Some Aspects of the Biology of the Aku, *Katsuwonus pelamis,* in the Hawaiian Islands

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THE AKU, *Katsuwonus pelamis* (Linné), is the most important species of fish taken commercially in Hawaii. It supports the only Hawaiian fishery which supplies a product, canned tuna, for export as well as for local consumption. It is, on the one hand, a species that affords the greatest promise for expansion of the Hawaiian fishing industry and, on the other, one of which little or nothing of the life history or biology is known.

Hence, the scientific staff of the Division of Fish and Game of the Territory of Hawaii, following an initial study of the length frequencies of Hawaiian aku by Bonham (1946), has been engaged in several projects concerned with the biology of this fish. Included among these projects are further studies of length frequencies, studies of the span and character of the spawning season, of the nature of schooling, and of the conduct of the fishery with a view toward establishing a basis for obtaining a fairly accurate measure of catch per unit of effort. The present paper is concerned with all these projects except the last.

Beginning in the late summer of 1946, aku obtained from the commercial landings were sexed and the length measured. The technique of sexing will be described later; the measurement of length obtained was from the tip of the snout to the end of the mid-caudal rays. This measurement was taken by means of calipers similar to those described by Marr and Schaefer (1949). In part, measurements made during 1950 and later were taken by marking the length on a celluloid strip by punching a hole in it. The lengths obtained are, for the same fish, very slightly less than the lengths obtained by the use of calipers. During the winter off-season period, both the number of fish measured in a sample and the number of samples obtained were affected by the availability of fish at the cannery; however, the frequency of sampling was chiefly affected. The number of fish entering into each of the percentage frequency curves plotted in Figure 1 is shown in Table 1. As individual samples usually represented some 100 fish, and sometimes much less, it is obvious that most of the percentage frequency curves of Figure 1 are composed of a number of samples combined together.

In the beginning of the program, estimates of the degree of maturity of the fish sampled were made by noting the appearance of the gonads; however, these estimates did not provide a measure of sufficient accuracy to show adequately the spawning season of this species. For this reason, beginning with the summer of 1948, ovaries were removed from 20 of the fish in each sample and preserved in formalin, and subsequently each ovary was drained and weighed to the nearest tenth of a gram. From each, 50 ova chosen at random were measured to the nearest one hundredth of a millimeter by means of an ocular micrometer in a compound microscope.

Beginning with the summer of 1949, a large part of the samples taken for length measurements were taken aboard the aku fishing vessels while landing the catch. These sam-

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TABLE 1
YEAR-CLASS MODAL LENGTHS IN CENTIMETERS AT VARIOUS MEAN DATES

MEAN SAMPLING DATES	YEAR-CLASSES (DATED BY PRESUMED YEAR OF ORIGIN)								NUMBER OF FISH MEASURED
	1943	1944	1945	1946	1947	1948	1949	1950	
Sept. 15, 1946	80.36	74.40	43.74						2,311
Dec. 8, 1946	81.46	75.96	51.95						3,463
July 3, 1947		79.30	68.10	43.96					5,364
Feb. 25, 1948			78.00	61.88					429
June 28, 1948			79.74	71.79	43.79				3,136
Dec. 8, 1948			80.00	74.64	57.68				160
Aug. 16, 1949				79.50	71.89	46.20			588
Dec. 26, 1949					73.84	53.78			853
July 12, 1950						71.91	44.08		4,878
Dec. 24, 1950						74.21	53.59		1,266
July 4, 1951							68.13	44.21	8,409
Total									30,827

ples were taken from such portions of the catch as, according to the captain of the vessel making the landing, had come from a single school of fish.

Acknowledgments

The field work for these studies was done by the employees of the Division of Fish and Game who deserve much of the credit for the results. Mr. W. Van Campen and Mr. J. P. Welsh took a large share of the length measurements. Mr. T. Shimizu took those length measurements from single school samples for 1949, 1950, and 1951, and Mr. F. W. Loo, statistician for the Division of Fish and Game, contributed to the statistical analysis herein. Dr. A. L. Tester of the University of Hawaii has offered a number of constructive suggestions. The fishermen, boat owners, and others engaged in the aku fishery have been most helpful. The officials of Hawaiian Tuna Packers, Ltd., have been, at all times, cooperative and interested in the program.

