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THE LIFE HISTORY AND ECOLOGY OF THE LONGFIN SMELT IN LAKE WASHINGTON

R. L. Dryfoos, 1965

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DRYFOOS, Robert Louis, 1939–
THE LIFE HISTORY AND ECOLOGY OF THE LONGFIN SMELT IN LAKE WASHINGTON.

University of Washington, Ph.D., 1965
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

THE LIFE HISTORY AND ECOLOGY OF THE LONGFIN SMELT IN LAKE WASHINGTON

by

ROBERT LOUIS DRYFOOS

A thesis submitted in partial fulfillment

of the requirements for the degree of

DOCTOR OF PHILOSOPHY

UNIVERSITY OF WASHINGTON

1965

Approved by Allan C. DeLacy

Department College of Fisheries

Date May 20, 1965

UNIVERSITY OF WASHINGTON

Date: April 12, 1965

We have carefully read the dissertation entitled The life history and ecology of the longfin smelt in Lake Washington submitted by Robert L. Dryfoos in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

In his dissertation on "The life history and ecology of the longfin smelt in Lake Washington" Mr. Dryfoos has demonstrated a pronounced ability to integrate the elements of his background into a solid basis for the investigation of a fishery biology problem which had gone virtually unnoticed at the very edge of the University of Washington campus. His recognition of the opportunity, his initiative in applying appropriate techniques for its study, and his awareness of the implications of his findings have resulted in a thesis that is not only of current interest but is certain to stand as a vital documentation of an important transitory condition in Lake Washington that might otherwise have passed without record. His further contribution to the taxonomy of the longfin smelt lies in a more usual research area but is also significant addition to knowledge about the fishes of the Pacific Coast of North America.

The particularly significant results of the thesis are the discoveries that (1) some populations of longfin smelt run their entire life cycle in fresh water; (2) the life cycle is completed in two years; (3) the present growth rate of smelt in Lake Washington is equal to or greater than that of some anadromous populations of longfin smelt; (4) there is a diel migration of smelt and of their chief food item, *Neomysis*; and (5) that structural deformities occur in an unexpectedly high proportion of longfin smelt from Lake Washington.

The study conducted and reported by Mr. Dryfoos is a worthy dissertation as it stands, but its value will surely be enhanced as present conditions in Lake Washington become modified, and future investigations seek to describe how the changing physical environment affects the biological components of the ecosystem.

DISSERTATION READING COMMITTEE: Allan C. DeLacy

Lauren R. Donaldson

R Van Cleve

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ACKNOWLEDGMENTS

I would like to express sincere gratitude to my major professor, Dr. Allan C. DeLacy. Dr. DeLacy provided excellent counsel and advice throughout the period of my graduate training. His suggestions and criticisms have significantly improved the quality of this thesis. I am indebted to Dr. Richard VanCleve, Dean of the College of Fisheries, Dr. Lauren Donaldson and Dr. Arthur Welander of the College of Fisheries, and to Dr. W. T. Edmondson of the Department of Zoology, who as members of my supervisory committee, aided by their constructive criticisms and always helpful suggestions. Dr. Max Katz of the College of Fisheries critically reviewed the manuscript and his helpful suggestions measurably enriched this thesis. Discussions with Dr. J. D. McPhail were both rewarding and thought provoking. The encouragement and kind assistance of other members of the faculty, staff, and graduate students of the College of Fisheries and the Zoology Department is sincerely appreciated.

During the field investigations the good-natured crew of the R. V. COMMANDO tolerated the many irregular hours which this study necessitated. My sincere thanks to Master Tom Oswold, Jr. and Engineer Olaf Rockness for their helpfulness and amiability.

The assistance of many other people in connection with the Harrison Lake collections and others who provided specimens of or data from longfin smelt from other areas is gratefully acknowledged. In addition, Dr. Thomas Northcote and Mr. Peter Ellickson of the University of British Columbia provided biological information regarding Harrison Lake.

This study was financed by a National Science Foundation Grant (GB-906). A fellowship awarded by the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service for the period September 1962--September 1964 was of material assistance. During the terminal phase of the analysis and writing of the thesis support was provided by a training grant from the Office of Resource Development (U. S. Public Health Service) to the College of Fisheries. The assistance of these organizations is gratefully acknowledged.

Finally, the understanding, cooperation, and steadfast encouragement of my beloved wife, Carol, contributed in many important ways to this study. Specifically she punched and verified 2,500 IBM cards, conducted the necessary correspondence, and typed the several drafts of this manuscript.

INTRODUCTION

The objectives of this study are (1) to describe the life history and ecology of the longfin smelt, Spirinchus thaleichthys (Ayres), in Lake Washington, (2) to determine the relationship between the Lake Washington population and populations of longfin smelt from other areas, and (3) to define the role of the smelt in the Lake Washington ecosystem.

Lake Washington is in the process of accelerating eutrophication due to the increasing input of treated sewage from Seattle and the suburbs surrounding the lake. A governmental body, the Municipality of Metropolitan Seattle, has been established to build new sewage treatment facilities and to divert the treated sewage into Puget Sound. This diversion will reduce the input of nutrients into the lake and will presumably reduce the productivity of the lake.

The limnology and zooplankton of Lake Washington have been studied several times in the past and the changes in limnological conditions with increasing eutrophication noted. Present conditions in the lake are being studied by Dr. W. T. Edmondson, of the University of Washington Department of Zoology, and the future changes in productivity will be documented. Although the zooplankton in the lake have received some attention, the resident fish populations have not been studied in detail.

There are no published data available on the growth rate, distribution, feeding, or predator relationships for any species of fish in Lake Washington. Even the species composition in the lake is not completely known. This study was conducted to provide this information for one species resident in the lake. Data obtained during this study will be the only data for fishes in Lake Washington collected systematically at the time of maximum production in the lake. As such, they will be of value for any future study concerning changes in the midwater fish populations as the lake reverts to a lower level of primary productivity.

Longfin smelt were first taken in Lake Washington in 1959 and 1960. This study was initiated in 1960 after examination of the specimens previously collected suggested a prolonged period of freshwater residence for a supposedly anadromous species. The first field collections of this study were made in the spring of 1962. The objectives of the field study were to learn something of the distribution of the smelt in the lake, to determine how much time they spend in the lake, and to obtain information on their growth in freshwater. This preliminary field study indicated that smelt were available in virtually all deep parts of the lake and that they underwent considerable diel changes of distribution. The data suggested that they were completing their entire life cycle within the lake, and that they were growing faster than some anadromous populations. Continuous freshwater residence had never been reported for this species or for the genus, although several other genera of smelt (Osmeridae) have freshwater representatives (McAllister, 1963). The evidence suggesting that freshwater residence was occurring, the fact that very little was known about the ecological requirements of any fish in Lake Washington, and the unique opportunity to study the lake at what may be its highest level of primary productivity made a full-scale research program desirable.

LITERATURE REVIEW

In 1863 Dr. W. O. Ayres described a new species of smelt, Osmerus thaleichthys from San Francisco Bay. He reported the fish to be quite common there and to be sold indiscriminately with other "smelt." He mentioned that he had never seen one over 7 inches in length and very few over 5 inches. A distribution from Monterey and then from San Luis Obispo, northward was attributed to this species by Jordan and Gilbert (1881, 1882). Gilbert (1895) identified with this species several young specimens from the Nushagak River, a tributary of Bristol Bay, Alaska. Jordan and Evermann (1896) erected the subgenus Spirinchus for O. thaleichthys Ayres and O. attenuatus Lockington. They gave the southern limit of distribution of O. thaleichthys as San Francisco and the northern limit as Bristol Bay. Evermann and Goldsborough (1907) referred to Gilbert's collection from the Nushagak River and added that Gilbert had obtained 5 more specimens. In their table giving the geographical distribution of fishes they indicated that O. thaleichthys were present in Puget Sound and British Columbia, southeastern Alaska, central Alaska, and the Bering Sea. Rutter (1908) reported that the adults ascended the Sacramento River to spawn in February and the young descended in April.

Kincaid (1919) reported O. thaleichthys to be common in Puget Sound waters, which in his definition included coastal

Schultz and Chapman also offered considerable information on life history. They stated that the species was anadromous and spawned in the Nooksack River from October to December. Young specimens, 41 to 53 mm., were obtained from the waters surrounding San Juan Island in August, 1932, and were described. Sexual dimorphism as indicated by the swelling of the scale pockets along the lateral line of the male was noted and described. They noted that this lateral swelling also occurred in mature males of S. lanceolatus and S. thaleichthys. Sexual dimorphism in coloration and enlargement of the fins was reported and it was observed that these sexually dimorphic characters were present only in breeding fish.

Spirinchus dilatus was distinguished from S. thaleichthys in having the pectorals shorter than the head and not extending beyond the insertion of the ventral fins. Schultz and Chapman mentioned that this was not always true for the immature and half-grown specimens. Spirinchus dilatus was reported to have a greater number of scales and anal rays than did S. thaleichthys.

Hart and McHugh (1944) provide additional notes on the life history of the longfin smelt. They examined a March, 1934, collection from Burrard Inlet, British Columbia, which included six males averaging 106 mm. and twenty-one females averaging 110 mm. The largest fish was 134 mm. long. These specimens were examined by them and found to be immature. They mentioned that the fish, assumed to be in their second year of life on the basis of their scale markings, were larger than those encountered in the spawning run in the Nooksack River. (Re-examination of the specimens by the author indicated they were post-spawning adults. This and the available evidence from the scales indicate these fish were in their third year of life. They were, therefore, comparable in length to those from Puget Sound of the same age.) Four specimens, 61 to 72 mm., were reported from the Fraser River at New Westminster. These young fish had fed entirely on the mysid, now called Neomysis awatchensis. The larger specimens from Burrard Inlet were found to have fed on euphausids while the smaller specimens had eaten copepods and cumaceans.

Rosa (1946) carefully compared large samples of S. starksi and S. thaleichthys from the San Francisco area and showed them to be distinct species. They differed in the length of the pectoral fin in relation to the origin of the ventral fin, the shape of the head, and in their spawning areas. He noted that collections of S. thaleichthys in San Francisco Bay did not show the sexual dimorphisms observed by Scofield (in Schultz and Chapman, 1934) in Sacramento River specimens taken near Walnut Grove. The largest specimen obtained by Rosa for S. thaleichthys was 92 mm. His data for length-frequency suggest that most of the adults were two years old.

McAllister (1963) recognized a cline in the characters used to distinguish S. dilatus from S. thaleichthys and found no valid characters for considering S. dilatus as a distinct species. He synonomized S. dilatus with S. thaleichthys. His conclusions were based upon specimens from Alaska (Dryfoos, 1961) as well as from California, Oregon, Washington, and British Columbia.

Spirinchus thaleichthys is only sparsely utilized by man throughout its range. However, Herald (1961) reports catches of more than 60,000 in a single 3-hour fishing period by oriental fishermen in San Francisco Bay. It is recognized as a food fish by the State of Washington Department of Fisheries. A local Indian and sport fishery--by dip net--exists in the Nooksack River each November. Clemens and Wilby (1961) mention that it has a fine flavor and has ready sale though the quantity is limited due to difficulty in locating the fish.

From the preceding discussion the following summary may be made. Spirinchus thaleichthys (Ayres) is an anadromous species occurring from the Gulf of Alaska to San Francisco Bay. Throughout this range a cline in some of their meristic and morphometric characteristics has been recognized. The fish spawn in the Nooksack River, Washington, from October to December and in the Sacramento River, California, in February. Young smelt, 61 to 72 mm. standard length taken near the mouth of the Fraser River, were found to be feeding on Neomysis awatchensis. The smallest specimen reported from saltwater was 41 mm. long and was collected in August in the waters adjacent to San Juan Island. A few localized fisheries represent the only utilization of this species by man.

Several limnological studies of Lake Washington have been made since the first one in 1911, which was limited to physical-chemical observations and notes on the phytoplankton (Kemmerer, Bovard, and Boorman, 1923). Scheffer and Robinson (1939) made the first thorough chemical and biological survey of the lake. Schultz and DeLacy (1935-1936) recorded the species of fish previously taken in Lake Washington. Scattergood (1949) gave data on the length and fecundity of kokanee (freshwater resident sockeye salmon, Oncorhynchus nerka) from North Bear Creek in the Lake Washington drainage for the year 1938. In 1949 and 1950 the planktonic copepods were studied by Comita (1953), and simultaneously, the seasonal variations in the phytoplankton were examined by Anderson (1954). Ajwani (1956) reviewed the literature pertaining to Lake Washington with special emphasis on the fishes. Edmondson, Anderson, and Peterson (1956) documented the first changes in biota associated with eutrophication of the lake. These changes in the zooplankton and phytoplankton were observed for the first time in 1955. A report on Metropolitan Seattle Sewerage and Drainage prepared by Brown and Caldwell (1958) contains considerable data on the nutrient inflow and outflow for

Lake Washington. The Municipality of Metropolitan Seattle (Metro) was established by a vote of the people in the Seattle area September 9, 1958. Metro was charged with the responsibility of developing a waste disposal program to end the pollution of adjacent salt- and freshwater bodies including Lake Washington. The present Metro construction schedule calls for the diversion of all treated sewage from the lake by 1966. Half of the treated sewage entering the lake was to be diverted by the end of 1965. Anderson (1961) and Edmondson (1961; 1963) reviewed the recent changes in Lake Washington up through 1958 as eutrophication continued. Shapiro (1960) suggested that a large population of nonmigratory *Diaptomus ashlandi* was the major factor producing a metalimnetic oxygen minimum in Lake Washington.

Although the limnology of the lake has been studied under the changing trophic conditions, the fish populations have received very little attention. No work has been published concerning the ecology, growth, distribution, or feeding of any resident fish population in Lake Washington.

METHODS

Sampling Program

The sampling program for Lake Washington was divided into standard sampling trips and irregular trips. The standard sampling trips were conducted each month from July, 1963, through July, 1964. The departure date for each of these 48-hour sampling periods was restricted to within seven days of the new moon. The average deviation from the night of the new moon was 2.3 days. The rationale for this restriction was to equalize, insofar as was possible, the nighttime light conditions throughout the year. This also maximized the effect of alternating daylight and darkness. Irregular sampling trips were conducted prior to the initiation of the standard sampling trips and were exploratory in nature. Later, they were conducted to provide data for specific purposes. Sampling was conducted with an Isaacs-Kidd midwater trawl. Table 1 gives pertinent data for all the midwater trawl sampling trips conducted on Lake Washington during this study.

Lake Washington arbitrarily was divided into four areas numbered from north to south (Figure 1). In this study no attempt was made to sample shallow marginal areas of the lake. The availability of the fish in the deep central area of the lake and the physical danger to the sampling gear near the precipitous

Table 1. Summary of midwater trawl sampling trips in Lake Washington

Vessel	Trip	Departure Date	Duration	Area	Day or Night	MWT Hauls
Commando	6209	May 7, 1962	3 hrs.	3	N	3
Commando	6212	June 19, 1962	3 hrs.	3	N	4
Commando	6216	July 10, 1962	4 hrs.	3	N	5
Commando	6218	Sept. 13, 1962	4 hrs.	3	N	6
Commando	6220	Oct. 11, 1962	6 hrs.	3, 4	N	9
Commando	6222	Dec. 7, 1962	7 hrs.	1, 2, 3	N	10
Commando	6223	Dec. 18, 1962	7 hrs.	3, 4	D	11
Commando	6302	Jan. 14, 1963	5 days	1, 2, 3, 4	D, N	80
Commando	6304	Mar. 8, 1963	6 hrs.	3, 4	N	9
HOH	6311	May 25, 1963	5 hrs.	4	D	5
HOH	6312	July 10, 1963	5 hrs.	3	D	10
Commando	6313	July 10, 1963	6 hrs.	3	D	13
*Commando	6314	July 18, 1963	2 days	1, 2, 3, 4	D, N	63
*Commando	6316	Aug. 13, 1963	2 days	1, 2, 3, 4	D, N	60
*Commando	6318	Sept. 17, 1963	2 days	1, 2, 3, 4	D, N	60
*Commando	6322	Oct. 14, 1963	2 days	1, 2, 3, 4	D, N	60
*HOH	6323	Nov. 14, 1963	2 days	1, 2, 3, 4	D, N	54
*Commando	6324	Dec. 17, 1963	2 days	1, 2, 3, 4	D, N	61
Commando	6325	Dec. 23, 1963	12 hrs.	3	D, N	14
Commando	6401	Jan. 2, 1964	11 hrs.	2, 3, 4	D, N	11
*Commando	6402	Jan. 14, 1964	2 days	1, 2, 3, 4	D, N	60
*Commando	6404	Feb. 6, 1964	2 days	1, 2, 3, 4	D, N	61
*Commando	6408	Mar. 17, 1964	2 days	1, 2, 3, 4	D, N	59
*Commando	6413	Apr. 15, 1964	2 days	1, 2, 3, 4	D, N	47
*Commando	6416	May 7, 1964	2 days	1, 2, 3, 4	D, N	50
*Commando	6420	June 11, 1964	2 days	1, 2, 3, 4	D, N	61
*Commando	6422	July 10, 1964	2 days	1, 2, 3, 4	D, N	63
Commando	6428	Oct. 21, 1964	8 hrs.	3	N	23

*Standard sampling trips

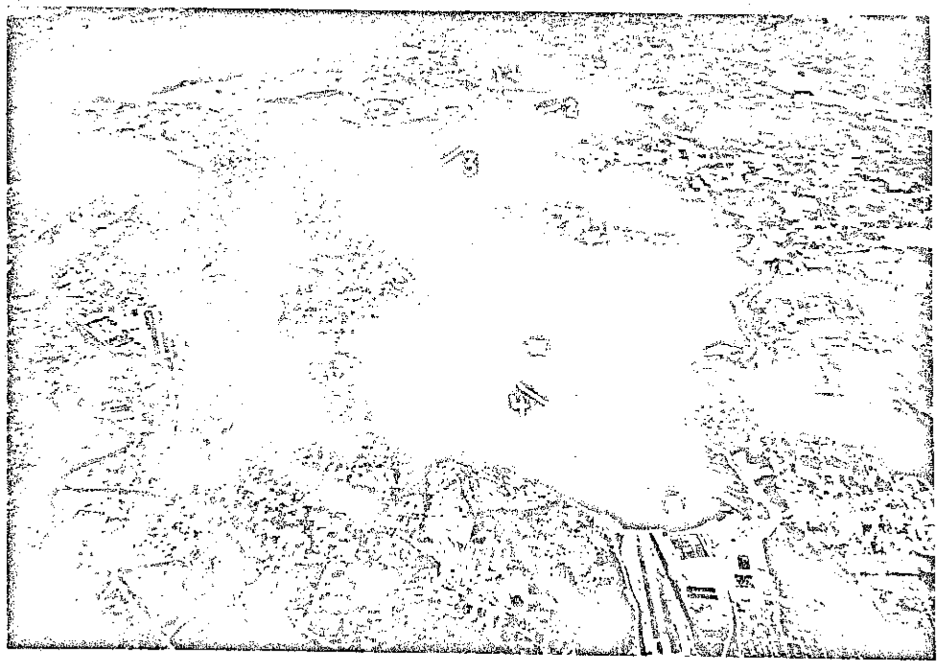


Figure 1. Aerial view of Lake Washington. The four sampling areas are designated by number. The standard stations are indicated by a white line. (Photograph by Pacific Aerial Surveys Inc., Seattle, was taken November, 1956.)

lake perimeter encouraged the study of the limnetic zone. The limnetic zone in the central part of Lake Washington (areas 2 and 3) is fairly uniform with a slight depression both east and west of a longitudinal axis near the center of the lake (Gould and Budinger, 1958). The average depth at these central stations was 30 fathoms. The division of this region into two areas (2 and 3) arbitrarily divided by the Evergreen Point Floating Bridge was not intended to indicate any expected differences between them but makes each sampling area more nearly representative of an equal portion of the limnetic zone. Areas 1 and 4 are representative of the shallower ends of the lake, each receiving the flow from one river and several smaller streams. The depth of the sampling stations in areas 1 and 4 averaged 20 and 18 fathoms, respectively. In each of the four areas a single standard station was sampled as an index of the distribution of smelt in that area. From the results of echo sounder surveys and sampling in other parts of each area, it was felt that the selected stations were adequately representative.

Sampling at each station was conducted in daylight and in darkness but not necessarily in that order. The sampling sequence was completed before moving to the next station. Each trip lasted 48 hours with about 12 hours at each station. With one exception the sequence of stations was fixed at 1, 2, 4, 3. The trawl was fished at discrete depth intervals determined before the start of the standard sampling program. Each tow lasted ten minutes at the desired fishing depth. During normal operating conditions, four tows could be completed in one hour. This included setting and retrieving the net and substitution of the collecting bucket.

The sampling depths were established after preliminary analysis of the data available in June, 1963. At all stations samples were taken from depths of 3, 7, 11, and 15 fathoms. In the two central stations, which were deeper, additional depths of 19, 23, and 26 fathoms were sampled. Generally only single tows were made at each depth. Replicate tows and tows at intermediate depths were made as time permitted. On certain trips more emphasis was placed on making replicate hauls. The actual fishing depth was determined by attaching a bathythermograph to the upper tow bar of the trawl. Confirmation was made by checking the bathythermograph depths with the records of a bathykymograph (time vs. depth recorder) which also was attached to the trawl. The boat speed during all tows was maintained at 6 knots (700 R.P.M.). The depth of the trawl was controlled by the amount of cable paid out.

Field Collections

With one exception all standard sampling trips were conducted aboard the College of Fisheries research vessel, COMMANDO.

The COMMANDO is a 67-foot, 69-ton vessel equipped with two echo sounders, radar, and dual trawl winches. The R. V. HOH, operated by the Department of Oceanography, was used as an alternate vessel for one standard sampling trip. Prior to this trip it was compared to the COMMANDO, during side by side towing experiments, and comparable speeds established.

The primary sampling gear for this study was a modified six-foot Isaacs-Kidd midwater trawl. The net and depressor are illustrated in Figure 2. Cotton netting of $1\frac{1}{2}$" mesh was used throughout the $20\frac{1}{2}$' body of the net. A $\frac{1}{2}$" mesh bait liner was used in the last 10'8" of the body. Behind this was a 20" stainless steel ring and a 1/8" mesh nylon bobbinetting cod end 5'8" long. A bayonet ring mounting was attached to the cod end and was connected with a plankton cup with two "0 gauge" wire mesh windows.

Several otter trawls were used during the study in order to catch additional specimens and to determine if longfin smelt were on or near the lake bottom. The trawls used were old nets which were considered to be expendable. They were balloon-type shrimp trawls of $1\frac{1}{2}$" mesh and were about 50' wide. The same trawl was not used on more than one trip. Otter trawls were used consistently in area 4 after March, 1964. Additional information could have been obtained if it had been possible to use them at each station and time of year.

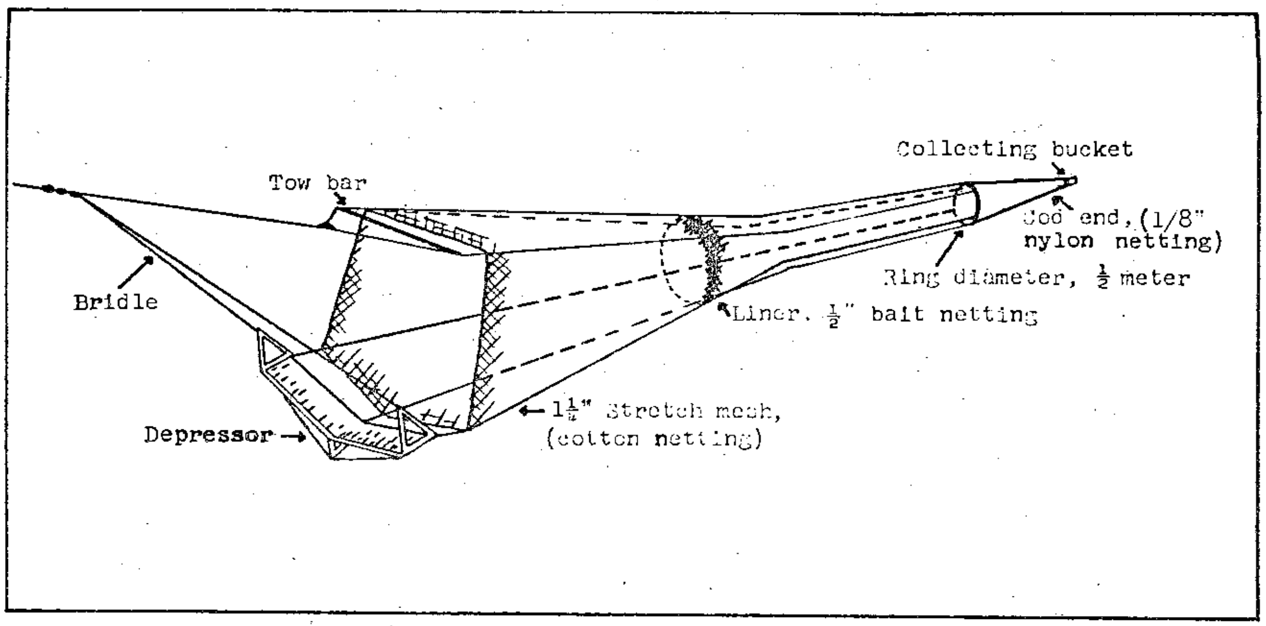


Figure 2. Modified six-foot Isaacs-Kidd midwater trawl (after Aron, 1960).

