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Fecundity of Walleye Pollock (*Theragra chalcogramma*) from the Shelikof Strait, Gulf of Alaska

by

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FECUNDITY OF WALLEYE POLLOCK (*Theragra chalcogramma*) FROM SHELIKOF STRAIT, GULF OF ALASKA

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ABSTRACT

The fecundity of walleye pollock, *Theragra chalcogramma*, from the Shelikof Strait, Gulf of Alaska, was investigated using specimens collected in the spring of 1982. Ovaries from mature pre-spawning females were found to contain two distinct and clearly separated size modes, indicating that the walleye pollock in Shelikof Strait are probably discontinuous, annual spawners; histological data also indicated once-a-year spawning. Fecundity (F) was found to be related to fork length in cm (L) by $F = 1.2604\ L^{3.2169}$ and to gutted weight in grams (W) by $F = 387.4551\ W^{1.0160}$. Fecundity estimates ranged from about 95,000 to 1,000,000 for fish ranging from 30 to 69 cm in length and 225 to 2000 grams in weight.

INTRODUCTION

Walleye pollock, Theragra chalcogramma, has in the past decade become one of the most important commercially exploited stocks in the Gulf of Alaska. All-nation landings climbed from less than 10,000 metric tons in 1970 to between 100,000 and 300,000 metric tons presently being harvested (Alton et al. 1985; Strickland and Sibley 1984). Successful management of the Alaska fishery depends upon a thorough understanding of the biology of walleye pollock. Of considerable importance is knowledge of the reproductive biology of walleye pollock which has been found to be lacking or poorly understood. Hughes and Hirschorn (1978) reported information on the growth, mortality, abundance, and sexual maturity of the Gulf of Alaska stock--sexual maturity was generally found to be reached at age three. Hirschberger and Smith (1983) reported pollock in spawning condition in the Shelikof Strait and Kodiak region and all along the outer edge of the continental shelf through the months between February and August, where the majority of these stocks appeared to spawn from late February through May. Peak spawning in Shelikof Strait appears to last only about 3-5 weeks (Dunn and Matarese 1985), occurring from the end of March to early April in 1981 and 1982 (Nunnallee, pers. communication). The objective of the present study is to determine the fecundity of walleye pollock collected from Shelikof Strait, Gulf of Alaska, in 1982.

We would like to acknowledge and thank Dr. Arthur Kendall, National Marine Fisheries Service, Seattle, who was responsible for arranging for this study to be done and for providing very helpful advice throughout the study. Foreign Vessel Observers from NMFS were responsible for

collecting some of the samples, and we thank them. Graduate students and biologists from the School of Fisheries, University of Washington, helped with this study and we would particularly like to thank Kathryn Garrison who initiated the field and lab work on the project and was responsible for the collection and processing of many of the samples, and also Robert Lauth for his valuable help in a variety of ways.

METHODS AND MATERIALS

Walleye pollock ovaries were collected in the Shelikof Strait area in the Gulf of Alaska from late February to April in 1982. Collections were made from two foreign processors (by NMFS observers) and from the NOAA research vessel CHAPMAN. Care was taken to standardize collection techniques and sample processing between collectors.

In the field, ovaries were divided into two main groups and treated separately. One group of ovaries, representing the various maturity stages (described below), were split into left and right lobes. One lobe was preserved in Dietrich's fluid or 10% buffered Formalin (for histological processing) and the other lobe was preserved in modified Gilson's solution (for oocyte size frequency distribution). The other main group of ovaries collected included mostly developing and mature ovaries (stages 2L and 3) which were taken from females representing the length range of pollock present and were preserved whole in modified Gilson's solution for fecundity estimates. Individual pollock were then gutted and weighed (grams) and measured (fork length in mm).

Definition of Maturity Stages

In order to standardize the ovary collections, it was necessary to define a maturity code and description for walleye pollock:

STAGE 1 Immature: Ovaries small, tapered, and transparent. Fish will not spawn in the current year. (Sex may be difficult to determine).

2 Developing: Early (2E) - ovaries tapered, forming two distinct, transparent lobes with well-developed blood vessels. No or few individual ova present. Late (2L) - developing lobes fill up to half of the body cavity, with distinctly visible opaque, orange eggs.

3 Mature: Ovaries fill more than half of the body cavity and contain distinctly visible eggs. Eggs are not extruded when ovaries are compressed. Most eggs are opaque, but scattered clear (hydrated) eggs may be present. Eggs cannot be easily separated from one another.

4 Spawning: Ovaries large, filling the body cavity. Most eggs are hydrated, although some opaque eggs remain. Eggs are extruded from the body under slight pressure or are loose in the ovary and easily separated from one another.

5 Spent: Ovaries are large, but flaccid, watery, and generally reddish. Scattered unspawned eggs can be seen. Ovaries which are "Recovering" will appear reddish-purple and contain scattered eggs, but will not be as large or as flaccid as recently spawned ovaries.

Representative photographs for these stages were provided to the personnel making the maturity observations.

Size-Frequency Distributions

Pairs of ovaries used to determine fecundity and oocyte size-frequency distributions were stored in individual jars of modified Gilson's solution for several months to break up the ovarian tissue. These samples were then screened through several mesh sizes to separate eggs and remove ovarian tissue. Once cleaned, the eggs were transferred to 5% Formalin.

To determine oocyte size-frequency distributions, the samples were rinsed, diluted to a known volume, and mixed using a magnetic mixer until a uniform suspension of eggs was obtained. A subsample was then

removed and placed on a cross-hatched petri dish. Oocyte diameters were measured along a transect using an ocular micrometer in a dissecting scope. Diameters were measured to the nearest 0.033 mm (0.1 ocular micrometer unit). To assure random measurement of non-spherical oocytes, diameters were measured across whichever axis lay along the transect line. At least 70 eggs were measured from each subsample. Samples were divided into 5 cm fish length groups and at least four samples from each length group were measured to determine the size-frequency distribution.