AKU LENGTH FREQUENCIES

The length measurements are plotted in Figure 1 and are grouped into units covering, for each length frequency curve, approximately a 6-month period. This grouping was selected for two reasons: (1) To insure the inclusion of an adequate number of measurements in each group, and (2) to make it convenient to plot, with the first consideration in mind, the length frequencies on an approximately uniform time scale. Some indications of the factors which made it seem best to place the length data in a few comparatively large groups will be given later.

The length data, as plotted in Figure 1, have a feature of considerable interest—the apparent progression of modal groups through the fishery with time. Such a group entering the fishery during the summer months at a modal length of 40 to 50 centimeters may be identified with a modal group of 55 to 60 centimeters which appears in the winter fishery, and in turn with a modal group of 68 to 72 centimeters which occurs in the following summer months' catch. There is an additional group at a modal length of 79 to 80 centimeters sometimes represented in the summer landings which may represent a group of fish a year older.

If it is assumed that these modal groups represent year-classes, the following interpretation of the length frequency data may be made:

At some age, perhaps one or two years, an age group or year-class is first taken in significant amounts by the fishermen during the summer fishing. By the second summer, this age group, at a length of 70 to 75 centimeters, is again taken and, as a matter of fact, is the size group most eagerly sought by the fishermen. This year-class appears again in the catch during the third summer but cannot be traced thereafter with any certainty from the available data.

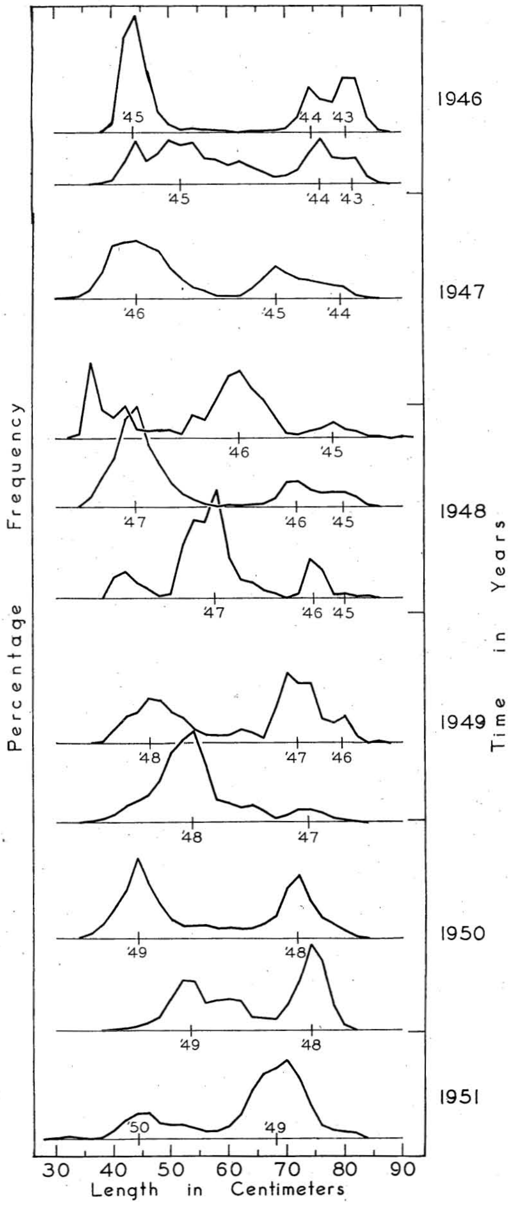

FIG. 1. Length frequencies of Hawaiian aku, 1946–51. The number identifying modal positions is the presumed year of origin of the modal group.