A brief statement to justify the use of the Isaacs-Kidd midwater trawl should be made. The earliest captures of longfin smelt were made using this type of gear. Subsequent sampling showed this net would capture specimens fairly consistently at certain depths and times. At the same time, both floating and sinking gill nets were tried and were found to be unsuccessful. The least effective sampling depth for the Isaacs-Kidd midwater trawl is near the surface. Presumably this is because the trawl fishes in the wake of the vessel. Trials using a surface tow net requiring two boats in Lake Washington on a spring night produced only a single larval smelt from five tows of standard length at a depth of from the surface to 3 fathoms. It was decided to use the Isaacs-Kidd midwater trawl as the primary gear but to limit the shallowest tow to 3 fathoms. The Isaacs-Kidd midwater trawl has advantages of speed in handling, reliable depth and behavior during fishing, and high trawling speed. It is relatively effective as a fish catcher, and has the advantage of catching reasonable quantities of smelt from 1" post larvae through adults in addition to zooplankton including mysids, amphipods, chironomids, copepods, and cladocera. In summary, the Isaacs-Kidd midwater trawl is the most effective sampling gear taking reasonable numbers of specimens of all size ranges of smelt and associated food and predator organisms. It can fish at all depths, is reliable, and requires very little deck time for each sample.

All samples were immediately preserved in the field with sufficient formalin to make a 10% solution (4% formaldehyde gas in water). Each sample was preserved in a 32-ounce glass jar with a label indicating the trip number, location, date, haul number, and number of fathoms of cable out.

The relationship between cable out and the actual depth of the trawl was determined using a bathythermograph (BT). The instrument was strapped onto the upper tow bar of the net and held in place by a safety line attached to the net. This instrument provided data on depth and temperature simultaneously. From this, the maximum depth of the trawl could be obtained. A bathykymograph (BKG) was used to determine if the net maintained a constant depth while fishing. This assumption was confirmed. The bathythermograph was most frequently used on the deeper tows and provided information on the temperature at various shallower depths. Occasional checks at shallower depths were also made and compared with simultaneous records from the bathykymograph. The actual depth relationship for all the standard tows was determined from a linear regression analysis of the net depth from the bathythermograph slides for tows at 700 R.P.M. on the R. V. COMMANDO. The depth was adjusted to the center of the trawl.

Least squares regression analysis of 97 midwater trawl hauls showed the depth of the trawl in fathoms to be related to the number of fathoms of cable paid out by the following equation:

$$Z = 0.2513X$$

Z = depth to the center of the trawl and X = amount of cable out. The slope coefficient was not significantly different from 0.25. The coefficient of variation, representing the standard deviation as a percentage of the mean, for the regression line in this analysis was 4.1%. When the cable out-trawl depth regression was divided into three equal parts corresponding to cable lengths of 0 to 40 fathoms, 41 to 80 fathoms, and 81 to 120 fathoms, the coefficient of variation showed no trend with increasing depth (3.1%, 4.4%, and 3.5% respectively). From this it may be concluded that the deviations from the average depth for any given length of cable tend to increase as the depth increases but that the increase is proportional to the increase in depth. The slope was not significantly different from 0.25 for any of the three regression lines. The overall regression equation given above is the best fit for all depths sampled; however, the simpler slope value of .25, or 4 fathoms of cable for each fathom of depth, is adequate for all practical purposes. It may also be concluded that the standard deviation for the depth determinations averages about 4% of the estimated depth.

Two echo sounders were used during the study. A Simrad (Model 510-5) echo sounder was used aboard the COMMANDO. This sounder operates on a pulse frequency of 38.5 k.c. Recordings were made for each tow on a wet type sounder paper and these records were labeled and stored. A Ross (Model 100/25) echo sounder was purchased and installed on the Mercer Island Floating Bridge in August, 1963. After completion of the Evergreen Point Floating Bridge, the set was transferred to that preferred location in April, 1964. This recorder was equipped with a recycling timer and operated on a cycle of "on" five minutes, "off" ten minutes, etc. The recorder operated for 1- to 3-day periods at bimonthly intervals for the duration of the study. This sounder operates on a frequency of 115 k.c.

Data for oxygen, carbon dioxide, and secchi disk readings were obtained from Dr. W. T. Edmondson for the Madison Park (area 3) station. The data for this station were obtained within one week of the time of midwater trawl sampling there.

All trawl collections were brought into the laboratory and were examined between July and December, 1964.

Laboratory Procedures

Two sets of data records were made. One set summarized the catch of each trawl haul and associated data. The other set summarized the data collected for each individual smelt. Examples of the data recording sheets and tables containing the numerical codes used are appended. These tables also indicate the criteria used for each observation. Also appended is a complete listing of the data.

A total of 972 midwater trawl hauls were made during this study. Of these, 934 were classified as being of 10 minute duration and successful. Tows which hit the bottom of the lake or during which some mechanical failure occurred were not considered to be successful.

A total of 1,324 smelt were examined from Lake Washington during this study. Not every smelt was examined completely. For each year class, if adequate samples were available, a minimum of 100 juveniles and 100 adults were examined. All midwater trawl samples taken before January, 1963, or after February, 1964, were completely examined. When more than adequate samples were available (i.e., July, 1963, through February, 1964) they were completely analyzed on an alternating month basis. In the months for which complete data were not taken, length, weight, age, number of vertebrae, and incidence of deformities were recorded. Otter trawl catches in 1964 provided additional adult specimens. Complete or nearly complete data were obtained for 615 smelt specimens.

From the record sheets, IBM cards were punched and verified. The analysis of the data on cards was accomplished on the IBM 7090 and 7094 computers at the Northwest Computer Center on campus. Extensive use was made of programs available at the

Computer Center or at the University of Washington Fisheries Research Institute. The programs used to scan the data were written at the U.C.L.A. Department of Preventive Medicine and are available in the BMD series (Dixon, 1964). The following BMD programs were utilized during the analysis of the data in this study: 01D, 02D, 05D, 07D, 01R, 02R, 01V, and 05V. In addition, a weighted regression program prepared for the Fisheries Research Institute, and a program for fitting the Chapman-Richards Generalized Growth Model written by Dr. K. S. Turnbull, University of Washington College of Forestry, were used. For all tests of significance the 5% significance level was used unless otherwise indicated.

RESULTS

Lake Washington Population

Freshwater Residence

A population of longfin smelt appears to be resident in Lake Washington throughout their life cycle. Seven year classes of this population have been sampled. Specimens of virtually every monthly age including larvae and spent adults have been obtained in the lake. During the study there was no indication of an influx of anadromous adult smelt. Mr. Richard Pressey, at the time with the Washington State Department of Fisheries, reports having seen adult longfin smelt in the Lake Washington ship canal locks in November, 1954. There is no way of knowing if these were strays from the resident Lake Washington population, anadromous adults from one of the other streams in Puget Sound, or part of an anadromous stock spawning in tributaries to Lake Washington. In spite of extensive collections in Puget Sound south of Everett there have been only 8 specimens of the longfin smelt taken. Three of these were taken in the Duwamish River, and the others in widely scattered locations. Concentrations of these smelt have been taken from the estuaries and bays near streams outside this area which have anadromous populations. This lack of collections from the surrounding saltwater and the presence of the smelt in the lake throughout their life suggest that the population studied is resident and that there are probably few if any anadromous smelt entering Lake Washington.

Age and Growth

Determination of the age of the longfin smelt was simplified because no overlap in length frequency between year classes occurred. Larval smelt were taken in the Cedar River in early April, 1963. Post larvae have been taken as early as late April and in May in the midwater trawl in Lake Washington. Smelt of two year classes have been taken in virtually every sampling trip made during May through February. Spawning appears to occur in January and February. March approximates the time of hatching and was selected as the date for age zero. The youngest specimens captured in the lake were taken in April and were considered to be one month old.

To determine if sexual differences in weight occurred, large samples obtained from otter trawl collections were compared by sex for each age available. Analysis of variance showed no significant sex effect for smelt of 13 or 14 months of age ($F_{1,44} = 0.6787$ and $F_{1,36} = 0.0064$) and a significant difference between sexes for smelt 15 and 16 months old ($F_{1,132} = 6.6034$ and $F_{1,41} = 4.8666$). The males were heavier at both ages. This could affect the estimate of average growth rate for a year class if the samples were not representative of the true sex ratio of the population or if the sexes were not considered separately. Samples from the otter trawl and from the midwater trawl both have approximately a 1:1 sex ratio. Sex could be distinguished after about the eighth-month stage. Comparisons between the sexes of average weight at a given age, using the small samples from the midwater trawl, show no consistent trend. If larger samples were available, the separation of the sexes would have been desirable; however, the difference between the sexes is small compared to the individual variation and the combination of the sexes is the best solution.

The effect of gear selectivity was investigated by a comparison of the average weights at comparable ages for samples taken by the otter trawl and the midwater trawl. Comparisons were made for smelt 13, 14, 15, and 16 months old. Analysis of variance indicated that for only one month was a significant difference present ($F_{1,52} = 4.1069$, $F_{1,47} = 0.0834$, $F_{1,145} = 0.1542$, $F_{1,56} = 1.3607$). This difference was barely significant at the 5% level and not significant at the 1% level. Considering also the small number of observations for the midwater trawl collections in this comparison (15 specimens) the real significance of this difference appears questionable. On the other hand, the significant difference is for the youngest age group compared and indicates a higher mean weight for smelt caught in the otter trawl. This may be considered to show a selectivity of the otter trawl for the larger fish near the lower limit of its effecitive fish-catching range. The more significant fact for this study, is that the midwater trawl was at least as effective as the otter trawl in collecting representative weight samples for the ages compared. The midwater trawl does capture large quantities of crustaceans such as the copepods, Diaptomus and Epischura, and the mysid, Neomysis, in addition to fish larvae smaller than those of the smelt. At the other extreme, captures of salmonids larger than adult smelt are not rare and even 3 adult salmon have been caught. The conclusion suggested by the above data and observations is that the midwater trawl is not selective for size within the range attained by the longfin smelt. It was assumed that the midwater trawl samples were representative of the length and weight of the smelt population for the analyses which follow.

A comparison of the weight at comparable ages for samples from the 1962 and 1963 year classes was made. Initial comparisons were made at ages for which the sample for each year class contained at least 15 observations. For all ages compared by analysis of variance (4, 9, 10, and 16 months) the 1963 year class was significantly heavier ($F_{1,87} = 9.5404$, $F_{1,87} = 25.0412$, $F_{1,126} = 12.4279$, $F_{1,55} = 17.5394$). Figures 3 and 4 show the descriptive statistics for each sample containing 8 or more observations of weights from the 1962 and 1963 year classes. These data suggested the basic similarity of the weights and weight

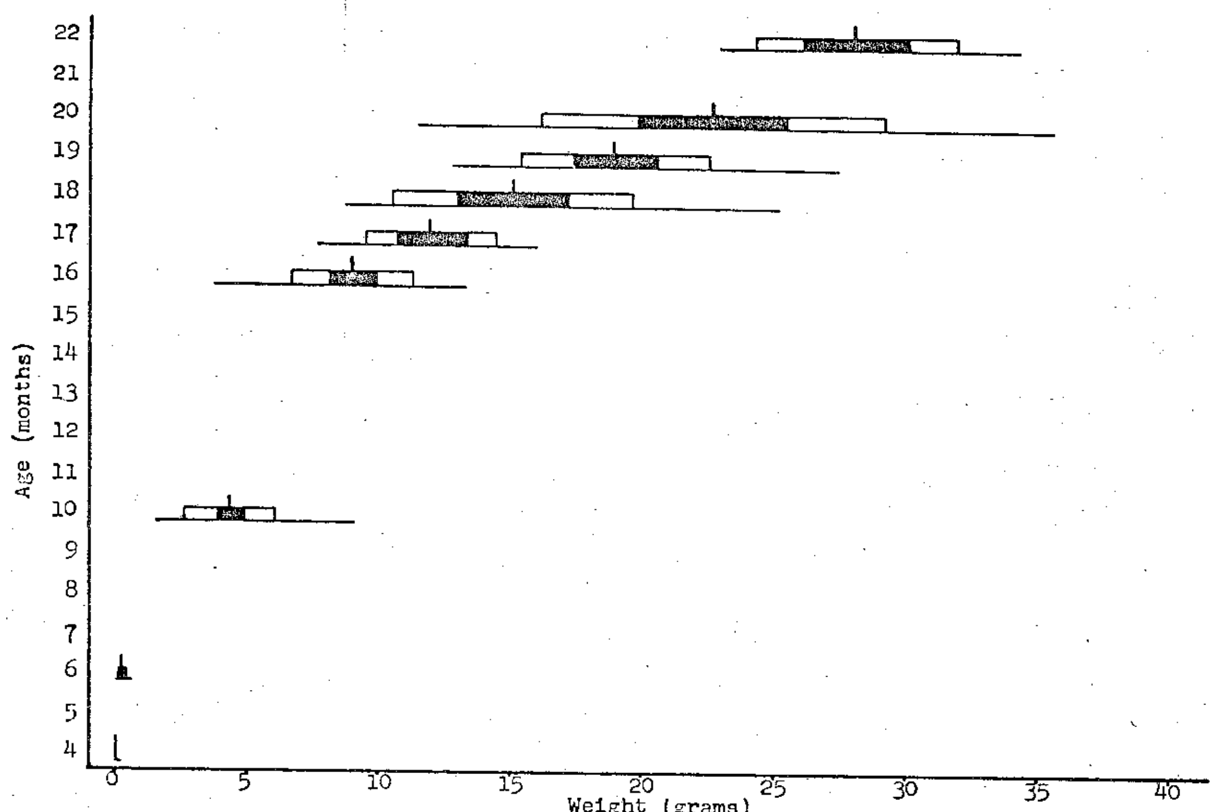


Figure 3. Growth in weight for the 1962 year class. Samples contain 8 or more observations. The graphical method of Hubbs and Hubbs (1953) is used. The observed range of the observations is indicated by the base line. The mean is represented by a vertical line. The black rectangle indicates ± 2 standard errors of the mean. The hollow rectangle represents ± 1 standard deviation from the mean.

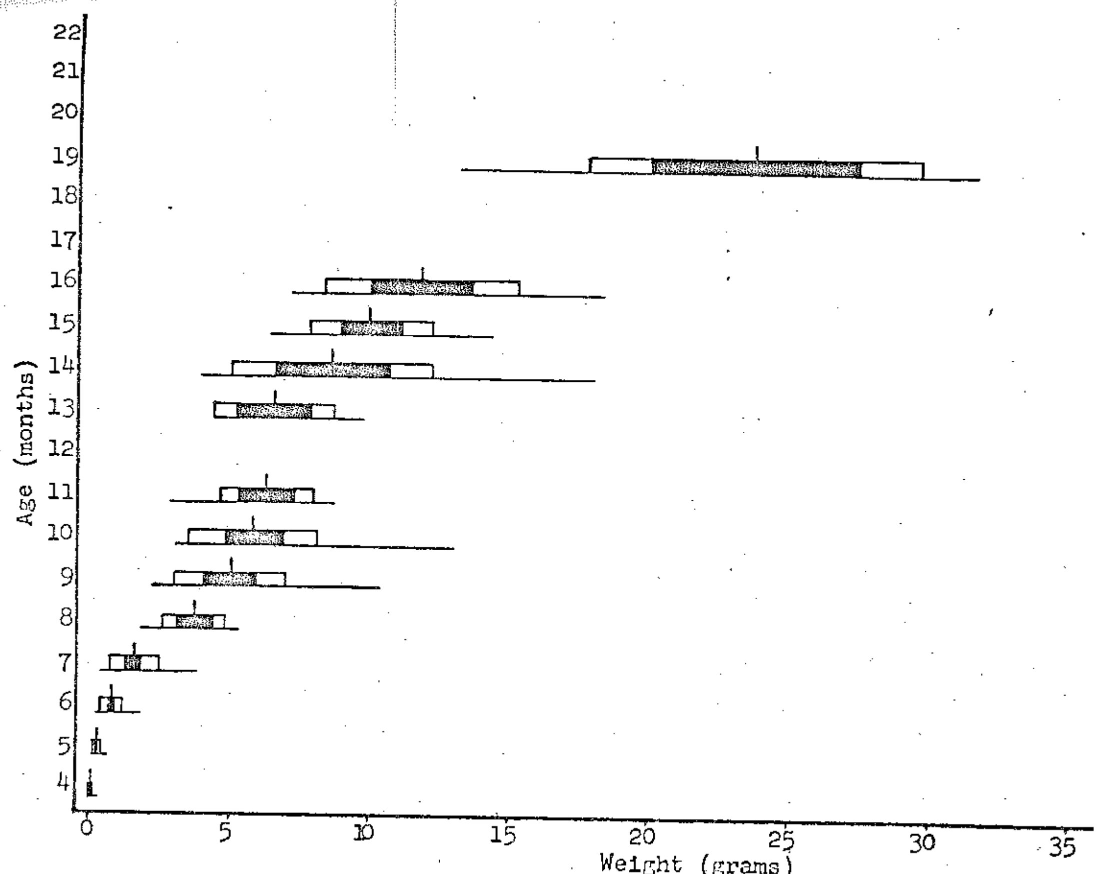


Figure 4. Growth in weight for the 1963 year class. Plotted as in Figure 3.

increments for the two year classes. Further, the data suggest the existence of two exponential growth periods separated by a short interval. This pattern is reasonable because the interruption of the exponential growth occurs during the winter months. To test this hypothesis and compare the two years' growth patterns, the two year classes were each divided into three groups (<9 months old, ≥ 9 <14 months old, and ≥ 14 months old) on the basis of the month of capture. Analysis of covariance was used to test the significance of differences between the slopes of the lines for each of these periods. The winter growth period (≥ 9 <14 months old) was tested in each case to see if the growth was significant (i.e., slope $>$ "0"). The weight data were transformed to logarithms for this analysis. The hypothesis of a common slope for year classes was rejected for the first growing period but was accepted for the winter and second growing period. The slope was found to be significant for all periods including the winter. The common slopes indicate a basic similarity in growth rate between the two year classes beyond the first 9 months. A comparison of the weights at an age of 7 months for the 1963 and 1964 year classes showed the 1964 year class to be significantly heavier at the same age than the 1963 year class ($F_{1,80} = 14.8958$). Figure 5 indicates the average growth in weight of the 1962, 1963 and 1964 year classes and is plotted on

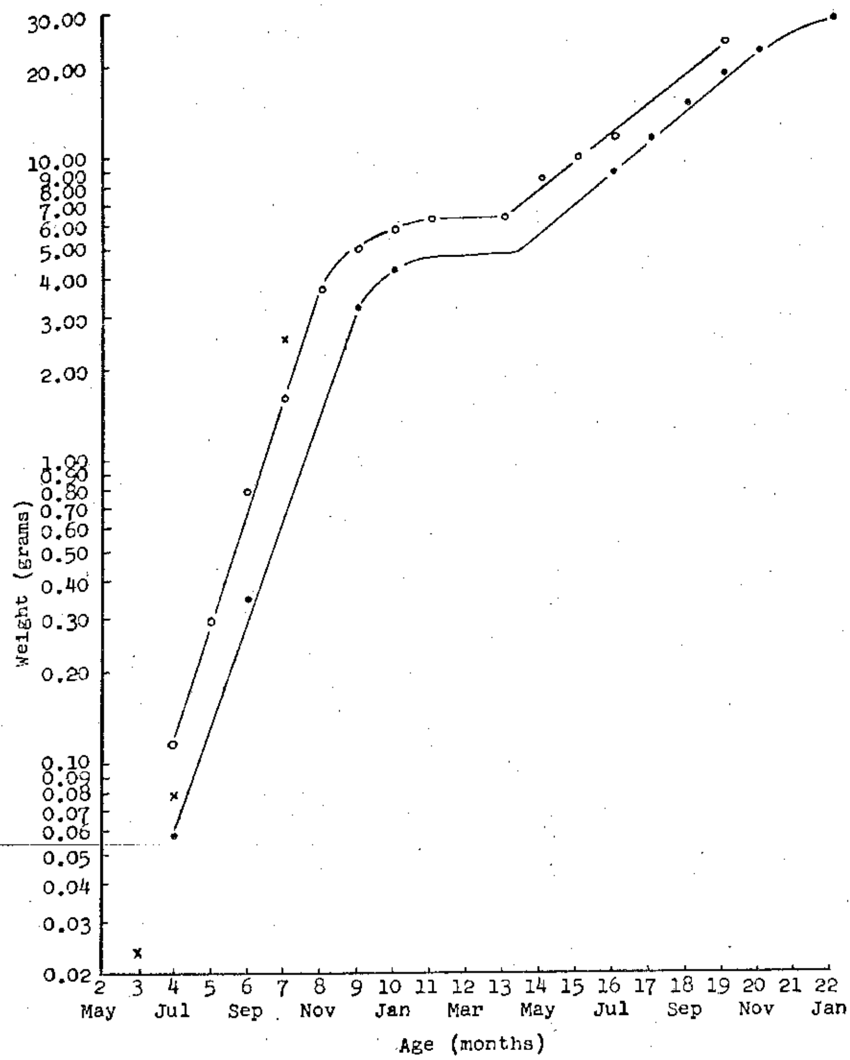


Figure 5. Average weight of smelt by age for the 1962 (•), 1963 (o), and 1964 (x) year classes. The average weights for monthly samples containing 8 or more observations were plotted on a logarithmic scale. Curves for the 1962 and 1963 year classes were fitted by eye.

a logrithmic scale.

The length-weight relationship was determined from the samples available regardless of year class. This relationship reflects the common exponential increase of weight with increasing length. The relationship was based upon the length and weight of 469 specimens greater than 70 mm. long and without vertebral deformities other than a replicated spine. The least squares fit of the transformed data gave a linear regression equation of:

$$\text{Log. weight} = -5.6260 + 3.3732 \text{ log. length.}$$

The slope was significantly greater than 3.00, the expected slope which would result from an isometric increase of weight with length. The standard deviation about the regression line was 1.1272 gm.

Growth in length shows a period of slow growth during the winter. Figures 6, 7, and 8 show the observed growth in length for the 1962 and 1963 year classes. The differences in growth between the two year classes are obvious in either the weight or the length growth data.

Scale formation was found to occur generally in July at a length of about 25 mm. At this time the scales were discs without any circuli. They first appear in a mid-lateral posterior position approximately even with the adipose fin. Collections of scales were made as close to this position as possible and near

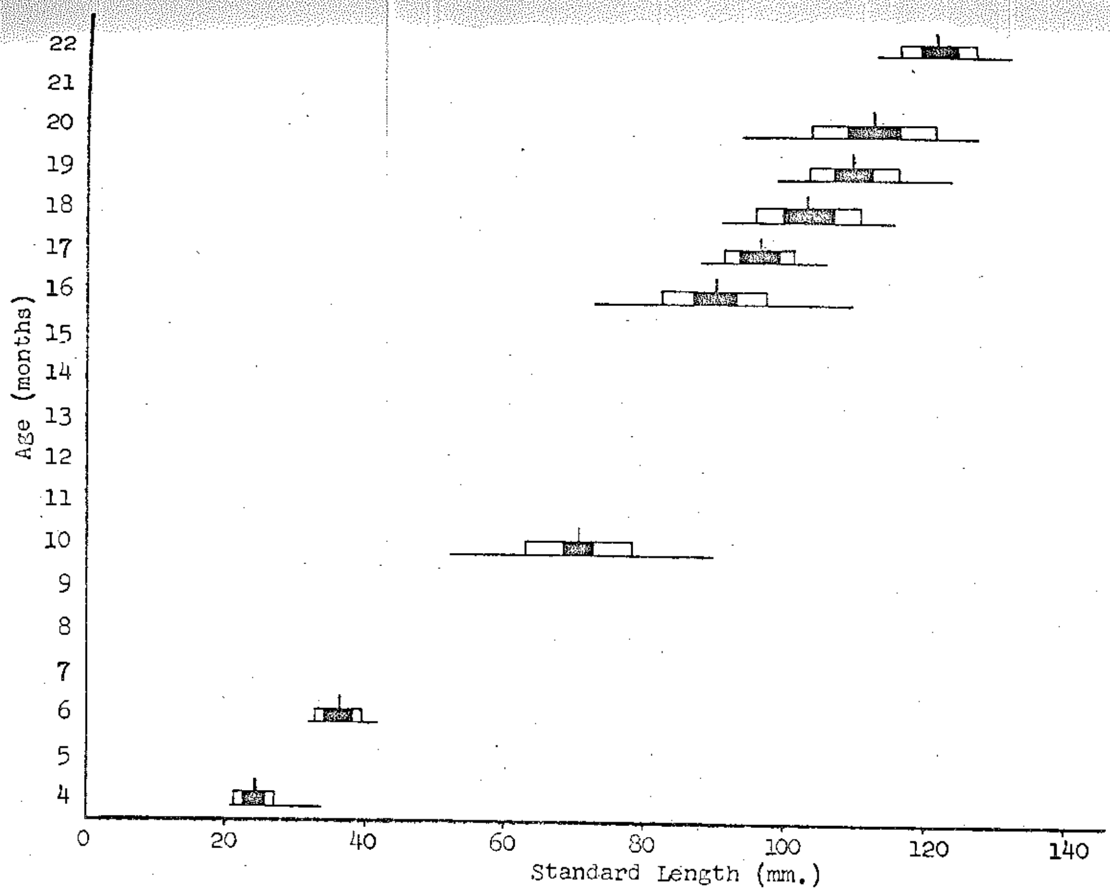


Figure 6. Growth in length for the 1962 year class. Plotted as in Figure 3.