From these measurements, two oocyte sizes were apparent. The size modes of samples from fish of maturity stage 2L overlapped somewhat (Fig. 1), but the modes of oocyte sizes from fish of maturity stage 3 were clearly separated with almost no overlap (Fig. 2). This initial finding was needed to determine which fish to use for fecundity estimates, i.e., only fish from maturity stage 3 were used to determine fecundity.

Counts of small and large eggs in entire subsamples indicated a bias in the transect counts. Therefore, the transect data could not be used for reliable estimates of the relative proportion between small and large eggs, although transect data was useful for estimates within samples of small and large eggs.

Histology Preparation

The ovaries from walleye pollock (Theregra chalcogramma) for histological analysis were separated into the five stages of grossly visible ovary maturity stages previously described. The anterior, center, and

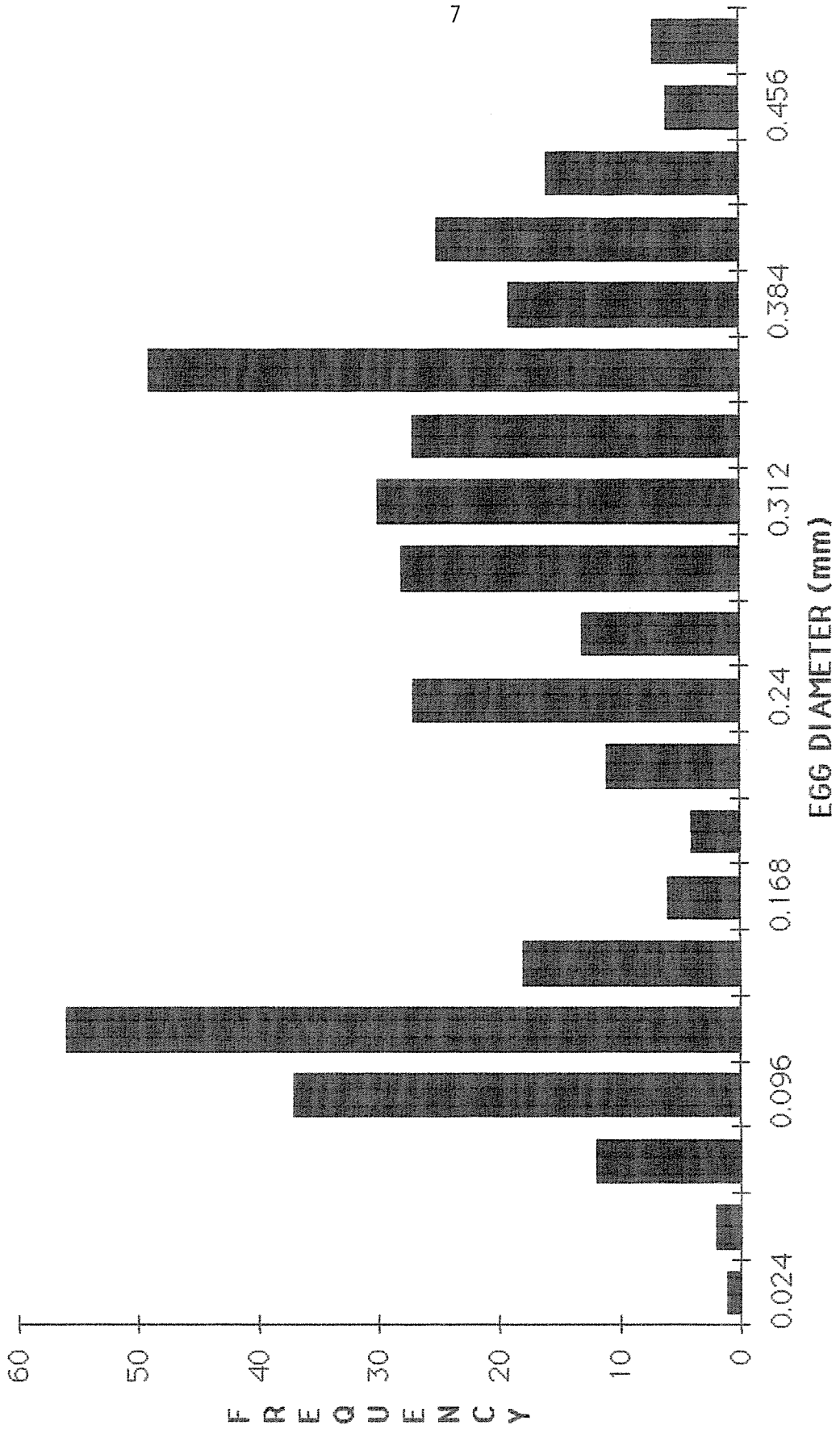

Fig. 1. Egg size-frequency distribution (Stage 2L samples).