The age of the modal group of smallest length, that of the youngest year-class fished, is of interest. It would appear to be possible to form some judgment of this age by fitting the observed modal length to a growth curve and extending the growth curve toward the origin. It is appreciated that the initial growth period, during the larval stages, will probably not be described by a simple growth curve adequate for the later period of growth; hence, this approach would not, of course, yield a certain answer, but it may, at least, give a likely estimate of the age of the fish. A growth curve of the type described by Walford (1946) was fitted to the length frequency data in the following manner: The obvious modes were selected (see Fig. 1) and the three highest classes for each mode were averaged. This average was thereafter taken as the modal length (these modal values are shown in part in Table 1). Then the modal lengths as obtained from the summer samples were paired with the modes presumed to be the same of a year later.

This relationship between length at age N and at age N + 1 which may be taken as a year or any other equal time interval later, as shown by Walford (1946), is usually a linear one. It was assumed to be linear for these data, and the line of best fit was computed by the method of least squares for the following paired values: Length at age N and N + 1, at age N + 1 and N + 2, and at age N + 2 and N + 3, if available. The equation of this line would permit, of course, the computation of the length at N + 1, given the length at N, or the length at N + 2, given the length at N + 1.

The average of all the mean sampling dates for the summer for the period of September

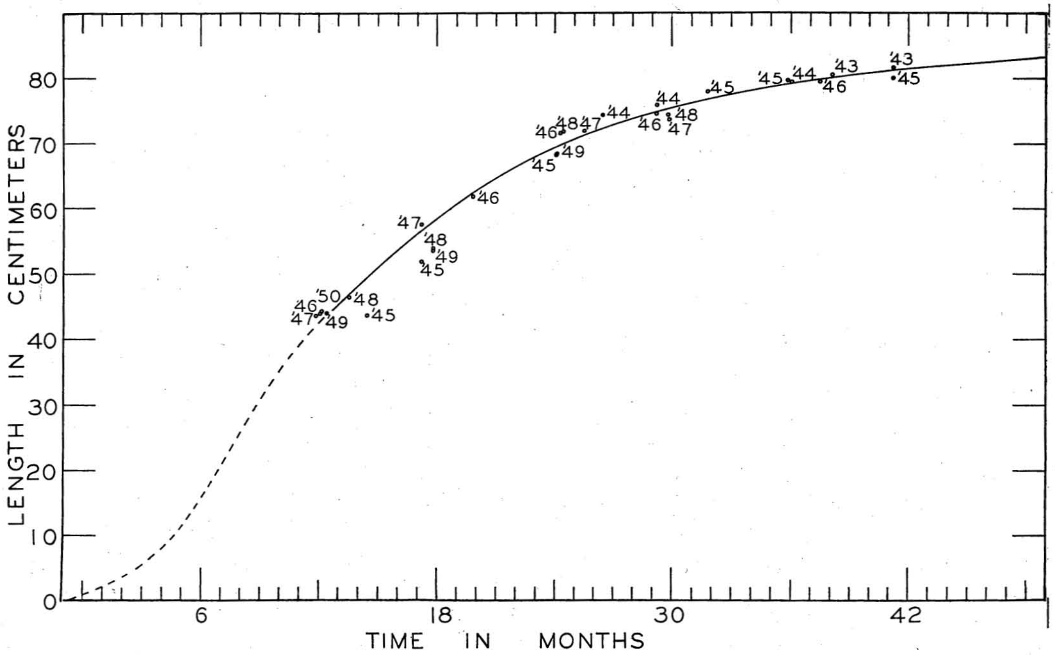

FIG. 2. Growth curve of Hawaiian aku. The number identifying modal lengths is the presumed year of origin of the modal group.

15, 1946, to July 4, 1951, was calculated, as well as the average of all the modal lengths of the modal group composed of fish of the smallest size, for these same sampling dates. This average modal value was taken as length at age N, which was assumed to be 1 year, and the growth curve shown in Figure 2 was computed, using the equation for the least square fit obtained as described above. Shown also on Figure 2 are the various modal values from Table 1 for which the computed growth curve would seem to provide a good fit.

The modal values obtained during the winter period were not used in the computation of the growth curve, as the mean sampling dates were usually much less than 6 months later than the mean sampling dates for summer, and, in addition, the number of fish represented by the winter samples was often small. Again the mode of smallest-size fish occurring in the winter samples was not included in Table 1, as it was felt that fish of these sizes or a little less were discriminated against by the fishermen and that these modal groups sampled during the winter represented, therefore, an incomplete part of the entering year-class. This judgment is, perhaps, strengthened by the fact that these particular modes do not seem to fit into the same pattern as the others. By summer the entering year-class would seem to be adequately represented in the catch in that the modal positions found for it do fit into the pattern of modal lengths of the older fish.

