ANNUAL PRODUCTION OF EVISCERATED BODY WEIGHT, FAT, AND GONADS BY PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*, NEAR AUKE BAY, SOUTHEASTERN ALASKA

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ABSTRACT

Pacific herring, *Clupea harengus pallasi*, grow according to the constant-proportion growth model, which requires that yearly growth in body length be a constant proportion of growth during the previous year. Herring have one or two growth stanzas (periods of constant-proportional growth) in the eastern Pacific Ocean and eastern Bering Sea, and grow faster in the eastern Bering Sea than in the northeastern Pacific Ocean.

With growth, total and eviscerated body weights of fresh Auke Bay herring bear an exponential relationship to body length (BL) that is slightly greater than cubic, and evisceration does not lower variability in length-weight relationships. With growth, an increasing part of the annual product (growth plus gonads) is partitioned into gonads so that in the largest fish most of the annual product is gonads. The annual product is constantly proportional to BL through ages 2-6 and also through ages 9-12, but the proportion is considerably smaller in the 9- to 12-yr-old fish. The two differing proportions may indicate that young and old Auke Bay herring occupy slightly different feeding niches and that the trophic environment in the Auke Bay vicinity may not support the older fish as well as the younger.

Pacific herring spawn in April or May in the Auke Bay vicinity, as zooplankton density rapidly increases to its peak in June. The time of spawning seems optimal for rapid building of fat reserves and feeding of newly hatched larvae.

Pacific herring, *Clupea harengus pallasi*, range off western North America, from the Chukchi Sea to San Diego, CA, and have been commercially exploited over the entire range (Rounsefell 1930; McLean and Delaney 1978; Spratt 1981). Pacific herring usually occupy extensive reaches of coast, from tens to hundreds of miles, and populations are particularly dense around the Alexander Archipelago of southeastern Alaska and the archipelago off British Columbia (from charts or fisheries maps in Rounsefell 1930, McLean and Delaney 1978, and Spratt 1981). Yet, even where dense, populations can be locally distinctive in vertebral number and spawning time (Rounsefell and Dahlgren 1935; Hourston 1980).

Pacific herring have been commercially harvested in Alaska since the late 1800's (Rounsefell 1930), principally for reduction to meal and oil. Herring were also pickled, starting in 1900, but the industry never became large and declined in the 1920's. A fishery for Pacific halibut, *Hippoglossus stenolepis*, bait had a similar rise and decline. The reduction fishery ended in the 1960's, and the principal fishery for Pacific herring in Alaska now is sac roe, which is exported to Japan.

The biology of Pacific herring in Alaska has not been thoroughly described. The study by Rounsefell (1930) is the most comprehensive work, and Rounsefell and Dahlgren (1935) separated stocks in southeastern Alaska on the basis of vertebral counts. Skud (1963) analyzed tag returns, and Carlson (1980) described the ecology of Auke Bay herring. Reid (1971) summarized some biological characteristics of herring taken for the reduction fishery from 1929 to 1966.

Because Pacific herring are economically and ecologically important in southeastern Alaska and there is little information on the growth, productivity, and life history of this species in this region, I undertook a 1-yr study of a population in the Auke Bay vicinity (Auke Bay is about 16 km northwest of Juneau). Goals of the study were to compare growth of Pacific herring in the Auke Bay vicinity with growth of Pacific herring from other locales in the eastern Pacific Ocean and relate annual production of fat, gonads, and eviscerated weight in the Auke Bay herring to the annual cycle of food supply.

Pacific herring of the Auke Bay vicinity are one of the innermost and northernmost populations in

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the Alexander Archipelago (Auke Bay is about 80 nmi [148 km] by water from the open coast). Although this population may contain more than one spawning stock, it will be identified with Auke Bay in the present study (local populations spawn within weeks of each other and within a few nautical miles).

METHODS

Auke Bay herring were sampled several times monthly from April 1973 to March 1974; however, no fish were taken in February 1974. The fish were captured principally by jigging with bright hooks or hooks wrapped with colored yarn. Samples were also taken during spring 1973 from nearby locales in southeastern Alaska, including Hood Bay (off Chatham Strait, southwest of Juneau), Carroll Inlet (near Ketchikan), and Katlian Bay (near Sitka), and also from the eastern Bering Sea west of Nunivak Island.

Auke Bay herring were usually examined fresh but sometimes were frozen and examined within 1 wk. Lengths were originally measured as standard lengths (SL, tip of upper jaw to end of hypural bones) but were later converted to body length (BL, tip of lower jaw to end of hypural bones) by multiplying SL by 1.0132, the average ratio in 126 specimens from Auke Bay.

Body lengths were back-calculated from scales taken from above the pectoral fins and posterior to the opercular flap. The calculations followed the proportional method of Whitney and Carlander (1956), which should reduce the variation in BL-scale size relationships because the method adjusts for possible differences in scale length in the same-sized fish. This method requires that the regression between BL and scale length be linear, which was satisfied (Fig. 1). The intercept of the regression (55 mm) was somewhat higher than the median BL (36.5 mm) for first squamation of 16 preserved specimens; however, the differences between estimates for BL at first squamation are probably important only for fish younger than 1 yr. The regression fit the data well for herring ≥ 1 yr old (Fig. 1). I also attempted to reduce variability in the back-calculations for the Auke Bay fish by averaging focus-to-annulus distances from left and right sides of the scales (annuli were as well defined at the sides as in the centerline of the scale), but only a centerline measurement was used in samples from other geographic regions.

After the growth data were analyzed by Walford graphs (Walford 1946), linear regressions (Walford regressions) were fit by least squares to adult sections of constant parameters (stanzas) that were indicated on the graphs. Both the Walford regression and von Bertalanffy formulation are variants of the constant-proportion growth model, which requires that growth in one year be a constant proportion of growth the preceding year (Ricker 1975). (The slope of a Walford regression equals the von Bertalanffy e^{-K}, and the intercept equals $L_\infty(1 - e^{-K})$.)

Annual changes in development of fat and gonads were evaluated by indices that were derived from total body weights, eviscerated body weights, and gonad weights. I estimated unbound water in the eviscerated body tissues and gonads as the percentage weight lost by drying 1 cm wide transverse body sections and entire gonads in a drying oven for more than 4 d at 27°C, a period that yielded weight stability. Visual estimates of visceral fat used a four-point scale (from none to heavy), and visual estimates of maturity used a seven-point scale, as follows (Roman numerals in brackets refer to a similar scale developed by Hay and Outram (1981) for Pacific herring): 1) Newly regenerating [VIII], 2) regenerating [III], 3) nearly mature [IV], 4) ripe [V], 5) ripe and running [VI], 6) partially spawned [VII], and 7) spawned out [VII]. Fresh body, eviscerated, and gonad weights were regressed on body lengths by least squares after logarithmic transformation of variates. Statistical tests were significant when $P < 0.05$.

Scales of Pacific herring from southeastern Alaska and the eastern Bering Sea probably have two annuli in the first growth year. When the annulus nearest to the scale focus of Auke Bay herring was used for back-calculations, the BL's were much smaller (average of 65 mm) for the first winter than the BL's of juvenile herring (at least 80 mm) captured at the end of their first year in Auke Bay by Jones (1978). Pacific herring in British Columbia attain a length of at least 80 mm by their first September (Hourston 1958). Furthermore, when the first annulus was used as the first year mark, Walford graphs of the growth data were erratic and differed markedly from graphs of the same type of data in the literature. When the second annulus was used as the first year mark, the graphs were simple and corresponded to graphs of similar data from the literature.

