UNIVERSITY OF WISCONSIN MILWAUKEE

College of Letters and Science
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UWM

September 10, 1994

Dr. Robert Behnke
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Dear Bob:

I enjoyed talking with you and Don, and am enclosing the manuscript from Jim Reist. I hope that we will be able to obtain some samples from the char of Lake Elgygytgyn for DNA analysis. My NSF grant comes up for renewal later this year, and I have been thinking about what I want to propose to do. It would be interesting to look at those samples and also the "intermediates" between northern and southern Dolly Varden which Jim Reist and Fred DeCicco have observed.

We finished everything I proposed for the last grant, so I am hopeful that I will be able to convince them to renew it. Future work will be expedited by the automated DNA sequencer which was recently acquired by our department. In fact, I mentioned to Don that we might be able to do some sequencing work for him for a price which would be substantially lower than what you can get commercially.

The ITS1 of the ribosomal DNA (575 base pairs long) turned out to contain some information regarding subspecies in the S. alpinus/S. malma complex. I am enclosing for you the PAUP tree showing bootstrap values (relationships in these trees are usually not taken very seriously unless bootstraps values exceed 85%). This is from my paper for the Norwegian symposium. We also have some preliminary information from 300 base pairs (bp) of the 5' ETS (external transcribed spacer) of the ribosomal DNA which is somewhere between 2,000 and 3,000 bp long. We believe this region should contain quite a bit of useful information. For example there are some microrearrangements in this region: if any of these are shared by at least two species they could possibly be more informative than single base changes. We have also sequenced the ND 3 gene of the mitochondrial DNA in Salvelinus species, but the sequences were all pretty similar, so did not contain very many informative sites. We will probably try another mitochondrial gene within the year, now that we have the automated sequencer.

Sincerely yours,

Ruth Phillips

Ruth Phillips

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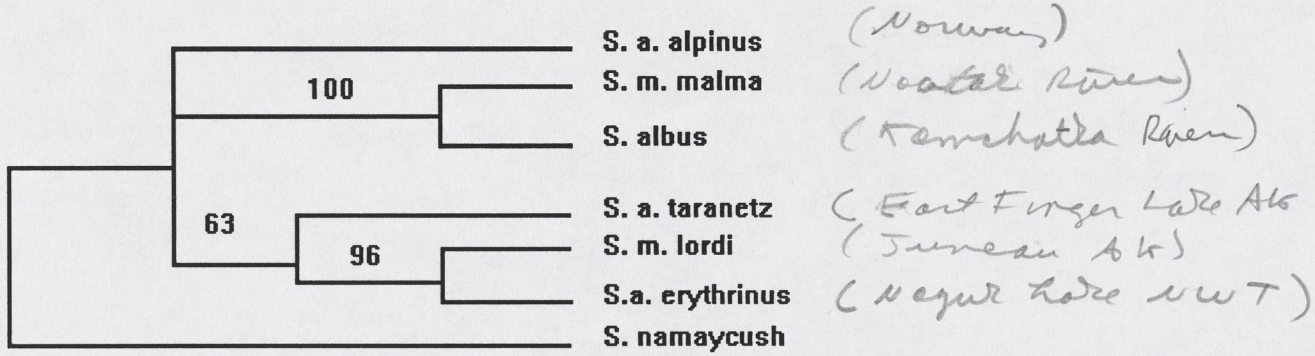
Phillips Sept 1994



Tree based on 575bp of the ITS1 of the ribosomal DNA (rDNA) — need more data from rDNA to draw firm conclusions

Variation and Specific Identity of char from Northwestern Arctic Canada.

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Abstract

Char from east of the Mackenzie River system in Canada are considered to be nominate Arctic char (Salvelinus alpinus). Anadromous char south of the Alaska Peninsula are, with few exceptions, considered to be nominate Dolly Varden char (S. malma). Considerable debate has occurred with respect to specific affinities of the char found between these two regions along the continental north slope from Point Barrow, Alaska eastwards to the Mackenzie River and the Alaskan coast from Point Barrow south to the Alaska Peninsula. Various authors have suggested these are taxonomic forms of either Arctic or Dolly Varden char and resolution of this issue both in the literature and with respect to common usage remains outstanding. Morphological and genetic variation were examined for char from locations in the western Arctic in order to assign specific identification to several char forms found on the Yukon north slope. Anadromous and isolated riverine resident char from the north slope exhibited great similarity both to each other as well as to nominate Dolly Varden from southeastern Alaska, but both were dissimilar from lacustrine north slope char and anadromous char from east of the Mackenzie River. Lacustrine north slope char exhibited greater similarity to nominate Arctic char than to Dolly Varden char. These results substantiate the view that riverine char (anadromous, residual, and isolated stream-resident forms) from the continental north slope west of the Mackenzie River are Dolly Varden char whereas lacustrine char from this area are relictual Arctic char.

Introduction

Fishes of the genus Salvelinus represent a generally confusing array of variation that has led to the description of numerous taxonomic forms throughout their Holarctic range. In northwestern arctic North America, three species have been formally identified or described: Arctic char, S. alpinus, assumed to be synonymous with the Eurasian taxon described by Linneaus; Dolly Varden char, S. malma, assumed to be synonymous with the Asian taxon described by Walbaum; and, Angayukaksurak char, S. anaktuvukensis, described by Morrow (1973). Additionally, numerous authors have described various geographically or ecologically defined sub-specific taxa and forms, and allied these with the above species. However, while general agreement prevails amongst authors with respect to the existence of the various sub-specific groups, considerable disagreement exists as to the specific affinities of both defined sub-specific taxa and of certain geographically defined groups. The taxonomic identity of several forms of chars found in the area of the Beaufort Sea is the subject of this contribution.

History of Salvelinus Taxonomy in western Arctic North America

In southwestern Alaska, two taxa of char co-occur - Arctic char with high pyloric caecae and gill raker counts, and Dolly Varden char with low counts for these characters (DeLacy and Morton 1942; McPhail 1961). McPhail (1961) considered these to constitute good biological species due to a lack of hybridization where they co-occurred. McPhail (1961) summarized the observed morphological variation for Dolly Varden char as follows: a) a northern form with more vertebrae and gill rakers distributed north of the Alaska Peninsula and on the Seward Peninsula, b) a southern form occurring south of the Alaska Peninsula, throughout the Aleutians and the remaining southern portion of the North American range; and, c) a central Alaskan form with low counts of pyloric caecae. Morphological variation for Arctic char was summarized as follows (McPhail 1961): a) the Bering Sea-western Arctic form with fewer pyloric caecae and lower gill rakers was distributed from the lower Kuskokwim River north and east to the Mackenzie River, Canada; b) the eastern form with higher counts was distributed east of the Mackenzie River; and, c) the Bristol Bay-Gulf of Alaska form occurred south of the Kuskokwim River and had counts similar to the eastern form. Two forms of char co-occurring in the Sagavanirktok River basin, north slope Alaska were equated with the Bering Sea-western Arctic and eastern forms of Arctic char by McCart and Craig (1971).