MODAL LENGTH AND AGE

If the age of the year-class entering the fishery during the summer is assumed to be 1 year, even though the growth attained during the first year seems high, it fits the pattern of growth which follows better than the assumption of some other age, such as 2 or 3 years, which may otherwise seem likely. If the judgment made here of the age of the fish in the entering year-class is in error by a year or more, then the initial accelerating portion of the growth curve would seem to persist for a year or more. It would be difficult to obtain an acceptable fit of a growth curve to these modes on any other basis. However, lacking data regarding the nature of the initial accelerating portion of the growth curve, the possibility that the entering year-class is more than 1 year old, even though deemed unlikely, cannot be disproved.

This interpretation of the length data would imply that the aku landed in Hawaii is a short-lived, rapidly growing fish and that the fishery depends on aku belonging largely to two adjacent year-classes and entirely to three. This interpretation is not proved here but is offered as a plausible hypothesis to account for some of the features of the length frequency data given in Figure 1. The most direct method of testing this hypothesis would seem to be by the tagging and recovery of fish of known size, as there is as yet no reliable means of age determination for this species. However, the albacore fishery of western North America also apparently draws its catch from a stock composed of but a few year-classes, as described by Brock (1944).

The appearance of distinct modal groups in these length frequencies, if due to year-classes, is somewhat surprising when the apparent rapid growth rate is considered together with the long spawning period, the evidence for which will be discussed later. The period of active spawning is perhaps much shorter than the occurrence in the landings of fish with fairly large ova would indicate. It is also possible that, although the period of spawning may be of considerable duration, only the fish which hatch during a limited part of that period survive in significant numbers.

LENGTH SEGREGATION IN SCHOOLS

As previously mentioned, beginning in the summer of 1949 a series of samples were taken in such a manner that each represented fish captured from a single school. This was practical inasmuch as only a single school would ordinarily be chummed up by live bait and fished at one time. This catch would often be stored by itself in an empty bait well. The fish were sampled aboard the vessel when it reached port, and samples were taken from those bait wells which, according to the captain, contained fish caught from a single school.

The "pure school" samples obtained during the summer of 1949 proved of sufficient interest to justify an increase in this sampling program. Between May 16 and September 30, 1950, some 120 samples with, on the average, 34 fish measured in each were obtained. As these length data for 1950 were more adequate and did not differ in the features of interest mentioned here from those for 1949, the 1950 data will be discussed. The 1951 data were, in all aspects considered here, also similar to the 1950 data.

The most striking feature of these samples is the comparatively small range of the length of fish within them which is in contrast to the range of the length of fish in the landings as a whole. For example, the mean range in length for the pure school samples was 11.3 centimeters, the least range 5 centimeters, and the greatest 21 centimeters. In contrast to these small ranges, the range of the seasonal summary of length measurements for the same period is 47 centimeters. It would appear that the school is a highly size-selected group in which those causes that select for size may well obscure the pattern of size distribution in the population as a whole. Hence, measuring a larger number of fish from a few schools would not reliably reveal the pattern of size distribution of the fishable stock; fish taken from a large number of schools must be measured. The fact that aku appear to school by size must, of course, be considered in the design of any program to obtain length samples. Although the effect may be less extreme, it may be suspected that schooling by size occurs in other tuna populations and species.

The causes of the observed size segregation by schools is a matter of interest, but they are not clearly evident from an examination of the length data. Of the various possible causes that may be advanced, the most probable one, in my opinion, is that the effect is a mechanical one dependent upon the fact that speed through water is, among other things, a function of size.[2] The cause of the relatively great similarity in the sizes of fish within a school also might be the result of fish of similar age and size remaining in a school together more or less permanently. It is likely that members of such a permanent school would resemble one another more nearly in growth rates than they would resemble members of other schools even though the ages were the same, since environmental differences would effect the school as a unit.