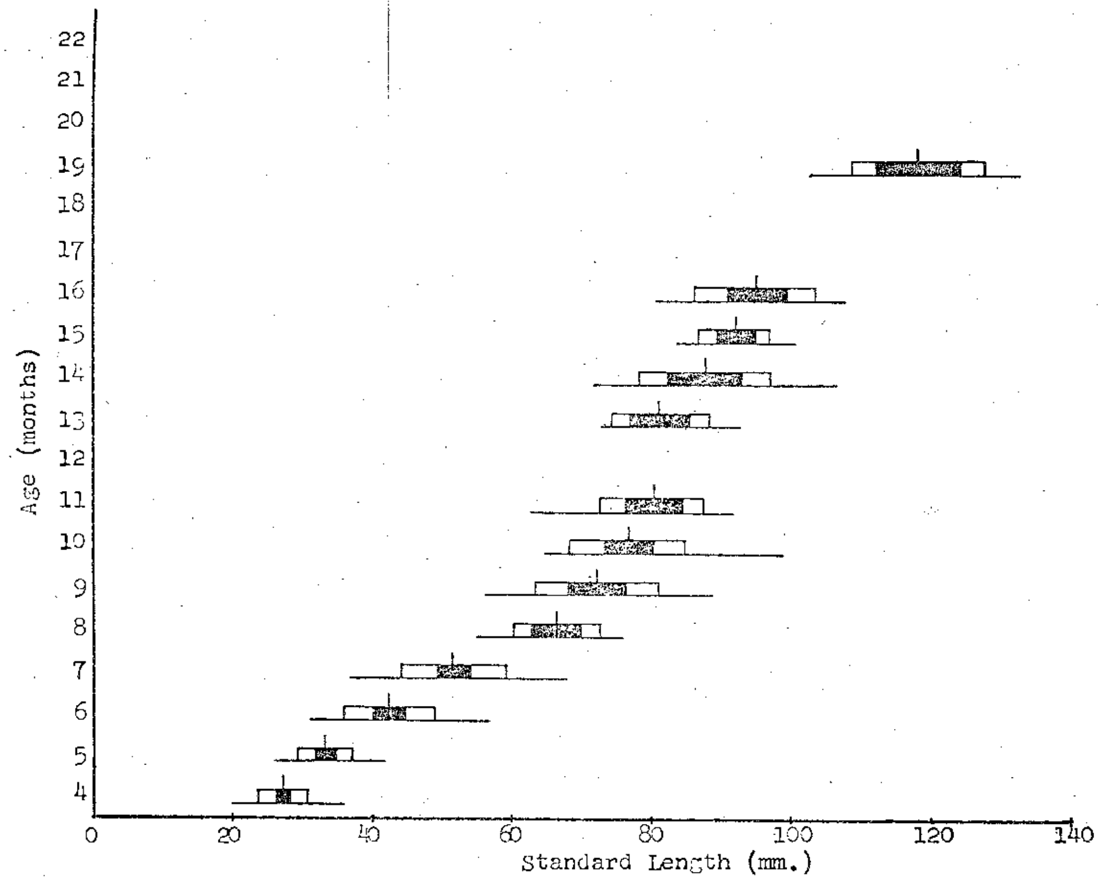


Figure 7. Growth in length for the 1963 year class. Plotted as in Figure 3.

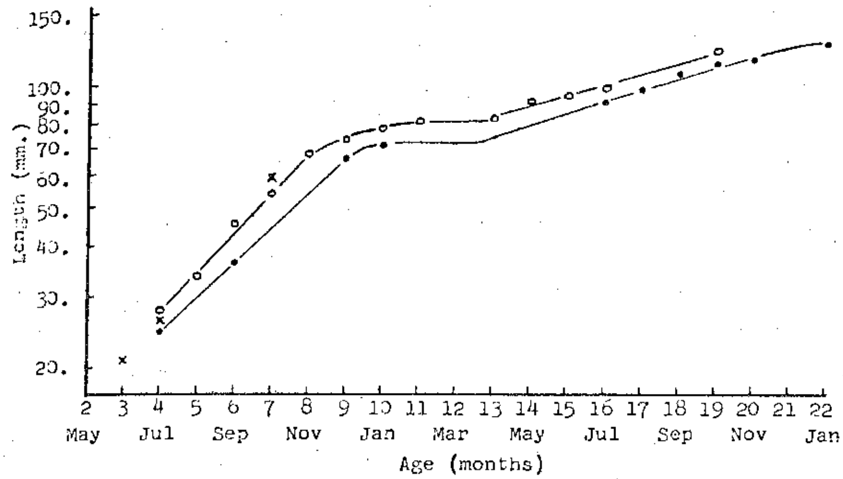


Figure 8. Average length of smelt by age for the 1962 (•), 1963 (o), and 1964 (x) year classes. The average lengths for monthly samples containing 8 or more observations were plotted on a logarithmic scale. Curves for the 1962 and 1963 year classes were fitted by eye.

the lateral line. The first summer's growth is quite apparent with about 14 circuli formed by November. Annulus formation is not consistent from fish to fish and frequently no annulus is present. The second summer's growth is also quite well represented on the scales. The adult smelt had about 30 circuli by November of their second year of life.

Reproduction

The fecundity of the longfin smelt was determined by a wet weight method. The ovaries were removed from preserved ripe fish which had been captured in January. An effort was made to select 10 females which showed no indication of previous spawning. For the total fecundity estimate, the right and left ovaries were combined, even though they contained very different numbers of eggs. The asymmetrical nature of smelt ovaries and their anatomy has been described by Kendall, 1927. Right ovaries from two fish were examined and the eggs individually counted; they were found to contain an average of approximately 1,550 eggs (1,455 and 1,655). The fecundity determinations were made by separating the ripe eggs from the trace of ovarian tissue. The loose eggs were then separated from the formalin solution by filtration with an aspirator. Aspiration continued for five minutes after the supernate fluid had been filtered off. Then the eggs were divided into two groups, the smaller containing

300 to 1,000 eggs. The two samples were weighed promptly on a Mettler analytical balance. After weighing, the eggs in the smaller sample were counted. The fecundity was determined by the ratio of the two weights and the number of eggs in the sample. The number of eggs in the sample was added to the fecundity estimate.

The results of the fecundity estimates indicated the method used was good. Five replicates on a single fish of 108 mm. standard length gave a mean of 16,216 with a standard deviation for the five estimates of 309. This is a coefficient of variation of 1.9%. The fecundity estimates for 10 nearly ripe specimens averaging 117 mm. (108 to 126 mm.) in standard length ranged from 9,621 for a 118 mm. fish to 23,624 for a 124 mm. individual. There was no relation between length and fecundity in the small, 2 cm., range of lengths available. The overall mean was 18,104 with a standard deviation of 4,458. Table 2 summarizes the fecundity observations. It is evident that there is a large variation in fecundity between individuals of nearly the same length. Two additional specimens were examined for fecundity. A mature two-year-old specimen was used which had a large number of fused vertebrae. The standard length of this fish was 89 mm. and its fecundity was 17,336. Thus, in this case, the vertebral deformity reduced the length of the fish by posterior foreshortening, but did not apparently affect the fecundity. One

Table 2. Fecundity of two-year-old longfin smelt from Lake Washington

Standard length (mm.)	Total Fecundity
89*	17,336
108	16,160
108	16,216
113	20,915
113	23,402
118	9,621
119	15,772
120	14,818
121	18,313
124	23,624
126	22,205

*Specimen with a very high number of vertebral fusions resulting in reduced body length.

specimen of a maturing one-year-old was also obtained. The specimen was 99 mm. long and had a fecundity of 9,332.

These fecundity estimates may be compared to those reported by Ito, 1959, for the Japanese species, S. lanceolatus. Fecundity estimates have not previously been reported for either North American species of Spirinchus. In samples from Akkeshi, where Ito found the fastest growing smelt of his seven study areas, 17% of his specimens of adult females were one year old. Their average standard length was 96.8 mm. and their fecundity 5,480 eggs. In this area the two-year-olds averaged 132.9 mm. and had an average fecundity of 12,700. The three-year-olds averaged 147.1 mm. and had 17,386 eggs on the average. Fecundity estimates in four of Ito's study areas indicated that two-year-olds averaging 122 mm. produced 8,900 eggs. For two areas, two-year-olds averaging 119 mm. produced 6,700 eggs. These fecundity estimates are much lower than those for S. thaleichthys from Lake Washington. No area or age combination of S. lanceolatus had an average fecundity greater than that for S. thaleichthys from Lake Washington.

Ova diameter measurements for mature fish from Lake Washington were made for those individuals with the largest eggs, and for those which were partially spent. The ova diameters averaged 1.0 mm. Other females of the same age which had larger numbers of smaller diameter eggs had ova diameters as low as 0.65 mm.

Whether these eggs were truly mature or not is not known. The onset of maturation of the ova, as determined by the first appearance of yolk in the eggs, appears to begin in October. A plot of total weight versus body weight is illustrated in Figure 9. Body weight was considered to be the weight of the carcass after the abdomen had been opened and the viscera in the body cavity removed. The ovaries weigh more than the other viscera after the start of maturation and were responsible for the greater difference between total weight and body weight for mature females than was the case for mature males. At a total weight of about 20 gms. the ovary occupies enough of the abdomen to make the sexual dimorphism in gonad weight evident. An average weight of 20 gms. was reached between October and November for the 1962 year class. These data support the visual determination of the onset of maturation.

Spawning for the Lake Washington population appears to extend from mid-December through mid-February. Only three adults have been taken after spawning--two of these were taken on December 18, 1962, the third was taken on April 16, 1964. All three were taken at the southern station. The former were nearly spent females which had retained only 86 and 3 eggs. Several dozen ova were being absorbed in the latter specimen. The spawning grounds were not precisely located and no dead smelt were found during the study. All indications suggest that the smelt

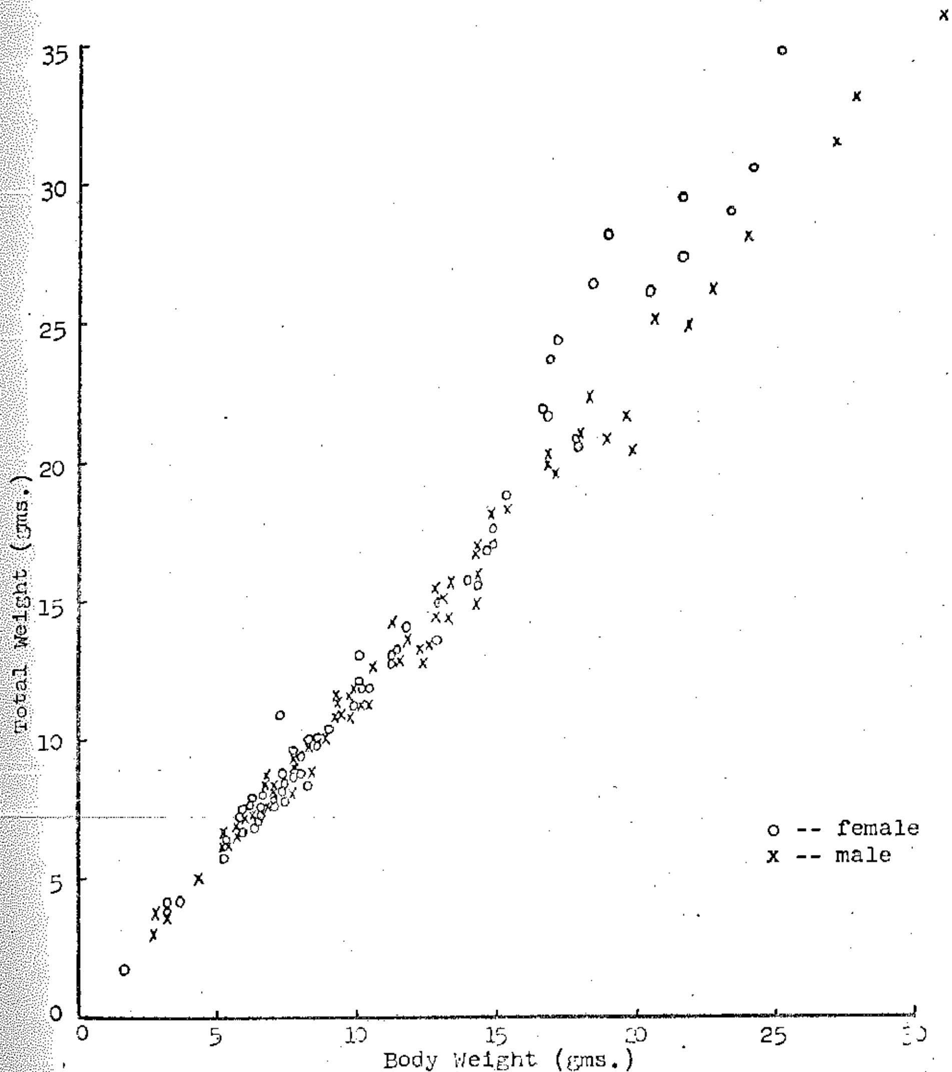


Figure 9. Relation of total weight to body or eviscerated weight for male and female smelt from Lake Washington.

modal 40 days
Complete 47 days

die after spawning with only a few surviving for any length of time after spawning.

On January 2, 1964, a ripe adult male and female were captured near the mouth of the Cedar River. About 200 eggs were extruded into a 32-ounce jar and artificially fertilized by addition of sperm from a male. Water was added and the eggs were observed to adhere to the jar bottom. After covering the top of the jar with nitex cloth it was suspended in Portage Bay behind the College of Fisheries. Initial survival after fertilization appeared to be quite high but due to mechanical problems no estimate was possible. The temperature during the developmental period was recorded continuously nearby. The temperature during the entire period averaged 44.5°F. with a maximum fluctuation of 1°F. An average ovum diameter of 1.2 mm. was found for the developing eggs. The average diameter of ova from this female which were preserved in the fish was 1.0 mm. Observation of the developing eggs indicated the presence of pigment in the eyes on about the 19th day. The first embryo hatched after 37 days and produced a larva 6.9 mm. long. The modal time to hatching was 40 days (17, or 46% of those hatching, hatched in one day). The size at hatching ranged from 6.9 to 8.0 mm. and hatching was completed by the 47th day.

Figure 10 illustrates the pigment pattern of the recently-hatched larva. The pigment pattern began developing in the

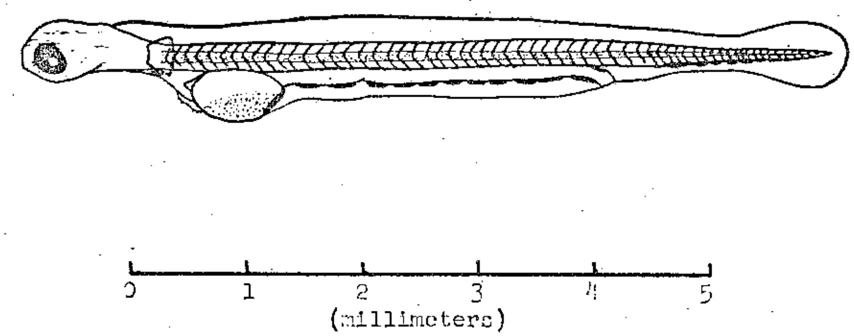


Figure 10. Pigment pattern of recently-hatched larva.

embryo by the 29th day. In the larvae the number and distribution of pigment spots on the yolk sac and intestine appeared to be quite consistent. The pigment spots on the caudal section were considerably more variable in number and form. The larvae all died within four days of hatching.

Larvae were captured in the mouth of the Cedar River on March 5 and 7, 1963 in a half-meter net. These larvae also were about 7 mm. long and were indistinguishable from those incubated at the College. The capture of ripe adults and spent adults in the southern area, near the mouth of the Cedar River, in conjunction with the finding of recently-hatched larvae in the mouth of the Cedar River, localizes at least one spawning area.

Hikita (1958) described the embryonic development of S. lanceolatus. The developing eggs of a 145 mm. female were 1.5 mm. in diameter or distinctly larger than those from Lake Washington fish. Apparently the difference in fecundity of the two species may in large part be attributed to the difference in volume of the ova. The resulting larvae also were larger (9.0 mm.). His observations ended five days after hatching. The incubation time from his experiment is not comparable with our conditions. Hikita could not control his experimental temperature with precision. Consequently, fluctuations as great as from 0°C. to 15°C. in a 6-hour period occurred. Fluctuations of temperature in his experiment were so great that determination of a mean temperature or day degree figure would likely be misleading.

Comparison of the Lake Washington larvae with those of S. lanceolatus at the time of hatching, shows a basic similarity. Both have two melanophores on the gut anterior to the gut constriction at the future site of the air bladder. Both have one melanophore approximately even with this constriction, and both have a fairly long row of melanophores from this point to the anus. In S. lanceolatus there appear to be about 13 in this posterior series while in the Lake Washington stock of S. thaleichthys there are about 8 to 10. The last of this series in each species appears to be a complex circumanal melanophore. The series of melanophores in the caudal region were difficult to count in the Lake Washington smelt larvae but seemed to be composed of fewer melanophores than those for S. lanceolatus. A maximum of seven distinct melanophores were observed but frequently the number of caudal melanophores was not discernible due to their expanded condition. In other respects the larvae appear very similar.

Dr. Robert Morris has fertilized, incubated, hatched and reared specimens of S. starksi during his studies on rearing of marine fish larvae. He kindly transmitted to the author considerable data for this species. Morris found the entire pigment row along the ventral margin of the gut to contain between 11 and 27 pigment spots (mean of 17). These data were based on 86 specimens. The caudal series contained between 3 and 9 spots (mean of 5).

Examination of the sex ratio of the specimens obtained throughout the study from the lake indicates that a 1:1 sex ratio is maintained throughout their lacustrine residence (457 males, 459 females, 398 immature specimens).

Food and Feeding

The feeding of the longfin smelt shows a definite seasonal pattern of intensity and there was also a definite change in composition of the food as the smelt increased in size. The examination of the stomach contents of the smelt included counting the number of each species of organism present. For comparison of intensity of feeding an average weight for each food organism was determined. Samples of preserved organisms known to be utilized as food were obtained from the midwater trawl samples. They were counted, dried, and weighed. In some cases, two separate samples were used to determine the accuracy of the method. The samples were all taken from September samples and coincide with the period of maximum feeding intensity. The average weights of the food organisms obtained are given in the following table. These weignt factors were multiplied by the number of such organisms per stomach and summed to obtain an estimate of the total dry weight of the stomach contents. Tables 4 and 5 present a summary of the data obtained by weight and frequency of occurrence for each food item.

Table 3. Average dry weights for species of zooplankton eaten by smelt*

Item	Sample size	Average weight μg.
Neomysis awatchensis	100	2,900
Chironomids (*Polypedilum fallax*)	3	1,100
Epischura nevadensis	100	39
Diaptomus ashlandi	75	3
Cyclops bicuspidatum	estimate	1
Diaphanosoma leuchtenbergianum	200	75
Pontoporeia affinis	7	1,200
Leptodora kindtii	10	160

*Samples were obtained from trawl catches in September.

The stomach contents of the smelt were examined according to the time of collection in an effort to determine the diel feeding pattern. The weight of food eaten and percent of empty stomachs were inversely related. A maximum average weight of food (8824 μg.) and lowest percent of empty stomachs (10%) were

Table 4. Summary of stomach contents by dry weight of food items

Age and Season	Number Examined	Intensity μg. food ÷ 1000 (g. body wt.)	Ave. wt. food per fish (μg.)	Percent of Total Weight of Food Items Per Stomach								
				Neomysis	Chironomids	Diaptomus	Epischura	Cyclops	Diaphanosoma	Leptodora	Pontoporeia	Fish
First Spring	20	1.38	34	0	0	22.0	0	0	78.0	0	0	0
First Summer	140	3.02	779	38.5	5.1	4.0	17.0	0.1	31.6	3.7	0	0
First Fall	99	0.72	2,119	77.5	3.7	3.3	4.6	Trace	11.0	0	0	0
First Winter	43	0.45	2,227	92.4	0	0.2	4.6	Trace	0.3	0	2.5	0
Second Spring	90	0.83	6,623	96.0	2.7	0.1	0.1	Trace	Trace	0	0	1.0
Second Summer	119	1.13	12,194	97.2	2.5	0.1	0.2	Trace	0.1	0.1	0	0
Second Fall	51	0.84	18,463	96.7	2.7	0.1	Trace	Trace	0.2	0	0.1	0
Second Winter	34	0.25	6,731	93.2	0.5	Trace	Trace	Trace	0	0	6.3	0
Average for one-yr.-olds	302	1.29	1,290	52.1	2.3	7.4	6.5	Trace	30.2	1.0	0.6	0
Average for two-yr.-olds	294	0.76	11,003	96.2	2.1	0.1	0.1	Trace	0.1	Trace	1.6	0.2
Overall Average	596	1.08	6,146	74.2	2.2	3.7	3.3	Trace	15.1	0.5	1.1	0.1

Table 5. Summary of stomach contents by frequency of occurrence of food items

Age and Season	Number Observed	Percent Empty Stomachs	Percent Frequency of Occurrence								
			Neo-mysis	Chiron-omids	Diap-tomus	Epis-chura	Cy-clops	Diaphan-osoma	Lepto-dora	Ponto-poreia	Fish
First Spring	24	29	0	0	67	0	0	8	0	0	0
First Summer	140	9	10	3	73	55	22	27	6	0	0
First Fall	102	8	32	6	77	45	19	53	0	0	0
First Winter	43	28	40	0	42	21	16	7	0	3	0
Second Spring	93	19	74	15	26	8	6	1	0	0	2
Second Summer	119	11	82	18	50	19	5	6	1	0	0
Second Fall	59	19	76	27	39	14	7	22	0	2	0
Second Winter	35	40	49	3	23	3	9	0	0	14	0
Average for one-yr.-olds	309	18.5	20.5	2.2	64.7	20.2	14.2	23.7	1.5	0.7	0
Average for two-yr.-olds	306	22.2	70.2	15.5	24.5	11.0	6.7	7.2	0.2	4.0	0.5
Overall Average	615	20.4	45.4	8.9	44.6	15.6	10.4	15.5	0.9	2.4	0.2

observed in fish collected between 6:00 p.m. and midnight. The lowest average weight of food (3514 µg.) and highest percent of empty stomachs (21%) occurred in fish taken between midnight and 6:00 a.m. During the day the smelt were found to have increasing weights of food eaten and decreasing percentages of empty stomachs. The fluctuation in percent of empty stomachs is not great enough to determine the period required for digestion of food items. It does suggest nearly continuous feeding with only a slight diel variation. Further refinement of this analysis was not attempted due to a basic weakness in the data for this type of study. The fixed sampling pattern could affect the results obtained in a detailed analysis of food by time. The shallow stations were always sampled between midnight and noon. These two sampling periods also coincide with the two lowest periods of feeding intensity. It is possible that these lows of feeding intensity reflect a difference in the availability of food in the shallower parts of the lake. This effect could not be isolated or balanced with the available data.

The data were examined to determine the relative magnitude of the fluctuation of feeding intensity by season of the year. For this analysis an intensity figure was obtained by dividing the average weight of food per fish (µg.) by 1,000 times the average body weight (gms.). This index reflects the weight of food eaten in proportion to the body weight. This index is given by age and season in Table 4. It is clear that the feeding intensity is highest during the summer for smelt of both ages. The spring and fall feeding was also intense for both age groups but less than that of the summer period, and the winter feeding intensity was lowest.

Digestion rates for the various food items was not determined, hence the relative importance of mysids and copepods or cladocera could not be determined without further assumptions. The combined pattern of frequency of occurrence and of weight are useful and indicative of the food organisms and their approximate importance. Diaptomus, Diaphanosoma, Neomysis, and Epischura were found in 20% or more of the stomachs examined from smelt one year old or less. Neomysis and Diaphanosoma, however, were the only species contributing more than 10% of the weight of food eaten for this age group. For the two-year-olds, Neomysis and Diaptomus were found in 20% or more of the stomachs examined. Neomysis was responsible for more than 96% of the weight of food eaten.

Distribution

Vertical and Horizontal Distribution of Smelt

The distribution of smelt was first analyzed by plotting catch per unit of effort with the midwater trawl for each depth, time of day, station, and season for adult and for juvenile smelt. Very little detail is lost, however, by considering only the standard trips and hauls. Both distribution and relative abundance may be considered from these standard hauls. Figures 11 through 16 present these basic data.

In 1964, post larval smelt were first captured in May. From the standard hauls four specimens were obtained--1 from area 1, 1 from area 3, and 2 from area 4; in June, 5 specimens were taken in area 1, 1 in area 2, 3 in area 3, and 11 in area 4. This distribution is suggestive of spawning in at least two regions. The Cedar River or its vicinity has been suggested previously as a major spawning area. The occurrence of a major spawning area located near the southern end of the lake is supported by the distribution of the post larvae. Furthermore, the early occurrence and relatively high number of post larvae in the north end suggest at least one spawning area in that region. There are several streams entering the north end which could be suitable for spawning. The two central regions of the lake are notably barren of spawning streams. This distribution of post larval smelt in areas of the lake adjacent to the mouths of tributary streams is suggestive of stream spawning or at least some preference or necessity for spawning near incoming streams. By July the distribution of post larval smelt is no longer localized.

