AGE AND GROWTH OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

The age and growth of Pacific hake, *Merluccius productus*, collected off California, Oregon, and Washington in 1964-69, were studied.

The age determination procedure was examined and considered to provide valid ages.

Several sources of variation in the age structure of the population were given cursory examination. Relative size of the year class and sampling area (average age tends to increase with latitude) contribute substantially to the variation of the population age composition while sex and sampling season have lesser effects.

Growth in length is rapid during the first 3 yr after which it slows and approaches an asymptote in the oldest ages, 10-13 yr. Females have a faster rate of growth than males and tend to survive 2 or 3 yr longer, to age 13. Growth in length can be adequately described by the von Bertalanffy growth equations: $l_t = 56.29\,(1-e^{-0.39\,(t-0.20)})$ for males and $l_t = 61.23\,(1-e^{-0.30\,(t-0.01)})$ for females. Year class variation in growth rate was detected by back-calculation, using the body length (Y)-otolith radius (X) relationship $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$. Growth in weight was determined by use of the length-weight equations: $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females. Males attain an average weight of about 1,211 g by age 11 and females reach an average weight of 1,374 g by age 13. Annual instantaneous growth rates in weight were computed and were found to decrease most during the fourth year for both sexes and very little growth occurred after the sixth year for males or after the ninth year for females.

The Pacific hake, *Merluccius productus*, is a common gadid fish that ranges from the Gulf of California to the Gulf of Alaska (Hart 1973) but is most abundant from Baja California to southern British Columbia (Alverson et al. 1964). There is apparently a single population offshore and another in Puget Sound, Wash. (Utter and Hodgins 1971). The Puget Sound population supports only a small fishery and is not considered in this report.

Feeding adult hake are usually found over the continental shelf and exhibit pronounced diel movement. During the day they are most commonly found in compact schools near the seabed, but as darkness approaches the schools rise and become more loosely structured. During their spawning period mature hake are more pelagic in behavior than during the rest of the year. They apparently spawn at intermediate depths in water 1,000 m deep or more and demonstrate little diel movement (Nelson 1967). Spawning occurs from January through April off northern Mexico and southern California (Ahlstrom and Counts 1955). Eggs and larvae are pelagic and are found mostly near the thermocline at depths of about 45 to 100 m. It is not clear at what age juvenile hake leave their pelagic phase and become more closely associated with the seabed. One-year-old hake are found in inshore waters off southern California, associated at times with schools of northern anchovy, *Engraulis mordax* (Dark et al. 1970). Hake, 1 to 3 yr old, are taken in shrimp trawls along the Oregon and California coasts (Morgan and Gates 1961). Pacific hake less than 4 yr old are rarely found north of Oregon. Most 4- to 13-yr-old hake mature and are found feeding off the coasts of Oregon, Washington, and southern British Columbia during the spring and summer. By early winter only a small portion of the summer population remains in these areas.

Temporal and areal distribution of the various life history stages suggest that adult Pacific hake undertake extensive annual migrations along the west coast of North America (Alverson and Larkins 1969). Most adult hake seem to move northward along the coasts of California, Oregon, and Washington in early spring on a feeding migration as far north as central Vancouver Island. In late fall the adults begin a return

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migration to the south which terminates in the spawning area off southern California and Mexico. The eggs and larvae drift onto the continental shelf and the young inhabit the waters of California and Oregon as 1-to-3 yr-olds. Some 3-yr-olds and most 4-yr-olds become sexually mature (Best 1963) and are recruited to the adult population.

Pacific hake were landed in small quantities in California ports as early as 1879. California landings from 1916 to 1951 varied from about 0.2 to 90 metric tons. An animal food fishery developed in 1952 creating an increased demand for low value species and hake landings increased to about 590 metric tons in 1956. From 1956 to 1968, landings averaged about 200 metric tons annually.

Prior to 1965 Washington and Oregon fishermen did not purposefully fish for hake and, in fact, considered them a nuisance species. In 1965 a small fishery was initiated under the guidance of the U.S. Bureau of Commercial Fisheries (BCF)[2] to examine the feasibility of efficiently harvesting Pacific hake off Washington and Oregon. Four vessels began fishing commercially in 1966 because favorable results were obtained from the feasibility study and a new fish reduction plant had begun operations at Aberdeen, Wash. During the same year a large Soviet trawl fleet appeared off the Washington-Oregon coast fishing for rockfish, *Sebastes* spp., and Pacific hake. Competition from the Soviet fleet was so severe that it seriously threatened the existence of the U.S. fishery. Negotiations between the United States and the Soviet Union in February 1967 resulted in an agreement which restricted the size of the Soviet fishing area off the southern Washington coast. The U.S. fleet was more successful in 1967 because of a reduction of Soviet competition and increased efficiency of U.S. vessels. This greater efficiency stemmed from the increased experience of fishermen, improved fishing gear, and greater scouting capability. The total U.S. catch in 1967 was 8,381 metric tons (catch-per-unit-effort [CPUE] = 4.5 metric tons/h), as compared to a total catch of 1,694 metric tons (CPUE = 3.0 metric tons/h) in 1966 (Nelson 1970). Soviet catches in 1966 and 1967 were about 136,050 and 170,590 metric tons, respectively. Since 1967 the Soviets have continued to fish for Pacific hake and annual catches have averaged about 140,000 metric tons. The U.S. fishery was discontinued in 1968 when the reduction industry, facing a depressed fish meal market, was unable to give vessel owners prices that were competitive with those offered by the shrimp and groundfish processors (Pereyra and Richards 1970).

[2]Presently, the National Marine Fisheries Service.

An agreement pertaining to the joint exploitation of groundfish in the northeast Pacific Ocean was negotiated between the United States and the Soviet Union in 1967 and renegotiated in 1969 and 1971. Scientific meetings have been held annually to discuss problems of mutual concern such as assessing the size of the Pacific hake population, determining the effects of the fishery, and estimating rates of growth, mortality, and maximum sustainable yield. Recommendations resulting from the scientific meetings provide a basis for modification of the bilateral fishery agreement—which can be done every 2 yr.

Initial growth estimates were based on preliminary data but served to provide essential real time estimates of maximum sustainable yield. Subsequently, additional data have been collected allowing for refinement of early growth estimates. The objectives of the present study were to provide new estimates of the growth rate of Pacific hake and to examine some of the potential sources of variation. An analysis was made of the reliability of the age determination method used since age information is basic to growth studies. The variability in the age structure of the Pacific hake population was also examined since age composition is frequently used to evaluate relative year class strengths, mortality rates, and the effects of fishing.

SAMPLING

Collection Methods

Biological data were collected from two sources: "commercial" samples from the commercial fishery and "research" samples taken aboard research vessels.

Commercial samples were taken mainly in 1966-67 when a U.S. hake fishery was conducted off the Washington coast during May-September. A sampling station was established at the reduction plant in Aberdeen, Wash., where essentially all hake taken off Washington and Oregon were landed. An attempt was made to man the station every other week and to sample the catches as they were unloaded at the plant. Irregular landing schedules, especially in 1966, resulted in sporadic sampling. In some sampling weeks, landings were made during 3 or 4 days while in other weeks there were no landings. Landings were sampled as fish moved from the vessel to the plant over a conveyor system. Approximately 200 specimens were collected for each sample. Specimens were first dissected to determine the sex, then were measured (to the nearest centimeter) from the snout to the fork of the tail. An otolith was removed for age determination and, when time allowed, whole specimens were weighed to the nearest decagram.

To simplify the collection of otoliths, most otolith samples were stratified by 1-cm body length intervals. Otoliths were taken from five males and five females in each length interval until the sample was exhausted. Although average length-at-age information can be taken directly from such stratified samples, randomization was necessary to obtain unbiased estimates of age composition.

Research vessel samples were collected from 1964 through 1969 and were both stratified and random. Most research vessel samples were processed at sea for the same biological data as those taken from commercial samples. When weights were taken a small hand-held steelyard was used which provided more consistent readings than did spring scales.

The research vessel samples used herein are geographically and temporally restricted simply because it was beyond the capability of a single vessel to conduct more extensive sampling. The samples taken at the reduction plant in 1966-67 provided the best temporal coverage over a season, but their areal distribution was restricted mainly to fishing grounds off Grays and Willapa Harbors, Wash.

Sample Representativeness

Whereas the nature of available samples places constraints on some aspects of the following study, the large number and size of samples collected over several years and over a large part of the species' geographical range render them valuable in examining the reliability of earlier estimates of growth (Best 1963; Tillman 1968). Also, some of the more conspicuous variations in both growth rates and age composition can be examined.

Figure 1 gives a general representation of the distribution of sampling effort in 1964-69. The adult portion of the population (4- to 13-yr-olds) occurring off the coast of Washington during the summer was the most intensively sampled, especially in 1966-67 when commercial samples were taken. Research vessels sampled adults off Washington, Oregon, and California, mostly during the summers of 1965-67. Juveniles (1- to 3-yr-olds) were sampled only sporadically and much less intensively. In the winters of 1965 and 1968, research vessels searching off southern California and northern Mexico for spawning hake obtained some samples of 1- and 2-yr-old specimens. Very few 3-yr-old hake were captured, probably because there was relatively little sampling effort in areas where they were likely to be most abundant.

