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Title: GROWTH AND REPRODUCTION OF THE LANTERNFISH STENOBRACHIUS LEUCOPSARUS

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Growth and reproductive patterns of the common lanternfish, Stenobrachius leucopsarus, are described by length frequency analysis, otolith analysis and examination of ovaries.

Length frequency analysis, employing the probability paper method of analysis of polymodal distributions, of three and one-half years of monthly midwater trawl collections off Oregon showed that fish in the fourth year of growth and younger form distinct length classes in collections. Growth is approximately linear during the second, third, and part of the fourth year of life. The average rate of growth during this time is 1.59mm (standard length) per month. Fish on their first birthday average 23mm long, on their second birthday 41mm long, and on their third birthday 59mm long.

Otolith analyses indicated that some fish live to be eight years old, but confidence in this method is limited to fish five years old

and younger. By fitting mean lengths of age groups defined by otolith analyses with the von Bertalanffy equation, the asymptotic length was estimated to be about 85mm, and the rate at which growth to the asymptote decreases to be about 0.34.

Back calculation of lengths at the times of annulus formations gave another set of estimated mean lengths of age groups. Fitting the von Bertalanffy equation to these data described a growth curve comparable to the one described by otolith analyses. Transforming the growth curve to growth in weight by a length-weight relationship indicated that the inflection in growth occurs at about age four years.

Spawning, determined from egg measurements, is thought to occur from December to March. Reproductively mature individuals are four years old and older. Recruitment of young size groups was also seasonal, 20-25mm individuals appearing in largest numbers in trawl samples in the winter, presumably about eight months after spawning.

Comparison with previously unpublished information from collections made in Monterey Bay, California, indicates that spawning may occur earlier there than off Oregon, but growth rates and sizes in age groups V and younger are very similar. Comparisons with published results of otolith analyses show similar age determinations for the younger age groups.

Growth and Reproduction of the Lanternfish *Stenobrachius leucopsarus*

by

William Williams Smoker

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

GROWTH AND REPRODUCTION OF THE LANTERNFISH STENOBRACHIUS LEUCOPSARUS

INTRODUCTION

Stenobrachius leucopsarus (Eigenmann and Eigenmann) is an abundant mesopelagic myctophid fish in the North Pacific Ocean. Aron (1962) reported it as the most abundant and most frequently caught fish in midwater trawl samples north of 45° N in the Pacific. Its zoogeographic range in the North Pacific extends north of about 35° N, into the Gulf of Alaska and the Bering Sea (Parin, 1961). Paxton (1967) called the species Transitional-Subarctic in its water mass associations and presented further evidence for correlating its distribution with Subarctic Water in his analysis of its vertical distribution in San Pedro Basin, California.

The vertical distribution of S. leucopsarus is affected by the vertical stratification of water masses (Paxton, 1967; Aron, 1962), its ontogenetic development, and its vertical migrations. Fast (1960) and Ahlstrom (1959) reported that S. leucopsarus larvae are concentrated in the upper 100m, localized particularly around 30-40m. Fast's daytime observations in Monterey Bay, California, suggest that metamorphosis takes place at 400-500m, juveniles rise to 200-300m, and the fish gradually seek lower levels with increasing age. Taylor (1968) also indicated that during daytime, large individuals may occupy deeper levels than small individuals (455-595m vs. 230-275m). During vertical migration, S. leucopsarus apparently moves into the upper 200m during darkness and descends to depths below 200m during daytime (Pearcy and Laurs, 1966). During this migration they may cross sharp hydrographic gradients. S. leucopsarus has also been associated with vertically migrating sound scattering layers (Taylor, 1968; Barham, 1957).

The major purposes of this study are to describe growth and age and season of spawning for S. leucopsarus off Oregon. Such knowledge is important to an understanding of the ecology of any species. Growth and age information are essential for estimating age group abundances and mortality rates. Age group abundances and growth rates can be used to estimate the productivity of a population. The amount of this production used by different predators of the various age groups can be estimated with mortality rates. The age of reproductive maturity can be used to estimate the size of the reproducing segment of the population and can help us to understand the ecology of reproducing individuals. The ecology of egg and larval stages, which are usually thought to have high mortality rates, can be understood only if the season of spawning is known.

Some information is available on age and growth of S. leucopsarus, but comprehensive data have not been published. Bolin (1956) and Fast (1960) determined growth by examining length frequency distributions from samples taken in Monterey Bay, California. Fast described a protracted spawning period from occurrence of larvae and mature females in these samples. Kulikova (1959) described growth by analyses of otoliths from 46 specimens collected in the Bering and Okhotsk Seas and the Kuril-Kamchatka trench.

METHODS

Sampling

Fish used in this study were collected with a six-foot Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953; Aron, 1962) equipped with a 5mm-mesh liner and a 0.571mm-mesh cod end. The trawl was equipped with a Depth-Distance Recorder, a pressure sensor and propeller driven device which records distance travelled vs. depth on a smoked glass slide (see Pearcy and Laurs, 1966).

Oblique tows of the trawl during nighttime hours were made to approximately 200m depth at about monthly intervals from February 1964 to July 1967 at stations on a line running west from Newport, Oregon. Stations 15, 25, 45, and 65 nautical miles from shore were occupied regularly. Stations as far as 450 miles from shore were sampled less frequently; one or more of these offshore stations was sampled in about one-third of the months. Normally one tow, but sometimes two and infrequently more, were made at a station. At stations 15 and 25 miles from shore the trawl was towed to depths shallower than 200m because of the shallowness of the water at these stations.

Specimens were fixed in 10% formalin in sea water at sea. Later they were transferred to 36% isopropyl alcohol in the laboratory.

Determination of reproductive state

Gonads were dissected from fish collected between July 1964 and November 1965. All available fish longer than 60mm were examined. Fish longer than about 40mm standard length had gonads which could easily be categorized as either ovary or testis. Testes were lobate, white in color, and seminal vesicles were seen in more mature males at the posterior confluence of the seminal ducts. Ovaries were skeins of opaque yellow eggs, ranging from 0.05mm to 0.70mm in diameter.

Mean egg diameter was chosen as an index of reproductive state. The size distribution of developing eggs was similar in various parts of the ovary, therefore a sample of the eggs in an ovary was taken by separating a few eggs from the ovary with forceps without regard for the part of the ovary from which they were taken. Mean egg diameter was determined by measuring at least ten eggs under a dissecting microscope with an ocular micrometer.

Large developing eggs were in a matrix of small (less than 0.10mm) eggs. In such cases only large eggs were measured. When two sizes of developing eggs (greater than 0.10mm) were found in an ovary, ten eggs of each size were measured to give two mean egg diameters for the fish.

Age determination: length frequency analysis

Fish were measured (standard length) to the nearest millimeter, grouped into five-millimeter length categories, and the number of fish in each length category from all the tows during a given month were added together. Only fish greater than 20mm in length were recorded in this part of the study because 1) the 20-25mm length category is represented by the greatest numbers found for any length category, hence is probably the smallest size that is sampled adequately and is a logical recruit length category; and 2) according to Fast (1960), Pertseva-Ostroumova (1961), Ahlstrom (1963), and my own observations, *S. leucopsarus* larvae metamorphose at about 18mm length. Thus 20-25mm fish are the youngest members of the population of juvenile fish.