The horizontal and vertical distribution of juvenile smelt during the summer and fall months is quite uniform. December

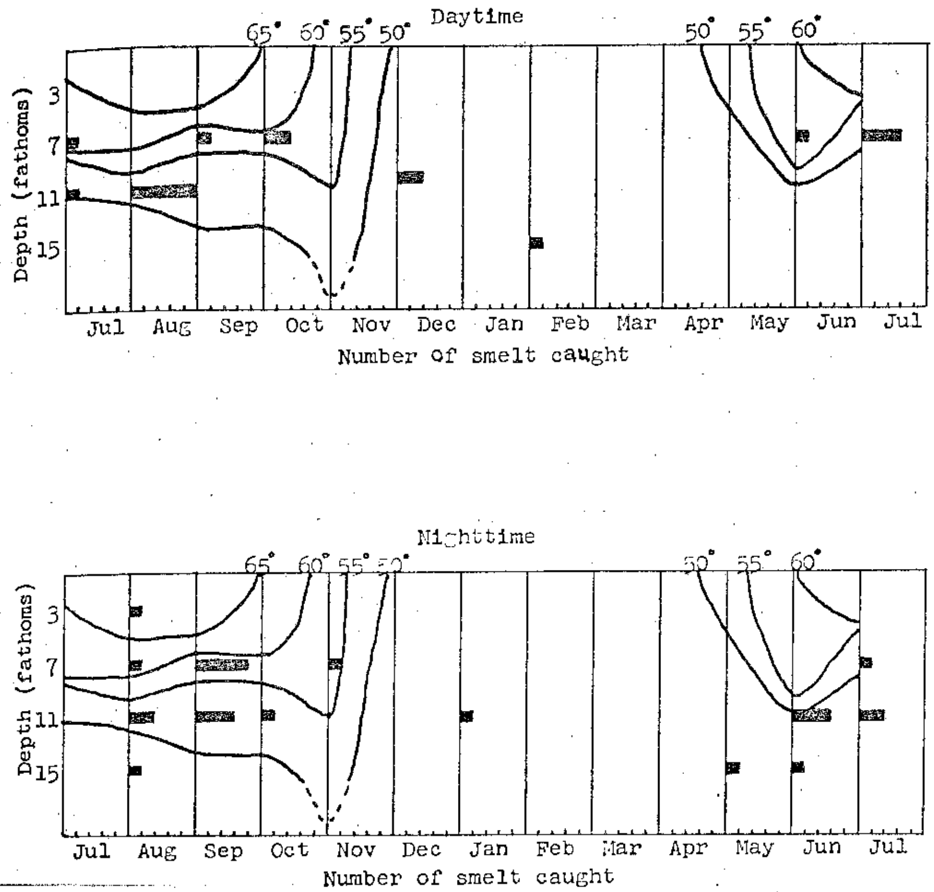
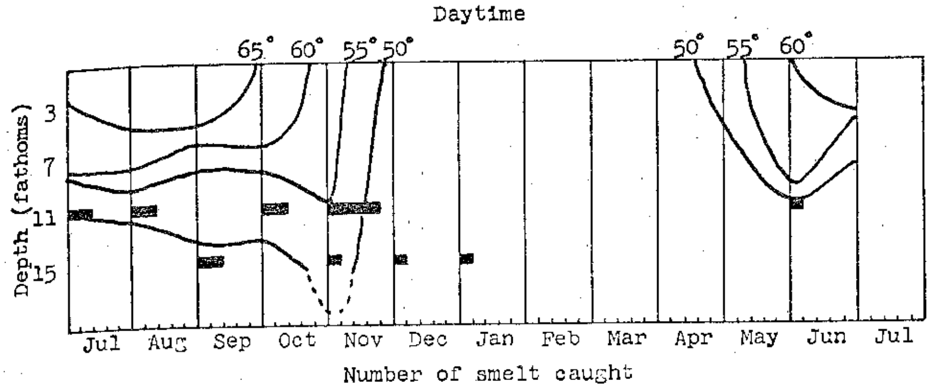


Figure 11. Day and night depth distribution of juvenile smelt catches for each standard trip and haul in area 1. Five degree isotherms are also plotted.



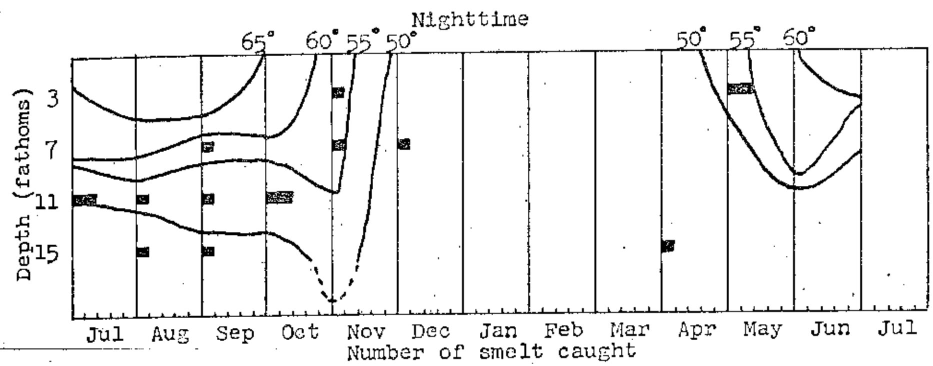
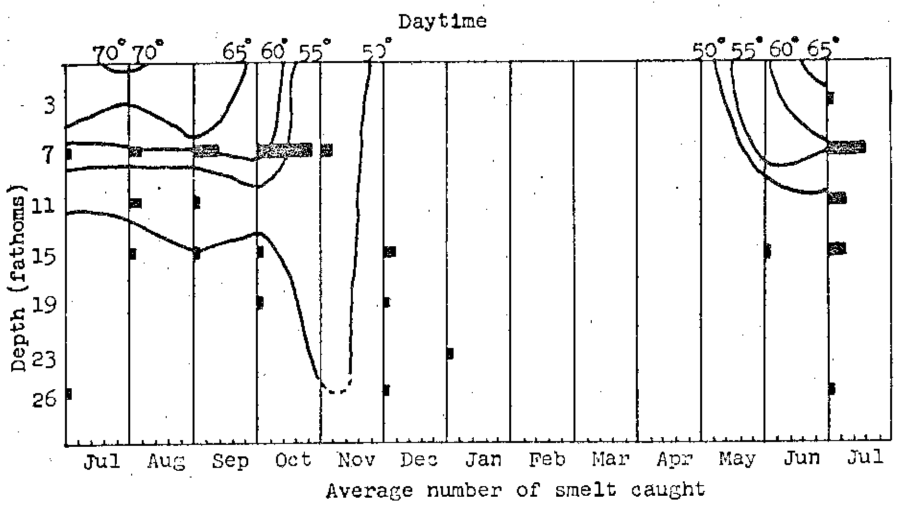


Figure 12. Day and night depth distribution of adult smelt catches for each standard trip and haul in area 1. Five degree isotherms are also plotted.



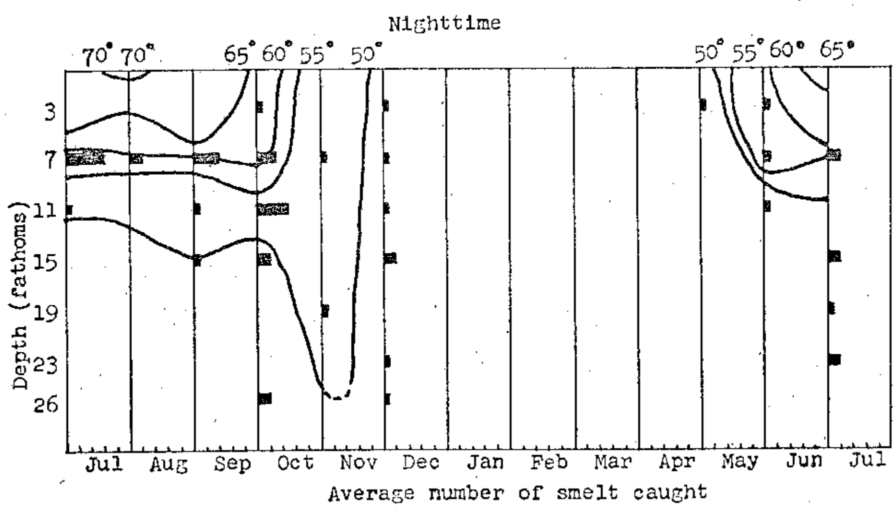


Figure 13. Day and night depth distribution of juvenile smelt catches averaged for each standard trip and haul in areas 2 and 3. Five degree isotherms are also plotted.

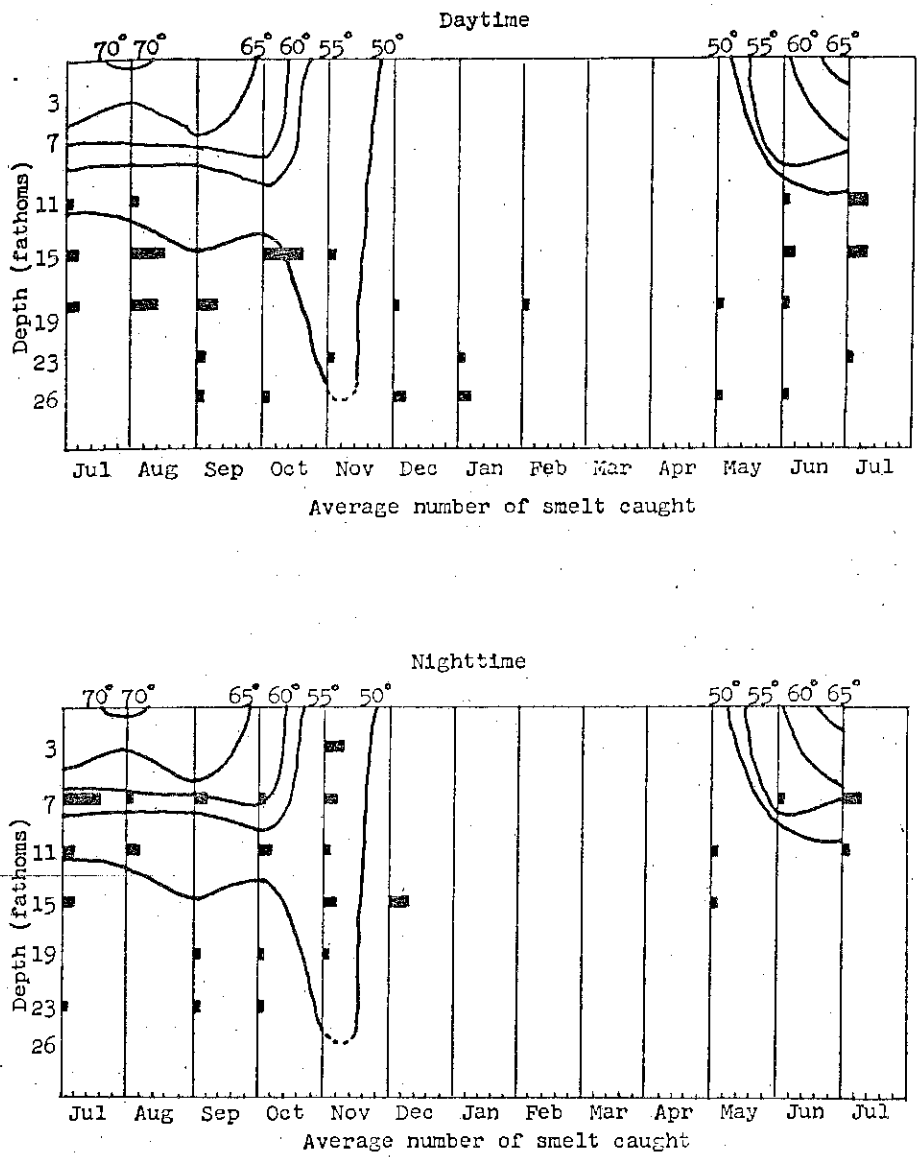
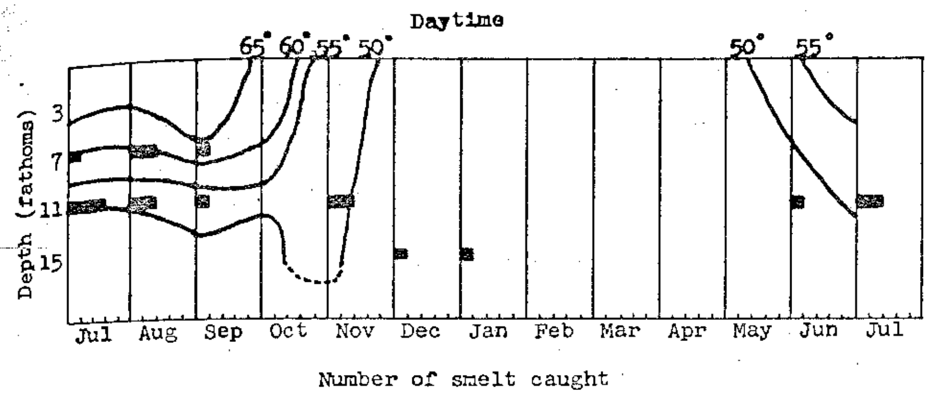


Figure 14. Day and night depth distribution of adult smelt catches averaged for each standard trip and haul in areas 2 and 3. Five degree isotherms are also plotted.



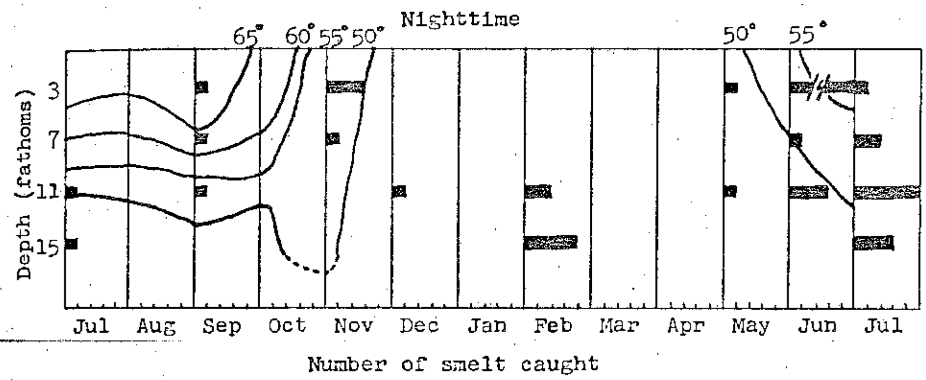


Figure 15. Day and night depth distribution of juvenile smelt catches for each standard trip and haul in area 4. Five degree isotherms are also plotted.

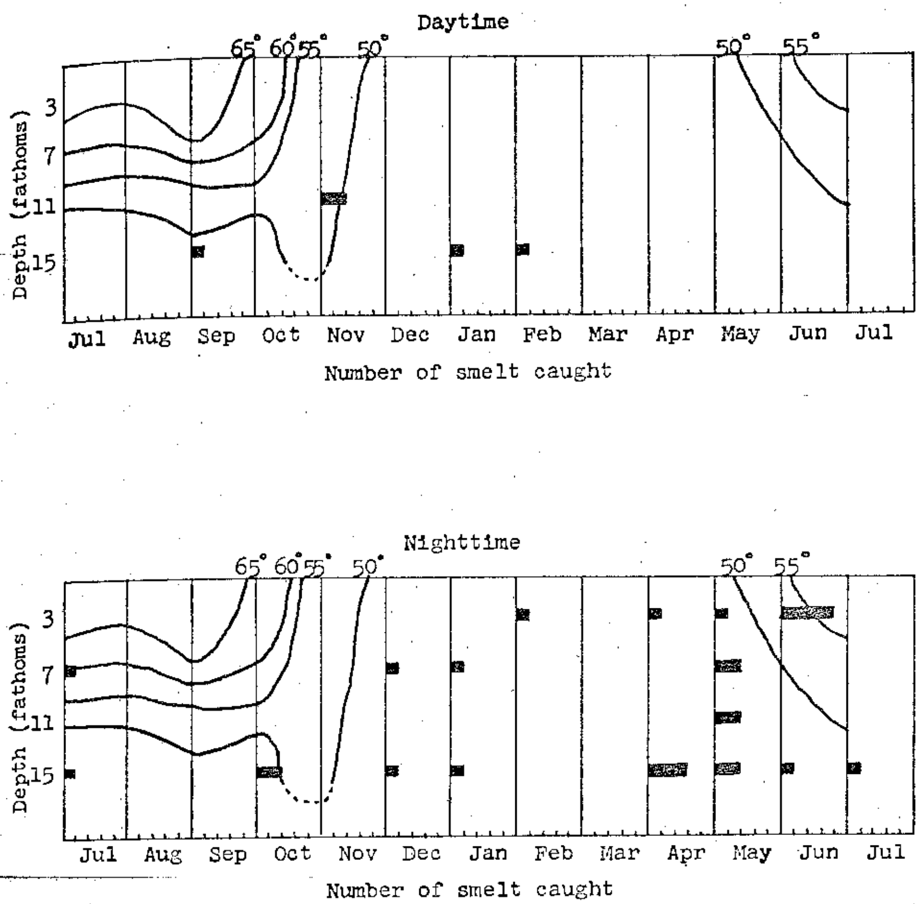


Figure 16. Day and night depth distribution of adult smelt catches for each standard trip and haul in area 4. Five degree isotherms are also plotted.

appeared to be a transition period between the fall and winter distributions. During the 6-month period, July through December, 75% of the juvenile smelt were obtained in tows made between 6 and 12 fathoms. During the day 92% of the smelt were taken in these strata, while at night the percentage dropped to 69%. These percentages were obtained from sampling during which only 36% of hauls were made in the strata containing the smelt. Considering only the first five months of this 6-month period, the percentage in the 6-12 fathom stratum was 81%. There does not appear to be any marked diel change in distribution for smelt of this age.

During the winter months, January through March, the sub-adult smelt were only partially available to the gear. From the standard hauls all sub-adult smelt taken during the day were captured at depths greater than 14 fathoms. During the night all sub-adults taken were caught at depths of less than 16 fathoms. The few smelt captured suggest the establishment of a diel migration.

In their second spring the smelt were still only partially available to the sampling gear. The daytime catches were small in number, and the fish were only taken in the deeper water. Nighttime catches were only abundant at the southern station and suggest a diel migration. Otter trawls that were used at this time in the south end revealed an abundance of specimens on or adjacent to the bottom during the day. This suggests where the smelt are during the winter and spring and also further supports the hypothesis of a diel vertical migration toward the surface at night.

The distribution of the smelt was similar during their second summer and fall. The smelt were widely distributed throughout the lake. They exhibited a marked diel vertical migration toward the surface at night. Compared to the younger smelt of which 81% were found between 6 and 12 fathoms in July through November, 60% of the adults at that time of year were found in the same strata at night. In the daytime, only 31% were taken between 6 and 12 fathoms, while 91% were taken between 10 and 20 fathoms.

In their second winter the adult smelt spawn and disappear. Winter catches of adults were not numerous but generally reflected the same diel migration pattern as did the sub-adults at that time of year.

Summarizing the distribution data, the young smelt first appeared at the north and south ends of the lake in May. By July they were widely distributed throughout the lake. From July through November they were generally found to be most abundant between 6 and 12 fathoms during both day and night. In December they changed to their January through June distribution pattern. Then they were taken only at comparably great depths (15 fathoms or greater) during the day. Otter trawls indicated a relatively high density on or very near the bottom during the day at this season. Nighttime catches were sparse but suggested a beginning of a diel vertical migration toward the surface at night. In their second summer and fall, a well-defined diel migration was established. During the day they were most abundant between 10 and 20 fathoms; at night they were found to be most abundant between 6 and 12 fathoms. They spawn during their second winter and during this time catches in the lake were not large. The winter catches suggest a deeper distribution during the day than at night. Figure 17 summarizes these data for the standard hauls. Figure 18 illustrates the distribution of smelt catches at the four standard stations.

The relative abundance of the smelt may also be examined using the data from the basic sampling program. A total of 572 standard tows had been planned for this analysis. Only 569 were completed as required. The three missing observations occurred in November as a result of equipment failures on the vessel used. Consideration of the data will proceed assuming no smelt were captured in those hauls. This is probably in error, as one would expect from the average catch during the trip (31 smelt ÷ 41 tows), but the error is not felt to be important. The tows missed were in area 4 at a depth of 15 fathoms during both day and night and in area 2 at a depth of 23 fathoms during the day. Table 6 gives the total catch regardless of area by day and night

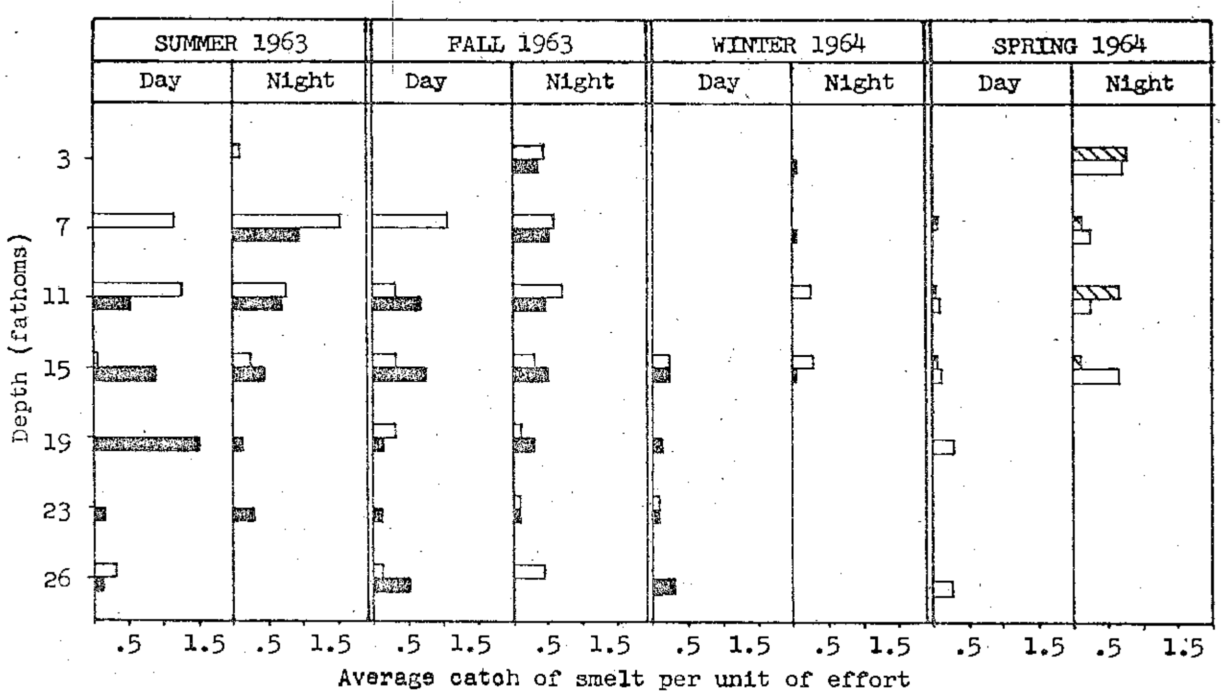


Figure 17. The average catch of smelt per unit of effort by depth, season, and time of day from the standard trips and hauls. The 1962 (▨), 1963 (□), and 1964 (▧) year classes are indicated separately. At each depth the younger fish are shown in the upper bar.

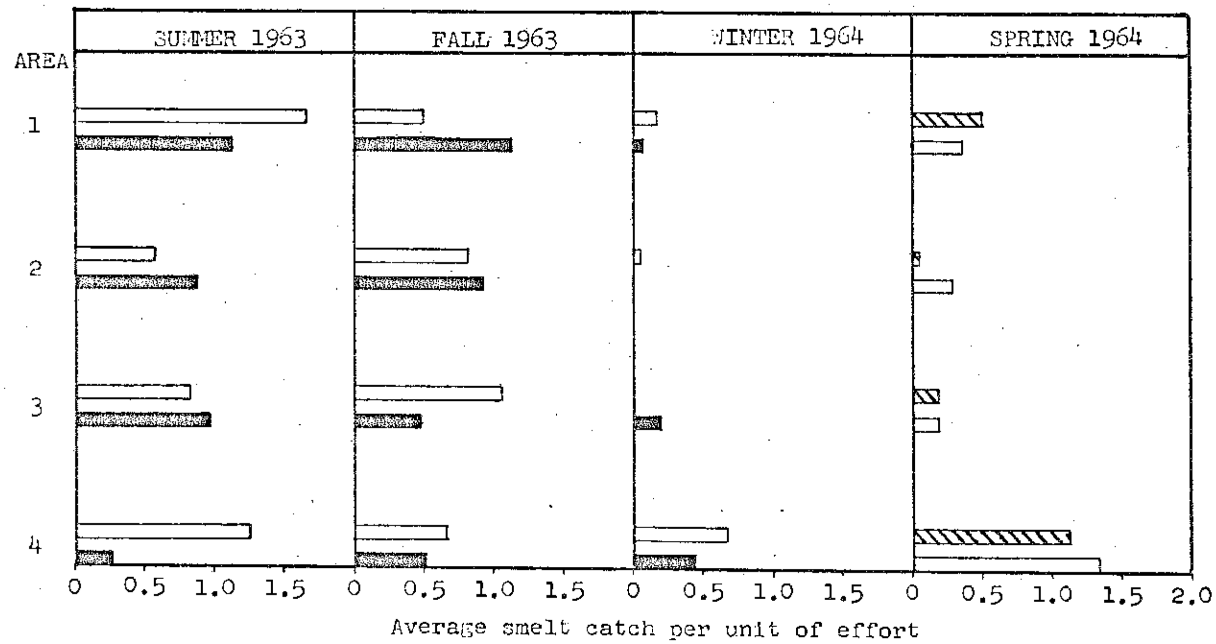


Figure 18. The average catch of smelt per unit of effort by sampling area and season for the standard trips and hauls. The 1962 (▨), 1963 (▭), and 1964 (▧) year classes are indicated separately. For each area the younger fish are shown in the upper bar.