Commercial vessels fishing for Pacific hake off Washington used Cobb pelagic and BCF universal trawls (Johnson and High 1970). The stretched mesh size varied from 5.1 to 7.6 cm in the trawl bodies and cod ends. Research vessels used the

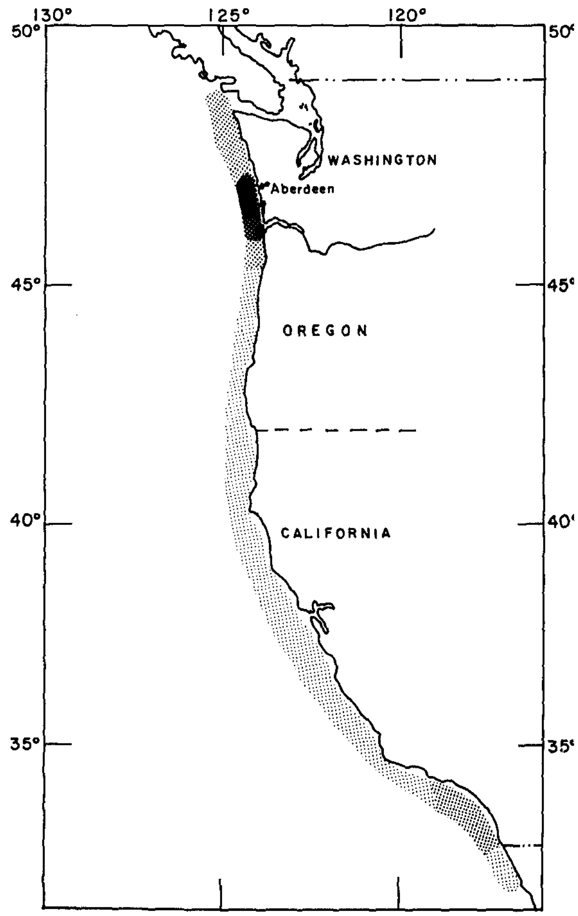

FIGURE 1.–Distribution of sampling effort for Pacific hake, 1964-69. (Darker stipling infers more intensive sampling.)

same trawls, but with 3.8-cm liners in the cod ends much of the time. Liners were used to determine the availability of the youngest age groups. Research and commercial samples were never taken in such a manner that length frequencies could be compared to isolate the effects, if any, of the 3.8-cm liner. But there was probably no significant selection for fish length without the liner since similar unlined trawls used in the Puget Sound hake fishery apparently retain all fish of 35 cm or greater.[3] Because very few hake off Washington were as small as 35 cm, sampling gear differences were not considered to be a significant source of sampling error. Therefore research and commercial samples taken in 1966-67 were combined at times to increase sample sizes and to improve temporal and areal sampling coverage.

DETERMINATION OF AGE COMPOSITION

Aging Technique

A prerequisite to any growth study is a method for reliably determining the age of individual fish. European investigators (Birtwistle and Lewis 1925; Hickling 1933; Bagenal 1954) found the otolith to be the most useful structure in determining the age of the European hake, *Merluccius merluccius*. Bigelow and Schroeder (1953) arrived at the same conclusion while studying the silver hake, *M. bilinearis*. Apparently Best (1963) was the first to age Pacific hake. He found that from the standpoint of availability otoliths were superior to scales as most scales were absent on trawl-caught specimens.

Our collection of otoliths was standardized in an effort to control sampling variation. Samplers attempted to always collect the otolith from the right side of the head to avoid any confounding effects due to possible otolith asymmetry. If the right otolith was damaged during the extraction process, the left otolith was accepted as an alternate (5-10% of all samples). Otoliths were thoroughly cleaned and preserved in a solution of 10-30% ethyl alcohol. Occasionally otoliths with a uniform chalky appearance were encountered and were cleared by dipping them in a weak solution of hydrochloric acid. This practice was followed with care to prevent the dissolution of annuli at the otolith edge.

[3]Larkins, H. A., H. H. Shippen, and K. D. Waldron. Features of a northern Puget Sound hake population. Unpubl. manuscr. Northwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

Otoliths were placed in a petri dish with the bottom painted black, illuminated with a reflected light, and read under a dissecting microscope at a magnification of 6.6×. Each otolith was read by two readers and if the ages did not agree, as was the case in 25-40% of the otoliths processed, the otolith was examined by a third reader. The best estimate of age was taken as the age agreed upon by any two readers. When all three readers disagreed (about 5% of the readings), the middle reading was used. If one reader could not make a determination and agreement could not be reached by the other two, the otolith was considered unreadable. Generally there was a 3-5% rejection rate.

The majority of the hake otoliths were collected during the summer (May-September). Assuming that the past winter was represented by the last (most recent) translucent zone, the age was taken to be simply the total number of translucent zones on the otolith. The few winter (February-March) samples collected were composed mainly of fish completing their first or second year of life. The same aging criteria cited above were applied to winter samples, except those otoliths without a translucent zone were assigned to age "1" instead of "0." This was done on the premise that the translucent zone would have been deposited shortly after the sample was taken, since young of the year would not have been captured by the sampling gear.

Validity of Aging Technique

Because the use of otoliths in aging Pacific hake had not been completely evaluated, some attention was devoted to determining the reliability of the procedure. Graham (1929) gives three indirect methods of evaluating the use of scales and otoliths for age determination: 1) agreement with Petersen's (1895) method; 2) seasonal changes in scale or otolith margins; and 3) observation of a strong year class over a period of years.

The Petersen's (1895) method, which compares the relative abundance of age groups as determined by length distribution with age groups as determined by analysis of scales, otoliths, or other structures, is generally only applicable to the first three or four age groups. For Pacific hake, the length distributions of the age groups overlap extensively after age 3, restricting the use of the method to the first three age groups. Because few 2- and 3-yr-old hake were present in the samples, Petersen's (1895) method could not be effectively applied.

According to Graham's (1929) second method, observations of the development of translucent and opaque zones on the perimeter of the otolith (based on data from a population that had been sampled periodically during a year) may provide an indication of the frequency with which the zones are formed. A single occurrence of a particular zone during a year would provide an annual mark which may be suitable for age determination. In European hake (Hickling 1933) opaque zones have been associated with good physical condition and growth whereas translucent zones have been associated with a lesser physical well-being and retardation or cessation of growth. Poor condition can result from a decrease in the food supply, the onset of maturation and spawning, or both.

For the present study a special effort was made to record the zone type on the edge of all hake otoliths collected during 1967. Samples were taken during March, April, May, June, and August. Otoliths from a sample collected in November 1969 were added to the above spring and summer samples for data on the winter appearance of the edge. It appears that there are long and overlapping periods when zones are deposited because most samples had some otoliths with opaque margins and others with translucent margins. One exception is the small, March 1967 sample that contains only 1-yr-olds. Even though opaque edges are plainly recognizable in the young age groups, all otoliths in this sample had translucent margins.

The persistent occurrence during the summer (the apparent growing season) of otoliths with a translucent edge may be at least partly because the newly deposited opaque material is not always detectable due to the thinness of the edge and the resulting transparency.

Figure 2 demonstrates that the frequency of opaque edges decreases rapidly with the age of the fish. This is almost certainly a bias resulting from the increased difficulty in distinguishing the zone type on the edge of the otolith as the fish becomes older. Opaque bands on the otoliths of young fish (1-4 yr) growing at a relatively fast rate are wide, dense, and readily distinguishable. As growth slows in older specimens, new opaque zones become narrower, and are not always apparent until late in the growing season or until bordered by a new translucent zone.

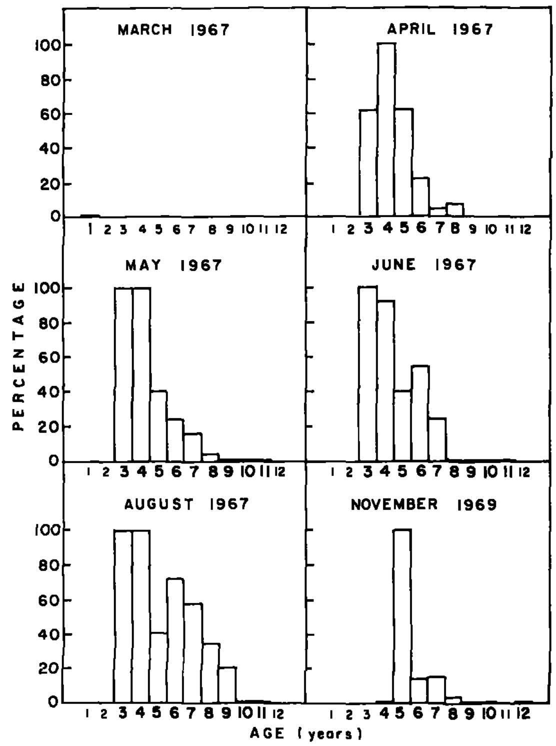

FIGURE 2.—Percentage of otoliths with opaque edges by age group (ages actually observed in bold print).

Because the zone type on the edge of the otolith is related to the age of the fish, a comparison of otoliths could be misleading if the sample age compositions vary to a large extent. Whereas the age compositions of the 1967 samples were similar, the age composition of the 1969 sample was noticeably different (Figure 3). To avoid the effects of advanced fish age on a reader's ability to accurately judge opaque zones at the otolith edge type, samples of 6-yr-olds taken in April-November and one sample of 1-yr-olds taken in March were compared in Figure 4. The graph suggests that Pacific hake start to deposit opaque material around April. The time of deposition may vary with age, but other age groups were not present in numbers adequate for comparison. The incidence of otoliths with opaque edges increased steadily through August when it peaked at about 72%. A dramatic decrease in otoliths with opaque edges occurred in the November sample. The foregoing analysis indicates that the physical well-being of Pacific hake improves in early spring

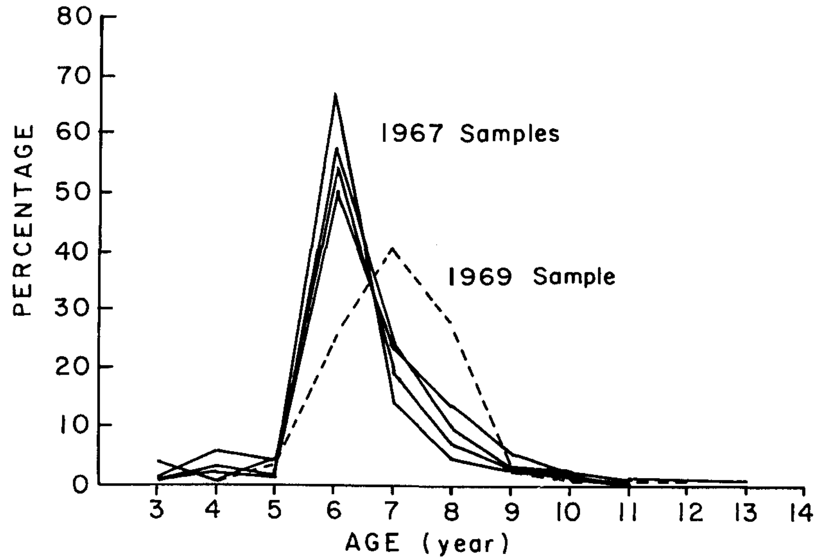

FIGURE 3.—Age composition of samples selected for analysis of zone type on the otolith edge.