Morrow (1973) described the angayukaksurak char, S. anaktuvukensis, as a distinct species. McCart (1980) re-examined the taxonomy of chars from the Prudhoe Bay area east to the Mackenzie River and considered S. anaktuvukensis to be a variant form of Dolly Varden. McCart (1980) concluded that only two forms of char were present in this area: all stream resident and isolated stream resident as well as a single lake resident population were equated with the Bering Sea-western Arctic form of Arctic char (McPhail 1961); and all remaining lake populations were eastern form of Arctic char. Genetic evidence further supported this in that allozyme variation in liver esterases of the eastern form was fixed for a fast allele and 98.6% of the Bering Sea-western Arctic form exhibited the alternative slow allele.

Morrow (1980) examined variation in Alaskan chars with the express aim of establishing the specific identity of the Bering Sea-western Arctic form. Multivariate comparison using meristic data indicated that nominal lake resident Arctic char from southern Alaska were distinct from both southern and northern forms of nominal Dolly Varden char. The latter pair overlapped each other but some degree of separation was evident. Almost complete overlap was observed between nominal Bering Sea-western Arctic Arctic char and the northern form of Dolly Varden, leading Morrow (1980) to conclude these constitute the same taxon which is Dolly Varden char.

Thus, we are left with two species-level taxa with conflicting composition and usage of char nomenclature in studies since 1980 reflects this confusion. For example, in comparing aging structures of char from the Wood River in interior Alaska, Baker and Timmons (1991) explicitly indicated that the taxon under consideration was the Bering Sea -western Arctic char of McPhail (1961) which Morrow (1980) would consider as northern form Dolly Varden. Barber and McFarlane (1987) compared aging structures from two populations of eastern form Arctic char (sensu McPhail 1961) from the central Northwest Territories and two populations from north slope coastal Alaska (northern Dolly Varden sensu Morrow 1980 or Bering Sea-western Arctic form of Arctic char sensu McPhail 1961) and equated all with Arctic char. De Cicco (1989) considered the char from the Kotzebue area of western Alaska to be northern form Dolly Varden (sensu Morrow (1980) but equivalent to the Bering Sea-western Arctic form of Arctic char of McPhail (1961). Other examples of such confusion of taxa exist in the literature.

Regardless of the specific designation of these taxonomic forms of char, all exhibit a wide range of alternative life history strategies. These include anadromous, residual (non-anadromous), both isolated and non-isolated stream resident, and lacustrine life history types (Bain 1974; Armstrong and Morrow 1980; McCart 1980; Johnson 1989; Reist 1989; Reynolds and Gregory 1989).

In summary, three taxonomic forms of char are widespread throughout northwestern North America and likely represent two species. Agreement prevails in that, char occurring in lacustrine habitats west of the Mackenzie River are Arctic char (with one exception). For southern Dolly Varden, agreement prevails in that, this form occurs in riverine habitats south of the Alaska Peninsula. For char distributed in riverine habitats north of the Alaska Peninsula to the Mackenzie River, agreement occurs as to taxonomic distinctness but disagreement prevails as to the specific affinity of this taxon.

Objectives of the Study

The objectives of this study are as follows. Objective 1 is to determine whether chars from northwestern arctic areas of North America represent two or more taxonomically recognizable forms. Objective 2 is to determine whether ecologically defined life history types represent either distinct taxa or differentiation within taxa defined by tests of objective 1. Assuming more than one taxon is present, Objective 3 is to develop criteria for the recognition of the taxa and to assign individuals from various locations and life history types to the correct taxon. Objective 4 is to establish the limits of distribution of the taxonomically recognizable forms present.

These objectives can be reformulated into the general null hypothesis 1) that all samples from the study area represent the same taxon. This in turn results in several testable predictions that meet the objectives. Prediction 1) is that no discontinuity in variation should be present across the samples. That is, 1a) within samples exhibiting similar life histories, at most any variation should be clinal regardless of the type of data examined. Between life history types, prediction 1b) is that variation may be clinal or discontinuous, but is attributable to ecological rather than taxonomic sources. Assuming hypothesis 1) is rejected and thus that two or more taxa exist, hypothesis 2a) is that all life history types of char (anadromous, non-anadromous residual, isolated) from riverine habitats along the continental north coast west of the Mackenzie River are the northern form of Dolly Varden char. The accompanying prediction is that these will exhibit greater similarity to Dolly Varden char from elsewhere than to Arctic char. Hypothesis 2b) is that lacustrine char from this same area are eastern form Arctic char with the prediction that these will associate with Arctic char from elsewhere.

Materials and Methods

Logic of the Study

The logical sequence of the study follows directly from the objectives outlined previously. The initial step was to establish two reference sample groups - Group A, Klutina R., AK.; and Group H, Cambridge Bay, NWT. - to be used as indicators of the possible taxa present. In the absence of examining the type specimens themselves, these reference samples were established relative to their geographical situation and comparison to literature descriptions of char from the same general area. The second step was to identify the reference samples relative to pre-existing taxonomic criteria. Of necessity, this was accomplished using meristic criteria only. To simplify presentation of results, the remaining individual samples (see Appendix Table 1) were grouped on the basis of similar geographic location, life history and habitat to form six groups of unknowns: Group B, Nome R., AK.; C anadromous, D residual, and E isolated life history types of char from riverine habitats west of the Mackenzie R., NWT.; F lacustrine char from isolated lakes west of the Mackenzie R.; and, G anadromous char from locations east of the Mackenzie R. Third, using a linear discriminant function for meristic data from the two reference samples, the six groups of unknowns were classified to specific morphological groupings. Fourth, the results of steps 1-3 were examined in reference to the null hypothesis outlined previously and discontinuities representing taxonomic boundaries sought. Because the establishment of reference samples, the classification of unknowns, and the existence of taxonomic boundaries all represent a hypothesis based upon morphological data, the final step was to re-test these morphological results using different data - in this case, genetic variation at isozyme loci.

This analytical logic establishes that groups exist and to some extent establishes the membership of those groups. However, it does not specify the taxonomic level of those groups - for example, species rather than some sub-specific taxon. Existence of groups is a fact that can be established by discontinuities in the data. However, the assignment of a particular taxonomic level is a matter of philosophical interpretation imposed upon the observations. Such interpretation is of course open to much debate which has been the norm in the taxomony of chars.

Data Utilized

Eight meristic variables were counted for all fish: upper (UGR) and lower (LGR) gill rakers with the middle raker included in the latter; pyloric caecae (PYL); branchiostegal rays (BRC); dorsal (DRC), anal (ARC), pectoral (PRC) and pelvic (VRC) principal fin rays. Total gill raker and pyloric caecae counts have traditionally been used to differentiate the taxa of char in this area. However, due to the known influence of environment on meristic characters, clinal variation in such characters is possible. Therefore, these meristic results were corroborated with a parallel set of allozyme genetic data. Two enzyme systems and a total of three loci exhibited variation, repeatable results, and adequate models: Superoxide dismutase (SOD-E.C. no. 1.15.1.1) showed one locus and Phosphoglucomutase (PGM-E.C. no. 2.7.5.1) was resolved for two loci (PGM-1, PGM-2).

Analyses Employed

Meristic variation in the two reference samples was analyzed using multivariate discriminant analysis (Norusis 1990). Such analysis is a three step process. 1) The null hypothesis of centroid equality is tested and if rejected, 2) a linear discriminant function is constructed between the groups. 3) A posteriori, the individuals used to construct the function can be scored and classified as to group membership by proximity to a group centroid and/or distribution, thus providing a measure of the discriminating power of the function. Alternatively, using the unstandardized coefficients for the function, individuals extrinsic to the analysis (i.e. true unknowns) can be scored and similarly classified. To ensure that the results obtained were representative of real variation in the data and not imposed by the constraints of the analysis, principal component analysis and scoring was employed that paralleled this discriminant analysis.