Table 6. Catch of smelt by age, time of day, and month for standard depths and trips

	Month	Juvenile		Adult		Juvenile	Adult
		Day	Night	Day	Night		
Summer 1963	July	8	9	7	15	64	54
	Aug.	14	7	12	5		
	Sept.	10	16	8	7		
Fall 1963	Oct.	13	14	9	9	53	48
	Nov.	4	7	9	11		
	Dec.	7	8	4	6		
Winter 1964	Jan.	2	1	5	2	11	10
	Feb.	2	6	2	1		
	Mar.	0	0	0	0		
Spring 1964	Apr.	0	0	0	5	23	30
	May	0	4	2	11		
	June	3	16	6	6		
Summer 1964	July	19	21	7	5	40	12
TOTALS		82	109	71	83	345	

for juvenile and adult smelt for each month. The fact that there is no significant difference between day and night catches for the adults of the 1962 year class or the young through sub-adults of the 1963 year class indicates that they were representatively sampled regardless of their diel depth distribution. It is of importance to note also that three year classes are involved in the catches. Figure 19 illustrates these standard catches by age for each year class regardless of diel time of capture. From Figure 19 it may be noted that the 1963 year class was relatively less abundant than either the 1962 or the 1964 year classes. Unfortunately, there is only one month of direct overlap during the study but the data obtained in the preceding and following months in each case support the above statement. Seasonal availability to the gear is indicated by the low catches of January, February, March, and April. It is not justifiable to estimate survival rates from the abundance at successive ages if the initial abundance varies from year class to year class. Furthermore, the assumption of constant availability to the gear beyond the period of recruitment is not tenable for at least a four-month period commencing in winter. The period of recruitment unfortunately was not sampled completely for any one year class. The time when the young fish may be considered fully available cannot be determined from the data collected. A consideration of the catches of the 1963 year class alone would suggest that recruitment is

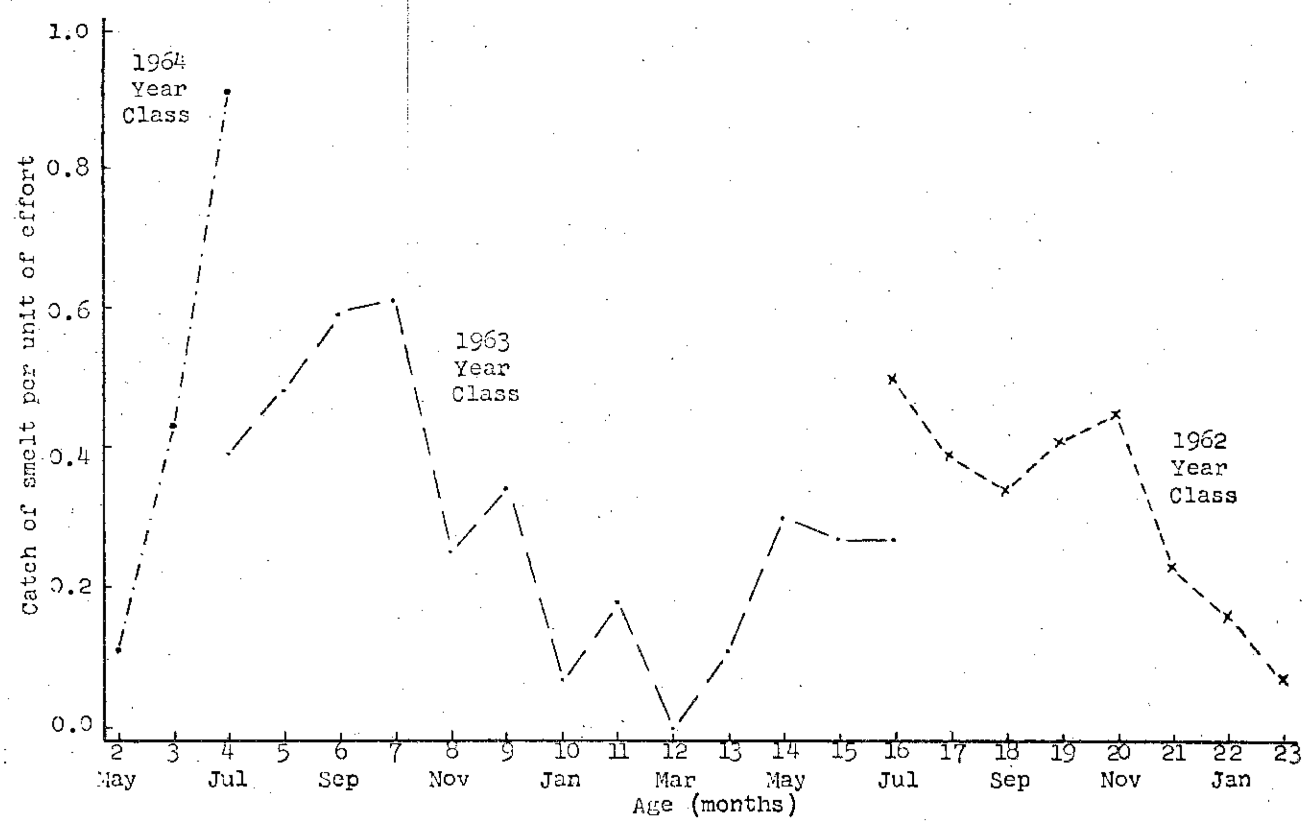


Figure 19. Catch of smelt per unit of effort by age and year class for the standard trips and hauls on Lake Washington.

complete by September or October. Very little confidence can be placed on a survival estimate made under these conditions. However, the survival between the September through December period of their first year and the May-July period of their second year can be estimated for the 1963 year class. Assuming the fish to be of equal availability during these times and the catching power of the gear to be comparable, the survival would have averaged about .625.

Relationships with Other Organisms

Three species of fish were responsible for about 95% of the midwater trawl fish catches. In numerical order these would be ranked Cottus sp., Oncorhynchus nerka, and Spirinchus thaleichthys. A list of the fish species taken during midwater trawling and a rough estimate of their relative abundance in the sampling area are given in Table 7.

The sculpin (Cottus sp.) is an undescribed species which is adapted for a pelagic existence in the lake. Throughout the year this species shows a diel vertical migration toward the surface at night (3-15 fathoms) and toward the bottom during the day (usually greater than 18 fathoms). Only 28% of the specimens taken were beyond the larval stage, but these juveniles and adults still were slightly more frequent than smelt in the catches. The species matures at a length of about 5 centimeters;

Table 7. Species of fish taken during midwater trawling in Lake Washington

Scientific name	Common name	Relative abundance
Cottus sp.	Pelagic sculpin	Very common
Oncorhynchus nerka	Sockeye salmon	Common
Spirinchus thaleichthys	Longfin smelt	Common
Cottus asper	Prickly sculpin	Common on lake bottom
Gasterosteus aculeatus	Three-spine stickleback	Occasional
Mylocheilus caurinus	Peamouth chub	Occasional
Oncorhynchus tschawytscha	King salmon	Rare
Oncorhynchus kisutch	Silver salmon	Rare
Salmo gairdneri	Rainbow trout	Rare
Ptychocheilus oregonensis	Northern squawfish	Rare
Entosphenus tridentatus	Pacific lamprey	Rare
Perca flavescens	Yellow perch	Rare
Pomoxis nigromaculatus	Black crappie	Rare
Cottus aleuticus	Aleutian sculpin	Rare
Lepomis machrochirus	Bluegill	Rare

the females were gravid in January and February. The first larval specimens were taken in February. Catches of adults fell to very low levels in the spring.

The sockeye salmon, including both resident kokanee and anadromous sockeye, were found to show no marked diel migration pattern. In the fall there was some suggestion of a diel vertical migration with the largest nighttime catches being somewhat closer to the surface, but the general trend was toward a relatively consistent diel distribution pattern with a maximum of abundance between 10 and 16 fathoms. More noticeable, however, was a seasonal shift in the area of maximum sockeye abundance. In the winter and spring months the south end provided nearly all the specimens. Mostly this was due to an abundance of fry which were first taken in February; however, the yearlings captured also were predominantly from this area. In the summer catches, the north end of the lake dominated in sockeye abundance. In the fall the summer concentrations of the north were partially dissipated and areas 1 and 3 were most productive. Indications of this cycle repeating itself were found in the overlapping July trips.

Another dominant organism in the midwater trawl catches was the mysid, Neomysis awatchensis. This organism, a major food of the smelt, was found to make diel vertical migrations toward the surface at night throughout the year.

Considering the 934 successful midwater trawl hauls made during the entire study, sample correlation coefficients were obtained for all combinations of the catches of the major limnetic fish species and the mysids. The coefficients are given in Table 8. It is not surprising to find significant but low correlation coefficients between the catches as the populations do tend to have diel migrations in the same direction. The smelt do not appear to be very closely related to any other organism. The total catch of smelt and their primary food organisms, the mysids, do have the highest correlation coeffecient (0.2844). Other associations revealed by this analysis are between Cottus sp. and mysids, within the smelt population, between juvenile smelt and Cottus sp., and between sockeye salmon and adult smelt.

There was no indication of any fish populations in the limnetic area which would be considered predators on the smelt. The sockeye salmon were only occasionally examined for stomach contents but were consistently found to be feeding primarily on the copepod, Diaptomus ashlandi. From the available data, it appears that predation on the smelt after they reach the lake is low. The present data indicate the smelt to be a primary predator on a rather large population of Neomysis. Interspecific competition may occur during the period when the smelt and the kokanee are feeding heavily on the copepod and possibly the cladocera populations. This predation period tends to occur

Table 8. Correlation coefficients for simultaneous catches of the dominant nektonic species

Species	Mysids	Juvenile Smelt	Adult Smelt	Total Smelt	Sockeye salmon
Total smelt	0.2844*				
Juvenile smelt	0.2747*				
Adult smelt	0.1497*	0.2366*			
Sockeye salmon	-0.0303	0.0800	0.1220*	0.1193*	
Cottus sp. (juvenile to adult)	0.2523*	0.1386*	0.0382	0.1260*	0.0275
Cottus larvae	-0.1313*	0.0296	0.0840	0.0623	0.0057
Total *Cottus*	0.0290	0.1123*	0.1002*	0.1345*	0.0195

*Correlation coefficients are significant above approximately |.085| at the 1% level with 932 degrees of freedom.

during the spring-summer period of high abundance of the zooplankton. For the smelt it does not appear that food is limited at any time of year; apparently, inter- or intraspecific competition for food is not severe. This is also indicated by the rapid growth rate and survival of the smelt.

Relationships with the Physical Environment

There are several environmental factors which can influence fish distribution. Three of the more frequently studied are temperature, light, and oxygen. During this study only temperature was taken directly during the sampling program. Secchi disk readings, oxygen, and carbon dioxide data were obtained from Dr. W. T. Edmondson for area 3. These environmental parameters are summarized for selected depths in Table 9. Figures 20 and 21 plot the available oxygen and carbon dioxide data on a grid of depth versus time for area 3. The temperature data are similarly plotted in Figures 11 through 16.

Adult and juvenile smelt were most abundant in the metalimnion at night during the summer and fall. They were only occasionally taken in the epilimnion during the summer when the temperature was above 65°F. During the day the juvenile smelt remained in the metalimnion while the adults were most abundant in the hypolimnion. From these observations it may be concluded that temperature gradients per se are not significant barriers to

Table 9. Summary of physical environmental factors for area 3

Month	Depth ftm.	Temp. °F.	Oxygen mg/l.	CO_2 mg/l.	Secchi Disk meters
July 1963	5 16 27	66 49 48	7.76 8.76 7.7	0 3.4 4.8	0.9
Aug.	5 16 27	64 50 48	4.16 7.27 5.5	0.8 5.1 6.5	1.0
Sept.	5 16 27	67 50 49	4.16 7.27 5.5	3.0 6.2 8.8	1.3
Oct.	5 6 27	65 50 48	8.10 6.88 5.3	0 6.6 8.4	1.3
Nov.	5 16 27	53 53 50	8.7 8.20 5.0	2.8 3.0 8.0	2.6
Dec.	5 16 27	49 49 49	8.36 8.38 8.2	4.1 4.4 4.6	3.5
Jan. 1964	5 16 27	48 48 48	9.22 9.22 9.2	3.7 3.7 3.7	3.6
Feb.	5 16 27	45 45 45	10.42 10.32 10.4	2.6 2.6 2.5	3.3
Mar.	5 16 27	45 45 45	11.29 11.19 11.2	2.0 2.0 2.1	3.6
Apr.	5 16 27	46 46 46	12.16 11.17 10.8	1.4 1.8 2.3	3.1
May	5 16 27	47 47 45	11.47 11.23 10.3	1.0 1.6 2.7	3.1
June	5 16 27	57 47 45	11.46 9.85 9.1	0 3.0 3.2	1.5
July	5 16 27	62 47 46	9.68 8.97 8.3	0 3.8 4.8	1.0

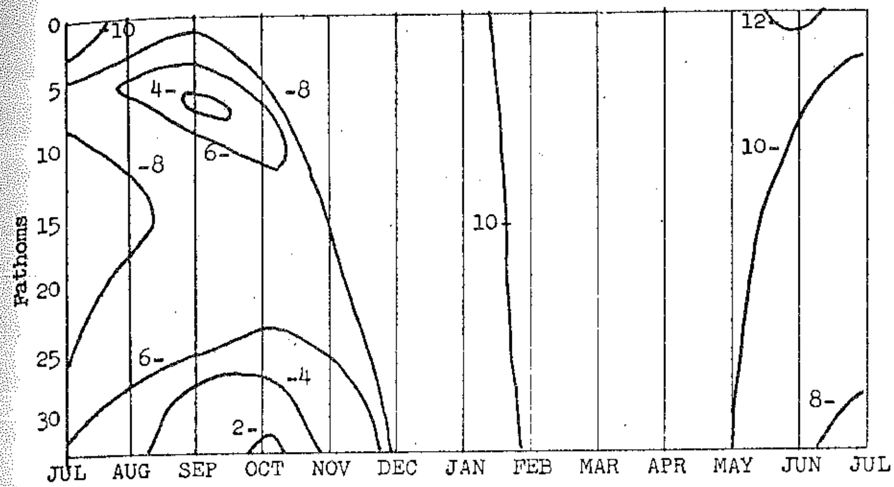


Figure 20. Oxygen concentration in mg./l. for area 3 during the period July 1963 through July 1964. Equal concentration lines are drawn for even interger values of oxygen concentration.

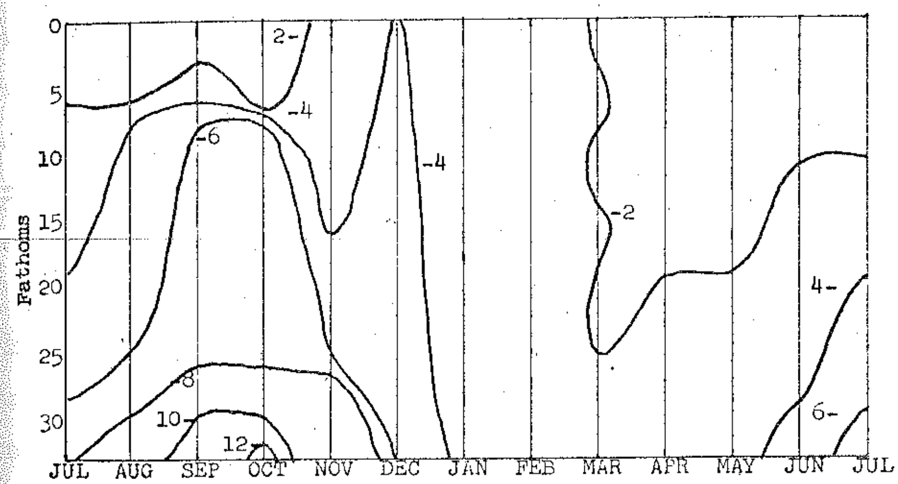


Figure 21. Free carbon dioxide concentration in mg./l. for area 3 during the period July 1963 through July 1964. Equal concentration lines are drawn for even interger values of carbon dioxide concentration.

the smelt but that the smelt may avoid temperatures above 65°F.

There is a marked relationship between the temperature and the dissolved oxygen at 27 fathoms. At higher temperatures the oxygen concentration drops to low levels. In part this is due to the increased rate of decomposition of organic material at the higher temperature, and, in part, it is due to the mass of material with a biological oxygen demand which settles to the bottom during the spring, summer, and fall. Also, there is a direct negative relationship between the oxygen concentration and the carbon dioxide concentration. These three factors are, therefore, all strongly related to one another. It is possible that the high carbon dioxide or low oxygen concentrations near the bottom in the summer and fall is responsible for the avoidance by the smelt of the bottom at that time. It is only possible to conclude that a relationship does exist between these environmental factors and the distribution of the smelt. The causal factor cannot be determined at this time.

Secchi disk readings are an index of the transmission of light through water. At higher secchi disk readings more light will penetrate to a given depth than at low secchi disk readings. In Lake Washington the seasonal decrease in secchi disk readings is caused by an increase in the particulate matter which scatters the light and decreases the depth of penetration of a given initial quantity of light. The concentration of adult smelt near the bottom during the day is closely related to the time of highest secchi disk readings. When the secchi disk readings drop abruptly in the spring, the daytime adult smelt distribution also appears to change. The smelt are found at a relatively shallower depth during the day in the summer. Also in the fall, when the secchi disk readings increase, the adult smelt concentrations during the day tend to go deeper. Again, no causal relationship can be claimed, but the relationship is present. It is the author's personal opinion, based on this and additional observations in Harrison Lake, that light penetration may be more directly related to the depth distribution of the adult smelt than were the observed concentrations of oxygen or carbon dioxide.

Distribution of Fishes and Echo Sounder Marks

Considerable data on the catch of the midwater trawl and simultaneous echo sounder recordings have been obtained during this study. Preliminary study was devoted to determining the best corrections to use on the echo sounder data. The basic Simrad data were counts of marks on the echo sounder records at the depth fished by the trawl. It was necessary to correct these counts for two factors. The expansion of the echo sounder beam with increasing depth may be corrected by multiplying the basic count by (2 ÷ depth in fathoms). This corrects all counts to a basic depth of two fathoms. The other necessary correction is for the attenuation of the sound impulse with increasing depth. This necessitated a correction factor of [(depth in fathoms)^2 ÷ 2^2] to adjust the counts to those at the 2-fathom reference level. The complete correction factor is (depth in fathoms ÷ 2). This factor multiplied by the Simrad counts for a haul gave a slightly higher sample correlation coefficient when related to the sum of the catch of smelt and sockeye salmon than did the original counts. The adjustment was considered more accurate than the original data on theoretical grounds, and the observed relationship with the combined smelt and sockeye catch supports this hypothesis. A comparison of the correlation coefficients for the basic Simrad counts, the adjusted counts, and logarithmic transformations of these data with the catches of smelt and sockeye revealed the highest correlation between the catch and the adjusted counts without any additional transformation.

Table 10 lists the dominant species and the correlation coefficients of the quantity caught to both the original Simrad counts and the adjusted counts. It should be noted that neither mysids nor pelagic sculpins are significantly correlated with the adjusted Simrad counts at the 99% significance level. The other dominant species are significantly correlated with these counts. The low coefficient for the catch of all fishes and for all fishes less the post larvae results from the inclusion of large numbers of sculpin larvae and the pelagic sculpin in the counts.

Table 10. Correlation of dominant species in 595 midwater trawl hauls and simultaneous Simrad marks from objects at the depth of the haul

Species	Original Simrad Counts	Adjusted Simrad Counts
Mysids	0.0912	0.0806
Pelagic sculpin	0.1137	0.0792
Juvenile smelt	0.2571	0.2631
Adult smelt	0.3545	0.2755
Total smelt	0.3992	0.3422
Sockeye salmon	0.7320	0.7676
All fishes	0.5194	0.4743
All fishes except postlarvae	0.7397	0.7447
Total sockeye and smelt	0.7746	0.7949

Clearly, the larger air bladder type fish are responsible for the bulk of the correlation between the catch and the Simrad marks. The correlation of 0.7949 between total smelt and sockeye salmon catch and Simrad marks is based on 695 collections made at different seasons, times of day, and depths. Linear regression analysis of this relationship provided the following equation:

$$\text{Catch}_{\text{smelt + sockeye}} = -0.50111 + 0.02145 \quad (Z) \quad (N)$$

Z = the depth of the tow in fathoms, and N = the number of fish marks at the depth of the trawl on 15 cm. of the Simrad record. The significance of this relationship suggested further analysis toward delimiting the effects of contamination and, especially for the sockeye salmon, of avoidance of the net during the day.

Observations of the depth of the haul in relation to the maximum concentration of marks on the Simrad records had been made. To detect contamination the hauls were divided into three categories. The hauls above the main concentration of fish marks, the hauls made in or near the main concentration of fish marks, and those below the main concentration of fish marks were separated and the correlations between the total number of smelt and sockeye in the haul and the Simrad counts determined for each (Table 11). The following analysis was based upon the adjusted Simrad data. There is no significant difference in the correlation coefficients for the upper two zones but a significantly lower correlation is derived from the zone below the main concentration of fish. A decrease in the number of marks per fish was

Table 11. Simrad analysis of smelt and sockeye salmon catch for possible contamination

Depth	Number of Hauls	Original Simrad Counts		Adjusted Simrad Counts	
		Correlation Coefficient	#marks ÷ #fish caught	Correlation Coefficient	(#marks) x ($\frac{depth}{2}$) ÷ #fish caught
Net above main concentration of fish	284	0.6620	6.0	0.7271	26.7
Net in main concentration of fish	234	0.7930	4.4	0.7931	28.8
Net below main concentration of fish	123	0.4195	2.0	0.3663	20.0

also noticeable. This is quite suggestive of contamination resulting in a more variable correlation (lower correlation coefficient) and a reduction in the number of Simrad marks necessary for a given fish catch. Correlations were also determined for the hauls considering the actual depth of the tow. The correlation between the total smelt plus sockeye catch and Simrad marks was 0.4423 at 0 to 9 fathoms, .8382 at 10 to 18 fathoms, and .4441 at greater than 18 fathoms. The absence of a consistent trend with depth and the higher correlation coefficient for the deepest hauls than was obtained from the previous analysis for the tows below the main concentration of fish suggests that the change in the correlation with depth was not caused by a failure of the echo sounder to record the smelt and sockeye at greater depths. The variability in the correlation between catch and marks by depth may be related to the species and distribution of the fish. The data suggest that contamination is most severe when towing below the depth of the maximum concentration of fish. The importance of the echo sounder in locating these regions of contamination should be evident. In the future it may be possible to use such information to "adjust" catch data for the concentration of fish above the towing depth.

The smelt were found to be nearly equally available either day or night. The catches of sockeye salmon, however, showed rather large and consistent differences between day and night.

The daytime catches were consistently low. The Simrad records should not have been subject to avoidance reactions by the salmon. For this reason, a comparison of catches of salmon and the correlation between salmon catch and Simrad records was made for day and night collection periods. Table 12 summarizes the results of this analysis and includes similar data for the smelt and for the total catch of smelt plus sockeye. From this analysis it should be noted that the mean catch of smelt shows relatively little variation between day and night while the catch of salmon varies considerably. Relatively more marks are required during the day for each salmon caught than at night. These factors force the proportion of marks to the number of smelt caught to vary between day and night also. The average number of marks on the echo sounder records decreased by 44% during the day. The average catch of sockeye salmon decreased by 62%, and the average smelt catch decreased by 23%. In addition, the correlation between sockeye salmon catch and the number of marks on the echo sounder records was significantly lower during the day. It appears from this analysis that some of the sockeye are capable of avoiding the trawl during the day, although no such phenomenon appears to be the case for the smelt. It is also significant that the average number of adjusted Simrad marks decreased by 44% between the nighttime and the daytime hauls. This indicates a real change in the distribution of the fish.

Table 12. Analysis of diel availability of sockeye, smelt, and total sockeye plus smelt

Species and Time	Number of Hauls	Mean Catch	Adjusted Simrad Counts: Correlation Coefficient	Adjusted Simrad Counts: $(\#marks)(\frac{depth}{2}) \div \#fish\ caught$
Sockeye salmon (day)	337	1.05	0.5922	51
Sockeye salmon (night)	358	2.32	0.8200	34
Smelt (day)	337	0.67	0.3807	79
Smelt (night)	358	0.87	0.3208	110
Sockeye and smelt (day)	337	1.73	0.6604	31
Sockeye and smelt (night)	358	3.09	0.8381	26

It is suggested that two factors are responsible for the lower daytime catches of sockeye salmon. First of all, nearly half appear to have left the area; they are not recorded on the sounder. Second, a significant proportion of those present are more capable of avoiding the net during the daytime than at night.

The correlation between the catch of smelt plus sockeye salmon and the adjusted Simrad counts can be increased significantly to 0.8381 by consideration of nighttime hauls only. This eliminates the difference in catchability of the salmon by time of day. A further increase in the correlation can be made by considering only those hauls made in or above the major concentration of fish and thereby reducing contamination. A correlation coefficient of 0.8415 for 289 observations is obtained with these two restrictions. The variability of the catches and of the technique of counting the Simrad marks and other variables impose some limits on the correlation.

A Ross echo sounder was installed on the Evergreen Point Floating Bridge and operated during a part of this study. This sounder operated with a recycling timer so that it recorded for five minutes and was off for ten minutes. The records from this sounder revealed some information on the timing and duration of the diel vertical migrations of the fishes. The records also indicated an increase in the number of fish present in the central part of the lake at night. This sounder and location should hold promise for further studies of distribution and seasonal abundance of fish species, especially the sockeye salmon.

In summary, the Simrad echo sounder records made in conjunction with the midwater trawl hauls provided considerable supporting information. A sample correlation coefficient of 0.7949 was obtained between the catch of smelt plus sockeye salmon and the adjusted counts of marks on the Simrad records. This correlation could be increased to 0.8415 by controlling the effect of two demonstrated variables, contamination and daylight net avoidance. It was revealed that at the sensitivity settings used during this study the mysids, fish larvae, and small pelagic sculpins were not detected by the echo sounder. A Ross echo sounder provided records from a fixed location in the center of Lake Washington. It showed promise for future studies of seasonal and diel changes in distribution and abundance of detectable fish species.

Deformities

The Lake Washington smelt population was found to have a very high incidence of deformities by any standard of comparison. The deformities considered were all structural in nature and do not appear to be pathological syndromes.

Two types of vertebral deformities were found to be common with several other less frequent types of deformities also occurring. The occurrence of vertebral deformities in fish is not rare and has been reported from smelt on at least two occasions (Templeman, 1948; DeLacy and Batts, 1963); however, deformities of the more severe types found abundantly in Lake Washington have never been reported in such high frequency for any other natural population of smelt or related fishes.

The type 1 vertebral deformity may be described as a symmetrical fusion of vertebrae. No intervertebral disk is evident and the joint is not functional. As many as 13 vertebrae were fused into one unit. There were as many as 16 separate fusions occurring in a single fish. In one vertebral column, as many as 31 vertebrae were found to be involved in fusions. These are admittedly the extreme cases; the most frequent occurrence was a single fusion involving two vertebrae. The distribution of these fusions along the vertebral column is not random. Vertebrae 17, 18, 19, and 20 form one region of frequent fusions and vertebrae 46, 47 form another. These vertebrae, counted from the anterior end, were each involved in a minimum of 30 fusions. The occurrence and distribution of this type of vertebral deformity are shown in Figures 22 through 25. Figure 26 illustrates the structural nature of the deformity. The count of the number of vertebrae for these fish was made from the number of neural spines. Comparisons of all meristic characters for normal and type 1 vertebral deformity fish showed no significant differences.