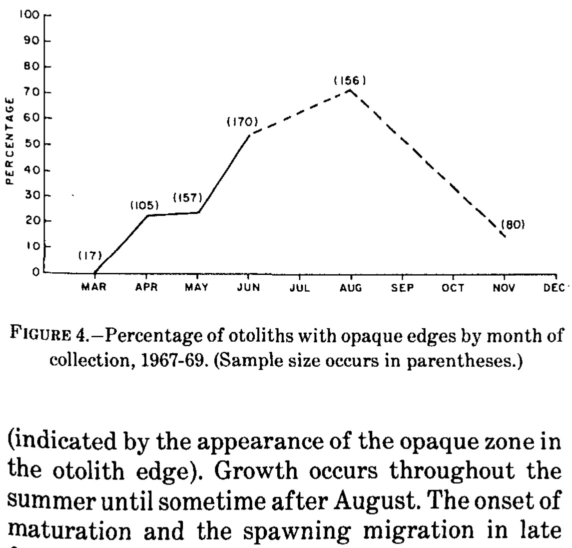

FIGURE 4.—Percentage of otoliths with opaque edges by month of collection, 1967-69. (Sample size occurs in parentheses.)

(indicated by the appearance of the opaque zone in the otolith edge). Growth occurs throughout the summer until sometime after August. The onset of maturation and the spawning migration in late fall probably place additional demands on the energies of the animal, resulting in slowed growth which is reflected in the appearance of the translucent zone at the otolith edge.

Although observations are not available during all months, the unimodal characteristic of the curve in Figure 4 strongly suggests that one opaque and one translucent zone are deposited each year and that the zones provide reliable annual marks. However, comprehensive monthly sampling is required to confirm unimodality.

The third method suggested by Graham (1929) is based on the rationale that if a predominant year class enters a population of fish and if the aging technique is reasonably reliable, then the year class should be observed progressing normally through the population age structure for several years.

Fortunately the 1961 year class of Pacific hake was extremely strong when it was partially recruited (designated as 4-yr-olds) to the adult hake population in 1965. In that year the 4-yr-olds comprised 15% of the adult population off Washington, while in other years from 1964 to 1969, 4-yr-olds contributed only 0-2%. In 1966 sampling indicated that over 50% of the adult population off Washington was composed of 5-yr-old hake. The dominance of the 1961 year class evidently continued through 1967, when over 70% of the population was 6-yr-olds; 1968 when about 64% was 7-yr-olds; and 1969 when about 24% was 8-yr-olds (Figure 5). In contrast, from 1964 to 1968, 8-yr-olds comprised only 2.4-13.7% of the population. This movement of the 1961 year class through the population age structure is accepted as additional evidence that the translucent zone represents a single annual mark.

Randomization of Age Samples

As noted previously some otolith samples used herein were collected aboard research vessels and are considered to be random, but the majority were commercial samples in which otoliths were

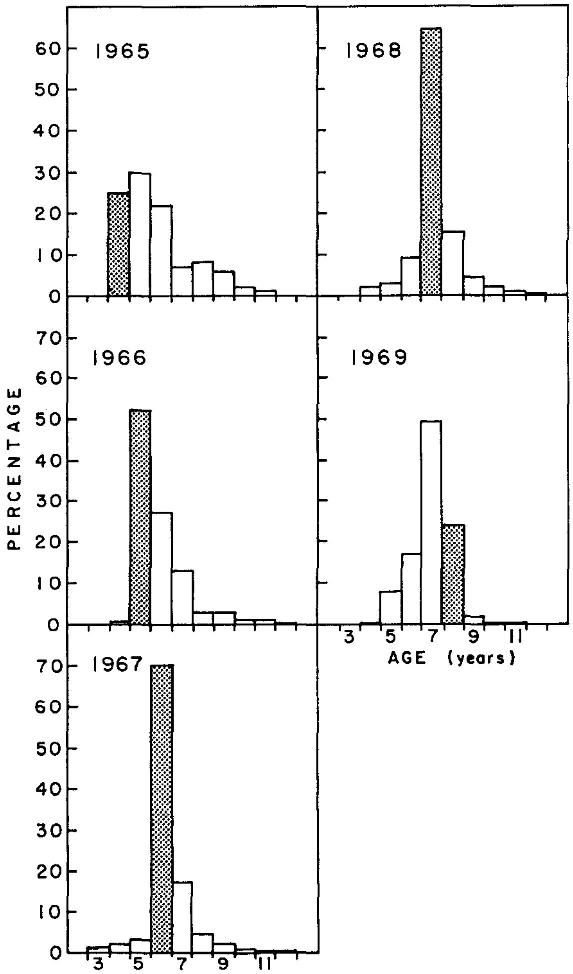

FIGURE 5.—Age composition of Pacific hake taken off Washington during May-August, 1965-69. (Shaded bar denotes the 1961 year class.)

collected in a stratified manner. Before the commercial samples could render representative age compositions, they had to be randomized. This was accomplished by constructing an age-length key for each sample. The percentage age frequency per length interval observed in stratified subsamples was applied to the length frequency distribution of the entire sample.

VARIABILITY IN AGE COMPOSITION

Several potential sources of variation in age composition were analyzed using research and commercial samples. Age composition is used for evaluation of the effects of fishing, estimation of recruitment, growth, and mortality. Therefore the major sources of sampling variation should be identified. The effects of annual, seasonal, latitudinal, and sexual variation are considered in this section.

Annual Variation

Annual variation in age composition was studied using samples collected off the Washington coast during May-September 1965-69. It has been assumed (Tillman 1968; Nelson and Larkins 1970) that Pacific hake are fully recruited to the fishery at age 5. If this assumption is valid and if recruitment and mortality rates are constant then one would expect, from a relatively unexploited population, a typical catch curve with the 5-yr-olds most numerous and the succeeding ages decreasing at a rate equal to the rate of natural mortality. This pattern was apparent in 1965 (Figure 5). The partially recruited 4-yr-olds were not as numerous as the 5-yr-olds which predominated. From age 5 there was a progressive decrease in the relative abundance of succeeding age groups until only a few 13-yr-olds remained. By examining the age compositions in subsequent years, it became obvious that the 4-yr-old age group in 1965 was considerably larger than usual. This was the first indication that the 1961 year class was unusually large. In 1966 the 1961 year class (5-yr-olds) was probably fully recruited and strongly dominated the age structure. The relative abundance of the incoming 1962 year class (4-yr-olds) was much smaller than the 1961 year class in the 1965 samples. The 1961 year class can be followed through the age composition in 1967-69. In 1969 the 1961 year class lost its dominance to the 1962 year class, but still produced extraordinarily large numbers of 8-yr-olds. Apparently the 1965-66 year classes were smaller than those observed previously since in the 1969 sample no 4-yr-olds were observed.

Obviously annual variation in age composition does occur in Pacific hake and is at least partly due to varying levels of recruitment of incoming year classes.

Seasonal Variation

In 1966-67 regular sampling of Pacific hake from off the southern coast (lat. 46°00′-46°59′N) of

Washington occurred throughout the fishing season. These samples were combined as "early" (collected in May-June), "middle" (July), and "late" (August-October) samples for the purpose of identifying any gross seasonal changes in age composition (Figure 6). The 1966 early sample contains somewhat fewer 5-yr-olds and more 6-yr-olds than either the middle or late samples which are very similar. For all practical purposes, the age compositions of the three 1967 samples are identical. There is little evidence in these comparisons to suggest that there is significant change in age composition during the time the Pacific hake are present in commercial quantities off southern Washington. The paucity of samples appropriate for further comparisons precludes assessment of seasonal age composition variation which may occur at other times and places.

Latitudinal Variation

Variation occurs in the age composition of Pacific hake samples taken from different portions of the latitudinal distribution (Nelson 1967; Tillman 1968). Table 1 is adapted from Tillman's table 14 to show the percentage age composition

