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Electrophoretic, Morphometric, and Meristic Comparisons of Walleye Broodstock in South Dakota

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ELECTROPHORETIC, MORPHOMETRIC, AND MERISTIC COMPARISONS OF WALLEYE BROODSTOCK IN SOUTH DAKOTA

By

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This thesis is approved as a creditable and independent investigation by a candidate for the degree Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Introduction

In South Dakota, the exclusive use of Missouri River walleyes (Stizostedion vitreum) as broodstock for statewide stocking programs has raised questions about whether there are genotypic, as well as phenotypic, differences between the Missouri River stock and the native glacial lake stock. In the past, survival of Missouri River fry and fingerlings has been poor when stocked into some of the state's northeastern glacial lakes. Others have experienced similar results; Laarman (1978) found, after reviewing over 100 case histories of walleye stockings, that only about 5% of supplemental and 32% of maintenance stockings were considered successful. The ability of the stocked fish to survive and reproduce may be determined by the amount of genetic variability within the stocked fish (Krueger et al. 1981). Stocking failures are more likely to occur when the donor population is not correctly matched to the new environment (Everhart et al. 1975). Matching salmonid broodstocks to the receiving environment has been suggested because salmonid strains are highly variable in physiological and morphological traits and performance characteristics (Kincaid and Berry 1986). I hypothesized that a genetic "mismatch" could be one factor explaining the poor survival of supplemental walleye stockings in the north-

eastern lakes of South Dakota, because the glacial lake and Lake Oahe environments differ greatly in the quality and quantity of habitat, prey species, and water chemistry characteristics.

My study utilized electrophoretic and morphometric analyses to compare South Dakota walleyes originating from the Minnesota River drainage with walleyes from the Missouri River drainage. Walleyes from Blue Dog Lake and three westside tributaries of Lake Oahe on the mainstem Missouri River were sampled to provide baseline data on the genetics of glacial lake and Missouri River stocks. When combined with data on the comparative growth and survival of progeny of Blue Dog Lake and Missouri River broodstocks (Wolters 1988), stock identification will be useful in making future decisions regarding the management and stocking programs for walleye in South Dakota.

Goals and Objectives

The primary goal of this study was to determine genetic and phenotypic variability among walleye stocks in South Dakota. This following objectives address this goal:

1. By using methods of electrophoresis, meristic counts, and morphological measurements, determine the amount of genotypic and phenotypic variability between native stocks of walleyes in northeastern glacial lakes and Lake Oahe.
2. By using methods of electrophoresis, meristic counts, and morphological measurements, determine the amount of genotypic and phenotypic variability of walleyes spawning in the Grand, Moreau, and Cheyenne River tributaries of Lake Oahe.
3. Compare the genetic variability of the South Dakota walleye stocks to those of the upper Mississippi River, pools 5 and 8.

Stock Identification of Fishes

In recent years, the identification of fish stocks has become an important part of freshwater and marine fisheries management. Stock identification has been used to distinguish wild stocks from hatchery-reared fish, thus allowing further studies of their performance (Reisenbichler and McIntyre 1977; Allendorf and Phelps 1980; Hjort and Schreck 1982). Stock identification has also been used to distinguish hybrids (Clayton and Gee 1969; Clayton et al. 1973; Strauss 1986; Todd 1986), to determine the success of supplemental stockings (Schweigert et al. 1977; Murphy et al. 1983; Seeb et al. 1986), to genetically compare different strains (Busack et al. 1979; Milner et al. 1979), and to ascertain the stock structure of existing populations (Beacham et al. 1985a; Beacham et al. 1985b).

A stock may or may not be genetically discrete from other groups of the same species. In the most liberal sense, a stock is defined as a group of randomly mating individuals of the same species, with temporal or spatial integrity (Ihssen et al. 1981; Krueger 1986). Some stocks, although not genetically distinct, may be of special management interest because of particular population parameters and/or physiological and behavioral characteristics (Ihssen et al. 1981; Krueger 1986). In most circumstances, however,

a stock is assumed to be genetically distinct. Therefore, its genetic integrity persists whether the fish remain spatially and temporally isolated as a group, or whether they segregate only for breeding and otherwise intermix with members of other stocks of the same species (Kutkuhn 1981). Genetic stock identification has been used by those interested in salmonids (Allendorf et al. 1977; Moller 1970; Allendorf and Utter 1979), northern anchovy (Engraulis mordax, Vrooman et al. 1981), walleye, (Clayton et al. 1971; Murphy 1981), sunfishes (Avise and Smith 1974), Atlantic cod (Gadus morhua, Mork et al. 1985), and a variety of other freshwater and marine species.

Philipp et al. (1986) surveyed state fish and wildlife agencies to determine the level of interest in genetic conservation of their fishery resources, the policies in effect, and the presence and adequacy of state genetic research facilities. From the responding 42 states, they found that 17 were genetically assessing their fish stocks. Assessment activities included evaluation and comparison of hatchery strains and identification and preservation of native stocks. Twenty-one states were involved with some level of genetic manipulation, either the production of hybrids and crosses between genetic stocks, or in the culture of specific stocks with desirable performance characteristics.

Genetic variability is thought to be the adaptive mechanism to constantly changing or fluctuating environmental conditions (Leary et al. 1985; Philipp et al. 1986). However, management techniques which subsequently reduce or eliminate heterozygosity have constantly been used. Examples are: introducing genetically-manipulated fertile species, introducing hybrids, and stocking non-native fish. Each practice could potentially result in back-crossing and loss of evolutionarily-evolved characteristics that made the parent species unique (Philipp et al. 1986; Wattendorf and Holcomb 1986).

Protein electrophoresis and mitochondrial DNA analyses are perhaps the most definitive methods of stock identification. Stock identification on the basis of morphology or meristic counts alone has been less conclusive, because the expression of the characters is dependent upon both genetic and environmental factors (Moller 1970) and has not been directly related to particular genome differences (Clayton 1981). Electrophoretic, morphometric, and meristic analyses, used in conjunction, are being utilized by research agencies in order to determine whether specific morphological characters are useful in field situations to distinguish genetically discrete stocks.

Electrophoresis Method

Electrophoresis is a method whereby enzymes or proteins located in tissue homogenates are subjected to an electric current, causing them to migrate through a conductive medium at a rate determined by their charge and subunit structure. In a protein, each amino acid chain is the product of a single gene (Murphy 1981). Therefore, by using specific enzyme staining, protein variants (alleles) at particular loci can be observed, and the frequencies with which they occur can be used to characterize a population or quantify the genetic differences between populations or species. Primary applications of information generated by the electrophoretic identification of fish stocks include 1) identification of stock structure, 2) identification of electrophoretically-distinguishable stocks for harvest management in mixed fisheries, and 3) genetic marking for the purpose of stock identification (Seeb et al. 1981).

Several studies have used electrophoresis to evaluate gene flow and stock structure. Campton and Utter (1987) found evidence of restricted gene flow among populations of coastal cutthroat trout (Salmo clarki) inhabiting two areas of Puget Sound. Yoshiyama and Sassaman (1987) found sufficient gene flow between three species of intertidal cottids. Mork et al. (1985) concluded that sufficient gene flow had prevented substantial genetic divergence of

Atlantic cod over its geographic range.

Electrophoresis has been used to identify heterozygosity among fish stocks, thus allowing further study of unique performance traits. Allendorf and Phelps (1980) found a loss of genetic variability in a hatchery stock of cutthrout trout. Leary et al. (1985) later used these results to assess the morphological deformities or reduced developmental stability of this stock, caused by the reduced genetic variation. Berry and Hudy (1983) used information gained from electrophoresis to compare survival to the creel of three groups of fingerling rainbow trout (Salmo gairdneri), each with a unique phenotype of lactate dehydrogenase (LDH).

Zimmerman and Richmond (1981) found an increase in polymorphism at a locus of malate dehydrogenase (MDH-B) in red shiner (Notropis lutrensis) that occupied areas of the Brazos River which were affected by the cold-water discharge from a hydroelectric dam. This, they concluded, was a result of an adaptive strategy in a multilocus system, of which heterozygotes had a higher fitness in the fluctuating thermal environment. Hallerman et al. (1986) employed electrophoresis to determine the genetic identity of a population of largemouth bass (Micropterus salmoides), with unusually small adults that had high condition factors.