Several techniques were employed to summarize the variation observed and to address questions of similarity between groups. These included UPGMA clustering, principal coordinates analysis, and multidimensional scaling of Euclidean distances for meristic data and Nei's genetic distance for genetic data (Rohlf 1990). Each of these techniques has idiosyncratic assumptions that may affect interpretation of results, thus similarity of results between techniques indicates true relationships inherent in the data.

Results

Identification of the Reference Samples

Comparison of total gill raker and pyloric caecae counts was used to establish identity of the reference samples (Klutina R. and Cambridge Bay) (Figure 1). Char from the area near Klutina R. were characterized by low counts for total gill rakers and pyloric caecae similar to counts for nominate Dolly Varden char (McPhail 1961; Morrow 1980). Char from Cambridge Bay are characterized by high counts of both variables and were similar to counts for nominate Arctic char from the central Canadian Arctic (McPhail 1961).

Meristic Discriminant Analysis of Reference Samples

The discriminant analysis of meristic variation between the two reference groups indicated a highly significant multivariate difference ($P<0.0001$) between the representatives of Dolly Varden char (Klutina River) and Arctic char (Cambridge Bay). The best discriminating variables were pyloric caecae, lower and upper gill rakers, with minimal contribution from the remaining meristic variables (Table 1). The two groups were completely separate and a posteriori classification accuracy was 100% (Figure 2). Fish representative of Dolly Varden all exhibited negative scores whereas those representative of Arctic char exhibited positive scores. Principal component analysis in which no a priori grouping structure was imposed gave similar results. With the exception of four individuals from Cambridge Bay that occupied the intermediate area, two groups of fish were evident and this separation was primarily due to gill raker and pyloric caecae variation.

Discriminant Analysis Classification of Unknowns

Using the unstandardized discriminant coefficients from the above analysis (Table 1) fish from all other samples were treated as unknowns and classified. This procedure involves computing the discriminant score as the sum of the unstandardized coefficients multiplied by the respective character values from each individual including the constant. Thus, the scores for the unknowns are expressed relative to the centroids and the distributions of scores for the reference samples used to construct the function.

A bimodal distribution of scores resulted when all fish extrinsic to the discriminant analysis were plotted simultaneously (Figure 2A). Such bimodality is primary evidence of the existence of two taxa present in the samples and further indicates that the reference samples are not the extremes of simple clinal variation. Further examination of scoring of groups within these unknowns revealed the following pattern of differences.

Fish from the Nome River all scored negatively and overlapped the distribution of scores of the Klutina R. reference sample but were displaced somewhat towards zero (Figure 2B). Anadromous char from locations west of the Mackenzie R. (Group C including Joe Ck., Firth R., Canoe R., Cache Ck., and Rat R. as well as coastal locations near Herschel Is. -- Ptarmigan Bay, Thetis Bay, and Pauline Cove) primarily exhibited negative scores between -4 and -1 (Figure 2B). Thus, as were the Nome R. fish these were not exactly synonymous with, but substantively overlapped the Klutina reference sample. Fish from some of these samples also exhibited scores for a few individuals in the 0 to +1 range of the function thus overlapping minimally with the distribution of scores for Cambridge Bay fish. However, these scores represent outliers distant from both the sample centroid and the majority of the distribution of scores.

Anadromous char collected from locations east of the Mackenzie R. (Group G including mainland coastal samples - Wood Bay; mainland riverine samples - Hornaday R., Horton R.; and, arctic island samples - unnamed lake on Banks Is., Kuujjua R., Kuuk R., Kagloryuak R., Kagluk R., Naloagyuak R.) scored positively and exhibited overlap with the scores of the Cambridge Bay reference sample (Figure 2B). A few individuals from these samples scored in the 0 to -1 area of the discriminant function thus overlapping minimally the distribution of scores for the Klutina R. fish. These scores represent outliers distant from both the sample centroids and the primary distribution of scores.

Fish representing the residual life history type from rivers west of the Mackenzie R. (Group D including Joe Ck., Firth R., Babbage R., Canoe R., and Cache Ck.) scored negatively and overlapped the distribution of scores of Klutina R. fish (Figure 2C). Fish from riverine habitats isolated above impassable falls west of the Mackenzie R. (Group E - Babbage R. and Cache Ck.) exhibited similar scores (Figure 2C). However, lacustrine fish from the north slope west of the Mackenzie R. (Group F - Lakes 103 and 104) exhibited complete overlap of discriminant scores with those of the Cambridge Bay reference sample (Figure 2C).

Numerical Taxonomy of Meristic Variation

Clustering, principal coordinates, and multi-dimensional scaling analyses of the Euclidean distances between the eight groups of fish for meristic mean values gave similar results (Figure 3). The most obvious feature on the phenogram was the formation of two groups of fish: 1) all riverine fish from west of the Mackenzie River and Alaska, and 2) all char from east of the Mackenzie plus the lacustrine fish from the north slope west of the Mackenzie River. Within both of these groups two sub-groups were apparent. For group 1), two sub-groups associated at a Euclidean distance of 3.2 - the first consisted of the Klutina R. fish and the isolated life history type from the Yukon north slope rivers, and the other consisted of the Nome R., anadromous and residual life history types from west of the Mackenzie R. For group 2), the two sub-groups were anadromous and Cambridge Bay fish associated with lacustrine fish at a Euclidean distance of 4.0.

The principal coordinates analysis resulted in a similar arrangement in which axis I (60% of total variation) separated chars from riverine habitats west of the Mackenzie R. from the lacustrine fish and chars east of the Mackenzie R. (Figure 3). Axis II (30%) separated the sub-groups within these two groups similarly to that seen for the clustering. Axis III (6%, not illustrated) indicated that the isolated fish were somewhat distinct from all others, thus the implied relationships of these with the Klutina R. sample observed in the phenogram is likely artifactual. The multi-dimensional scaling analysis reinforced the results observed in the previously noted phenetic analyses and further suggested that the association between the isolated group and Klutina R. fish as seen in the phenogram was artifactual (Figure 3).

Genetic Results

In general, with the exception of the isolated fish, the lacustrine fish and both groups from east of the Mackenzie R. exhibited low variation for the enzymes examined relative to the remaining samples from west of the Mackenzie R. (Table 1). Superoxide dismutase-1 exhibited two alleles a and b with mobilities of 100 and 84 respectively (Allelic mobilities were established relative to the Klutina R. sample). Between groups the pattern of variation indicated that all lacustrine char, Cambridge Bay char, and with the exception of two heterozygous fish out of 342 anadromous fish, complete fixation occurred for the b allele which was commonest overall. The isolated riverine group from west of the Mackenzie R. was also fixed for b. The a allele was present at a moderate frequency (5%+) in the residual and anadromous fish from west of the Mackenzie R., but was very frequent in both the Nome and Klutina samples. Three alleles (a,b,c) with relative mobilities of -100, -117 and -92 respectively were observed for PGM-1. With the exception of one heterozygous fish out of 360, all char east of the Mackenzie R. as well as the lacustrine char from west of the Mackenzie R. were fixed for the c allele. All other fish exhibited high frequencies of the a allele. The third allele (b) was only observed in the Klutina R. sample. Three alleles (a,b,c) with relative mobilities of -100, -70, and -119 respectively were observed for PGM-2 with a being the most frequent in all groups. The rare c allele was observed only in anadromous fish from west of the Mackenzie R. and the Klutina R. fish.

