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Stock Structure of Rainbow Smelt in Western Lake Superior: Biochemical Genetics

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Abstract

Serum transferrin (TFN) and glucosephosphate isomerase from white muscle were examined in rainbow smelt *Osmerus mordax* from Lake Superior and from nine tributary streams along the lake's Minnesota shoreline. Significant differences in allelic frequencies at the *TFN* locus were observed among locations. These differences suggest either that there are at least three discrete populations along the Minnesota shoreline or that differential selection for *TFN* alleles occurs within the lake.

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Rainbow smelt *Osmerus mordax* is a successful introduced species in the Great Lakes. Origin of the Lake Superior rainbow smelt population is attributed to planting of eggs from Green Lake, Maine, into Crystal Lake, Michigan, and subsequent dispersal to the upper Great Lakes (Creaser 1925). Rainbow smelt first were discovered in eastern Lake Superior in 1930 and within 16 years had spread to the Minnesota waters of western Lake Superior (Hale 1960). Since the decline of lake trout *Salvelinus namaycush* and cisco *Coregonus artedii*, rainbow smelt has emerged as a primary commercial species in western Lake Superior and also supports a large sport fishery in Minnesota (Hassinger 1976).

Rainbow smelt are potential competitors with and predators on native and introduced fishes (Selgeby et al. 1978). It has considerable spatial overlap with some of these species (Craigie 1971) and is prey for others, including burbot *Lota lota* and salmonids (Anderson and Smith 1971). The importance of rainbow smelt stems from these interactions which may be important in the rehabilitation of the Lake Superior fish community.

As part of a study of rainbow smelt population dynamics, the present study was conducted to determine if the species is divided into discrete stocks along the Minnesota shoreline of Lake Superior. Genetic variation among samples of spawning rainbow smelt was examined for evidence of stock structuring. Stocks of rainbow smelt, if they exist, may react differently to predation, competition, fishing pressure, and changing species composition in Lake Superior. Information about stock structure of rainbow smelt in western Lake Superior might permit more effective management of the species as well as predator species, most notably lake trout and Pacific salmon *Oncorhynchus* spp.

Methods

Rainbow smelt samples (30–36 individuals) were collected from the lake and tributary streams along the Minnesota shoreline of Lake Superior from Duluth to Grand Portage, Minnesota, during the spawning seasons (late April to early May) of 1977, 1978, and 1982 (Fig. 1). Fish were taken from streams by dip net and from the lake by commercial pound nets. In addition, a bottom trawl catch from the Duluth area (Duluth Flats) provided an offshore rainbow smelt sample in October 1978.

Within 2 hours after they were captured, blood was collected from live rainbow smelt by cardiac puncture with heparinized capillary tubes (Krueger and Menzel 1979). Whole fish

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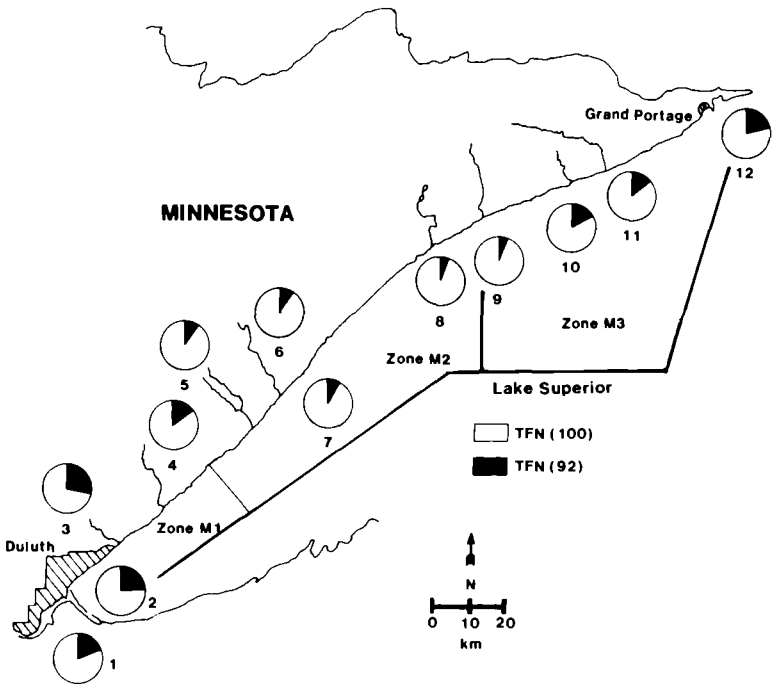