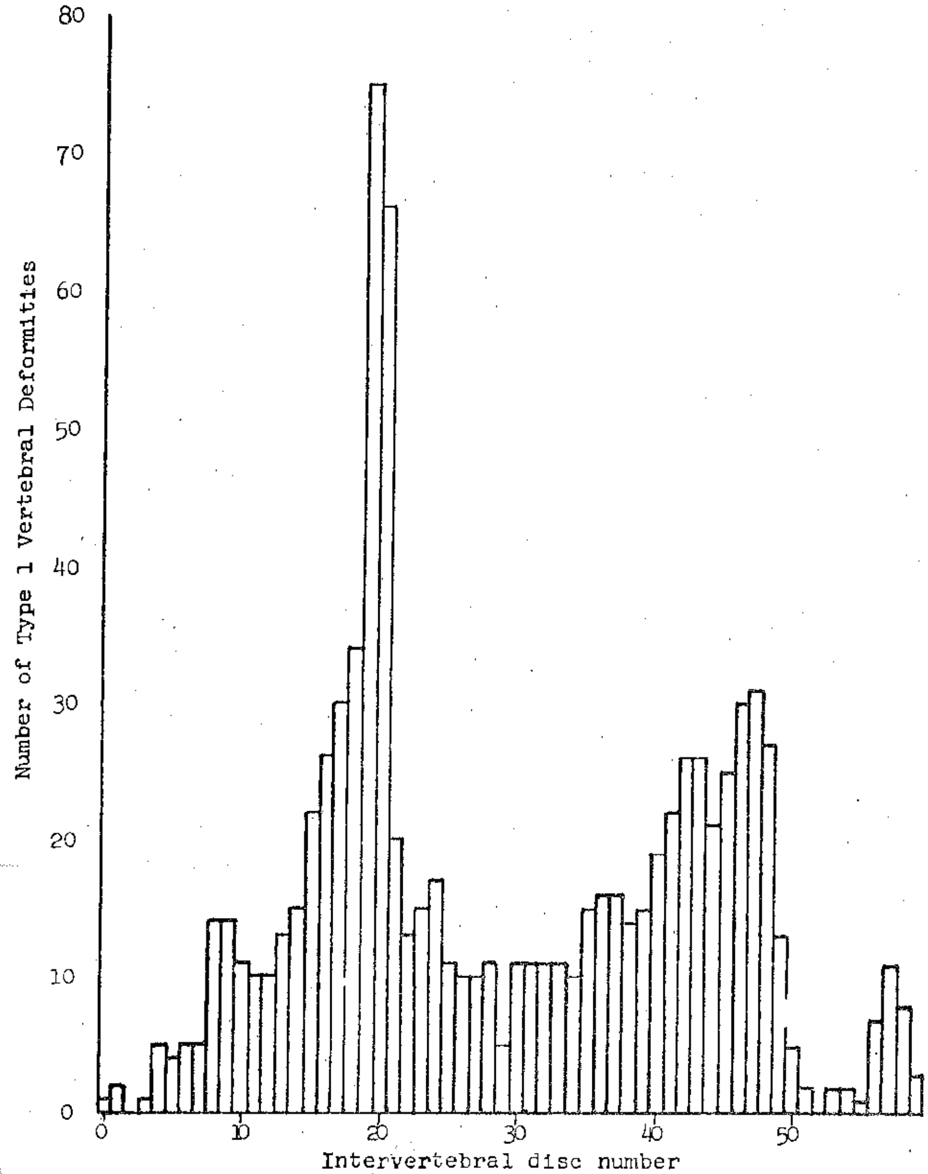


Figure 22. Location of vertebral fusions of Type 1 in 216 smelt from Lake Washington.

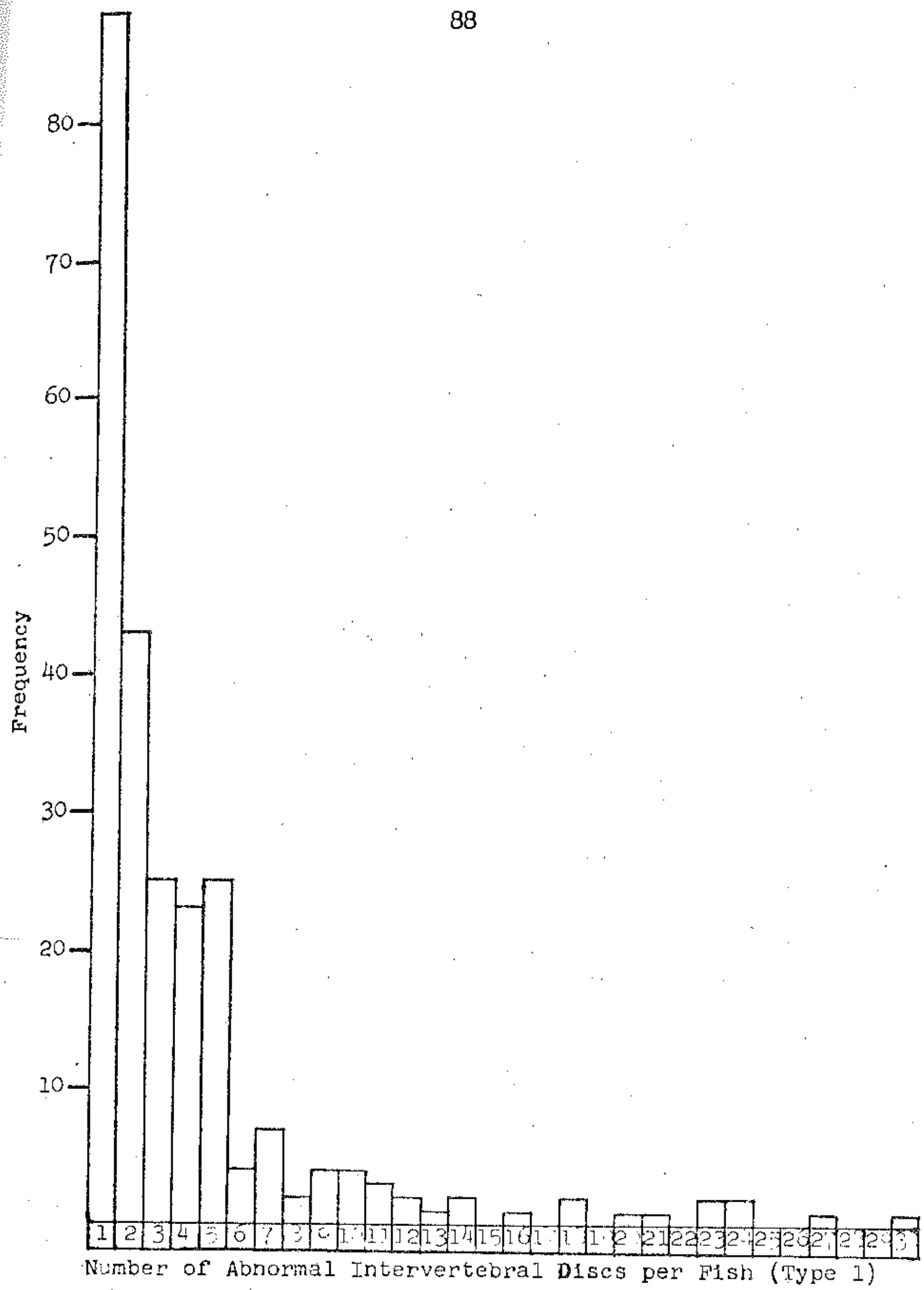


Figure 23. Number of abnormal intervertebral discs per fish.

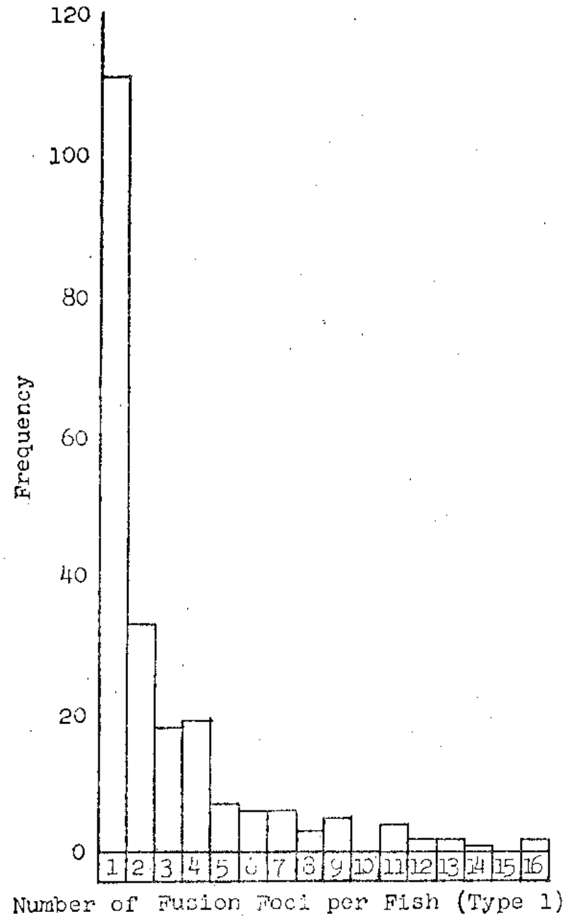


Figure 24. The number of fusion foci per individual fish.

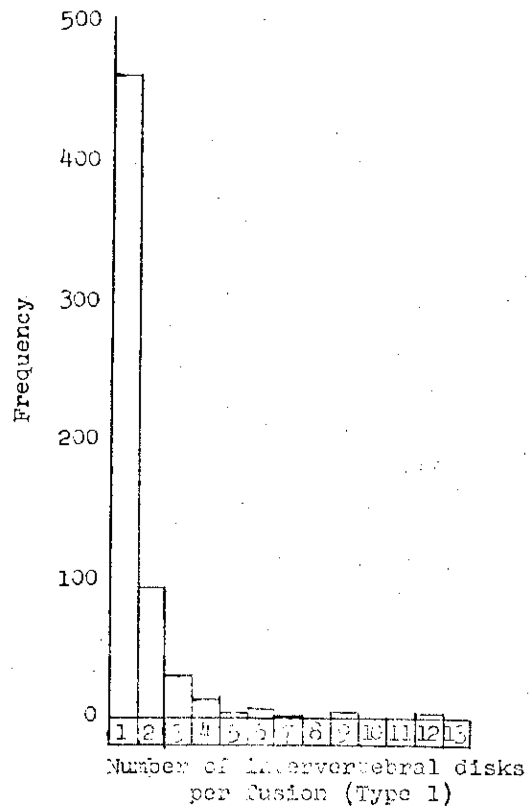


Figure 25. The number of intervertebral discs involved in complex vertebral units

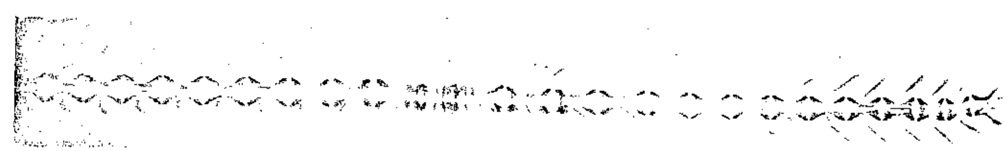


Figure 26. An illustration of a moderately severe Type 1 vertebral deformity.

There was no difference in frequency of the occurrence of deformities between males and females. Figure 27 illustrates normal smelt and severe cases of this type of deformity. Because of their stumpy nature in the severe cases, no fish with this type of deformity were included in the morphometric analysis or in the growth data. Of the 999 smelt examined for vertebral deformities, 21.6% contained type 1 deformities.

A second common deformity (18.7%) was the occurrence of an additional spine on one of the last two vertebrae (type 2 vertebral deformity). Counts of vertebrae, when this deformity was present, were based on the number of haemal spines. This deformity was associated with a significantly higher vertebral count. Other meristic characters were not significantly different from those for normal fish. There was no significant difference in frequency of occurrence by sex. It is likely that the counting method for this deformity was a source of error. The occurrence of such an accessory spine has been found in several other fish species. Other investigators have treated it in various ways. McHugh (1942) counted each spine as a vertebral element in herring vertebrae. The higher-than-normal vertebral counts for these fish were attributed to a propensity for such a deformity in fish with higher-than-average number of vertebrae. Other authors have not counted the accessory spine at all and have obtained significantly lower-than-normal vertebral counts

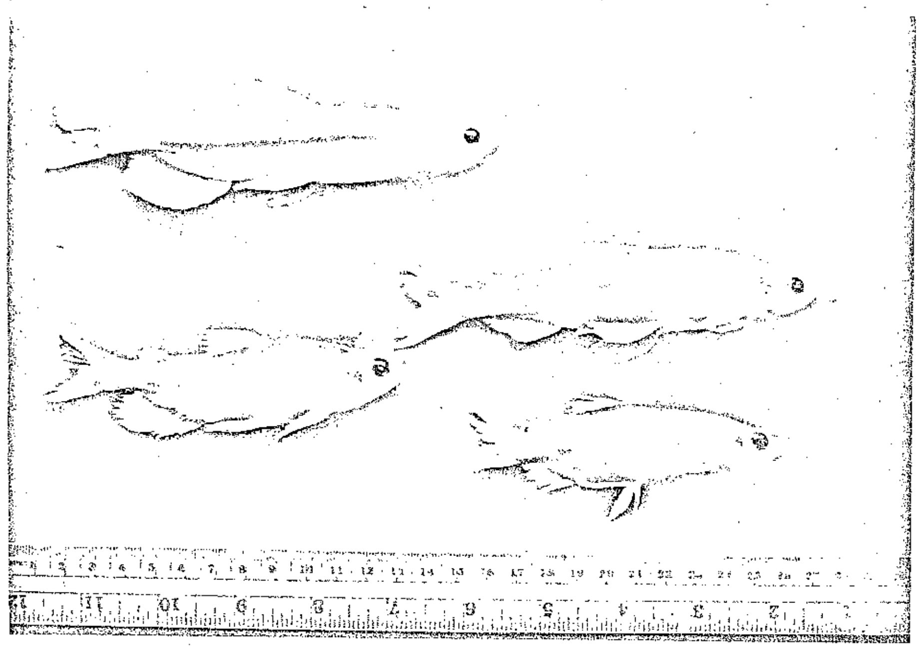


Figure 27. Photograph illustrating normal and severely deformed fish with Type 1 vertebral deformities.

(DeLacy and Batts, 1963). Some European authors working on brown trout and herring have compromised and added 0.5 vertebrae for each accessory spine rather than 1.0 vertebrae as used by McHugh and in this study (Schmidt, 1921; Ford, 1933). This adjustment would give the Lake Washington smelt with additional spines approximately the same average number of vertebrae as normal smelt from the lake.

Other vertebral deformities were found but were of comparably low incidence. These deformities were of two principle types. One was an asymmetrical vertebral element (13 cases), the other was a spiral suture between the vertebrae (10 cases). Mis-shaped vertebral centra or accessory spines were recorded in 21 cases but were not always recorded during the observation of the vertebrae. No analysis of the relationship between these less frequent deformities and the meristic characters was attempted.

The occurrence of these major vertebral deformities by year class is given in Table 13. The overall average frequency of smelt with some type of deformity during the study was 39%. The smelt may for all practical purposes be considered as odd and even year stocks. It will be noted that the occurrence of vertebral deformities shows no genetic trend. There is no relationship between incidence of deformities in the parental-progeny line. The two vertebral deformities also do not show a strong relationship to one another. From these data it would appear that the environmental influences on the incidence of deformities may be important.

Table 13. Frequency of occurrence of major vertebral deformities by year class

	1961	1962	1963	1964
Type 1	27%	31%	14%	3%
Type 2	23%	18.5%	19%	13.5%
Any vertebral deformity	45%	47%	33%	16%
Number of smelt examined	62	405	469	37

The absence of the dorsal fin was another major deformity observed. Thirty-eight fish with no dorsal fin were captured. Ten more fish had a reduced dorsal fin (i.e., 3 to 6 fin rays instead of the typical 9 or 10 rays). These fish with abnormal dorsal fins had no supporting skeletal elements for the missing fin or fin rays. The occurrence of these dorsal fin abnormalities was not a direct function of either common vertebral deformity. Examination of the meristic characters for fish without a dorsal fin and for those with a reduced dorsal fin revealed an association with a significantly lower-than-normal number of anal fin rays. In addition, a significantly higher-than-normal number of pectoral fin rays were revealed. The complete loss of the dorsal fin was also associated with a significantly higher number of vertebrae. Table 14 shows the frequency of occurrence of these abnormalities by year class.

Table 14. Frequency of occurrence of dorsal fin abnormalities by year class

	1961	1962	1963	1964
No dorsal	4%	1%	5%	0%
Reduced dorsal	3%	1%	.3%	.7%
Total number of smelt examined	75	470	606	147

Only in the loss of the dorsal fin is there a regularity of occurrence in parent and offspring. Whether this is indicative of genetic influences or a fortuitous combination cannot be resolved by the data. There is a reasonably high probability that this regularity in dorsal fin loss is due purely to chance. Since four different abnormalities have been obtained when including the vertebral deformities and three of them do not indicate a direct genetic effect, the significance of the fourth is doubtful. Until further evidence of a genetic origin of the deformities and abnormalities is gathered, the probability that they are environmentally induced will be accepted. If a high incidence of vertebral deformities continues to exist after the cessation of discharges of treated sewage and industrial wastes into the lake it should warrant further attention.

Meristics and Morphometrics

As noted earlier, the taxonomic status of this species recently has been changed. The change in nomenclature was brought about by McAllister's recognition of a cline in the characters used to distinguish S. dilatus from S. thaleichthys. Consequently, it was desirable to define the amount of variation in the taxonomic characters within a relatively homogeneous population. Considerably more morphometric data were obtained than are included in this discussion. The complete data were scanned for the more meaningful information to the taxonomic questions raised. Tables 15 and 16 present a summary of the analysis of the meristic data for age, sex, and year class differences.

The numbers of anal fin rays, gill rakers and pyloric caeca change with age. The numbers of anal rays and gill rakers apparently become fixed after about 6 months; the pyloric caeca after about 9 months. No differences were found in the other characters by age. For consideration of sex and year class differences the age may be disregarded since the sex could not be determined until about 8 or 9 months of age. After this age, very little change in the meristic characters was observed. Sexual dimorphism in meristic characters was not significant.

Table 15. Meristic characters by three-month age groups to the adults and their differences from the adult counts

	1-3 mos. N=19-36	4-6 mos. N=11-142	7-9 mos. N=33-118	10-12 mos. N=27-92	Adults 13-24 mos. N=176-367
	Means	Means	Means	Means	Means
Vertebrae	-----	59.36	59.42	59.5	59.5
Pectoral	-----	12.21	11.90	12.11	11.90
Dorsal	9.05	9.17	9.26	9.25	9.16
Anal	19.05*	19.60*	19.81	19.66	20.2
Total gill rakers	16.69*	30.01*	41.31	41.35	41.4
Lower gill rakers	15.14*	23.05*	29.53	29.75	29.15
Pyloric caeca	0.03*	1.58*	4.40*	4.70	4.73

*Difference significant at 5%.

Table 16. Comparison of meristic characters by sex and year class for 1962 and 1963

	Year class	Sex: Male Means	Sex: Female Means	Difference Significant at 5%	
Vertebrae	1962	59.31	59.48	Year class	Yes
	1963	59.75	59.59	Sex	No
Pectoral fin rays	1962	11.98	11.90	Year class	No
	1963	11.90	11.92	Sex	No
Dorsal fin rays	1962	9.24	9.13	Year class	No
	1963	9.04	9.14	Sex	No
Anal fin rays	1962	20.0	19.78	Year class	No
	1963	19.99	19.91	Sex	No
Total gill rakers	1962	42.07	41.86	Year class	No
	1963	41.49	41.84	Sex	No
Lower gill rakers	1962	29.84	29.73	Year class	No
	1963	29.65	29.79	Sex	No
Pyloric caeca	1962	4.53	4.53	Year class	Yes
	1963	4.83	4.82	Sex	No

For the two year classes (1962 and 1963) which could be compared, only the numbers of vertebrae and pyloric caeca showed significant differences.

The samples collected from different parts of the lake were also compared to determine if any difference in counts occurred in the different areas. No significant differences in the meristic characters were found in adult smelt caught in different areas of the lake. The young fish did show significant differences in the number of gill rakers present between the four collecting areas. Vertebrae and pyloric caeca could not be properly analyzed for these young fish. Table 17 presents the results of this analysis. This difference reflects the capture of more very young fish in the south end than in the other areas.

The morphometric data were examined by plotting character length against standard length. Some characters were plotted against head length. The length of the adipose fin base, depth, distance from the snout to the origin of the dorsal fin, head length, upper jaw length, orbit width, pectoral fin length, pelvic fin length, the distance between the pectoral and pelvic fin insertion, and the length of the seventh from the last anal fin ray were all considered. The most striking result from this analysis concerned one of the key taxonomic characters previously used to distinguish S. dilatus from S. thaleichthys.

The length of the pectoral fin divided by the distance

Table 17. Analysis of meristic differences by area of capture for smelt less than 9 months old and for those 9 months old or older

	Area Average 1	2	3	4	Analysis of Variance d.f.	F
< 9 months old						
Pectoral fin rays	12.14	12.12	12.19	12.12	3,92	0.0475
Dorsal fin rays	9.12	9.08	9.23	9.13	3,179	0.9525
Anal fin rays	19.61	19.76	19.52	19.48	3,172	0.97[illegible]
Total gill rakers	31.08	32.27	29.37	25.04	3,190	4.5295**
≥ 9 months old						
Vertebrae	59.49	59.29	59.48	59.49	3,646	1.5643
Pectoral fin rays	11.80	11.80	11.92	11.96	3,261	1.1043
Dorsal fin rays	9.13	9.18	9.24	9.22	3,264	0.2174
Anal fin rays	20.07	19.90	19.92	19.36	3,264	0.7026
Total gill rakers	41.77	41.74	42.04	41.60	3,26[illegible]	0.6660
Pyloric caeca	4.78	4.86	4.39	4.63	3,252	2.3577

**Significant at 1%.

between the insertions of the pectoral fin and the pelvic fin was plotted against standard length. Figure 28 shows the resulting plot. This ratio is quite dependent on the length of the fish. Plots of the components of this ratio with standard length (Figures 29 and 30) show different allometric growth relationships. It will be noted that S. thaleichthys was described and is currently represented in its type locality by adult fishes of about 78 mm. standard length. Spirinchus dilatus was described and is currently represented in its type locality by adult fishes of about 115 mm. standard length. The cline noted by McAllister (1963) for this character appears to be a reflection of another well-known cline in temperate marine fishes--that of final size (Gunter, 1950). The results of the examination of the remaining morphometric data are presented in Table 18. Three additional ratios were plotted against standard length. Upper jaw length divided by head length was constant and had a mean value of .492 for 276 specimens. Ninety-five percent of the observations were between .400 and .545. Orbit length divided by head length was constant with a suggestion of a slight decrease at lengths greater than about 95 mm. The overall average from 268 specimens was .220. The interval 0.187 to 0.253 contained 95% of the observations. Adipose length divided by head length decreased between 20 mm. and 40 mm. standard length. The ratio did not change beyond a length of 40 mm. The mean for the ratio for 212

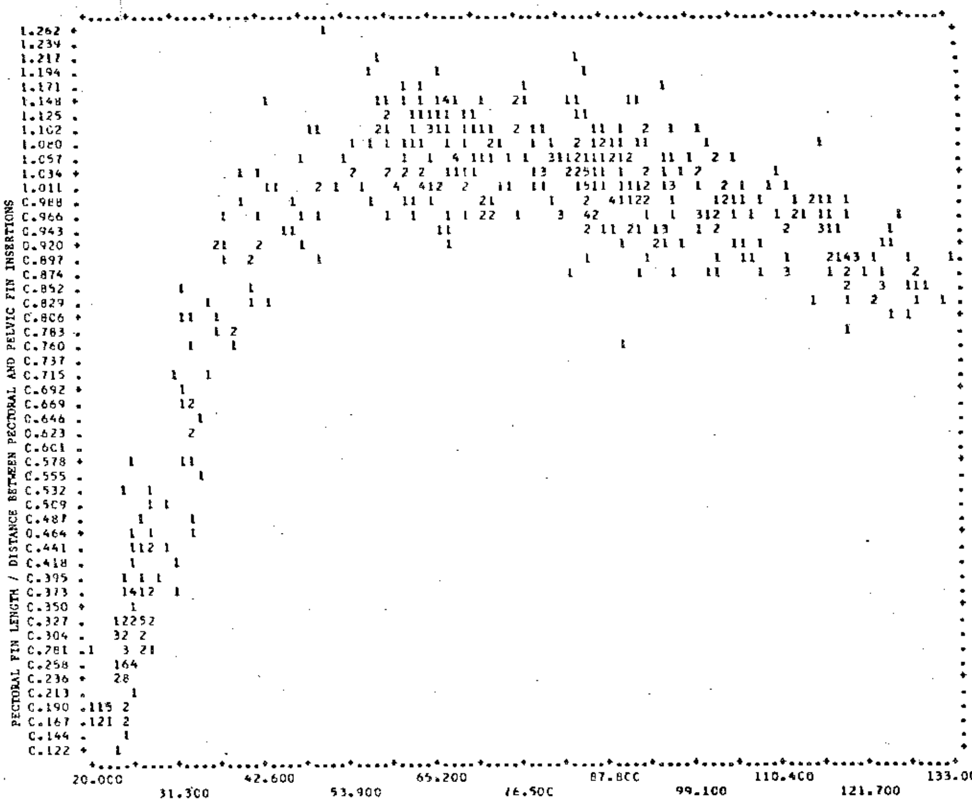


FIGURE 23. PLOT OF THE LENGTH OF THE PECTORAL FIN DIVIDED BY THE DISTANCE BETWEEN THE INSERTIONS OF THE PECTORAL FIN AND THE PELVIC FIN AGAINST STANDARD LENGTH.

