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A METHOD OF ESTIMATING SPAWNING BIOMASS FROM EGG SURVEYS WITH AN APPLICATION TO WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN SHELIKOF STRAIT, ALASKA

by

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ABSTRACT. The annual egg production method of estimating spawning biomass was applied to the population of walleye pollock that spawn in Shelikof Strait, Alaska. Ichthyoplankton surveys are routinely conducted by the National Marine Fisheries Service in Shelikof Strait during peak spawning time of walleye pollock. Survey data from 1981 and from 1985 to 1988 were used in this analysis. The annual production of eggs was estimated in two steps. First, the average spawning season was described by a bell-shaped curve relating egg production to date within the season. This was estimated by regressing total abundance of young eggs from each cruise against the mean date of the cruise. Only those years with multiple cruises during the spawning season were used to estimate parameters of the annual egg production curve. Peak spawning was found to occur between 15 March and 2 May. Next, egg mortality and annual egg production were estimated by integrating a model over the spawning season that combines the annual egg production curve with an exponential mortality model. This model allows for the different production rates of eggs of different ages from the same survey and was fit to the one survey from each year that occurred during peak spawning. Annual egg production appears to have declined since the highest level in 1981. Annual fecundity per gram female varied over years but was linear with female weight. Sex ratio was assumed to be 0.5 in numbers of fish, but was scaled to average male and female weights. The resulting spawning biomass estimates follow the same downward trend as the annual egg production estimates and follow the same trend as biomass estimates for walleye pollock based on other methods and surveys.

CONTENTS

INTRODUCTION

Walleye pollock, *Theragra chalcogramma,* belong to the family Gadidae. Adults are primarily demersal and juveniles are primarily pelagic, but both life stages occur over the full depth range of the species. Pollock become fully mature at four to six years of age. Pollock are determinate spawners (Hinckley, 1987), that is, the potential number of eggs to be spawned in a season is determined physiologically before spawning begins. They spawn mainly in spring and each mature female pollock releases several batches of eggs during the season, but limited spawning occurs almost year-round throughout the Gulf of Alaska. A major portion of Gulf of Alaska walleye pollock spawn in Shelikof Strait (Fig. 1a) based on observed distributions of pollock eggs throughout the Gulf of Alaska (Kendall and Picquelle, 1990). Eggs occur between depths of 150 m and 250 m; they hatch in about two weeks into larvae that reside in the upper part of the water column (Kendall and Kim, 1989). The highest density of spawning adults and eggs have been found in deep water in the sea valley on the Alaskan Peninsula side of Shelikof Strait (Fig. 1b) (Kendall and Picquelle, 1990).

The walleye pollock fishery in the North Pacific is the largest single species fishery in the world (Megrey, 1991). The largest portion of this fishery is in the Bering Sea, but the Gulf of Alaska walleye pollock fishery is very important to the local economy. Fishery managers need accurate and precise biomass estimates to provide rational management. In the case of Gulf of Alaska walleye pollock, reliable biomass estimates are especially critical

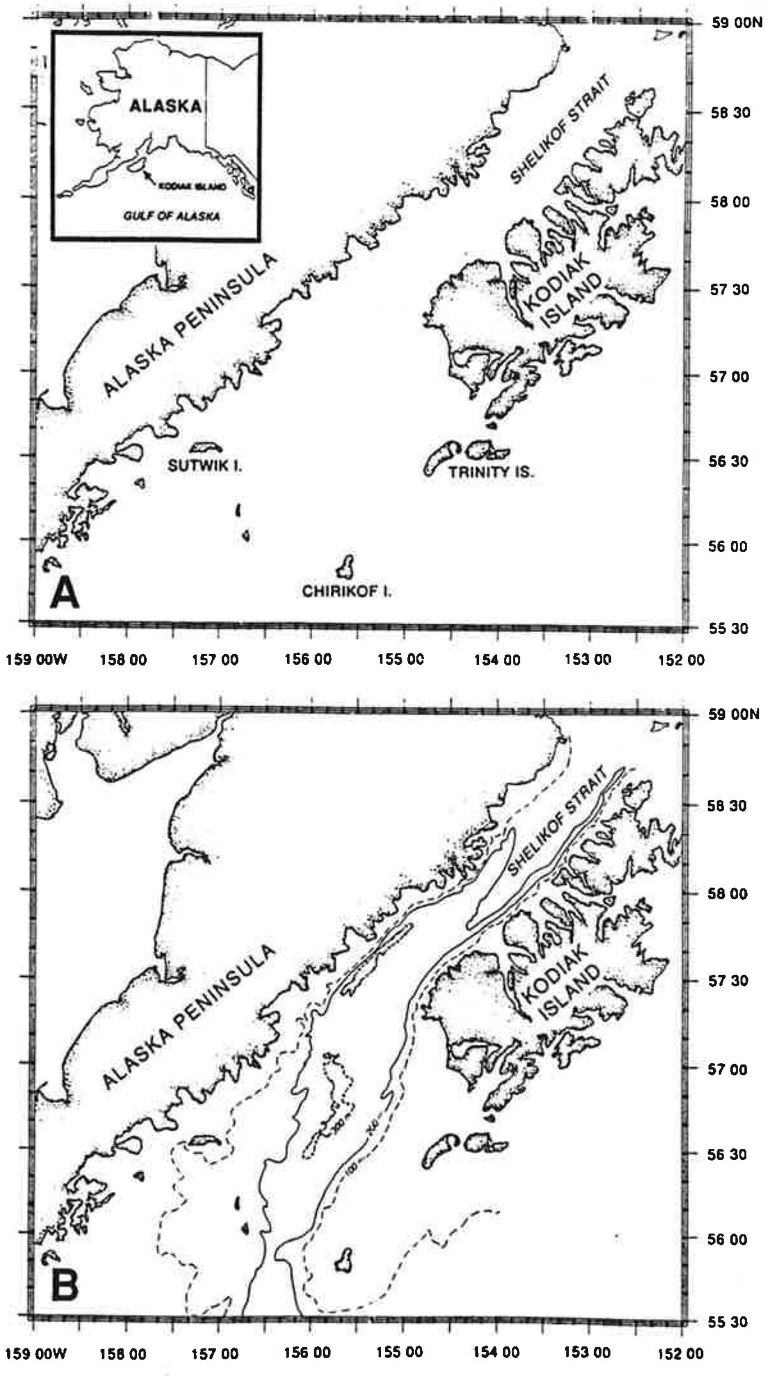

Figure 1. 1a: Gulf of Alaska and Shelikof Strait. 1b: Bathymetry of Shelikof Strait (100 m, 200 m, and 300 m depth contours).

in light of the decline in pollock population abundance since the early 1980's (Hollowed and Megrey, 1990, 1991).

