[Journal of the Arkansas Academy of Science](https://scholarworks.uark.edu/jaas)

Volume 39 | Article 15

1985

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HETEROGENEITY OF THE SPAWNING POPULATIONS OF SURF SMELT IN THE STATE OF WASHINGTON

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ABSTRACT

Biometric comparisons of three spawning populations of surf smelt, one from Pacific Coast and two from Puget Sound, were made. The Puget Sound populations (Hood Canal and Utsaladdy) were more similar to each other compared to the ocean populations. The Hood Canal and Utsaladdy smelt exhibited least distance function, D^2, and greater overlap of meristic characters compared to the Lapush fish. It was postulated that the Puget Sound smelt populations were derived from the ocean smelt some 13,000 or more years ago.

INTRODUCTION

The surf smelt, *Hypomesus pretiosus* is distributed in the eastern Pacific from Prince William Sound, Alaska to Monterey Bay, California (McAllister, 1963). The surf smelt occurs on the Washington coast as well as in Puget Sound.

Thompson (1936) observed surf smelt spawning season to extend from May to September on the outer coast of the Olympic Peninsula, Washington, in the vicinity of Cedar Creek; in Puget Sound it extends from May to the following March but smelt do not spawn on all of the beaches at the same time (Schaefer, 1936).

There has been no detailed biometric study to investigate population heterogeneity. This paper discusses the biometric comparisons of three spawning populations and evaluates the origin of the surf smelt populations in the State of Washington.

