THE REPRODUCTIVE BIOLOGY OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN THE BERING SEA, WITH REFERENCE TO SPAWNING STOCK STRUCTURE

SARAH HINCKLEY[1]

ABSTRACT

The reproductive biology of walleye pollock. *Theragra chalcogramma*, in the Bering Sea was studied from collections of ovaries and observations of spawning in 1984. Spawning occurred in the Aleutian Basin from January through March. in the southeastern Bering Sea from March through June. and northwest of the Pribilof Islands from June through August. Spawning concentrations found in these areas showed significant differences in length at age and fecundity. Histological evidence indicated that the spawning period of an individual female probably lasts less than 1 month. Results indicate at least three separate spawning stocks of walleye pollock within the Bering Sea. These are located in the Aleutian Basin, over the southeastern continental shelf and slope and northwest shelf areas, and over the continental slope northwest of the Pribilof Islands. Mixing of stocks between widely separated spawning grounds due to extended spawning and migration is not likely.

Walleye pollock, *Theragra chalcogramma*, a member of the gadid family found in the North Pacific Ocean, currently supports the largest single-species fishery in the world. In the eastern portion of its range, catches of pollock average 100,000 to 300,000 metric tons (t) per year in the Gulf of Alaska (Alton et al. in press) and 1,000,000 t per year in the Bering Sea (Bakkala et al. in press). The walleye pollock resource in the Bering Sea is presently managed as a single stock but there is increasing evidence that substocks may exist (Lynde et al. 1986[2]). If substocks exist, this information should be considered in management strategy.

If a stock is defined as a production unit or a group of fish showing similar responses to environmental conditions within a certain geographic area, then population characteristics such as growth rates, fecundity, and size or age at maturity may provide the most practical means of differentiating these units. As these parameters determine the yield of a stock to a fishery, identification of production units based on some or all of them may improve the effectiveness of fisheries management.

A clearer understanding of the reproductive process in walleye pollock may also aid in differentiating stocks or production units. Nishiyama and Haryu (1981) proposed that walleye pollock in the Bering Sea may migrate and spawn over extensive distances during the long spawning season, implying that spawning groups mix over large areas. Sakurai (1982) has shown in laboratory experiments that walleye pollock spawn a single group of matured eggs in successive batches, possibly over a period of 1 month. It is not known, however, whether an individual female is capable of repeating vitellogenesis with more than one separate group of eggs in 1 year (i.e., of rematuring the ovary). Evidence of batch spawning or rematuration in Bering Sea walleye pollock may indicate the duration of individual spawning and the potential for mixing between spawning concentrations found in widely separated areas.

In this study, the spatial and temporal distribution of spawning for 1984 has been documented and the length at age and fecundity of walleye pollock from spawning concentrations in different areas has been determined. Walleye pollock ovaries were examined histologically to clarify the process of oocyte development, to learn whether annual fecundity is determinate or indeterminate and to learn the optimal stage for estimating fecundity, and to determine whether

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[2]Lynde, C. M., M. Van Houghton Lynde, and R. C. Francis. 1986. Regional and temporal differences in growth of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea and Aleutian Basin with implications for management. NWAFC Proc. Rep. 86-10. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Manuscript accepted April 1987.
FISHERY BULLETIN: VOL. 85, NO. 3, 1987.

batch spawning or rematuration occur in Bering Sea pollock.

METHODS

Data and Sample Collection

Data and specimens of walleye pollock were collected from December 1983 to October 1984 by National Marine Fisheries Service (NMFS) observers aboard foreign commercial fishing vessels and by NMFS pesonnel aboard NOAA research vessels. Data collection was divided into three phases. First, fisheries observers logged the time and location of commerical hauls in which spawning walleye pollock (those with running eggs or milt) were observed. A total of 1,538 observations was made between January and October. Second, otoliths were collected from walleye pollock in hauls where spawning was observed. Third, walleye pollock ovaries were collected for histology and anaylsis of fecundity. Three ovaries per maturity stage (Hinckley 1986) were collected and preserved in 10% neutral buffered formalin for histological analysis. A separate collection of late developing or mature ovaries was made for the fecundity analysis. Five ovaries per 5 cm length interval were collected over the entire length range encountered. These ovaries were preserved in modified Gilson's solution (Ito 1977[3]). A total of 345 ovaries were collected for histology and 294 for fecundity analysis.

Data and Sample Processing

Location of Spawning and Length at Age of Spawners

Spawning locations of walleye pollock were plotted by month. The distribution of fishing effort by the foreign commercial fleet over the spawning season was examined and compared with locations where spawning was found. Water temperatures and depths of capture at spawning locations were also examined.

For the length-at-age analysis, five areas were defined within the Bering Sea based on oceanographic features (after Lynde et al. fn. 2): the southeast continental shelf, the southeast continental slope, the northwest shelf, the northwest slope, and the Aleutian Basin (Fig. 1). Northwest and southeast areas were divided at the Pribilof Islands and buffer zones were defined in order to clearly separate them. Ages were assigned to a maximum of 200 otoliths per area by readers at the Northwest and Alaska Fisheries Center (NWAFC) age and growth laboratory.

Lynde et al. (fn. 2) found that walleye pollock from the Aleutian Basin and the northwest slope were generally slower growing than pollock from the southeast shelf and slope areas. Based on this observation, R. Francis and A. Hollowed[4] classified walleye pollock as "northern" (slow-growing) or "southern" (fast-growing), and developed two corresponding growth curves. In the present study, the growth of walleye pollock from spawning concentrations in different areas was compared to the two growth curves described in Francis and Hollowed's unpublished study. The geographical distribution of the two growth types was then examined.

To derive their "northern" and "southern" growth curves, Francis and Hollowed (unpubl. data) used age data collected by foreign fisheries observers from 1978 to 1983. Age samples were separated into $\frac{1}{2}°$ latitude by 1° longitude cells. The mean length at age was estimated for each cell by year, quarter, and sex.

Estimates of mean length at age for each cell were used to classify the cell as "northern", "southern", or "unknown". The "northern" classification indicated that the distribution of mean length at age in a given cell was similar to that seen by Lynde et al. (fn. 2) in the northwest slope and Aleutian Basin areas (Fig. 1). The "southern" classification indicated that growth was similar to that observed by Lynde et al. (fn. 2) in the southeast slope and shelf areas (Fig. 1).

For this classification, the von Bertalanffy (1938) growth model was fitted to the weighted mean length-at-age data for the "northern" and "southern" areas for each quarter and sex over a period of 6 years (1978-83) (Lynde et al., fn. 2). The model was fitted using the BMDP PAR derivative-free nonlinear least squares estimation procedure (Dixon 1983) to produce predicted mean lengths at age for "northern" and "southern" fish.

---

[3]Ito, D. H. 1977. Fecundity of the copper rockfish, *Sebastes caurinus* (Richardson), from Puget Sound, Washington. Unpubl. manuscr. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[4]Robert Francis and Anne Hollowed, Northwest and Alaska Fisheries Center, National Marine Fisheries Service NOAA, 7600 Sand Point Way N.E, Seattle, WA 98115, pers. commun. January 1985.