Genetic marking also has been used with success. Murphy et al. (1983) introduced a stock with significantly different malate dehydrogenase (MDH) allele frequencies to determine stocking success of walleye in Claytor Lake, Virginia, and Schweigert et al. (1977) used walleye with unique MDH phenotypes to determine the effects of fry and fingerling introductions in West Blue Lake, Manitoba. Seeb et al. (1986) selected spawning male chum salmon (Oncorhynchus keta) with a unique allele of aspartate aminotransferase to fertilize the eggs of females. These hatchings produced smolts which were genetically marked for this allele. The contribution of the marked fish to subsequent spawning runs could then be determined.

Meristic and Morphological Methods

Meristic characters are countable repetitions of some morphological features, such as scale patterns or fin rays. These traits are usually unaffected by age or nutritional state of the individual fish and are visible on preserved specimens as well as on fresh ones. However, meristic counts may be affected during development by environmental factors such as temperature, light, and dissolved substances (Fowler 1970). Phenotypic expression of meristic traits thus indicates a complex involvement of epigenetic, physiological, and environmental factors (Ihssen et al. 1981).

Morphometrics represent dimensional measurements of the body and its associated structures, such as fin ray lengths or various head lengths. The data generated are continuous, thus the predictive ability of morphometrics is likely to be greater than that generated by meristic counts and their non-continuous data. The series of measurements can easily be made by use of calipers and represent the synergism between size and shape (Ihssen et al. 1981).

Several studies have shown the efficacy of using morphometrics and meristics in discriminating populations or stocks of fish. Beck and Biggers (1983) used discriminant function analysis to determine the ploidy of grass carp (Ctenopharyngodon idella) x bighead carp (Hypophthalmichthys nobilis) hybrids. Of the 26 characters measured and counted, they found that although no single character allowed diploids to be distinguished from triploids, 12 of the characters could be used in combination to correctly classify 97% of the hybrids as diploids or triploids. Taylor and McPhail (1985) found that discriminant function analysis of morphological characters of several populations of juvenile coho salmon (Oncorhynchus kisutch) allowed the identification of the home stream with 71% accuracy. Juveniles identified as either belonging to coastal or interior streams could be identified with 93% accuracy.

Similarly, Taylor (1986) used discriminant function analysis to identify juvenile coho salmon as either originating from hatchery or wild populations with over 90% accuracy. He found that hatchery juveniles were less variable morphologically than the wild populations, which he attributed to environmental differences and greater homogeneity of the hatchery environments compared to natural rivers and streams.

Morphometrics have been used in combination with biochemical analyses to yield greater discriminatory information. Kelsch and Hendricks (1986) used electrophoretic and morphometric comparisons to separate headwater catfish (Ictalurus lupus) from channel catfish (I. punctatus). They found biochemical evidence and morphological discreteness which supported the independent-species status of the headwater catfish. Haug and Fevolden (1986) found that both genetic and morphological data for Atlantic halibut (Hippoglossus hippoglossus) were in agreement on the homogeneity of the stocks.

Genetic Investigations of Walleye

Although there is a vast amount of literature pertaining to the genetics of salmonids, little work on walleye genetics has been published. This is somewhat surprising because transfer of walleye from one geographic region to another are common (Murphy and Lee 1986). Colby and Nepszy (1981) noted out that although evidence for discrete walleye stocks does exist, stock differentiation is usually based on differences in population parameters (age, growth, fecundity, maturity) -phenotypic expressions that are largely environmentally induced.

Vely (1970) employed electrophoresis of plasma proteins in an effort to determine whether walleyes from eastern Lake Erie moved throughout the lake or were a localized subpopulation, which would require different management strategies. He found that although differences in minor protein bands could be detected in walleyes inhabiting separate bodies of water, no significant differences could be found among those inhabiting the same or closely connecting bodies of water. This finding was confirmed by Ulrikson and Laarman (1971).

Uthe and Ryder (1970), in an electrophoretic survey of walleyes from several lakes in central Canada, found only the three previously reported phenotypes of muscle myogen,

AA, AB, and BB. They found that phenotype frequencies varied from lake to lake, but always agreed with Hardy-Weinberg expected values, indicating genetic control of this polymorphic enzyme by two non-dominant alleles. However, when body measurements and counts of interneural and interhemal spines and of vertebrae were used to try to distinguish between the three phenotypes, they found no significant differences between the electropherogram types, and thus concluded that there was no relationship between the morphological traits and protein phenotypes.

Clayton et al. (1971) found that six phenotypes of malate dehydrogenase (MDH) isozymes could be isolated from extracts of the white skeletal muscle of walleye. Clayton et al. (1973) used the mitochondrial and supernatant forms of MDH to distinguish walleyes from sauger (S. canadense) and their hybrids. Clayton et al. (1974) also used the varying supernatant MDH alleles to discriminate populations of walleye within and near Prince Albert National Park in western Canada, in order to determine whether or not the frequency and geographical distribution of the c^1 allele would allow for the evaluation of fry stocking success in waters depleted of their natural population. Eight spawning populations were distinguished within the 241-km radius of their study.

Murphy and Lee (1986) sampled walleyes from the Mississippi River, the Hudson Bay, and the Lake Superior watersheds in Minnesota. They found all samples to be notably different, but the fish from the Mississippi River watershed closely resembled the Lake Superior watershed fish, which followed the geologic history of the area. Seeb et al. (1981) found much variation in Lake Erie walleyes and determined that the variability could be useful for the identification of stocks in the Great Lakes.

Walleyes may form discrete stocks in a large body of water by homing to specific spawning areas (Regier et al. 1969; Ferguson and Derksen 1971; Ney 1978). Homing behavior is defined as the tendency for spawning walleye to return to the same spawning sites each year in preference to other sites, although during the remainder of the year individual members of different stocks may intermix (Olson and Scidmore 1962; Crowe 1962; Forney 1963). In very large waters, walleyes may largely remain spatially isolated (Regier et al. 1969) with movements confined to restricted "home areas" throughout most of the year, and migrations made just prior to and after spawning seasons (Forney 1963; Ferguson and Derksen 1971; Olson et al. 1978). Olson et al. (1978) proposed that walleye homing is an adult-learned behavior, as natal imprinting is highly unlikely, given walleye reproductive characteristics and early life history. Thus,

they suggested, the destination of the initial spawning migration may be determined by the chance encounter with walleyes having already established spawning migrations. This initial spawning migration is then reinforced by repeated migrations, so that populations with a large proportion of older fish may display stronger homing tendencies than those of younger fish (Olson et al. 1978).

Todd and Haas (1988) tagged walleyes to determine homing and used protein electrophoresis to determine heterogeneity among spawning sites. They found that walleyes from four spawning sites in Lake Erie and four spawning sites in Lake St. Clair exhibited homing behavior, but within Lake Erie, significant heterogeneity was not present among populations. However, when comparing Lake Erie walleyes to those of Lake St. Clair, they found significant heterogeneity, and concluded that the two walleye populations represented distinct gene pools. Terre (1985) found that during the non-reproductive periods, walleyes appeared to randomly mix in a Texas reservoir. However, during the spawning periods, he detected weak genetic differentiation, which he concluded may have been due to either homing behavior, or to changes in the spawning habitat caused by the fluctuating water levels. Murphy (1981), in determining heterogeneity within Claytor Lake, Virginia, found that at least two distinct stocks of

walleyes were present in the lake. However, given the complexity of the stocking history of the lake, the cause of this discreteness could not be determined.

Glacial and Ichthyofaunal History of South Dakota

The Coteau des Prairies

The state of South Dakota can be subdivided into several distinct topographical regions, the Black Hills, the Great Plains, and the Prairie Plains (Visher 1918). The Prairie Plains, east of the Missouri River may be further subdivided into three parts: the southeastern river valleys, the Dakota Valley, and the coteaus. The southeastern river valleys include the lower portions of the Sioux, Vermillion, and Missouri Rivers. This area is comprised of broad flood plains which lie 50 to 100 ft below the rolling uplands on either side (Visher 1918).

The Dakota Valley is a broad, nearly-level region extending from the Wessington Hills and Coteau du Missouri on the west, to the Coteau des Prairies on the east. The nearly-level area of central Dakota Valley is due, in part, to glacial Lake Dakota, which occupied this region. Lake Dakota was formed by unequal deposition of glacial drift, as were the majority of South Dakota's lakes. It extended from Mitchell northward 150 miles, and had an average width of 30 miles (Visher 1918). In the early stages of the late Wisconsinan glaciation, the Sheyenne River in North Dakota carried meltwater from glacial lobes in the northern and eastern part of that state southerly into Lake Dakota, which

then drained into the Missouri River (Brophy and Bluemle 1983).