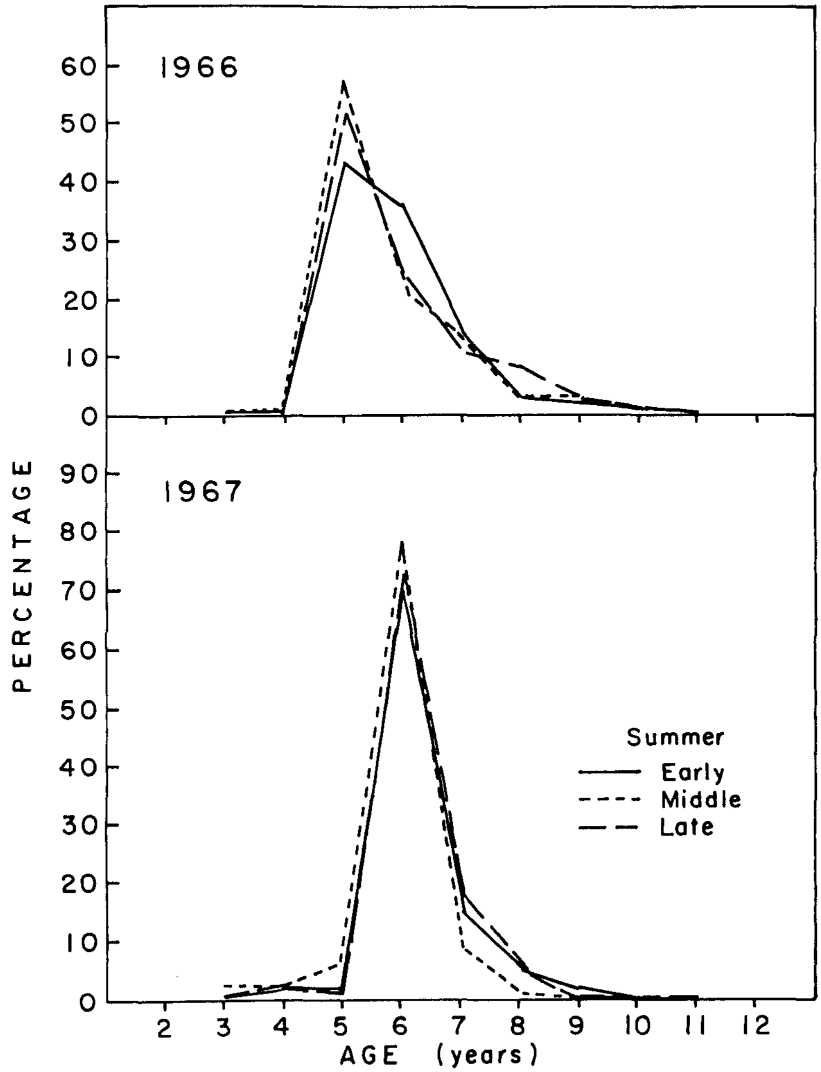

FIGURE 6.—Age composition of Pacific hake collected off southern Washington (lat. 46°00'-46°59'N) by early, middle, and late summer periods.

TABLE 1.—Age composition (percentage) of hake taken off Washington, Oregon, and California in 1965 by research vessels (adapted from Tillman 1968).

Age (years)	Washington			Oregon			California		
	Male	Female	Sexes combined	Male	Female	Sexes combined	Male	Female	Sexes combined
1	—	—	—	—	—	—	0.2	1.5	0.6
2	—	—	—	—	—	—	1.8	4.0	2.4
3	—	—	—	—	—	—	3.8	6.9	4.7
4	13.0	22.5	17.7	26.8	46.4	37.2	44.4	38.2	42.6
5	28.9	20.6	24.7	37.0	27.6	32.0	29.8	25.1	28.4
6	27.2	23.8	25.1	22.8	11.9	17.0	8.1	10.6	8.8
7	13.5	5.2	8.5	4.1	4.6	4.4	5.1	5.5	5.2
8	12.9	10.6	11.5	9.1	4.3	6.6	3.5	5.1	4.0
9	3.0	10.3	7.4	0.1	3.9	2.1	2.7	2.5	2.6
10	1.4	4.9	3.5	—	0.6	0.3	0.4	0.6	0.4
11	—	1.4	0.9	—	0.5	0.3	0.1	—	0.1
12	—	0.6	0.4	—	—	—	0.1	—	0.0
13	—	—	—	—	0.1	0.1	—	—	—
Sample size	1,474	2,196	3,670	810	914	1,724	1,586	670	2,256

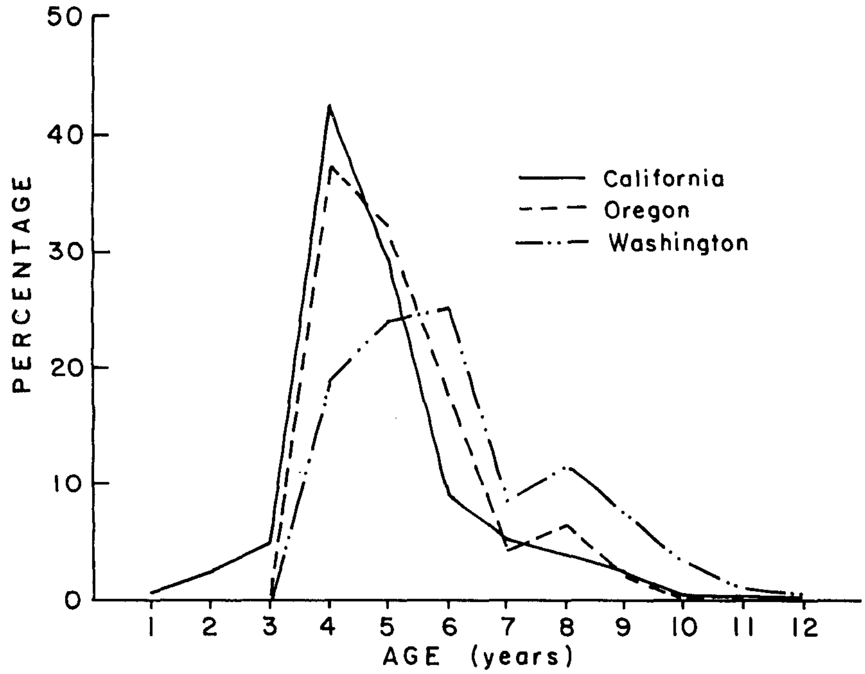

FIGURE 7.—Age composition of Pacific hake collected off California, Oregon, and Washington in 1965.

for research vessel samples taken off Washington, Oregon, and California in 1965. These samples were used because they provided the best geographic coverage and were taken with similar trawl gear, equipped with small-mesh cod end liners capable of capturing juvenile hake. The age composition of the California sample probably does not truly reflect the relative abundance of the age groups. The southern distribution and abundance of adult hake was a primary consideration at the time of sampling and, because the very young hake normally are not found associated with the adults, they probably were not taken in proportion to their abundance. Figure 7 shows, however, that samples taken off California included 1-, 2-, and 3-yr-olds, which did not occur in Washington and Oregon samples. Washington and Oregon samples composed of fish 4-yr-old and older were considered to be representative of the population in those areas. There is a smaller percentage of 4-yr-olds and a greater percentage of 5- and 6-yr-olds in the Oregon sample than in the California sample. Similarly, the Washington sample contains a much smaller percentage of 4-yr-olds and a greater percentage of nearly all the older age groups than does the Oregon sample. It cannot be clearly demonstrated whether there are in fact fewer 4-yr-olds in the hake population off Washington or whether additional older specimens are recruited, depressing the relative abundance of the 4-yr-olds. However, since 3-yr-old hake are not recruited to the Washington fishery and it is difficult to rationalize the sudden occurrence of additional large numbers of older, adult fish not found off Oregon and California, the most likely event is that the 4-yr-olds are only partially recruited off Washington and are not as numerous as they are off Oregon.

In May, July, and October 1965 and in August 1966, samples were available from off the Washington coast from lat. 46°00′N to 48°59′N. For each year the samples were grouped by half degree intervals of latitude and compared in Figure 8 to determine if changes in age composition among smaller spatial units than used in the foregoing discussion could be detected. The 1965 samples were collected during a period of several months but, as indicated in a previous section, seasonal (spring-fall) variation should not be a significant factor. Although there is considerable random variation in the relative abundance of an age group among areas, there appear to be some

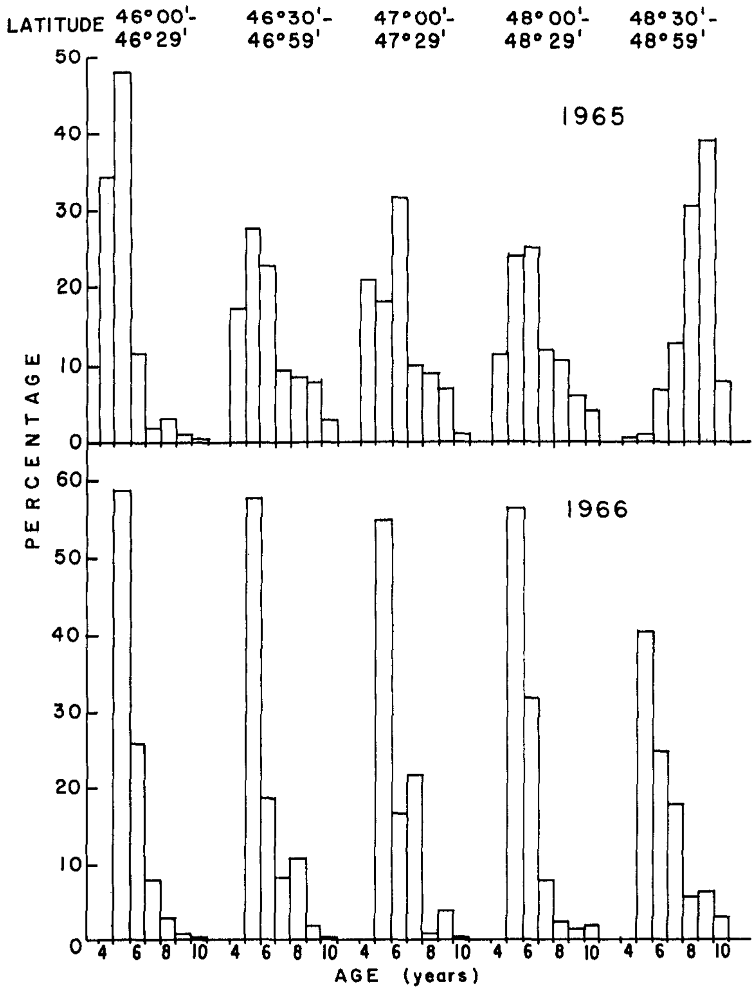

FIGURE 8.—Age composition of Pacific hake taken at various latitudes off Washington in 1965-66.

trends associated with latitude. Generally, the relative abundance of 4- and 5-yr-olds tended to decrease as sampling progressed from south to north while the relative abundance of 7- to 10-yr-olds tended to increase. This is consistent with observations over a larger sampling area.