The probability-paper method of graphical analysis of polymodal distributions, first suggested for ageing members of a population by Harding (1949), was used to analyze length frequency distributions in this study. This method not only helps to separate overlapping size groups but also gives an easy estimate of the mean, standard deviation and standard error of the mean for each size class (Cassie, 1954). Partlo (1955) and Duncan (1967) used this technique with success in studies of fish populations.

The length-frequency distribution obtained for a given month was plotted on probability paper and the means and standard deviations were recorded. The percentage in each age class is determined from the probability paper plot. The number of fish in each length class was calculated by multiplying the total number caught during the month by the percentage of the catch belonging to each length class. The standard error of each length class mean was derived from S. E. $= 2\sigma/\sqrt{n}$, where sigma is the standard deviation and n is the number of fish in the length class.

Otolith analysis

Saccular otoliths (see Romer, 1962, p. 434) were dissected from fish frozen at sea. The gills and operculum on one side of a fish's head and the palate were removed, exposing the floor of the braincase and the thin bony bulbs on either side of the midline of the braincase containing the otoliths. These cavities were ruptured with fine forceps and the otoliths removed.

Otoliths were immersed in xylene and examined under a dissecting microscope at 66 magnifications. Both transmitted and reflected light made the layers apparent, and the alternate use of both kinds of light made the deciphering of the layers in larger otoliths easier. Annulus diameters were measured with an ocular micrometer along the longest dimension of the otolith, i. e. through the center and generally perpendicular to the groove extending from the center of the otolith.

RESULTS

Reproduction

The time of spawning and the size (hence age) at which *S. leucopsarus* spawns were estimated primarily from egg diameters and changes in reproductive state. The months of recruitment of small fish provided secondary evidence of spawning seasonality. Stages of gonad maturity were determined according to the "universal scale" of Nikolsky (1963, p. 160) as shown in Table I.

Table I. Stages of gonad maturity

	Nikolsky's Universal Scale	*S. leucopsarus* Ovaries (Mean Egg Diameter & Description)
Stage I.	Young individuals, have never spawned.	No eggs visible, not distinguishable as an ovary.
Stage II.	Quiescent, gametes have not begun developing or have been discharged.	Less than 0.10mm, eggs are yellow, opaque.
Stage III.	Ripening, eggs visible to the naked eye.	IIIa 0.10-0.20mm IIIb 0.20-0.40mm IIIc 0.40-0.60mm eggs are yellow and opaque
Stage IV.	Ripeness, gametes are ripe but do not run out under pressure.	Greater than 0.60mm, eggs are translucent, granular, and grey containing globular yellow bodies.
Stage V.	Reproduction, eggs run out under pressure.	None observed.
Stage VI.	Spent, ovary is swollen, contains a few left-over eggs.	As in Stage II.

The maturity stages of fish in different length categories during various months of the year are entered in Table II. Some fish's ovaries had two sizes of developing eggs. In such cases the stage of maturity indicated by the larger eggs was entered in Table II. During 1964-1965 females greater than 40mm in length were all in Stage II until October when fish longer than 65mm began to reach Stage III. Stage III occurred from October to April. Only two ripe fish (Stage IV) were observed, one each in December and March. By April 1965 early Stage III and Stage II fish were found. From May to September 1965 only Stage II fish were noted.

These results suggest that 1) S. leucopsarus becomes reproductively mature when it reaches about 65mm length (later results will show that this length corresponds to four years of age), 2) maturation of gonads begins in October and 3) spawning occurs between December and March.

The occurrence of ovaries with two sizes of developing eggs was high in December, January, February, and intermediate in March (Table III). Such ovaries were not found between March and December. Three hypotheses might explain this occurrence of two sizes of eggs in an ovary: 1) the smaller eggs are destined to be spawned in a later year (see Hickling and Rutenberg, 1936), 2) the smaller eggs are spawned later during the same year, or 3) the smaller eggs are resorbed without being spawned.

Table II. Maturation stages of *S. leucopsarus* during 1964-1965[1]

Length	Jul-Sep 1964	Oct 1964	Nov 1964	Dec 1964	Jan 1965	Feb 1965	Mar 1965	Apr 1965	May-Sep 1965	Oct 1965	Nov 1965
91-95	(1)II					(1)IIIc					
86-90									(2)II		
81-85	(3)II	(1)II (1)IIIa		(2)IIIb (4)IIIc	(1)IIIc	(4)IIIb (2)IIIc	(1)IIIb	(2)II	(5)II	(1)IIIb	
76-80		(1)II (1)IIIa (1)IIIb	(2)IIIb	(2)IIIb (1)IIIc (1)IV	(2)IIIc	(1)IIIb (1)IIIc	(1)IIIb (2)IIIc	(2)II	(10)II		(1)IIIb (1)IIIc
71-75		(1)IIIb	(1)IIIb	(4)IIIb	(1)IIIb	(4)IIIb (1)IIIc	(2)IIIb (1)IIIc (1)IV	(1)IIIa	(11)II	(1)II (1)IIIb	
66-70	(1)II	(1)II	(2)II	(2)II (5)IIIb	(1)II (5)IIIb	(2)IIIa (1)IIIb (1)IIIc	(4)II (1)IIIb	(1)IIIa (3)II	(7)II	(1)II	(1)II (1)IIIa
61-65	(1)II	(3)II	(4)II	(6)II	(1)IIIa	(4)II	(1)II	(3)II	(3)II		(1)II
41-60	(2)II	(9)II	(5)II	(21)II	(9)II	(3)II	(12)II	(15)II	(15)II	(14)II (3)I	(2)II
20-40									(10)I		

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[1] Arabic numerals indicate the number of fish examined in each category. All fish examined are entered on the table.

Table III. Percent of females greater than 65 mm in length with two sizes of eggs in ovaries.

MONTH (year)	PERCENT WITH OVARIES WITH TWO SIZES OF EGGS	NO. FEMALES OBSERVED	NO. RIPENING FEMALES OBSERVED
July (1964)	0	5	0
August (1964)	0	1	0
October (1964)	0	6	4
November (1964)	0	5	3
December (1964)	28	21	19
January (1965)	40	10	10
February (1965)	42	19	18
March (1965)	14	14	9
April (1965)	0	10	2
June (1965)	0	13	0
July (1965)	0	19	0
August (1965)	0	3	0

The first hypothesis is rejected because no fish in a maturity stage later than Stage II were observed during summer months. If the smaller size eggs observed in winter were to be spawned during a later year, the same size or larger eggs should be observable during summer months.

The second hypothesis, that the smaller eggs represent a second spawning during the same season, is possible. If the first spawning were to continue until March the observed decline in ovaries with two sizes of eggs (Table III) would be expected. It would also be expected, however, that ovaries in ripe stages would be seen after the decline in ovaries with two sizes of eggs. This was not observed. Although it cannot be entirely discounted because the smaller eggs might develop quickly and be spawned, the second hypothesis is not well supported.

The third hypothesis, that the smaller eggs are resorbed, is best supported (Table III). If spawning were to occur between December and March, the decline in ovaries with two sizes of eggs observed in March would be expected. The intermediate or small stage eggs would also continue to occur until they were resorbed. Two fish collected in April provide further evidence for this resorption hypothesis. These fish had Stage III ovaries with grey and translucent eggs rather than yellow and opaque eggs. This suggests that the yolky material in these eggs had been resorbed. Resorption of eggs is not uncommon. Nikolsky (1963, p. 151) states that "In many fishes the small eggs remain in the ovary after spawning and are gradually reabsorbed ..."