The coteau regions include most of eastern South Dakota. The western coteau extends from the Missouri River to the Dakota Valley. The eastern coteau, Coteau des Prairies, is more popularly known as 'the lake region of South Dakota'. The Coteau des Prairies (Hill of the Prairie) was given its name by early French explorers (Leap 1974). It is a broad, flat divide between the Dakota Valley, to the west, and the Red, Little Minnesota, and lower Sioux valleys to the east (Visher 1918; Leap 1974). The coteaus may be considered, topographically, as broad mesas, rising 500 to 700 ft above the Dakota Valley. Both of the coteaus were mostly glacier-covered, at least for a short time. The coteau regions are largely undrained, and contain numerous lakes (Visher 1918). In fact, the majority of the natural lakes in South Dakota are glacial lakes located in these coteau regions. Their formation was due to an irregularity in the bedrock surface which impeded the flow of several glacial advances and caused a pile-up of glacial material which deposited irregularly, forming many lake basins (State Lakes Preservation Committee 1977).

During the late Wisconsinan ice sheet, approximately 25,000 years ago, glacial ice advanced southwesterly into the Hudson Bay Lowland of Manitoba and Ontario, damming the

northward-draining rivers of the United States and central Canada. Sometime around 12,300 years ago, this impoundment produced glacial Lake Agassiz, a proglacial lake along the front of the ice sheet that covered, with its drainage basin, nearly two million km^2 from northeastern South Dakota to Hudson Bay (Teller and Clayton 1983). As the ice sheet advanced southward, Lake Agassiz was displaced and the impounded water expanded southward. River Warren was one of the main outlets for the glacial meltwater in the first few thousand years of the lake's existence (Matsch 1983; Teller and Clayton 1983). River Warren flowed southerly, through the valley now occupied by Lake Traverse, Bigstone Lake, and the Minnesota River, before discharging into the upper Mississippi River (Bailey and Allum 1962; Matsch 1983). By 9,500 to 9,200 years B.P., as the glacier wasted, outlets in the lowlands to the east opened, and Lake Agassiz poured into the Lake Superior basin (Brophy and Bluemle 1983).

The ichthyofauna of South Dakota is thus of recent origin. Ice-free refugia and proglacial waters allowed for active immigration into new habitats (Bailey and Smith 1981). Fish utilized River Warren for northward dispersal from the Upper Mississippi River basin to the Arctic drainages (Greene 1935). Southward draining streams across western Manitoba and southern Saskatchewan also provided waterways through which ichthyofauna of the Missouri River

drainages dispersed (Stewart and Lindsey 1983).

In South Dakota, hydrographically, the Missouri River basin covers 97% of the area of the state. Two percent comprises the Minnesota River drainage, and the remaining one percent is Red River drainage. Of the ichthyofauna in the Missouri River basin, 76 are native forms which entered the basin post-glacially from the Missouri River and those which entered via hydrographic exchange with the Upper Mississippi River basin. The Upper Mississippi and the middle Missouri Rivers are suspected to have been at least temporarily joined. The tributary streams of the Big Sioux and the Little Sioux rivers of the Missouri basin in southeastern South Dakota may have been, at several points, hydrographically connected to the Minnesota and the Des Moines rivers of the Upper Mississippi basin (Bailey and Allum 1962).

The native fishes of the Minnesota River drainage in the eastern part of the state probably entered that area by dispersal northward and westward in the upper Mississippi River drainages. Fishes native to the Red River basin probably entered by postglacial dispersal northward and westward in River Warren from the upper Mississippi River drainage (Bailey and Allum 1962).

Regarding the presence of walleye in South Dakota, Bailey and Allum (1962) concluded that they entered by

postglacial dispersal from both the Upper Mississippi and the Missouri Rivers. During their survey of fishes of the Missouri River basin, Evermann and Cox (1896) collected specimens of walleye in Crow Creek, which empties into the Missouri south of Chamberlain; Rock Creek, which empties into the Dakota (now known as the James) River near Mitchell; and in Choteau Creek, which empties into the Missouri west of Springfield. Churchill and Over (1938) also found walleye in several of the lakes in eastern South Dakota.

Lake Oahe

Oahe Reservoir is the third and largest impoundment on the mainstem Missouri River in South Dakota (Fogle 1961). It was formed by closure of Oahe Dam on July 31, 1958 (Fogle 1961; Gabel 1974; Selgeby and Jones 1974; June 1976; Riis 1985). Oahe Dam is the largest rolled earth dam in the world, and was constructed by the U.S. Army Corps of Engineers for multiple use (Fogle 1961). Nearly 10 years after closure of the dam in the fall of 1967, the reservoir reached operational pool level and now backs water 402 km to Bismark, North Dakota (Riis 1985). The shoreline of Lake Oahe is rugged and irregular, with large finger-like bays formed by the draining of four large westside tributaries, the Cheyenne, Moreau, and Grand Rivers in South Dakota, and

the Cannonball River in North Dakota (June 1976).

During filling, the fishery was dominated by rough fish and other fish species requiring or using areas with flooded littoral vegetation for spawning and nurseries, such as common carp (Cyprinus carpio), black bullhead (Ictalurus melas), white crappie (Pomoxis annularis), black crappie (P. nigromaculatus), northern pike (Esox lucius), yellow perch (Perca flavescens), and various minnows. During the post-filling stages, most of these species decreased in abundance and other species, with less restrictive reproductive and nursery requirements persisted or increased in abundance, including goldeye (Hiodon alosoides), sauger, walleye, white bass (Morone chrysops), and freshwater drum (Aplodinotus grunniens) (June 1976).

In the second year of impoundment in 1959, Fogle (1961) found that rough fish were the predominant catch; only four walleyes were taken during the entire netting period, June - September, in the lower portion of the reservoir. By the fifth year of impoundment (Fogle 1963), catch of walleyes slightly increased while the rough fish had declined to make up a smaller percentage of the catch than in previous years. Gabel (1974) postulated that the low numbers of walleyes in the early years of impoundment occurred because the bottom material of Lake Oahe was primarily clay and silt. This lack of suitable spawning habitat was probably the factor

limiting their abundance. As the reservoir enlarged, suitable walleye spawning habitat increased, as extensive shoreline erosion exposed areas of sand, gravel, and rubble.

Fishery investigations continued with the filling of the reservoir, and strong year classes of walleyes were produced in 1964, 1965 (Gabel 1974), and in the early 1970's (June 1976). Riis (1985), in reporting results from an angler use and harvest survey conducted on Lake Oahe during the years 1981-1983, stated that walleye comprised a major component of the catch (69%; 95,797 walleye harvested in 1983 alone), and were the most sought after sport fish in South Dakota.

Stocking Reports

Walleyes are an abundant and important part of the South Dakota sport fishery, with 80-120 million eggs taken from spawning stations and 30-60 million stocked as fry and fingerlings yearly (Bob Wagers, Blue Dog State Hatchery Manager, Waubay, South Dakota, personal communication 1987). Early spawning operations began in the northeastern part of the state. The first state-run, warm-water hatchery was located near Pickerel Lake and began its operations in 1929. The facilities were solely for the purpose of hatching eggs from warm-water fish, walleye, and northern pike. Eggs hatched at the Pickerel Lake Hatchery originated from

walleye stocks in many of the northeastern lakes, the majority coming from Bigstone, South Buffalo, and Roy Lakes. A smaller percentage of the eggs may also have been taken from walleyes spawning in Blue Dog, Enemy Swim, and Pickerel Lakes. Progeny from the glacial lakes fish were then stocked back into northeastern lakes. In 1982, because of decreasing success in obtaining an adequate egg supply from the northeastern lakes, the state began supplementing its egg supply with eggs spawned from Lake Oahe walleyes. A new state hatchery, Blue Dog State Fish Hatchery, was constructed near Waubay to meet the increasing demands for walleye eggs in the state. It became operational in 1983, and with its larger capacity, larger and more reliable egg sources were explored. Spawning operations were discontinued in the northeast, and focused on the stations set up on the Grand and Cheyenne Rivers (Doug Hansen, Department of Game, Fish and Parks, Webster, South Dakota, personal communication 1988).