The UPGMA phenogram of Nei genetic distances exhibited two major groups associated at a distance of 0.5: 1. anadromous fish east of the Mackenzie R., lacustrine fish from west of the Mackenzie R., and the Cambridge Bay sample; and, 2. all remaining groups (Figure 4A). Within group 2., two groups that were associated at a distance of 0.1 were apparent: a) Klutina-Nome fish, and b) Yukon north slope anadromous, residual and isolated groups. Principal coordinates analysis and multi-dimensional scaling duplicated the results observed in the phenogram (Figure 4B,C).

Summary

In summary, all analyses whether morphological or genetic as well as all types of analysis (discriminant, clustering, principal coordinate, multi-dimensional scaling) indicated the presence of two taxa in these fish. The groups composing these taxa were consistently the same with one taxon being the anadromous char from areas east of the Mackenzie R., Cambridge Bay fish, and the lacustrine samples from the Yukon north slope west of the Mackenzie R. The other taxon was composed of the riverine fish from west of the Mackenzie R. including the two samples from Alaska.

Discussion

Presence of Two Taxa

The presence of a discontinuity in meristic variation, that is, the bimodality of discriminant scores, indicates two taxa are present in northwestern arctic North America. The association of ecologically defined life history types with their taxon of presumptive origin indicates that the variation is primarily driven by taxonomic rather than ecological causes. Thus as originally formulated hypothesis 1 (all represent the same taxon) is rejected. Life history types of riverine char (anadromous, non-anadromous, residual) from the continental coast west of the Mackenzie River exhibited greater similarity to the reference Dolly Varden char sample as did the sample of char from the Nome River, than either did to the reference Arctic char sample. Thus, it can be concluded that these morphologically all are members of the Dolly Varden taxon. Anadromous char from east of the Mackenzie River as well as lacustrine char from isolated lakes west of the Mackenzie River exhibited greater similarity to the reference Arctic char sample than either did to the reference Dolly Varden char sample. Thus, it can be concluded that these morphologically all are members of the Arctic char taxon.

The support of this morphological hypothesis by genetic results, in particular the almost complete fixation of alternative alleles for two enzyme loci, further strengthens the existence of the two taxa indicated above. All analyses of these genetic data reiterated the presence of at least two taxa. However, some results suggested the presence of two lower level taxa within the Dolly Varden group. Resolution of this issue awaits future work.

This evidence supports the contention of Morrow (1980) that all riverine dwelling char west of the Mackenzie R. and throughout Alaska are forms of Dolly Varden. There is no evidence for the presence of a riverine dwelling, often anadromous, form of Arctic char (i.e. Bering Sea-western Arctic form of McPhail 1961) anywhere west of the Mackenzie R. Thus this taxon as originally formulated by McPhail (1961), reiterated by McCart (1980), and in prominent usage since 1980 should be equated with Dolly Varden. Future usage of this taxon as a form for Arctic char is not warranted. Alternatively, there is excellent evidence for the presence of a lacustrine form of char that is very similar morphologically and genetically to eastern form Arctic char (McPhail 1961; Morrow 1980; this study). These are distributed in several lakes across the continental north slope (McCart 1980) and throughout western and southern Alaska (Morrow 1980).

Identification of the Taxa

In view of this taxonomic distinction and in view of the continuing ambiguity with respect to exactly which taxon is being examined in a given study, interpretation of previous literature must proceed with caution. To avoid ambiguity in the future, information regarding the habitat occupied, the degree of isolation if any, total gill raker and pyloric caecae counts should be presented in all publications regarding char from the area. This will permit clear unambiguous identification of the taxa being examined. To aid this process the following protocol for field identification is given.

Field Identification of Individuals

To establish criteria for the rapid field identification of char from this area, a linear discriminant function was constructed between two groups - 1) all anadromous and residual north slope Dolly Varden char, and 2) all anadromous char east of the Mackenzie River. Two meristic variables, total gill raker (TGR) count and pyloric caecae (PYL) count, were used because of their discriminatory power and for rapid field convenience.

The function was highly significant (P <0.0000) and the standardized coefficients were 0.8111 and 0.6195 respectively for gill rakers and caecae. The a posteriori classification accuracy was very high although not perfect for Dolly Varden 99.4% (687 out of 691) were correctly classified and 96.8% (337 out of 348) Arctic char were correctly classified. Thus, in most cases, this discriminant function will result in accurate classification of unknown individuals from the area of the continental north slope and coastal regions to the east of the Mackenzie River.

To classify unknowns, the unstandardized coefficients must be used as follows: DA Score = 0.5297 (TGR) + 0.1167 (PYL) -16.3680. These scores are compared to the group centroids and ranges of scores to hypothesize the identity of the individual. For correctly classified Dolly Varden and Arctic char, these values respectively were: centroid, -1.534 and range, -3.97 to +0.66; and, 3.045 and +1.13 to +6.06. The uppermost score for Dolly Varden and the lowermost score for Arctic char represent individuals which were not misclassified to an inappropriate group. The scores of misclassified individuals ranged from 1.19 to 1.49 for Dolly Varden (4 individuals) and 0.14 to 0.85 for ten of 11 misclassified Arctic char. One of the misclassified Arctic char scored at -0.51 representing an extreme outlier. Thus, the region of 0.14 to 1.49 represents an ambiguous zone for purposes of classifying individuals and identifications of unknowns therein should be suspect. Discriminant scores less than 0.14 and especially negative values represent Dolly Varden char. Discriminant scores greater than 1.49 represent Arctic char.

Level of the Taxa

The discovery of two taxa does not automatically determine the taxonomic level to which those taxa should be assigned. Rather, as pointed out previously, determination of taxonomic level is a philosophical point of view imposed on the system by human interpretation. However, in applying the biological species concept, coexistence without widespread hybridization as seen for Dolly Varden char and Arctic char in southwest Alaska (McPhail 1961) provides strong evidence for the taxa described herein to be considered distinct at the species level. This interpretation is reinforced by the ecological and biological differences apparent: e.g., riverine versus lacustrine spawning for Dolly Varden and Arctic char respectively in this area; age of first seaward migration of 3-4 years for Dolly Varden (McCart 1980) and 4-7 for Arctic char (Johnson 1980); greatest ages attained of ~17 for north slope anadromous Dolly Varden (McCart 1980) compared to >24 for Nauyuk Lake Arctic char (Johnson 1980); and, development of a kype in Dolly Varden char but not Arctic char (personal observation).

Distribution and Sub-specific Diversity of the Taxa

From the evidence presented herein and insofar as coastal char populations are concerned, the Mackenzie River apparently forms a demarcation in the distribution of the taxa. In particular, Dolly Varden char apparently do not occur east of the Mackenzie River, and the only Arctic char populations that occur west of the Mackenzie River are relictual populations confined to lakes.

