	16.27 (16-18)	16.67 (16-17)	16.64 (16-17)	29.92 (29-31)
44.	29	9.03 (9-10)	20.27 (19-21)	16.59 (15-17)	16.86 (16-18)	16.83 (16-17)	29.31 (28-30)
45.	12	9.00 (9)	20.17 (20-21)	16.83 (16-18)	16.75 (15-18)	16.50 (15-18)	29.18 (29-30)
46.	16	9.25 (9-10)	20.31 (20-21)	16.25 (15-17)	16.50 (15-18)	16.38 (15-18)	29.56 (29-31)
47.	21	9.10 (8-10)	20.71 (20-22)	16.52 (15-17)	16.29 (15-17)	16.45 (15-17)	29.81 (28-31)
48.	9	9.22 (9-10)	20.00 (19-21)	16.12 (16-17)	---	---	29.22 (29-30)
49.	10	8.80 (8-9)	20.70 (20-22)	17.10 (16-18)	16.90 (16-17)	---	29.50 (29-30)
50.	22	8.52 (7-10)	20.64 (16-23)	16.67 (15-17)	17.14 (13-18)	17.50 (17-18)	29.14 (28-32)
51.	42	8.98 (8-10)	20.76 (20-21)	17.31 (16-20)	16.93 (14-18)	16.86 (14-19)	29.74 (29-32)
52.	40	9.00 (9)	20.82 (20-22)	17.02 (16-18)	16.60 (16-18)	16.50 (16-17)	29.83 (29-31)
53.	28	9.00 (8-10)	20.82 (20-21)	16.93 (16-18)	16.93 (16-18)	16.74 (16-18)	29.82 (28-31)
54.	41	8.98 (8-9)	20.90 (19-22)	16.98 (15-18)	16.44 (15-18)	16.39 (15-17)	29.88 (28-31)
55.	37	8.95 (8-9)	20.70 (19-22)	16.89 (16-18)	16.43 (16-17)	16.32 (15-17)	29.65 (28-31)
56.	27	8.89 (8-9)	20.89 (20-22)	17.18 (16-18)	16.30 (15-17)	16.41 (16-17)	29.78 (28-31)
57.	15	8.80 (8-9)	20.93 (20-22)	17.00 (16-18)	16.67 (14-18)	16.53 (14-17)	29.73 (29-31)
58.	30	8.87 (8-9)	20.13 (19-22)	16.27 (15-17)	16.73 (16-18)	16.80 (16-18)	29.00 (27-31)
59.	20	9.06 (8-10)	20.31 (19-21)	16.81 (16-18)	16.67 (14-18)	16.16 (14-18)	29.45 (28-31)
60.	16	8.69 (8-9)	20.87 (20-22)	16.81 (15-18)	16.44 (16-17)	16.38 (15-17)	29.53 (28-31)
61.	21	8.81 (8-10)	20.60 (19-22)	17.24 (16-19)	16.29 (15-18)	15.86 (15-17)	29.50 (28-31)
62.	13	9.08 (9-10)	20.69 (20-22)	17.15 (16-18)	16.00 (15-17)	16.00 (15-17)	29.77 (29-31)
63.	24	9.00 (8-10)	20.29 (19-21)	16.58 (15-18)	16.25 (16-17)	16.21 (15-17)	29.29 (28-31)
64.	9	8.89 (8-9)	20.56 (20-21)	17.00 (16-18)	16.00 (15-17)	15.89 (15-16)	29.45 (28-30)
65.	22	8.68 (8-9)	20.23 (19-21)	17.18 (16-18)	16.14 (15-17)	16.18 (16-17)	28.91 (28-30)
66a.	3	8.00 (8)	19.67 (19-20)	16.67 (16-17)	16.00 (15-17)	15.67 (15-16)	27.67 (27-28)
66b.	3	8.00 (8)	20.00 (20)	17.00 (17)	16.00 (16)	16.33 (16-17)	28.00 (28)
67.	3	8.00 (8)	19.67 (18-21)	16.33 (16-17)	15.67 (14-17)	16.00 (15-17)	27.67 (26-28)
68.	2	8.00 (8)	20.00 (20)	17.50 (17-18)	16.00 (16)	15.00 (14-16)	28.00 (28)
69.	14	8.21 (7-9)	19.00 (19)	16.64 (16-18)	15.64 (15-16)	15.50 (14-16)	27.21 (26-28)
70.	8	8.00 (8)	19.12 (18-20)	17.00 (16-18)	16.50 (16-17)	16.25 (16-17)	27.12 (26-28)
71.	3	8.00 (8)	19.33 (19-20)	16.67 (16-17)	16.33 (16-17)	16.33 (16-17)	27.33 (27-28)
72.	4	8.00 (8)	18.75 (18-20)	16.50 (16-17)	16.00 (15-17)	16.00 (15-17)	26.75 (26-28)
73.	28	8.82 (8-10)	19.93 (19-21)	16.54 (15-18)	16.21 (15-17)	16.11 (15-17)	28.75 (27-31)

Appendix Table 7. Monthly Mean Temperature in °C for Selected Coastal and Inland Localities.*

Locality	Latitude	J	F	M	A	M	J	J	A	S	O	N	D	Annual Range
<u>Coastal</u>														
Valdez	61° 07' N.	- 7.1	- 5.9	- 2.6	+ 1.4	6.3	10.2	11.3	10.9	7.8	3.0	- 3.9	- 7.5	18.8
Prince Rupert	54° 17' N.	1.7	2.9	4.2	6.3	9.8	12.0	13.4	13.9	12.0	8.7	5.1	2.7	12.2
Victoria	48° 25' N.	3.6	5.7	7.2	9.6	12.4	14.3	15.9	15.7	14.4	10.9	7.3	5.2	12.3
San Francisco	37° 47' N.	10.0	11.0	11.9	12.5	13.3	14.4	14.3	14.7	15.9	15.3	13.6	10.9	5.9
Santa Barbara		11.8	--	--	--	--	--	19.1	--	--	--	--	--	7.3
San Diego	32° 44' N.	12.3	13.4	14.8	16.2	17.8	19.0	21.0	21.7	20.9	18.6	15.6	13.2	9.4
N-S Range		19.4	19.3	17.4	14.8	11.5	8.8	9.7	11.8	13.1	15.6	19.5	20.7	--
<u>Inland</u>														
Watson L.	60° 07'	-22.0	18.4	- 8.9	- 0.4	8.0	13.6	14.8	12.8	9.0	1.1	-13.7	-22.1	36.8
Prince George	53° 54'	- 9.9	6.6	- 1.4	+ 4.6	9.9	13.4	14.9	13.7	9.9	4.8	- 2.7	- 7.5	24.8
Spokane	47° 37'	- 4.4	+0.4	3.8	8.7	13.1	16.3	20.9	20.0	15.4	9.2	2.7	- 1.1	25.3
Red Bluff	40° 09"	6.9	9.2	11.4	14.6	19.8	23.0	27.1	25.4	23.5	17.4	11.6	7.7	20.2
Sacramento	38° 35'	7.6	10.0	12.2	16.3	18.0	21.3	23.9	23.2	22.3	17.6	12.2	8.3	16.3
Fresno		7.5	--	--	--	--	--	27.4	--	--	--	--	--	19.9
N-S Range		29.6	28.4	21.1	15.9	11.8	9.6	12.6	12.6	14.5	16.5	25.9	30.4	--

*10 year-averages, 1941-1950 (World Weather Records, U.S. Weather Bur. Wash., D.C. 1959:1-1361)