In the 1960's and 1970's, walleye eggs and fry entering South Dakota waters in the southern two-thirds of the state were obtained primarily from out-of-state sources, especially Nebraska, Kansas, and New Mexico. A small number of eggs was occasionally added to the pool from the lower Missouri River near Yankton, hatched at the Gavins Point National Fish Hatchery in Yankton, and later transported as

fry and fingerlings to the surrounding state waters as well as to out-of-state agencies (Roger Copper, Gavins Point National Fish Hatchery, Yankton, South Dakota, personal communication 1987).

Spawning Activity

In light of the information that walleyes have an adult-learned homing behavior, Riis (1985) conducted a tagging study on Lake Oahe walleyes during the years 1981-1984. Walleyes were tagged with plastic disc tags in 1982 and 1983 during spring spawning runs up the Cheyenne, Moreau, and Grand Rivers. In 1983, 90% of the walleyes recaptured were recaptured at their tagging sites. In 1984, 85.4% of the 1982 tagged walleyes and 91.3% of the 1983 tagged walleyes were recaptured at their tagging sites. Riis concluded that a homing behavior in walleyes does indeed trigger a return to the same spawning site in Lake Oahe, and, based on angler tag returns, found that the tagged walleyes intermingle in the open reservoir during the remainder of the year, thus indicating there may be discrete sub-populations identifiable with particular spawning area (Riis 1985).

Today the state has expanded spawning operations and has set up permanent spawning stations on two of the three major westside tributaries of the Missouri River, the

Cheyenne River near Pierre, and the Grand River north of Mobridge. Walleyes are also spawned on the third tributary, the Moreau River south of Mobridge, with a "spawntoon" boat. Because of the availability of eggs and the ease of operations from Lake Oahe spawning stations, all attempts to spawn walleyes from the northeastern lakes have ceased, and only Missouri River-spawned walleye eggs are hatched at Blue Dog State Fish Hatchery. Subsequently, fry and fingerlings from Missouri River-spawning fish are now stocked into South Dakota waters all across the state.

Stock Identification of South Dakota Walleyes

Materials and Methods

A total of 82 walleyes (24 from the Grand River, 30 from the Cheyenne River, and 28 from the Moreau River) were taken from stations on Lake Oahe during spawning operations in April, 1987 (Figure 1). The fish were captured in trap nets set by the South Dakota Department of Game, Fish and Parks biologists and put into raceways until morphological measurements and meristic counts could be made. Samples of eye, liver, white skeletal muscle, and heart were removed from each fish, placed on ice immediately, and frozen overnight prior to transport back to the laboratory. Six walleyes (3 males and 3 females) were collected by trap nets in early April, 1987, in Blue Dog Lake, a shallow, glacial lake located on the Prairie des Coteau in northeastern South Dakota (Figure 1). The fish were measured immediately, and the tissue samples were placed on ice and later frozen at the laboratory. Fourteen fish were collected from fishermen participating in the Blue Dog Lake Association Fishing Derby in June, 1987. Measurements and tissue samples were taken immediately following weigh-in each day. Twelve walleyes were collected during the course of the summer from anglers. These fish were frozen and sent to me for analysis. All

fish used in this study were aged from scales and otoliths (procedure following Miller and Storck 1982) and sexed when mature gonads were present.

Just prior to analysis, one part of Tris-EDTA buffer, pH 7.0 was added to two parts of tissue, and the mixture was homogenized and placed in an ice bath. The homogenates were then centrifuged for 10 minutes, and the samples were again placed in an ice bath and used immediately.

Electrophoresis

Horizontal starch gel electrophoresis, described by Selander et al. (1971), was used to detect enzyme variation. All gels were Electrostarch (Lot No. 87) and Sigma hydrolyzed potato starch (5:4 ratio) in a 15% buffer solution. Two buffer systems were used:

(I) AMP - (Clayton and Tretiak 1972) - gel: 0.02M citric acid, pH 6.1; electrode: 0.04M citric acid, pH 6.1; both buffers were adjusted to the specific pH with N-(3-amino-propyl)-morpholine.

(II) RW - (Ridgeway et al. 1970) - gel: 0.03M Tris-0.06M citric acid, pH 8.5; electrode: 0.06M lithium hydroxide-0.3M boric acid, pH 8.1.

Stain formulations were modified from Harris and Hopkinson (1976). Twenty-one enzyme and protein systems were surveyed (Appendix 1). Allelic designations follow the

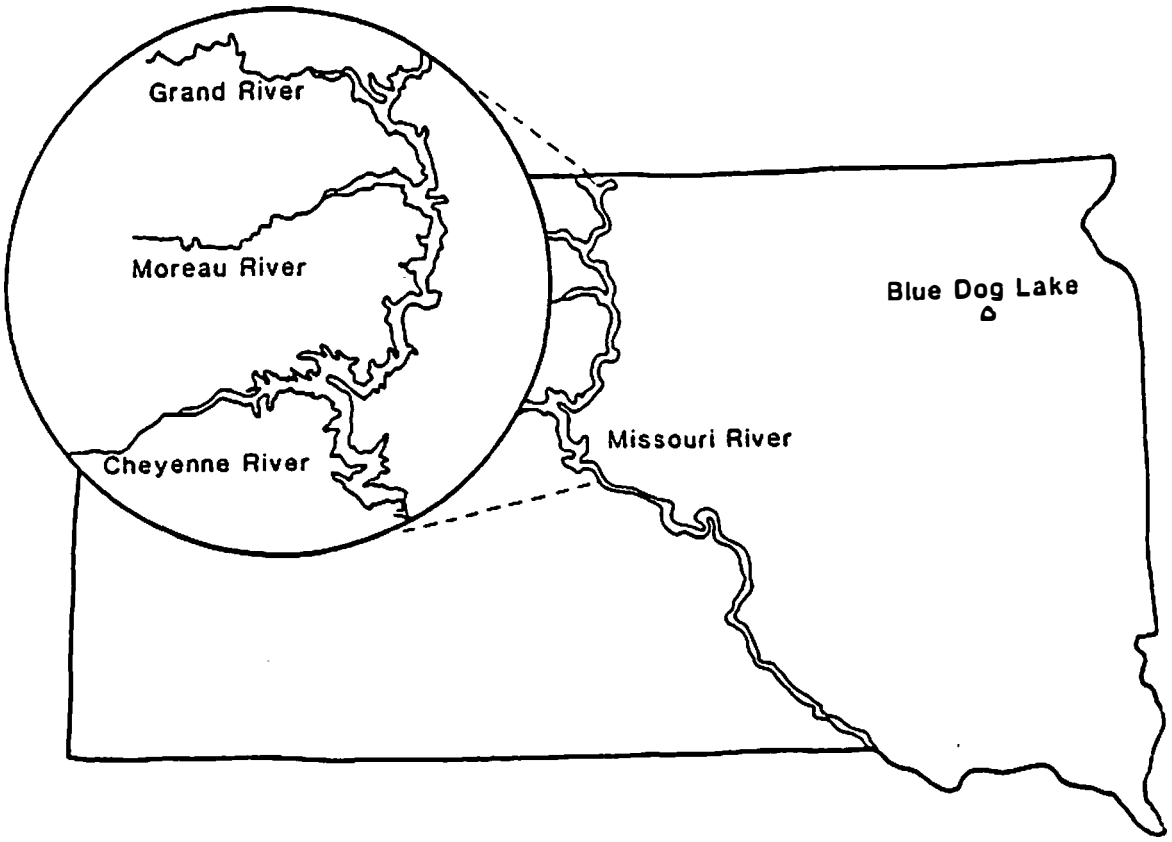

Figure 1. Map of South Dakota showing the three major westside tributaries of Lake Oahe, on the mainstem Missouri River. Tissue samples and morphometric measurements were taken from walleyes (Stizostedion vitreum) in each of the three tributaries and Blue Dog Lake during 1987 to determine genotypic and phenotypic variability.

system outlined by Allendorf and Utter (1979). If multiple loci encode the enzyme or protein, the loci are numbered beginning with the one which encodes isozymes with the least anodal migration. The most common allele therefore was designated 100; the other alleles were assigned mobilities relative to that of the common (100) allele. The interpretation of the banding patterns for this species follows that of Thomas Todd (National Fisheries Center - Great Lakes, Ann Arbor, MI, unpublished data), Murphy and Lee (1986), Terre (1985), Seeb et al. (1983), and Murphy (1981).