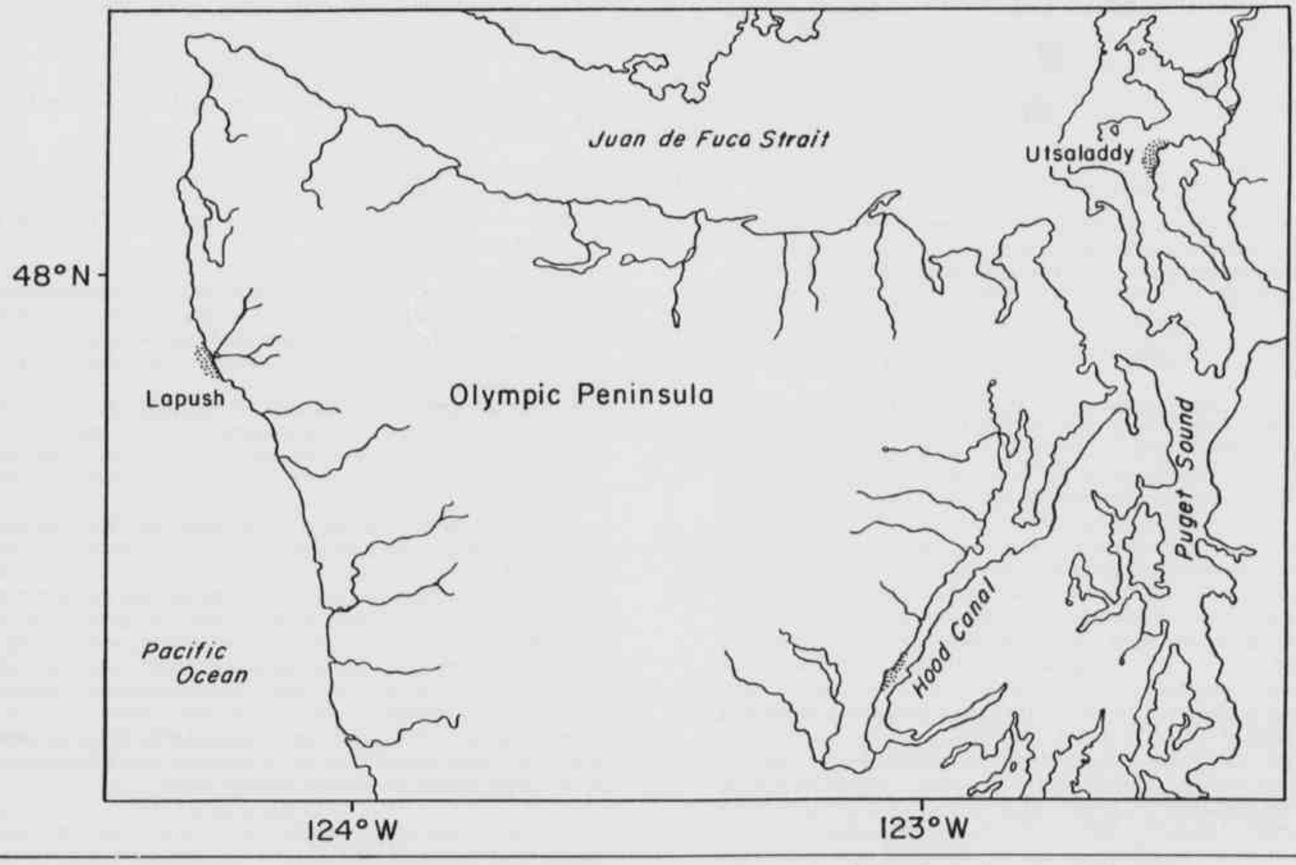

Figure 1. Spawning localities for surf smelt at Hood Canal and Utsaladdy in Puget Sound and Lapush on the coast of Washington.

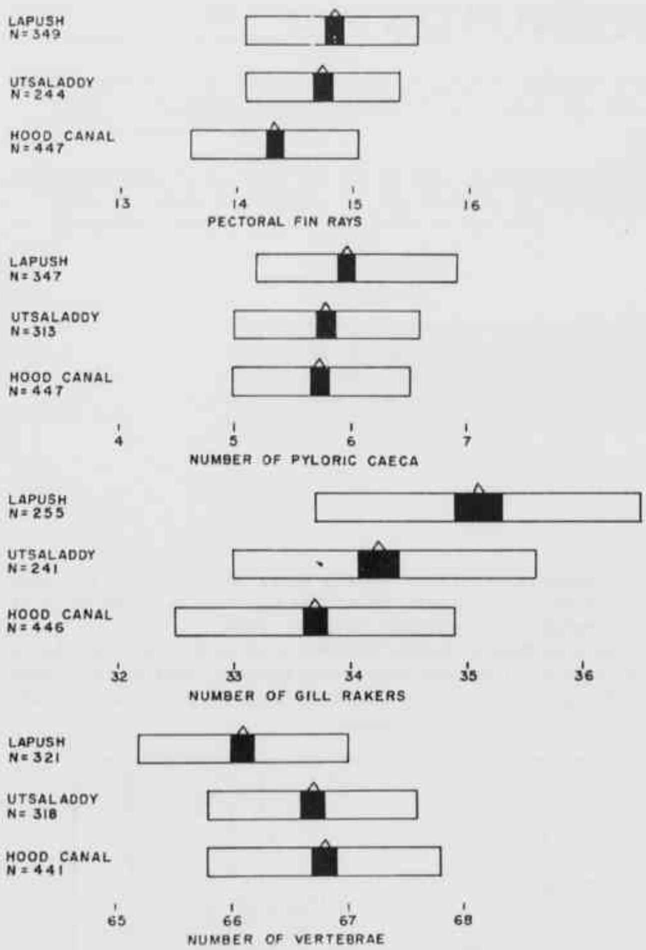

Figure 2. Meristic statistics plots showing mean (central triangle), two standard errors on either side of the mean (solid bar), and one standard deviation on each side of the mean (hollow bar).

MATERIALS AND METHODS

Three spawning populations, from Lapush on the Pacific Coast, and Utsaladdy and Hood Canal in Puget Sound were selected for a detailed study (Fig. 1). The smelt spawn during summer (May - October) at Lapush and Utsaladdy and in the fall (August - December) in Hood Canal. All the smelt samples for this study were collected in 1962 and 1963 as the fish moved toward the beaches for spawning.

Smelt from Utsaladdy were obtained from the catches of a commercial fisherman who fished under my supervision using a 61 m long beach seine having 3.5 cm stretched mesh size in the wings and 3.2 cm mesh size in the 30.5 m long center portion of the seine. I collected the Hood Canal samples by a 37 m long beach seine having 3.8 and 1.9 cm stretched mesh size in the wings and the bag, respectively. The Lapush samples were obtained by the seine used at Hood Canal, from the Seattle fish market, and from the Quillayute Indians who used a 110 m long beach seine of 2.5 cm stretched mesh size.

