



Genetic Relationships among Smelt, Genus *Osmerus*

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GENETIC RELATIONSHIPS AMONG SMELT, GENUS *OSMERUS*.—The genus *Osmerus* is represented by anadromous and landlocked forms in the Pacific, Arctic and Atlantic oceans and their drainages. Despite numerous efforts to clarify taxonomy within the genus including a systematic revision of the *Osmeridae* (McAllister, 1963), the relationships remain obscure. McAllister (1963) divided *Osmerus* into a European *O. eperlanus eperlanus* and an Arctic, Pacific and western Atlantic *O. e. mordax*, but indicated that should sympatric noninterbreeding populations of these two subspecies be found, it would be necessary to consider them full species.

Scott and Crossman (1973) and McAllister et al. (1980) divided the genus into two species, *O. eperlanus* of the European Atlantic coast and *O. mordax* of the Pacific, Arctic and western Atlan-

tic coasts. The latter was separated into two subspecies, *O. m. mordax* for the western Atlantic smelt, and *O. m. dentex* for the Pacific and Arctic forms. These divisions were based on descriptions by Kliukanov (1969) of meristic and morphometric characters as well as his reported sympatry of *O. m. dentex* and *O. eperlanus*. The present taxonomy is not in accord with that presented by McAllister (1963), and Scott and Crossman (1973) regarded the data of Kliukanov (1969) as less than satisfactory. Additionally, McAllister (pers. comm.) has unpublished data under study which suggest there are at least two taxa in Europe which are now called *O. eperlanus*, a western anadromous form ranging from Ireland and France to Poland and an eastern lacustrine form found in lakes and the less saline portions of the Baltic from Denmark to the USSR. Gill raker counts distinguish most and multivariate analysis almost all specimens. Whether these are full species or subspecies remains to be determined.

Further perplexity in systematic relationships is evidenced in a size dimorphism in freshwater forms. A doctoral thesis by Delisle (1969) reports on pygmy and normal-sized populations of *Osmerus* in Heney Lake, Quebec, which differed in growth rate, spawning time and morphology. Copeman (1977) found the Heney pygmy was morphologically nearly identical with a Green Lake, Maine, pygmy population, and that normal-sized populations clustered together with some separation of anadromous and freshwater forms. The pygmy and anadromous populations may comprise two distinct species, with the normal-sized freshwater populations simply representing landlocked populations of the anadromous species. McAllister (pers. comm.) is currently comparing known populations of the pygmy form, including a population in Utopia Lake, New Brunswick, with the normal-sized species and believes the name *O. spectrum* Cope may be available for the pygmy should it be accorded specific status. The conclusion of McPhail and Lindsey (1970) that *Osmerus* probably forms a systematic complex which is not yet understood, continues to exemplify the confusion and need for further information.

The purpose of this report is to present the results of a preliminary electrophoretic investigation of the genetic relationships of *O. mordax* and *O. eperlanus* and as such represents the first comparative study within the genus.

TABLE 1. PROTEINS, LOCI, AND BUFFER-TISSUE COMBINATIONS USED IN THE PRESENT STUDY. Enzyme Commission numbers are listed after each enzyme.

Proteins	Loci	Tissue	Buffer ²
General Protein	GP	Muscle	CT
Glucosephosphate isomerase (5.3.1.9)	GPI-1	Muscle	CT
	GPI-2	Muscle and liver	CT
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3PDH	Muscle and liver	CT
Isocitrate dehydrogenase (1.1.1.42)	IDH-1	Muscle	CT
	IDH-2	Liver	CT
Lactate dehydrogenase (1.1.1.27)	LDH	Muscle and liver	R
Malate dehydrogenase (1.1.1.37)	MDH-1	Muscle and liver	CT
	MDH-2	Muscle	CT
Peptidase (3.4.11) ¹	PEP-1	Liver	R
	PEP-2	Muscle and liver	R
Superoxide dismutase (1.15.1.1)	SOD-1	Muscle and liver	CT
	SOD-2	Muscle and liver	CT

¹ Glycyl-L-Leucine as substrate.