There are currently two methods of estimating biomass for the walleye pollock stock in Shelikof Strait, Gulf of Alaska: 1) echo integration midwater trawl surveys (Nunnallee and Williamson, 1989), and 2) application of an age-structured stock assessment analysis (Hollowed and Megrey, 1989, 1990, 1991) using the stock synthesis model (Methot, 1989, 1990). The stock synthesis model is a new method of stock assessment that uses age-composition and catch-biomass data from the commercial fishery of the entire Gulf of Alaska, and biomass estimates from both the annual echo-integration midwater trawl (acoustic) surveys and the triennial bottom trawl surveys. A description of stock synthesis is beyond the scope of this paper, the reader can find more detailed information in Methot (1989, 1990). Stock synthesis biomass estimates are presently being used for management decisions. Even though the stock synthesis model integrates information from acoustic and bottom trawl surveys with commercial fisheries data, the three data sources taken by themselves each suggest different trends in the pollock stock dynamics (Megrey et al., 1990). The study presented in this paper has produced fishery-independent spawning biomass estimates for walleye pollock in Shelikof Strait, Gulf of Alaska, for the years 1981 and 1985 through 1988, using the annual egg production method. Two earlier studies have also produced egg production spawning biomass estimates for this population of pollock for 1981 (Kim and Gunderson, 1989; Bates, 1987).

OVERVIEW OF THE ANNUAL EGG PRODUCTION METHOD FOR ESTIMATING SPAWNING BIOMASS

The annual egg production method may be used to estimate spawning biomass of walleye pollock because it is a determinate spawner, which allows total fecundity (the standing stock of advanced yolked oocytes in the ovary) to be measured directly. If total fecundity is estimated prior to the onset of spawning it provides an estimate of potential annual fecundity (Hunter et al., 1985; Hunter et al., 1992), an important parameter in the annual egg production method.

The annual egg production spawning biomass estimate is based on the following relationship:

$$P_a = B_f * E \qquad \text{[Eqn. 1]}$$

that is, the total number of eggs produced in the spawning season (P_a) is equal to the total biomass of spawning females (B_f) multiplied by the number of eggs produced per unit weight of mature female (E). Equation 1 is modified to include total spawning biomass by incorporating the relationship between female spawning biomass and total spawning biomass:

$$B_f = B_S * R \qquad \text{[Eqn. 2]}$$

where R = proportion of the total spawning biomass that is female, and

B_s = total spawning biomass.

Combining Equations 1 and 2 and solving for spawning biomass produces the annual egg production estimate of spawning biomass (Saville, 1963):

$$B_S = P_a * E^{-1} * R^{-1} * 10^{-6} \qquad \text{[Eqn. 3]}$$

where B_s = spanwing biomass (metric tons),

P_a = total egg production over the spawning area and season,

E = number of eggs produced per gram of female weight (annual relative fecundity),

R = sex ratio, fraction of spawning biomass that are mature females, and

10^{-6} = factor to convert grams to metric tons.

Estimation of the variance of the spawning biomass estimate is given by

$$\begin{aligned} Var(B_s) &= 10^{-12}*Var(P_a * E^{-1} * R^{-1}) \\ &= 10^{-12}*\left[P_a^2*R^{-2}*Var(E^{-1}) + R^{-2}*E^{-2}*Var(P_a) + P_a^2*E^{-2}*Var(R^{-1})\right. \\ &\quad + R^{-2}*Var(P_a)*Var(E^{-1}) + P_a^2*Var(R^{-1})*Var(E^{-1}) \\ &\quad \left. + E^{-2}*Var(P_a)*Var(R^{-1}) + Var(P_a)*Var(R^{-1})*Var(E^{-1})\right] \end{aligned}$$

[Eqn. 4]

This is the variance of a product of three independent random variables (Hogg and Craig, 1970): total egg production (P_a), the inverse of relative fecundity (E^{-1}) and the inverse of sex ratio (R^{-1}). If the assumption that these parameters are independent is false then the variance will be biased and the direction of the bias depends on the covariance terms for each pair of parameters.

METHODS AND MATERIALS

DATA SOURCES AND PROCESSING

This analysis used data collected during 12 ichthyoplankton surveys conducted throughout the walleye pollock spawning season (March through May), covering five years (1981 and 1985 through 1988). All surveys but one were conducted aboard the NOAA research vessel *Miller Freeman*; cruise 1DN88 was a cooperative survey aboard the Soviet research vessel *Darwin*. Table 1 lists the cruises and the dates they occurred.

Egg surveys have been conducted each year during the peak of the spawning season in early April (Kendall and Picquelle, 1990) and these surveys were used to estimate egg mortality (Table 1). Some years had multiple cruises over the spawning season, and these surveys were used to estimate the annual egg production curve (Table 1).

Acoustic surveys have been conducted just prior to the ichthyoplankton surveys (February and March) to estimate the abundance of the spawning walleye pollock population in the Shelikof Strait spawning area. Acoustic surveys provide samples of pre-spawning females for the fecundity estimates. Mature female fish were sampled with midwater trawls. Fecundity data are available for the years 1986 through 1989. Acoustic surveys also provided estimates of sex ratio from the midwater trawl samples from 1985 to 1991.

TABLE 1

Cruise periods and data summary. Column headings are as follows: YEAR: year the survey was conducted, CRUISE: cruise name, STA: number of stations used in this analysis, Z: indicates which cruises were used to estimate mortality, and AEPC: indicates which cruises were used to fit the annual egg production curve. The body of the table shows the dates of the cruises, with a different shading pattern for each year.

					MARCH							APRIL										MAY						
YEAR	CRUISE	STA	Z	AEPC	10			20			30	1			10			20			30	1			10			20
81	1MF81	31		Y		▨	▨	▨																				
81	2MF81	86	Y	Y								▨	▨	▨	▨													
81	3MF81	76		Y																▨	▨	▨						
85	1MF85	88	Y									▨	▨	▨	▨													
86	1MF86	80	Y	Y										▨	▨	▨												
86	2MF86	50		Y																		▨	▨	▨	▨	▨	▨	
87	2MF87	121	Y										▨	▨	▨													
88	1DN88	43		Y						▨	▨	▨	▨															
88	1MF88-A	37		Y								▨																
88	1MF88-B1	105	Y	Y									▨	▨	▨													
88	1MF88-B2	46		Y										▨														
88	1MF88-C	31		Y											▨	▨												
88	2MF88	45		Y																▨	▨							

During ichthyoplankton surveys, a column of water was sampled at each station using standard MARMAP oblique tows with 60 cm bongo nets (Smith and Richardson, 1977). Nets of smaller diameter (20 cm) were used on one of the 12 cruises (1MF85). Mesh size was 505 µm on the cruises in 1981, 1987, and 1988, and 333 µm on the cruises in 1985 and 1986. Since pollock eggs are 1.3 - 1.4 mm in diameter (Hinckley, 1990), no extrusion through 0.505 or 0.333 mm mesh should occur (Smith and Richardson, 1977).