Recruitment of young fish 20-25mm in length into trawl samples is also seasonal (Figure 1). This is additional evidence for seasonal spawning: if spawning were spread over all seasons it would be expected that recruitment of young fish would continue throughout the year.

To summarize: fish greater than 65mm long (four years and older) begin to develop ripe gonads in October and spawn between December and March. In some females some eggs apparently develop only partially and are resorbed. The greatest recruitment of juveniles into trawl samples occurs in November.

Growth

The average growth of *S. leucopsarus* was described by three methods: (1) the increase in mean length of year classes from successive samples, (2) from the mean lengths of fish aged by otolith analysis, and (3) from back-calculating the lengths of age groups at the time of annulus formation. In all methods a regression curve was fitted to the mean lengths.

Graham (1928) reviewed in some detail the earlier literature concerned with ageing fishes. Rounsefell and Everhart (1953) gave a

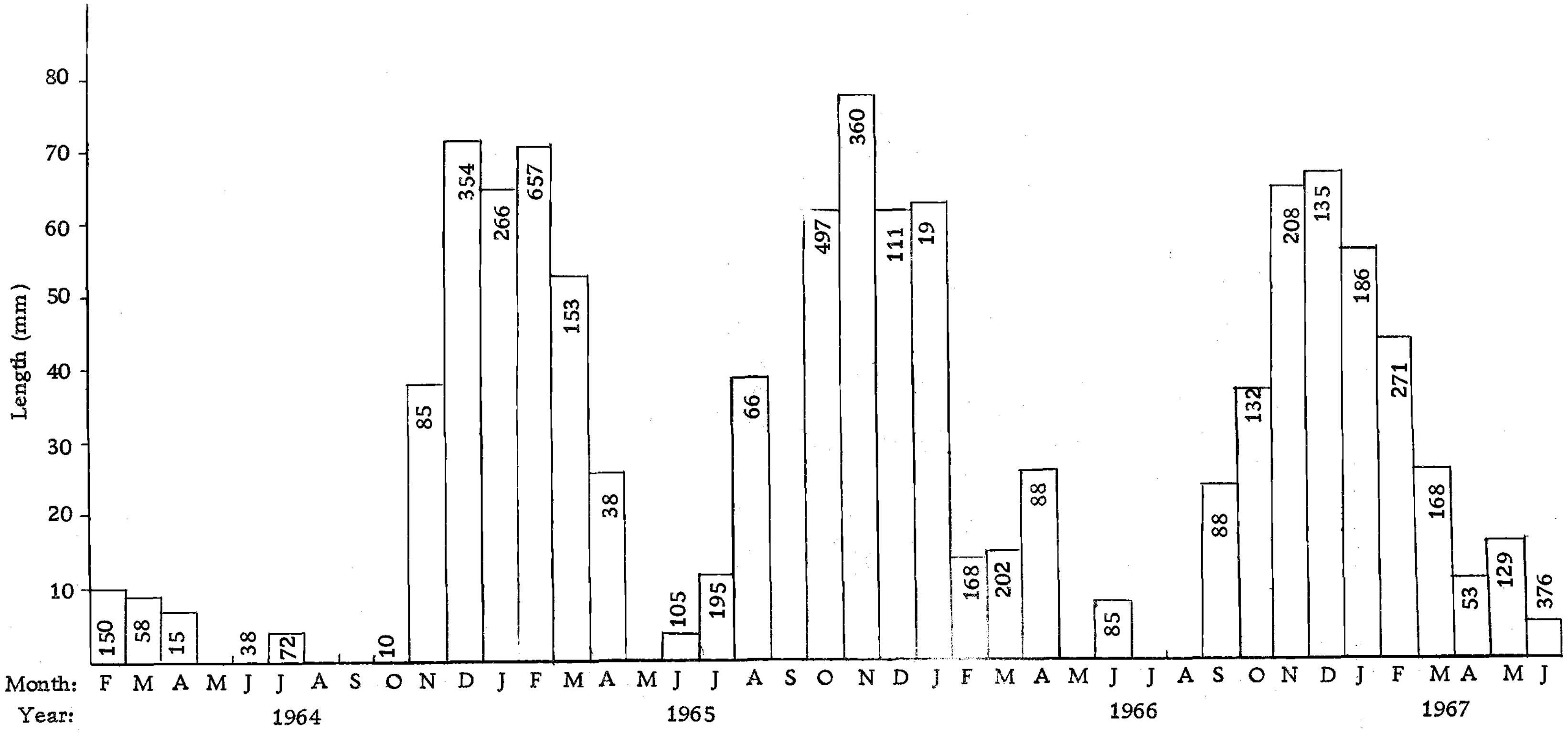


Figure 1. Percent recruits (20-25 mm fish) in monthly samples. Numbers inside bars are total number of fish in sample.

more general review of the methods, including the two used in this study: length frequency analysis and interpretation of the layers deposited during otolith formation.

Length frequency analysis

Length frequency analysis, or the Petersen Method, "... is based on the fact that the lengths of fish of one age tend to form a normal distribution." (Rounsefell and Everhart, 1953, p. 297). One simply draws a length frequency distribution for a sample of a population and counts the peaks; each peak or length class corresponds to an age group. This method assumes that 1) spawning of year classes be isolated enough in time so that the length frequencies of succeeding year classes do not overlap too much; 2) numbers of a year class all experience roughly the same growth conditions so that the length frequency of a year class is not polymodal; and 3) all year classes be well enough represented in the samples that incorrect ages are not assigned to length classes due to the absence of one or more year classes in the sample (after Rounsefell and Everhart, 1953).

Length frequency distributions of fish from tows taken to greater depths (200-1000m) did not indicate a higher proportion of fish in any length categories, suggesting that the standard 0-200m tows are representative in all length categories.

Graphical analysis of monthly samples gave estimates of length class means and their standard errors (Figure 2). Recruitment of juveniles occurs early in each year, and each year class is discernible until sometime between its third and fourth birthdays.

Attempts to fit a curvilinear relationship to the mean lengths of age groups I-III (the age groups which could be identified) using computer techniques were unsuccessful because the means too closely approximated a straight line. The mean lengths less than 70mm for each year class were therefore superimposed on a common time scale using January of the year following spawning as the common point. Linear regression of length on time gave:

$$\text{Length} = 20.78 + 1.59X$$

$$r^2 = 0.97$$

where X is months numbered beginning with January of the year following spawning, the first birthday. This line is drawn in Figure 2 as a reference line by repeating it with the same slope and "January intercept" for each of the year classes represented.

Comparison of the year classes to this reference line shows that growth of *S. leucopsarus* is approximately linear during the second, third and fourth years. Apparently none of the year classes differs greatly from the others in sizes or in growth rate, and each year class passes through the same length categories during the same months of the year.