In summary, 1-, 2-, and 3-yr-old Pacific hake are rarely encountered north of California and, as sampling progresses northward along the Washington coast, the younger age groups (4- and 5-yr-olds) contribute less to the population while the relative abundance of the older age groups (7- to 10-yr-olds) increases.

Such latitudinal stratification of age groups, apparently occurring to some extent even within 3 degrees of latitude, compounds the problem of representatively sampling the age composition of not only the entire hake population, but also the commercially available portion of the population. This spatial variation should be considered when comparing annual changes in age composition.

Sexual Variation

Pacific hake samples taken off Washington in 1965-69 were used to examine the variation in age composition between male and female components. The percentage of each sex by age group was calculated (Table 2) and plotted in Figure 9. The age compositions for males and females are similar in all years. The greatest difference occurred in 1965 when females contributed a larger proportion of the 4-yr-old group. In all years, a greater percentage of the females occurred in the older age groups (8 yr and older). These results correspond well with earlier observations (Best 1963; Tillman 1968) that females live longer and may be the sole survivors by age 11 and 12. Therefore sampling that is highly selective for sex would provide biased estimates of the relative abundance of older age groups.

GROWTH OF PACIFIC HAKE

Growth in Length

To determine the general shape of the growth curve for Pacific hake, average lengths-at-age by sex were computed using combined data from samples taken off Washington, Oregon, and California during 1965-69 (Table 3).

Growth of both sexes is quite rapid during the first 3 yr, then slows abruptly (Figure 10). Deceleration of the growth rate probably is not as pronounced as indicated. Latitudinal stratification of ages discussed previously is probably a result of stratification by size; therefore, mainly the larger members of the younger age groups would be recruited to the Washington-Oregon area where most samples were collected. Best (1963), for instance, computed the average lengths for small samples of hake (age groups 4-13 consisted of females only) taken off northern California and the 3- to 6-yr-olds were somewhat shorter than those in the Washington-Oregon samples (Figure 10). The most accurate growth curve for 2- to 6-yr-olds would probably fall somewhere between that based on Best's (1963) data and the curves generated from my data. Asymptotic growth has been shown for Cape hake, *M. capensis* (Botha 1969); silver hake (Fritz 1962); and Pacific hake in Puget Sound (see footnote 3). For the purpose of this study it is assumed that the growth curve for the length of coastal Pacific hake is also asymptotic.

Sexual differences in the size at age occur in most hake species (Hickling 1933; Hart 1948; Fritz 1962; Botha 1969), and the Pacific hake is no exception (Figure 10). Females are noticeably longer by age 4, but may be longer even at an earlier age. Larkins et al. (see footnote 3) reported that female Pacific hake of the Puget Sound population are slightly longer than males even as 1-yr-olds. This cannot be demonstrated for coastal hake because sex information was not available for 1-yr-olds and so few 2- to 3-yr-olds were collected that one cannot accept the estimated mean lengths by sex with confidence. Although sexual differences in growth exist, these differences are not large. The maximum difference in mean lengths is 3.12 cm occurring at 11 yr of age (Table 3).

Year class variation with respect to growth was examined by two means: 1) the comparison of age-length data collected in 1965-69, and 2) the back-calculation and comparison of growth rates for five year classes.

Mean body lengths by age for the 1956-62 year classes are found in Table 4 and compared in Figure 11. Only samples taken off the Washington coast were used so that successive year classes could be compared while minimizing any spatial effects. These growth curves generally fall into two sets. Individuals of the 1956-59 year classes were considerably larger at age than the members of the 1961-64 year classes. The growth curve for the 1960 year class falls between the two sets.

TABLE 2.—Age composition (percentage) of male and female hake taken each year off Washington, 1965-69.

Age (years)	1965 Male	1965 Female	1966 Male	1966 Female	1967 Male	1967 Female	1968 Male	1968 Female	1969 Male	1969 Female
2	—	—	0.1	—	0.1	0.1	—	—	—	—
3	—	—	0.1	0.1	1.4	1.2	—	—	—	—
4	13.0	22.5	0.3	0.3	1.6	2.6	1.4	2.5	0.1	0.2
5	28.9	20.6	44.2	46.0	5.2	4.5	1.9	2.9	6.9	9.0
6	27.2	23.8	33.1	23.7	62.1	53.6	11.5	7.0	16.6	18.5
7	13.5	5.2	14.5	15.9	22.2	19.7	68.6	60.3	55.7	41.3
8	12.9	10.6	3.1	6.7	5.4	10.2	13.3	17.2	19.7	28.2
9	3.0	10.3	3.2	3.3	1.2	4.8	2.3	4.8	1.0	2.5
10	1.4	4.9	0.7	1.8	0.6	2.2	0.9	3.2	—	0.1
11	—	1.4	0.7	1.5	0.1	0.9	0.2	1.4	—	0.1
12	—	0.6	—	0.5	0.1	0.2	—	0.4	—	—
13	—	—	—	0.1	—	—	—	0.3	—	—
Sample size	1,474	2,196	1,355	1,724	1,195	1,432	1,047	1,546	1,009	811

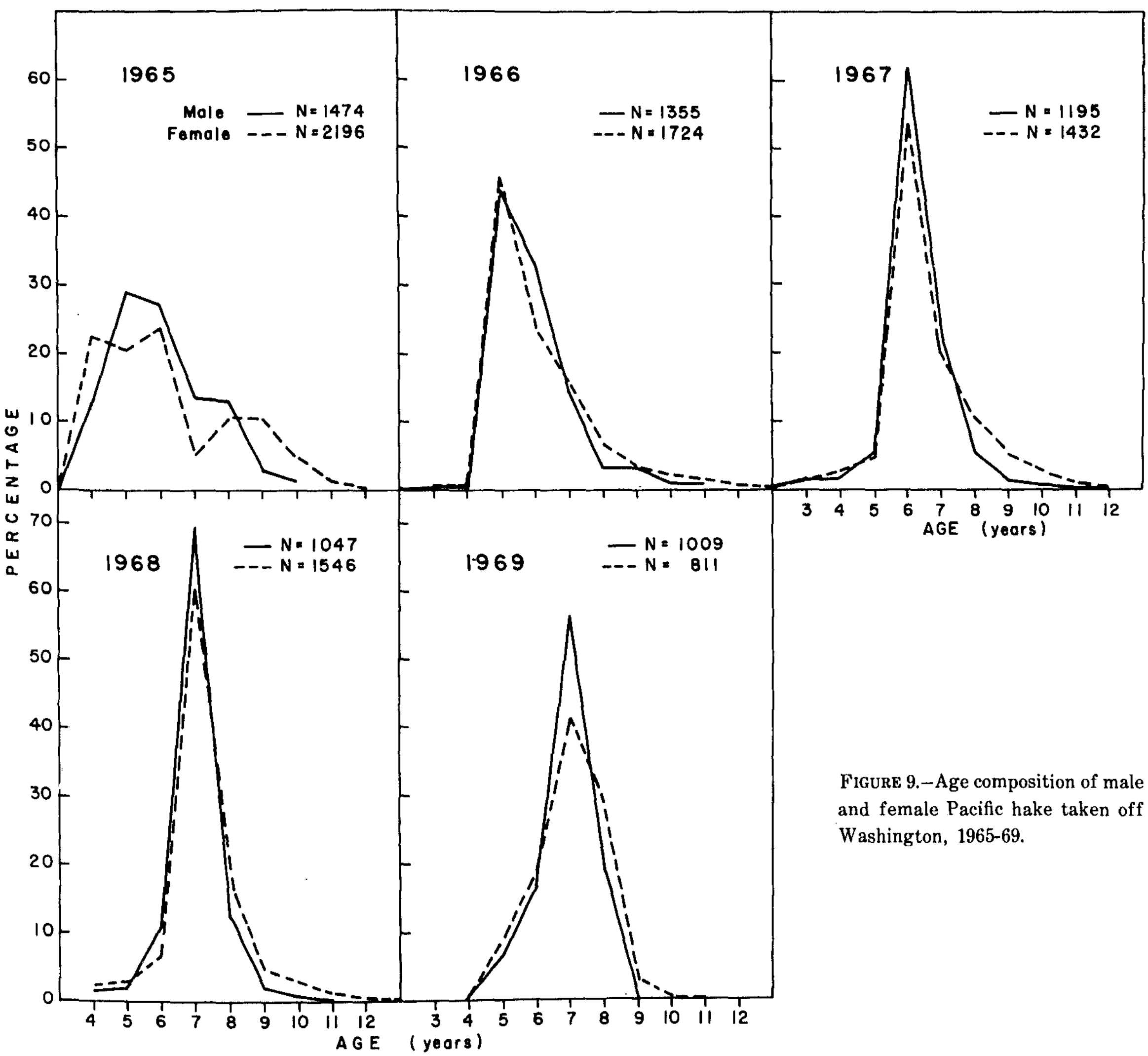

FIGURE 9.—Age composition of male and female Pacific hake taken off Washington, 1965-69.

TABLE 3.—Average body length at various ages for male and female hake taken off California, Oregon, and Washington during 1965-69.

Age (years)	Female: Sample size	Female: Mean length (cm)	Male: Sample size	Male: Mean length (cm)
1.0	385	[1]15.40	385	[1]15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	—	—
13.3	6	61.83	—	—
	[2]4,453		[2]4,201	

[1]Assigned value based on the mean of all 1-yr-old hake; sex determinations were not available for 1-yr-olds.
[2]Does not include the unsexed 1-yr-old group.

While there is little variation apparent within year class groups, length at age may vary by as much as 4 cm between year class groups.

These data suggest that some variation in growth can occur among year classes, but the irregular sampling of all ages, particularly the youngest, precludes construction of complete growth curves by year class using length-at-age data. Therefore a back-calculation technique was utilized to reconstruct the growth curves for several year classes as a means of further examining year-class variation.