There was no indication of Lee's phenomenon (slower growth in longer lived individuals) in the back-calculated BL's, but there was evidence of a changing relation between growth back-calculated for ages 1 and 2 and the span of years that was used

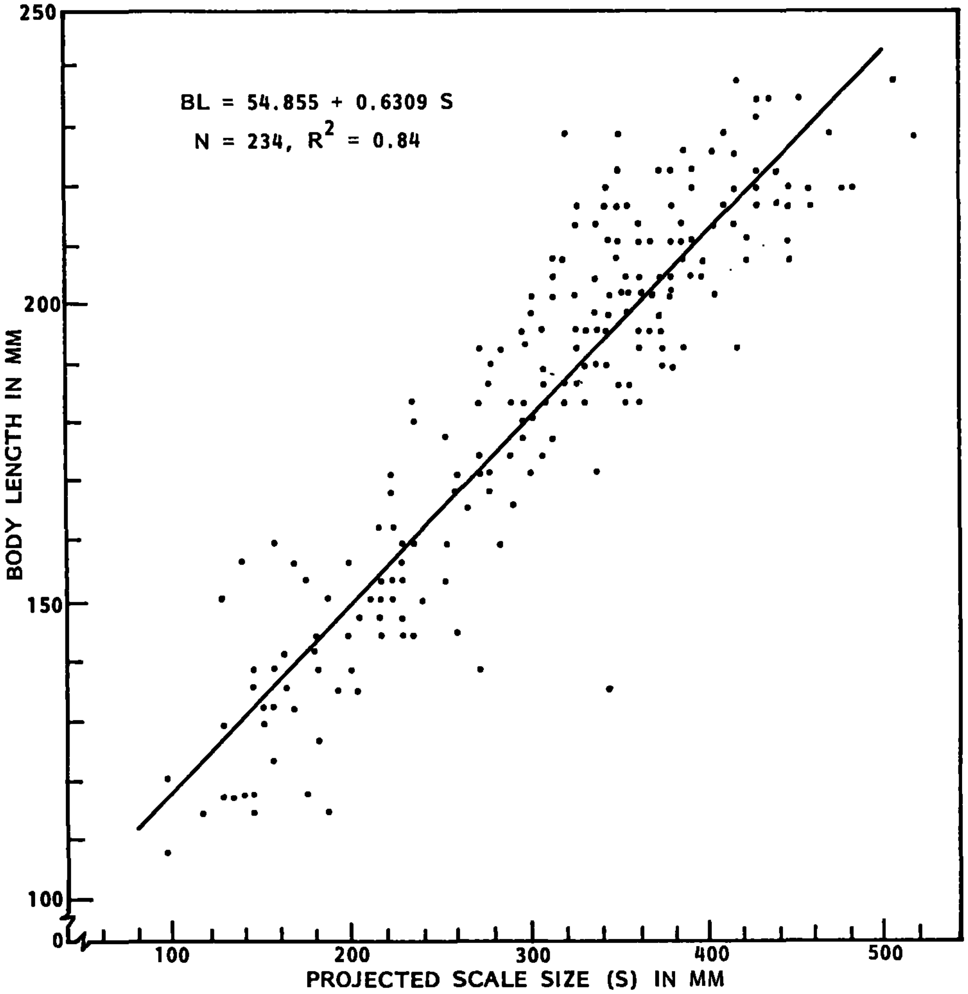

FIGURE 1.—Relationship between body length (BL) and projected scale size (S) of Pacific herring from Auke Bay, AK.

in the back-calculations. When the estimates of growth to ages 1 and 2 were compared for all specimens, those from herring aged 2-4 at time of capture (back-calculated over a span of 0-2 yr) had slower-than-average growth, and those herring aged 4-7 (back-calculated over a span of 3-5 yr) had faster-than-average growth (Fig. 2). Estimates for the oldest herring (back-calculated over a span of ≥6 yr), however, gave mixed results. The trends in fish of 5 yr and younger may have been caused by environmental influences because the trends occur in sets of years (fish aged 2-4, when captured, spent their first or second growth years in 1970-72, and those aged 4-7 spent their first or second growth years principally in 1966-69).

GROWTH

The average size-at-age data in my samples of Pacific herring from the eastern Pacific and eastern Bering Sea and data from the literature for those regions usually formed two stanzas on Walford graphs and inflected at ages 2 or 3 (see Figure 3 for examples). The data for Norwegian and Murman stocks of Atlantic herring, *Clupea harengus harengus*, (Svetovidov 1952) also formed two stanzas and intersected at age 2. Although the stanzas for all of my back-calculated data from the eastern Pacific Ocean intersected at age 2, stanzas for two populations from California (data from Spratt 1981) intersected at age 3, and a plot of Naumenko's

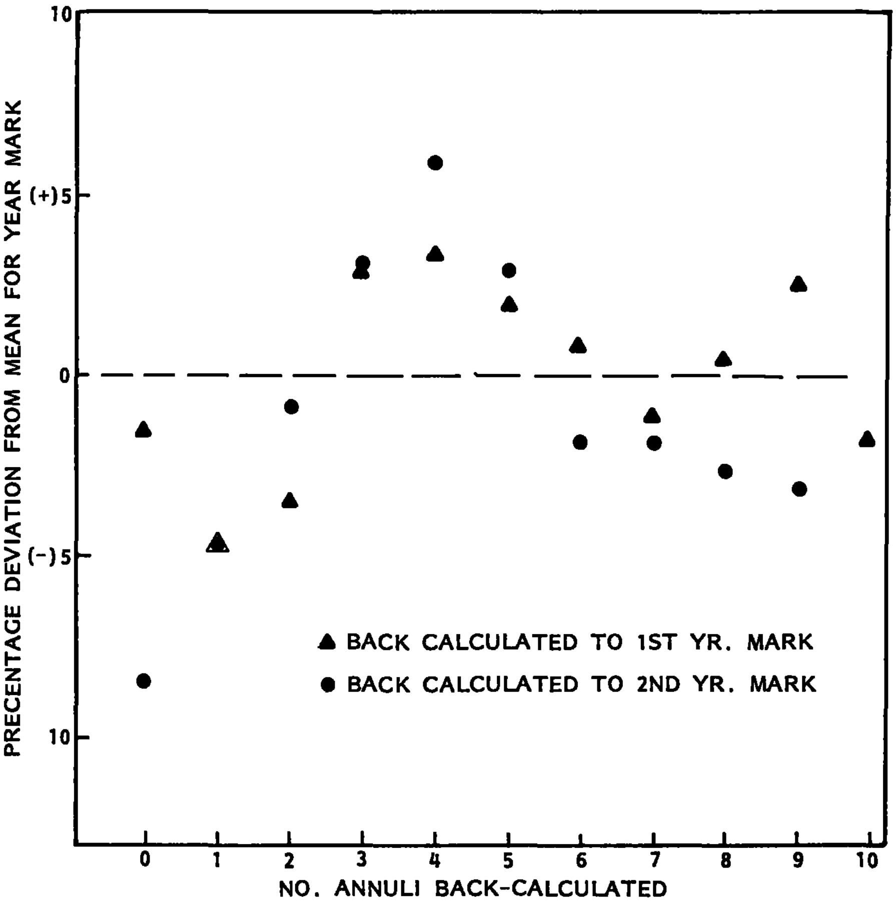

FIGURE 2.—Relationship between extent of back-calculation from scales and the body length estimated at 1 and 2 yr in Pacific herring from Auke Bay, AK. Points indicate the deviation of size estimates for age-1 and age-2 Pacific herring from the average for all annuli (the second annulus was taken as the first year's mark).

(1979) data from the eastern Bering Sea had only one stanza. Regardless of the data source, linear regressions (Walford regressions) closely fit the data in the growth stanzas (Tables 1, 2).

The method of aging Pacific herring can influence estimates of growth. In the data that I examined for this study, adult stanzas based on back-calculated lengths usually had lower slopes than adult stanzas based on terminal-lengths-at age (Table 1). Furthermore, the plots of back-calculated data inflected either at 2 yr or not at all, in contrast to plots of lengths-at-terminal-age, which inflected at 3 yr in three of six examples (Table 1). Important factors, however, remain uncontrolled in this comparison. For instance, the lengths-at-terminal-age from the literature were based on summer sampling; hence, they include additional growth after annulus formation. The lengths-at-terminal-age were from populations near or on the open coast, which may grow faster than populations from protected and possibly less productive waters within the Alexander Archipelago. Furthermore, it is not clear that the Alaskan data for lengths-at-terminal-age used the second scale annulus as the first year's mark.