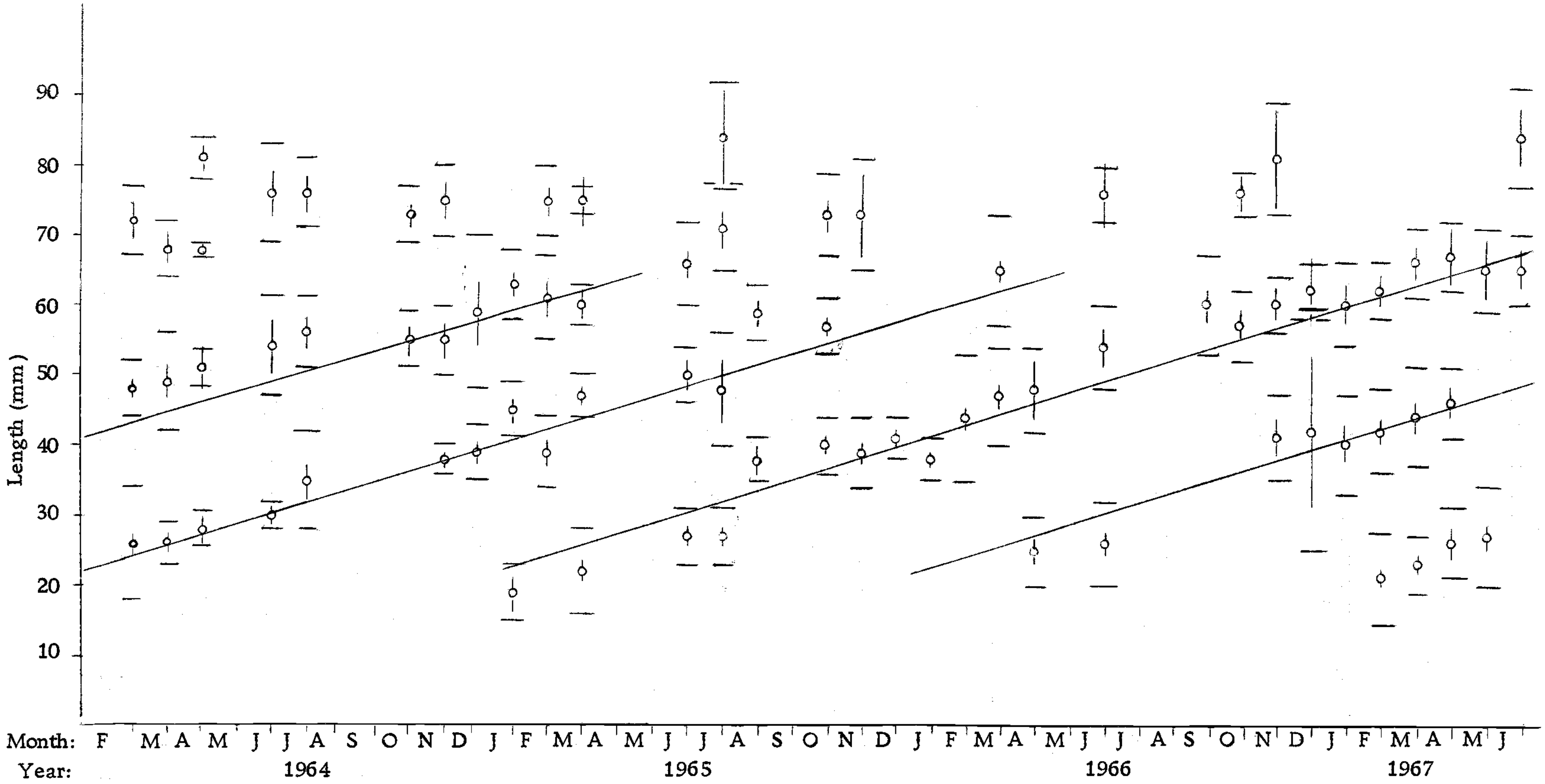


Figure 2. Length class means. Horizontal lines indicate ± one standard deviation. Vertical lines are ± $2\sigma/\sqrt{n}$ (standard error). Oblique lines are length = 20.78 + 1.59 (months) for fish under 70 mm.

Otolith analysis

Teleost otoliths are formed by deposition of calcium carbonate (aragonite) from the endolymph filling the membranous labyrinth. They function in sensing acceleration and tilt of a fish's head by stimulating sensory hairs on the inside surface of the sacs in which they form (Romer, 1962). Otolith structure has been described by Hickling (1931), Irie (1955a, b) and Dannevig (1956). The otolith consists of alternately opaque and translucent concentric layers (see Figure 3). The layers are separated by a proteinaceous membrane. Opacity to transmitted light is due to the inclusion of conchiolin, a protein, in the layer; translucency to the absence of the protein (Dannevig, 1956).

A fish's age can be determined from examination of its otoliths if an annular pattern of alternation of opaque and translucent layers exists. The number of alternations gives the fish's age. Such a pattern is demonstrated for S. leucopsarus in Table IV: the largest percentages of otoliths with opaque peripheries occurred during summer months, the largest percentages with translucent peripheries during winter. The reason that no month showed 100% opaque peripheries is that the otolith margin may appear to be translucent because of its thinness, though an opaque layer may be forming.

Table IV. Percentage of otoliths with translucent and/or opaque peripheries during various months of the year.

Month (year)	Percent Translucent	Percent Opaque/ Translucent	Percent Opaque	Number Examined
January (1966)	100	0	0	2
February (1966, 1969)	70	18	13	55
April (1966)	62	13	25	8
June (1966, 1969)	27	32	41	22
October (1965, 1968)	43	31	25	28
November (1968)	95	0	5	38
December (1966)	71	0	29	21

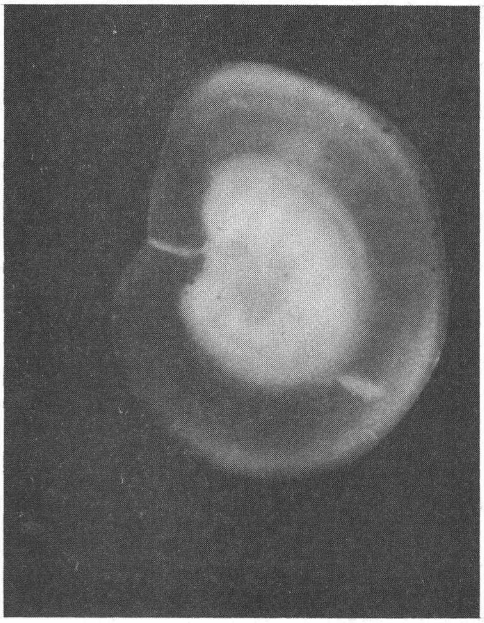
Figure 3. Photographs of Stenobrachius leucopsarus otoliths.

A. Date Collected: June 1966
Standard Length: 34mm
Age Group: I
Otolith Diameter: 0.83mm
Periphery: Opaque

B. Date Collected: June 1966
Standard Length: 41mm
Age Group: II
Otolith Diameter: 0.99mm
Periphery: Opaque

C. Date Collected: October 1968
Standard Length: 56mm
Age Group: III
Otolith Diameter: 1.25mm
Periphery: Translucent

D. Date Collected: October 1965
Standard Length: 73mm
Age Group: IV
Otolith Diameter: 1.57
Periphery: Translucent



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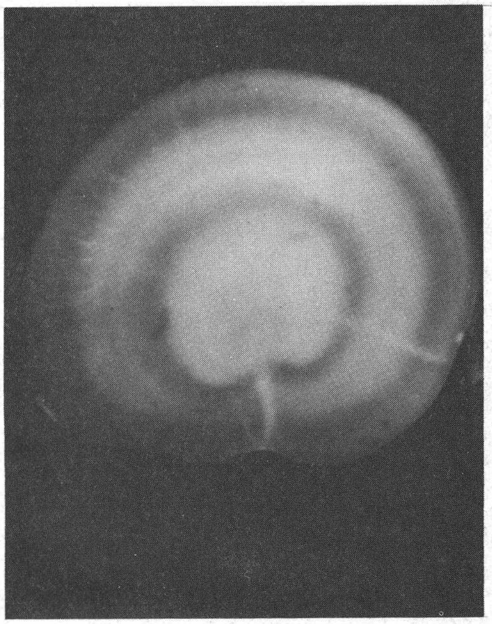