Morphometrics and Meristics

Data were recorded for 25 morphological and 14 meristic characters from each walleye (Table 1). All measurements and counts were made in a systematic manner on the left side of the body unless that body part was missing. Measurements were made to the nearest 0.1 mm using a vernier caliper and followed Hubbs and Lagler (1967) and Cailliet et al. (1986).

Data Analysis

Electrophoretic data were converted to allele frequencies and analyzed by BIOSYS-1, a FORTRAN program created by Swofford and Selander (1981). Because genotypic frequencies in actual populations can only be predicted

Table 1. Meristic and morphometric characters assessed on each walleye (Stizostedion vitreum) from Lake Oahe and Blue Dog Lake in South Dakota in April 1987.

Morphometrics	Meristic Counts
Standard length	First dorsal fin spines
Total length	Second dorsal fin rays
Weight	Pelvic fin rays
Head width	Pectoral fin rays
Head length	Anal fin spines
Post-orbital head length	Anal fin rays
Cheek length	Pyloric caecae
Snout length	Branchiostegal rays
Upper jaw length	Principle gill rakers - top
Gape	Principle gill rakers - bottom
Body depth	Lateral line scales
Eye diameter	Scales above lateral line
Horizontal orbit width	Scales below lateral line
Vertical orbit width	Scales before dorsal fin
Interorbital width	
Suborbital width	
Pre-dorsal fin length	
Dorsal fin length	
Pelvic fin length	
Pectoral fin length	
Anal fin length	
Caudal peduncle length	
Caudal peduncle depth	
Caudal peduncle width	
Length of longest dorsal spine	

under the conditions of Hardy-Weinberg equilibrium, each polymorphic locus was tested for conformance to Hardy-Weinberg equilibrium expectations with a chi-square goodness-of-fit test using Levene (1949) correction for small sample size. A locus is said to conform to Hardy-Weinberg equilibrium values if after one generation of random mating, the frequency of any genotype in the population is the product of the parental allelic frequencies. By using the equation $p^2 + 2pq + q^2$, where p is the frequency of the A allele and q is the frequency of the a allele, the genotypic frequencies can be predicted (Kapuscinski and Jacobson 1987). Departure from the expected values may be caused by pooling samples from two discrete populations, tissue degradation, or scoring errors.

Contingency chi-square tests were employed to test for inter- and intrapopulational heterogeneity. Nei (1978) unbiased genetic identity was calculated from allele frequency differences, and a dendogram was constructed from the matrix of the identity values.

Morphometrics represent continuous data and are largely size dependent, while meristics are not size dependent and represent discrete data. Analyses for morphometrics and meristics were performed separately using procedures provided by the Statistical Analysis System (SAS 1985). All morphometrics were first plotted against standard length to

check for linearity. All of the variables used in the subsequent analyses had a linear relationship with standard length, so no log transformations of the data set were made.

The morphometric data sets were subjected to stepwise discriminant analysis (Proc STEPDISC, SAS 1985) using a stepwise selection. At each step, a variable contributing the most to the discriminatory power of the model (as measured by Wilks' Lambda) was entered. STEPDISC was used to determine which subset of variables could be selected to most accurately separate the identified groups or sampling locations.

The least squares analysis of variance (Proc GLM, SAS 1985) was then employed for uni- and multivariate analysis of variance with a standard length as the covariate. The univariate (ANOVA) was used to determine significance ($P \leq 0.05$) in means for the subset of variables identified by STEPDISC. Multivariate analysis of variance (MANOVA) was also used with a covariate so that each dependent morphometric variable from the subset would be regressed on the independent covariate standard length. Using ANOVA and MANOVA with standard length as the covariate enabled the detection of significant ($P \leq 0.05$) differences in morphology among locations, while reducing the effects of size on the morphological measurements. Roy's Maximum Root was used as an upper bound on the F value to determine whether MANOVA

was superior to univariate analysis of variance in discriminating the fish by location (SAS 1985).

Discriminant function analysis (Proc DISCRIM, SAS 1985) was carried out on the same subset of variables. The DISCRIM procedure developed a classification criterion using a measure of generalized squared distance that was based on within-group covariance matrices. Each observation was placed in the location from which it had the smallest generalized squared distance. The posterior probability of an observation belonging to each location was then computed.

The categorical modeling procedure (Proc CATMOD, SAS 1985) was used to analyze the meristic data. The sum of each variable was adjusted for the overall mean sample size and tested for significance ($P \leq 0.05$).

Genetic Variability

A polymorphic locus was defined as one in which the frequency of the common allele did not exceed 0.95. Only four of the loci examined exhibited consistently-scorable polymorphisms based on this criterion (Table 2). These proteins were (abbreviation with locus and Enzyme Commission No. in parentheses): malate dehydrogenase (MDH-3; 1.1.1.37, previously described in walleye by Clayton et al. (1971)), isocitrate dehydrogenase (IDH-1; 1.1.1.42), alcohol dehydrogenase (ADH-1; 1.1.1.1), and a general protein found in the muscle (GMP-3). None of the sample locations differed greatly in mean heterozygosity (0.106-0.123) or in percent polymorphism (28.5%).

Heterogeneity Within Lake Oahe

Walleyes spawning in the three tributaries of Lake Oahe were genetically similar; the probability of homogeneity among Oahe tributary stocks was insignificant ($P>0.05$) for all alleles (Table 3). Deviations from Hardy-Weinberg expectations were observed in allele frequencies of Cheyenne River walleyes at the ADH-1 locus and in Grand River walleyes at the IDH-1 locus. These deviations were both due to an excess of heterozygotes and probably occurred as a result of degraded tissues, because they occurred only in

Table 2. Frequencies of variant alleles at the polymorphic loci of walleye (Stizostedion vitreum) sampled from the Grand, Moreau, and Cheyenne Rivers and Blue Dog Lake in South Dakota, and the Mississippi River. Alleles are designated by their mobilities relative to that of the common (100) allele. A minus (-) sign indicates cathodally-migrating enzymes.

Locus and Allele	Blue Dog Lake	Lake Oahe Tributaries: Grand River	Moreau River	Cheyenne River	Mississippi River: Pool 8	Pool 5
ADH-1						
(N)	22	22	26	29	50	50
-75	0.159	0.250	0.212	0.190	0.220	0.240
-100	0.841	0.750	0.788	0.810	0.780	0.760
IDH-1						
(N)	22	24	23	25	50	50
80	0.432	0.458	0.413	0.440	0.510	0.479
100	0.568	0.542	0.587	0.560	0.490	0.521
120	0.000	0.000	0.000	0.000	0.000	0.000
MDH-3						
(N)	23	24	28	30	49	48
80	0.000	0.000	0.000	0.000	0.000	0.000
100	0.609	0.688	0.750	0.733	0.765	0.823
120	0.391	0.313	0.250	0.267	0.235	0.177
GMP-3						
(N)	23	24	28	30	50	50
75	0.652	0.854	0.839	0.883	0.410	0.410
100	0.348	0.146	0.161	0.117	0.590	0.590

Table 3. Allele frequencies for four polymorphic loci in walleyes (Stizostedion vitreum) from the three tributaries of Lake Oahe, probability of deviation from expected Hardy-Weinberg equilibrium values (HDYWBG), and probability of homogeneity of samples (P), when df=2.

Locus	Moreau River	Cheyenne River	Grand River	P
ADH-1				
(N)	26	29	22	
-75	0.212	0.190	0.250	
-100	0.788	0.810	0.750	
(HDYWBG)	(0.925)	(0.012)	(0.404)	
				0.761
IDH-1				
(N)	23	25	24	
80	0.413	0.440	0.458	
100	0.587	0.560	0.542	
(HDYWBG)	(0.863)	(0.562)	(0.011)	
				0.906
MDH-3				
(N)	28	30	24	
100	0.750	0.733	0.688	
120	0.250	0.267	0.313	
(HDYBWG)	(0.724)	(0.064)	(0.237)	
				0.765
GMP-3				
(N)	28	30	24	
75	0.839	0.883	0.854	
100	0.161	0.117	0.146	
(HDYWBG)	(0.343)	(0.506)	(0.342)	
				0.785

allele frequencies of liver enzymes, and liver samples are quickly and easily degraded.

When these data for walleyes from the three tributaries were combined into one Lake Oahe sample (Table 4), there were no significant ($P>0.05$) departures from Hardy-Weinberg expectations. These three spawning populations appeared to be genetically very similar (Table 5; Figure 2).