Walford graphs for Pacific herring from Tomales Bay, CA (data from Spratt 1981), and the eastern Bering Sea (this study) indicated that juvenile growth success and age at inflection (intersection of juvenile and adult stanzas) are more important determinants of adult size at age than either length at year 1 or the slope of the adult stanza, the adult growth proportion (Table 1; Fig. 3). The data indicate that herring from the Bering Sea quickly outgrow those from Tomales Bay although the BL's of the two groups were almost identical at ages 1

TABLE 1.—Growth characteristics and growth parameters of Pacific herring from the northeastern Pacific Ocean and eastern Bering Sea, based on data from the present study and from the literature. Growth is portrayed by the Walford version of the constant-proportion growth model (see text). Because Reid's (1971) data were gathered from a summer fishery, body lengths are longer than they were at the time of annulus formation and may not be comparable to back-calculated data or to lengths-at-terminal-age collected on or near the time of annulus formation. The inflections column refers to the junction of juvenile stanzas with stanzas for adults. Juvenile stanzas on the Walford graphs were fit by eye to sizes at ages 1 and 2, or ages 1-3; adult stanzas were fit by least squares.

Capture location	Size at age 1 (mm)	Inflection at year	Adult stanza			Aging method	Source
			Intercept	Slope	R^2		
Back-calculated lengths:							
Auke Bay vicinity	93.3	2	64.89	0.709	0.998	scales	this study
Hood Bay, Chatham Strait	90.8	2	66.31	0.664	0.995	scales	this study
Katlian Bay	101.5	2	81.50	0.659	0.991	scales	this study
Carroll Inlet	102.7	2	83.61	0.632	0.999	scales	this study
Eastern Bering Sea	112.8	2	79.26	0.727	0.993	scales	this study
Eastern Bering Sea	90.3	?[1]	88.79	0.722	0.999	scales	Naumenko 1979
Lengths-at-terminal-age:							
Auke Bay vicinity	—	2	64.94	0.716	0.983	scales	Blankenbeckler 1979[2]
Prince William Sound, AK	131.4	3	40.60	0.859	0.985	scales	Reid 1971
Kodiak vicinity, AK	132.1	2+	55.99	0.792	0.990	scales	Reid 1971
Southeastern Alaska	145.1	2+	52.14	0.788	0.967	scales	Reid 1971
San Francisco, CA	113	3	44.87	0.816	0.989	otoliths	Spratt 1981
Tomales Bay, CA	113	3	36.95	0.871	0.996	otoliths	Spratt 1981

[1] No inflection apparent.

[2] Blankenbeckler, D. 1978. Age, growth, maturation, and parasite occurrence of Pacific herring (*Clupea pallasi*) from southeastern Alaska, 1974 through 1976. Alaska Dep. Fish Game, Tech. Data Rep. 39, 88 p.

and 2, and the adult stanza was steeper for herring from Tomales Bay. The Bering Sea herring, however, inflected to a steeper slope at age 2 rather than age 3. Environment may not determine the time of inflection in Pacific herring because juveniles both from the Bering Sea and Tomales Bay had similar BL's during the first 2 yr (Fig. 3) although the environments of the locales probably differ greatly.

Weight-Length Relationships

Total weight (W, grams) relates to BL (millimeters) in fresh Pacific herring from the Auke Bay vicinity as $W = (4.4467 \times 10^{-6})\mathrm{BL}^{3.2232}$ ($N = 491$; $R^2 = 0.97$). The lower confidence limit for the exponent exceeds 3.0, and the exponent exceeds 3.0 in reports for herring in most locales; e.g., Pacific herring from Tomales Bay, 2.93 (Spratt 1981); San Francisco Bay, 3.23 (Spratt 1981); the east coast of Vancouver Island, 3.26 (Hart et al. 1940), and Barkley Sound, British Columbia, 3.46 (Hart et al. 1940); and in Atlantic herring, 3.15 and 3.5 (Hart et al. 1940). Many differences between exponents, as cited, may not be biologically significant because weight-length relationships vary seasonally and between sexes, even in eviscerated fish. The exponent for the relationship between BL and total weight probably exceeds 3.0 in healthy herring populations because, as noted in later paragraphs, both eviscerated and gonad fresh weights also have exponents >3.0 when related to BL.

Eviscerated weight of Auke Bay herring also had an exponential relationship to BL that significantly exceeded 3.0 [($W = 5.0894 \times 10^{-6})\mathrm{BL}^{3.16640}$; Fig. 4]. In theory, evisceration avoids large potential weight variations caused by seasonal changes in gonads and fat deposits about the viscera, and variable food content; yet, eviscerated weight ($Sy \cdot x = 0.1030$) was at least as variable a function of BL as total weight ($Sy \cdot x = 0.0953$) in the same specimens, and both total weight and eviscerated weight had the same coefficient of determination (0.97). The lack of decreased variability in the weight of eviscerated herring, as a function of BL, compared with whole fish is evidence that building of visceral fat and gonads does not simply add weight, but rather that some compensatory mechanism may act between these apparent weight sources and the eviscerated body.

In contrast to the results of Hart et al. (1940), Hickling (1940) found markedly low exponents, 2.13 and 2.37, for the relationship between eviscerated weight and BL for Atlantic herring from the North Sea, values that are strikingly lower than those expected for fishes in general. For example, Quast (1968) gave exponents of 2.7-4.5 for 32 species of marine fishes in southeastern California, including 3.9 for the northern anchovy, *Engraulis mordax*. Hickling's exponents may be too low because the

TABLE 2.—Body lengths (BL's) of Pacific herring from the Alexander Archipelago and the eastern Bering Sea, AK. Found lengths are mean BL's at capture (Blankenbeckler's[1] data) or mean back-calculated BL's; fitted lengths are predicted by the constant-proportion growth model (see text) from found lengths. Parentheses indicate sample sizes <5 (found data) or extrapolations with the growth models. Average differences between the fitted and found data (bottom line) were based on absolute values and exclude values in parentheses. For Pacific herring in the Auke Bay vicinity, average differences between fitted lengths based on length at capture (col. 3) and fitted lengths based on back-calculations (col. 5) was 1.96%.

			Back-calculated lengths (mm)									
	Terminal lengths (mm) Auke Bay vicinity		Auke Bay vicinity		Hood Bay, Chatham Strait		Katlian Bay		Carroll Inlet		Eastern Bering Sea	
Age	Found	Fitted	Found	Fitted	Found	Fitted	Found	Fitted	Found	Fitted	Found	Fitted
1	—	—	93.3	—	90.8	—	101.5	—	102.7	—	112.8	—
2	133.0	—	130.8	131.0	125.9	126.6	153.3	152.3	148.5	148.5	163.3	161.3
3	163.6	160.2	159.2	157.8	151.9	150.4	182.6	181.9	176.7	177.5	198.4	196.5
4	176.0	179.6	178.0	176.8	165.6	166.2	196.7	201.4	196.9	195.8	221.4	222.1
5	190.6	193.6	189.5	190.2	175.1	176.6	213.4	214.2	208.9	207.3	236.5	240.7
6	203.7	203.5	198.0	199.8	183.7	183.6	223.6	222.7	214.4	214.6	247.8	254.3
7	211.5	210.7	203.6	206.5	(181.1)	(188.2)	228.7	228.2	219.2	219.3	261.2	264.1
8	215.6	215.8	209.2	211.3	(186.1)	(191.3)	(223.4)	(231.9)	(221.5)	(222.2)	274.2	271.3
9	219.9	219.4	214.5	214.7	—	(193.3)	—	(234.3)	(220.9)	(224.0)	(284.4)	(276.5)
10	220.7	222.0	217.8	217.1	—	(194.7)	—	(235.9)	(223.8)	(225.2)	(288.4)	(280.3)
11	225.4	223.9	221.2	218.8	—	(195.6)	—	(237.0)	(229.0)	(225.9)	(293.0)	(283.0)
12	(213.2)	(225.3)	220.9	220.0	—	(196.2)	—	(237.7)	(248.2)	(226.4)	—	(285.0)
13	(231.7)	(226.2)	(229.3)	(220.9)	—	(196.6)	—	(238.1)	—	(226.7)	—	(286.5)
Average difference (%)	0.86		0.66		0.56		0.73		0.32		1.28	

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[1] Blankenbeckler, D. 1978. Age, growth, maturation and parasite occurrence of Pacific herring (*Clupea pallasi*) from southeastern Alaska, 1974 through 1976. Alaska Dep. Fish and Game Tech. Data Rep. 39, 88 p.