Back calculation of body lengths was based on an otolith radius-body length relationship derived from hake samples collected in 1966-68. Approximately 10 otoliths (5 male and 5 female) per 1-cm body length interval were selected for

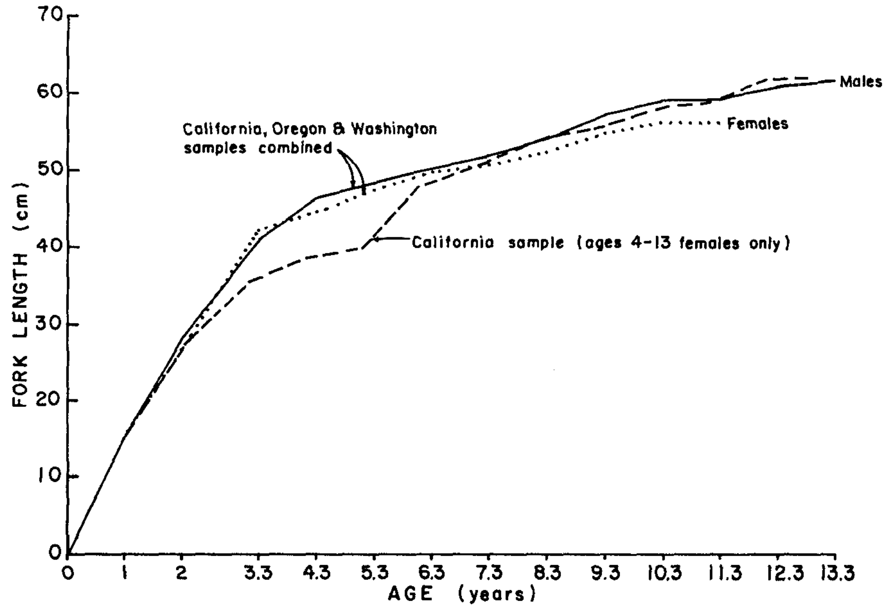

FIGURE 10.—Average fork lengths at various ages for Pacific hake collected off California, Oregon, and Washington combined, and from California alone (Best 1963).

TABLE 4.—Mean body length (cm) at various ages (in years) for 1956-62 year classes of hake.

1956: Age	1956: Length	1957: Age	1957: Length	1958: Age	1958: Length	1959: Age	1959: Length	1960: Age	1960: Length	1961: Age	1961: Length	1962: Age	1962: Length
—	—	—	—	—	—	—	—	—	—	—	—	3.0	35.6
—	—	—	—	—	—	—	—	—	—	4.3	44.9	4.5	47.8
—	—	—	—	—	—	5.7	52.5	5.3	48.9	5.5	48.2	5.3	48.7
—	—	—	—	6.7	53.9	6.3	52.6	6.5	51.6	6.3	49.2	6.3	49.7
—	—	7.7	54.2	7.3	53.9	7.5	54.8	7.3	53.2	7.3	50.6	7.5	50.6
8.7	54.9	8.3	55.2	8.5	56.1	8.3	55.9	8.3	54.1	8.5	51.8	—	—
9.3	57.4	9.5	56.8	9.3	56.5	9.3	56.6	9.5	54.2	—	—	—	—
10.5	57.8	10.3	59.7	10.3	58.2	10.5	57.0	—	—	—	—	—	—
11.3	58.7	11.3	58.0	11.5	60.0	—	—	—	—	—	—	—	—
12.3	60.0	—	—	—	—	—	—	—	—	—	—	—	—

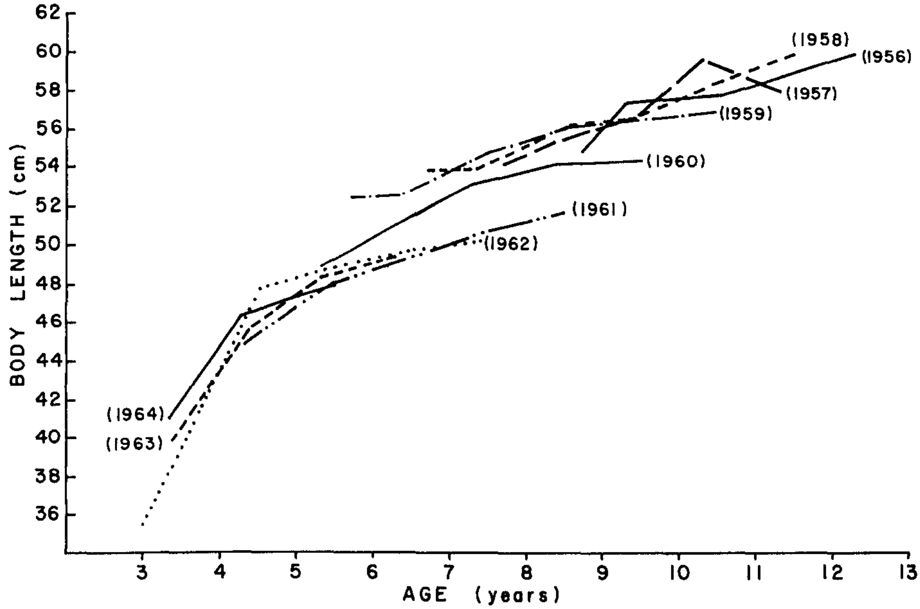

FIGURE 11.–Average fork lengths at various ages by year class (in parentheses) for Pacific hake taken off Washington, 1964-69.

analysis. A sample of 10 was not attained in those centimeter groups near the extremes of the length distribution nor in those length groups where 10 samples were taken but not all otoliths were readable. Fork lengths represented ranged from 11 to 68 cm. To facilitate the measuring all otoliths were photographed and enlargements made so that the prints were 16 times the size of the otoliths. Measurements were taken directly from each print. A midpoint was determined on the photograph of each otolith by measuring the distance from the anterior edge to the posterior edge of the first translucent zone and halving that measurement (Figure 12). Measurements were made from this midpoint to the anterior margin of each annulus and to the anterior edge of the otolith. When annuli were not clearly defined, measurements were not made.

The mean body length per centimeter of otolith radius was computed and plotted in Figure 13. A curve constructed from the individual observations ($n = 370$) is superimposed on the means. The curve was constructed from a third degree polynomial equation of the form $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$, where Y = estimated body length and X = otolith radius. This equation provided the best fit (smallest residual sum of squares and mean square) of the several functions examined (Table 5). The correlation

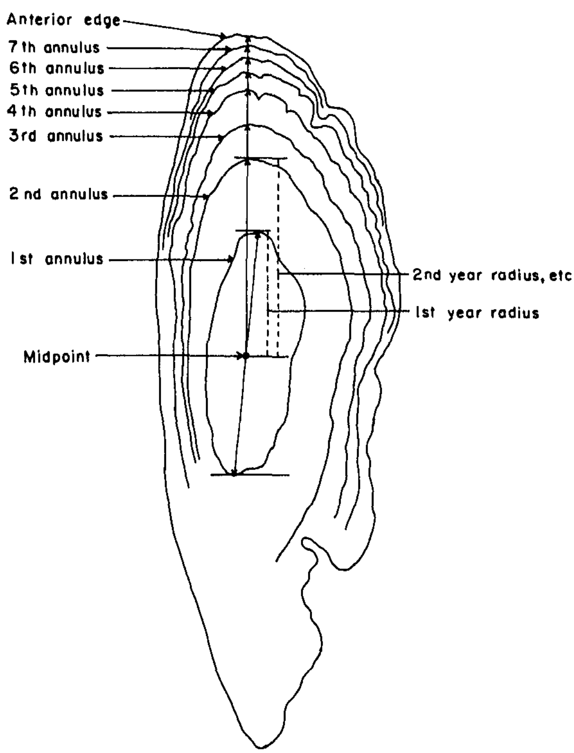

FIGURE 12.–Pacific hake otolith showing the calculated midpoint and measurement intervals from the midpoint to the anterior margins of successive annuli.

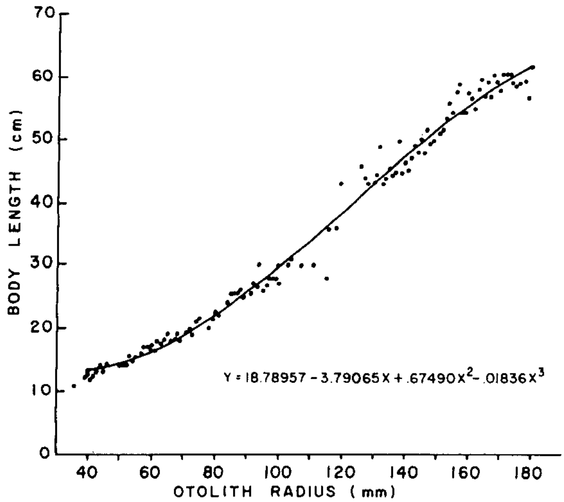

FIGURE 13.—A scattergram of mean body lengths per millimeter of otolith radius (as taken from a 16× photographic enlargement) and superimposed curve of the function used to back-calculate growth.

TABLE 5.—Functions examined for the best fit of otolith radius–body length data, corresponding residual sums of squares, and mean squares.

Function	Residual sum of squares	Mean square
$y = a + bx$	3,865	10.44
$y = a + bx + cx^2$	3,700	10.03
$y = a + bx + cx^2 + dx^3$	3,146	8.55
$y = ab^x$	7,611	20.57
$y = e^a x^b$	3,768	10.18

between estimated and observed values is 0.9860, so an improved fit was not attempted. The Y intercept is at 18.78957 cm indicating that the function does not adequately represent the otolith radius-body length relationship in fish less than 1 yr of age. Therefore the back calculation of body lengths beyond the range of the data fitted is obviously not meaningful.

The mean total otolith radii by age were used to back calculate lengths at age which are presented in Table 6 and compared in Figure 14 with observed lengths at age from combined 1965-69 samples. The atypical 1961 year class was excluded in this comparison. In spite of a certain amount of variation in the back-calculated curve (probably induced by the small sample size), the two curves correspond very well.