If association of fish by length within a school is dependent upon a real difference in the top speed attainable by fish of different size, then other events must necessarily occur for this effect to express itself in the manner described here. There must be a schooling instinct or reflex which impels the fish to school. (Of the nature of its mechanism or function nothing will be discussed here, but the assumption of its existence is fundamental to the argument.) The fish must spend some of the time swimming at or near top speed or at an optimum speed differing for each size of fish which in turn should result in fish of like sizes schooling together and apart from fish of unlike sizes. This hypothesis would not be incompatible with fish of various ages but similar sizes occurring together or with the occurrence of schools of mixed sizes; the mechanism of size segregation could be effective intermittently, depending on the frequency of sustained rapid swimming by the fish. If the explanation is correct, then schools of fish of mixed sizes may occur. The fact that the range of lengths for fish sampled from presumably pure schools is somewhat variable would strengthen the likelihood that some pure schools of mixed sizes do occur. If, on the other hand, occurrence of fish of much the same size together in a school is due to the relatively great stability and duration of such schools, then the occurrence of mixed sizes of fish in pure school samples in any number would not be expected. If mixed sizes of fish do occur in the pure school samples, the variance of those samples should not be homogeneous. Bartlett's test of the homogeneity of the variance was computed from the length frequency data for both the pure school samples measured in 1950 and 1951 (Snedecor, 1948: 251–252), and the probability that the variances were homogeneous was found to be less than .001 for both years. Hence, of the two explanations for the observed size segregation in schools, the hypothesis that the effect is due to a speed differential in fish of different sizes would seem to accord best with the nonhomogeneity of the variance of these samples. However, the above analysis is not conclusive, and it cannot be denied that other explanations as well are possible.

SPAWNING SEASON

The program initiated in 1948 of weighing an ovary from each of the first 20 female fish of a sample and then measuring the diameters of some 50 ova from it was preceded by routine subjective observations on the degree of maturity for those samples sexed and measured during 1946 and 1947. However, these observations did not indicate the existence of a definite spawning cycle, possibly because the period of observation was insufficient.

In immature fish the gonads appear as two slender strips lying along the dorsal part of the visceral cavity. It is difficult or impossible to sex them by a gross examination of the gonads. As the fish mature, the gonads increase greatly in size and come to fill most

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[2] Designated by Sir Isaac Newton as the *Principle of Similitude*. As applied to ships, it may be stated that the speed of a model and of its full-size counterpart should be proportional to the square roots of their dimensions. The dimension usually taken is the length, and the ratio $\frac{S}{\sqrt{L}}$ is employed in naval architecture to convert the speed observed for a model to that expected for the full-size counterpart, where S equals speed and L length.