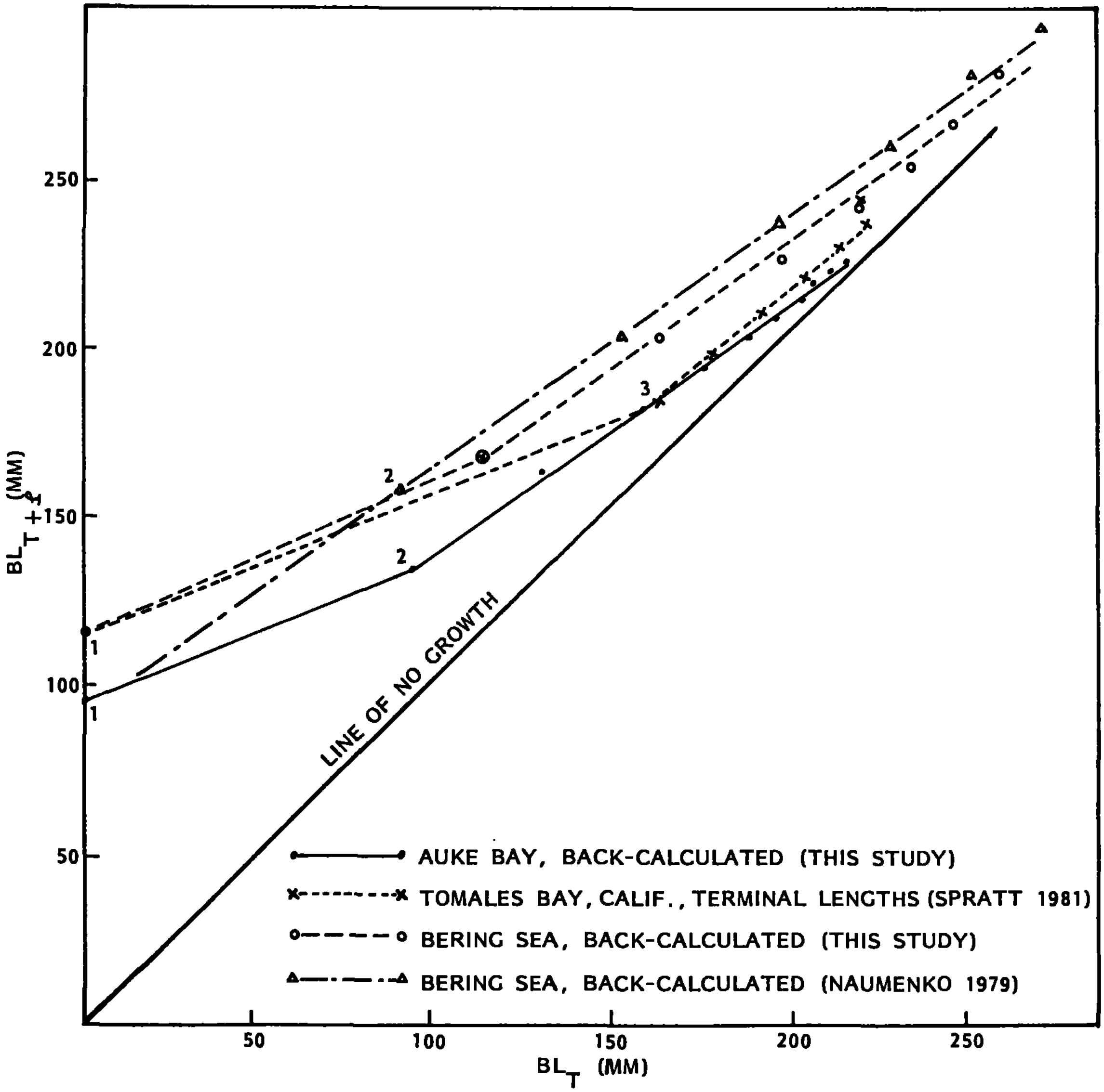

FIGURE 3.—Examples of Walford trends in body length of Pacific herring from widely separated locales in the eastern Pacific Ocean and Bering Sea. Heavy solid line through origin is the line of zero growth, and numbered points indicate ages in years. Adult stanzas were fit by least squares, and the juvenile stanzas were fit by eye. Data from Naumenko (1979) represent 25 yr of collections.

effective range of BL's was limited (near 50 mm) in his data sets and his data were grouped in 10 mm size classes. (In contrast, BL's extended over about 130 mm in the Auke Bay herring, and lengths were taken to 1 mm.)

In Pacific herring, the relationship between eviscerated weight and BL varies with season and sex (Fig. 5), and the relationship for Atlantic herring should vary similarly. Although Hickling (1940) concluded that regressions of eviscerated weight on BL differed by sex in Atlantic herring (W = 0.0661 $BL^{2.312}$ in males, and W = 1.1471 $BL^{1.456}$ in females), his samples probably were too restricted seasonally to estimate reliably the relationship between eviscerated weight and BL for all seasons. Because of seasonal variation in fat content of the musculature (discussed in the next section), data for a single season cannot represent an average over all seasons in Pacific or Atlantic herring of either sex.

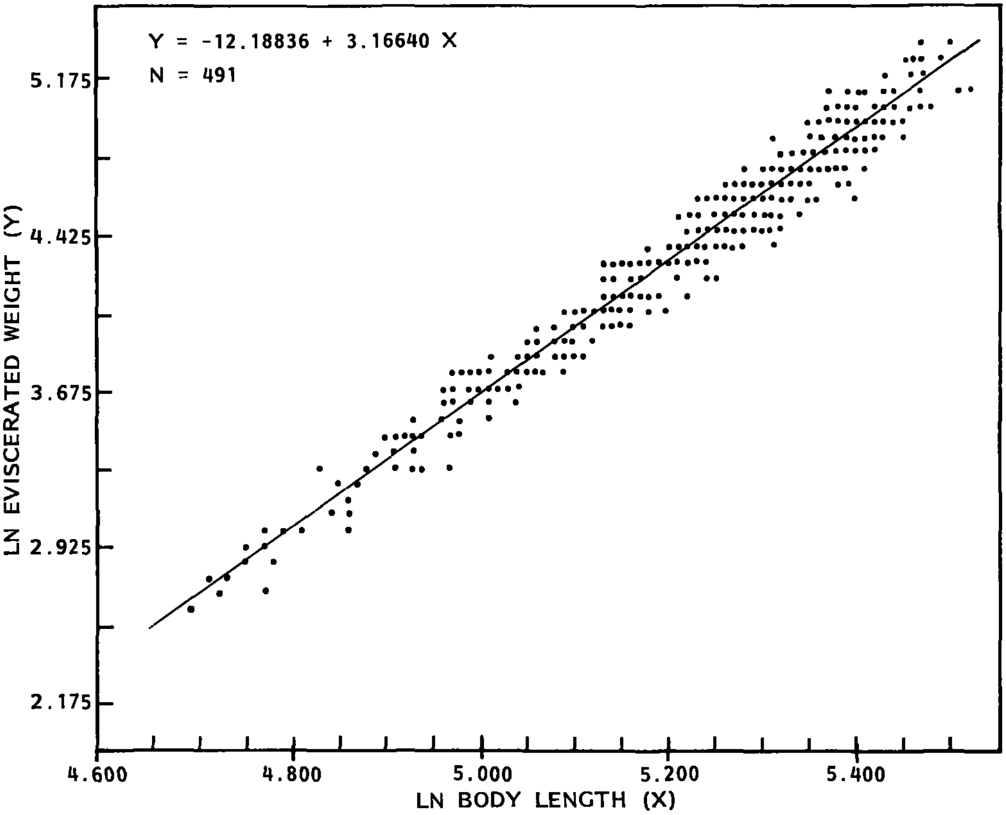

FIGURE 4.—Relationship between body length and eviscerated body weight in fresh Pacific herring in the vicinity of Auke Bay, AK, sexes combined. Variates transformed to their natural logarithms (LN). Points represent 1-9 specimens.

Seasonal Cycles in Fat and Gonads

Adult Pacific herring feed chiefly on zooplankton and small fishes (Hart 1973). In the Auke Bay vicinity, zooplankton peak in abundance in June or July and are virtually absent from November to March (Fig. 6; fig. 3 in Carlson 1980). In an unpublished study of Auke Bay herring, stomachs were mostly empty during late fall and winter (R. E. Haight, cited in Carlson 1980).