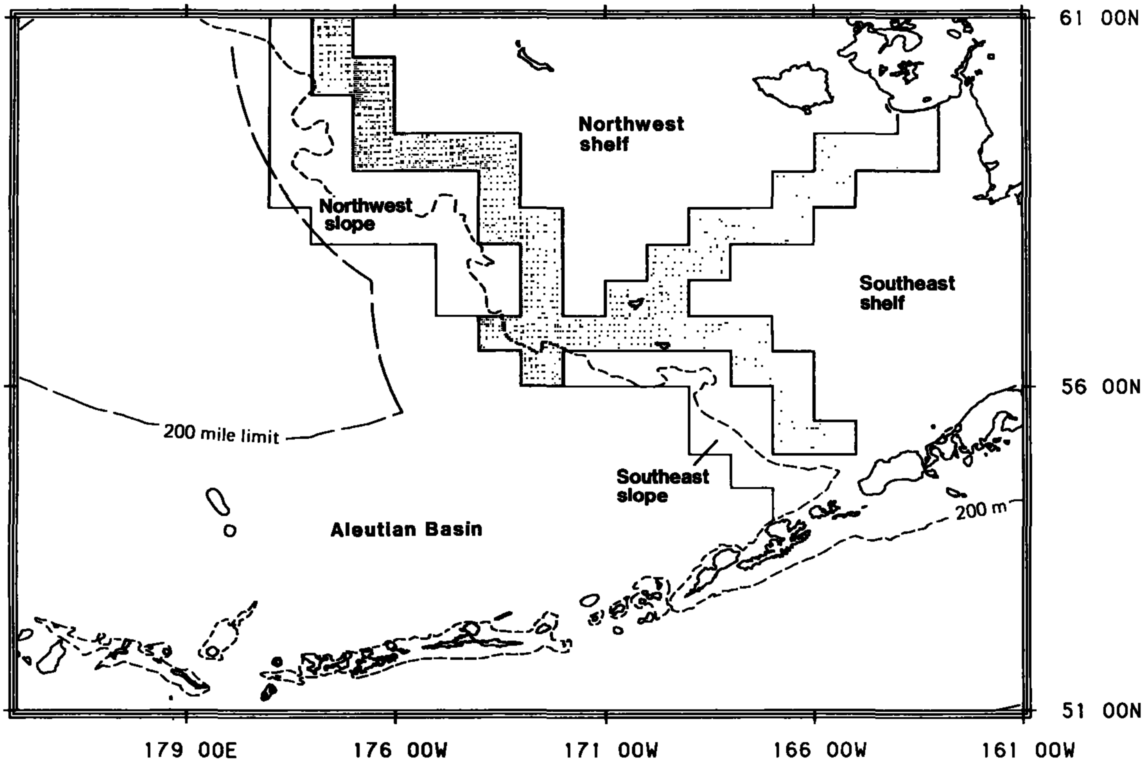

FIGURE 1.—Sampling areas within the Bering Sea. Shaded areas are buffer zones.

The cells were then classified for each sex and quarter using an index of similarity, $Pr(s)$. This index was based on the ratio of the sum of squared deviations of the observed mean length at age from the 6-yr fitted average for the southern region, to the sum of the squared deviations of the observed mean length at age from the southern and northern regions combined:

$$Pr(s) = 1 - [SS(s)/SS(s) + SS(n)]$$

where $SS(s) = \sum_{i=1}^{k} [X(i) - ES(i)]^2$ and

$$SS(n) = \sum_{i=1}^{k} [X(i) - EN(i)]^2.$$

$SS(s)$ = the sum of squared deviations for the southern regions,
$SS(n)$ = the sum of squared deviations for the northern regions,
$ES(i)$ = the 6-yr fitted average from the southern region,
$En(i)$ = the 6-yr fitted average from the northern region,
i = age,
$X(i)$ = the observed mean length at age (i),
k = the maximum age observed.

Thus, $Pr(s)$ is the likelihood of the cell being a southern cell. Arbitrary cut-off values of 0.75 and 0.25 were imposed to classify the southern and northern cells, respectively. Any value >0.25 and <0.75 defined an unknown cell.

New 6-yr average growth curves were fitted for each region by quarter and sex using only those estimates of mean length at age from cells that were classified as northern or southern (i.e., excluding all unknown cells). Partial F-tests showed ($P < 0.001$) that there are significant regional differences in growth between the "southern" (southeast shelf and slope) and the "northern" (Aleutian Basin and northwest slope) areas.

Using the new 6-yr average growth curves, the 1984 data were divided into cells, compared to Francis and Hollowed's (unpubl. data) growth curve, and were classified as northern, southern, or unknown, based on the index of similarity [$Pr(s)$] for both sexes combined:

$$Pr(s) = 1 - [SS(s)_{♀} + SS(s)_{♂}/SS(s)_{♀} + SS(s)_{♂} + SS(n)_{♀} + SS(n)_{♂}]$$

The classification of the 1984 data was examined to see whether the northern and southern cells fell into the same geographic areas as those which originally defined the growth types described by Lynde et al. (fn. 2) and the growth curves of Francis and Hollowed (i.e., the northwest slope and Aleutian Basin areas or the southeast shelf and slope areas).

Analysis of Fecundity

Collections of walleye pollock ovaries for fecundity analysis were subsampled by geographic area to provide at least four ovaries in each 5 cm length interval over the entire available length range. Ovaries were collected from walleye pollock in all areas except the northwest shelf, where observer coverage was inadequate. The oocytes were separated from the ovarian tissue by washing them through successively finer meshed sieves; and a volumetric subsampling method, similar to that described in Gunderson (1977), was used to estimate the total number of oocytes in each ovary. In all ovaries examined, there was a clear separation in the sizes of unyolked (uncounted) and yolked (counted) oocytes. The histological analysis (described below) indicated that ovaries showing this separation in egg size modes were at the stage of maturity suitable for fecundity counts. A minimum of five subsamples were counted for each ovary; if the coefficient of variation between subsample counts exceeded 10%, more counts were done, to a maximum of 10 counts. It was discovered that recounts of individual subsamples accounted for very little of the overall variation between counts, so these were not done on a regular basis.

The average coefficient of variation between subsample counts for each ovary was 5.20% (range, 0.87 to 10.30%). The number of oocytes was estimated for a total of 115 ovaries.

Fork length, ovary-free weight, and the mean of the subsample estimates of fecundity for each fish were used to derive three relationships for each area within the Bering Sea: length-fecundity, length-weight, and weight-fecundity. Nonlinear least-squares regression methods (Dixon 1983) were used to estimate parameters for each relationship. Unequal error variances were observed in the dependent variables of weight and fecundity. This was accounted for by the use of weighting factors in the nonlinear regression procedure. The weighting factor used was the inverse of the variance of the dependent variable.

Because comparison of linear regressions is the most direct method and because the linear and nonlinear regressions showed the same relative positions for each area, Newman-Keuls multiple range tests (Zar 1974) were done on the slopes and intercepts of the equations resulting from the linear regressions, to examine differences in the relationships by area. The regressions were fitted to a length range (38 to 60 cm) common to all areas before comparison.

Tests performed included an overall test for coincidental regression, Newman-Keuls multiple range tests on the slopes of the lines, and multiple range tests for equality of the intercepts of those relationships found to have equal slopes. The procedures outlined in Zar (1974) were followed for all of these tests. If the tests indicated that the relationship under examination did not differ significantly between two or more areas, the data from the areas were combined and a curve fitted to the new set of data using the nonlinear procedure.

Histological Analysis

The ovaries of walleye pollock collected for histological analysis were classified by area, following the same geographic scheme used for the length-at-age and fecundity analyses. The collection was subsampled to obtain ovaries in a complete range of development from each of the five geographic areas. Sections were removed from the central portion of the ovaries. Tanino et al. (1959) have shown that there is no difference in the size composition of oocytes throughout walleye pollock ovaries. All sections were 6 to 10 μm in thickness and were stained with Mayer's haemotoxylin and eosin. In all, 122 ovaries were examined histologically.

Oocytes were classified into 12 categories of development (Hinckley 1986). The overall maturity of each ovary was based on the most advanced oocytes present, and each ovary was assigned to one of 10 maturity classes (Hinckley 1986).

Egg-stage frequency counts, as determined from the histological slides, were used to examine the process of oocyte development. A transect grid was drawn on each slide, and oocyte counts for each stage of development were made at each intersection on the grid. Stage 8 (tertiary yolk) and stage 9 (nuclear migration) oocytes were called stage 8; stage 11 (maturation) and stage 12 (ovulation) were called stage 11, owing to the difficulty in consistently differentiating these stages. Counts from all points on the grid were combined into a total egg-stage frequency for each ovary. Development of the maturing oocytes could be followed by comparing the egg-stage frequencies for each level of maturity.

Slides were also examined for evidence of ovarian rematuration. Rematuring ovaries were defined as those containing identifiable postovulatory follicles (the remnant of the egg membrane left after ovulation and release of the oocyte); thick ovarian walls; and resorbing, unspawned, fully yolked oocytes in ovaries that also contained vitellogenic oocytes.

RESULTS

Spatial and Temporal Distribution of Spawning

Observer information showed that walleye pollock spawning in the Bering Sea began in the Aleutian Basin in January. As the year progressed, spawning was observed further inward over the continental slope and shelf (Fig. 2A through 2H). Spawning occurred between January and March in the basin, between March and June over the southeastern Bering Sea slope and shelf, and between June and August over the northwest slope and shelf. Scattered spawning was noted in the northwestern areas as late as October.

Spawning walleye pollock were caught at depths ranging from 46 to 360 m, most commonly between 100 and 250 m. Temperatures at these depths ranged from $-1.8°$ to 6.0°C ($\bar{x} = 2.34$°C).

The monthly distribution of the commercial fishing fleet in the Bering Sea was examined to assess whether observer reports from the fleet represented the true distribution of spawning. If significant portions of the Bering Sea were not fished by the fleet, concentrations of spawning walleye pollock could have been missed. In January and February, coverage of the continental shelf was scattered and in May most fishing occurred in the southeast portion of the Bering Sea. Coverage of the Aleutian Basin was minimal after March because harvestable concentrations of spawning walleye pollock could not be found in the area after this time (R. Nelson[5]). Nevertheless, the fishing fleet distribution appears to have been sufficiently extensive to detect the majority of spawning walleye pollock, and the reports of spawning obtained from the fleet appear to reasonably represent the true spawning distribution for 1984.