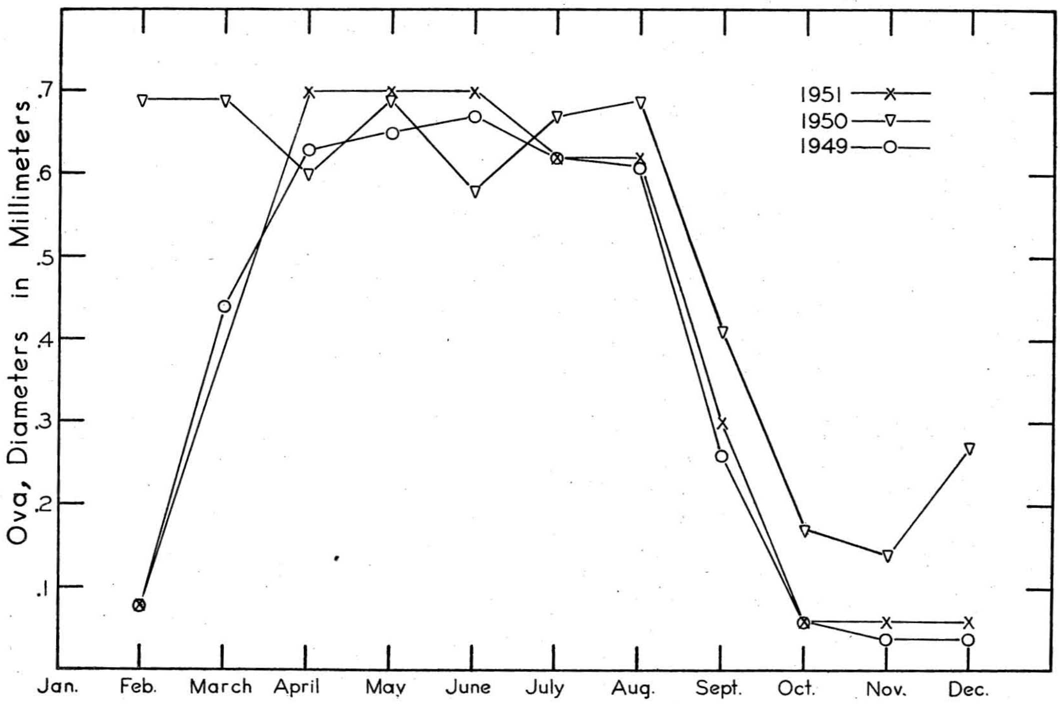

FIG. 3. Average modal diameter of the largest group of ova present in ovary samples for 1949, 1950, and 1951

of the space lateral to the visceral mass. The ovaries become bright yellow, deepening almost to orange in very mature specimens. The small eggs can be seen clearly through the ovarian membranes, and the small blood vessels become increasingly prominent in such fish. The testes of mature males are smooth in texture, pure white, and of more fragile texture than the ovaries. The sex of a mature or maturing fish is easily determined by a gross examination of the gonads.

The ovaries of spawned-out females usually appear large but flabby and empty, are often dark and somewhat bloody, and contain a few large disintegrating ova.

Fully ripe fish were very rare in the landings; such fish are apparently not commonly available to the fishery. One fish 43.2 centimeters long, examined on June 20, 1947, appeared to be fully mature. When it was opened, a gelatinous mass of eggs came foaming out of the visceral cavity in sufficient quantity to make a fair double handful. These eggs, assumed to be mature, were the largest seen in quantity in any of the gonads observed, averaging about 1.125 millimeters in diameter. They were smooth and round (or slightly oval) and contained a single yellow oil globule which varied from 0.22 to 0.45 millimeter in diameter. In contrast, the larger ova from maturing aku as taken by the commercial fishery measure only from 0.4 to 0.9 millimeter in diameter and have a cluster of two or three oil globules.

The beginning of the spawning season was not observed in 1948, as the program of taking ova diameters and ovary weights revealed that the fish sampled at the beginning were as mature as ordinarily are available to the fishery. From the beginning of the program, June 16, 1948, until the middle part of September, spawned-out fish were also very rare; after that time they dominated the catch.

However, the spawning season studies did begin early enough in subsequent years to span the entire spawning season, with the possible exception of 1950; hence, the analysis of the data for those seasons will be presented. However, the study of the data for the 1948 season gave equivalent results for the short period covered.

Given in Figure 3 are the mean of the ova diameters measured, averaged for each month for 1949, 1950, and 1951. Large ova first appear in late February, March, or April and are found until September. During the remainder of the year the ova are small. Presumably, eggs are maturing between March and September but not during the other months of the year. Not until after the presumed end of the spawning season in September are fish with flabby, empty ovaries encountered. During the summer when the ovaries attain their greatest growth, spawned-out fish are evidently not available to the fishery. The spawning season, as indicated by Figure 3, is a long one, and aside from its length there are a number of other characteristics which may guide some guesses regarding its important features. These are: (1) The great rarity of fish containing fully matured eggs in the commercial fishery; (2) the lack of fish with ovaries sampled within the spawning season which present the spawned-out appearance to be observed in those fish ovaries sampled after mid-September; (3) the apparent absence of a trend in mean ova diameters during the spawning season which is shown in Figure 3; and (4) the multimodal frequency distribution of ova diameters during the spawning season, as shown in Figure 4, in which the diameters of 1,000 ova measured from a single ovary are plotted. At other times, aside from a few large eggs being resorbed immediately following the spawning season, only a single modal diameter of ova is in evidence, and this is quite small—less than 0.1 millimeter.