Pacific herring spawn in Auke Bay in late April or May but may spawn as late as 4 June (Wing[2]). Eggs hatch 14-20 d after spawning, based on incubation temperatures for herring in British Columbia (Outram 1965[3]) and temperatures for mid-April and May in Auke Bay, which are similar to those for British Columbia (Wing[4]). The time of spawning seems optimal to allow spawned fish and their newly hatched larvae to feed during the heaviest zooplankton concentrations of the year (Fig. 6).

Because the peak in zooplankton abundance is relatively brief, the period immediately after spawning is critical for fattening of adults and for growth and survival of newly hatched larvae. Feeding and fattening of all life stages of Auke Bay herring may also be aided by the submarine illumination afforded by the longest days and highest levels of light, early in the summer.

Fat accumulated about the viscera during the period of maximum zooplankton abundance and reached highest indices shortly afterward, about mid-July (Fig. 6). It then declined rapidly but slightly differently in each sex. There is evidence, also, based

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[2] B. L. Wing, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. November 1981.

[3] Outram, D. N. 1965. Canada's Pacific herring. Dep. Fish. Can., Ottawa, Fish. Res. Board Can., Biol. Stn., Nanaimo, B.C., 23 p.

[4] B. L. Wing, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. July 1983.

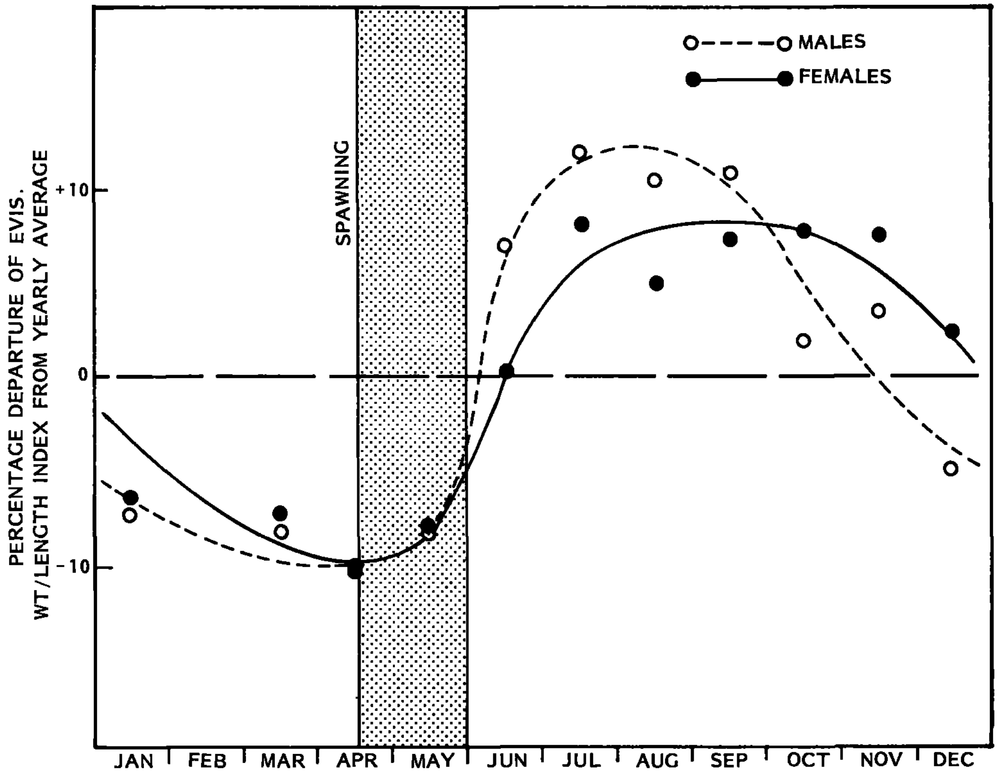


FIGURE 5.—Seasonal variation in eviscerated weight as shown by monthly samples of fresh Pacific herring near Auke Bay, AK, given as percentage departure from the weight predicted by the general eviscerated weight/BL regression for these fish (see Figure 4). The percentage departure is given relative to its yearly average to highlight seasonal changes. Data fit by eye.

on the water content of the musculature, that intramuscular fat varied seasonally and paralleled the development of visceral fat—water content of eviscerated body sections for the sexes behaved in an opposite fashion to visceral fat, being highest in April-May and at low levels between June and October (Table 3). In contrast to the water content of the musculature, eviscerated weight increased relative to BL after May (Fig. 5). If the increase in eviscerated weight were caused by increased somatic hydration, variation in hydration would have paralleled variation in eviscerated weight, but instead, the values for hydration decreased after May. Some other factor must be responsible for the increased eviscerated weights after May, and a likely candidate is fat, because eviscerated weight increased over the same period that visceral fat was building. Hart et al. (1940) also described an apparent reciprocal relationship between water and oil content in Pacific herring from British Columbia, and Love (1970) discussed the same relationship in Atlantic herring and other fish species with fatty tissues.

TABLE 3.—Average hydration of musculature as a percentage of wet weight, by month in Pacific herring from Auke Bay, AK.

	Males		Females	
Month	*N*	Percent	*N*	Percent
January	15	69.2	6	68.4
March	17	71.1	19	71.0
April	26	75.3	25	76.0
May	29	77.0	29	76.0
June	8	61.7	12	66.5
July	8	60.8	12	61.5
August	10	60.7	10	61.1
September	23	61.7	30	62.7
October	12	61.9	18	61.5
November	1	62.6	6	60.6
December	3	65.0	25	63.1

The timing of gonad development, as indicated by seasonal development of gonads, differed in the sexes in Pacific herring from Auke Bay. Males were