The lengths-at-age for five year classes (1957-61) were compared by back calculating the lengths of approximately equal numbers of males and females from each year class. Because there is some evidence in Table 7 that the radii of the first one or two annual marks increase as the total age increases, only otoliths from 7-yr-olds were used to avoid any possible age-related effects. Older specimens could not be used because they were not available in sufficient numbers and younger specimens had a growth history which was too brief. Fifteen otoliths of each sex for each of the 5 yr were selected. The desired sample size (30 per year class) was seldom obtained because many of the otoliths had deteriorated in storage so that opaque and hyaline zones could not be distinguished on the photographs.

Back-calculated lengths are presented in Table 8, and a comparison of back-calculated growth curves for the five year classes is made in Figure 15. It appears that year class variation was not great among the 1957-60 year classes, but that the members of the 1961 year class were on the average noticeably smaller at age than members of the other year classes. This latter observation

TABLE 6.—Mean otolith radii and back-calculated body lengths at various ages for Pacific hake.

Age (years)	Mean otolith radii (cm)	Calculated body lengths (cm)
1	6.08	16.57
2	9.06	26.19
3	12.53	41.13
4	13.50	45.44
5	13.60	45.88
6	14.43	49.45
7	14.80	51.00
8	16.44	57.30
9	15.79	54.92
10	17.29	60.11
11	17.74	61.44
12	18.30	62.92
13	17.90	61.88

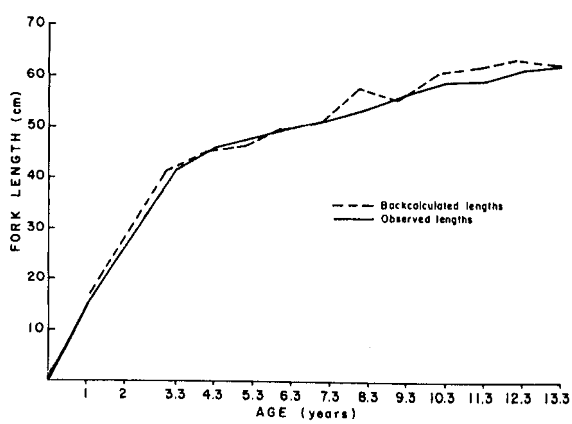

FIGURE 14.—A comparison of growth curves as constructed from observed and backcalculated fork lengths at various ages.

TABLE 7.—Mean radii (cm) of photographed otolith annuli by total age group.

Total age (years)	Annuli 1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th
1	5.96	—	—	—	—	—	—	—	—	—	—	—	—
2	5.85	8.87	—	—	—	—	—	—	—	—	—	—	—
3	7.10	10.13	12.53	—	—	—	—	—	—	—	—	—	—
4	6.34	9.73	11.66	13.13	—	—	—	—	—	—	—	—	—
5	6.57	10.03	11.50	12.87	13.57	—	—	—	—	—	—	—	—
6	6.38	9.73	11.51	12.79	13.79	14.32	—	—	—	—	—	—	—
7	6.16	9.59	11.60	12.97	13.89	14.37	14.71	—	—	—	—	—	—
8	6.18	9.86	12.02	13.63	14.90	15.61	16.15	16.50	—	—	—	—	—
9	6.33	9.80	11.56	12.89	14.05	14.53	14.94	15.39	15.66	—	—	—	—
10	6.44	9.92	11.65	13.39	14.57	15.66	16.21	16.73	17.14	17.50	—	—	—
11	6.60	9.84	11.38	13.08	14.42	15.52	16.00	16.54	16.94	17.36	17.66	—	—
12	6.75	10.85	12.75	14.50	15.50	16.10	16.60	17.60	17.90	18.10	18.40	18.60	—
13	7.15	10.45	12.20	13.40	14.35	14.95	15.35	15.75	16.20	16.55	16.90	17.25	17.65

TABLE 8.—Back-calculated body length (cm) at various ages for the 1957-61 year classes of Pacific hake.

Age (years)	Year class and (in parentheses) sample size 1957 (27)	1958 (15)	1959 (22)	1960 (27)	1961 (30)
1	19.02	18.64	16.45	16.85	16.95
2	31.16	31.01	30.36	29.92	28.50
3	38.71	39.05	38.65	37.11	37.06
4	44.61	40.66	46.09	46.12	43.58
5	49.31	50.14	50.92	50.38	47.60
6	52.28	50.98	53.74	52.65	49.88
7	54.10	54.61	55.51	54.20	51.48

corroborates the slow growth rate of the 1961 year class suggested by the length-age data presented previously. The 1961 year class was an extremely large year class numerically, exceeding by far the size of other year classes of record. Perhaps density-dependent growth was operative in this instance. The size of the 1961 year class may have been so large that the competition for food and space noticeably restricted the growth of individuals. It cannot be ascertained whether the members of smaller year classes might undergo density-dependent growth to a lesser extent or if the phenomenon is triggered only by unusually large year classes.

The von Bertalanffy growth equation is commonly used to describe asymptotic growth. It is used herein because it fits the data well and is readily incorporated in certain yield models. Von Bertalanffy's equation is $l_t = l\infty\ 1\text{-}e^{-k\ (t-t_0)}$, where l_t = body length at time t; $l\infty$ = estimated average maximum body length; k = rate of growth; t_0 = theoretical age when growth conforms to the von Bertalanffy equation. Since sexual differences in growth characteristics exist in Pacific hake, separate curves were fitted to male and female length data. Average length at age data from Table 3 were used to compute the growth curves. In this instance the growth of the 1961 year class was considered atypical and it was excluded from the analysis. A computer program[1] utilizing the method of Stevens (1951) was used to compute the constants for the von Bertalanffy equation. The resulting equations are: $l_t = 56.29\ (1\text{-}e^{-0.39\ (t-0.20)})$ for males and $l_t = 61.23\ (1\text{-}e^{-0.30\ (t-0.01)})$ for females. By comparison, Tillman's (1968) estimates of k were 0.41 for males and 0.19 for females. He reported that treatment of Best's (1963) data also yielded 0.19 for females. In the present study $l\infty$ for both sexes are reasonable estimates of average maximum body lengths. Males as long as 66 cm and females as long as 80 cm have been observed. Growth of Pacific hake is adequately represented by the von Bertalanffy equations as the curves fit the observed lengths-at-age very well (Figure 16). The curves are nearly superimposed until about age 5 when they begin to diverge and continue to do so with age. Although sex-specific growth rates are apparent, the growth rate of the entire Pacific hake population may be best represented by an equation based on data with the sexes combined. The growth equation with sexes combined is $l_t = 60.85\ (1\text{-}e^{-0.30\ (t-0.03)})$.

Growth in Weight

In 1964-69 length and weight data were collected on 2,417 male and 3,117 female Pacific hake taken from Washington to southern California. Lengths and weights were taken from fresh fish as they were unloaded from vessels at the processing plant and from research samples at sea. Fork lengths were taken to the nearest centimeter and weights to the nearest decagram. The majority of

[1]Program developed by George Hirschhorn, Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash.

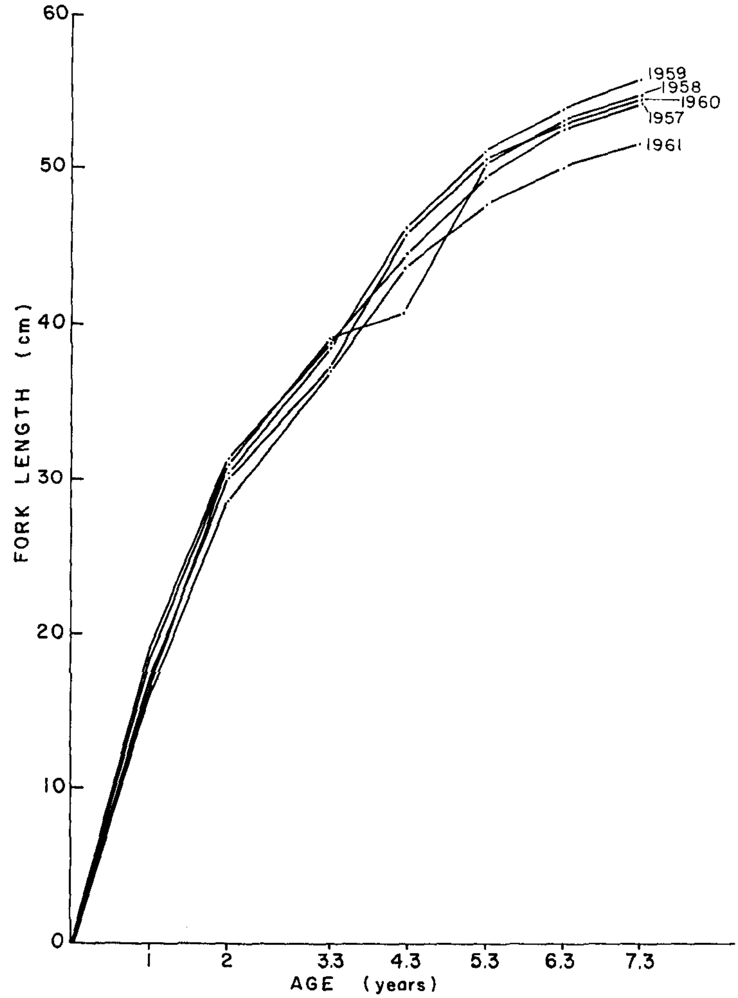

FIGURE 15.–Back-calculated growth curves for 1957-61 year classes. (Only otoliths from 7-yr-old specimens were used.)