Length-Age Characteristics of Walleye Pollock from Spawning Concentrations

The plots of mean length at age for walleye pollock males (Fig. 3) and females (Fig. 4) suggest that length at age was similar for both sexes in the Aleutian Basin and over the northwest slope. Lengths for the older ages were smaller in these areas than in the other three. Although the data were widely scattered, length at age was similar in the southeast shelf, southeast slope, and northwest shelf, and was larger in these areas than in the basin and the northwest slope.

Comparison of the length-at-age data from $\frac{1}{2}°$ by 1° cells with the growth curves generated by Francis and Hollowed showed that most of the cells assigned to the "northern" group were in the northern slope and buffer areas and in the Aleutian Basin (Fig. 5). Walleye pollock in these areas were characterized by a smaller mean length at age. Cells designated as "southern" were mostly from the southeast and northwest shelf areas and southeast buffer zone (Fig. 5) and contained walleye pollock with a larger mean length at age. The spawning concentrations of walleye pollock, therefore, show the same geographic distribution of the two growth types as seen by Lynde et al. (fn. 2) and Francis and Hollowed (unpubl. data).

Length-Fecundity Relationship

In all areas of the Bering Sea, the length-fecundity relationship for walleye pollock (Fig. 6) was found to be curvilinear ($F = aL^b$, Table 1), similar to that observed for walleye pollock from other regions. The overall test for coincidental regression indicated ($F = 5.51$, $P < 0.001$) that the length-fecundity relationships for the four areas were not identical.

Multiple range test results (Table 2) indicated that the northwest and southeast shelf and slope area regression slopes did not differ significantly.

[5]R. Nelson, Observer Program, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

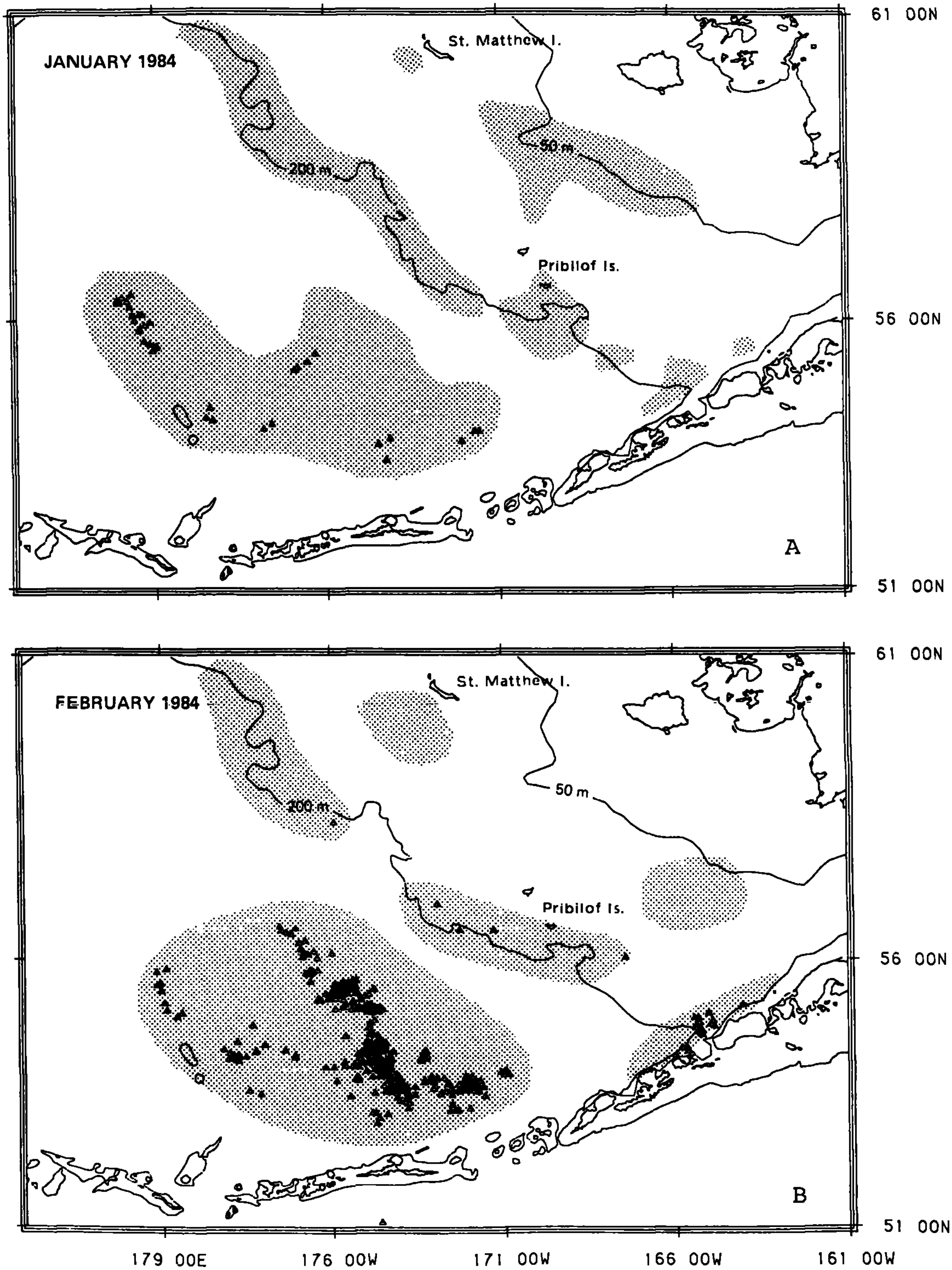

FIGURE 2.—Observed distribution of spawning walleye pollock in 1984, by month. Shaded areas indicate distribution of the

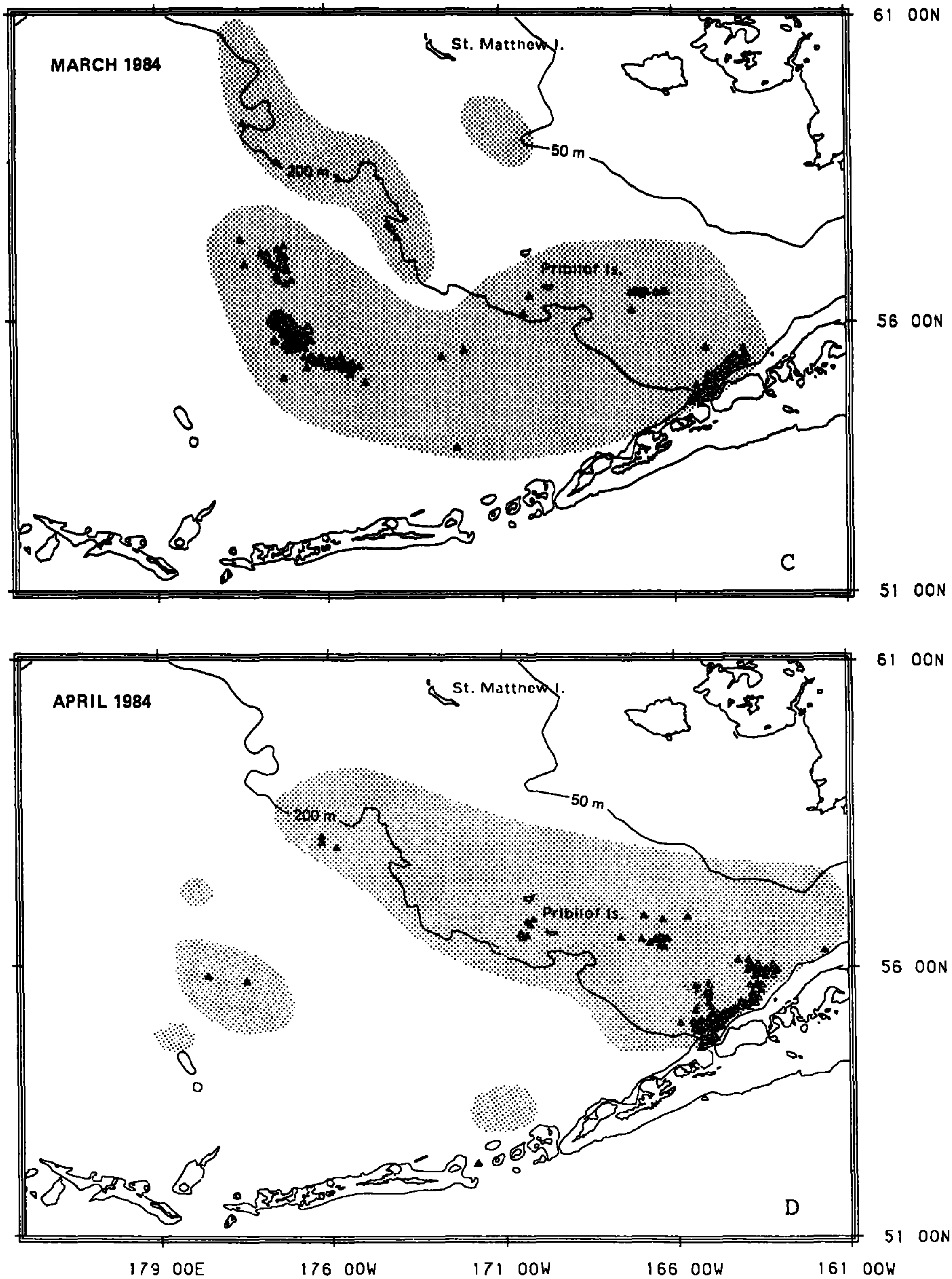

FIGURE 2.—*Continued*—foreign commercial fishing fleet. Triangles indicate hauls in which spawning walleye pollock were caught.