At each station, walleye pollock eggs were counted from one of two bongo nets. Counts were standardized to the number of eggs beneath 10 m^2 of sea surface area based on tow depth and volume of water filtered (Smith and Richardson, 1977). A subsample of 100 eggs (or the entire catch if less than 100) was randomly selected and each egg was assigned to egg stages based on the 21 walleye pollock egg stages described in Blood et al. (in review). No estimate of damage or rupture of the eggs during collection is available, however, generally less than 5% of the eggs that are staged are damaged (i.e. have ruptured yolks) (A. Matarese, Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070, pers. comm., 1991). These damaged eggs were assigned to stages based on the stage distribution at that station.

Bongo tows were usually deployed to within 10 m of the bottom because walleye pollock eggs have been found to occur close to the bottom or to a maximum depth of 250 m (Kendall and Kim, 1989). The depth distribution of walleye pollock eggs was unknown when the 1981 cruises were conducted, hence in that year the water column was only sampled to a depth of 200 m. Consequently, a portion of the eggs at the stations in 1981 were not sampled, and the observed density of eggs was underestimated. This bias was corrected by estimating the total number of eggs per station by Equation 5 (Kendall and Picquelle, 1990). The correction, which models the depth distribution of eggs based on the maximum depth of the gear and the number of eggs caught, compensates for the fact that eggs below the tow depth were not sampled.

$$N_j = N_j^* * \frac{p_{0,\min(bottom\ depth,\ 250)}}{p_{0,tow\ depth}} \qquad \text{[Eqn. 5]}$$

where N_j = estimated catch at station j if the gear had sampled to the bottom or 250 m,

N_j^* = observed catch at station j from gear that sampled to tow depth,

$p_{0,\min(\text{bottom depth, } 250)}$ = proportion of eggs in entire water column that occur between the surface and bottom depth or 250 m (whichever is shallower),

$p_{0,\text{tow depth}}$ = proportion of eggs in water column that occur between the surface and tow depth.

These proportions were estimated by a model that describes the depth distribution of eggs:

$$p_{a,b} = (0.0006883) * (e^{0.02913*b} - e^{0.02913*a}) \qquad \text{[Eqn. 6]}$$

where a and b define the depth interval and is conditional on a bottom depth of at least 250 m. This model was developed by S. Kim (Korea Ocean Research & Development Institute, Polar Research Laboratory, Ansan, P.O. Box 29, Seoul 171-14, Korea, pers. comm., 1988) and is documented in Kendall and Picquelle (1990). It was assumed that all stations have the same distribution of eggs over depth and that no eggs occur below 250 m (Kendall and Kim, 1989). The measurement error about the estimated egg catches (N_j) introduced by Equations 5 and 6 was assumed to be negligible when compared to other sources of error and was ignored. For consistency this adjustment was made to all stations from all cruises because occasionally stations were sampled to insufficient depths, but the adjustment had no effect on tows that were taken to 250 m and it only generated large adjustments for cruises in 1981. There were two stations in 1981 where the sampled water columns were so shallow that Equation 5 estimated that less than 10% of the eggs in the water column were sampled, thus giving a very unreliable estimate of how many eggs were actually there. As a result, these two stations were treated as missing and their egg densities were estimated by the weighted average of egg densities from the adjacent stations. Weights were set to the inverse of the distance between the missing and adjacent station.

Application of the annual egg production method to walleye pollock was a complicated undertaking requiring several steps and models. To assist the reader, the procedure is outlined in Figure 2; then each step is explained in greater detail in the following sub-sections of the Methods and Materials section. All nonlinear and linear regression analyses were performed using SYSTAT Version 5.0 (Wilkinson, 1990) statistical analysis software on a 386 microcomputer.