These distributions suggest that Arctic char was once more widely distributed in western North America. This species is cold adapted being found in northernmost freshwaters (Johnson 1980), and seems to require environments that include lacustrine habitats. Thus in areas that are cold, where lakes are present and in areas of a former more widespread distribution, Arctic char presently occur. Conversely, Dolly Varden char is a species adapted to warmer environments (e.g. distribution south to Washington State, Haas and McPhail 1991), present primarily in riverine environments, and exhibits limited use of lacustrine habitats. Range expansion of this taxon to areas east of the Mackenzie River appears to be limited by either ecological factors (e.g. unsuitable habitat in that cool non-turbid mountain rivers are not found) or by biological factors (e.g. environments are colder or co-existence with anadromous forms of Arctic char is unsuccessful).

Dolly Varden distribution in the study area is virtually synonymous with the habitat available during the Wisconsin glaciation (Lindsey and McPhail 1986). Presumably isolation in northern and southern Beringian refuges has contributed to sub-specific diversification into the northern and southern forms. The reconstruction of Beringian physiography during the Wisconsin glaciation includes major rivers draining now submerged lands under the Chukchi and Bering Seas (Lindsey and McPhail 1986). Areas on the north side and the western tip of the Seward Peninsula and those further north were drained by the Chukchee Sea River. Areas immediately south were drained by the Gulf of Anadyr River, and those further south by the Yukon and Kuskokwim Rivers. Thus, in contrast to Morrow (1980) the Seward Peninsula appears to be the area of demarcation between these two forms. The association of Nome River fish with north slope Dolly Varden in some analyses and with Klutina River fish in others indicates the possibility of greater diversity within this taxon. Perhaps three forms are present: southern - from the Yukon River southwards; Anadyrian - southern portion of the Seward Peninsula and areas on the south side of Norton Sound, as well as southern drainages of the Chukotka Peninsula in Siberia; and, a northern form distributed to the north of the Seward Peninsula and both the Siberian and North America continental north coasts. Further examination of sub-specific diversity within Dolly Varden is warranted.

The distribution of relictual populations of Arctic char throughout the study area is poorly known but apparently widespread. Presumably this indicates a previous, likely pre-Illinoian glaciation, more widespread distribution. The glacial extent was greater and thus a cooler climate prevailed during the Illinoian glaciation (Lindsey and McPhail 1986). Because Arctic char can survive at glacial fronts (Priede 1989), there would be ample opportunity for trans-basin movement during ice retreat either throughout interior Beringia or along coastal margins as well as for isolation in mountainous lakes as deglaciation occurred. Detailed examination of sub-specific diversity in Arctic char populations throughout the study area is warranted.

Thus similar to the conclusions of Morrow (1980) all present results indicate that riverine dwelling char from areas west of the Mackenzie River are representatives of Dolly Varden char (Salvelinus malma). Lacustrine fish from this area, with one exception, all represent relictual forms of Arctic char (Salvelinus alpinus (Morrow 1980). The existence of the Bering Sea-western Arctic taxon of Arctic char (McPhail 1961, McCart 1980) present in riverine habitats in this area is not supported by any results obtained herein.

Acknowledgements

We acknowledge the financial support for this study from implementation funds of the Inuvialuit Settlement Agreement administered by the DFO/Inuvialuit Fisheries Joint Management Committee and by regular DFO funding. Substantive logistical support was received from the Science Institute of the Northwest Territories - Inuvik Research Centre. The assistance of the following individuals is greatly appreciated: for providing samples from their own studies - R. Baker, W. Bond, A. Kristofferson, B. Stewart; for aid in collecting Canadian samples - D. Bodaly, R. Fudge, B. Macdonald; for aid in collecting Alaskan samples - K. Alt, F. DeCicco; and, for arranging for sample collections - V. Gillman. The efforts of M. Koshinsky and her crew in processing the fish are appreciated. D. Ostlere, T. Stevens, B. Tilwari all contributed to the electrophoretic work. Permission to collect in Northern Yukon National Park was given by Parks Canada. The efforts of G. Decterow in text-editing the many versions of the manuscript are greatly appreciated.

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Figure Captions

Fig. 1. Identification of reference samples to taxon by comparison of meristic variation with samples from the same area. Individual samples are centered on the bivariate mean values for total gill rakers (TGR) and pyloric caecae (PYL) and the range of each character is given by the respective line. Arctic char (ARCH) values are derived from McPhail (1961) for Sapuladjuk, Kathewachaga, Bloody Falls and Bernard Harbour localities. Dolly Varden (DVCH) values are derived from McPhail (1961) for Summit L. and Turnagain Arm and from Morrow (1980) for Tutka Bay, Bear Ck., and Ketchikan area.

Fig. 2. Discriminant scores of groups: A. reference samples (top) and all other, unknown char (bottom); B. groups of unknowns - Nome R. (top), anadromous fish from west of the Mackenzie R. (middle), and anadromous fish from east of the Mackenzie R. (bottom); and, C. life history types from the Yukon north slope residual-riverine (top), isolated riverine (middle), and lacustrine (bottom) forms.

Fig. 3. Phenetic results obtained for meristic data. A. UPGMA clustering, B. principal coordinates analysis, and C. multidimensional scaling analysis of Euclidean distances for standardized meristic mean values.

Fig. 4. Phenetic results obtained for genetic data. A. UPGMA clustering, B. principal coordinates analysis, and C. multidimensional scaling analysis of Nei's genetic distance.