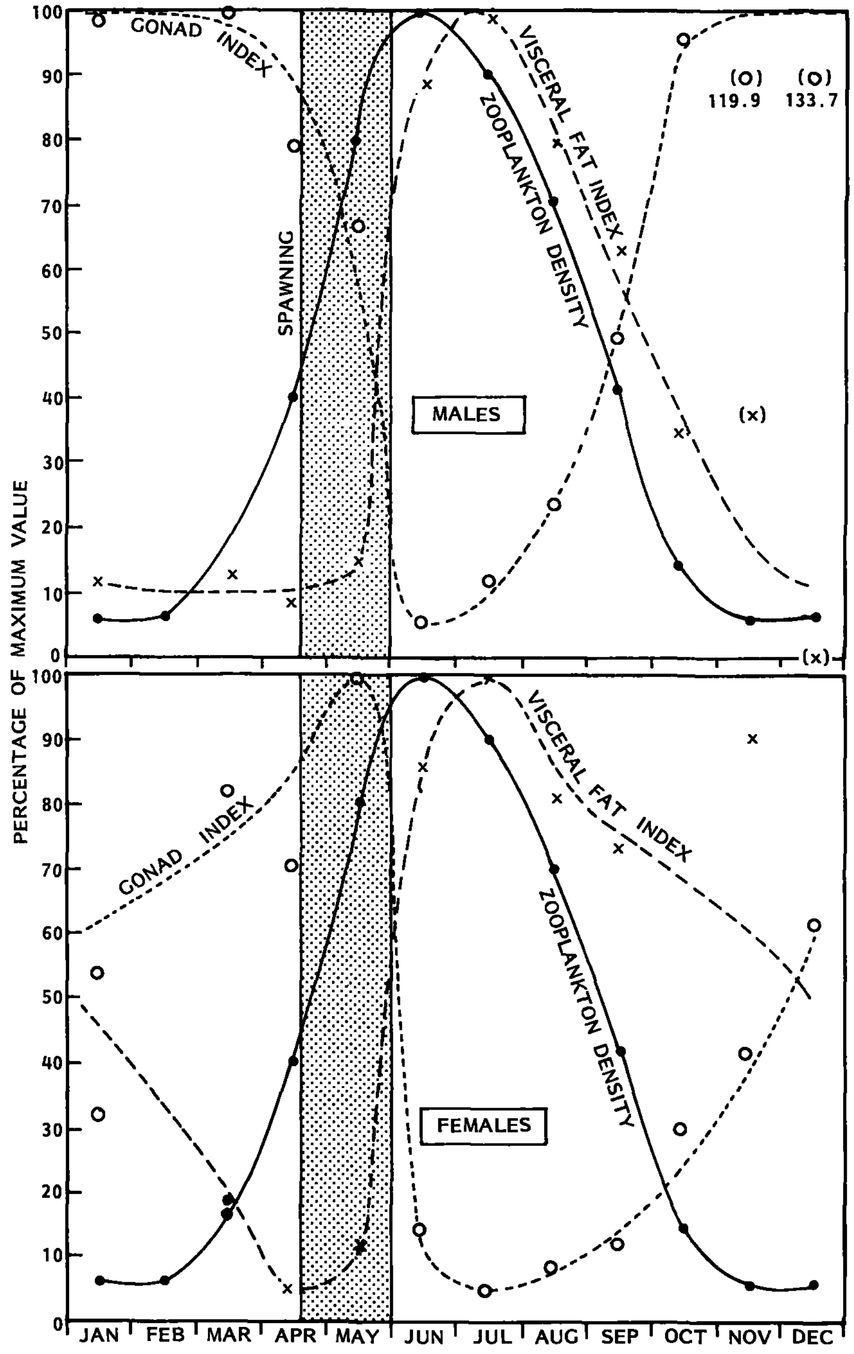


FIGURE 6.—Three annual cycles that relate to the condition of Pacific herring in the vicinity of Auke Bay, AK: A visual index of visceral fat (see text); gonad indices based on (wet) gonad weights as a percentage of the eviscerated (wet) body weights that would be expected at various BL's (see Figure 4); and an annual cycle of zooplankton density, from displacement volumes for 1962-64 given in Wing and Reid (1972). Points based on less than five specimens are enclosed in parentheses. Curves fit by eye.

nearly ready to spawn in November but females delayed readiness until perhaps 4 mo later (Fig. 6), a delay that was confirmed by visual judgments of maturity, see table below (sample size in parentheses):

Percentage of herring judged ripe

	Sept.	*Oct.*	*Nov.-Jan.*	*Mar.*
Males	4(23)	92(12)	95(19)	94(18)
Females	0(31)	11(18)	79(38)	90(20)

These data differ in some important respects from those of Hay and Outram (1981) for Pacific herring in British Columbia. Their gonadosomatic index has sharper peaks in maturity of gonads and different timing of the peaks than the Pacific herring from Auke Bay. For example, in their data, testes were only developing (a low gonadosomatic index) in October (the fish spawned in late February and early March), but testes were near maximum fullness (high index values) in October in herring from Auke Bay (Fig. 6). However, Hay and Outram used total weight in their index. If total weight is used for the index, the divisor will include a considerable weight of fat about the viscera in the fall and negligible weight in the spring, with the result that even if gonad weights remain the same from November to February, the decline in the amount of fat would cause the index to increase. In my study of the Pacific herring in Auke Bay, I divided gonad weight by eviscerated body weight, which should avoid an appreciable error in the gonadosomatic index that would be caused by variation in visceral fat.

Within each sex, seasonal profiles for gonad indices are nearly opposite the profiles for indices of visceral fat (Fig. 6). The annual cycles in fat and gonad indices (Fig. 6) in Pacific herring from Auke Bay resemble those noted by Blaxter and Holliday (1963) for spring spawning in Atlantic herring: "In winter-spring herring the good feeding conditions in late spring and early summer (after spawning) build up the fat reserves. With development of the gonads in late autumn feeding stops and spawning in December-March means that the fish overwinter and spawn with fat reserves considerably lower than the autumn spawners." Visceral fat in male Auke Bay herring is lowest in winter (perhaps as early as November), but in females does not reach lowest values until April. Correspondingly, the testes build rapidly in late summer and fall and appear to be heaviest by October or shortly after, but the ovaries are not at their heaviest until shortly before spawning, in April or May. Hydration is not responsible for sexual differences in development of gonad weight from January to March because, as the following table indicates, hydration remains virtually constant from November to March in both sexes (Table 4).

TABLE 4.—Average hydration of gonads, as a percentage of wet weight, by month in Pacific herring from Auke Bay, AK.

	Males		Females	
Month	*N*	Percent	*N*	Percent
January	14	76.2	5	73.6
March	16	76.1	17	71.3
April	39	82.6	33	84.5
May	24	83.7	24	77.2
June	6	75.5	9	77.7
July	18	73.6	19	76.2
August	25	77.9	21	80.7
September	19	77.6	25	78.6
October	12	76.9	18	74.5
November	1	76.1	6	72.7
December	3	74.2	25	71.2

This seasonal, mirror imagery between development of fat and gonads, with the images differing for sexes, is evidence for a strong physiological coupling between fat depots and gonads. Fat depots enable Pacific herring to accommodate two critical cycles in their life history that are badly out of phase: The zooplankton cycle, with its brief, summer peak that builds fat depots rapidly and is followed by low levels of food abundance from October to March; and the gonad cycle that slowly removes fat from the depots with the slow building of testes from July through October and the slower building of ovaries from July through March.

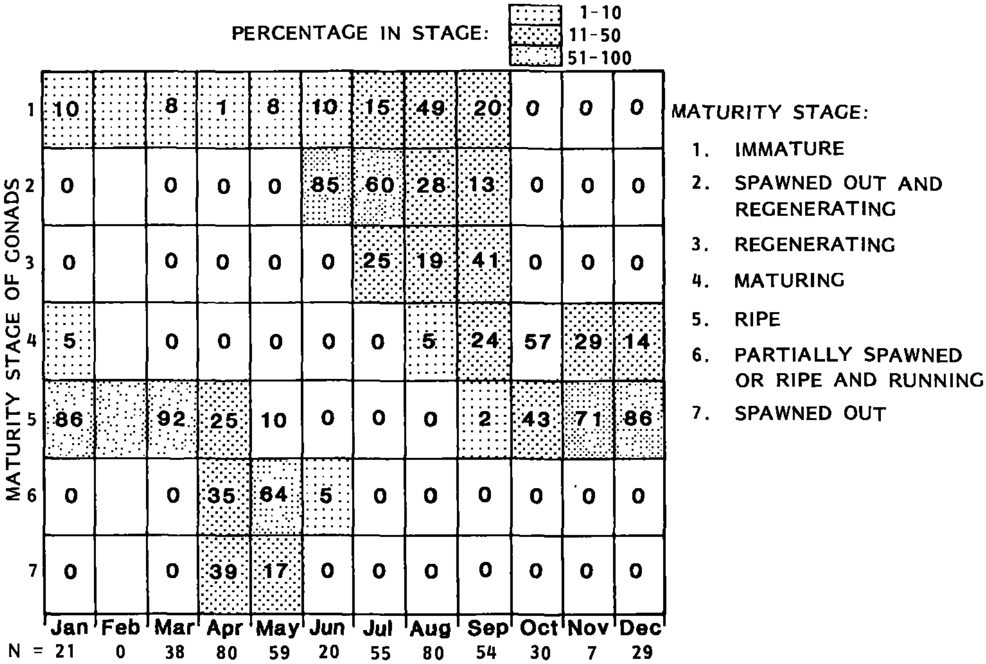
Are the seasonal cycles of gonad maturity in Pacific herring from Auke Bay determined by genetics or are the gonads responding principally to cyclical changes in the immediate environment? Iles (1984) felt that Atlantic herring are remarkably independent of their environment. Genetic control of gonad maturity seems likely except for spawning, which appears to respond to local temperatures (Outram 1965, see footnote 3). Gonads must build well in advance of spawning, and spawning dates vary from November in the southern limits of the eastern Pacific range (Spratt 1981) to June in Auke Bay. Female Auke Bay herring mature sexually and use fat deposits later in the fall than do males and thus anticipate a later spawning date. Male herring in the eastern Pacific Ocean, in contrast, appear to build testes early enough to spawn at any date between November and June. Only the ovarian cycle seems to correspond closely to the local environmental conditions that seem optimal for larval growth and survival. Possibly, the genes that are responsible for local adaptation of spawning stocks are sex linked for females and are selected through larval survival.