Soon after collection, fish were preservd in 10% formalin. From these collections, samples of 100-150 smelt were taken to include the extreme size range represented in the collections and equal numbers of males and females if available. From each fish, data were recorded for the counts of vertebrae, gill rakers, pyloric caeca, and pectoral fin rays; for measurements of standard length, predorsal length, pectoral fin

Table 1. Mahalanobis D^2 and percent overlap between populations.

Populations Compared	D^2	Percent Overlap
Hood Canal vs Utsaladdy	0.34	77.2
Hood Canal vs Lapush	2.04	47.4
Utsaladdy vs Lapush	1.08	60.4

length, head length, body depth, and eye diameter, all in millimeters. Statistical significance was expressed at the 0.01 level.

RESULTS

Meristic Characters: Regression analyses of standard length on the numbers of vertebrae, gill rakers, pyloric caeca and pectoral fin rays showed no correlations. For any given character, differences between any two spawning populations were tested by the least significant difference (1st) analysis (Steel and Torie, 1960).

Vertebrae — There were no differences in the mean vertebral counts among the sexes or among the samples within the localities. The numbers of vertebrae were not different between the year classes but the differences among the localities were significant. There was no significant difference between the Hood Canal and Utsaladdy smelt, but these two populations showed significant differences with the Lapush fish that had the lowest mean vertebral count (Fig. 2).

Gill rakers — Within each of the spawning localities, the average numbers of gill rakers were not different either for the sexes or among the samples. Yearclass differences within the localities approached significance. Each spawning population differed significantly from the others with the Hood Canal smelt having the lowest and the Lapush fish the highest count (Fig. 2).

Pyloric caeca — No differences were evident between the sexes, samples, and year classes within the localities. The Lapush fish had significantly higher average pyloric caecal counts than did those of Utsaladdy and the Hood Canal smelt (Fig. 2).

Pectoral fin rays — Within each of the spawning populations the average pectoral fin ray counts were the same among the sexes, the samples, and the year classes. The Lapush and the Utsaladdy populations had similar counts (Fig. 2) that were significantly higher than that of the Hood Canal smelt.

The Lapush smelt can be separated from the Hood Canal fish by all four (100%) of the meristic characters used in this study and from the Utsaladdy fish by three characters (75%). The Puget Sound (Utsaladdy and Hood Canal) spawning populations showed heterogeneity in only two characters (50%).

Generalized distance function, D^2 (Mahalanobis, 1936) was used to separate the smelt spawning populations. This function provides a measure of distance between two populations based on a combination of characters and from this function percent overlap was determined, an indication of the maximum extent to which two populations share identical characters (Royce, 1957; Mais, 1972; Sharp et al., 1978). The D^2 and overlap estimates for the smelt populations using all the four meristic characters are given in Table 1. The Puget Sound (Hood Canal and Utsaladdy) populations exhibited the least distance function and greater percent overlap of characters compared with the Lapush population. The Hood Canal and Lapush populations were widely separated as indicated by high D^2 and low overlap values.

Morphometric Characters: Linear regression analyses were used for all the relationships. If the differences between sexes in one area are significant for a particular character, then, for convenience sexes are

Table 2. Details of regression of body part (Y) on standard length (X) for male surf smelt and body part adjusted to 125 mm standard length.

Body Part	Locality	N	Regression Equation	S_{yx}	Adjusted Body Part (mm)
Head Length	Hood Canal	251	0.1593 X + 4.8024	1.3501	24.71
	Utsaladdy	231	0.1901 X + 0.2941	1.5702	24.05
	Lapush	176	0.1997 X + 0.8872	1.2385	25.84
Predorsal Length	Hood Canal	251	0.4971 X + 0.2485	1.0696	62.38
	Utasladdy	231	0.5067 X - 2.0052	1.2385	61.33
	Lapush	176	0.5106 X - 1.7024	1.1986	62.12
Body Depth	Hood Canal	202	0.1856 X + 0.9412	0.9681	24.14
	Utsaladdy	181	0.2394 X - 5.0967	1.1726	24.83
	Lapush	127	0.1576 X + 4.4988	1.5348	24.20
Pectoral Fin Length	Hood Canal	251	0.1460 X + 1.4713	0.6365	19.72
	Utsaladdy	231	0.1267 X + 3.4630	0.7584	19.30
	Lapush	176	0.1316 X + 1.8290	0.7348	18.27

treated separately for that character in all three areas. For the pectoral fin length-standard length of the females and the eye diamester-head length comparison, error mean squares were used in convariance analyses for testing locality differences. For the rest of the comparisons, mean squares due to samples and years were used in the covariance analyses, as the differences between the samples and between the years or both were significant within the localities. Adjusted means were calculated for a standard length of 125 mm and a head length of 25 mm which were approximately the averages of the smelt from all the areas. The regression equations are given in Table 2, 3, and 4.