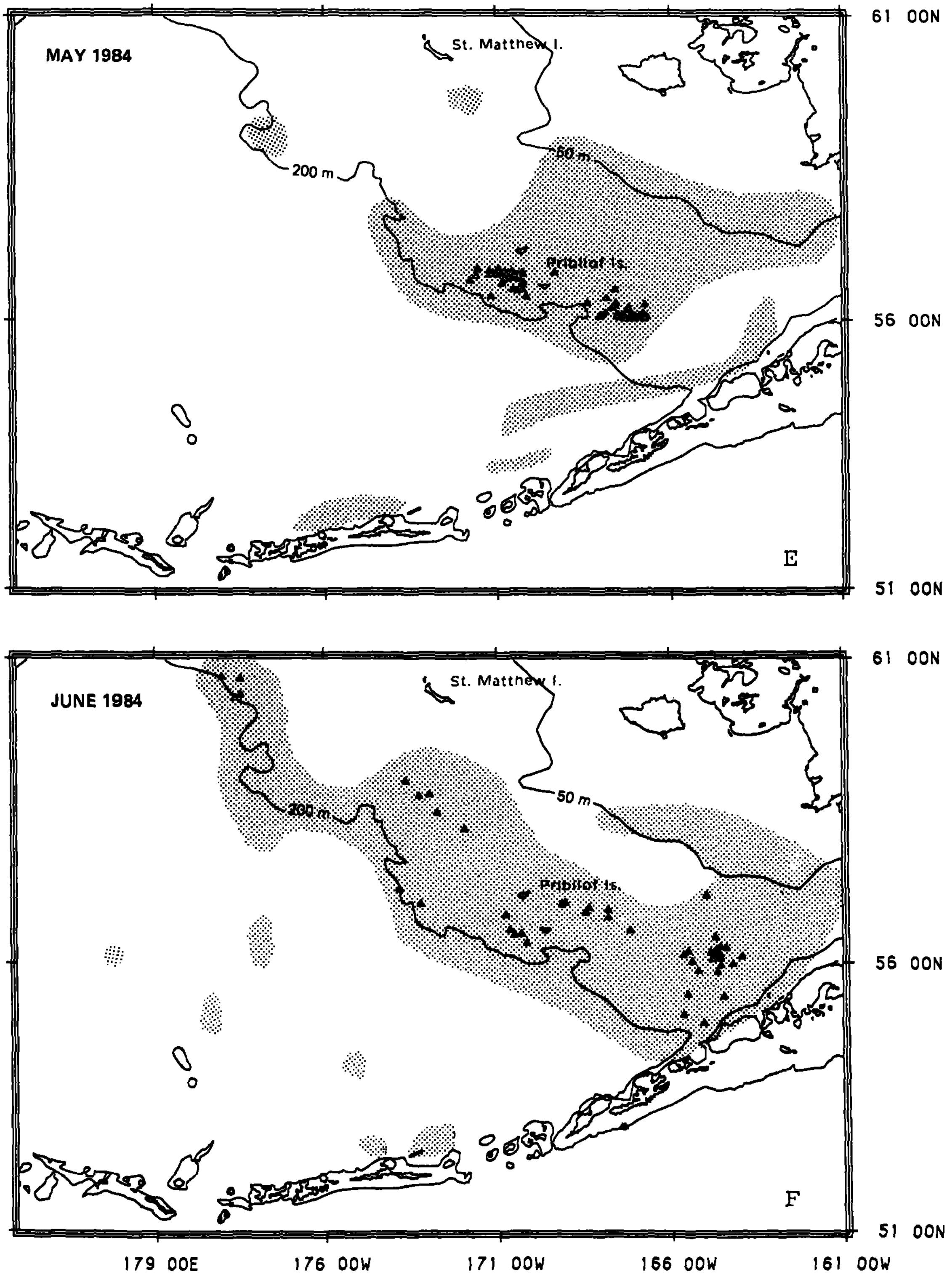

FIGURE 2.—*Continued.*

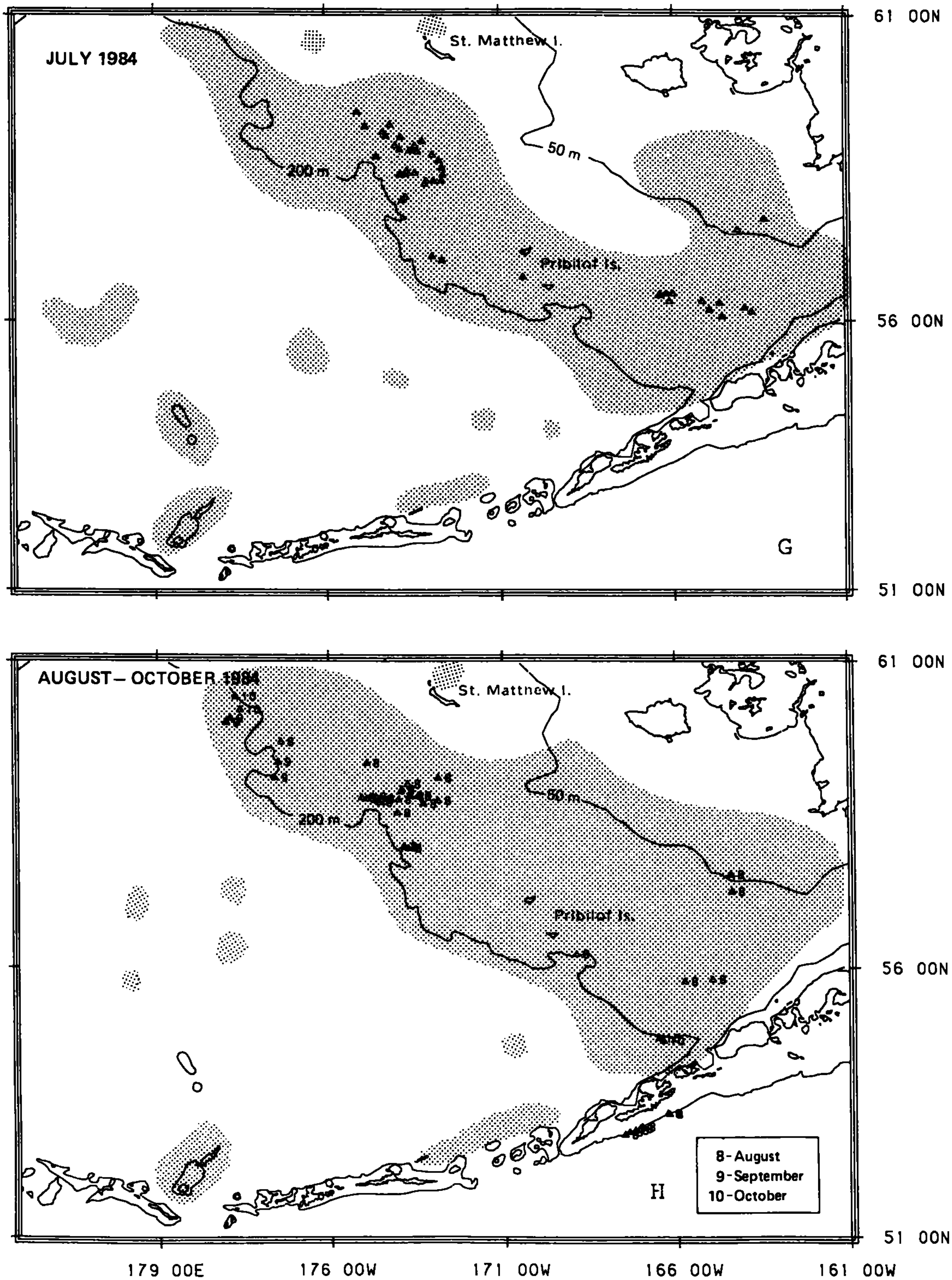

FIGURE 2.—*Continued.*

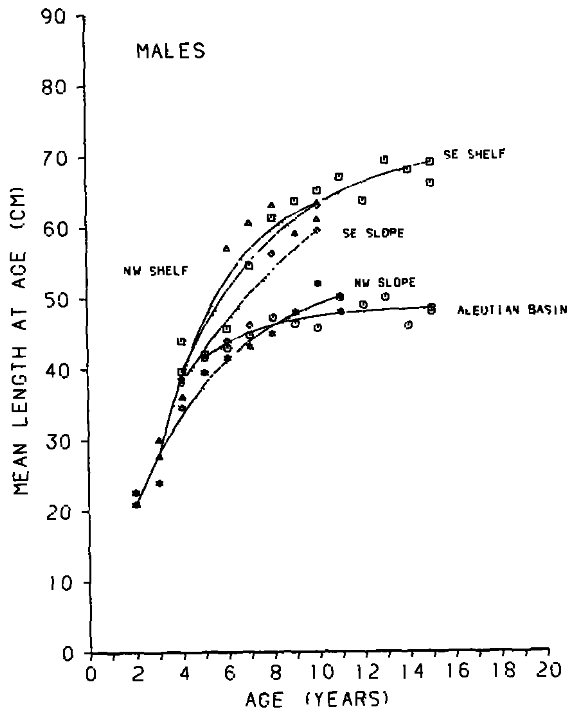

FIGURE 3.—Mean length at age for male walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

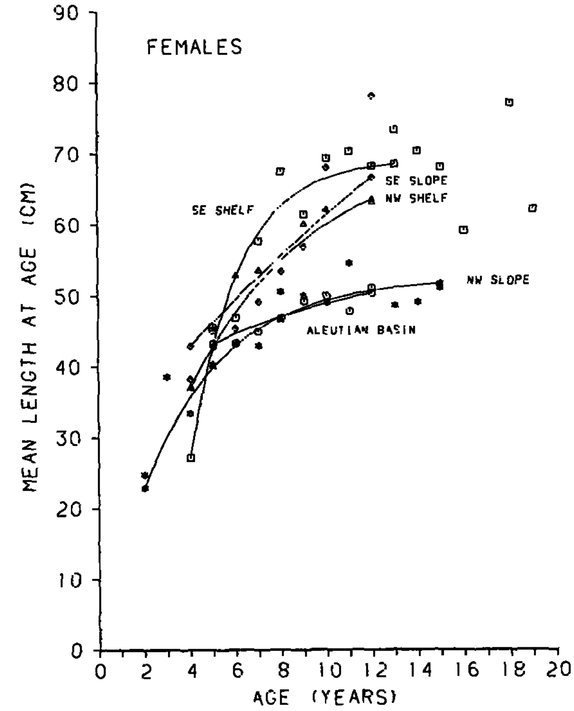

FIGURE 4.—Mean length at age for female walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

TABLE 1.—Length, weight (W), and fecundity (F) relationships for Bering Sea walleye pollock resulting from the nonlinear regression.

		Length-fecundity		Length-weight		Weight-fecundity	
Region	n	F	R^2	W	R^2	F	R^2
Southeast shelf	25	$0.1926L^{3.5439}$	0.865	$0.0120L^{2.8744}$	0.996	$91.7096W^{1.1423}$	0.877
Aleutian Basin	20	$469.2282L^{1.5575}$	0.769	$0.1257L^{2.2300}$	0.983	$9,119.3100W^{0.4570}$	0.737
Southeast slope	28	$4.6528L^{2.8066}$	0.944	$0.0041L^{3.1134}$	0.997	$906.4315W^{0.8534}$	0.935
Northwest slope	38	$0.0872L^{3.7869}$	0.995	$0.0001L^{3.4862}$	0.999	$118.6879W^{1.1439}$	0.995
Combined areas	91	[1]$0.1719L^{3.6046}$	0.907	[2]$0.0027L^{3.2743}$	0.996	[1]$174.9222W^{1.0765}$	0.900

The multiple range test on the regression intercepts could not distinguish the intercepts of the three lines from the slope and shelf areas. The multiple range test on regression slopes also showed that the slopes of the regressions from the Aleutian Basin and from the southeast slope areas could not be distinguished; however, the intercepts of the regressions from these two areas differed significantly.