FIGURE 1.—*Geographic variation in transferrin* (TFN) *allele frequencies (Table 2) in rainbow smelt from sites along the Minnesota shoreline of Lake Superior. Symbols represent proportion of alleles at each site. Sample sites are* ***1*** *Duluth Harbor,* ***2*** *Duluth Flats,* ***3*** *Talmadge River,* ***4*** *Knife River,* ***5*** *Split Rock River,* ***6*** *Beaver River,* ***7*** *East Beaver Bay,* ***8*** *Poplar River,* ***9*** *Cascade River,* ***10*** *Durfee Creek,* ***11*** *Brule River, and* ***12*** *Grand Portage. M1, M2, and M3 are fishery statistical zones.*

and blood samples were frozen immediately on dry ice in the field, transported to the laboratory, and stored at −20 C. Five proteins were examined by electrophoresis from rainbow smelt collected at 12 locations during 1977 and 1978 (Table 1). Twenty-one additional proteins were examined from fish collected during 1982 by dip net in the Beaver River and by commercial pound nets in Duluth Harbor (Table 1).

Blood serum was analyzed electrophoretically with 7.5% polyacrylamide gels (Balsano and Rasch 1974) and stained for transferrin (Menzel 1976; Ornstein 1976). Extracts of white muscle, eye, and liver tissue were analyzed by horizontal starch gel electrophoresis (May et al. 1979) with one of four buffer systems (Table 1). Gels were stained for various proteins according to the methods of Selander et al. (1971), Siciliano and Shaw (1976), Smith (1976), and Allendorf et al. (1977).

Genic nomenclature used here is that of Allendorf and Utter (1979). Each protein is abbreviated and the abbreviation is italicized when it refers to the locus of the gene that codes for the enzyme. Loci that produce different forms of the same enzyme are sequentially numbered from the gel origin to reflect the position of the respective enzyme products. Alleles at a locus are designated by their relative electrophoretic mobility. The most common allele is designated *100* and other alleles are assigned a numerical value that describes their position relative to the common allele.

The genotypic frequencies of samples were tested for conformance to Hardy–Weinberg equilibrium values by chi-square tests with Levene's (1949) correction. Chi-square analyses of allele counts were used to test for differences in allele frequencies among collections from the same site on different dates, and among collections from different locations (Conover 1971). Probability values less than 0.05 were required for rejection of the null hypothesis on all statistical tests. Genetic distances (Rogers 1972)

TABLE 1.—*Proteins examined for polymorphic expression in rainbow smelt. The proteins, tissues, and stains listed here were identified in a larger survey and had good activity and resolution.*

Protein	Tissue	Buffer[a]	Enzyme Council number
	1978–1979		
Superoxide dismutase	Eye	R	1.15.1.1
Malic enzyme	Eye	R	1.1.1.40
Phosphoglucomutase	White muscle	R	2.7.5.1
Glucosephosphate isomerase	White muscle	R	5.3.1.9
Transferrin	Blood serum		None
	1982		
Aldolase	Eye	TVB	4.1.2.13
Creatine phosphokinase	Eye	R	2.7.3.2
Creatine phosphokinase	White muscle	R	2.7.3.2
Esterase	White muscle	R	3.1.1.1
Peptidase (substrate glycyl-L-leucine)	White muscle	R	3.4.11–13
6-phosphogluconate dehydrogenase	White muscle	R	1.1.1.44
Adenylate kinase	White muscle	CT	2.7.4.3
Malic dehydrogenase	White muscle	CT	1.1.1.37
Malic enzyme	White muscle	CT	1.1.1.40
General protein	White muscle	TC	None
Isocitrate dehydrogenase	White muscle	TC	1.1.1.42
Glucosephosphate isomerase	White muscle	TC	5.3.1.9
Aspartate aminotransferase	White muscle	TVB	2.6.1.1
Aldolase	White muscle	TVB	4.1.2.13
Glutamic-pyruvate transaminase	White muscle	TVB	2.6.1.2
Phosphoglucomutase	White muscle	TVB	2.7.5.1
Creatine phosphokinase	Liver	R	2.7.3.2
Glucose-6-phosphate dehydrogenase	Liver	R	1.1.1.49
Lactate dehydrogenase	Liver	R	1.1.1.27
Mannosephosphate isomerase	Liver	R	5.3.1.8
Xanthine dehydrogenase	Liver	R	1.2.1.37
Glycerol-3-phosphate dehydrogenase	Liver	CT	1.1.1.8
Acid phosphatase	Liver	CT	3.1.3.2
Malic dehydrogenase	Liver	CT	1.1.1.37
Malic enzyme	Liver	CT	1.1.1.40
Catalase	Liver	TC	1.11.1.6
Isocitrate dehydrogenase	Liver	TC	1.1.1.42
Aspartate aminotransferase	Liver	TVB	2.6.1.1
Fructose-1,6-diphosphatase	Liver	TVB	3.1.3.11
Peroxidase	Liver	TVB	1.11.1.7
Phosphoglycerate kinase	Liver	TVB	2.7.2.3