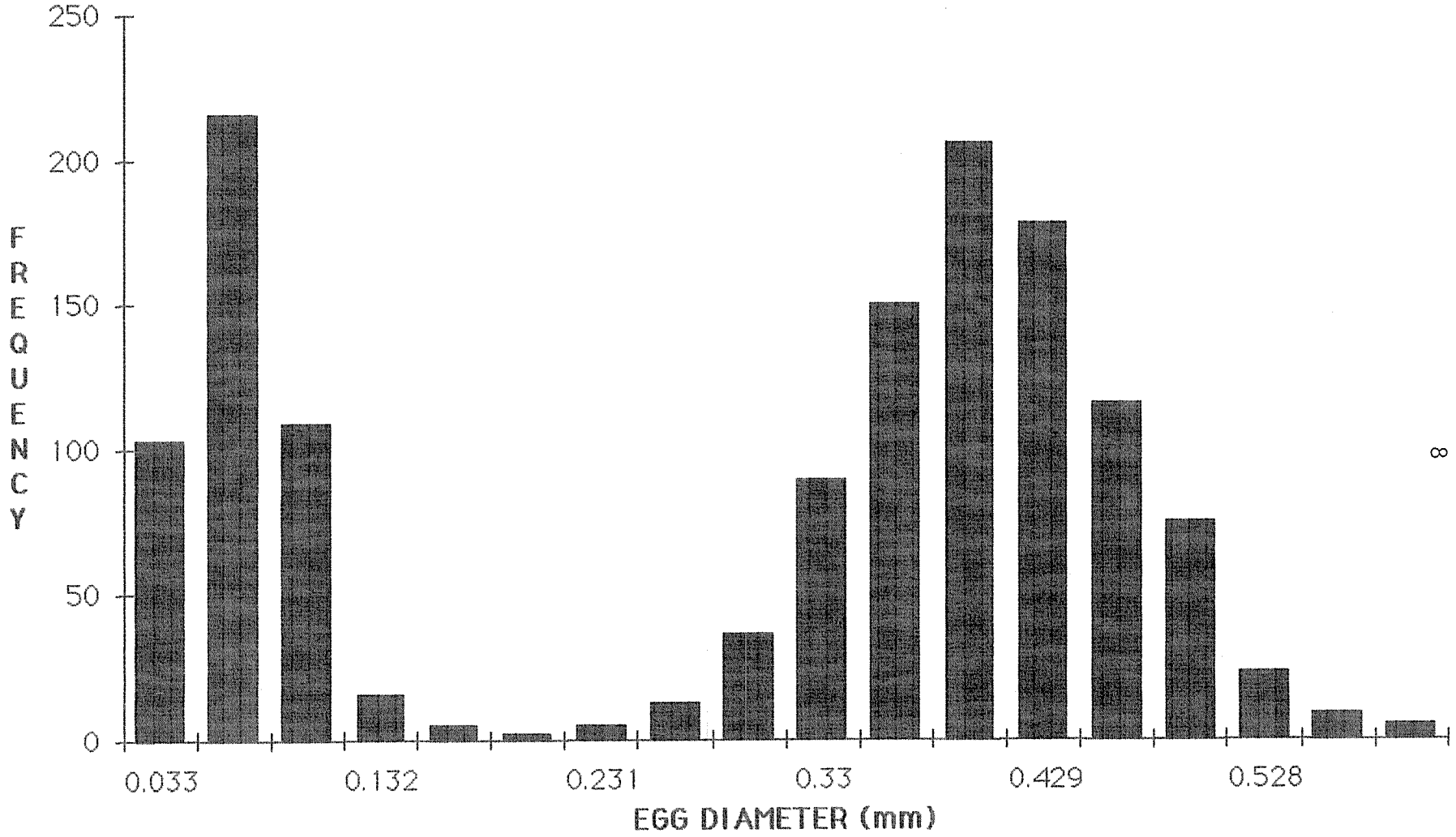

Fig. 2. Egg size-frequency distribution (Stage 3 samples).

posterior part of each ovary was cross-sectioned and removed for paraffin embedding. Representative samples were sectioned at 5 um, mounted on slides and stained with hematoxylin and eosin. Each sample was examined and characterized in terms of cellular development and organization.

Fecundity

Based on the observations made from the oocyte size-frequency distributions, only samples from fish of maturity stage 3 were used to estimate fecundity. Samples containing many hydrated eggs were not used as a precaution against underestimating fecundity due to egg loss from nearly ripe fish.

Maturing eggs were easily distinguished from the reserve fund eggs by size under the dissecting microscope. Few oocytes were of a size difficult to assign to developmental stage. To avoid confusion, eggs with a diameter of 0.198 mm or less were considered to belong to the reserve fund, and those greater than 0.198 mm were considered to be developing or maturing.

To determine the fecundity of the fish sampled, the eggs were rinsed, diluted, and mixed as previously described. A known volume subsample was withdrawn, taking care to sample the entire water column. The subsample was placed in a counting tray and all the maturing eggs in the subsample were then counted. At least three subsamples were counted from each sample. Each subsample was counted twice and the two counts were averaged. The mean number of eggs per ml, standard deviation, and coefficient of variation (CV) were computed based on the averaged

counts. If the CV exceeded 0.10 (10.0%), additional counts were made until the CV was reduced below 0.10 or the total number of subsamples counted was a minimum of five.

Ten samples were counted from each 5 cm length group of fish in the range of sizes from 30 cm to 55 cm. Fewer stage 3 samples from larger fish were available, and as a result, five samples were counted from the 55-59 cm group, two samples from the 60-64 cm group, and two samples from the 65-69 cm group. Fecundity was estimated by multiplying the mean number of oocytes per ml counted by the volume in ml of the sample:

$$F = (\text{Mean \# eggs/ml}) \times (\text{Vol (ml) of sample})$$

Analytic Methods

Data used in the analysis of fecundity relationship consisted of fork length measurements, gutted weight measurements and a fecundity estimate for each fish based on the average of several subsamples (n = 3 to 7).

Three empirical relationships were developed using least squares regression techniques. These were fecundity as a function of fork length (cm)

[1] $$F = a\ L^{b}$$

gutted weight (gm) as a function of fork length (cm)

[2] $$W = a\ L^{b}$$

and fecundity as a function of gutted weight (gm)

$$[3] \qquad F = a + W^b$$

Parameters for the relationships described by the above equations were estimated with nonlinear least squares regression techniques. Parameter values used to initialize the nonlinear least squares procedure were obtained by applying least squares regression techniques to the linearized form of the equations,

$$[4] \qquad \ln(Y) = \ln(a) + b \ln(X)$$

Weighting factors were incorporated into the nonlinear regressions to account for the unequal error variance observed in fecundity and weight variables for the different length intervals (Table 1). Weighting factors were set inversely proportional to the variance of the dependent variable. In the case of the fecundity-length and fecundity-weight relationships, weighting factors were set inversely proportional to subsample variances associated with each fecundity estimate. These values were available for each fish in the sample. In the case of the weight-length relationship, weighting factors were set inversely proportional to the variance of the weight variable observed in each 5 cm length interval (Table 1). With this approach, estimates of the dependent variable associated with length groups that were determined with high precision (low variance) were more heavily emphasized while estimates associated with length groups having larger variances received less emphasis. Theoretically, performing a weighted least squares analysis will give parameter estimates that are not markedly different

Table 1. Mean and variances (SD) of fecundity and weight by length categories.