² CT = Clayton and Tretiak (1972); R = Ridgway et al. (1970).

Materials and methods.—Separate collections of *O. m. dentex*, *O. m. mordax* and *O. eperlanus* (sensu McAllister et al., 1980) were obtained in 1979. Two samples of *O. m. dentex* were collected from the western coast of Alaska; one sample was from Kotzebue Sound near the Baldwin Peninsula and the other was from the Kuskokwim River near the city of Bethel. *O. eperlanus* were obtained from Lake IJssel in the Netherlands, and *O. m. mordax* were from Lake Huron, Canada, which resulted from plantings in Crystal Lake, Michigan, which were themselves obtained from New England (Van Oosten, 1937). Whole fish were shipped frozen on dry ice by collecting agencies and stored at -20 C in the laboratory. White muscle and liver samples were dissected from partially thawed smelt immediately prior to electrophoresis; tissue preparation methods followed those of Krueger (1980). Horizontal starch gel electrophoresis as outlined by May et al. (1979) was used to detect protein variants. Two buffer systems were used: 1) a discontinuous Tris, citric acid, lithium hydroxide, boric acid buffer system described by Ridgway et al. (1970); and 2) an amine citrate buffer described by Clayton and Tretiak (1972). Staining procedures generally followed those given by Allendorf et al. (1977). Genetic nomenclature used here is that proposed by Allendorf and Utter (1979), and bands on the gels were designated by their mobilities relative to those of Lake Huron samples which were designated 100.

Genetic distances (Rogers, 1972) were calculated based on data from 13 loci, and the estimated evolutionary tree produced by the distance Wagner procedure (Farris, 1972). The root of the Wagner tree was estimated as the midpoint between the two most divergent phyletic lines under the assumption of equal evolutionary rates.

Results and discussion.—Banding patterns observed for eight proteins represent the products of a minimum of 13 loci (Table 1). Six of these loci were polymorphic among the four collections **GP**, **GPI-1,2**, **IDH-2**, **MDH-2** and **PEP-2** (Table 2). Bands of identical mobility among samples were observed for **G3PDH**, **IDH-1**, **LDH**, **MDH-1**, **PEP-1** and **SOD-1,2**.

The genetic distances (Table 3) and the Wagner tree (Fig. 1) indicate a relatively large genetic distance between the Pacific and the Atlantic groups, while the distance between the two Atlantic forms is small. The results are not in accord with what would be predicted by current classification (Scott and Crossman, 1973; McAllister et al., 1980) under the hypothesis that conspecific and closely related species demonstrate consistent levels of genetic (allozyme) similarity (Aise, 1974). The two Alaskan samples show the expected minimal genetic distance for geographically proximate populations; however, the genetic distance between Lakes Huron and IJssel (0.135, Table 3) is smaller than would be expected for congeneric

TABLE 2. ALLELIC FREQUENCIES AND SAMPLE SIZES FOR SIX POLYMORPHIC LOCI WITHIN FOUR SAMPLES OF SMELT.

Locus		Kuskokwim River	Kotzebue Bay	Lake Huron	Lake IJssel
GP	100	0.0	0.0	1.00	1.00
	82	1.00	1.00	0.0	0.0
	n	4	4	4	4
GPI-1	100	0.0	0.0	1.00	1.00
	60	1.00	1.00	0.0	0.0
	n	4	4	4	4
GPI-2	100	0.0	0.0	1.00	0.0
	95	1.00	1.00	0.0	0.0
	83	0.0	0.0	0.0	1.00
	n	7	8	8	8
IDH-2	100	0.0	0.0	1.00	1.00
	113	1.00	0.93	0.0	0.0
	86	0.0	0.07	0.0	0.0
	n	4	7	7	3
MDH-2	100	1.00	1.00	1.00	0.12
	114	0.0	0.0	0.0	0.44
	87	0.0	0.0	0.0	0.44
	n	8	8	8	8
PEP-2	100	0.0	0.0	1.00	1.00
	108	1.00	1.00	0.0	0.0
	n	5	5	3	3

species. In addition, the genetic distances between the Alaskan samples and the Atlantic samples (0.382–0.443, Table 3) are in the range expected for congeneric species (Avice, 1974).