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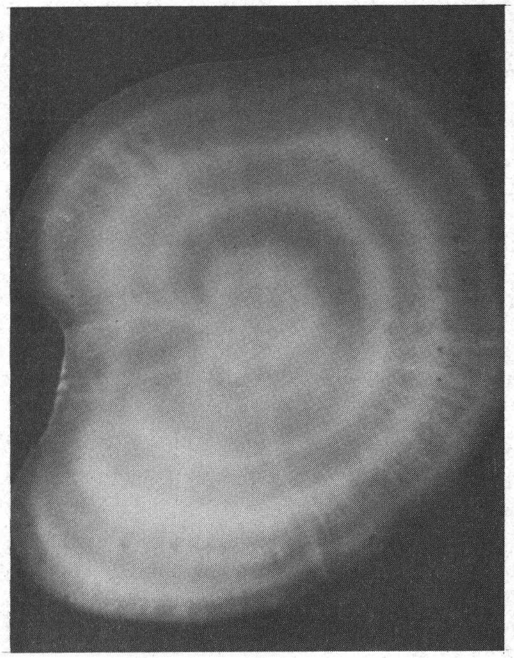
D



The birthday of S. leucopsarus is arbitrarily defined as January of each year. Translucent layers are forming on otoliths at this time of the year (Table IV). The outermost edge of opaque layers are the most conveniently measured annual demarcation in otolith structure, however, and were called "annuli." The formation of annuli does not coincide with the birthdays of the fish because opaque layers are formed in summer about six months before the corresponding birthday.

The opaque core of the otolith was considered to be the first annulus, i.e. deposited during the first year of life. Fish belonging to the recruit (20-25 mm) length category have an otolith consisting of an opaque center surrounded by some translucent material. Based on my length frequency data (Figures 1 and 2) and those of Fast (1960), and on knowledge of the larval development of S. leucopsarus (Fast, 1960; Pertseva-Ostroumova, 1961; Ahlstrom, 1963; and my observations), these individuals are about one year old.

Although otolith analysis indicated some fish are seven or eight years old, otoliths from fish older than five years could not be analyzed with reliability owing to the merging of peripheral annuli. Photographs of otoliths from age groups I-IV with both translucent and opaque peripheries are shown in Figure 3.

The mean lengths of fish in otolith analysis age groups were fitted to the von Bertalanffy equation (von Bertalanffy, 1938) (Figure

4).[1] In that equation the rate of change of length with time is proportional to the difference between the length of a fish at a given time and the length at which the growth curve closely approaches an asymptote. The equation for length at a given age is:

$$L_x = L_\infty - (L_\infty - L_o)\, e^{-kX}$$

where

L_x = the length at age X

L_∞ = the asymptotic length

L_o = the length at age zero

e = the base of the natural logarithms

k = the rate at which length approaches the asymptote.

X = age in years.

Curve fitting gives these estimates of the parameters:

$L_\infty = 34.96$, S. E. = 2.79

$L_\infty - L_o = 79.32$, S. E. = 3.12

$k = 0.34$, S. E. = 0.044.

Thus

$$\text{Length} = 84.96 - 79.32\, e^{-0.34\,\text{Age}}$$

variance = 3.06.

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[1] These age group means were fitted using the *CURVFIT program on Oregon State University's CDC 3300 computer. For a discussion of a method of obtaining least-squares estimates of the parameters in the von Bertalanffy equation see Draper and Smith (1966) and Allen (1966).

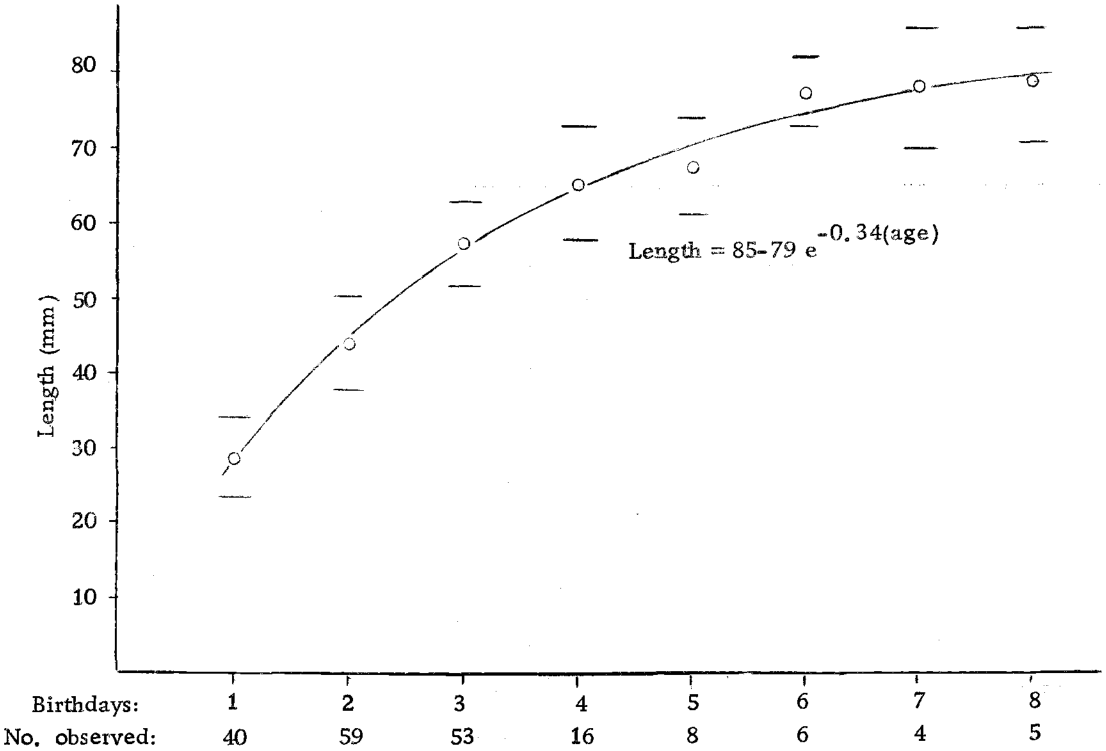

Figure 4. Means and standard deviations of lengths in otolith analysis age groups.