Length group number	Length range (cm)	Number data points	Fecundity (number eggs) Mean	Fecundity (number eggs) Std. Dev.	Weight (gm) Mean	Weight (gm) Std. Dev.
1	30-34	10	96,216	21,650	225.0	22.7
2	35-39	10	167,787	43,616	345.0	51.5
3	40-44	10	242,695	57,840	499.0	73.7
4	45-49	10	382,920	83,173	691.0	80.1
5	50-54	11	364,696	103,709	885.5	168.7
6	55-59	5	531,921	76,707	1130.0	177.6
7	60-69	4	1,079,540	117,421	1997.5	225.1

from those obtained from unweighted least squares; however, they will be subject to less sampling variation as indicated by lower estimated standard deviations of the regression coefficients. Moreover, more precise confidence intervals on values predicted from the fitted response function can be determined.

The final step involved an analysis of the residuals. This analysis was performed to determine if the residuals were normally distributed and additionally to identify observations that might unduly influence parameter estimates or deviate from the usual mortality assumption. If data points with large residuals were identified, they were removed and the data was reanalyzed to ascertain the effect of their removal.

Linear regressions were carried out using the Minitab interactive software package (Ryan et al. 1982) . Nonlinear regressions were performed using the derivative-free nonlinear least squares regression procedure (BMDPAR) of the BMDP statistical software library (Dixon 1985).

Approximate confidence bounds were constructed for predicted values using the formula derived by Working and Hotelling (Neter and Wasserman 1974)

[5] $$95\%\ \text{confidence limits} = Fec \pm W\ s(Fec)$$

where

[6] $$W^2 = 2\ F(1-p;\ 2,\ n-2)$$

and

FEC = estimated fecundity,
s(FEC) = standard deviation of the fecundity estimate,
p = probability level (set to 0.05),
n = number of observations (n = 60),
F = F-statistic

RESULTS

Egg Size-Frequency Distribution

Egg size frequencies were determined for 35 samples representing data from each of the three sampling vessels over the full range of fish lengths. In all the samples, the "developing" oocytes could be clearly distinguished from the smaller oocytes composing the "resting" reserve fund. The average size of the larger, developing eggs was over 6 times as large as the average size of the smaller eggs, and virtually no overlap was observed in the modes of egg sizes (Table 2).

The average sizes of resting and developing oocytes were clearly separated at .0677 mm and .4107 mm, respectively. The sizes of the resting oocytes ranged from .033 mm to .198 mm, and the sizes of developing eggs ranged from .231 to .594 (Fig. 3). No trends in egg sizes with length or weight were observed. Only six hydrated eggs, representing 0.26% of the total number of developing eggs measured, were encountered. The estimates of fecundity included the samples containing the few hydrated eggs since we believe that the existence of one or two hydrated eggs in a sample did not represent sufficient hydration to indicate significant loss of eggs due to the onset of spawning.

Observations Using Histology

One point that became immediately apparent was that the five maturity stages of visual classification used in the collection of the whole ovaries (Immature, Developing, Mature, Spawning and Spent) were not appropriate for cytological categorization. To avoid confusion, egg cell development will be described as one of six "phases" of growth.

Table 2. Egg size-frequency distribution.

Diameter (mm)	Number in samples	Proportion in samples
"Resting"		
.033	482	.2133
.066	1215	.5376
.099	526	.2327
.132	33	.0146
.165	4	.0018
.198	1	.0004
"Developing"		
.231	9	.0039
.264	35	.0150
.297	76	.0327
.330	202	.0868
.363	288	.1238
.396	549	.2360
.429	540	.2322
.462	358	.1539
.495	205	.0877
.528	52	.0224
.561	13	.0056