Annual Production of Eviscerated Weight and Reproductive Tissues

Although Pacific herring usually have only one major spawning per site in the Auke Bay vicinity, there may be a succession of lesser spawnings each spring. Unspawned fish are rarely seen as late as July (author's observations and comments by salmon fishermen who jig herring for bait). Although Wing (see footnote 2) recorded spawnings in Auke Bay between 24 and 29 April 1973, herring must spawn for at least 2 mo in Auke Bay because some fish sampled in 1973 were partially spawned or ripe and running in May and June (Fig. 7). Presumably, local conditions influence the number of eggs deposited on any date.

The relationship between fecundity, as indicated by mature ovarian weight, and BL was greater than cubic, in agreement with data on other clupeoid species (Blaxter and Hunter 1982). Samples of Auke Bay herring had an exponent of 3.94 (Fig. 8), within the range (3.07-4.50) for Atlantic herring as given by Paulson and Smith (1977), from the literature. These authors gave an exponent of 3.32 for Pacific herring they sampled in Prince William Sound. Perhaps, the exponent for fecundity would have been higher for the herring Paulson and Smith sampled in Prince William Sound had their collections included smaller fish (their smallest were near 180 mm long, but fish as small as 130 mm were available in samples from Auke Bay). The exponent for testicular weight was considerably higher than that for ovarian weight in Auke Bay herring (Fig. 8); however, the difference may not be real because the confidence limits for the two exponents overlapped considerably.

The scatter in the plots of gonad and testes weights on BL for Auke Bay herring (Fig. 8) and for Pacific herring from Prince William Sound (fig. 1 in Paulson and Smith 1977) indicate that some of the herring may have been partially spawned when they were collected (fully spawned fish were not used in my data). If samples for fecundity are taken in the spawning season, there is the risk that some



MATURITY STAGE OF GONADS	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	10		8	1	8	10	15	49	20	0	0	0
2	0		0	0	0	85	60	28	13	0	0	0
3	0		0	0	0	0	25	19	41	0	0	0
4	5		0	0	0	0	0	5	24	57	29	14
5	86		92	25	10	0	0	0	2	43	71	86
6	0		0	35	64	5	0	0	0	0	0	0
7	0		0	39	17	0	0	0	0	0	0	0
N =	21	0	38	80	59	20	55	80	54	30	7	29

MATURITY STAGE:

1. IMMATURE
2. SPAWNED OUT AND REGENERATING
3. REGENERATING
4. MATURING
5. RIPE
6. PARTIALLY SPAWNED OR RIPE AND RUNNING
7. SPAWNED OUT

FIGURE 7.—Maturity of Pacific herring near Auke Bay, AK, by month (sexes combined). Numbers in boxes are percentages of herring that were visually classified into maturity stages on examination. Total fish by month are given in the bottom line. Data for February were extrapolated from January and March.

fish will have spawned partially and that fecundity estimates will be too low.

When the relationships between BL, weight, and fecundity in Pacific herring from Auke Bay were used in a model of annual changes in gonad weight and eviscerated weight, production of eviscerated weight decreased rapidly with age or size (Table 5, col. 3). Gonad production (Table 5, col. 4), in contrast, increased yearly but appeared to approach an asymptote at about 31-34 g in the oldest fish. With age, more of the annual product (annual increment in eviscerated weight plus gonad weight) was par-

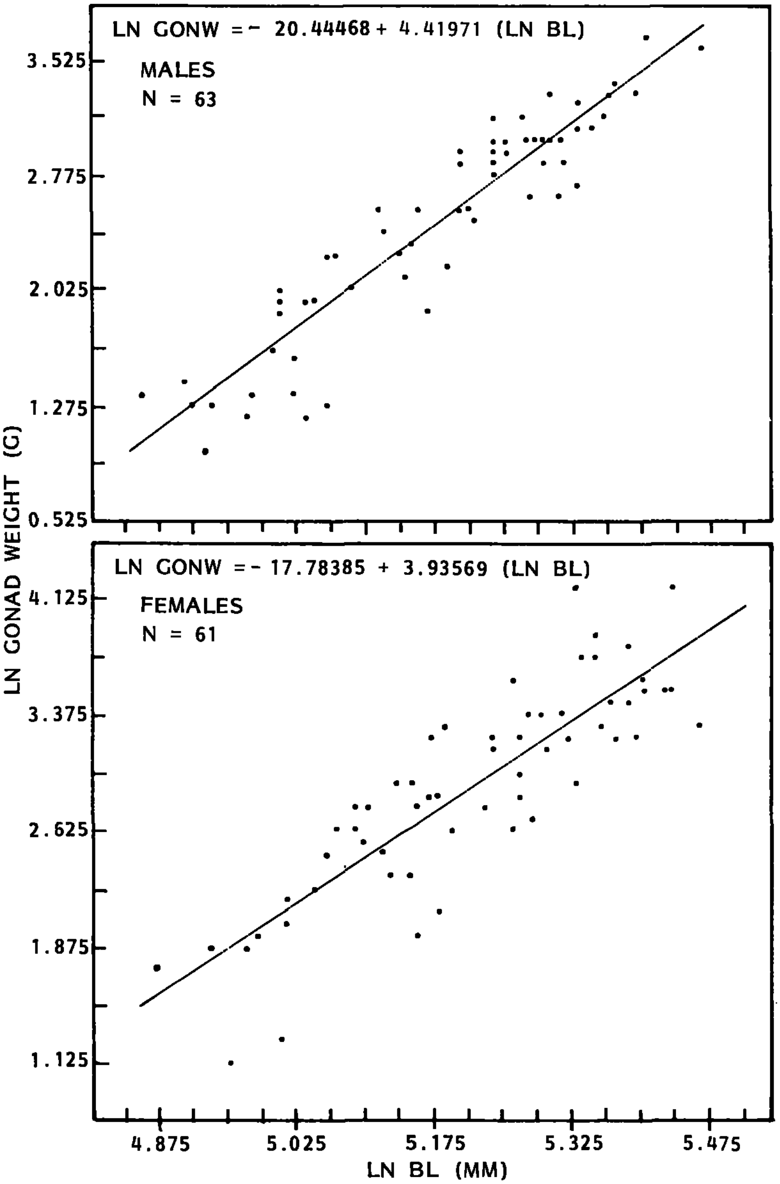


FIGURE 8.—Relationships between (wet) gonad weight (GONW) and BL in fresh Pacific herring collected from March to May 1973 near Auke Bay, AK (variates transformed by natural logarithms (LN). Data (not shown) that formed a separate cluster of points near the abscissa for each sex probably represented spawned fish and were not used in the regressions. Points represent 1-2 specimens.

TABLE 5.—Annual production of (wet) eviscerated weight and gonads in Pacific herring from the vicinity of Auke Bay, Alaska, as estimated from growth, length, and eviscerated-weight relationships, and length and gonad-weight relationships (Table 1, Figs. 4, 8). Column numbers are referenced in the text.

Annulus	(1) Fitted BL (mm)	(2) Estimated eviscerated weight (g)	(3) Eviscerated weight increment (g)	(4) Maximum gonad weight March-May		(5) Annual product (gonads plus eviscerated body weight)		(6) Annual product (5) as a percentage of BL the preceding year		(7) Annual product (5) as a percentage of eviscerated weight the preceding year		(8) Gonads as a percentage of annual weight product (5)	
				Males (g)	Females (g)	Males (g)	Females (g)	Males	Females	Males	Females	Males	Females
2	131.0	25.8	—	—	—	—	—	—	—	—	—	—	—
3	157.8	46.4	20.6	6.9	8.3	27.5	28.9	21	22	107	112	25	29
4	176.8	66.5	20.1	11.3	13.2	31.4	33.3	20	21	68	72	34	40
5	190.2	83.9	17.4	15.6	17.7	33.0	35.1	19	20	50	53	47	50
6	199.8	98.0	19.1	19.5	21.4	38.6	40.5	20	21	46	48	50	53
7	206.5	108.8	10.8	22.5	24.4	33.3	35.2	17	18	34	36	68	69
8	211.3	117.0	8.2	24.9	26.7	33.1	34.9	16	17	30	32	75	76
9	214.7	123.1	6.1	26.7	28.4	32.8	34.5	15	16	28	29	81	82
10	217.1	127.5	4.4	28.1	29.7	32.5	34.1	15	16	26	28	86	87
11	218.8	130.7	3.2	29.1	30.6	32.3	33.8	15	16	25	27	90	90
12	220.0	133.0	2.3	29.8	31.3	32.1	33.6	15	15	25	26	93	93

titioned into gonads, which by age 12 composed nearly all of the annual production (Table 5, col. 8). As the herring grew, the annual product was more closely related to BL than to eviscerated body weight (Table 5, cols. 6, 7), evidence that individual herring in the Auke Bay vicinity may use food more in proportion to their BL than their weight. Furthermore, although the relationship between annual product and BL was nearly constant within age groups 3-6 and 8-12 (Table 5, col. 6), productivity was much lower in the 8-12 group. Young Auke Bay herring may be more successful for their size in finding food than are older individuals, because important foods needed by older herring may be scarce in the Auke Bay vicinity, which is about 80 nmi (148 km) by water from the open ocean.