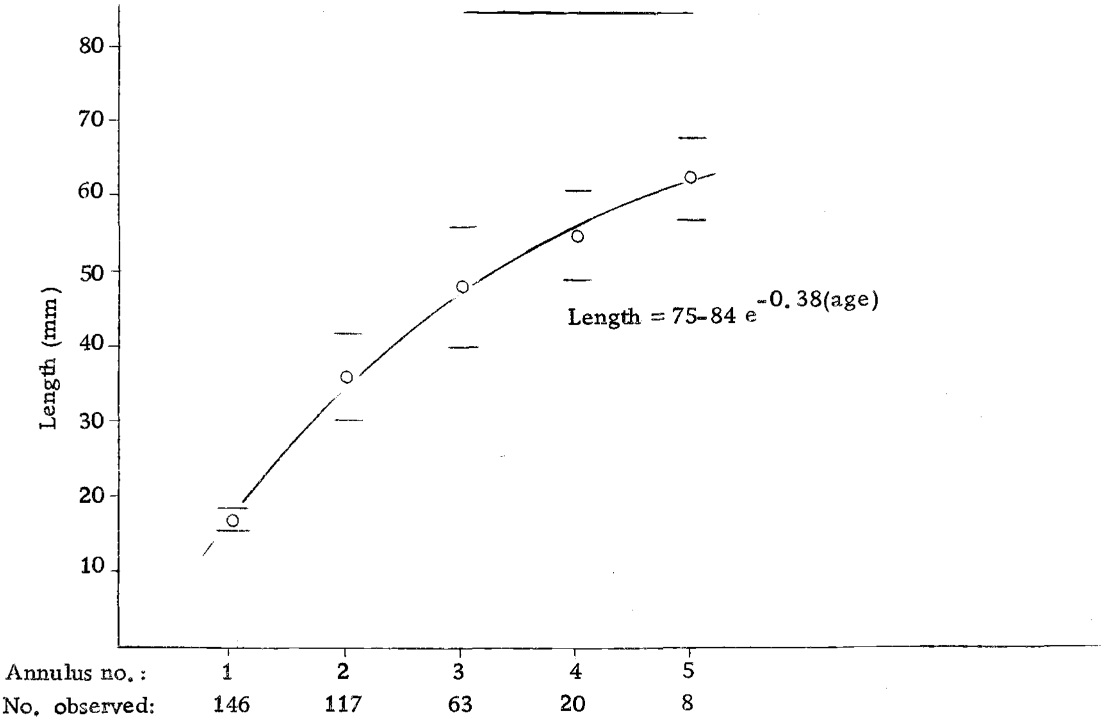

Figure 5. Means and standard deviations of lengths back calculation age groups.

Age groups V, VI, and VII were included. Though confidence in these age determinations is less than for the first four age groups, the mean lengths of fish in these age groups are consistent with the trend established by the younger age groups.

Back calculation of age group lengths

Diameters of otolith annuli were used to compute lengths of fish at earlier ages by deriving a formula relating annulus diameter to standard length. Assuming that length varies as some power of otolith diameter (Rounsefell and Everhart, 1953, p. 324), a linear relationship exists between the logarithm of length and the logarithm of otolith diameter. Linear regression analysis gave the equation:

$$\log \text{Length} = 1.6419 + 0.920 (\log \text{Annulus Diameter})$$

$$\text{Length} = 43.85 (\text{Annulus Diameter})^{0.920}$$

$$r^2 = 0.92130.$$

All measurements are in millimeters.

Mean lengths of age groups I-IV calculated by this method were fitted to the von Bertalanffy equation (Figure 5) giving these estimates of the parameters:

$$L_\infty = 75.01, \quad \text{S.E.} = 5.00$$

$$L_\infty - L_o = 84.17, \quad \text{S.E.} = 3.01$$

$$k = 0.377, \quad \text{S.E.} = 0.0629.$$

Thus

$$\text{Length} = 75.01 - 84.17\, e^{-0.377\,(\text{Age})}$$

$$\text{variance} = 1.468.$$

Only means from age groups I-IV were used because otoliths from older fish could not be confidently read.

Synopsis of growth determinations

The three growth curves, derived from length frequency analysis, otolith analysis, and back calculations, are superimposed in Figure 6. Since otolith annuli are formed about six months before the corresponding birthdays, and back-calculated lengths correspond to the time of annulus formation, the back-calculated curve must be shifted to the left about one-half year to be comparable to the line fitted to length class means which plots size at the different birthdays. The otolith analysis curve, however, is comparable to the length frequency line as it is drawn. The mean lengths of otolith analysis age groups correspond to the average lengths of fish during the year of growth between annulus formations. For this reason the mean lengths of otolith analysis age groups are plotted at the time of the fish's birthdays in Figure 6. In addition, most of the otoliths happened to be collected in midwinter (see Table IV) which gives added confidence to the plotting of mean lengths of otolith analysis age groups at the time of the fish's birthdays.

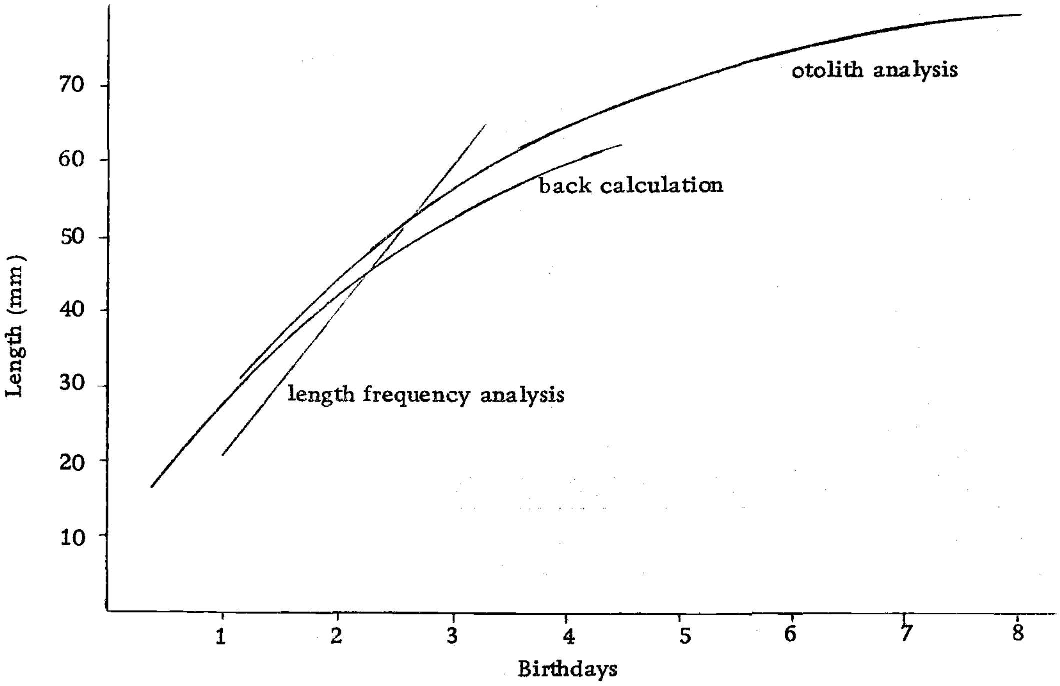

Figure 6. Comparison of three growth curves, Figures 2, 4, 5.