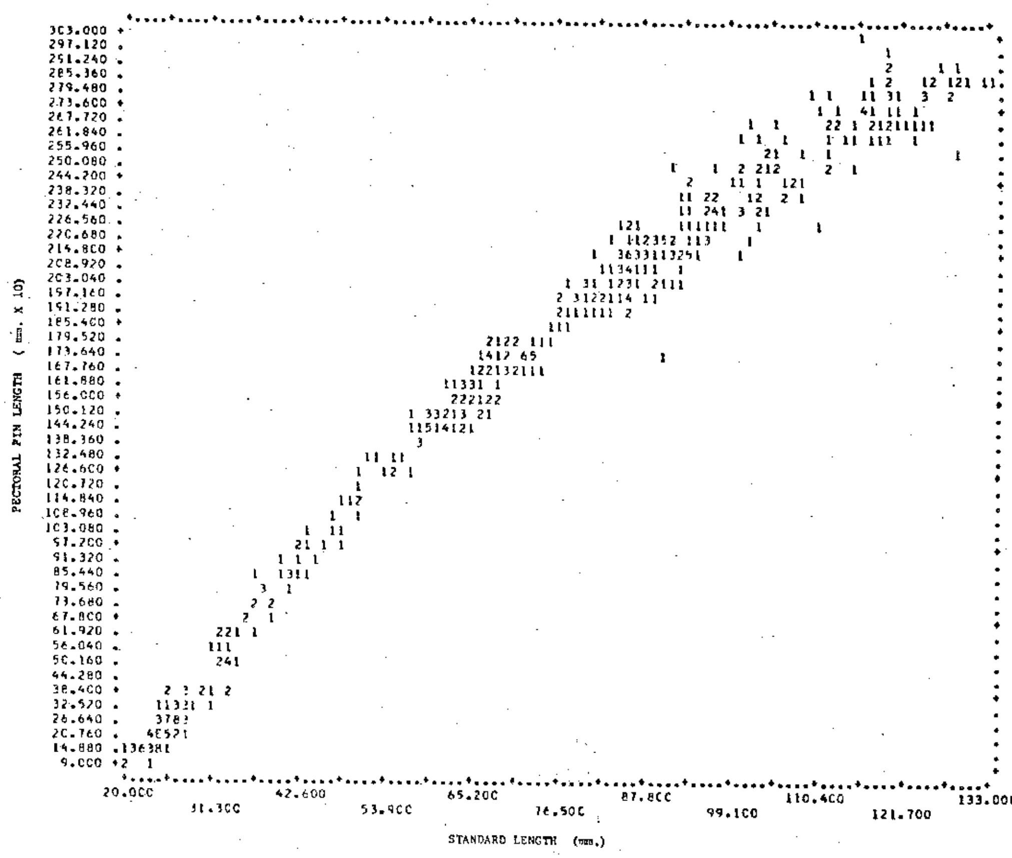


FIGURE 2[illegible]. PLOT OF THE LENGTH OF THE PECTORAL FIN VERSUS STANDARD LENGTH.

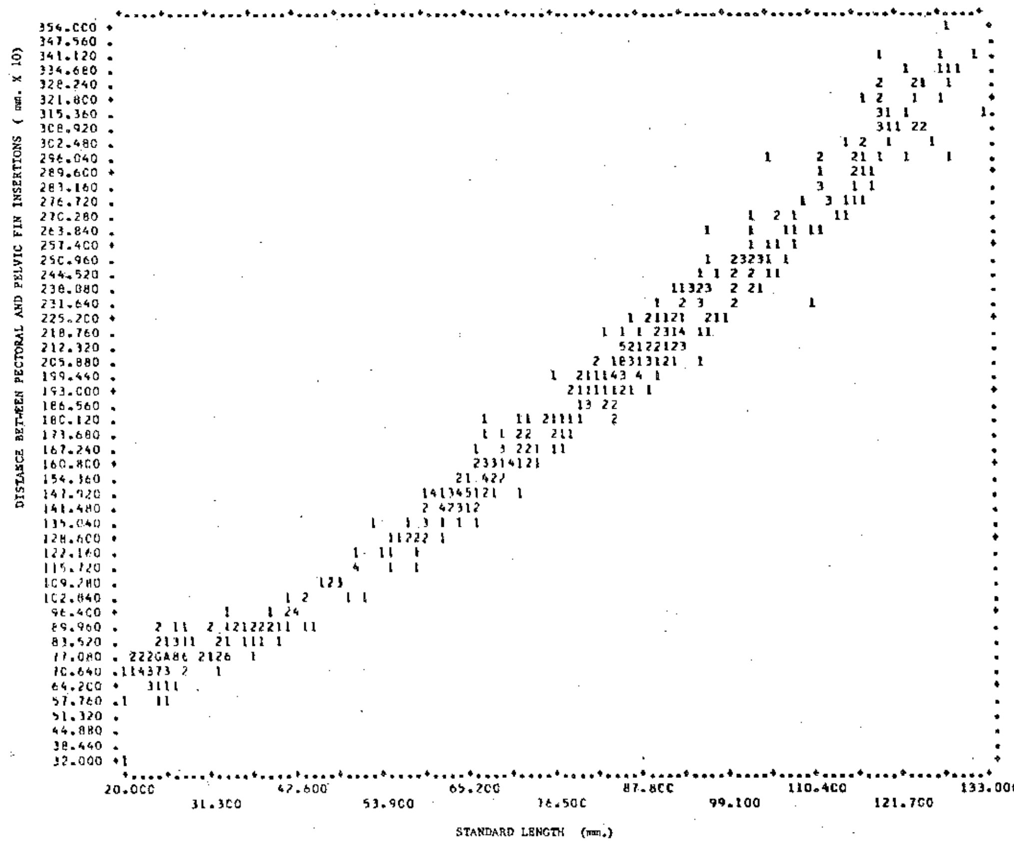


FIGURE [illegible]. PLOT OF THE DISTANCE BETWEEN THE INSERTION OF THE PECTORAL AND PELVIC FINS VERSUS STANDARD LENGTH

Table 18. General growth form of morphometric characters

Character	Growth form with increasing standard length (S.L.)	Equation
Adipose fin length	Linear	Y= 0.60701 +0.03177L
Depth	Linear	Y= -3.04629 +0.22799L
Distance from snout to dorsal origin	Linear	Y= 2.07140 +0.46479L
Head length	(≥ 40 mm. S.L.) linear	Y= 1.99613 +0.20341L
Upper jaw length	(≥ 40 mm. S.L.) linear	Y= 1.83452 +0.09295L
Orbit width	(≥ 40 mm. S.L.) linear	Y= 0.30030 +0.040[illegible]7L
Pelvic fin length	(≥ 40 mm. S.L.) linear	Y= -[illegible].13188 +0.24738L

specimens above 40 mm. standard length was 0.171. Ninety-five percent of the observations were between 0.10 and 0.20. All three ratios when plotted against standard length, showed a slight decrease in variance with increasing size.

The length of the seventh from the last anal fin ray was measured to determine the time of formation of the sexual dimorphism of the anal fin in the male. When these data were plotted against standard length it was observed that when the male attained a length of about 95 mm. the growth rate of their anal fin rays accelerated. Before this fish length was attained the male and female smelt anal fin rays grew at about the same rate. Table 19 indicates the magnitude of this change in rate as a change in the linear regression slope of the anal fin ray length versus body length. The average male smelt in the 1962 year class reached a length of 95 mm. in August of their second year.

Studies of Smelt from Other Areas

San Juan Islands, Washington

Collections were made in East Sound, Orcas Island, during the summer of 1963 and the winter, spring, and summer of 1964 by Mr. Bruce Miller of the College of Fisheries, University of Washington. An otter trawl was used to make these daytime collections. The smallest longfin smelt captured here was 40 mm.

Table 19. Sexual dimorphism in the length of the seventh from the last anal fin ray

Stage	Slope of the linear regression of fin ray length on standard length
Immature (no sex, < 75 mm.)	0.8387
Small ♀ (< 95 mm.)	0.7794
Small ♂ (< 95 mm.)	0.9665
Large ♀ (≥ 95 mm.)	0.5862
Large ♂ (≥ 95 mm.)	2.7885

standard length and was taken on June 27, 1963. A comparison of the lengths at comparable ages for the East Sound and the Lake Washington populations indicates that they reach approximately the same size at each age. September samples from East Sound had a distinct mode at about 112 mm. Examination of adults from East Sound revealed a significant difference in length of mature males and females. Adult females averaged 106 mm. and adult males averaged 117 mm. in January, 1963. The spawning area of this population is not known; however, a consideration of their size, time of maturity, and availability suggests that it is not far from East Sound and that it is not the Nooksack River. Catches made during the spring included several adult specimens which showed indications of having spawned. Females dominated among the catches made of smelt after they had spawned.

Port Gardner, Washington

Collections were made in this area by Dr. Thomas English, Department of Oceanography, University of Washington, using a 16' otter trawl. Specimens as small as 35 mm. were obtained in September, 1962; however, the modal length of the young smelt at this time was 42 mm. The adult smelt had a mode at 100 mm. These fish presumably spawn in the Snohomish River. Mr. Richard Pressey then with the Washington State Department of Fisheries, has provided records of his observation of longfin smelt in the

Snohomish River near Lowell in December, 1951.

Sacramento and San Joaquin Rivers, California

Mr. Clark Blunt, Jr. of the California Department of Fish and Game has provided considerable data on the distribution of the adult longfin smelt in the Sacramento and San Joaquin River delta area. The data were summarized very well by Mr. Blunt in a letter (February 17, 1964) to the author and his summary is quoted below:

> Generally from our work in the Delta..., we can make the following points:
>
> (1) Sacramento smelt began to work their way up into the Delta during December and January.
>
> (2) During February and March they are distributed throughout the Sacramento, Mokelumne and lower San Joaquin rivers.
>
> (3) None was taken in the San Joaquin River above the confluence with the Mokelumne or the southern Delta. This is significant and the reasons for this are unknown. Since this appears to be a spawning migration, it is possible that water temperature may have an effect on their distribution as the San Joaquin River and southern Delta are from 2-3°F. warmer than the Sacramento River.
>
> (4) Midwater trawling during April-November indicates almost a complete absence of this species in the Delta.
>
> (5) The first catches occurred in December 1963 in the lower Sacramento and San Joaquin Rivers.
>
> (6) Their occurrence in the Sacramento appears to be a spawning migration as specimens collected by us in January and February of this year are in a ripening

or ripe condition. Whether or not they die after spawning is not known.

Additional information was obtained from Mr. John Thomas, California Department of Fish and Game, pertaining to the distribution of the young smelt. He noted observing about 10,000 one-inch smelt in Carquinez Strait in May, 1962. This appears to represent an out migration of the larval smelt. Length data he collected on the adult smelt in January, 1962, are presented in Table 20. The mode between 70 and 90 mm. presumably represents mature two-year-olds, while that at 120 to 130 mm., represents three-year-olds.

The specimens received from the delta area, including some one-year-olds, confirm the age distribution indicated by Rosa (1946). The adults are predominantly two-year-olds with some three-year-olds, mostly females, also being present. Meristic and morphometric data of some of these smelt were obtained. Twenty-eight adults taken from several locations in the delta between December 30, 1963, and March 23, 1964, were used in this study. The average standard length was 78 mm., and the range from 71 to 91 mm. Those examined all appeared to be two-year-old adults. The meristic data for the 1964 collection of smelt is summarized in the following table.

Table 20. Length* frequency of January caught mature longfin smelt in Carquinez Strait, California, in 1962

Fork Length	Frequency	Percent
60 - 69 mm.	8	7.1
70 - 79 mm.	43	38.4
80 - 89 mm.	31	27.7
90 - 99 mm.	16	14.3
100 - 109 mm.	6	5.4
110 - 119 mm.	1	0.9
120 - 129 mm.	5	4.5
130 - 139 mm.	1	0.9

*Fork length data.

Table 21. Summary of meristic data for 28 longfin smelt from the delta of the Sacramento and San Joaquin Rivers*

Character	Mean	Range
Dorsal fin rays	9.28	9-10
Anal fin rays	19.57	18-21
Vertebrae	55.39	54-57

*Collected from December 30, 1963, through March 23, 1964.

The differences between these smelt and the Lake Washington population in the fin ray counts may readily be dismissed as they are relatively small compared to the variability in the counts. The differences in the number of vertebrae between smelt from Lake Washington and those from California are very large. McAllister (1963) has noted a cline in this character. (Note: In comparing data in this paper with that of McAllister's, account must be taken of the different methods and criteria used in counting.)

The only morphometric character examined in the California smelt sample was the ratio of the length of the pectoral fin divided by the distance between the insertions of the pectoral and pelvic fins. The average ratio was 1.06. All but one observation were equal to or greater than a ratio of one. Comparison of this ratio with that for smelt of the same length from Lake Washington shows them to have approximately the same ratio (Figure 19).

Nooksack River, Washington

A single dip net collection of adult smelt in the Nooksack River was made as a part of this study in November, 1963. Collections of spawning smelt from this river have almost invariably been made in November. This is the earliest time of spawning yet known for this species of smelt, although other streams in this area appear to have populations maturing in December and January. Those in Lake Washington are the latest spawning local population known and appear to spawn in December through February. The sample from the Nooksack River represented only one time in the spawning period and may not be representative of the aggregate population. It was made at a time and on a year class for which comparisons with other stocks could be made. The specimens are all adults predominantly two years old. A few three-year-old females were also taken. This collection reveals a sexual dimorphism in the length of the adults. The 21 males form a single mode at 112 mm. (range from 104 to 118 mm.), and the 15 females have a major mode at 94 mm. and a small second mode at 116 mm. (range from 93 to 119 mm.). The second mode appears to be composed of three-year-olds.

This collection was further analyzed to determine the average number of dorsal and anal fin rays and vertebrae. The following table presents these data.

Table 22. Summary of meristic data for 36 longfin smelt from the Nooksack River, November 24, 1963

Character	Mean	Range
Dorsal fin rays	9.86	9-11
Anal fin rays	20.31	19-22
Vertebrae	59.0	57-61

The differences between the Nooksack and the Lake Washington fish are most pronounced in the dorsal fin ray counts and the number of vertebrae. Both are significant differences. The ratio of the pectoral fin length to the distance between the insertions of the pectoral and pelvic fins was also determined. The average ratio for the morphometric characters was 0.91 with a range of from 0.83 to 1.00. This is similar to the ratio obtained in Lake Washington for fish of a comparable length.

Harrison Lake, British Columbia

Harrison Lake was selected for investigations because three specimens of the longfin smelt, 53-54 mm. long, had at some time been picked up on its beach. The collector and date of collection were not recorded, but the specimens were entered into the University of British Columbia Fish Museum in 1957. The specimens were larger than the smallest specimens which had been obtained from saltwater (35 mm.). This fact suggested the possibility that the smelt were resident in the lake. Originally only one trip to Harrison Lake was planned. Four seasonal trips were made as a consequence of the results from the first trip.

The first trip to Harrison Lake was made on September 21, 1963. A 165-hp. tugboat, the TIPELLA, was chartered and the midwater trawl was attached to the tow line. A rope was attached to the 20" ring in the cod end and tied to the upper tow bar of the net. The trawl could not be lifted out of the water and properly cleaned after each tow but the rope served to bring the cod end aboard the vessel at the end of each tow. The towing periods varied from 10 to 15 minutes and the contamination time was considerably greater than that in Lake Washington. Despite these problems, all trips to Harrison Lake were successful. Boat speed was maintained reasonably constant and the cable-to-depth relationship determined separately for each trip. The September, 1963, trip was made entirely under daylight conditions. Figure 31 presents the smelt catch data for the September trip by depth of capture.

It was apparent during the collection of these smelt that two groups were present in the population. The fact that they were actually a year apart in age was not obvious until the succeeding trip. The total catch in September was 122 juvenile smelt and 7 adults in 13 tows. The tows were not made in any one

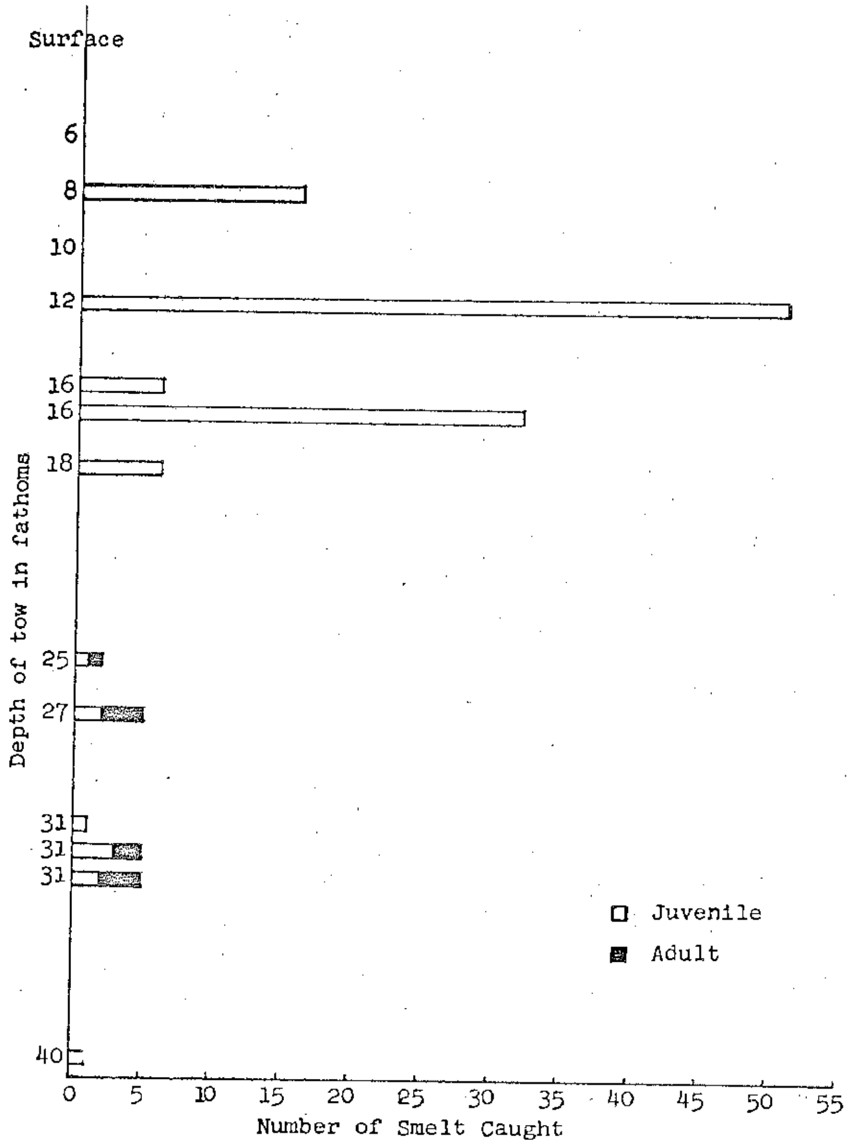


Figure 31. Depth of tow and numbers of juvenile and adult smelt captured in Harrison Lake, September 21, 1963.

part of the lake but rather were made on a track which covered about the lower half of the length of this 35-mile-long lake. When allowance is made for the contamination from haul to haul and during each tow, it emphasizes the difference in the daytime depth distribution of the adults and juveniles. It is clear that the juvenile smelt were most abundant at about 12 fathoms and the adults probably at about 30 fathoms. There was no thermocline within this depth range but there was a nearly linear decrease in temperature with depth. The juveniles were in water of about 58° F. while the adults were at about 46°F. Although no oxygen or carbon dioxide data are available for Harrison Lake, there is little question that these parameters are not limiting the distribution of the adult smelt in oligotrophic Harrison Lake.

It is noteworthy that, in addition to the 129 smelt, only 10 other fish were taken. Nine specimens of the three-spine stickleback and one adult specimen of Lampetra ayresi made up the other fish species. This is the farthest inland record for the lamprey. Mysids, Neomysis awatchensis, were present but the quantity was extremely small compared to that taken in Lake Washington. Approximately 30 individual mysids were obtained during this trip.

Smelt were subsampled, measured, and weighed. The average length of 32 juveniles was found to be 29 mm., the average weight was 0.14 gm. For the 7 adults, the average length was 50 mm.;

the average weight was 1.11 gm.

In November, a second trip to Harrison Lake was made. On this and succeeding trips sampling was confined to the southern part of the lake generally on a track between Long Island and Echo Island. The first four tows were made before dusk, the remaining nine after dark. Smelt of both age groups were taken in all but one haul. Figure 32 illustrates the catch of juvenile and adult smelt by depth and time of day. Little can be concluded regarding differences in distribution between day and night from these data; however, it does suggest that the nighttime maximum of abundance was in the vicinity of 25 fathoms. Both adults and young fish were widely distributed in depth.

The total catch at this time was 224 smelt which included 67 adults. Thirty-seven sticklebacks and 6 sockeye salmon comprised the other fish species caught. A subsample of 23 juvenile smelt was found to have an average length of 35.5 mm. and an average weight of 0.32 gm. A subsample of adults showed 11 males to average 54.1 mm. in length and 1.44 gm. in weight. Thirteen females had an average length of 51.1 gm. and an average weight of 1.18 gm. The differences between the males and females in length and weight were consistent and significant. Two females, 61 and 63 mm., were taken which were considered to be three-year-olds.

The typical sexual dimorphism in the anal fin was obvious in the November sample. In fact, this was the first indication that

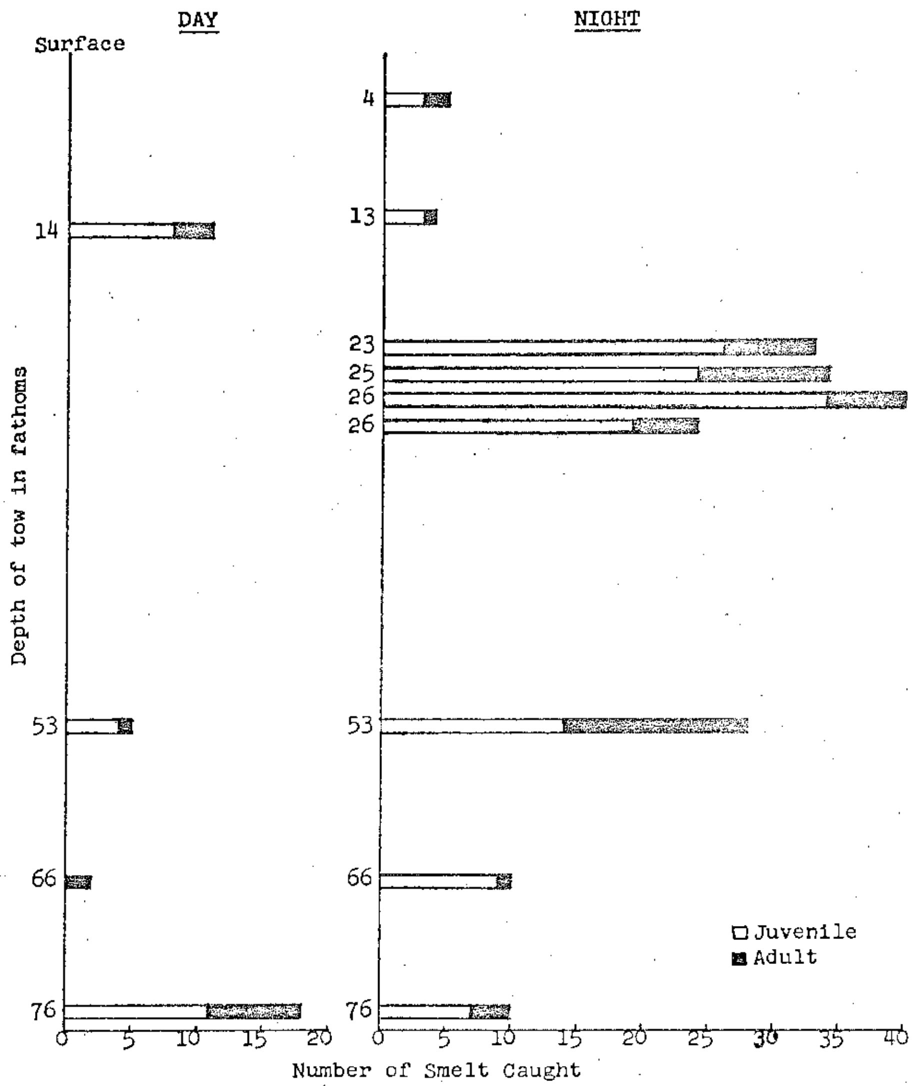


Figure 32. Depth of tow and numbers of juvenile and adult smelt captured in Harrison Lake, November 23, 1963.

the fish were sexually mature. Re-examination of the three small specimens previously found on the lake shore showed them to have been sexually mature males. They were the same size as those taken in November, 1963.

Fecundity was determined for mature adult smelt taken in November by direct count of the eggs. Six individuals from 46 to 61 mm. were used for this study. The following table presents the data obtained.

Table 23. Fecundity of adult smelt from Harrison Lake, November 23, 1963

Standard length (mm.)	Total fecundity
46	535
49	880
51	1,033
55	960
58	1,142
61*	2,425

*A three-year-old.

A subsample of 42 adult smelt from the November sample was used for meristic and morphometric comparison with the Lake Washington and other populations of the longfin smelt. The following table presents the meristic data obtained.

Table 24. Summary of meristic data for 42 longfin smelt from Harrison Lake, November 23, 1963

Character	Mean	Range
Dorsal fin rays	9.12	8-10
Anal fin rays	18.43	17-20
Vertebrae	56.05	54-58

The anal fin rays and the vertebrae are both significantly different from those in Lake Washington. The counts do not fit the cline reported by McAllister (1963). The number of vertebrae is remarkably close to the number found in the delta of the Sacramento and San Joaquin Rivers but is significantly higher. It is noteworthy that the three small specimens previously taken in Harrison Lake have vertebrae counts similar to those obtained in November. The single large specimen taken in Harrison Lake and designated a paratype of S. dilatus by Schultz and Chapman (1934) has 57 vertebrae.

The morphometric ratio of pectoral fin length divided by the distance between the insertions of the pectoral and pelvic fins averaged 0.98 for the November sample. This also is comparable to the ratio found for Lake Washington smelt of comparable length.