Heterogeneity Between South Dakota Stocks

Allele frequencies of walleyes collected from the tributaries of Lake Oahe and Blue Dog Lake differed significantly ($P \leq 0.001$) at only one locus, GMP-3 (Table 6). Nei (1978) unbiased genetic identity (Table 5) and the dendogram constructed from the similarity values (Figure 2) showed a separation of the two stocks at a genetic distance of 0.003.

Heterogeneity of Mississippi River Pools

Walleyes from pool 5 and pool 8 of the Mississippi River conformed to Hardy-Weinberg expectations (Table 7). Combining these samples into one Mississippi River sample (Table 4) revealed no significant ($P>0.05$) deviations, suggesting homogeneity of the pooled samples. Contingency chi-square tests of the allele frequencies substantiated a high probability of homogeneity (Table 7). Genetically, the

Table 4. Allele frequencies for four polymorphic loci found in walleyes (Stizostedion vitreum) sampled from Lake Oahe, Blue Dog Lake, and the Mississippi River, probability of deviation from expected Hardy-Weinberg equilibrium values (HDYWBG), and probability of homogeneity of samples (P), when df is equal to two.

Locus	Lake Oahe	Blue Dog Lake	Mississippi River	P
ADH-1				
(N)	77	22	100	
-75	0.214	0.159	0.230	
-100	0.786	0.841	0.770	
(HDYWBG)	(0.082)	(0.394)	(0.651)	
				0.584
IDH-1				
(N)	72	22	98	
80	0.438	0.432	0.495	
100	0.563	0.568	0.505	
(HDYWBG)	(0.262)	(0.984)	(0.096)	
				0.513
MDH-3				
(N)	82	23	97	
100	0.726	0.609	0.794	
120	0.274	0.391	0.206	
(HDYBWG)	(0.606)	(0.726)	(0.979)	
				0.027
GMP-3				
(N)	82	23	100	
75	0.860	0.652	0.410	
100	0.140	0.348	0.590	
(HDYWBG)	(0.608)	(0.218)	(0.588)	
				<0.001

Table 5. Matrix of Nei (1978) unbiased genetic identity and distance coefficients based on allele frequency differences among walleyes (Stizostedion vitreum) sampled from the Mississippi River, Blue Dog Lake, and the Moreau, Cheyenne, and Grand Rivers in South Dakota in April, 1987.

Above diagonal: Nei (1978) unbiased genetic identity[1]
Below diagonal: Nei (1978) unbiased genetic distance[2]

Population	1	2	3	4	5	6
1 Mississippi Pool 5	*****	1.000	0.993	0.986	0.983	0.985
2 Mississippi Pool 8	0.000	*****	0.995	0.986	0.983	0.985
3 Blue Dog Lake	0.007	0.005	*****	0.998	0.997	0.998
4 Moreau River	0.014	0.014	0.002	*****	1.000	1.000
5 Cheyenne River	0.017	0.017	0.003	0.000	*****	1.000
6 Grand River	0.016	0.015	0.002	0.000	0.000	*****

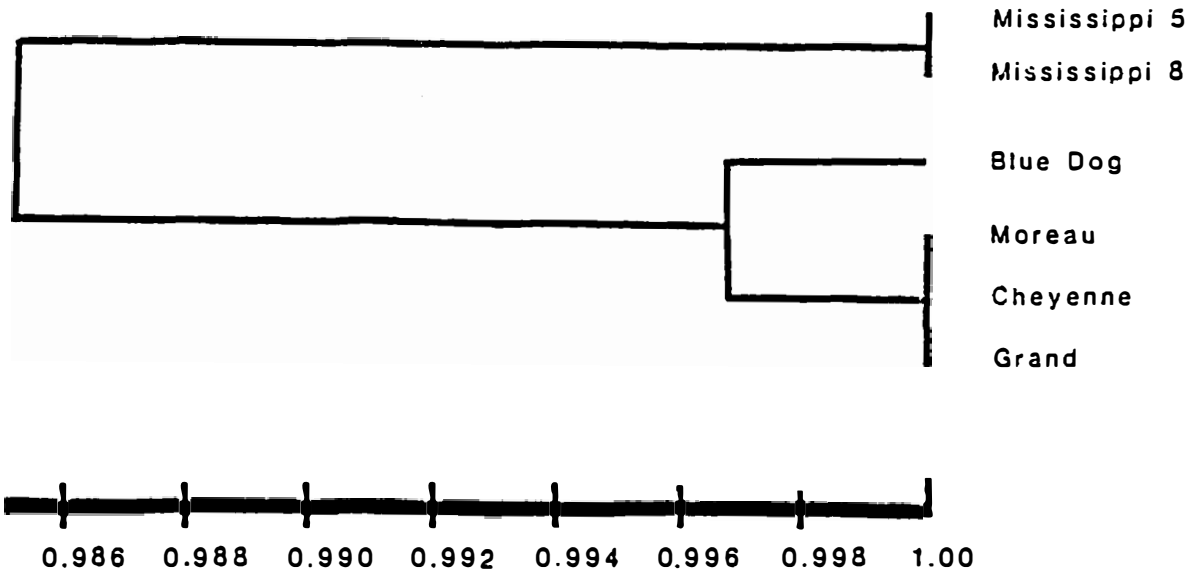

Figure 2. Dendogram depicting the genetic similarity among walleyes (Stizostedion vitreum) sampled in 1987 from the Mississippi River, and the Moreau, Cheyenne, and Grand Rivers in South Dakota. Similarity is derived from Nei (1978) unbiased genetic identity values based on allele frequency differences.

Table 6. Allele frequencies for four polymorphic loci found in walleyes (Stizostedion vitreum) sampled from Lake Oahe and Blue Dog Lake in South Dakota, probability of deviation from expected Hardy-Weinberg equilibrium values (HDYWBG), and probability of homogeneity of samples (P), when df=1.

Locus	Lake Oahe	Blue Dog Lake	P
ADH-1			
(N)	77	22	
-75	0.214	0.159	
-100	0.786	0.841	
(HDYWBG)	(0.082)	(0.394)	
			0.421
IDH-1			
(N)	72	22	
80	0.438	0.432	
100	0.563	0.568	
(HDYWBG)	(0.262)	(0.984)	
			0.947
MDH-3			
(N)	82	23	
100	0.726	0.609	
120	0.274	0.391	
(HDYBWG)	(0.606)	(0.726)	
			0.126
GMP-3			
(N)	82	23	
75	0.860	0.652	
100	0.140	0.348	
(HDYWBG)	(0.608)	(0.218)	
			0.001

Table 7. Allele frequencies for four polymorphic loci in Mississippi River pool 5 and pool 8 walleyes (Stizostedion vitreum), probability of deviation from expected Hardy-Weinberg equilibrium values (HDYWBG), and probability of homogeneity of samples (P), when df=1.

Locus	pool 5	pool 8	P
ADH-1			
(N)	50	50	
-75	0.240	0.220	
-100	0.760	0.780	
(HDYWBG)	(0.868)	(0.579)	
			0.736
IDH-1			
(N)	48	50	
80	0.479	0.510	
100	0.521	0.490	
(HDYWBG)	(0.223)	(0.230)	
			0.666
MDH-3			
(N)	48	49	
100	0.823	0.765	
120	0.177	0.235	
(HDYBWG)	(0.567)	(0.626)	
			0.321
GMP-3			
(N)	50	50	
75	0.410	0.410	
100	0.590	0.590	
(HDYWBG)	(0.869)	(0.315)	
			1.000

two localities are very similar, as depicted by the dendogram (Figure 2) based on Nei (1978) unbiased genetic identity values (Table 5).

Heterogeneity Among All Localities

Significant heterogeneity was observed at two of the four polymorphic loci ($P \leq 0.05$ for MDH-3 and $P \leq 0.001$ for GMP-3) when the Lake Oahe, Blue Dog Lake, and Mississippi River walleye were compared to each other (Table 4). The dendogram, based on similarity values derived from Nei (1978) unbiased genetic identity (Table 5), defined two groups of walleyes, a Mississippi River stock and a South Dakota stock; with the South Dakota stock less distinctly separated (Figure 2).

Morphometric and Meristic Variability

No single morphometric character allowed walleyes from one location to be distinguished from those of other localities as differences in the means, although statistically significant ($P \leq 0.05$), were all too small to be of practical importance. Stepwise discriminant analysis removed a subset of 8 of the original 22 morphometric variables to explain 89% of the variability in morphology among sampling locations, as indicated by a final Wilks' Lambda value of 0.1143 (Table 8). This same subset of eight variables contributed to the discrimination of walleyes among the four sampling locations (Table 9). Using discriminant function analysis, I correctly classified Cheyenne River walleyes 96.8% of the time, and Blue Dog Lake fish with 95.7% accuracy. Grand River fish were correctly classified as to their location with only 82.6% accuracy. Two of the fish were incorrectly identified as Cheyenne River walleyes, and one each as Moreau River and Blue Dog Lake fish.