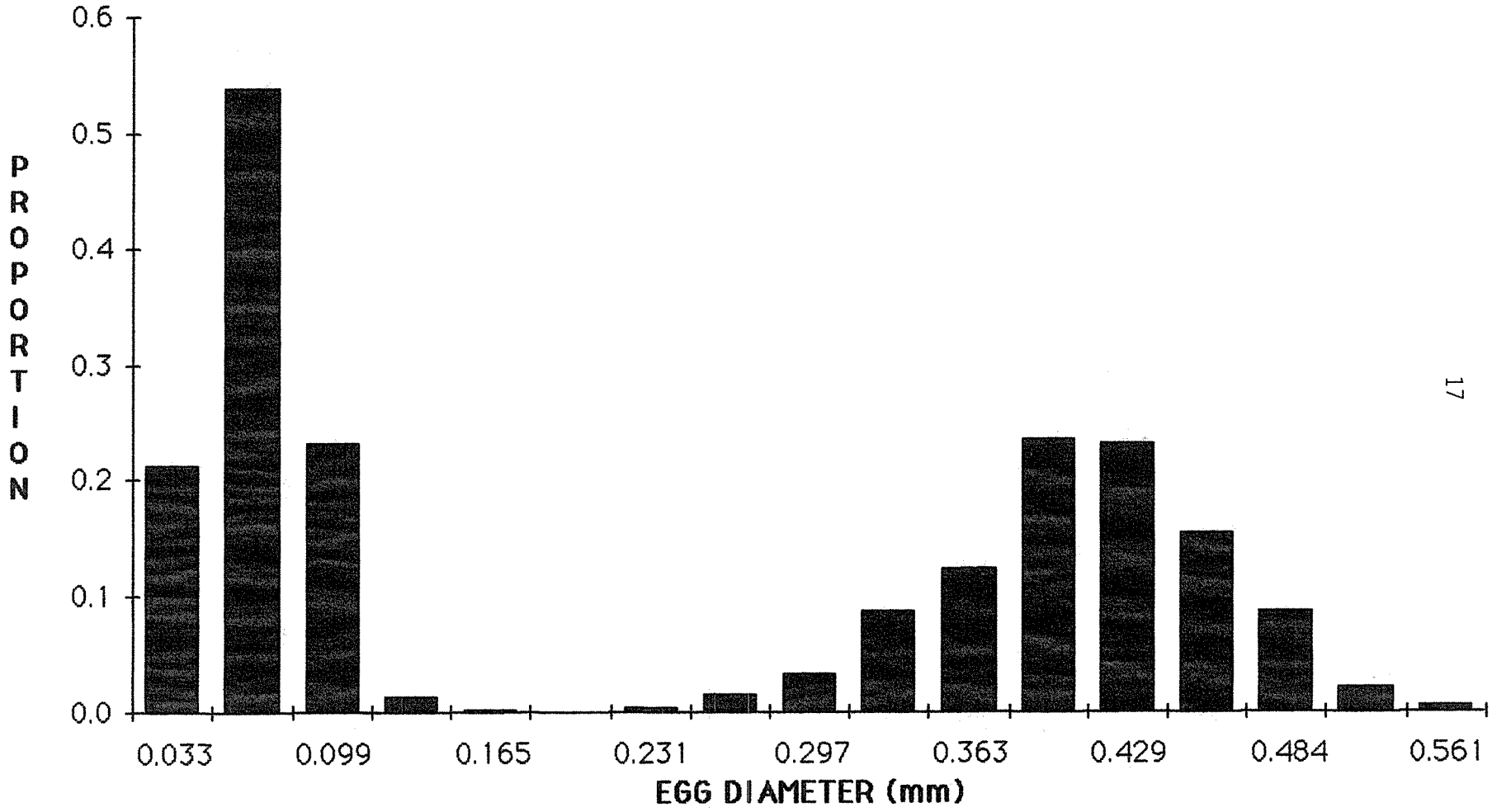

Fig. 3. Egg size-frequency distribution, all samples.

These phases are similar to those described for striped bass by Groman (1982).

Phase I oocytes include germinal cells, primary oogonia and resting oocytes. These are the earliest and smallest stage of ova development. Commonly, these cells are located in focal "nests" adjacent to connective tissue and are oxygenated by one or two capillaries. The cytoplasm of phase I oocytes stains lightly pink with eosin (acidophilic). The oogonia arise from the germinal cells which undergo mitosis. The oocytes are produced by the oogonia precursors in the first stage of meiosis.

Phase II oocytes are characterized by cytoplasmic enlargement of the phase I cells. The intiation of cellular growth is accompanied by early differentiation of the follicular cells which will support the developing ova. The oocytes of this stage exhibit a lightly basophilic cytoplasm (ovaplasm) with a disproportionately large nucleus containing diffuse chromatin.

Phase III oocytes are characterized by a more strongly basophilic ovaplasm than the phase II cells. The follicular epithelium becomes more developed, surrounding the oocyte with a series of laminated membranes supplied by an adjacent blood vessel. Ribonucleic protein particles appear as provitelline nucleoli that migrate toward the margin of the karyoplasm. This stage of development usually occurs at the same time as lipogenesis in most teleosts.

Phase IV oocytes exhibit the most strongly stained basophilic ovaplasm of all the developmental phases. The nucleus stains acidophilic and contains prominent euvitelline nucleoli adjacent to the nuclear membrane. A distinct zona radiata layer containing microvilli, that gives the appearance of striations when examined histologically, is first evident in this phase. The formation of yolk vesicles containing polysaccarides (not true yolk) and vitellogenesis begin near the end of phase IV development.

Phase V oocytes exhibit a rapid growth in oviplasm due to large increases in the amount of yolk vesicles consisting of cortical alveoli. The acidophilic nucleus is enlarged and surrounded by a band of blue ovaplasm devoid of the yolk vesicles in the early part of this phase. Near the end of this phase, the nucleus begins to degenerate and move to the margin of the ova near the micropyle in the zona radiata.

Phase VI is the final stage of development of the ova before release. Phase VI oocytes contain a homogenous mixture of acidophilic yolk granules and fat granules. A thin layer of lightly basophilic cytoplasm is still visible all along the zona radiata. Presumably, the first polar body is formed during the completion of the initial meiosis followed by the formation of three polar bodies in the second meiosis. The mature ovum is haploid and fully developed for spawning.

A comparison of the anterior, middle, and posterior ovarian cross-sections revealed nearly identical patterns and stages of development within individual organs. This was anticipated because of the systematic nature of hormonal control in reproduction. The earliest cell

stages tend to rest close to the connective tissue of the trabecular projections and the inside margin of the tunica albuginea.

The question of synchronous versus asynchronous development must be carefully addressed because of the implications made regarding single versus multiple spawning seasons within a single spawning season. In the slides prepared, early development is indicated to be asynchronous, but becomes synchronous once vitellogenesis begins. The synchrony of development allows a fecundity estimate to be made based on an oocyte count in the most advanced egg phase under the assumption that these ova will be released that season.

The walleye pollock ovaries exhibited large size (and phase) differences between the most prevalent advanced stage and the less common early phase oocytes. An examination of the most developed pre- and post-spawned walleye pollock revealed a small population of early phase IV oocytes during and after the release of the mature phase VI ova.

The post-spawning residual oocytes appeared irregular in shape and poorly supported by the trabecular connective tissue. During the late maturity and spent ovarian stages, atretic follicles were commonly observed. We assume these foci are to be resorbed by macrophages for energy and reuse by the adult female.

The oocytes remaining after spawning do not appear to be numerous or developed enough to allow a second spawning within a 2-3 month spawning period. The fish examined from this population are most likely

single batch spawners and the oocytes develop synchronously after the onset of vitellogenesis.

Fecundity

Fecundity estimates were made for 60 Shelikof Strait walleye pollock, using samples collected aboard three vessels operating in the area. The fish sampled (Table 3) ranged in total length from 31 cm to 68 cm and in weight from 0.19 kg to 2.32 kg. Number of fish sampled by length and weight group were spread fairly evenly throughout the range, although fish of the largest sizes were under-represented. The coefficient of variation (CV) was used as a measure of variance between subsamples for each fish. The percent deviation from the mean CV ranged from 1.3% to 17.3% with 82% of the samples under 10.0% (Table 4).