Based on these analyses, the length-fecundity relationships from all shelf and slope areas appeared to be similar, and the relationship in these areas was different from that seen in the Aleutian Basin. Fecundity increased almost linearly with length in Aleutian Basin walleye pollock; however, pollock larger than about 60 cm are not found in the basin (Okada 1977[6], 1983[7]; J.

[6]Okada, K. 1977. Preliminary report of an acoustic survey of the pollock stock in the Aleutian Basin and the adjacent waters in the summer of 1977. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, September 1977. Fishery Agency of Japan.

[7]Okada, K. 1983. Biological characteristics and abundance of the pelagic pollock in the Aleutian Basin. Document

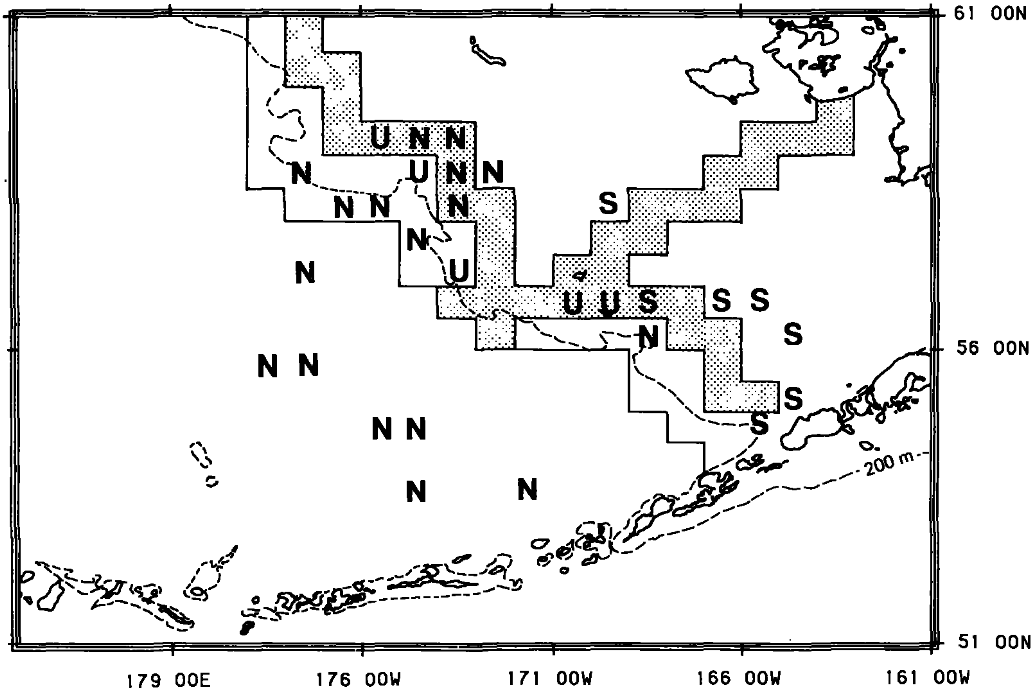

FIGURE 5.—Locations of cells containing walleye pollock from spawning concentrations with growth rates similar to "northern" (N), "southern" (S), or "unknown" (U) groups of Lynde et al. (text footnote 2).

Traynor[8]). The great increase in fecundity, seen in fish larger than 60 cm, resulted in the observed curvilinear relationships found in the other areas.

Length-Weight Relationship

The multiple range test results on the length-weight relationship for walleye pollock were inconclusive (Table 3). The hypothesis that the length-weight relationship was the same in all areas was rejected ($F = 3.4156$, $0.0025 < P < 0.005$), but the slopes of the regression lines did not differ significantly. A test of intercept equal-

submitted to the annual meeting of the International North Pacific Fisheries Commission, 1983. Far Seas Fisheries Research Laboratory, Japan.