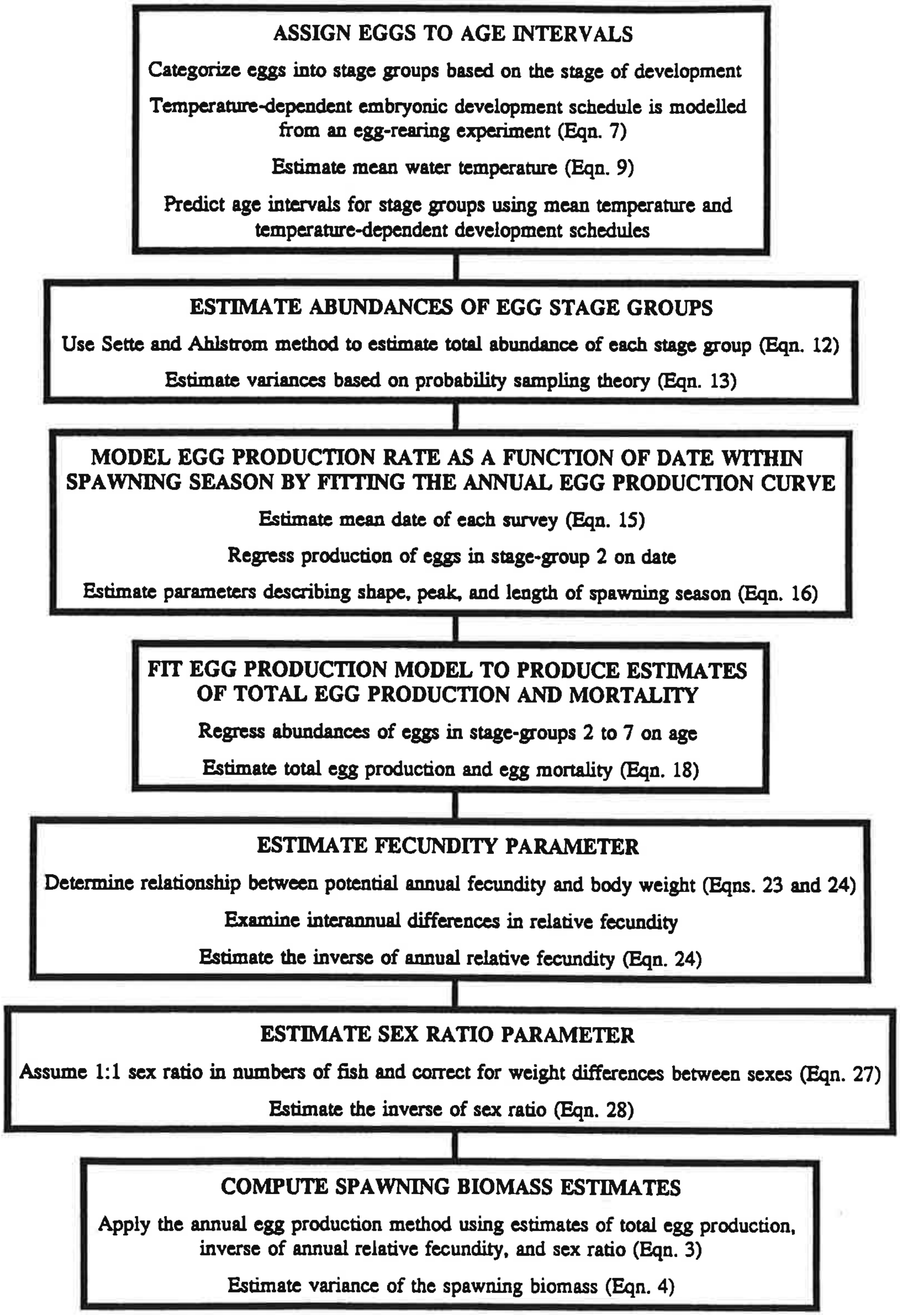

Figure 2. Outline of procedure employed in this study to produce annual egg production method estimates of spawning biomass of walleye pollock.

EGG STAGES AND STAGE DEVELOPMENT TIMES

The estimation method for total egg production (P_a) required estimates of total egg abundance in age categories. This in turn required that eggs be aged from each sample. Egg age was estimated by identifying the stage of development. Twenty-one distinct stages of development have been identified for walleye pollock eggs (Blood et al., in review); these were used to categorize a subsample of eggs from each station.

Egg stages were grouped into eight stage groups of approximately equal time intervals (about 1.5 days of development at 5°C) (Fig. 3). Stage groups were selected to be at least 24 h (except stage-group 1) to increase the likelihood that eggs of all stage groups would occur in each sample no matter what time of day the sample was taken.

Only stage-groups 2 through 7 were used in the analysis. Stage-group 1 (stages 1 through 5) was omitted because the stages in this group were not sampled completely. Observed densities of eggs in these stages are consistently lower than expected based on their duration and on the observed densities of eggs in the older stage groups. The short duration of these stages should not produce a bias, but would increase the variance of observed densities because their occurrence in a sample depends on the time of the sample relative to the time eggs were spawned. Observed variances of the densities of stages 1 through 5 were higher than those of the older stage groups; there also appeared to be a sampling bias as indicated by the lower than expected densities. Stage-group 8 was also excluded because hatching begins at stage 20 and data on the age of stage 19 eggs are inconsistent in that

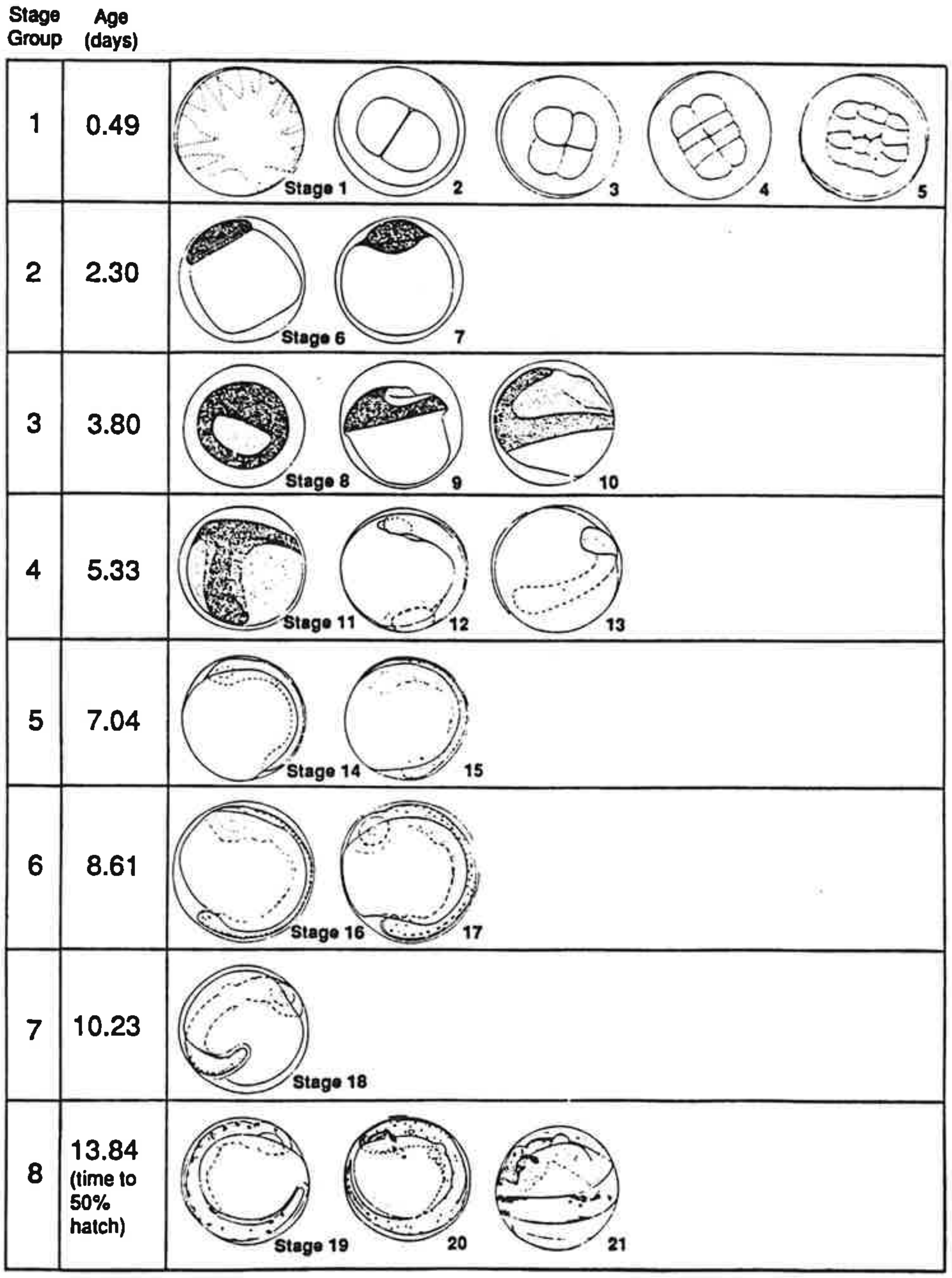

Figure 3. Grouping of egg stages into age intervals (Blood et al., in review). Ages are at the end of the stage group for eggs incubated at 5°C.

development time for this stage appears to increase instead of decrease with higher water temperature (Blood et al., in review). It was assumed that stage-groups 2 through 7 were sampled by the bongo nets with 100% efficiency. Similarly, it was assumed that there was no bias in selecting subsamples of eggs for staging.