Implications of a protein based bipartite division of the genus *Osmerus* into Atlantic and Pacific forms might necessitate revision of zoogeographical accounts under current phylogeny. McAllister (1963) attributed derivation of all smelt genera to an origin in the North Pacific or adjacent Arctic Ocean. The European Atlantic form (*O. eperlanus*) was proposed to have

TABLE 3. COEFFICIENTS OF GENETIC IDENTITY (ABOVE DIAGONAL) AND ROGERS (1972) GENETIC DISTANCE (BELOW DIAGONAL) FOR SMELT.

	Kuskokwim River	Kotzebue Bay	Lake Huron	Lake IJssel
Kuskokwim River	—	1.000	0.615	0.562
Kotzebue Bay	0.005	—	0.619	0.565
Lake Huron	0.385	0.382	—	0.877
Lake IJssel	0.443	0.440	0.135	—

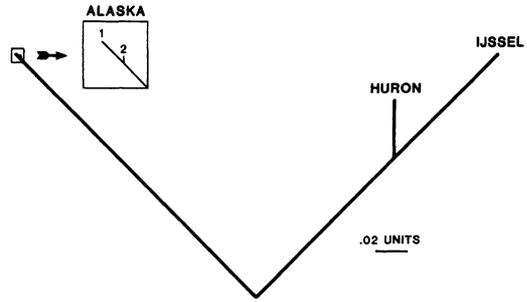


Fig. 1. Tree diagram produced by the distance Wagner procedure (Farris, 1972) based on Rogers genetic distance coefficients (Rogers, 1972) between smelt collections. Branch lengths are proportional to inferred patristic distances. The root was estimated as the midpoint of the path from *O. m. dentex* (Kuskokwim River) and *O. eperlanus*, those two samples being separated by the greatest estimated patristic difference. Inset is enlarged five times to show branch lengths.

developed from a westward movement along Arctic Russia to the White Sea, with subsequent spread to the Baltic region prior to or during Pleistocene glaciation. After deglaciation, the Baltic populations were geographically isolated and became the present *O. eperlanus* type. The origin of the eastern North American form was ascribed to a migration from the Pacific across Arctic Canada during a more recent interglacial period. Subsequent cooling resulted in the isolation of Pacific and eastern North American populations. The incomplete differentiation of these forms was assumed to be the result of either their recent origin during the hypsithermal or hypsithermal introgression of populations which had separated earlier during an interglacial period. The inferred patristic differences in the Wagner tree (Fig. 1) would make the postulated routes of migration and past isolating mechanisms seem less probable. However, the conflict between protein and morphological data should be resolved.

The present study represents a preliminary venture in *Osmerus* taxonomy, future investigations should certainly include greater numbers of loci (Gorman and Renzi, 1979) and perhaps other members of the Osmeridae to more effectively evaluate systematic relationships. The implications of the present study could be extensive in terms of the taxonomy and phylogeny within the genus *Osmerus*, and warrant further study. Protein data, it appears, can make a useful contribution to smelt taxonomy.

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KARYOLOGICAL STUDIES IN FIVE TETRAODONTIFORM FISHES FROM THE INDIAN OCEAN.—The tetraodontiform fishes are specialized teleosts of the tropical and subtropical Atlantic and Indo-Pacific oceans. This order comprises eight families with nearly 65 genera and approximately 320 species (Nelson, 1976; Breder and Clark, 1947; Fuhrman, 1967; Tyler, 1968). In an attempt to resolve some systematic problems, chromosomal studies have been undertaken in five species of Indian tetraodontiforms.