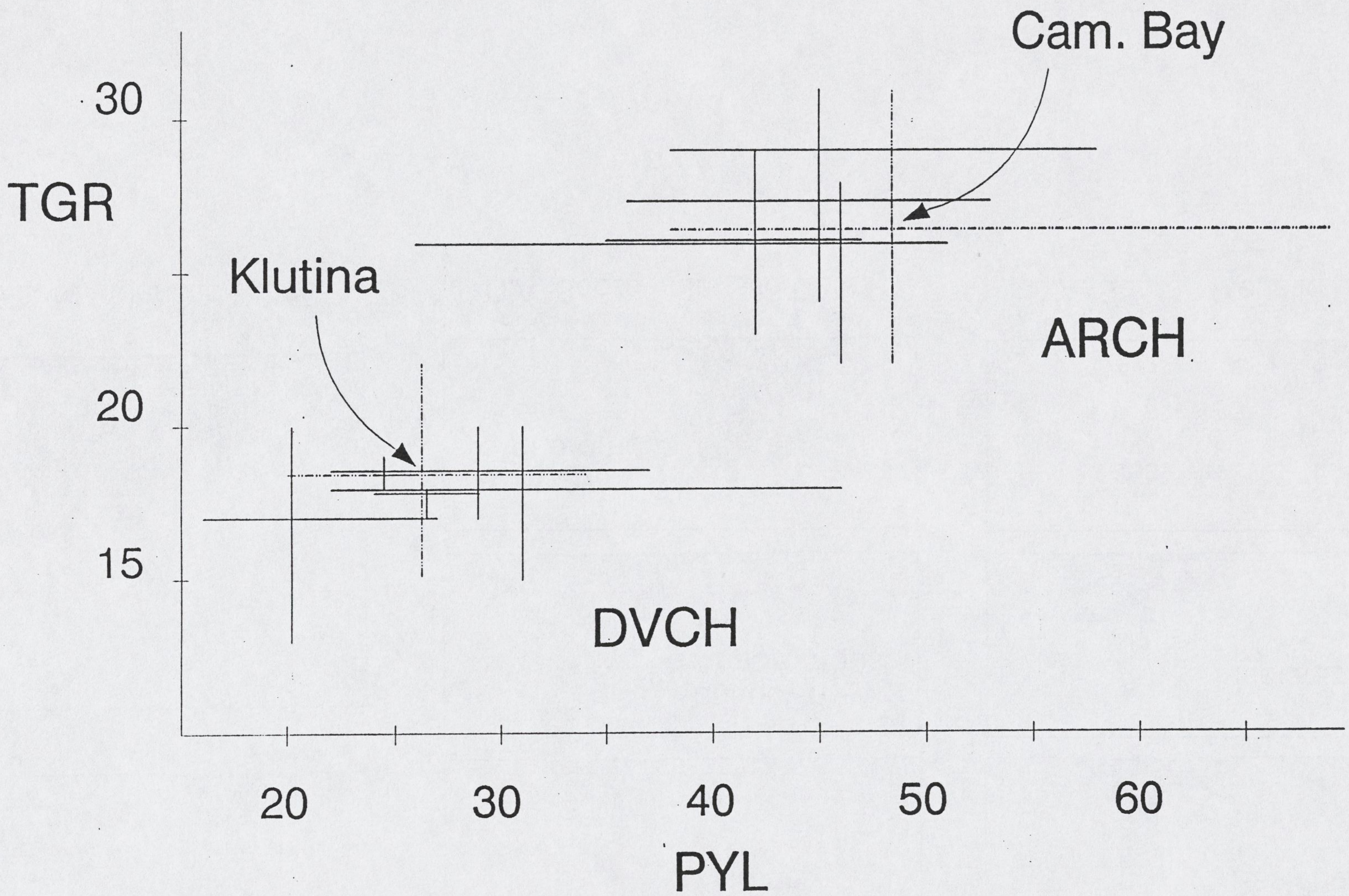
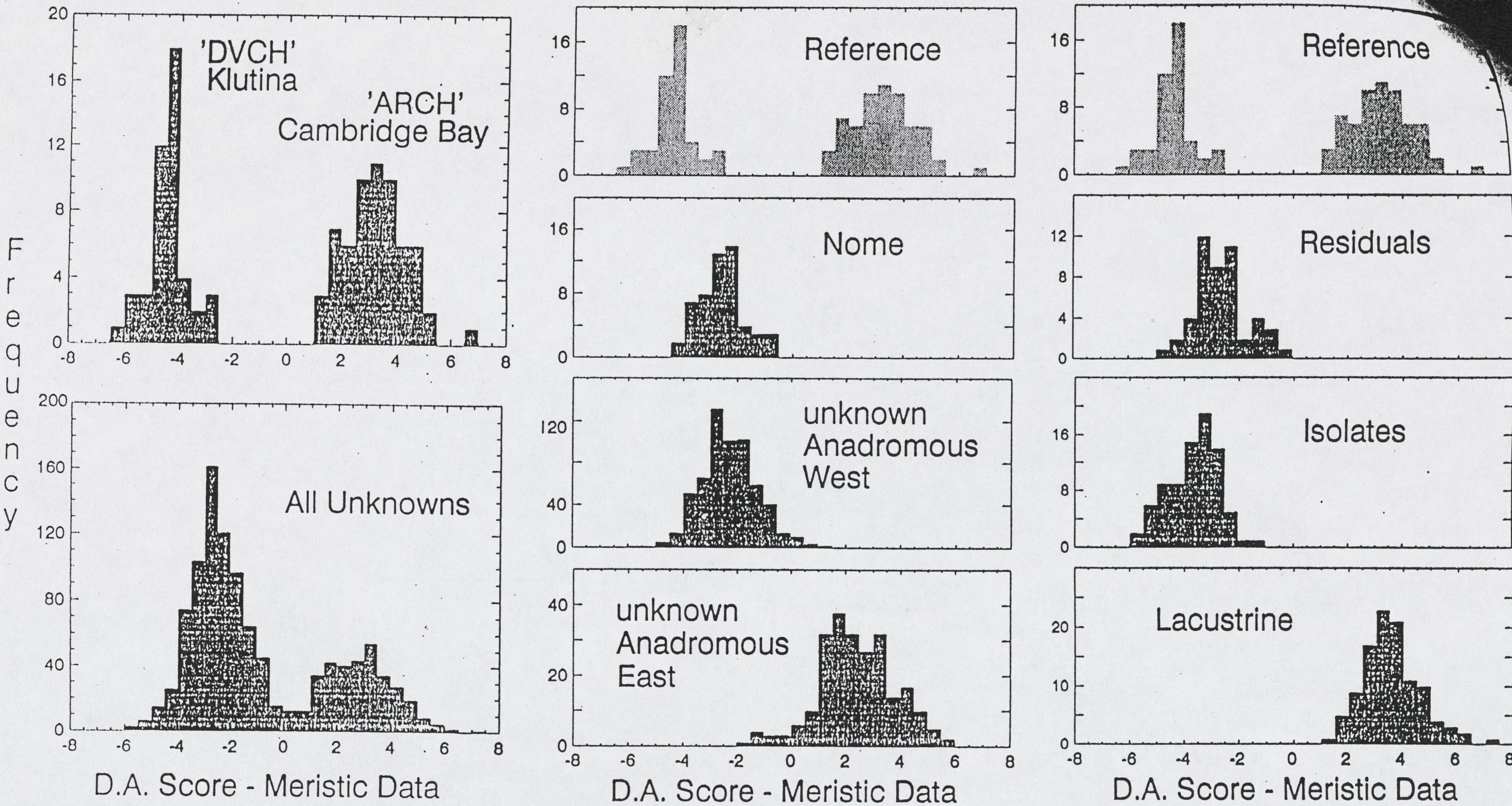