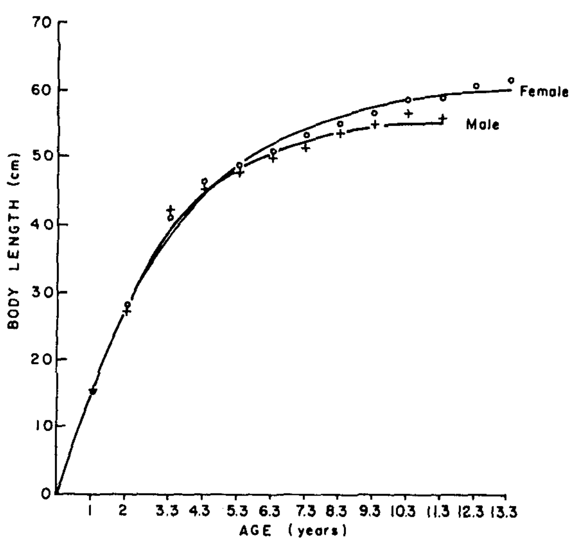

FIGURE 16.–Von Bertalanffy growth curves for male and female Pacific hake superimposed on mean body lengths at various ages. (o = females; + = males.)

observations were made from mature specimens in commercial samples, and therefore hake less than about 40 cm long were inadequately represented or not represented at all. The commercial data were fitted using the length-weight equation $W = aL^b$, where W = weight in grams, L = length in centimeters, and a and b are constants. In linear form this equation becomes $\log W = \log a + b (\log L)$. The length-weight relationships were calculated to be $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females (Figure 17).

Typically the exponent in the length-weight equation for most fusiform fishes approximates 3, implying isometric growth. On the basis of data

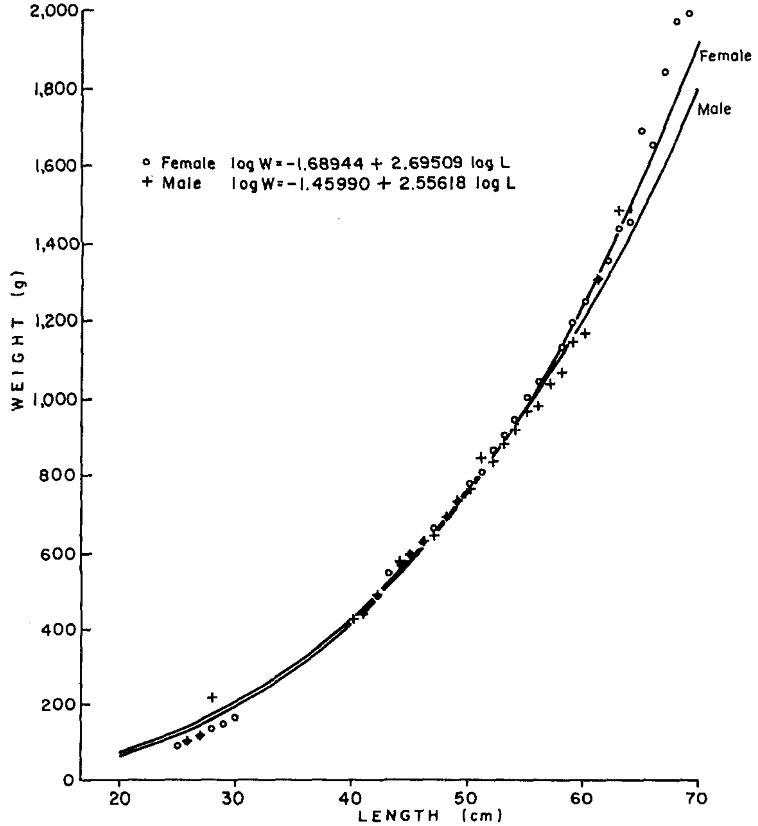

FIGURE 17.–Length-weight curves for male and female Pacific hake superimposed on mean body weights ($n \geq 5$).

from 58 female hake from California ports, Best (1963) estimated the exponent of the length-weight equation to be 3.0668. On the chance that the hake in commercial samples had lost weight between capture and delivery through the loss of body fluids, another pair of equations was fit to less extensive length-weight data taken aboard research vessels off Washington from freshly caught specimens. Student's t-test was used to test the null hypothesis that regression slopes calculated from research and commercial samples did not differ significantly from 3. All tests were significant at the 1% level (Table 9) and the hypothesis was rejected. A possible explanation is that because most specimens are in an immediate postspawning state as they arrive off Washington and Oregon, their weight relative to their length is less than it might be later in the year.

Growth in weight for males and females was calculated from the length-weight equations (Figure 18). These curves suggest that Pacific hake gain weight at an increasing rate until they are 3 yr old. After age 3 the rate of growth in weight decreases and remains roughly constant until death. By age 3, males have grown to approximately 50% of their total weight at 11 yr of age, whereas females by age 3 have attained about 40% of their total weight at 11 yr of age. The growth rates are sex specific and the curves begin to diverge noticeably between ages 3 and 4. At 11 yr of age females weigh on the average about 200 g

TABLE 9.–Results of t-tests to determine if slopes of length-weight regressions calculated from commercial and research samples differ significantly from 3. All comparisons were significant at the 1% level.

Sample type	Sum of deviations from mean (Σx^2)	Variance (Sxy^2)	Slope (b)	Sample size (n)	t
Commercial:					
Male	6.4064	0.0049	2.55618	2,417	16.02
Female	10.5651	0.0032	2.69509	3,117	17.62
Research:					
Male	2.6224	0.0154	2.63189	432	4.80
Female	4.2177	0.0075	2.65436	587	8.20

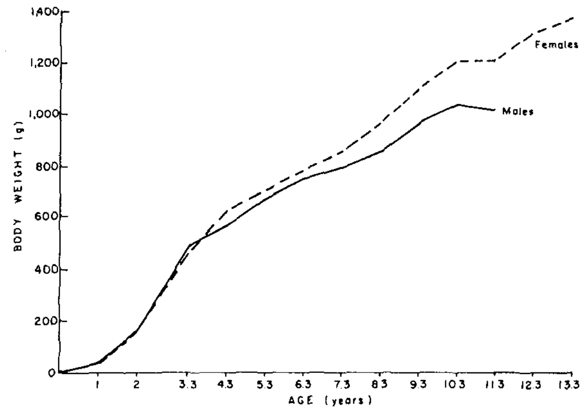

FIGURE 18.—Average body weight at various ages for Pacific hake collected off California, Oregon, and Washington, 1965-69.

more than males. For each sex, Table 10 gives average weight at age values, annual growth rates, and annual instantaneous growth rates, assuming exponential growth in weight.

SUMMARY AND CONCLUSIONS

Biological data from samples of Pacific hake taken in 1964-69 off the coasts of Washington, Oregon, and California were utilized to study the age and growth of the species.

TABLE 10.—Mean weight, annual increase in weight, and instantaneous growth rate at various ages for male and female hake taken off California, Oregon, and Washington, 1964-69.

	Male			Female		
Age (years)	Body weight (g)	Annual increase (%)	Instant. growth rate	Body weight (g)	Annual increase (%)	Instant. growth rate
1	37.6			32.4		
		318	1.43		400	1.61
2	157.0			162.9		
		216	1.15		183	1.04
3.3	496.0			459.5		
		15	0.14		36	0.31
4.3	570.0			626.5		
		18	0.17		13	0.12
5.3	674.6			703.5		
		12	0.11		12	0.11
6.3	751.0			786.2		
		6	0.06		8	0.08
7.3	798.2			853.6		
		7	0.07		13	0.12
8.3	856.8			966.8		
		13	0.12		14	0.13
9.3	964.1			1,102.5		
		8	0.08		9	0.09
10.3	1,040.6			1,207.2		
		0	0.00		0.3	0.00
11.3	1,014.8			1,211.1		
		—	—		8	0.08
12.3	—			1,319.6		
		—	—		4	0.04
13.3	—			1,374.0		
		—	—		—	—

The method of age determination from annuli on otoliths was examined, and all evidence suggests that the method provided reliable age data.

Several sources of variation in the age structure of the population were considered. The relative size of newly recruited year classes varied substantially, creating noticeably annual variation in the age composition. There was no detectable seasonal variation in the age composition of the hake population found off Washington from spring through fall. Latitudinal stratification of hake by age (known to occur over large geographical areas) was further examined, and some variation in age composition was found even among ½ degree intervals of latitude off the Washington coast. The relative abundance of the 4- and 5-yr-olds decreased as sampling progressed northward from the mouth of the Columbia River to the Strait of Juan de Fuca, while the relative abundance of 7- to 10-yr-olds increased. This stratification of ages by latitude supports the theory that there is a northward migration of hake in the early spring along the Pacific coast of North America with the older (larger) individuals tending to migrate farthest. There is little variation in age composition due to sex, except that the longer lived females tend to predominate from 8 to 10 yr of age and are usually the sole survivors at 11-13 yr of age.

Pacific hake grow rapidly in length during their first 3 yr after which growth slows and becomes asymptotic. At about 4 yr of age, females grow noticeably faster and by age 11 may average 3.12 cm longer than males. Individual males may reach 66 cm, while some females may reach 80 cm in length. Year class variation in growth rates was detected by analysis of age-length data and back calculation of growth from otoliths. The equation $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$ was used to describe the relationship of body length (Y) and otolith radius (X).

The extraordinarily large 1961 year class grew at a substantially slower rate than the 1957-60 year classes. This difference possibly is indicative of density-dependent growth. Growth in length can be expressed adequately by the von Bertalanffy growth equations:

$l_t = 56.29\,(1 - e^{-0.39\,(t-0.20)})$ for males,
$l_t = 61.23\,(1 - e^{-0.30\,(t-0.01)})$ for females, and
$l_t = 60.85\,(1 - e^{-0.30\,(t-0.03)})$ for the sexes combined.

Growth in weight was determined by applying the length-weight equations:

$$\log W = -1.45990 + 2.55618 \log L \text{ for males, and}$$
$$\log W = -1.68944 + 2.69509 \log L \text{ for females}$$

to average length-at-age data. By age 3, males have grown to about 50% of their total weight at age 11, and females to about 40% of their total weight at age 11. At 11 yr of age females weigh on the average 200 g more than males. Males attain an average weight of about 1,015 g by age 11 and females reach an average weight of 1,374 g by 13 yr of age.

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