The third sampling trip to Harrison Lake occurred on March 21, 1964. As in Lake Washington, the catch had fallen off appreciably from the summer and fall sampling trips. The sampling during this trip was conducted only during the daylight hours. Twenty-eight smelt including one three-year-old female were taken. In addition, 5 sticklebacks and 1 sockeye salmon were caught. Figure 33 gives the depth distribution of the smelt caught.

From Figure 33 it appears as if the greatest concentration of smelt during the day was between 20 and 32 fathoms. The difference in abundance of these smelt compared to the high abundance as juveniles in November suggests either a rather high mortality during the winter or a real change in distribution.

The collections of smelt again were subsampled and length and weight data obtained. Nineteen yearling smelt averaged 36.8 mm. and had an average weight of 0.28 gm. The single three-year-old, a female, was 53 mm. long and weighed 1.15 gm.

The fourth sampling trip to Harrison Lake was conducted in June, 1964, to complete a seasonal sampling pattern and to obtain specimens of the larval smelt. Six tows were made before dark and 12 after dark. The depth distribution of the catch for the larvae and adults is given in Figure 34.

It is evident that during the June sampling program the smelt were concentrated relatively near the surface, at a depth of about 5 fathoms. The daytime distribution is not so clearly defined and the data are not adequate for analysis. The June sampling provided 57 smelt including 15 adults, 103 sticklebacks, 3 Cottus

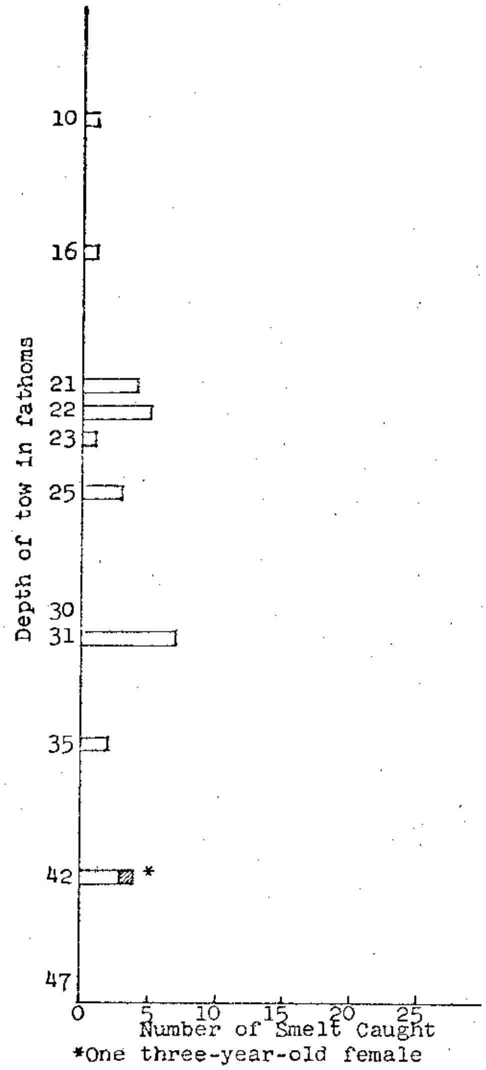


Figure 33. Depth of tow and numbers of smelt beginning their second year of life captured in Harrison Lake, March 21, 1964.

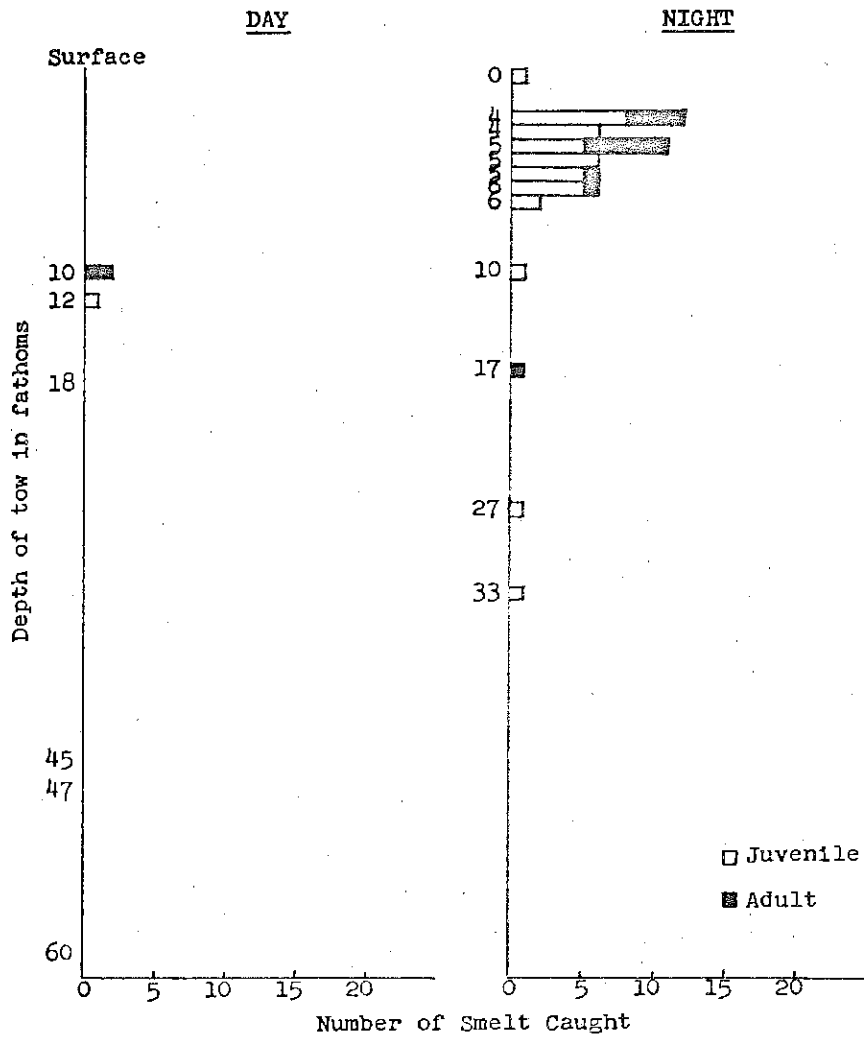


Figure 34. Depth of tow and numbers of juvenile and adult smelt captured in Harrison Lake, June 19-20, 1964.

asper larvae, and a second *Lampetra ayersi* from a total of 18 hauls. The smelt specimens were weighed and measured. The average length of 39 juveniles was 19 mm. and their average weight was 0.02 mm. The 15 adults averaged 42 mm. standard length and weighed on the average of 0.61 gm.

The general growth pattern of the Harrison Lake smelt regardless of year class is illustrated in Figure 35. It is evident that this population is stunted in growth. Indications that this is due to a high population density and the low productivity of the lake are found in the very high catches of smelt and very small amount of zooplankton, either mysids or copepods, taken in the trawl. Harrison Lake is typically an oligotrophic lake. Glacial silt reduces the transparency of the water during periods of melting ice. It is of some significance that no vertebral deformities were observed while reading the x-ray films for the adult smelt. One could assume that with high intra-specific competition for food, deformed fish would be eliminated. The small size at maturity has apparently reduced the fecundity; however, the reduction in individual fecundity must be made up in numbers of smelt. The ratio of fecundity to body weight is slightly higher for the Harrison Lake population than for the Lake Washington population.

The seasonal trend in availability in Harrison Lake is similar to that for Lake Washington smelt, except that recruitment

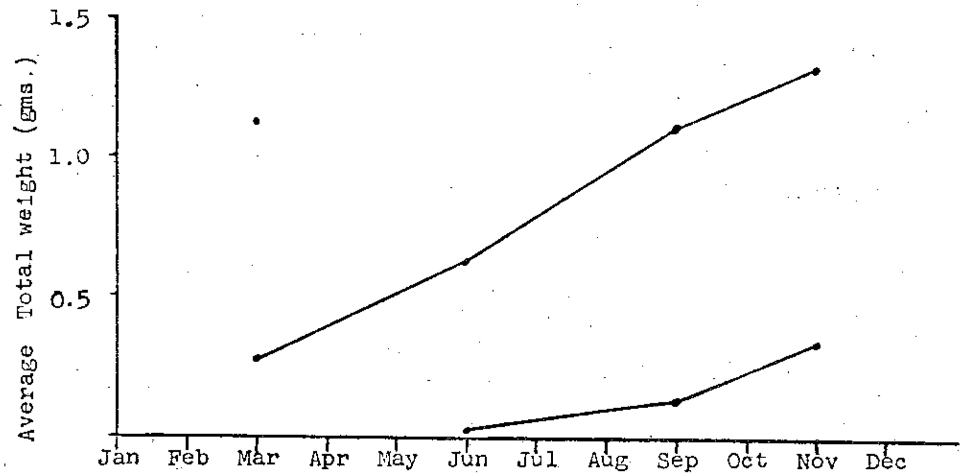


Figure 35. General growth pattern of the Harrison Lake smelt regardless of year class.

to the population that is sampled appears to be later. The decline in abundance or availability with age is relatively greater in Harrison Lake. Figure 36 illustrates the fluctuation in catch per unit of effort in Harrison Lake.

The depth distribution of the smelt in Harrison Lake shows some parallels to that in Lake Washington; however, marked differences also occur. No adequate data were obtained to determine the diel vertical migration pattern. Considerable additional data which are not available would be required to more closely relate the vertical distribution of the smelt in the two lakes. Suffice it to say that regardless of the actual depth of the maxima concerned, the relationship between the most productive depths for the juvenile and adult smelt at a given time of day and season showed the same basic pattern in Harrison Lake as in Lake Washington. The daytime adult distribution in the summer suggested a relationship with light.

In summary, the Harrison Lake smelt population has provided considerable insight into the factors involved in the Lake Washington population. The existence of a second resident stock increases the importance and significance of the Lake Washington study. It supports the thesis that the Lake Washington population is not an artifact caused perhaps by man's alteration of the Lake Washington drainage system. It has indicated that the species has a remarkable range of adaptability to different

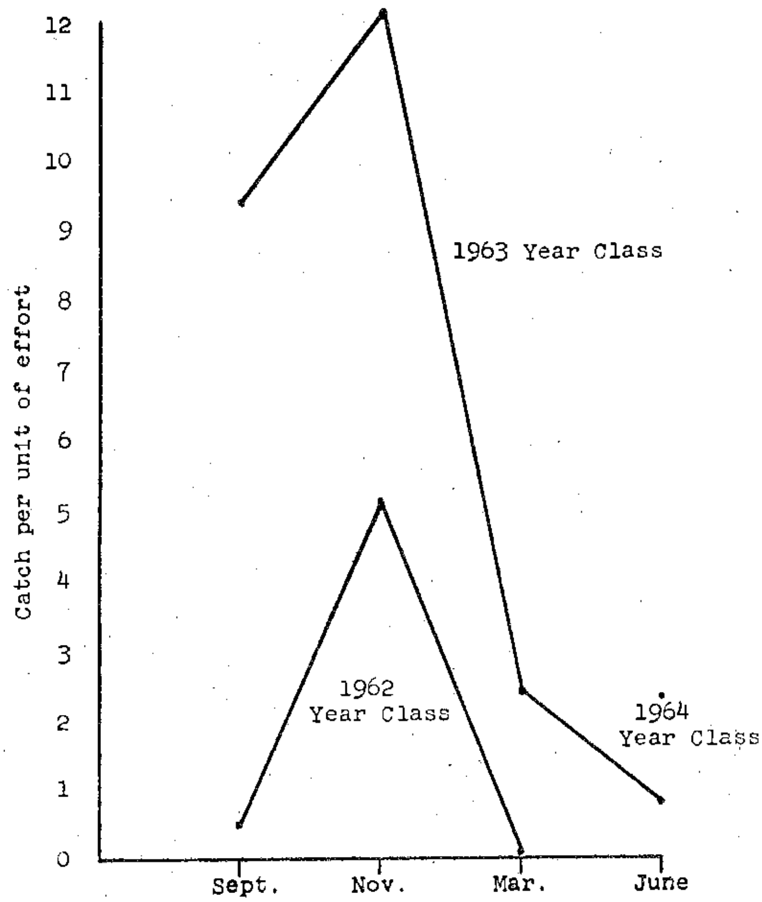


Figure 36. Fluctuation in catch of smelt per unit of effort in Harrison Lake.

levels of productivity and that it can compete with the other native limnetic species, such as the sockeye salmon, under these varied conditions. The occurrence of another freshwater resident population without a high incidence of vertebral deformities suggests that this need not be a syndrome of freshwater residualism.

Taxonomic Considerations

It is concluded that the meristic differences between the lacustrine and anadromous stocks examined are statistically significant but that they do not warrant taxonomic separation. The differences between the resident and anadromous stocks are not consistent and the lake forms resemble each other less than they resemble different anadromous stocks. The clinal nature of the proportion of pectoral fin length to the distance between the pectoral and pelvic fins has been found to be more closely related to body length. A cline in body length is present among the anadromous populations, apparently being the cause of the cline in the aforementioned ratio.

Meristic differences between populations only indicate that there is not completely random mating among the individuals of different populations. It does not mean that the populations cannot interbreed. Local environmental factors and selection may be quite important in the determination of the meristic characters and yet the populations may belong to the same species and be capable of interbreeding with impunity. It is felt that the gene pool of the species is probably nearly complete in each population. Of interest in this regard is that the Harrison Lake population deviates from the cline in vertebrae and approaches the lowest count known for the species as found in California samples. Unless this population is spawning in or near the Harrison Hot Springs there is little environmental evidence to suggest physical or chemical factors as the cause of this deviation. The possibility of a selection or secondary adaptation for a low number of vertebrae under the very different conditions in Harrison Lake is present. If this is the case, it reinforces the hypothesis of a common gene pool which would permit the expression of such a low number of vertebrae.

The similarities between the populations should be considered in this section. All populations studied mature predominantly in their second year regardless of their size at this time. Figure 37 illustrates mature smelt from four of the study areas. Survival after spawning was rare. Those surviving to be three years old were dominated by females, a fact not uncommon in fishes. Sexual dimorphism in anal fin ray length and other characters begins to develop only a few (up to 6) months before spawning. This sexual dimorphism is absent in Spirinchus starksi. The morphometric ratio previously used to separate two species, S. thaleichthys and S. dilatus, was found to be nearly constant for the populations studied when the length of the fish was considered.

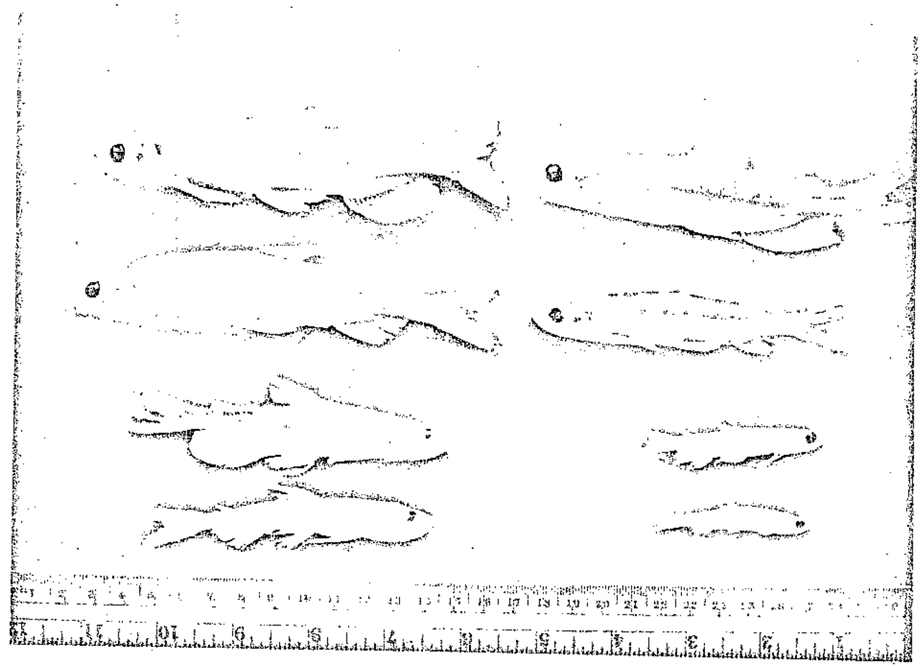


Figure 37. Mature, two-year-old, longfin smelt from four study areas. In each case the male is shown above the female. The specimens in the upper left were taken in Lake Washington and those in the upper right were from the Nooksack River. The lower left specimens came from the Sacramento River Delta and those in the lower right were collected in Harrison Lake.

The glacial history of both Harrison Lake and Lake Washington suggests that the smelt may be relics of marine origin and could not have occupied these lakes as freshwater residents until 8,000 to 13,000 years ago. For these reasons, the author feels the name, Spirinchus thaleichthys (Ayres) is appropriate for the longfin smelt throughout the geographic range of the species as defined by McAllister (1963) and Dryfoos (1961).

The Role and Future of the Smelt in the Lake Washington Ecosystem

The smelt in Lake Washington is a limnetic species, feeding virtually entirely on zooplankton. In Lake Washington under the conditions existing during this study, food did not appear to be limiting, and the smelt population density was not high. Interspecific competition did not appear to be a significant factor. Competition between the young smelt and the sockeye salmon populations may develop at higher population densities.

The smelt are not associated with any other species except perhaps their major food item--the mysids--although the diel and seasonal distribution patterns of the dominant fish species do occasionally overlap. The smelt appear to be a major predator upon the mysids. During the course of this study, there did not appear to be a significant predator on the smelt in Lake Washington or in Harrison Lake.

From the data now available for the smelt in Lake Washington and the supporting data from Harrison Lake, it appears that the species has the ability to alter its growth rate under conditions of low food supply and still mature at two years of age. In Harrison Lake the population is large and the individuals are stunted in growth.

At present in Lake Washington, the growth is excellent even surpassing that of some local anadromous populations. Indications of comparatively low levels of predation and competition in the lake have been obtained. The question of why the population in Lake Washington is not greater cannot be conclusively answered with the available data. Survival in the lake appears to be better than that in Harrison Lake. The data would indicate some source of very high mortality between the time the adult smelt leave the lake and the larvae return to it. In connection with this, the very high incidence of deformities which showed no indication of being of genetic origin is of interest. It is probable that in a more severe environment these fish would not survive as they do in Lake Washington. Nevertheless, their high incidence is suggestive of some environmental factor probably operating during the time of incubation which induces these deformities and probably also is responsible for a very high rate of embryonic mortality. The identification of the cause of this phenomenon was not possible during this study. Two potential causes do stand out above several other possibilities. An inadequate spawning environment is one possibility; the other, an actual pollutant. Since the diversion of domestic wastes from the lake and incoming streams is nearly complete at this time, the future occurrence of structural deformities and the smelt population density may be subjected to change. It is doubtful that the changes in lowered productivity of the lake will eliminate the smelt population; it is more likely that the population density will increase and the growth rate decrease. If, however, the population density does not increase due to a continuing high mortality, the smelt population may reach a point where slowed growth and lowered fecundity cannot cope with the mortality rate. Under these conditions, the population density would decline. Most likely, however, the species will not become extinct but will reach a lower equilibrium point. The extinction of the population, therefore, seems doubtful. If the foregoing prognosis is correct, a study of the smelt population in the future may provide an interesting commentary on the changes in the lake.

SUMMARY

Longfin smelt are resident in Lake Washington throughout their life. The smelt virtually without exception matured, spawned, and disappeared at the end of their second year. The growth of the smelt in Lake Washington surpasses that of some anadromous stocks of the same species. Growth of the longfin smelt may be represented by two periods of exponential growth at different rates separated by their first winter of very slow growth. Faster growth in the first nine months for the 1963 year class resulted in heavier and longer fish at successive ages than in 1962. The differences in rate of growth between the two year classes were confined to the first nine months.

Fecundity estimates were made for adults captured in January. The average fecundity for ten specimens between 108 and 126 mm. standard length was 18,104. There was no relation between length and fecundity in the small length range examined.

Smelt eggs were obtained on January 2, 1964 from a ripe female and fertilized. The smelt eggs hatched after 40 days at 44.5° F., and the length of the larvae at hatching was generally between 7 and 8 mm.

Larvae, 7 mm. long, were captured on March 5 and 7, 1963, in a half-meter net in the Cedar River. The distribution of mid-water trawl catches of larvae less than 2 cm. long in the lake suggests spawning at both ends of the lake. The Cedar River

is probably the major spawning location.

Eight species of zooplankton composed virtually all the food organisms eaten. The continuity in weight of stomach contents throughout the day and night suggests nearly continuous feeding. Seasonally, the summer is the most active feeding period, and the winter is the least active. Neomysis and Diaphanosoma accounted for most of the weight of food eaten by the juvenile smelt but frequently Diaptomus and Epischura were also eaten. For the adult smelt, Neomysis was the most important food item.

The youngest smelt were taken at the north and south ends of the lake in May. By July they were widely distributed throughout the lake. Both day and night during the summer and fall months the young smelt were most abundant between 6 and 12 fathoms. In the winter and spring they were usually at a depth of 15 fathoms or greater during the day. At night they were most abundant between 10 and 16 fathoms. During their second summer and fall the smelt were most abundant between 6 and 12 fathoms at night and between 10 and 20 fathoms during the day. In the winter they again were found at greater depths during the day than at night. The catch of adult smelt decreased during the winter period, presumably as they migrated to their spawning areas.

The data from a set pattern of depths and stations indicated the 1963 year class to be somewhat less abundant than either the 1962 or the 1964 year class. The difference in abundance however was not large.

Analysis of the catch composition for each tow showed the smelt and mysids to be significantly correlated. The smelt catch, when compared with other fish taken in the same haul, showed correlations between juvenile and adult smelt, between juvenile smelt and Cottus sp., and between adult smelt and sockeye salmon. These correlation coefficients were statistically significant but were not high, and the distribution of the smelt probably was not directly related to that of any other fish.

The distribution of the smelt depends partially on certain physical characteristics of the environment. The daytime depth distribution of the adult smelt appears to be related to the depth of light penetration. The summer depth distribution may be limited near the surface by high water temperatures.

Echo sounder records made simultaneously with the midwater trawl hauls provided considerable evidence supporting the distribution data obtained from the trawl catches. The catch of smelt and sockeye salmon was correlated with the number of marks recorded on the echo sounder from the depth of the trawl. A correlation coefficient of 0.795 was obtained for this relationship which was based on data collected during 695 tows made at all depths, times, and seasons of the year. The correlation could be increased to 0.842 by considering only the 289 tows least subject to avoidance of the net and contamination from overlying concentrations of fish. The smelt and sockeye salmon were responsible for the great majority of the fish marks on the Simrad. At the sensitivity setting used, the catches of neither mysids nor sculpins were significantly related to the Simrad marks.

Structural deformities occurred in the Lake Washington population at a very high frequency. One common vertebral deformity was characterized by the symmetrical fusion of two or more vertebrae. Of the 999 smelt examined for vertebral deformities, 21.6% expressed one or more fusions of this type. In the more severe cases, which also resulted in a stumpy body form, as many as 13 vertebrae were fused together in one unit. As many as 16 separate locations of fusions in a single vertebral column were noted. The most severe case had 31 vertebrae (of a total of 60) involved in fusions.

Another common but less severe deformity was the replication of a spine on one of the last two vertebrae before the urostyle. This deformity was found in 18.7% of the smelt examined.

The complete or partial loss of the dorsal fin was also observed. This abnormality was not related to the vertebral deformities, but was also structural in nature. No basal elements, which normally support the fin, were present. Fish with this abnormality also had significantly higher-than-normal pectoral fin ray counts, and lower-than-normal anal fin ray counts. The complete loss of the fin was also associated with a significantly higher-than-normal number of vertebrae. The frequency of the dorsal fin abnormalities varied between 0.7% and 7% of the smelt examined from the different year classes.

All deformities were found to vary in abundance from year class to year class. Although there is almost complete genetic separation of the odd and even year classes, there was no perceptible genetic trend in the occurrence of these deformities. The possibility that they are environmentally induced was accepted pending further evidence of a genetic origin.

The meristic and morphometric characters of the Lake Washington smelt population were determined. The addition of anal fin rays and gill rakers was completed at six months and the numbers of pyloric caeca present in adults were established at nine months. No meristic differences were found between the sexes; however, vertebrae and pyloric caeca varied significantly between the two year classes studied. The length of the posterior anal fin rays of the male began to diverge from that of the females at a length of about 95 mm. This usually occurred in August which is five months before the spawning season. Other morphometric characters were examined and generally found to be linear functions of the increase in length. The growth of the pectoral fin was not linear, and a ratio of pectoral fin length to the distance between the pectoral and pelvic fin insertions was found to be allometric. This ratio had been used for taxonomic purposes without concern for the length of the fish.

Meristic data obtained from smelt samples from California, the Nooksack River in Washington, and Harrison Lake in British Columbia, were compared with the data for the Lake Washington stock. Significant differences in these characters were found between smelt from all areas. It was concluded, however, that these differences did not necessitate taxonomic separation. The general life history pattern of growth, maturation, sexual dimorphism, time of spawning, and survival after spawning appear to be relatively constant between the anadromous populations and the population in Lake Washington. Although stunted in growth, the resident Harrison Lake population matures at the same age as do the Lake Washington smelt. This stunting is felt to be due to a very high population density and a low food supply.

The Harrison Lake population was studied seasonally and is the dominant limnetic species there. The seasonal availability in both Harrison Lake and Lake Washington follows the same general trend; however, the seasonal and diel depth distribution patterns are not directly comparable.

This study has provided data which indicates the condition of the smelt stock at a high level of primary productivity. Under the present conditions, the smelt population appears to be limited in number by a high mortality which may occur between the time the adult smelt migrate to the spawning area and the time the larvae are first available for collection in the lake. Once in the lake, competition and predation are very low and both growth and survival appear to be exceptional. The persistance of structural vertebral deformities, some of which appear to be rather severe, in an average of 39% of the smelt examined suggests that predation is not high and that competition is not adequate to "thin" the stock. These deformities did not appear to be of genetic origin but the variability in their frequency of occurrence and type suggested an environmental cause. A study of the smelt population in Lake Washington in the future may provide valuable insight into some effects of reduced productivity of a lake on its fish populations.

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