Ages were assigned to stage groups using the concept that development time decreases with increasing temperature. Development times for the egg stage groups were modelled by an exponential relationship between development time and water temperature (Bates, 1987):

$$t_{s,T} = \alpha_s * e^{-\beta_s * T} \qquad \text{[Eqn. 7]}$$

where $t_{s,T}$ = development time from fertilization to the end of stage-group s at temperature T,

α_s, β_s = parameters of the model for stage-group s, and

T = temperature (°C) at which eggs developed.

Equation 7 was fit to data from an experiment where three groups of eggs were reared at 3, 5, and 7 °C (Blood et al., in review) using nonlinear regression. Residuals appeared to increase with development time, so a multiplicative error term was assumed. This indicated the use of the Equation 8 for the objective function instead of the usual least squares:

$$\text{minimize} \sum_{all\ obs} (\ln(t_{s,T}) - \ln(\hat{t}_{s,T}))^2 \qquad \text{[Eqn. 8]}$$

where $\hat{t}_{s,T}$ = predicted development time to end of stage-group s incubated at temperature T, using Equation 7, and

$t_{s,T}$ = observed development time to end of stage-group s incubated at temperature T.

The fitted models (Eqn. 7) were used to predict the age interval of stage-groups 2 through 7 for eggs from the ichthyoplankton surveys using the mean water temperature during the cruise as the independent variable in Equation 7. Temperature data was not collected at all ichthyoplankton stations, so it was necessary to use mean cruise temperature instead of the actual temperature at each station. Temperatures at 1 m depth intervals were collected using conductivity-temperature-depth instruments (CTD) taken during the egg surveys. First, mean temperature for each CTD station was computed by averaging temperature over depth and weighting each depth interval by the density of eggs at that depth as predicted by Equation 6. Then, mean cruise temperatures ($\bar{T}_h$) were estimated by the simple mean of the CTD station temperatures:

$$\bar{T}_h = \frac{\sum_{j=1}^{n_{T_h}} T_{h(j)}}{n_{T_h}} \qquad \text{[Eqn.9]}$$

$$Var(T_h) = \frac{\sum_{j=1}^{n_{T_h}} (T_{h(j)} - \bar{T}_h)^2}{(n_{T_h} - 1)} \qquad \text{[Eqn.10]}$$

where n_{T_h} = number of CTD stations within the egg survey region during survey h,

$T_{h(j)}$ = weighted mean temperature at station j in survey h,

$$T_{h(j)} = \frac{\sum_{d} T_{h(j),d} * P_{d-1/2,d+1/2}}{\sum_{d} P_{d-1/2,d+1/2}} \qquad \text{[Eqn. 11]}$$

$T_{h(j),d}$ = temperature at 1 m depth increment d at station j in survey h, and

$P_{d-1/2,d+1/2}$ = proportion of eggs in the water column that occur between depths $d-1/2\ m$ and $d+1/2\ m$ as predicted by Equation 6.

EGG ABUNDANCE ESTIMATION BY STAGE GROUP

Estimates of total abundances for each egg stage group (N_s) were required for the estimation of the total egg production parameter (P_a) in Equation 3. Total abundances for each egg stage group were estimated for each survey.

This estimation was complicated by the fact that the available survey data were accompanied by a variety of sampling peculiarities. The 12 surveys were not all designed for the primary purpose of estimating egg production and each survey covered a slightly different area. Although many surveys included stations sampled for special studies, this analysis included only stations that were originally designed to be used to estimate abundance. The survey area was standardized for this analysis by selecting only stations within a specified region that historically contained the majority of the eggs spawned in Shelikof Strait (Figs. 4

and 5). It was assumed that the standardized area missed only a small portion of eggs and this bias was ignored. The spatial distribution of eggs in Shelikof Strait is very consistent over years; changes in total egg abundance among years manifests itself with changes in egg densities and not changes in the area of spawning (Kendall and Picquelle, 1990), in contrast with other fish species (Smith, 1990).

An additional problem is that there was no consistent sampling scheme in the past; some surveys were systematic, while others targeted areas of high walleye pollock egg density. Station densities in these cruises were frequently uneven but not random. Survey designs need to be taken into account when estimating abundance. The Sette and Ahlstrom polygon method for estimating abundance (Richardson, 1981) was used to correct for the unequal probabilities of selecting a column of water for the survey. This method weights each station by the area it represents and is consistent with methods from probability sampling (Jessen, 1978). Weights are the areas of the polygons associated with each station as described in Richardson (1981). Figure 6, as an example, shows the polygons associated with each station for cruise 2MF87. Total abundance and the variance of the total abundance of a stage group from a survey were estimated as follows (Richardson, 1981; Kendall and Picquelle, 1990):

$$N_{sh} = \sum_{j=1}^{J_h} N_{sh(j)} * A_{h(j)} \qquad \text{[Eqn. 12]}$$

$$Var(N_{sh}) = \frac{J_h}{J_h - 1} \sum_{j=1}^{J_h} \left(N_{sh(j)} * A_{h(j)} - \frac{N_{sh}}{J_h} \right)^2 \qquad \text{[Eqn. 13]}$$