[8]J. Traynor, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

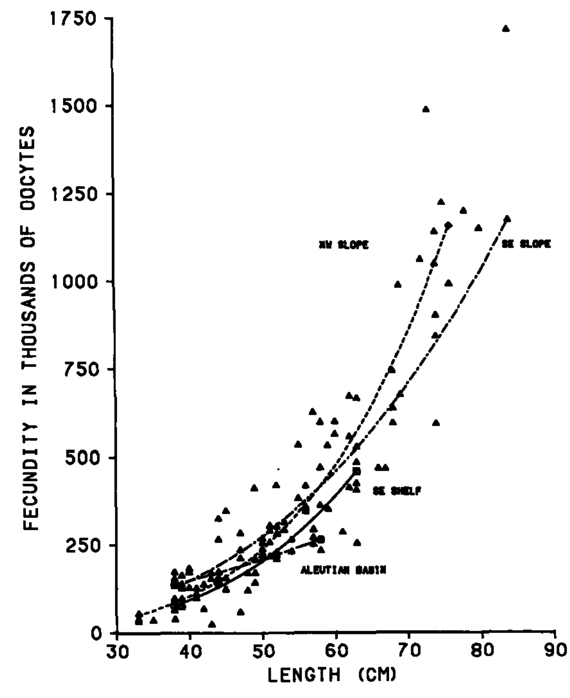

FIGURE 6.—Observed and predicted relationships between fecundity and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

TABLE 2.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-fecundity regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1		2	3	4
Ranked slopes:	1.6554		2.7661	4.0967	4.2659
Area:	Aleutian Basin		SE slope	SE shelf	NW slope

Comparison	Difference	SE	q	p	q(0.05,78,p)
4 vs. 1	2.6105	0.5320	4.9070	4	3.70
4 vs. 2	1.4998	0.5735	2.6152	3	3.37
4 vs. 3	Do not test				
3 vs. 1	2.4413	0.4926	4.9559	3	3.37
3 vs. 2	Do not test				
2 vs. 1	1.1107	0.5928	1.8737	2	2.81

INTERCEPTS

A. Ranks of intercepts:	1	2	3
Ranked intercepts:	−4.211	−3.864	1.711
Area:	NW slope	SE shelf	SE slope

Comparison	q	p	q(0.05,60,p)
3 vs. 1	1.3870	3	3.40

B. Ranks of intercepts:	1	2
Ranked intercepts:	1.711	5.784
Area:	SE slope	Aleutian Basin

Comparison	q	p	q(0.05,35,p)
2 vs. 1	3.6720	2	2.88

TABLE 3.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-weight regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	2.7927	2.8883	3.1635	3.3161
Area:	Aleutian Basin	SE shelf	SE slope	NW slope

Comparison	Difference	SE	q	p	q(0.05,107,p)
4 vs. 1	0.5234	1.7581	0.2977	4	3.70

INTERCEPTS

Ranks of intercepts:	1	2	3	4
Ranked intercepts:	−6.3145	−5.6965	−4.5605	−4.1570
Area:	NW slope	SE slope	SE shelf	Aleutian Basin

Comparison	q	p	q(0.05,107,p)
4 vs. 1	6.2685	4	3.70
4 vs. 2	4.1848	3	3.37
4 vs. 3	1.4944	2	2.81
3 vs. 1	4.3880	3	3.37
3 vs. 2	2.5906	2	2.81
2 vs. 1	0.4340	2	2.81

ity showed a significant difference ($F = 3.608$, $0.01 < P < 0.025$); however, the multiple range test on intercepts was inconclusive and showed overlaps in the equality of intercepts by area. The curves in Figure 7 all appear similar. A nonlinear regression on the combined data from all areas explained a high percentage of the overall variation (99.63%) (Table 1). It seems reasonable to use one equation to describe the length-weight relationship for all areas combined.

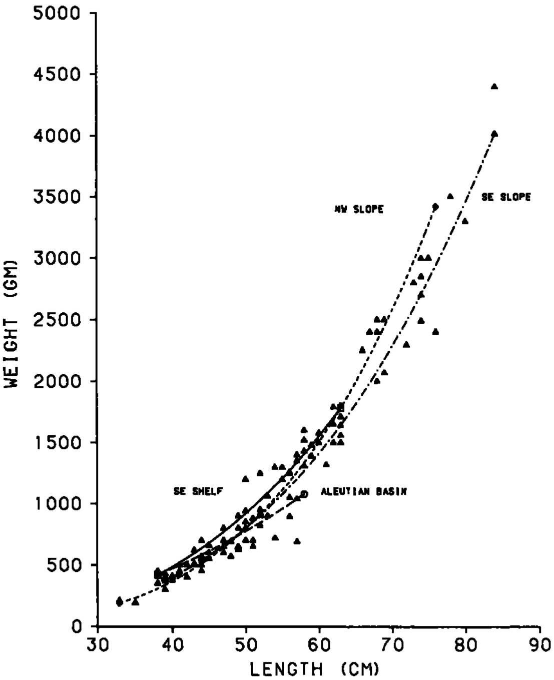

FIGURE 7.—Observed and predicted relationships between weight and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the weight of the sampled fish.

Weight-Fecundity Relationship

The weight-fecundity relationship for walleye pollock in all areas was nearly linear (Fig. 8). The overall test for coincidental regressions indicated that the weight-fecundity relationship differed significantly between areas ($F = 7.6534$, $P < 0.001$). Comparison of the linearized equations showed that the regression slopes were similar in the northwest continental slope, the southeast continental shelf, and the southeast continental slope areas (Table 4). The multiple range test on the intercepts of the regressions from the two continental slope areas indicated that they were similar, but different from the regression intercept of the line from the southeast shelf area. The multiple range test on the regression slopes showed that the slope of the weight-fecundity regression for Aleutian Basin pollock was similar to that seen in the southeast continental slope area; however, a comparison of the intercepts did show a significant difference between these two areas.

As with the length-fecundity relationship, the weight-fecundity relationship appeared similar in the continental shelf and slope areas, and differed from the relationship seen in the Aleutian Basin. The weight-fecundity relationship for the Aleutian Basin showed the same trend that was seen for length-fecundity, i.e., a much more gradual increase in fecundity with weight than in other areas.

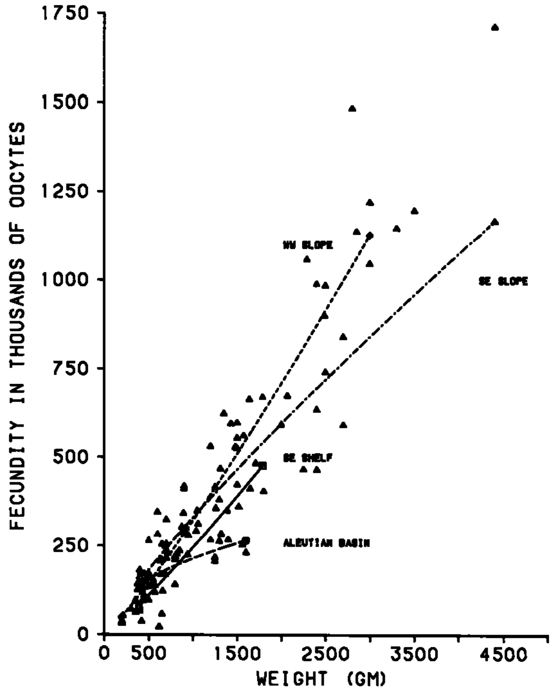

FIGURE 8.—Observed and predicted relationships between fecundity and weight for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

Ovarian Maturation

Examination of the egg-stage frequencies indicates that the process of ovarian development in Bering Sea walleye pollock (Fig. 9A through 9M) is one of partial synchrony. A "reserve" fund (Foucher and Beamish 1980) of small, unyolked oocytes exists at all times in the ovary; this consists of oocytes at the early and late perinucleus stages. The reserve fund is represented by the single mode in Figure 9A. A portion of this group begins the process of yolk formation, advancing asynchronously to the fully yolked tertiary yolk stage (stage 8). This developing mode is visible in Figure 9B, C, and D. When vitellogenesis is complete, the mode of developing oocytes is com-

TABLE 4.—Newman-Keuls multiple range tests on the slopes and intercepts of the the notation

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	0.5169	0.9577	1.2280	1.3978
Area:	Aleutian Basin	SE slope	NW slope	SE shelf

Comparison	Difference	SE	q	p	q (0.05,78,p)
4 vs. 1	0.8809	0.1555	5.6650	4	3.70
4 vs. 2	0.4401	0.1698	2.5919	3	3.37
4 vs. 3	Do not test				
3 vs. 1	0.7111	0.1574	4.5178	3	3.37
3 vs. 2	Do not test				
2 vs. 1	0.4408	0.1847	2.3866	2	2.81