[a] R denotes Ridgway buffer (Ridgway et al. 1970).
TVB denotes tris–versene–borate buffer (Siciliano and Shaw 1976).
CT denotes Clayton–Tretiak buffer (Clayton and Tretiak 1972).
TC denotes tris–citrate buffer (Siciliano and Shaw 1976).

were calculated for all pairs of collection locations based on allele frequencies at transferrin and glucosephosphate isomerase loci and subjected to unweighted pair group cluster analysis (Sneath and Sokal 1973) so that genetically similar groups could be identified.

Results and Discussion

Among the 26 proteins examined for polymorphic expression, there were differences among individuals for esterase (EST), isocitrate dehydrogenase (IDH), glucosephosphate isomerase (GPI), and transferrin (TFN). The other 22 proteins examined were monomorphic in their electrophoretic expression. Banding patterns for individuals were identical in heart and white muscle, but there were many variations in patterns among muscle, liver, and eye tissues. Esterase variations observed among individuals could not be replicated and this enzyme was excluded from further analysis. Two three-banded IDH phenotypes observed were typical of heterozygotes for a dimeric enzyme. The mobility of the IDH variant relative to the mobility

TABLE 2.—*Genotype distributions and allele frequencies for transferrin* TFN *and glucosephosphate isomerase* GPI-1 *in rainbow smelt from sample sites in western Lake Superior during 1977–1978. Sites are ordered from south to north along the Minnesota shoreline. Lower numbered allele codes for the slower-migrating protein. All samples were collected during the spawning run (April–May) except one trawl sample (Duluth Flats) during October.*

	Transferrin					Glucosephosphate isomerase				
	Genotype distribution			Allele frequency		Genotype distribution			Allele frequency	
Sample sites	(92/92)	(92/100)	(100/100)	(92)	(100)	(100/100)	(100/243)	(243/243)	(100)	(243)
Duluth Harbor	4	37	96	0.164	0.836	62	10	0	0.930	0.070
Duluth Flats	2	10	20	0.219	0.781	30	2	0	0.969	0.031
Talmadge River	1	15	16	0.266	0.734	32	0	0	1.000	0.000
Knife River	0	10	22	0.156	0.844	31	1	0	0.984	0.016
Split Rock River	0	6	26	0.094	0.906	31	1	0	0.984	0.016
Beaver River	0	6	26	0.094	0.906	62	2	0	0.984	0.016
East Beaver Bay	1	16	76	0.097	0.903	61	5	0	0.962	0.038
Poplar River	1	1	30	0.047	0.953	31	1	0	0.984	0.016
Cascade River	0	4	27	0.065	0.935	30	2	0	0.969	0.031
Durfee Creek	1	9	22	0.172	0.828	30	2	0	0.969	0.031
Brule River	0	9	23	0.141	0.859	29	3	0	0.953	0.047
Grand Portage	5	26	65	0.187	0.813	57	7	0	0.940	0.060

of the most common allele was 0.71. The rare homozygote (*71/71*) was not observed. The frequency of *IDH(71)* in samples collected during 1982 from Duluth Harbor and the Beaver River was too low (0.0083) to be useful for stock discrimination.