Table 5 summarizes the results of weighted and unweighted fits of the relationships $F = a\ L^b$, $W = a\ L^b$, and $F = a\ W^b$ using both linear and nonlinear regression procedures. Tabulated are parameter estimates, standard deviations, and coefficient of variation. This latter statistic is a relative variance measure and provides a means to compare fits when scales (i.e., logarithmic/arithmetic) are different. Also tabulated is a measure of the percent of the variability observed in the dependent variable explained by the independent variable.

Fecundity-Length Relationship

All forms of the fecundity-length relationship explained about the same amount of variation in fecundity. The weighted nonlinear relationship did the best job with an R^2 of 98.7 percent. The constant parameter (a) was estimated with less precision when compared to the

Table 3. Sample sizes by length and weight group and by vessel.

Fork length (cm)	Vessel[a] 1	Vessel[b] 2	Vessel[c] 3	Total
30-34	2	4	4	10
35-39		4	6	10
40-44	1	5	4	10
45-49	2	5	3	10
50-54	1	2	8	11
55-59	2		3	5
60-69	3		1	4
Total	11	20	29	60

Weight (gm)	Vessel 1	Vessel 2	Vessel 3	Total
0 - 249	2	3	4	9
250 - 499	1	7	7	15
500 - 749	2	5	8	15
750 - 999		5	6	11
1000 -1224			3	3
1250 -1499	3			3
1500- 2500	3		1	4
Total	11	20	29	60

[a]Vessel 1 is the Chapman.
[b]Vessel 2 is represented by samples collected by Draves.
[c]Vessel 3 is represented by samples collected by Hostetler.

Table 4. Number of samples falling into ranges of coefficients of variation, CV. Coefficient of variation expressed in %.

CV	Sample frequency
<4.9	14
5.0 - 9.9	35
10.0 - 14.9	7
15.0 - 19.9	4

Table 5. Results from linear and nonlinear least squares analysis of the full pollock fecundity data set.

Parameter estimates and statistics	Linear regression		Nonlinear regression	
	Unweighted	Weighted	Unweighted	Weighted
	Fecundity-length relationship			
	$\ln(F) = \ln(a) + b \ln(L)$		$F = a L^b$	
ln(a)	0.7174	0.2840	--	--
Std Dev ln(a)	0.6677	0.6871	--	--
CV ln(a)	0.9307	2.4194	--	--
a	--	--	1.2848	1.2604
Std Dev a	--	--	1.0616	0.6882
CV a	--	--	0.8262	0.5460
b	3.1038	3.1933	3.2308	3.2169
Std Dev b	0.1760	0.1902	0.2048	0.1392
CV b	0.0567	0.0596	0.0634	0.0433
R^2	84.3	82.9	82.4	98.7
	Weight-length relationship			
	$\ln(W) = \ln(a) + b \ln(L)$		$W = a L^b$	
ln(a)	-5.0308	-4.9403	--	--
Std Dev ln(a)	0.2656	0.3129	--	--
CV ln(a)	0.0528	0.0633	--	--
a	--	--	0.0041	0.0059
Std Dev a	--	--	0.0015	0.0013
CV a	--	--	0.3659	0.2203
b	2.9994	2.9747	3.1192	3.0273
Std Dev b	0.0700	0.0881	0.0912	0.0592
CV b	0.0234	0.0296	0.0292	0.0196
R^2	96.9	95.2	95.7	97.9

Table 5. Results from linear and nonlinear least squares analysis of the full pollock fecundity data set - cont'd.

Parameter estimates and statistics	Linear regression		Nonlinear regression	
	Unweighted	Weighted	Unweighted	Weighted
	Fecundity-weight relationship			
	$\ln(F) = \ln(a) + b \ln(W)$		$F = a W^b$	
ln(a)	5.8997	5.8963	--	--
Std Dev ln(a)	0.3267	0.3474	--	--
CV ln(a)	0.0554	0.0589	--	--
a	--	--	374.1367	387.4551
Std Dev a	--	--	141.3190	98.2910
CV a	--	--	0.3777	0.2537
b	1.0386	1.0211	1.0384	1.0160
Std Dev b	0.0514	0.0598	0.0532	0.0372
CV b	0.0495	0.0586	0.0512	0.0366
R^2	87.6	83.4	87.3	97.7

power coefficient (b). As expected, weighting the fit increased the precision of the parameter estimates as measured by the coefficient of variation (CV). Residuals from the unweighted nonlinear fit had the typical fan shaped appearance associated with the condition of unequal error variances. Residuals from the weighted nonlinear fit had a more random appearance suggesting that performing the weighted fit dealt with the unequal variance problem.

Despite which form of regression was tried, data points from the large length interval (>60 cm) had the largest residuals. Under the assumption that the errors are normally distributed, we would expect most standardized residuals to fall within two standard deviations of the average residual (assumed to be equal to zero). Often standardized residuals from this length interval exceeded a value of 2.0.

Because data points from the larger length interval did not fit the model well, two data sets were analyzed. The first data set contained all data points. A truncated data set in which observations from length interval 60-69 cm (Table 1) were removed was also used. This length group only had four observations, so the truncated data set had 56 observations.

There was little improvement in the fit when using weighted non-linear regression on the truncated data set. Results from the truncated data set resulted in a slightly lower R^2 value (97.3) and slightly more variable parameter estimates. The parameter estimates themselves changed little. The constant coefficient increased (1.42) and the power coefficient decreased (3.18) relative to the same fit on the full data

set. Essentially what has happened is that without the large fecundity estimates, the estimated line is more closely approaching a linear form (i.e., the constant coefficient has increased and the power coefficient decreased). In the nonlinear fits, the precision of the parameter estimates increased with weighting and the percent variation explained by the regression increased relative to the unweighted case.