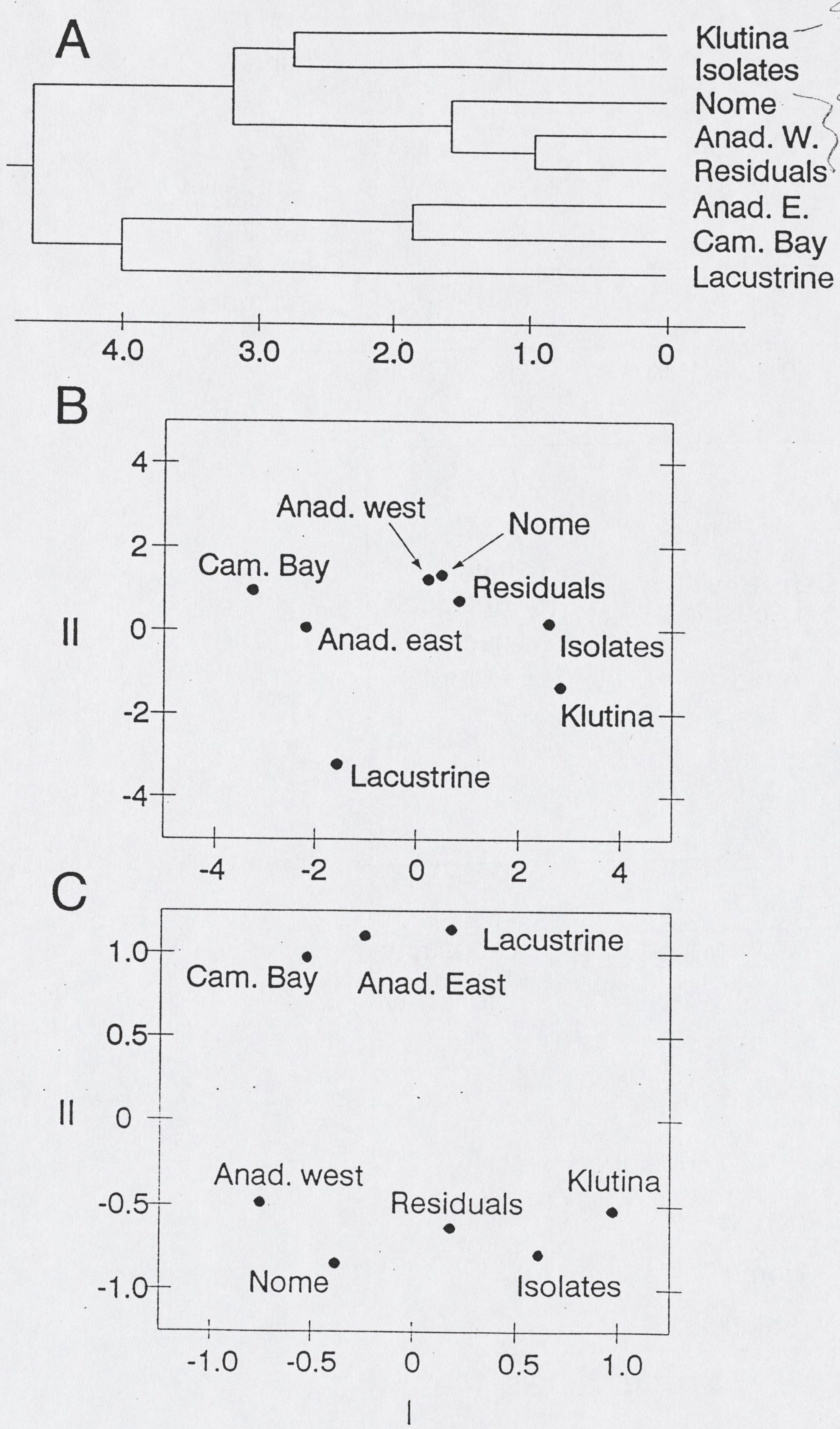
Fig 1

18


'DVCH'
Klutina
'ARCH'
Cambridge Bay
All Unknowns
Frequency
D.A. Score - Meristic Data
Reference
Nome
unknown
Anadromous
West
unknown
Anadromous
East
D.A. Score - Meristic Data
Reference
Residuals
Isolates
Lacustrine
D.A. Score - Meristic Data

19 Fig 2

20 Fig 3


A
Klutina
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Anad. E.
Cam. Bay
Lacustrine
4.0
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1.0
0
B
4
2
0
-2
-4
II
Anad. west
Nome
Cam. Bay
Residuals
Anad. east
Isolates
Klutina
Lacustrine
-4
-2
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2
4
C
1.0
0.5
0
-0.5
-1.0
II
Lacustrine
Cam. Bay
Anad. East
Anad. west
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Residuals
Nome
Isolates
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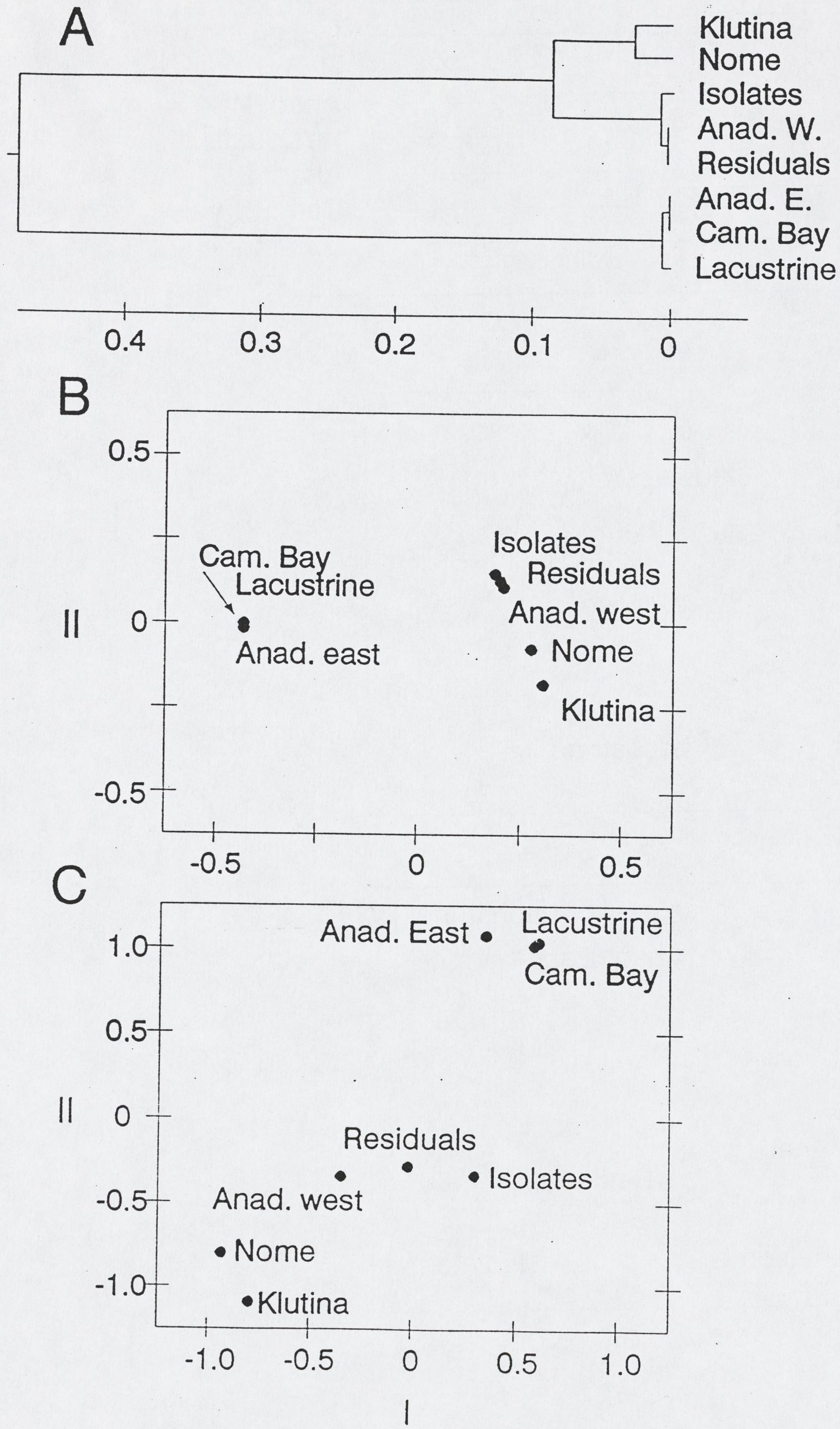
I

21 Fig 4



A
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Nome
Isolates
Anad. W.
Residuals
Anad. E.
Cam. Bay
Lacustrine
0.4
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B
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Cam. Bay
Lacustrine
Anad. east
Isolates
Residuals
Anad. west
Nome
Klutina
-0.5
0
0.5
C
1.0
0.5
0
-0.5
-1.0
II
Anad. East
Lacustrine
Cam. Bay
Residuals
Isolates
Anad. west
Nome
Klutina
-1.0
-0.5
0
0.5
1.0
I

Table 1. Meristic mean values for the groups and coefficients for discriminant analysis between Klutina and Cambridge Bay reference samples. See text for groups and variable acronyms. Std = standardized and Unstd = unstandardized coefficients. Group acronyms are: KL - Group A, Klutina R. char; NO - Group B, Nome R. char; AW - Group C, anadromous fish from rivers west of the Mackenzie R.; AE - Group G, anadromous fish from east of the Mackenzie R.; IW - Group E, isolated riverine char from west of the Mackenzie R.; RW - Group D, residual char from west of the Mackenzie R., and, CB - Cambridge Bay char.