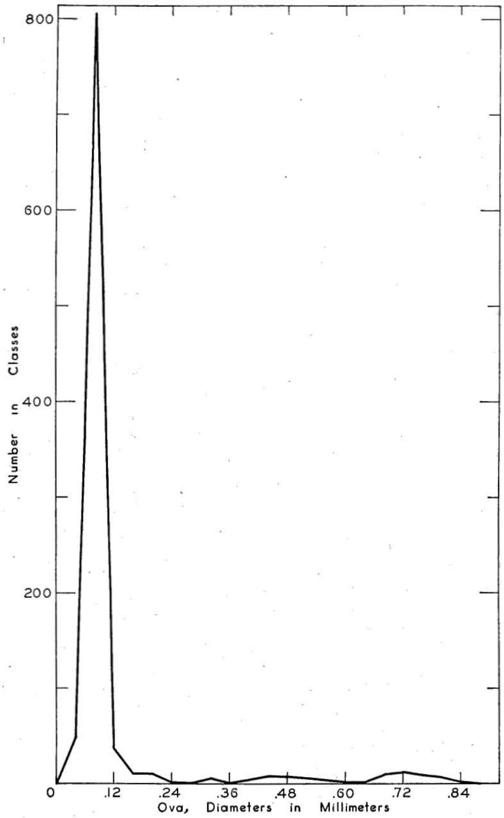

FIG. 4. Size frequency of ova taken from a single ovary, summer of 1949.

Assembling these observations into a partern is nôt difficult; however, there are admittedly other patterns possible. The multimodal distribution of ova diameters during the spawning season and its absence at other times would infer that individual fish spawn several times. This inference is strengthened by the absence of an over-all trend in ova diameters during the spawning season (that is, the dominate diameters do not progressively increase or decrease) and perhaps also by the absence of fish that are obviously spawned-out until after the end of the spawning season.

Table 2 gives the relative proportion in the samples of ova diameters of certain sizes. Although fish with ova approaching 0.7 or 0.8 millimeter in diameter were quite rare, fully mature ova are over 1 millimeter in diameter. This may imply that fish with ova diameters of 0.7 millimeter and above become

TABLE 2
COMPARATIVE ABUNDANCE OF OVA MODAL GROUPS OF VARIOUS DIAMETERS IN THE SAMPLES TAKEN FOR THE SUMMER OF 1949

MODAL DIAMETER OF THE GROUP OF LARGEST OVA FOUND	PERCENTAGE OCCURRENCE OF OVARIES WITH SUCH OVA GROUPS IN THE SAMPLES
Millimeters	
0.48	5
0.60	30
0.68	55
0.80	6
0.88	4

progressively less available to the fishermen until a short time after spawning and that when they again enter the catch the dominate ova diameters in their gonads are 0.4 to 0.5 millimeter. In turn, these ova may grow and mature and the spawning cycle repeat itself. Inasmuch as the data do not include information concerning the histories of individual fish but represent a statistical cross section of the ovarian situation at various irregular stages for various fishes, it is difficult to obtain a valid basis for judging the rates of growth of ova and the number of times fish may spawn. If the spawning act was a periodic matter, occurring at the same time for all fish, it would be possible to judge when it occurred and how often; however, if it occurs irregularly with relatively small groups of fish spawning together as the ova mature, data of the nature obtained during the present study cannot adequately describe the situation.

SIZE OF FISH AT MATURITY

The smallest fish that possessed maturing ova during the spawning season were around 40 to 45 centimeters long. Fish 35 to 40 centimeters in length had ovaries that, with a few exceptions, seemed immature. Immature fish are rare in the commercial landings during the spawning season, as are likewise fish less than 40 centimeters in length. It therefore appears likely, considering also the information on age and rate of growth, that aku may mature in 1 year.

SEX RATIOS

The sex ratios obtained while sampling ovaries are of interest in that a significant departure from an expected 1:1 ratio occurs in the fall months.

The number of male and female fish obtained during the course of this sampling, together with the probability that the observed sex ratio was 1:1 as indicated by chi-square, is given in Table 3 for spring, summer, and fall.