The weighted nonlinear fit of the fecundity-length relationship using the full data set appears to be the best fit based on values of R^2 and the precision of the parameter estimates. Fecundity estimates for selected lengths, standard deviations, and 95% confidence intervals are given in Table 6.

Weight-Length Relationship

The weight-length relationship was well defined. Parameters were estimated with greater precision than they were in the fecundity-length relationship as indicated by lower CV's and the linear and nonlinear fits explained a large amount of the variation (Table 5). Results showed similar trends as in the analysis of the fecundity-length relationship. Weighting the nonlinear fit produced parameter estimates with lower CV's and the weighted nonlinear fit explained more of the variation in the dependent variable compared to the unweighted fit.

Analysis of the truncated data set (omitting 60-69 cm fish) also showed similar trends; the constant coefficient increased (0.0074) and the power coefficient decreased (2.9657). Both parameters were more variable compared to corresponding estimates derived from the full data set.

Table 6. Ninety-five percent confidence limits for fecundity estimates. Fecundity estimates and standard deviations were derived from the fecundity-length relationship using weighted nonlinear regression on the full fecundity data set.

Length (cm)	Estimated fecundity	Std. dev. of estimate	Lower limit	Upper limit
30	71,164	5,578	57,163	85,165
35	116,832	6,938	99,418	134,271
40	179,546	8,048	159,346	199,746
45	262,221	9,254	238,993	285,449
50	368,013	11,752	338,515	397,511
55	500,055	17,225	456,820	543,290
60	661,673	27,033	593,820	729,526
65	855,991	41,626	751,510	960,472

Analysis of residuals revealed trends similar to those observed from the fecundity-length analysis. The weighted nonlinear fit using the full data set appears to be the best fit based on values of R^2 and the CV's of the parameter estimates. Weight estimates for selected lengths, standard deviations, and 95% confidence intervals are provided in Table 7.

Fecundity-Weight Relationship

The weighted nonlinear fecundity-weight relationship explained the largest precentage of the variation in fecundity. As in the previous two cases, the constant parameter was estimated with less precision when compared to the power coefficient and weighting the fit increased the precision of the parameter estimates as measured by the coefficient of variation (CV).

The value of the power coefficient estimated from the nonlinear regressions was very close to 1.0 implying the relationship between fecundity and weight is linear. It cannot be determined if 1.061 is statistically different from 1.0 based on the results from nonlinear regression because standard statistical tests are not appropriate when the model is nonlinear (Draper and Smith 1966). However, valid statistical tests can be performed on the results from the linear fits. This seems reasonable since estimates of the power coefficient from the linear and nonlinear procedures are very close in value and precision and because the power coefficient is estimated without bias using linear regression. The null hypothesis that the power coefficient equals 1.0 cannot be rejected at the 0.05 probability level.

Table 7. Ninety-five percent confidence limits for weight estimates. Weight estimates and standard deviations were derived from the weight-length relationship using weighted nonlinear regression on the full fecundity data set.

Length (cm)	Estimated weight (gm)	Std. dev. of estimate	Lower limit	Upper limit
30	174.79	4.37	163.82	185.76
35	280.61	4.98	268.11	293.11
40	417.61	5.84	402.95	432.27
45	600.49	8.17	579.98	621.00
50	826.09	13.40	792.46	859.72
55	1102.39	22.05	1047.04	1157.74
60	1425.11	34.75	1337.89	1512.33
65	1815.86	51.81	1685.82	1945.90

Analysis of the residuals show large residuals associated with observations from the large length interval. Analysis of the truncated data set indicated that the constant coefficient decreased (358.0128) and the power coefficient increased (1.0281) relative to applying the weighted nonlinear procedure to the full data set. These changes are modest but are opposite to the results from analyzing the fecundity-length and weight-length relationships using the truncated data set. As before, both parameters were more variable compared to corresponding estimates derived from the full data set.

The weighted nonlinear fit of the fecundity-weight relationship using the full data set appears to be the best fit based on values of R^2 and the precision of the parameter estimates. Fecundity estimates for selected weights, standard deviations, and 95% confidence intervals are provided in Table 8.

Table 8. Ninety-five percent confidence limits for fecundity estimates. Fecundity estimates and standard deviations were derived from the fecundity-weight relationship using weighted nonlinear regression on the full fecundity data set.

Weight (gm)	Estimated fecundity	Std. dev. of estimate	Lower limit	Upper limit
200	84,347	5,201	71,292	97,402
500	213,981	7,382	195,452	232,510
1000	432,734	11,676	403,427	462,041
1500	653,326	22,452	596,971	709,681
2000	875,120	36,002	784,755	965,485

DISCUSSION

Histological analysis and the existence of two strong modes of egg size, one mature, the other immature and yolkless, suggests that these stocks of walleye pollock are annual spawners. It has generally been concluded that species at high latitudes spawn once a year (Qasim 1956). However, multiple size modes of oocytes have been interpreted in some studies as indicating more than one spawning per year (Foucher and Beamish 1980). Although one wonders how probable it is that pollock could produce sufficient yolk material for a second spawning in these latitudes, conclusive evidence of single spawning would require histological observations of post-spawning fish. Goldberg (1981) has suggested that the presence of a mode of mature oocytes and a mode of vittellogenic oocytes (indicating yolk deposition in process) may indicate a fish is capable of spawning more than once a year. Preliminary investigations of histological sections do not suggest such a combination of modes in these fish. An examination of individuals throughout the year may possibly be required to determine the degree of oocyte development over time.

Fecundity of species displaying clearly separated modes of egg sizes has generally been estimated by determining the number of eggs in the most advanced mode and assuming these eggs represent all that is spawned in a season (Hodder 1963; Raitt 1933; May 1967; Gunderson et al 1980). Such an approach has been taken in this study.

In the Shelikof Strait, walleye pollock fecundity was found to be proportional to gutted weight and to vary at a rate proportional to

length cubed. The value of the exponent in the latter relationship is similar to that commonly reported in other species.