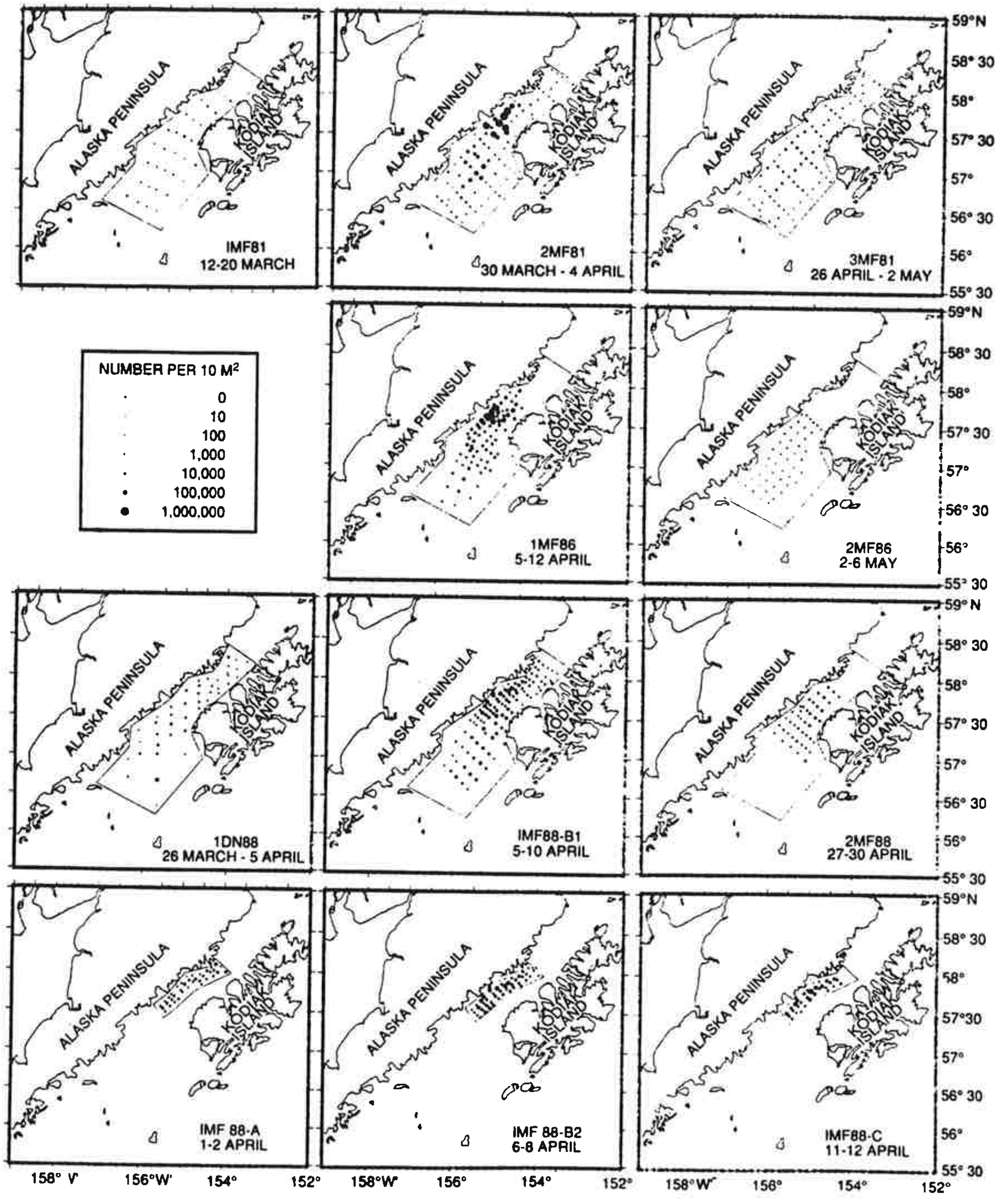

Figure 4. Surveys used to fit the annual egg production curve. Dots indicate station locations and dot size indicates observed density of pollock eggs (eggs/10m^2). Polygon delimits standardized survey region. Cruises are arranged in rows according to the year. The year 1988 has two series: Series 88-1 (1DN88, 1MF88-B1, 2MF88) and Series 88-2 (1MF88-A, 1MF88-B2, 1MF88-C).

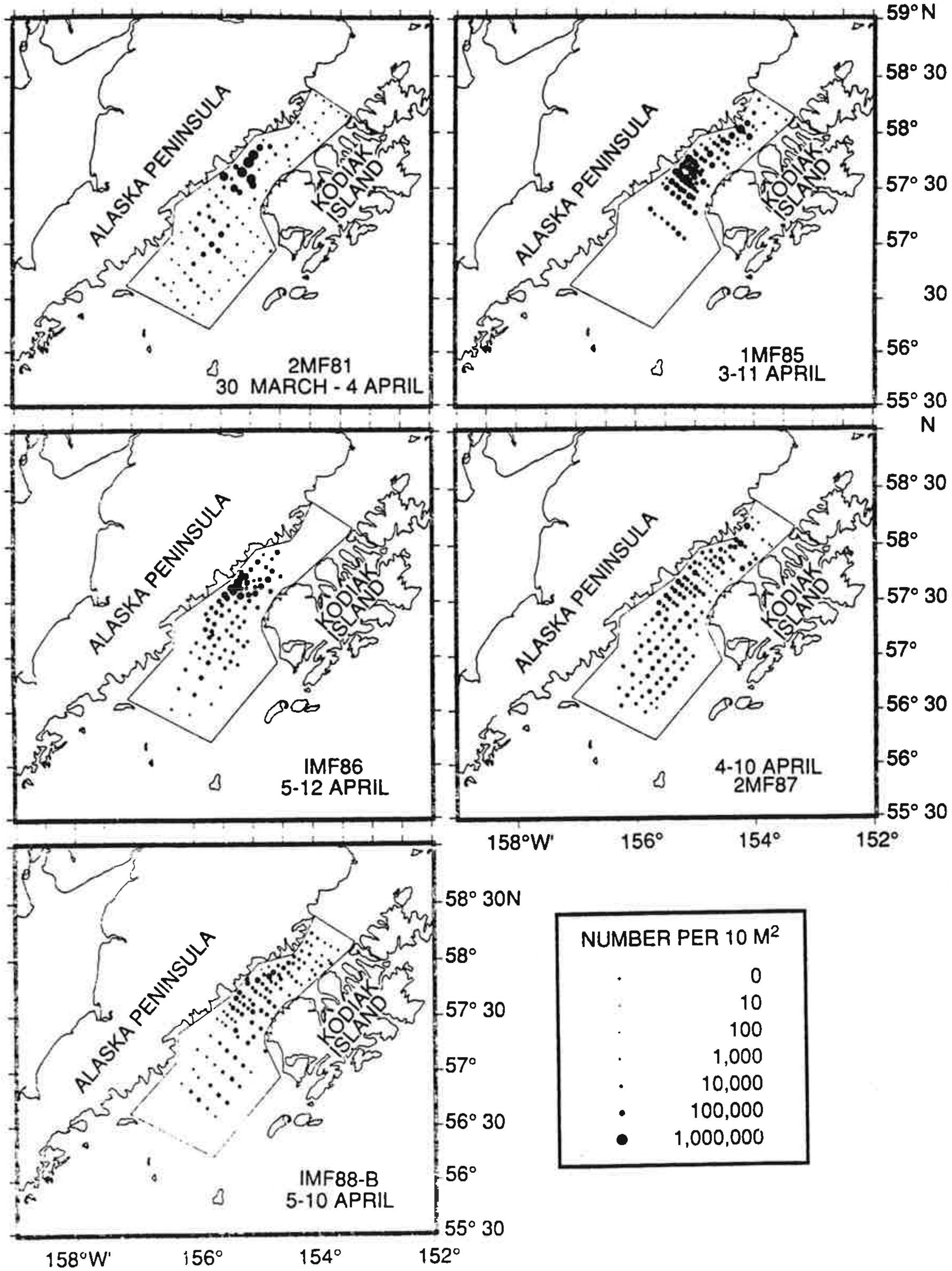

Figure 5. Surveys used to fit the egg production model. Dots indicate station locations and dot size indicates observed density of pollock eggs (eggs/10m^2).