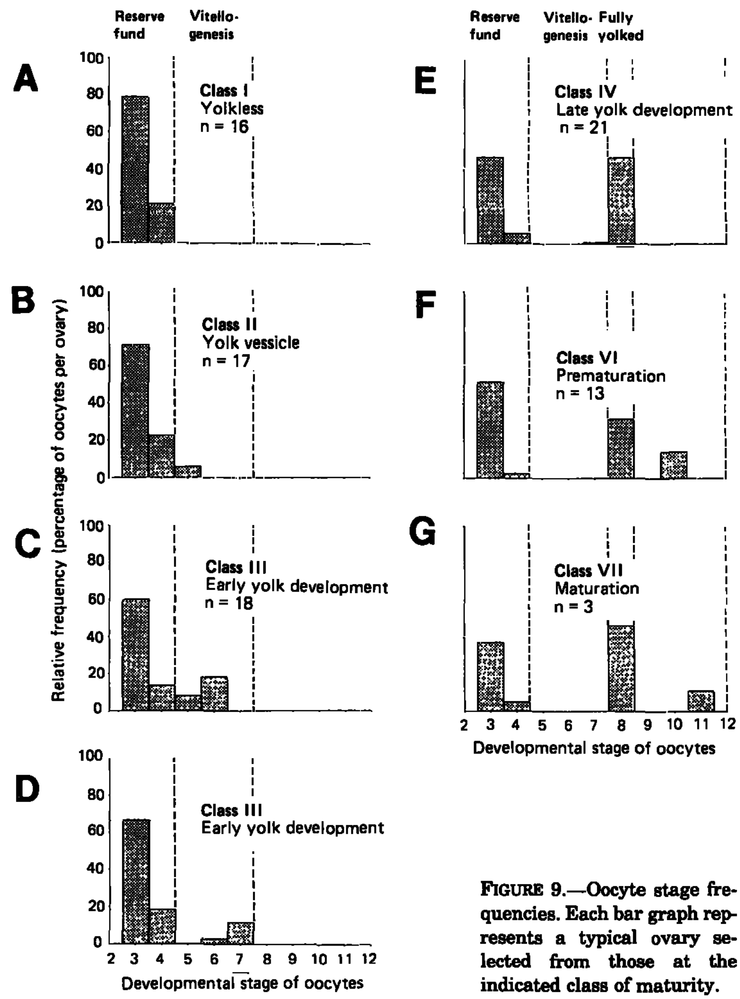

FIGURE 9.—Oocyte stage frequencies. Each bar graph represents a typical ovary selected from those at the indicated class of maturity.

inearized weight-fecundity regressions from four areas in the Bering Sea (following of Zar 1974).

INTERCEPTS

A. Ranks of intercepts:	1	2	3
Ranked intercepts:	2.7420	4.2815	6.1588
Area:	SE shelf	NW slope	SE slope
Comparison	q	p	q(0.05,60,p)
3 vs. 1	6.4957	3	3.40
3 vs. 2	1.3520	2	2.83
2 vs. 1	5.4330	2	2.83
B. Ranks of intercepts:	1		2
Ranked intercepts:	6.1588		8.7805
Area:	SE slope		Aleutian Basin
Comparison	q	p	q(0.05,35,p)
2 vs. 1	5.2249	2	2.88

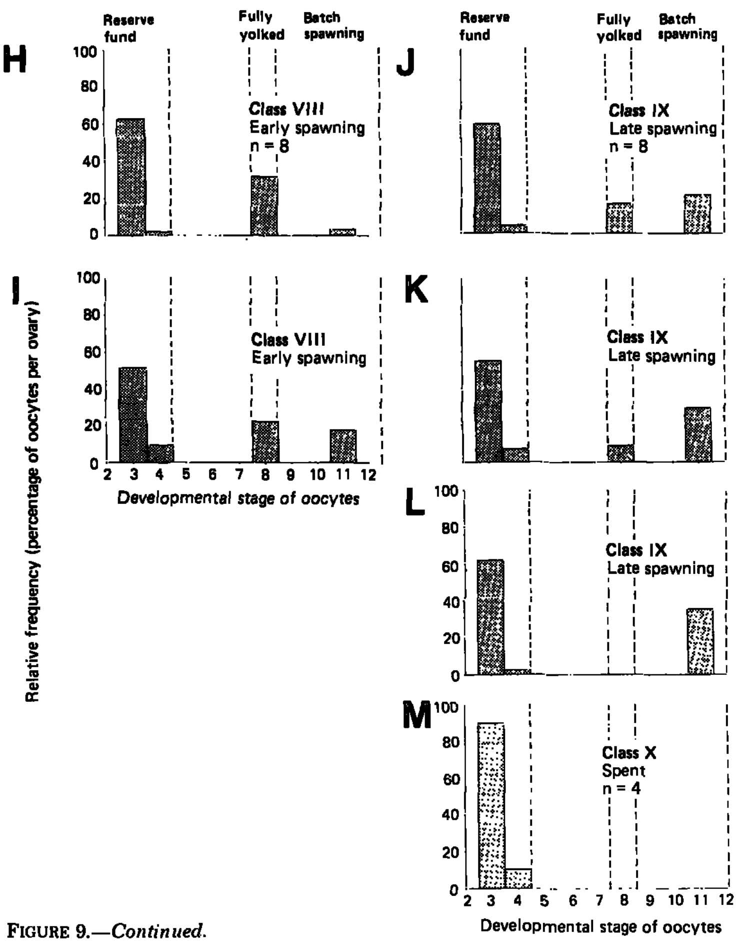

FIGURE 9.—*Continued.*

pletely separated from the remaining reserve fund (Fig. 9E). This appears to be the best stage to estimate fecundity, as no more eggs will be recruited into the developing mode, and spawning has not yet begun.

The final part of the maturation process appears to occur in a synchronized manner, with successive groups of fully yolked oocytes proceeding through the last stages (homogenization of yolk, hydration, ovulation, and release) in discrete batches. During the spawning period, the proportion of nonhydrated (stage 8) oocytes gradually decreases, and that of hydrated oocytes (stage 11) increases, until only hydrated oocytes remain. This progression is visible in Figure 9H through L. The spawning of matured oocytes in discrete groups appears to represent the "batch spawning" process in walleye pollock.

Spent ovaries contain oocytes in the early and late perinucleus stages (the reserve fund), postovulatory follicles, and, in some cases, yolked but unspawned oocytes undergoing resorption. Redeveloping ovaries, i.e., those containing signs of prior spawning and vitellogenic oocytes, were found in small numbers (9 out of 122 ovaries examined). Of the 18 ovaries examined for March, only one appeared to be developing new oocytes, possibly early enough for a second spawning that year. The rest of the redeveloping ovaries were collected from June to September from walleye pollock in the southeast shelf area. Redeveloped ovaries found in the summer with oocytes at the yolk vessicle stage may spawn in the autumn or during the next year (small numbers of walleye pollock have been observed in spawning condition throughout the year). Rematuring ovaries containing oocytes at the primary and secondary yolk stages were found only in August and September. More than one-half of these ovaries (5 out of 8) showed signs of resorption of the developing oocytes, and would probably not spawn again that year.

DISCUSSION

The results of this study appear to indicate that at least three separate spawning stocks of walleye pollock exist in the Bering Sea. One is located in the Aleutian Basin, a second over the northwest continental slope, and a third in the southeast shelf, southeast slope, and northwest shelf areas.

As noted by Ogawa (1956), geographical isolation or ecological separation of spawning concentrations may indicate population separation. Overall, the spawning season in the Bering Sea lasts about 8 months, and spawning within the different areas is separated by 500 to 1,000 km. Within the different areas, spawning lasts 2 to 3 months.

Dissimilarities in several population characteristics were observed between groups spawning in the different areas, supporting the concept of multiple stocks. Length at age differed by area, with larger length at age seen in walleye pollock spawning over the southeast shelf, southeast slope, and northwest shelf, and smaller length at age seen in walleye pollock spawning in the Aleutian Basin and over the northwest slope. These results were also found by Lynde et al. (fn. 2).

Fecundity relationships in all shelf and slope areas were similar, and differed from that seen in the Aleutian Basin. Aleutian Basin walleye pollock showed the lowest fecundity. Walleye pollock from the northwest and the southeast slope areas showed the highest fecundity. Fecundity estimates for walleye pollock in Shelikof Strait in 1982 (Miller et al. 1986[9]; $F = 1.2604L^{3.2169}$) and in British Columbia waters in 1979 (Thompson 1981; $F = 6.771L^{2.981}$) are higher than the Bering Sea estimates from this study. A general trend of declining fecundity exists towards the northern range of walleye pollock. Due to possible interannual variability in fecundity, caution should be taken in comparing studies done in different regions and years.

Further research is needed for walleye pollock, in the Bering Sea and elsewhere, to determine the proportion of annual fecundity actually realized, i.e., whether resorption of yolked oocytes during maturation and after spawning is significant. Preliminary histological analysis of walleye pollock ovaries from Shelikof Strait (Hinckley unpubl. data) suggests that resorption of yolked oocytes may not be significant.