Head length on standard length — Sexual demorphism was exhibited by the Hood Canal and Lapush populations. Males showed significant differences between the Utsaladdy and Lapush smelt and the Lapush fish had greater head length than the Puget Sound populations (Table 2). The female smelt of Utsaladdy and Hood Canal were not different in this character but differed significantly from the Lapush fish. The Hood Canal and Utsaladdy females had the longest and smallest head lengths, respectively (Table 3).

Peredorsal length on standard length — Sexual dimorphism was present among the Utsaladdy and Hood Canal populations. There were no differences between the three populations and adjusted predorsal lengths are shown in Tables 2 and 3.

Body depth and standard length — The Lapush and Hood Canal populations showed no differences between sexes but the Utsaladdy smelt exhibited sexual dimorphism with the the females having deeper bodies than the males (Tables 2 and 3). Males of the three populations showed no significant difference but among the females, the Utsaladdy population had significantly deeper bodies than did the Lapush populations (Table 3).

Pectoral fin length on standard length — The three smelt populations showed sexual dimorphism. Comparison of the populations by sexes indicates no differences between Hood Canal and Utsaladdy but these Puget Sound populations were significantly different from the Lapush smelt in having longer pectoral fins (Tables 2 and 3).

Eye diameter on head length — No sexual dimorphism was present within the populations, hence data for sexes were combined for further analysis. Each spawning population was different from the other two and the Utsaladdy smelt had the largest eye diameter followed by Lapush and Hood Canal (Table 4).

Of the five morphometric characters, the males of the Hood Canal population showed significant differences in one (20%) and two (40%) characters with the Utsaladdy and the Lapush populations, respectively, whereas the Utsaladdy and the Lapush populations differed in three (60%) characters. As for the females, the Hood Canal differed in one (20%) and three (60%) characters with those of Utsaladdy and Lapush fish, respectively. The Utsaladdy and Lapush females differed significantly in four (80%) characters.

Table 3. Details of regression of body part (Y) on standard length (X) for female surf smelt and body part adjusted to 125 mm standard length.

Body Part	Locality	N	Regression Equation	S_{yx}	Adjusted Body Part (mm)
Head Length	Hood Canal	198	0.1660 X + 4.3468	0.8034	25.09
	Utsaladdy	90	0.1836 X + 0.9572	1.3642	23.90
	Lapush	187	0.2019 X - 0.2722	1.1642	24.96
Predorsal Length	Hood Canal	198	0.4985 X + 0.6888	0.8995	63.00
	Utsaladdy	90	0.5191 X - 3.0854	1.1648	61.80
	Lapush	187	0.5183 X - 2.5543	1.2973	62.23
Body Depth	Hood Canal	198	0.1902 X + 0.6162	1.0735	24.39
	Utsaladdy	66	0.2177 X - 0.3606	1.8918	26.85
	Lapush	136	0.1719 X + 2.4986	2.0365	23.99
Pectoral Fin Length	Hood Canal	198	0.1135 X + 3.3850	0.6065	17.57
	Utsaladdy	90	0.1131 X + 3.5931	0.7483	17.73
	Lapush	187	0.1118 X + 3.2633	0.6704	17.23

DISCUSSION AND CONCLUSIONS

Recognition of populations is based on the establishment of recognizable and significant differences between them. One of the problems encountered in differentiating fish populations is that meristic characters may vary with size of fish. Such a relation was found for the vertebral counts (Tester, 1937; McHugh, 1942; Gosline, 1947) and gill rakers (Krefft, 1958). The smelt of my study showed no such relationship between the meristic counts and the fish lengths.

Utilization of more than one sample over a two-year period and two to three year classes within any one population maximized evaluation of usefulness of characters in differentiating the surf smelt populations.