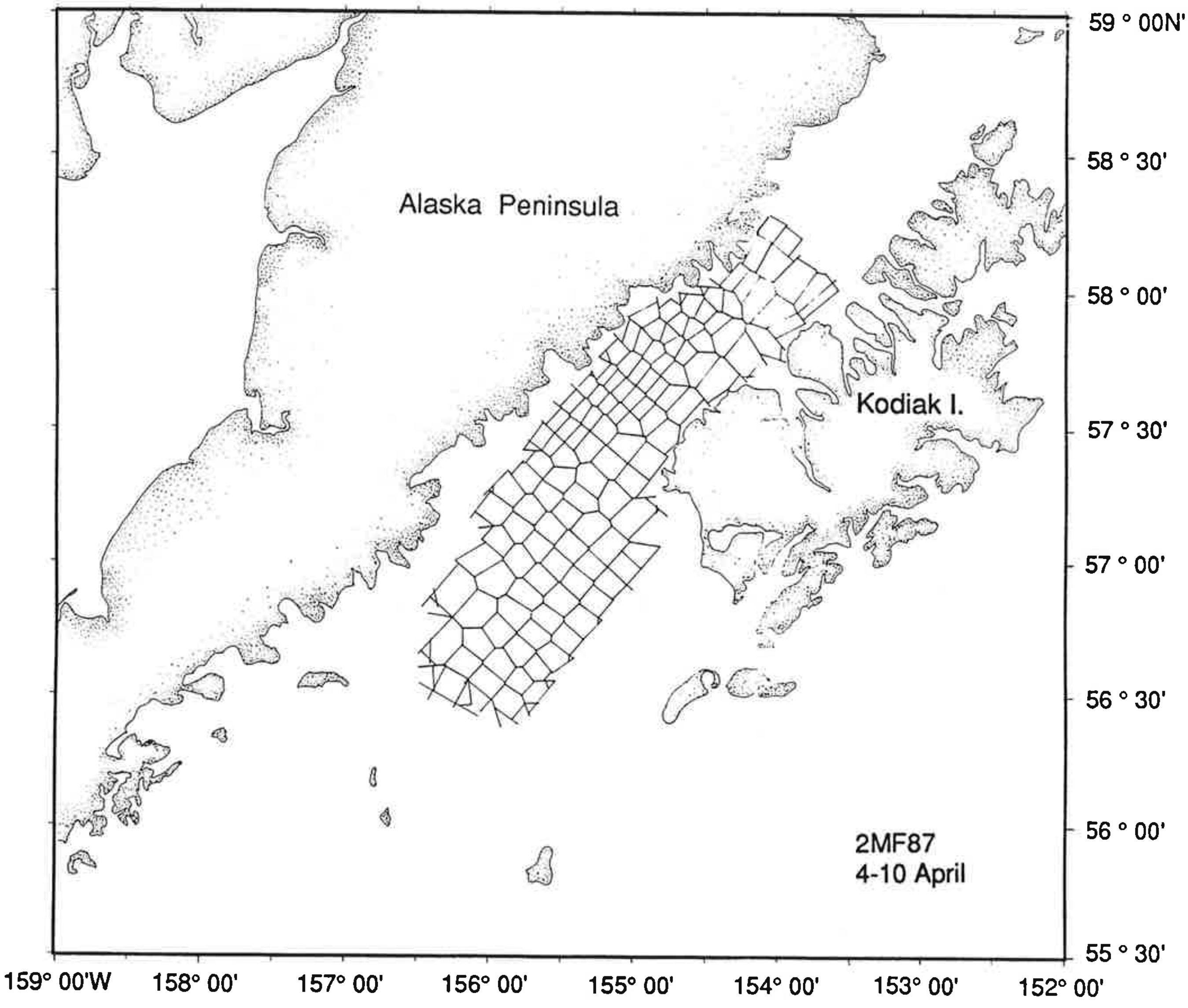

Figure 6. Example of polygonal areas. Each polygon is associated with one station. Area of the polygon is the station weight.

where N_{sh} = estimated total number of stage-group s eggs in survey area in survey h,

s = stage-groups 2 through 7,

J_h = number of stations in survey h,

$N_{sh(j)}$ = number of eggs per 10 m^2 of stage-group s at station j in survey h (adjusted by Equation 5),

$A_{h(j)}$ = polygonal area of station j in survey h, in units of 10 m^2, and

$Var(N_{sh})$ = estimated variance of the total number of stage-group s eggs in the survey area in survey h.

The Sette and Ahlstrom method allows the survey design to put more stations where egg densities are higher (hence more variable), as was done for several of the surveys. That particular survey design is called sampling with probabilities proportional to a measure of size (Jessen, 1978); this is a special case of probability sampling and the main advantage is that it reduces the variance about abundance estimates.

ANNUAL EGG PRODUCTION CURVE

Age-specific abundances estimated by Equation 12 were used to estimate total egg production by fitting a mortality curve to the decline in abundance with age, and extrapolating back to age 0. There are two problems with applying this method to walleye pollock. The first problem is a fundamental weakness in the method; extrapolating beyond the range of the data to estimate egg production is dangerous because you must assume that the model is still valid where you have no data to verify it. This risk is minimized by having data points close to age 0, thereby reducing the distance the model is extrapolated. The second problem is that walleye pollock eggs of different ages, and hence of different spawning dates, are produced at different rates. Ideally, mortality and egg production are estimated by following a cohort through time and monitoring its decline. However, this is difficult to do with walleye pollock because of sampling constraints. Usually it is assumed that the production rate is constant over the time when the sampled eggs were produced; then the eggs in the sample can be treated as if they are from one cohort. This assumption is not valid for pollock because the egg production rate changes quickly over the short spawning season (Bates, 1987, 1990). The production rate of a cohort depends on the date of spawning relative to the peak spawning date, hence eggs spawned on different days are produced at different rates. This necessitates estimating production rate as a function of the date within the spawning season as suggested by Bates (1987, 1990); this is the annual egg production curve.