Variation of GPI and TFN in samples collected during 1977 and 1978 was useful for potential identification of stocks (Table 2). The three phenotypes of TFN were interpreted as the expression of a monomeric protein with two alleles, *TFN(92)* and *TFN(100)*, at a single locus. Genotypic frequencies at *TFN* (Table 2) did not deviate significantly from Hardy–Weinberg equilibria. The banding patterns for GPI suggested a dimeric enzyme genetically controlled by two loci, *GPI-1* and *GPI-2*. Locus *GPI-1* was polymorphic for two alleles designated *GPI-1(100)* and *GPI-1(243)*. The rare homozygote (*243/243*) was not observed in this study; however, it was found in rainbow smelt from Whitefish Bay in eastern Lake Superior (Schreiner 1980). The frequencies of phenotypes at *GPI-1* (Table 2) conformed to Hardy–Weinberg expectations in all samples. Schmidtke et al. (1975) examined 17 individuals of *Osmerus eperlanus* and found that products of the faster migrating locus (*GPI-2*) were polymorphic. In this study, only *GPI-1* was polymorphic.

There were no significant differences in frequencies of *TFN* and *GPI-1* alleles at given locations within or between years (Table 3). Therefore, samples collected during both years from an individual site were combined. Further analyses were based on the pooled data sets.

There was no significant evidence of genetic heterogeneity among locations for *GPI-1*. At *TFN*, however, highly significant differences ($P < 0.005$) in allele frequencies were observed among the collection locations; frequencies changed abruptly at the middle section (statistical zone M2) of the sampling area (Fig. 1).

Cluster analysis of genetic distances revealed two distinct clusters (Fig. 2). One consisted of samples from the pound net and streams in the East Beaver Bay area (zone M2), the other included pound net and stream samples taken in the Grand Portage (zone M3) and Duluth (zone M1) areas. The Talmadge River was not grouped in either cluster due to a high frequency of *TFN(92)* and fixation at *GPI-1* (Table 2).

Analysis of 60 individuals (each) collected from East Beaver Bay and Duluth Harbor during 1982 failed to detect any variation at *GPI-1* (*TFN* was not analyzed during 1982). Failure to observe the rare allele *GPI-1(243)* probably was due to inadequate sampling during 1982.

The data suggest that at least three rainbow smelt stocks exist along Minnesota's shoreline. Although genetic differences were not detected between rainbow smelt from northern and southern areas, it seems unlikely that migration and subsequent mating between these groups could occur without affecting allele frequencies in the middle area. The rainbow smelt from the

TABLE 3.—*Chi-square analyses of allele-frequency differences for transferrin* TFN *and glucosephosphate isomerase* GPI-1 *in rainbow smelt within and between years. Duluth Harbor, East Beaver Bay, and Grand Portage were sampling locations for commercial pound nets. Rainbow smelt from the Beaver and French rivers were sampled by dip net.*

		TFN		*GPI-1*	
Sample site	Dates compared	χ^2 (df)	*P*	χ^2 (df)	*P*
Duluth Harbor	Apr 29, 1977 May 9, 1977	1.19 (2)	>0.50		
East Beaver Bay	Apr 29, 1977 May 8, 1977	1.56 (2)	>0.40		
Grand Portage	May 7, 1977 May 13, 1977	2.80 (2)	>0.25		
Duluth Harbor	Apr 25, 1978 May 9, 1978	0.75 (2)	>0.75		
Duluth Harbor	1977 1978	2.81 (2)	>0.25	0.46 (1)	>0.50
East Beaver Bay	1977 1978	2.82 (2)	>0.25	0.16 (1)	>0.70
Grand Portage	1977 1978	2.96 (2)	>0.25	1.44 (1)	>0.20
Beaver River	1977 1978			0.00 (1)	>0.99
French River	1977 1978			1.97 (1)	>0.15

northern and southern areas probably represent separate stocks because the areas are separated by over 240 km of shoreline. We are unaware of any evidence for natal homing by rainbow smelt (as a result of imprinting in the natal stream). However, the potential for reproductive segregation through reappearance of adults in the vicinity of the natal stream has been documented. McKenzie (1964) found that rainbow smelt in the Miramichi River system of