There is indirect evidence from the characteristics of growth and production in Auke Bay herring and growth characteristics of other Pacific herring in the northeastern Pacific Ocean and Bering Sea that not only growth but the annual product relative to herring size and the partitioning of the annual product may vary with the population. If the relationship between eviscerated weight and BL in Auke Bay herring is used with growth data of Pacific herring from other locales in the eastern Pacific Ocean and Bering Sea (Table 1), striking differences are visible in the annual product of eviscerated weight (Fig. 9). For example, if 190 mm herring (3-yr-olds) in the Bering Sea produce gonads in the same proportion to eviscerated weight as 190 mm herring in Auke Bay (5-yr-olds; Table 5, col. 8), gonads and eviscerated weight would each form about one-half of the annual product of Bering Sea herring. However, this proportion would be much too high for herring in Bering Sea during their first year of gonad production, according to the model based on Auke Bay herring, if Bering Sea herring mature as 2- or 3-yr-olds. If production of eviscerated weight and gonads is scheduled according to age, rather than proportion of annual product, similar conflicts result; thus, Pacific herring from different regions probably differ in characteristics for production of eviscerated weight and gonads.

CONCLUSIONS

Pacific herring grow in the eastern Pacific Ocean according to the constant-proportion model; i.e., growth in one year is a constant proportion of the amount grown the previous year. Growth stanzas (regions of constant growth parameters) for juveniles and adults usually inflect near age 2, and the change in growth is probably related to sexual

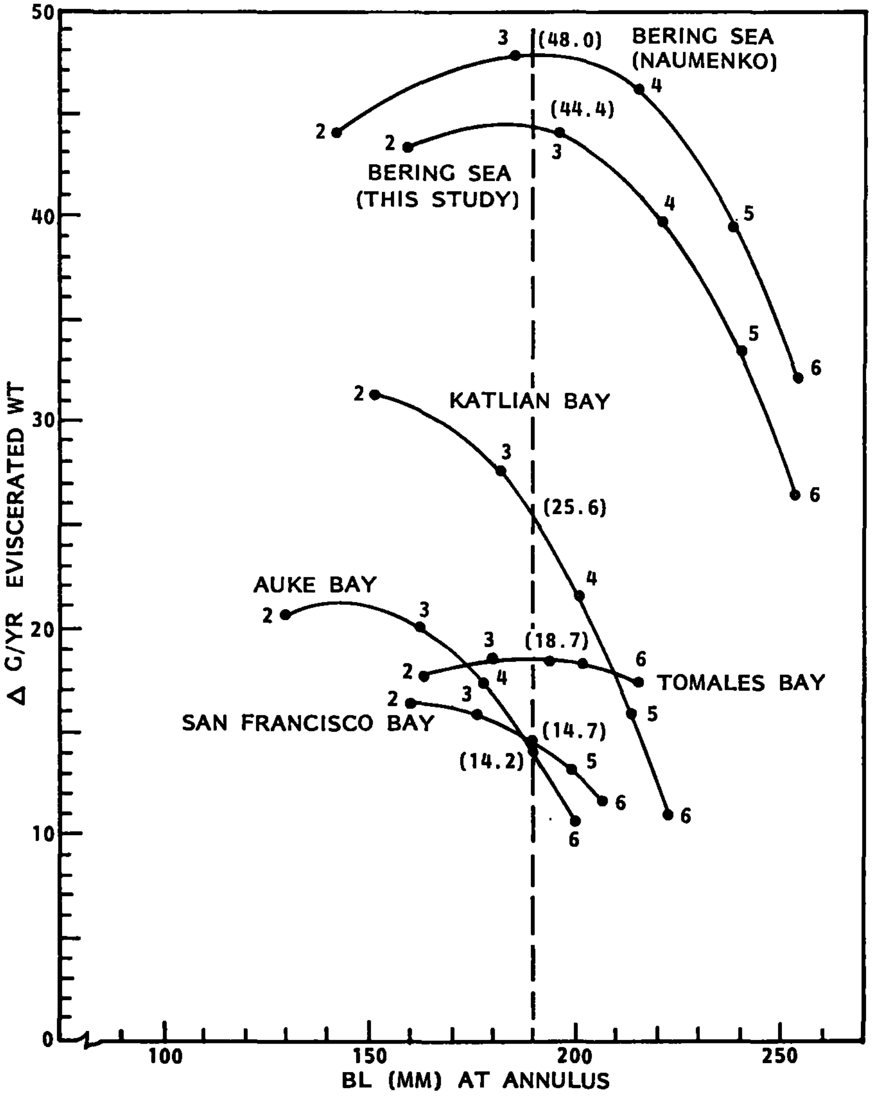


FIGURE 9.—Hypothetical growth in (fresh) eviscerated body weight by Pacific herring at locales in the eastern Pacific Ocean and eastern Bering Sea. Data were based on relationships between eviscerated body weight and BL in samples from the Auke Bay vicinity and data on growth reported in the literature (see Table 1). Numbered points are ages at the beginning of annual growth increments. The dashed vertical line is for comparative purposes and intersects the graphs at 190 mm BL. The second annulus was taken as the first year mark in specimens from Auke Bay, Katlian Bay, and Bering Sea (this study).

maturity. Size of adults is influenced more by growth rate of juveniles and the size at inflection of growth stanzas than by the constant of proportional growth after inflection.

In the Auke Bay vicinity, a sharp increase of zooplankton abundance in June is the determinent for the annual cycles of fattening and spawning in Pacific herring, and spawning in April or May seems optimally timed for growth of newly hatched fry. In summer, fat builds rapidly about the viscera and in the musculature of adults, as a reserve for gonad development and metabolism in fall and winter when food is scarce and herring do not feed. Iles (1984) found that in Atlantic herring fat is assimilated and deposited almost unchanged during the feeding cycle and is not utilized for metabolism until the metabolic pool of protein is exhausted. He also hypothesizes that annual somatic growth declines with gonad growth and ceases with depletion of the protein pool.

Male Pacific herring from Auke Bay build gonads and use their fat reserves more rapidly than do females. Testes may be near spawning condition in November, but ovaries are not full sized until April. Males may be ready or nearly ready to spawn in November over the entire eastern Pacific Ocean, but females delay spawning until local conditions of temperature and food abundance are optimal for larval growth.

The exponents for total and eviscerated body weights, as functions of BL, exceed 3.0 in Pacific herring from Auke Bay, and probably in Atlantic herring as well because of their similar morphology. Weight of mature gonads also have a greater-than-cubic relationship to BL in Auke Bay herring (the exponent was 4.4 for testes; the exponent of 3.9 for ovaries was within the range for ovaries in Atlantic herring).

The annual product (eviscerated body weight and gonad weight) is constantly proportional to BL through ages 2-6 and also through ages 8-12 in Pacific herring from Auke Bay, but the proportion is considerably lower in the 8-12 group. However, despite the two levels of production relative to BL, annual production corresponds more closely to BL than to eviscerated weight. Annual production may be lower relative to BL in the older group because suitable foods for adults may not be abundant in the Auke Bay vicinity. Most annual production in young Auke Bay herring goes into growth of eviscerated body weight. After age 6, production of sex products predominates, and by age 12, sex products compose over 90% of annual production.

Pacific herring probably develop genetic stocks that are distinguished by locale, spawning time, and cycles of gonad maturity and fat utilization in the females. The stocks probably are distinguished also by growth rate, age, or size at growth inflection and by partitioning of annual product between eviscerated body weight and gonads.

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