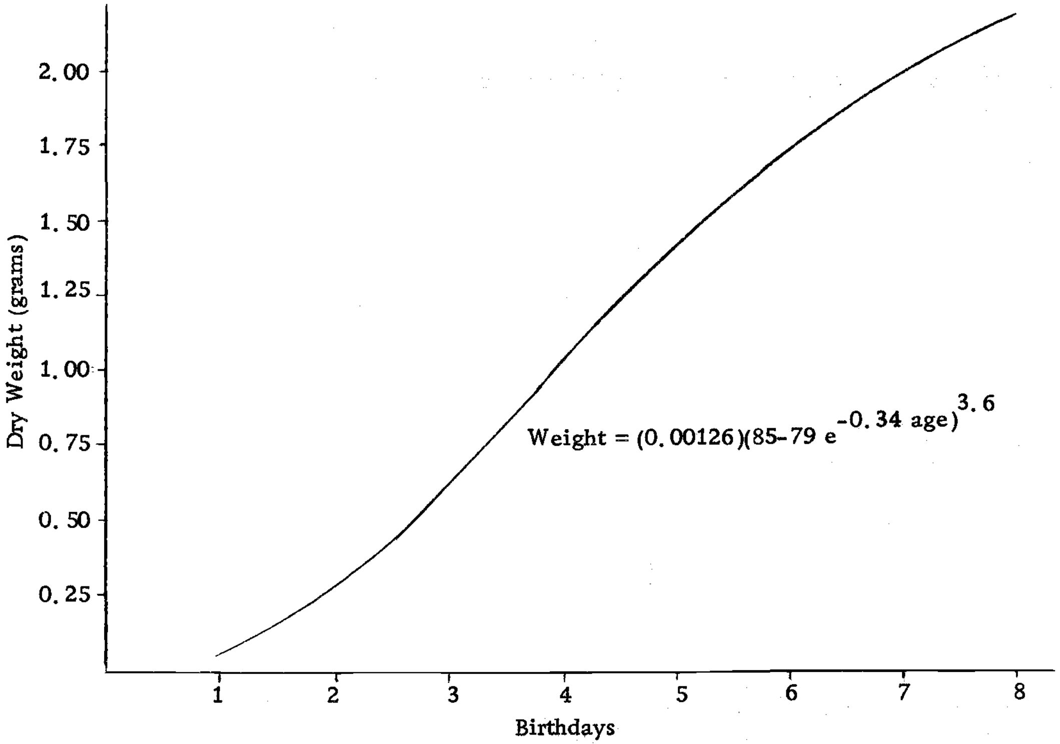

Figure 7. Growth in weight.

There is good agreement among the curves. The apparent discrepancy between the curves derived from otolith analysis and back calculation in the fourth and fifth years is not due to any inadequacy in the methods of back calculation, but to the inclusion of older age groups in the otolith analysis curve. Comparison of Figures 4 and 5 shows that means of back-calculated lengths for each age group are somewhat less than mean lengths of age groups described by otolith analyses. This is to be expected because back calculation is the computing of the length of a fish at the time of an annulus formation, the time of the very beginning of growth during the time between succeeding annulus formations. Otolith analyses, however, are made at some later time, between annulus formations.

Growth in weight

Fish from which otoliths were to be removed were dried to a constant weight on glass slides in an oven at 65° C (three or four days), scraped from the slide and weighed to the nearest milligram. If it is assumed that weight is proportional to some power of length (Ricker, 1953, p. 191), linear regression of the logarithm of weight on the logarithm of length should give a regression line with an intercept equal to the logarithm of the constant of proportionality and a slope equal to the power of length with which weight varies. This analysis of data gave:

$$\log \text{Weight (grams)} = -2.898 + 3.595 \log \text{Length (centimeters)}$$

or

$$\text{Weight (grams)} = 0.001264\ (\text{Length})^{3.595}.$$

The growth curve obtained from otolith analyses is transformed into growth in weight in Figure 7 by the relationship between length and weight.

DISCUSSION

Fast (1960) also investigated the age, growth and spawning season of S. leucopsarus. His samples, taken at weekly intervals in Monterey Bay, California, between 1951 and 1955, included larval fish as well as juveniles and adults. Fast sampled with a circular meter net made of 30mm grit gauze, and a "Tucker-Balesteri net", a net six by six feet square at the mouth and 30 ft. long (see Fast, 1960; Barham, 1957).

Fast's results on the seasonal occurrence of S. leucopsarus are illustrated in Figure 8. From several years of sampling he found that larvae 5-10mm long were present from November through July and were most common between December and March. Larvae 10-20mm long were present from March through October and were most abundant between April and July. Juveniles 20-25mm long were present from June into February and were common between August and December. Fast found ripe females during the entire year: "... mature individuals possessing eggs which appeared in a spawning condition were found randomly spread throughout the period that the larval S. leucopsarus were present in the nets." (Fast, 1960, p. 29). Despite this, seasonal variation in occurrence of young length classes indicates that the intensity of spawning varied seasonally.

Peak numbers of 20-25mm juveniles occurred from July to

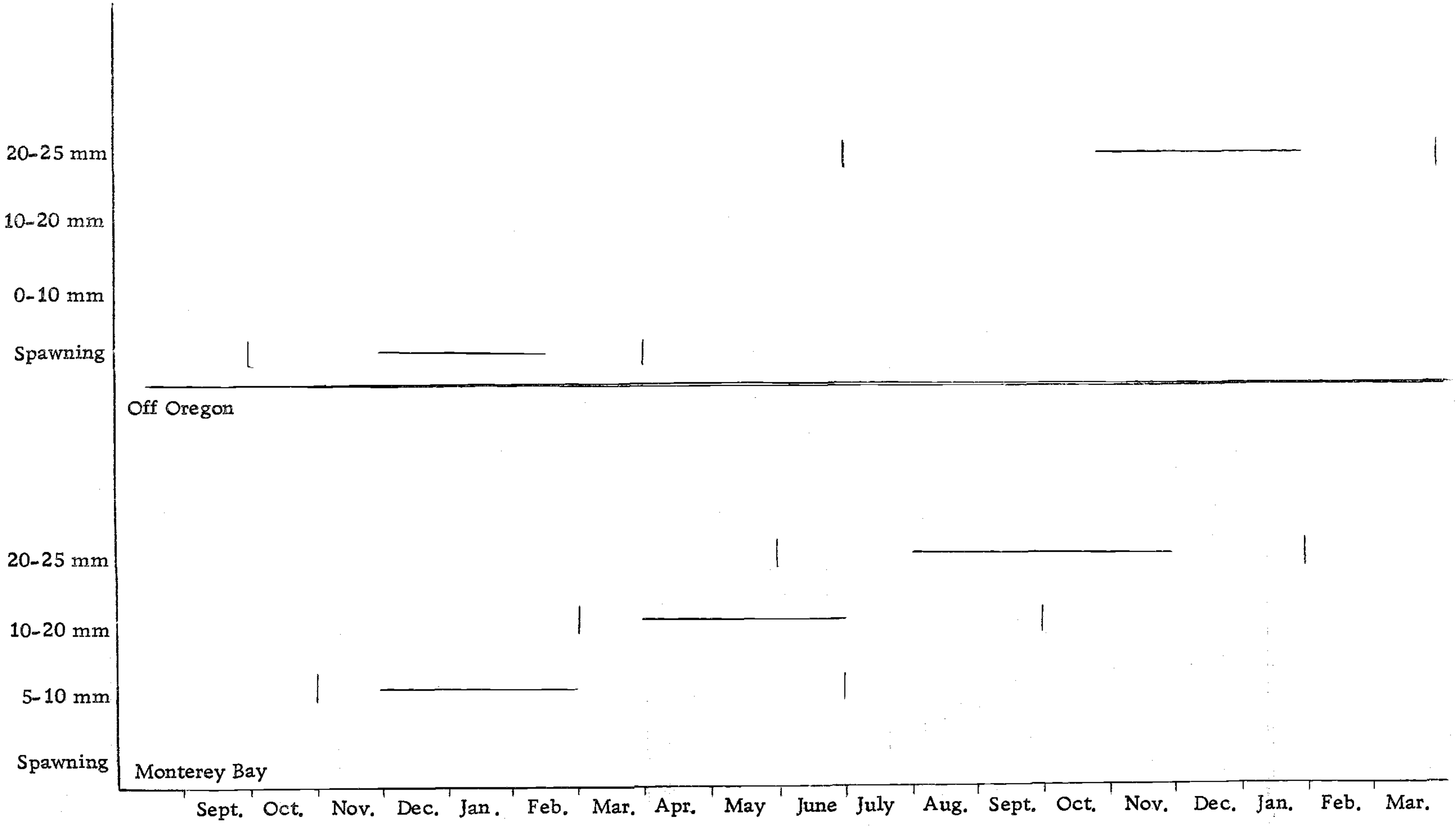

Figure 8. Comparison of periods of spawning, catches of larvae, and catches of small juveniles in Monterey Bay and off Oregon. Vertical lines are ranges of occurrence, horizontal are periods of abundance.