Variable	Mean for Group								Coefficient	
	KL	NO	AW	AE	IW	RW	LW	CB	Std	Unstd
Meristic Data										
DRC	10.7	11.1	10.9	10.9	11.1	10.9	10.4	10.8	-0.005	-0.007
ARC	9.1	9.8	9.7	9.7	9.2	9.5	9.2	10.1	0.113	0.169
PRC	13.2	13.9	13.8	14.0	13.0	13.8	13.3	14.2	-0.097	-0.150
VRC	8.9	9.1	9.1	9.5	8.8	9.0	9.7	9.7	-0.068	-0.129
BRC	10.6	11.0	11.4	11.2	11.0	11.2	10.9	11.5	0.106	0.148
UGR	7.6	9.0	8.9	11.2	8.4	8.6	10.3	10.9	0.438	0.486
LGR	10.8	12.7	12.6	15.9	12.1	12.7	17.0	15.5	0.368	0.358
PYL	26.3	28.1	30.2	42.8	24.7	29.1	49.1	48.4	0.767	0.194
Constant	-	-	-	-	-	-	-	-	-	-16.925
Genetic Data										
SOD-1a	0.535	0.411	0.081	0.001	0	0.049	0	0		
b	0.465	0.589	0.919	0.999	1.0	0.951	1.0	1.0		
PGM-1a	0.812	0.961	0.999	0.002	1.0	1.0	0	0		
b	0.188	0	0	0	0	0	0	0		
c	0	0.039	0.001	0.998	0	0	1.0	1.0		
PGM-2a	0.925	1.0	0.999	0.998	1.0	1.0	1.0	1.0		
b	0.075	0	0.001	0	0	0	0	0		
c	0	0	0	0.002	0	0	0	0		

Appendix Table 1: Locations of samples used in this study and the group to which they were assigned (see text). The Number represents the number of fish used in the morphological portion of the study.

Group	Location	Latitude °N	Longitude °W	Date Mo. Yr	Life History Type[a]	Habitat[b]	Number	Presumptive taxon [c]	Location code
A	Klutina R, AK	61 45	145 45	9 91	?	S?	49	DVCH-S	91-12
B	Nome R, AK	64 40	165 20	9 91	A	S	54	DVCH-n	91-13
C	Joe Creek, YT	68 56	140 58	9 86	A	S	52	DVCH-n	91-13
D	"	68 56	140 58	9 86	R	S	26	DVCH-n	86-58
C	Firth R, YT	68 40	140 55	9 86	A	S	54	DVCH-n	86-59
C	"	68 40	140 55	9 88	A	S	17	DVCH-n	88-07
D	"	68 40	140 55	9 88	R	S	9	DVCH-n	88-07
F	Lake 103, YT	69 26	139 34	9 88	L	L	60	ARCH	88-06/1
F	Lake 104, YT	69 26	139 36	9 88	L	L	49	ARCH	88-06/2,3,4
C	Babbage R, YT	68 40	139 13	9 88	A?	S	4	DVCH-n	88-10/1
E	Babbage R, YT	68 34	139 19	9 86	I	S	26	DVCH-n	86-60
E	"	68 38	139 22	9 88	I	S	26	DVCH-n	88-10/3
C	Canoe R, YT	68 46	138 44	9 86	A	S	68	DVCH-n	86-61
C	"	68 46	138 45	9 88	A	S	56	DVCH-n	88-09
C	"	68 46	138 45	9 88	R	S	11	DVCH-n	88-09
C	Cache Creek, YT	68 17	136 21	9 86	A	S	62	DVCH-n	86-62
D	"	68 17	136 21	9 86	R	S	4	DVCH-n	88-62
C	Cache Creek, YT	68 17	136 21	9 88	A	S	66	DVCH-n	88-05/1,2,3
D	"	68 17	136 21	9 88	R	S	3	DVCH-n	88-05/1,2,3
E	Cache Creek, YT	68 16	136 23	9 88	I	S	31	DVCH-n	88-05/4
C	Ptarmigan Bay, YT	69 26	139 01	8 88	A	S	32	DVCH-n	88-57
C	"	69 28	139 01	8 89	A	S	23	DVCH-n	88-05
C	Thetis Bay, YT	69 33	139 02	8 89	A	S	13	DVCH-n	89-03
C	Pauline Cove, YT	69 35	138 52	8 89	A	S	59	DVCH-n	89-04
C	Shingle Point, NWT	68 59	137 31	8 89	A	S	16	DVCH-n	89-20
C	Rat River, NWT	67 47	136 19	9 86	A	S	58	DVCH-n	86-63
C	"	67 47	136 19	9 88	A	S	51	DVCH-n	88-11
G	Wood Bay, NWT	69 48	129 42	8 89	A	?	8	ARCH	89-08
G	Horton R., NWT	69 56	126 48	9 88	A	?	12	ARCH	88-31
G	Hornaday R, NWT	69 24	123 35	8 86	A	?	50	ARCH	86-64
G	Unnamed L, NWT	73 05	118 15	8 87	A?	L?	52	ARCH	87-83
G	Kuuk R, NWT	70 34	112 38	9 87	A	L?	31	ARCH	87-82
G	Kagluk R, NWT	70 13	112 58	9 88	A	L?	30	ARCH	88-36
G	Kagloryuak R, NWT	70 18	111 24	8 89	A	L?	28	ARCH	89-18
G	Naloagyak R, NWT	70 13	112 13	8 89	A	L?	31	ARCH	89-19
G	Kuujjua R, NWT	71 15	116 30	10 91	A	L?	35	ARCH	91-25
H	Ferguson L, NWT	69 22	105 03	12 87	A	L?	51	ARCH	87-85
H	30 Mile Ck, NWT	69 16	108 00	12 87	A	L	13	ARCH	87-86
H	Byron Bay, NWT	69 04	109 14	12 87	A	L	4	ARCH	87-87
H	Surrey, L, NWT	69 40	106 40	12 87	A	L	5	ARCH	87-88

[a] Life history types are: A-anadromous; R-residual member of anadromous populations; I-isolated river resident (non-anadromous), L-isolated lake resident (non-anadromous).
[b] Habitats where spawning/residence occurs are: S-streams and rivers, L-lakes.
[c] Presumptive taxon as established herein: DVCH-s - southern form of Dolly Varden char, DVCH-n - northern form of Dolly Varden char, ARCH-arctic char.

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