The significant change in the sex ratio which occurs during the period from September through December corresponds to the nonspawning period (see Fig. 3) and may indicate a differential availability between male and female fish during this period. This

TABLE 3
COMPARISON OF SEX RATIOS OF AKU FOR SPRING, SUMMER, AND FALL, 1949 AND 1950

	1949			1950		
	MARCH TO MAY	JUNE TO AUGUST	SEPT. TO DEC.	MARCH TO MAY	JUNE TO AUGUST	SEPT. TO DEC.
Males	237	691	351	42	275	418
Females	205	722	214	40	240	316
Totals	442	1,413	565	82	515	734
Probability	.13	.41	<.0001	.82	.12	<.001

TABLE 4
COMPARISON OF SEX RATIOS FOR BOTH LARGE AND SMALL FISH FOR MARCH–AUGUST AND SEPTEMBER–DECEMBER, 1949 AND 1950

	LENGTH GREATER THAN 650 MILLIMETERS		LENGTH LESS THAN 650 MILLIMETERS	
	MARCH–AUGUST	SEPT.–DEC.	MARCH–AUGUST	SEPT.–DEC.
Males	1,077	304	168	465
Females	1,063	208	144	322
Total	2,140	512	312	787
Probability	.76	<.0001	.17	<.0001

is likewise a period of reduced availability, and, if the reduction in catch commonly experienced during the fall and winter months arises from the departure of part of the population from the areas fished, it might be suggested that a disproportionate number of female fish are among those departing.

The possibility that the observed changes in the sex ratio might be linked with changes in the sizes of fish available to the fishery was explored, as significant changes in the average size of fish in the catch does seem to occur during the year and some error may be expected in sexing the smaller sizes.

The fish sampled were placed in two groups by size—those larger than 65 centimeters and those smaller than 65 centimeters; however, the same pattern of sex ratios was displayed by both groups. (See Table 4.) If the length frequency curves (Fig. 1) are examined, it will be seen that fish of 65 centimeters are not abundant in the catch. This particular length, therefore, seems to be a natural point of division between large and small fish, at least for the dominant summer fishery.

SUMMARY

The length frequency measurements of Hawaiian aku (*Katsuwonus pelamis*) for the period from the summer of 1946 to that of 1951 contained definite modal groups which, when properly associated from summer to summer, indicated the probability of the existence of two and sometimes three year-classes in the landings which were possibly 1, 2, and 3 years of age, respectively (fish referred to as 1 year old have probably reached or are about to reach the end of their first year and are, therefore, beginning their second year of life), with modal lengths of 42 to 45 centimeters, 68 to 73 centimeters, and 79 to 80 centimeters for each of the ages given above.

A study of the schooling pattern of the aku indicated a strong tendency to school by size; no fish within a school, in the samples studied, differed by more than 20 centimeters, whereas fish present in the whole population sampled differed by as much as 50 centimeters. The possibility that the mechanism of this size segregation might depend upon the existence of a higher swimming speed for the same proportionate effort for larger fish was suggested. An alternate hypothesis, that the schools were relatively stable aggregates, seemed less likely as the variances for these pure school samples were found to be significantly nonhomogeneous.

The measurement of ova indicated that the spawning period probably extended from late February, March, or April to the first part of September, and the existence of several modes in the frequency distribution of ova diameters within individual ovaries indicated the likelihood of multiple spawnings. Fully ripe and spawned-out fish were both quite rare in the commercial catch during the spawning season, and, although these observations would indicate that fully ripe fish were not available

to the fishery, they would also imply a pattern of multiple spawning. The data did not allow an estimation to be made of the number of times aku may spawn each season.

It would appear probable, in consideration of the minimum size at maturity together with the growth rate as estimated from the length frequency curves, that aku require a year in which to reach maturity.

The significant reduction in the proportion of female fish in the landings during the fall and early winter months, coupled with the reduced catches experienced during this period, may indicate that the female fish become less available to the fishermen at this time than the males. This differential availability of females would seem to occur coincident with the end of the spawning period. This change was found not to be associated with shifts in the sizes of fish landed.

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