April, with largest numbers concentrated from November through February. Ripe females occurred between October and April, and spawning is believed to occur from December through March (Figure 8). Therefore both spawning and the occurence of young apparently peak earlier in Monterey Bay than off Oregon.

According to Fast S. leucopsarus in age group I during their second year of growth average 32mm in length, age group II during their third year of growth average 50mm in length, and age group III average 66mm long. These estimates agree very precisely with the regression line fitted to length frequency data from Oregon collections (Figure 9). Since the appearance of 20-25mm fish occurs earlier in the year in Monterey Bay, Fast's growth curve would be displaced to the left of the one from this study on an absolute time scale but would have the same slope. They coincide when plotted against birthdays in Figure 9.

Fast does not assign ages to large fish -- "... individuals which attain lengths of 70-89mm are not readily assigned to the appropriate age groups" (Fast, 1960, p. 23). Examination of his "modified length frequency distribution," however, suggests that age group IV fish are about 72mm long and age group V fish are about 76mm long. These observations are in agreement with growth described in my study.

Kulikova (1957) examined otoliths from 46 S. leucopsarus

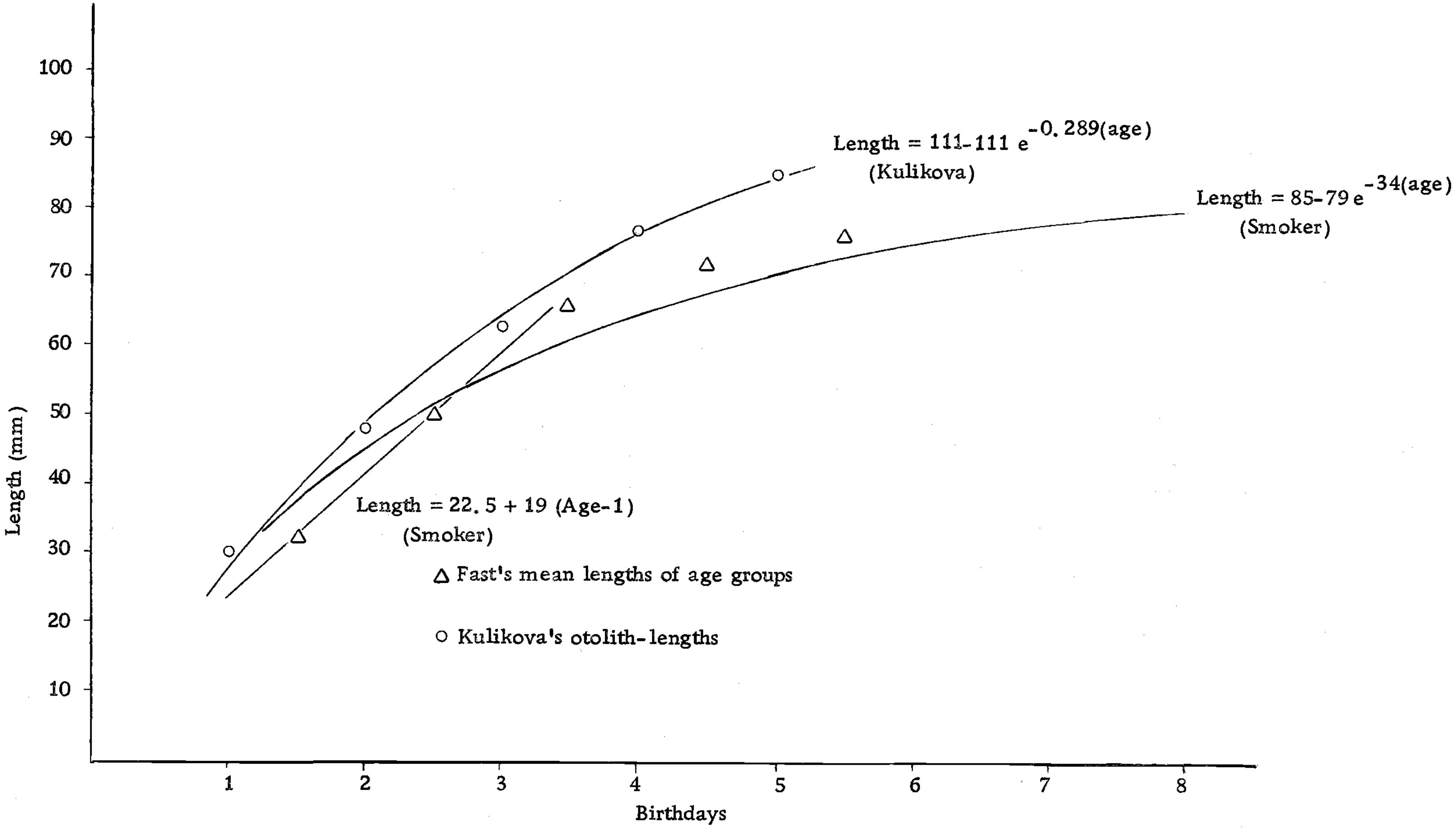

Figure 9. Comparison of Kulikova's otolith analysis, Fast's length frequency analysis, and my length frequency analysis and otolith analysis.

collected in the western North Pacific. To compare with results of this study, I fitted the von Bertalanffy equation to the mean lengths of Kulikova's age groups (Figure 9). The estimate of L_∞ (111mm) is much higher than the estimate from my study, and the estimate of k (0.29) is somewhat lower. Kulikova's data agree well with my results and those of Fast during the first three years og growth, but they indicate a greater growth rate for age groups IV and V.

The major discrepancies among the various studies of growth of S. leucopsarus concern the maximum age of the fish and the size of older fish. In a preliminary report on the data later analyzed by Fast, Bolin (1956) thought the maximum age of S. leucopsarus is four years and the maximum length 78mm. Kulikova's results agree with Bolin's interpretation, but she added two more age groups (V and VI) which averaged 86 and 89mm in length. Fast's interpretation and my results indicate somewhat smaller sizes for age groups IV and older. Fast finds a maximum age of five years; I find the maximum age to be as many as seven or eight years.

Neither method of age determination, length frequency analysis or otolith analysis, is reliable for older age groups. The slower growth rates of older age groups found by Fast and me have often been found in studies of growth of other animals. For example, an attempt was made in this study to fit the von Bertalanffy equation to means of length classes in the monthly samples. It was assumed that the largest length class represented four year old fish, i. e. that the maximum age of _S. leucopsarus_ was four years. The resulting estimate of L_∞ (125mm) is much higher than the estimate derived from mean lengths from otolith analysis age groups; the estimate of k (0. 02) is much lower than derived from otolith analysis. When this was transformed into growth in weight, the inflection point, i. e. the point at which the rate of growth stops increasing and begins decreasing, occurred at an age corresponding to a length longer than most of the fish in the collections. According to Brody (1945) the inflection point in the growth curves of many species including fishes occurs at the time of sexual maturation. Therefore it would be surprising if _S. leucopsarus_ matured sexually and grew nearly to its largest observed size before its growth rate began to slow.

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