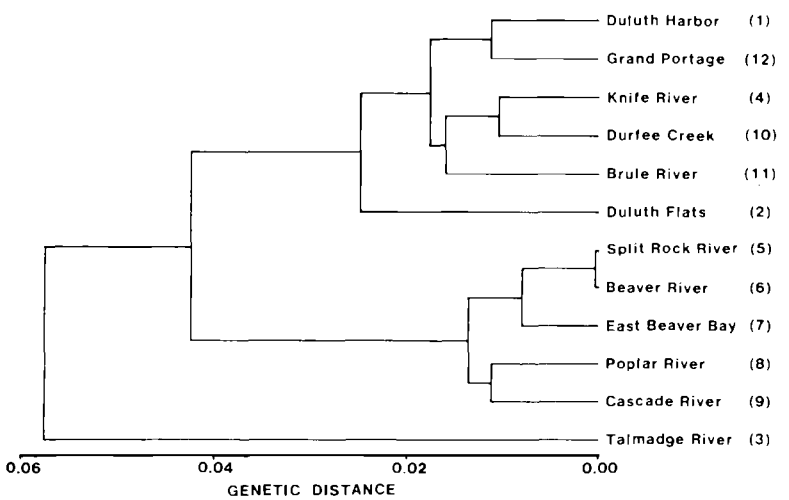

FIGURE 2.—*Cluster analysis based on Roger's genetic distance, calculated from transferrin* TFN *and glucosephosphate isomerase* GPI-1 *allele frequencies for rainbow smelt from 12 sampling locations in western Lake Superior during 1977–1978. Site numbers are those of Fig. 1.*

eastern Canada returned and spawned in the same stream or in streams within 8–12 km in subsequent years, and that only 0.05% moved as far as 80 km after spawning. Fréchet et al. (1983) provided evidence that anadromous rainbow smelt do not home to the natal stream, based on minimal biological differences among spawners from geographically proximate rivers in the St. Lawrence River system. Their analyses of variability in meristics, growth, and fecundity, however, revealed the existence of geographical groupings of spawning rainbow smelt and indicated that open-water migrations were limited to the geographical area of origin and adjacent areas. An earlier study of rainbow smelt in the St. Lawrence River (Magnin and Beaulieu 1965) suggested that spring and fall migrations were commonly as great as 100–200 km upstream and downstream, though no movement into the open water of the Gulf of St. Lawrence was noted. No detailed studies of rainbow smelt movements in western Lake Superior are available. Despite the extensive movements of rainbow smelt reported in the St. Lawrence, it appears that spatial isolation associated with residence in or returns to the vicinity of natal areas (as compared to more precise homing to natal streams) is a possible mechanism for maintenance of stock differences within this species.

An alternative hypothesis is that the low frequency of the *TFN(92)* allele in the central region is due to the existence of selective pressures. An example of the potential for selection involves the documented association of TFN phenotypes with differential resistance to bacterial kidney disease in coho salmon *Oncorhynchus kisutch* (Suzumoto et al. 1977) and with differential weight gain in rainbow trout *Salmo gairdneri* (Reinitz 1977). Large postspawning mortalities of rainbow smelt have occurred periodically along sections of the shoreline of Lake Superior. After a die-off in 1977, Schaefer et al. (1981) found the greatest number of dead fish near Duluth and none between the Beaver and Cascade rivers in zone M2. No observations were made in zone M3. They suggested that temperature stress on spawning rainbow smelt increased their susceptibility to fungus infections and promoted osmoregulatory imbalance. The regional differences in TFN phenotypes may be related to the frequent postspawning die-offs in the southern region and indicate selective differences among TFN phenotypes (Suzumoto et al. 1977). The available information suggests a potential selection mechanism for the difference observed between zones M1 and M2. No explanation is available for the similarity between zones M1 and M3.

Although studies of a comparable number of loci are not available, rainbow smelt in Minnesota waters of Lake Superior appear to be relatively monomorphic when compared to other fishes (Nevo 1978), at least with regard to electrophoretic characters (only four loci were polymorphic among those sampled). This observation is similar to that reported for rainbow smelt from Lake Erie where no polymorphisms were detected in an electrophoretic examination of seven enzymes (MacCrimmon et al. 1983). The apparent low level of genetic diversity in Great Lakes rainbow smelt may be a result of a founder effect that occurred if only a few individuals colonized each lake. The apparently discrete stocks in Lake Superior and the apparent low level of genetic diversity should be considered in future studies and management of the species. Stock structure of Lake Superior rainbow smelt is examined further in terms of population characteristics by Luey and Adelman (1984, this issue).

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