The meristic characters, gill rakers, pectoral fin rays, and pyloric caeca exhibited clinical variation with the direction of the line being from Lapush to Hood Canal, i.e., from ocean to most interior. The vertebral counts demonstrated clinical variation from the interior (Hood Canal) to the ocean (Lapush). Schaefer (1936) also found a lower vertebral number for the ocean populations than the Puget Sound populations. Vladykov (1934) stated that meristic counts generally decreased from open to closed regions and marine to freshwater; with the exception of the vertebrae, the surf smelt essentially conformed to the above postulation.

Comparison of the three surf smelt populations by the meristic and morphometric characters revealed that the Utsaladdy population differed in more characters from the Lapush population spawning in the same season (Summer) than from Autumn spawning Hood Canal population. The D square function and the percent overlap yielded similar findings for the meristic character. Schaefer (1936) found the ocean smelt populations to differ from the Puget Sound populations in the vertebral counts and that not all the Puget Sound populations were different from each other.

Kilambi and DeLacy (1967) reported that the infestation by larval *Anisakis* was common among the Lapush smelt, rare in the Hood Canal fish, and the Utsaladdy population was free of this parasite. They postulated that these three surf smelt populations existed as distinct entities during at least part of the feeding phase, the Lapush population feeding along the outer coast and the Utsaladdy and Hood Canal populations in Puget sound. The absence of *Anisakis* from the Utsaladdy smelt indicates that feeding areas differed in some degree between the Puget Sound populations. Leong (1967) found that the Lapush smelt population differed from the Utsaladdy and Hood Canal populations in producing smaller but more eggs for a given weight of the smelt.

Choice of characters that are relatively free from the environmental influences is desirable when evaluating genetic differences. Blood factors are generally believed to be under genetic control. Stormont (1961) stated "...It is axiomatic in immunogenetics that all blood factors are inherited traits which are subject to little or no influence by the environment. Consequently, any differences which two or more subpopulations exhibit with respect to the incidence of common blood factors are fully meaningful even in the absence of information concerning the inheritance of blood factors....". Based on quantitative serological tests, Kilambi et al. (1967) concluded that the Utsaladdy and the Hood Canal smelt populations had similar erythrocyte antigen composition and therefore similar genetic composition but these two Puget Sound populations differed from those of Lapush.

Table 4. Regression of eye diameter (Y) on head length (X) and eye diameter adjusted to 25 mm head length.

Locality	N	Regression Equation	S_{yx}	Adjusted Eye Diameter (mm)
Hood Canal	449	0.1390 X + 1.9403	0.3101	5.41
Utsaladdy	321	0.1065 X + 3.2686	0.5112	5.93
Lapush	363	0.1943 X + 0.9322	0.4367	5.78

It is evident from the study of meristic and morphometric characters, parasite incidence and serology, that the Puget Sound smelt populations are more similar to each other than they are to the Lapush population. This greater similarity among the Hood Canal and Utsaladdy populations and their dissimilarity with the Lapush population might be related to the glacial history and the origin of Puget Sound. During the late Pleistocene (some 15,000 years ago), the Cordilleran ice sheet advanced from the mountains of western Canada into the Straight of Juan de Fuca and southward forming the Puget lobe. As the glacier retreated, sea water entered the glacially scoured troughs shortly before 13,500 years ago (Crandell, 1965). Accepting the concept of the eastern Pacific as the center of origin for osmerids (McAllister, 1963), the following concept is postulated for the origin of the Puget Sound smelt populations and for the extent of divergence of the populations.

Some 13,000 or more years ago, surf smelt must have entered Puget Sound during the recession of the Puget lobe in the Vashon Stade. After their entry, the smelt moved freely in the then estaurine sound waters. They must have attained maturity at different times of the year as a result of physiochemical and biological factors. Mixing of smelt in the Puget Sound must have continued over a long period after their original entry, whereas further invasion by the ocean smelt stopped. Possibly, with the passing of time, the smelt homed to different places in Puget Sound. Characters were influenced by the environmental conditions and were acted upon by natural selection. Divergence between the Lapush and Utsaladdy-Hood Canal populations is more than that between the Utsaladdy and Hood Canal because common ancestry for these two latter populations presumably continued for some time after their entry into Puget Sound.

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