Univariate analysis of variance was used to test the null hypothesis of equality of means regardless of sampling location. There were significant ($P \leq 0.001$) differences in means among locations for each of the 22 morphometric characters. Uni- and multivariate analysis of variance were

Table 8. Summary of the subset of variables selected by stepwise discriminant analysis which explain the most variability in morphology among walleyes (Stizostedion vitreum) sampled from Lake Oahe and Blue Dog Lake in South Dakota, the probability level of their significance to the model, and the Wilks' Lambda values.

Variable	Probability level	Wilks' Lambda
Interorbital width	0.0001	0.4798
Upper-jaw length	0.0001	0.3097
Eye diameter	0.0001	0.2126
Body depth	0.0024	0.1791
Head length	0.0166	0.1584
Post-orbital head length	0.0169	0.1400
Head width	0.0381	0.1263
Cheek width	0.0441	0.1143

Table 9. Discriminant function analysis classification summary of walleyes (Stizostedion vitreum) sampled from the Grand, Cheyenne, and Moreau Rivers and Blue Dog Lake in South Dakota, and posterior probability of membership in each location using the generalized squared distance function. Number of observations classified into each location is indicated by parenthesis.

From Location	Moreau	Blue Dog	Cheyenne	Grand
Moreau River (N=28)	(26) 92.9%	(0) 0.0%	(0) 0.0%	(2) 7.1%
Blue Dog Lake (N=23)	(1) 4.4%	(22) 95.7%	(0) 0.0%	(0) 0.0%
Cheyenne River (N=31)	(0) 0.0%	(0) 0.0%	(30) 96.8%	(1) 3.2%
Grand River (N=23)	(1) 4.4%	(1) 4.4%	(2) 8.7%	(19) 82.6%

then used with standard length as the covariate to test the variability in the subset of eight measurements among locations, while correcting for size differences. The measurements were significantly ($P \leq 0.05$) different among locations (Table 10). Using Roy's Greatest Root as an upper bound on the F tests showed that univariate statistics were superior to multivariate statistics in discriminating fish by locations (Table 11). With Fisher's protected least significant difference (FLSD) test for identifying the sources of the significance in means, I found that Blue Dog Lake walleyes had a greater eye diameter, and longer head and upper-jaw length than the other fish (Table 12). Means and standard errors were calculated for all characters and are listed in Table 14.

In using the CATMOD procedure for testing the sums of the meristic data, I found one character significant ($P \leq 0.01$). Blue Dog Lake walleyes had a mean of 19.2 scales below the lateral line, whereas all three Missouri River tributaries had mean values of about 21.2 (Table 13).

Table 10. Univariate Analysis of Variance of eight morphology variables measured on walleyes (Stizostedion vitreum) sampled from Blue Dog Lake and Lake Oahe in April 1987, and their sources of variability.

Independent Variables and their Sources of Variability	df	Mean Square	F value
Interorbital width			
location	3	48.89	25.24**
standard length	1	934.40	482.33**
error	100	1.94	
Upper-jaw length			
location	3	42.88	7.39**
standard length	1	6339.61	1092.93**
error	100	5.80	
Eye diameter			
location	3	30.25	18.76**
standard length	1	311.11	192.93**
error	100	1.61	
Body depth			
location	3	200.99	2.76*
standard length	1	24308.11	333.37**
error	100	72.92	
Head length			
location	3	301.02	11.06**
standard length	1	33247.57	1221.59**
error	100	27.22	
Cheek width			
location	3	0.65	0.14
standard length	1	2858.16	611.15**
error	100	4.68	
Head width			
location	3	109.80	5.01**
standard length	1	5788.77	264.26**
error	100	21.91	
Post-orbital head width			
location	3	56.16	4.86**
standard length	1	11307.23	978.43**
error	100	11.56	

* Denotes significance at the 0.05 level of probability.
** Denotes significance at the 0.01 level of probability.

Table 11. Multivariate Analysis of Variance (MANOVA) of eight morphology variables measured on walleyes (Stizostedion vitreum) sampled from Blue Dog Lake and Lake Oahe in April 1987, test criteria and exact F statistics with standard length as the covariate.

To test the hypothesis of no overall standard length effect:

Statistic	Value	F Value
Roy's Greatest Root	14.74	171.36**

To test the hypothesis of no overall location effect:

Statistic	Value	F Value
Roy's Greatest Root	2.06	24.49**

** Denotes significance at the 0.01 level of probability.

Table 12. Means (mm) of the morphology measurements most variable in walleyes (Stizostedion vitreum) sampled from the Moreau, Cheyenne, and Grand Rivers, and Blue Dog Lake in South Dakota in April 1987.

Variable	Location	Mean
Interorbital width	Moreau River	21.10[a*]
	Blue Dog Lake	20.62[a]
	Cheyenne River	24.05[b]
	Grand River	21.28[a]
Upper-jaw length	Moreau River	55.54[a]
	Blue Dog Lake	57.94[b]
	Cheyenne River	55.12[a]
	Grand River	55.11[a]
Eye diameter	Moreau River	17.06[a]
	Blue Dog Lake	19.65[b]
	Cheyenne River	18.86[c]
	Grand River	17.87[d]
Body depth	Moreau River	92.83[ab]
	Blue Dog Lake	90.20[a]
	Cheyenne River	91.38[a]
	Grand River	97.09[b]
Head length	Moreau River	128.20[a]
	Blue Dog Lake	133.55[b]
	Cheyenne River	126.29[a]
	Grand River	125.58[a]
Head width	Moreau River	54.18[a]
	Blue Dog Lake	55.17[a]
	Cheyenne River	59.30[b]
	Grand River	54.63[a]
Post-orbital head length	Moreau	73.50[a]
	Blue Dog Lake	76.50[b]
	Cheyenne River	74.47[ab]
	Grand River	72.96[a]

*Means with the same superscript are not significantly different ($P \leq 0.05$); Fisher's protected least significant difference test (FLSD).

Table 13. Means of each meristic character counted on walleyes (Stizostedion vitreum) sampled from the Moreau, Cheyenne, and Grand Rivers, and Blue Dog Lake in South Dakota in April, 1987.

Meristic Variable	Moreau River	Cheyenne River	Grand River	Blue Dog Lake
First dorsal spines	13.71	13.81	13.48	13.83
Second dorsal rays	21.68	20.43	20.74	19.82
Anal fin spines	2.00	2.06	2.00	1.96
Anal fin rays	13.36	13.03	12.91	12.91
Pectoral fin rays	14.50	13.35	14.57	13.70
Pelvic fin rays	5.00	5.06	5.09	5.04
Branchiostegals	7.00	7.06	7.04	6.87
Principle gill rakers-top	3.14	3.94	3.35	3.39
Principle gill rakers-bottom	8.18	8.61	8.17	8.09
Lateral line scales	84.79	86.39	85.39	85.71
Scales above lateral line	13.93	14.29	14.70	12.94
Scales below lateral line	21.21	21.26	21.70	19.24**
Scales before dorsal fin	19.89	18.32	20.39	18.24
Pyloric caeca	2.86	3.00	3.00	2.89

** Significantly different (P<0.01) from the Grand, Cheyenne, and Moreau River mean

Table 14. Means and standard errors (in parentheses) of each morphometric character measured on walleyes (Stizostedion vitreum) sampled from the Moreau, Cheyenne, and Grand Rivers, and Blue Dog Lake in South Dakota in April 1987.