Fecundity estimates with which to compare the results of this study are not available for Shelikof Strait walleye pollock stocks. Data on the fecundity of Bering Sea walleye pollock is available in a report by Shew (1978, unpublished). The relationship between fecundity and length in centimeters was expressed as: $F = .29L^{3.462}$. Recently Hinckley (1986, unpublished) determined the F-L relationship to be $F = 0.1719L^{3.6046}$ for the combined shelf and slope area of the Bering Sea, and to be $F = 469.2282L^{1.5575}$ for the Aleutian Basin. Thompson (1981) found the relationship between the same variables for pollock stocks in the Strait of Georgia (British Columbia, Canada) to be: $F = 6.771L^{2.981}$. Zvèrikova (1977) reported the relationship for stocks in the northeast Sea of Japan as: $F = 0.16\ L^{3.72}$, and Sakurai (1982, unpublished) calculated the relationship as $F = 8.73 \times 10^{-6}L^{3.98}$ for pollock sampled off Kumaishi and the surrounding waters of Funka Bay in the Sea of Japan side of Hokkaido.

These relationships between length and fecundity were compared with the results from the present study (Fig. 4). Fecundity at a given length for the various stocks appears to be quite variable. The numbers of eggs produced by British Columbia fish is about double that produced by a Shelikof Strait female of comparable length, while the numbers reported from the Bering Sea are almost half that in the Shelikof Strait area. The curves representing the stocks from the area north of the Sea of Japan and those presented for this study are very

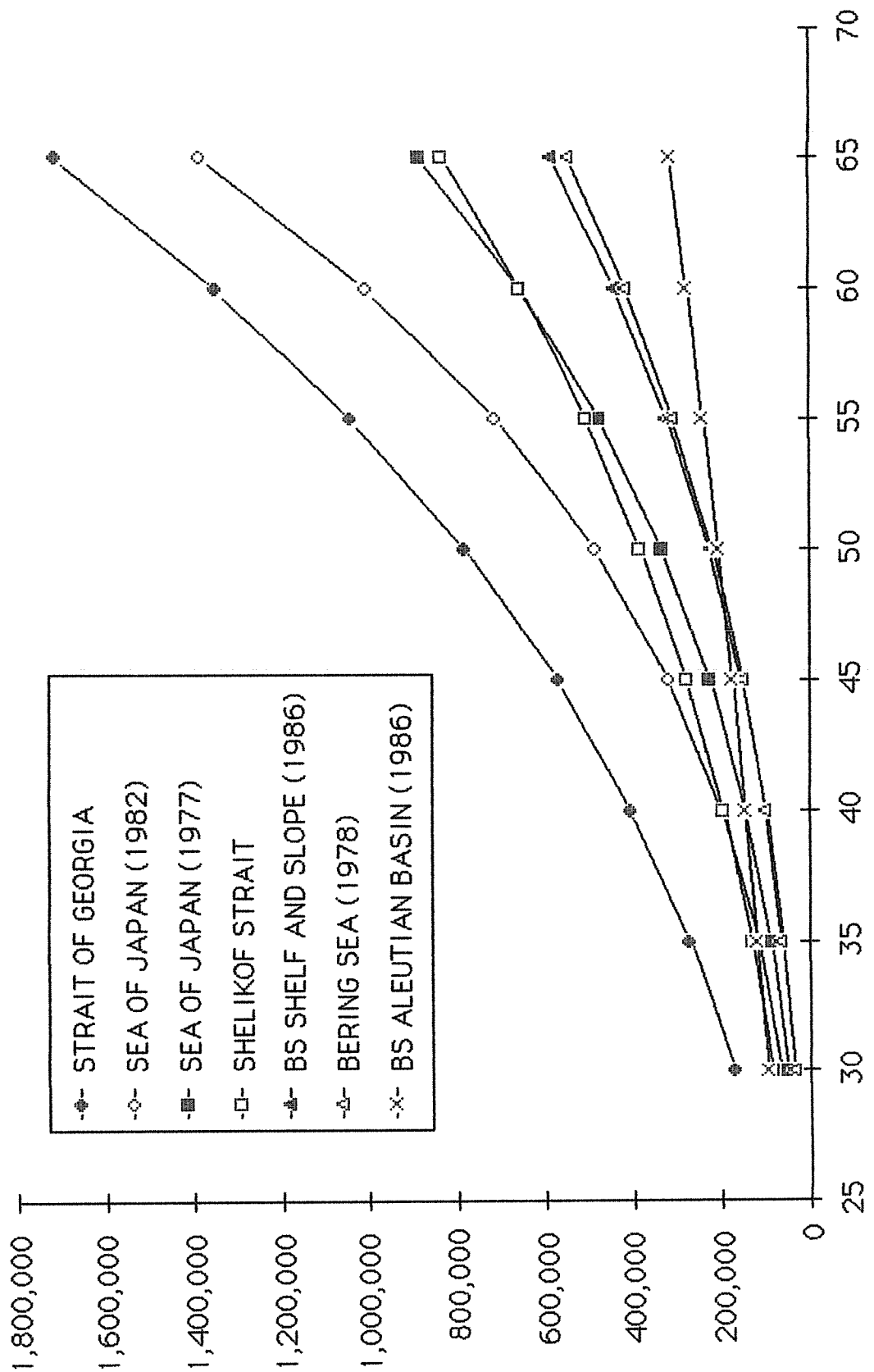

Fig. 4. Length-fecundity relationships calculated from this study (Shelikof Strait) and from the literature.

similar, while the F-L relationship from the Sea of Japan side of Hokkaido is similar for smaller fish, but fecundity increases at a much faster rate for the larger fish.

Fecundity has been defined as the number of viable oocytes actually released for fertilization (Foucher and Beamish 1980). This requires that histological studies be conducted to estimate the number of oocytes remaining in the ovary after spawning to determine the proportions of viable and non-viable oocytes. As a result of future histological studies for Shelikof Strait fish, the estimates of fecundity presented here may have to be adjusted to reflect the number of viable eggs remaining in the ovary at spawning.

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