Based on similarities in growth, Lynde et al. (fn. 2) proposed that mixing of walleye pollock stocks occurs between the Aleutian Basin and the northwest slope; however, the findings of this study indicate the mixing does not occur during the spawning season. Spawning over the basin and the northwest slope is separated by about 5 months and 500 km, yet there was no sign of

[9]Miller, B. S., D. R. Gunderson, D. Glass, D. B. Powell, and B. A. Megrey. 1986. Fecundity of walleye pollock (*Theragra chalcogramma*) from Shelikof Strait, Gulf of Alaska. Fish. Res. Inst. Rep. FRI-UW-8608. Univ. Washington, Seattle, WA 98195.

rematuration in walleye pollock ovaries collected from the northwest slope late in the season, which could have indicated that these fish spawned first in the basin and then later on the northwest slope. The difference in fecundity between these areas also supports the theory that spawners found in the northwest slope area form a separate group from those found in the Aleutian Basin. The similarities in growth found by Lynde et al. (fn. 2) may be a result of mixing occurring at other times of the year.

A reduced food supply may produce the smaller length at age and lower fecundity of Aleutian Basin walleye pollock. The reduced growth of walleye pollock in the basin is probably due to the lack of fish, particularly juvenile walleye pollock, in the diet (Okada fn. 7; Traynor and Nelson 1985; Dwyer et al. in press). Dwyer (1984) also found that the mean weight of stomach contents of basin-caught fish was low compared with that of fish caught over the shelf and slope. Reduced food supplies have been shown to lower fecundity in several species (Scott 1962; Hester 1964; Bagenal 1969; Leggett and Power 1969; Wootton 1973, 1977; Hislop et al. 1978).

Histological examination of walleye pollock ovaries further supports the theory that spawning concentrations found in widely separated areas do not mix extensively. Walleye pollock spawning in the Bering Sea can be classified as partially synchronous, with one discrete group of oocytes brought to maturation and then spawned in successive batches. This is similar to the process described for walleye pollock from Japan (Sakurai 1977). The maturation of a second group of oocytes from vitellogenesis to spawning within 1 year does not appear to be common. Maximum walleye pollock fecundity is therefore annually determinate, and the duration of an individual female's spawning period is limited by the duration of the batch spawning process. If an individual does batch spawn a group of matured oocytes over 1 month, as Sakurai's (1982) laboratory studies suggest, it seems unlikely that it would migrate any great distance over this time while actively spawning.

To infer stock separation from the results of this study (i.e., that fish return to the same discrete areas each year to spawn) requires assuming that the timing and distribution of spawning, the dynamics of ovarian maturation, and the differences in growth and fecundity remain relatively constant from year to year. The timing and location of spawning have been similar from 1982 to 1986 (Hinckley unpubl. data; R. Nelson fn. 5). The process of maturation is basically the same for walleye pollock found in the Bering Sea, in the Gulf of Alaska (Miller et al. fn. 9), and in Japanese waters (Sakurai 1977, 1982). Differences in mean length at age represent cumulative differences in growth over the life of a fish, and systematic variation by area such as that seen in this study probably reflects separation over a period of years. The study by Lynde et al. (fn. 2) documented the same differences in growth by area over a period of 8 years as was seen in this study for 1984. It is not known at what point annual fecundity is determined in walleye pollock, but as egg production is influenced by food supply in many species, and as walleye pollock feed mostly during the spring and summer and less during the winter (Dwyer et al. 1986) and the spawning season, yearly fecundity may be determined about 1 year before spawning. The results of this study suggest that the assumption of stock separation over a period of years is reasonable.

This study has outlined the timing and distribution of walleye pollock spawning in the Bering Sea for 1984, and postulates the existence of at least three separate spawning stocks. Further research is needed on the biological and oceanographic conditions occurring in the different spawning areas in order to understand the reasons for the apparent separation of stocks, and to clarify differences in recruitment and production by these stocks.

ACKNOWLEDGMENTS

I would like to express my thanks to Kevin Bailey and Robert Francis for their guidance and support. Russell Nelson and the U.S. foreign fisheries observers made possible the collection of data and samples. Anne Hollowed assisted in the length at age analysis, Linda Rhodes and Beverly Macewicz gave advice on histology, and Berne Megrey assisted with the analysis of fecundity. Arthur Kendall, William Karp, and Gary Stauffer made useful comments on the manuscript.

LITERATURE CITED

ALTON, M. S., M. O. NELSON, AND B. A. MEGREY.
In press. Changes in the abundance, composition, and distribution of pollock (*Theragra chalcogramma*) in the western Gulf of Alaska (1961-1984). Fish. Res. (Amst.)

BAGENAL, T. B.
1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish. Biol. 1:167-182.

BAKKALA, R. G., V. WESPESTAD, AND L-L. LOW.
In press. Historical trends in abundance and current condition of walleye pollock in the eastern Bering Sea. Fish. Res. (Amst.)

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth. Human Biol. 10:81-113.

DIXON, W. J. (editor).
1983. BMDP Statistical Software. Univ. Calif. Press, Berkeley, CA., 735 p.

DWYER, D. A.
1984. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. M.S. Thesis, Univ. Washington, Seattle, 102 p.

DWYER, D. A., K. BAILEY, AND P. LIVINGSTON.
In press. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci.

DWYER, D. A., K. BAILEY, P. LIVINGSTON, AND M. YANG.
1986. Some preliminary observations on the feeding habits of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, based on field and laboratory studies. Int. North Pac. Fish. Comm. Bull. 45:228-246.

FOUCHER, R. P., AND R. J. BEAMISH.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41-48.

GUNDERSON, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull., U.S. 75:369-403.

HESTER, F J
1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish. Res. Board Can. 21:757-764.

HINCKLEY, S.
1986. Spawning dynamics and fecundity of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. M.S. Thesis, Univ. Washington, Seattle, 104 p.

HISLOP, J. R. G., A. P. ROBB, AND J. A. GAULD.
1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish. Biol. 13:85-98.

LEGGETT, W. C., AND G. POWER.
1969. Differences between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland. J. Fish. Res. Board Can. 26:1585-1596.

NISHIYAMA, T., AND T. HARYU.
1981. Distribution of walleye pollock eggs in the uppermost layer of the southeastern Bering Sea. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 2, p. 993-1012. Univ. Wash. Press, Seattle.

OGAWA, T.
1956. Studies on fisheries and biology of important fish Suketo-dara (Pollock). Bull. Jpn. Sea Reg. Fish. Res. Lab. 4:93-140.

SAKURAI, Y. (formerly known as T. H. Yoon)
1977. Sexual maturity and spawning process of Alaska pollock, *Theragra chalcogramma* (Pallas) in Funka Bay, Hokkaido. M.S. Thesis, Hokkaido Univ., Hakodate, Hokkaido, Japan. (Translation by A. Shiga and A. M. Shimada, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, 7600 Sand Point Way NE, Seattle, WA 98115.)
1982. Reproductive ecology of walleye pollock *Theragra chalcogramma* (Pallas). Ph.D. Thesis, Hokkaido Univ., Hakodate, Hokkaido, Japan. (Translation by T. Nishida, N. D. Davis, and T. Nishiyama for National Marine Fisheries Service, Northwest and Alaska Fisheries Center, 7600 Sand Point Way NE, Seattle, WA 98115.)

SCOTT, D. P.
1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 19:715-731.

TANINO, Y., H. TSUJISAKI, K. NAKAMICHI, AND K. KYUSHIN.
1959. On the maturity of Alaska pollock, *Theragra chalcogramma* (Pallas). (In Jpn.) Hokkaido Reg. Fish. Res. Lab. 20:145-164.

THOMPSON, J. M.
1981. Preliminary report on the population biology and fishery of walleye pollock (*Theragra chalcogramma*) off the Pacific coast of Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1031.

TRAYNOR, J. J., AND M. O. NELSON.
1985. Results of the U.S. hydroacoustic survey of pollock on the continental shelf and slope. *In* R. G. Bakkala, and K. Wakabayashi (editors), Results of cooperative U.S.-Japan groundfish investigations in the Bering Sea during May-August 1979, p. 192-199. Int. North Pac. Fish. Comm. Bull. 44.

WOOTTON, R. J.
1973. The effect of size of food ration on egg production in the female three-spined stickleback, *Gasterosteus aculeatus* L. J. Fish. Biol. 5:89-96.
1977. Effect of food limitation during the breeding season on the size, body components and egg production of female sticklebacks (*Gasterosteus aculeatus*). J. Anim. Ecol. 46:823-834.

ZAR, J. H.
1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.