Morphometric Variable	Moreau River	Cheyenne River	Grand River	Blue Dog Lake
Standard length	39.82 (9.90)	499.58(13.86)	406.04(14.35)	418.78 (9.85)
Head length	117.35 (3.00)	145.14 (3.92)	117.66 (4.59)	129.28 (2.90)
Head width	49.65 (1.25)	67.16 (1.81)	51.32 (2.29)	53.39 (1.48)
Snout length	31.07 (0.77)	37.47 (0.92)	31.16 (0.95)	33.51 (0.73)
Post-orbital head length	67.18 (1.84)	85.46 (2.31)	68.34 (2.67)	74.01 (1.61)
Sub-orbital width	4.32 (1.84)	5.84 (0.20)	4.02 (0.24)	5.27 (0.25)
Cheek width	34.41 (1.04)	43.30 (1.21)	35.05 (1.31)	36.40 (0.73)
Interorbital width	19.28 (0.55)	27.21 (0.67)	19.95 (0.84)	19.90 (0.49)
Horizontal orbital width	19.80 (0.39)	24.06 (0.51)	19.83 (0.50)	22.46 (0.41)
Vertical orbital width	17.38 (0.44)	22.55 (0.55)	18.39 (0.52)	20.81 (0.51)
Gape	43.55 (1.18)	60.80 (2.20)	46.30 (2.34)	47.69 (1.46)
Body depth	83.56 (2.26)	107.49 (3.43)	90.31 (5.26)	86.54 (2.34)
Caudal peduncle depth	29.95 (0.81)	39.98 (1.08)	31.24 (1.18)	32.18 (0.70)
Caudal peduncle width	23.83 (0.64)	32.90 (0.95)	25.04 (1.09)	25.75 (1.04)
Caudal peduncle length	47.58 (1.27)	72.56 (2.80)	51.51 (1.90)	49.58 (1.43)
Eye diameter	16.01 (0.33)	20.68 (0.44)	17.10 (0.48)	19.24 (0.43)
Upper-jaw length	50.81 (1.37)	63.35 (1.74)	51.65 (1.96)	56.07 (1.22)
Predorsal length	127.21 (3.22)	156.12 (4.30)	128.13 (4.66)	144.27 (6.29)
Dorsal fin length	247.50 (6.23)	300.39 (7.81)	249.22 (8.49)	252.65 (5.28)
Pectoral fin length	59.70 (1.57)	77.46 (2.02)	61.32 (2.21)	67.09 (1.28)
Pelvic fin length	60.23 (1.50)	76.31 (1.96)	62.96 (1.84)	68.72 (1.71)
Anal fin length	69.43 (1.87)	87.72 (2.21)	71.27 (2.31)	74.30 (1.53)
Longest dorsal spine	57.40 (1.25)	66.12 (1.57)	56.65 (1.38)	59.75 (0.83)

Discussion

Geological history indicates that walleyes entered the glacial lake district of northeastern South Dakota from the Mississippi River via the Minnesota River drainage, while those inhabiting Lake Oahe are remnants of the Missouri River stock. While walleyes from the Mississippi River were observed to be genetically distinct from the South Dakota stocks (Figure 2), very little enzyme variability was observed among the South Dakota fish. Of the 21 loci examined, only four produced consistently-scorable polymorphisms. Only one of these polymorphic loci was significant in discriminating the South Dakota stocks (Table 6; GMP-3 probability of homogeneity $P \leq 0.001$). Stock identification studies based on electrophoretic data are limited, however, by the amount of observable genetic differences between populations (Kapuscinski and Jacobson 1987). Not all proteins can be resolved using electrophoretic techniques. Because of this limitation, electrophoresis can never be used to prove that stocks of fish are identical; it can only be used to detect and show genetic differences. In this study, Nei (1978) genetic distances based on the allele frequency differences of the Blue Dog Lake walleyes and those of the Lake Oahe tributaries were around 0.002 (Table 5). This distance indicates that the

two stocks are genetically distinct, although only at one locus. Unfortunately, no clear cut definition of a significant genetic distance exists. The significance is rather relative to the objectives of the study. A manager contemplating future stocking strategies would have to take this small discreteness into account and decide whether this genetic integrity is worth preserving.

Genetic heterogeneity among spawning populations of walleyes in Lake Oahe was not detected (Nei (1978) genetic distances for all three populations were zero, Table 5). Based on these findings and the species early life history, the hypothesis that the Lake Oahe spawning populations represent genetically distinct stocks can not be supported, given the limitations of electrophoresis.

Morphometric analysis indicated that Lake Oahe spawning populations and Blue Dog Lake fish are phenotypically distinct (Tables 9 and 12). This difference in morphology may be of adaptive significance. For example, some salmon stocks differ morphologically as a result of adaptation to local conditions in the natal river (Hjort and Schreck 1982; Taylor and McPhail 1985; Beacham et al. 1988). My data suggests a similar phenomenon in walleyes. Blue Dog Lake walleyes had a significantly ($P \leq 0.05$) longer upper jaw, head length, eye diameter, and post-orbital head length (although the latter was not significantly ($P>0.05$)

different from Cheyenne River walleyes) than did walleyes from the other localities (Table 12). These larger characters may represent an adaptation to feeding efficiency in the shallow, turbid waters of Blue Dog Lake, where prey is less abundant and of a more variable body size than in Lake Oahe. The lack of genotypic differences does not imply a lack of phenotypic differences, because the correlation between genotype and phenotypic variability is still uncertain (Ryman et al. 1979). Coho salmon, although not highly variable at electrophoretically detectable loci, show inter-populational differences in body morphology (Rosenau and McPhail 1987). The phenotypes I observed were probably due to a gene x environment interaction, which results in the expression of a complex of covarying traits (Riddell and Legget 1981). Without data provided from breeding studies, however, it is difficult to ascertain whether phenotypic differences are under genetic or environmental control, or an interaction of the two.

Because of the promiscuity in stocking programs, it is important that the genetic differentiation of walleye populations, and the relationship between this differentiation and fitness be understood (Koehn 1970). Further studies on performance, feeding, and survival should be undertaken to determine the adaptive significance of characteristics related to head size. Wolters (1988)

compared post-stocking performance between fingerling Blue Dog Lake and Missouri River stocks, and concluded that fingerling growth and survival (July, 1987 - April, 1988) differences were small and probably not controlled by genotype. However, he compared only about 250 fish of each stock in an unreplicated study. Other performance differences may be revealed by more comprehensive studies.

The high degree of genetic homogeneity among walleyes in South Dakota prevents the recommendation of a different management strategy in South Dakota. However, the electrophoretic separation of South Dakota stocks from those of the Mississippi River clearly indicates genetic dissimilarity, and I believe that the state must be wary of bringing in new stocks, particularly those from riverine habitats. Stocks are independent, self-perpetuating biological units and these riverine stocks may have distinctive characteristics. Continued promiscuity in stocking may result in cross-breeding that limits and subsequently eliminates genetic diversity (Murphy and Lee 1986). Discrete stocks should be identified and their unique traits recognized, especially when used as broodstock.

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APPENDIX 1

ENZYME SYSTEMS SURVEYED

ENZYME	ABBREVIATION	ENZYME COMMISSION NUMBER	TISSUE TESTED	BUFFER SYSTEM
Adenylate kinase	AK	2.7.4.3	Liver	RW
Alcohol dehydrogenase	ADH	1.1.1.1	Liver	AMP
Aldolase	ALD	4.1.2.13	Liver Muscle	AMP
Creatine kinase	CK	2.7.3.2	Muscle	RW
Diaphorase	DIA	1.6.2.2	Liver	AMP
Esterase	ES	3.1.1.1	Liver	AMP
Fumarase	FH	4.2.1.2	Muscle	AMP
General Protein	GMP		Muscle	RW
Glucose dehydrogenase	GDH	1.1.1.47	Muscle	AMP
Glucose-6-phosphate dehydrogenase	GD	1.1.1.49	Muscle	RW
Glucose phosphate isomerase	GPI	5.3.1.9	Muscle	RW
Glutamate dehydrogenase	GLUD	1.4.1.3	Muscle	AMP

APPENDIX 1 - CONTINUED

ENZYME	ABBREVIATION	ENZYME COMMISSION NUMBER	TISSUE TESTED	BUFFER SYSTEM
Isocitrate dehydrogenase	IDH	1.1.1.42	Muscle Liver Heart	AMP
Lactate dehydrogenase	LDH	1.1.1.27	Muscle	AMP
Malate dehydrogenase	MDH	1.1.1.37	Liver Muscle	AMP
Malic enzyme	ME	1.1.1.40	Muscle	AMP
Phosphoglucomutase	PGM	2.7.5.1	Muscle	AMP
Phosphogluconate dehydrogenase	6PGD	1.1.1.43	Muscle	RW
Sorbitol dehydrogenase	SORDH	1.1.1.14	Liver	RW
Superoxide dismutase	SOD	1.15.1.1	Liver	AMP
Xanthine dehydrogenase	XDH	1.2.1.37	Liver	AMP