The annual egg production curve was modelled by a symmetrical uni-modal cosine curve:

$$P_0(D) = \rho_0 * \frac{b}{2\pi} * [1 + \cos(b * (D - \mu))] + \gamma \qquad \text{[Eqn. 14]}$$

where $P_0(D)$ = egg production per day at day-of-the-year D,

ρ_0 = total production of eggs over the spawning season (excluding the background rate of spawning (γ)),

b = parameter determining the length of the spawning season,

$\frac{2\pi}{b}$ = length of spawning season in days,

μ = day-of-the-year when peak spawning occurs, and

γ = constant background rate of egg production.

Note that

$$\int_{\mu-\frac{\pi}{b}}^{\mu+\frac{\pi}{b}} \frac{b}{2\pi}\,[1 + \cos(b(D-\mu))]\,dD = 1 .$$

To fit the annual egg production curve (Eqn. 14), it is necessary to have estimates of the egg production rate from several points of time within the spawning season. Without estimates of production rate of newly hatched eggs, we used the production rate of stage-group 2 eggs (P_2) as an index of egg production (P_0). This is valid if the mortality rate between age 0 and stage-group 2 is constant over the season and between years. Stage-group 2 eggs are between 0.5 and 2.3 days old (at 5°C), so the mortality rate would have to be drastically different to result in an important difference in the proportion of age-0 eggs surviving to stage-group 2.

The annual egg production curve was fit by regressing the production rate of stage-group 2 (P_2) on mean survey date (D) for the cruises marked in the AEPC column in Table 1. Production rate of stage-group 2 was estimated by the abundance of stage-group 2 (as estimated by Equation 12) divided by the duration of this stage-group (as estimated by Equation 7). Mean survey date was estimated by the weighted average of station dates, weighted by the station abundance of eggs in stage-group 2, thus it is the mean date that stage-group 2 eggs were caught.

$$D_h = \frac{\sum_{j=1}^{J_h} D_{h(j)} * N_{2,h(j)} * A_{h(j)}}{\sum_{j=1}^{J_h} N_{2,h(j)} * A_{h(j)}} \qquad \text{[Eqn. 15]}$$

where D_h = mean day-of-the-year for survey h,

$D_{h(j)}$ = day-of-the-year for station j in survey h,

$A_{h(j)}$ = polygonal area of station j in survey h, in units of 10 m^2, and

$N_{2,h(j)}$ = number of stage-group 2 eggs per 10 m^2 at station j in survey h.

There are not sufficient numbers of surveys within each year to estimate the annual egg production curve independently for each year (Table 1), so Equation 14 was modified to be fit simultaneously to all survey years using indicator variables and nonlinear least squares:

$$P_{2,y}(D_h) = \left(\sum_y \rho_{2_y} * I_{yh}\right) * \frac{b}{2\pi} * \left[1 + \cos(b * (D_h - \mu))\right] + \gamma + \varepsilon_{yh} \qquad \text{[Eqn. 16]}$$

where $P_{2,y}(D_h)$ = production per day of stage-group 2 eggs at day-of-the-year D_h in year y;

this is estimated by the production rate of stage-group 2 eggs in survey h,

$$= \frac{N_{2,h}}{(t_{2,\bar{T}_h} - t_{1,\bar{T}_h})}$$ as estimated by Equations 7 and 12,

D_h = mean day-of-the-year for survey h, as estimated by Equation 15,

ρ_{2_y} = total production of stage-group 2 eggs over the spawning season for year y

(excluding the background rate of spawning (γ)),

I_{yh} = indicator variable for year y and survey h,

$$I_{yh} = \begin{cases} 1 \text{ if survey h occurred in year=y} \\ 0 \text{ otherwise} \end{cases}$$, and

ε_{yh} = additive error term.

Equations 14 and 16 are valid over the time interval $\mu - \pi/b \leq D_{yh} \leq \mu + \pi/b$; beyond this range $P_{2,y}(D_h)$ is estimated by γ. Equation 16 has four parts:

1) $\sum_{y} \rho_{2_y} * I_{yh}$ [Eqn. 16.1]

This is a scaling parameter that allows each year to have a different total egg production (ρ_{2_y}) using indicator variables (I_{yh}).

2) $\frac{b}{2\pi}*[1+\cos(b*(D_{yh}-\mu))]$ [Eqn. 16.2]

This part is a modification of a cosine wave with the peak at μ and with the period $2\pi/b$. A cosine function was chosen to describe the egg production rate over the spawning season because it is a symmetrical bell-shaped curve, and it allows an analytical solution to the integral in Equation 17.

3) γ [Eqn. 16.3]

This term allows for a background level of spawning to continue beyond the spawning season. There is evidence of limited spawning occurring over an extended period of time (Kendall and Picquelle, 1990). Equations 14 and 16 model this background level with a constant term.

4) ε_y [Eqn. 16.4]

This term models the error about the egg production rate. The errors are assumed to have a mean of zero and constant variance over years.

This model produced estimates of the ρ_{2_y}'s for y=1981, 1986, 1988-1, and 1988-2 and of b, μ, and γ common for all years. The estimates of the parameters b, μ, and γ are used in the next step in the analysis. The estimates of the ρ_{2_y}'s are not used further in the analysis; they are included in the model only to allow for the interannual differences in total egg production. It is assumed that in each year the distribution of egg production over time has the same shape (cosine wave), the same length of spawning season ($2\pi/b$), and the same day of the peak of the annual egg production curve (μ); only the height of the curve was allowed to vary among years (Fig. 7). It is also assumed that the production rate of stage-group 2 eggs is a valid index of the production rate of eggs at time of spawning.

There were only three years (1981, 1986, and 1988) that had multiple cruises over the spawning season. The 1988 cruises were divided into two series covering two different but overlapping areas; 1DN88, 1MF88-B1, and 2MF88 (Series 88-1) covered the standard area, and three passes in 1MF88 (1MF88-A, 1MF88-B2, and 1MF88-C, comprising Series 88-2) covered a smaller area in the region of highest egg densities (Fig. 4). Data from the three passes in 1MF88 closely bracket the peak spawning date and contribute important information about the shape of the annual egg production curve. The total abundances of stage-group 2 eggs were much less for the 88-2 series than for the 88-1 series because these passes covered a much smaller area, hence this series was not comparable to the 88-1 series; this inconsistency was overcome by treating two series as two different years in Equation 16.

EGG PRODUCTION

The egg production model (Eqn. 17) has two components: the egg production rate as a function of date (the annual egg production curve, $P_0(D)$ in Equation 14) and an exponential survival model with a constant mortality rate Z over time t (e^{-Zt}) (Bates, 1987, 1990).

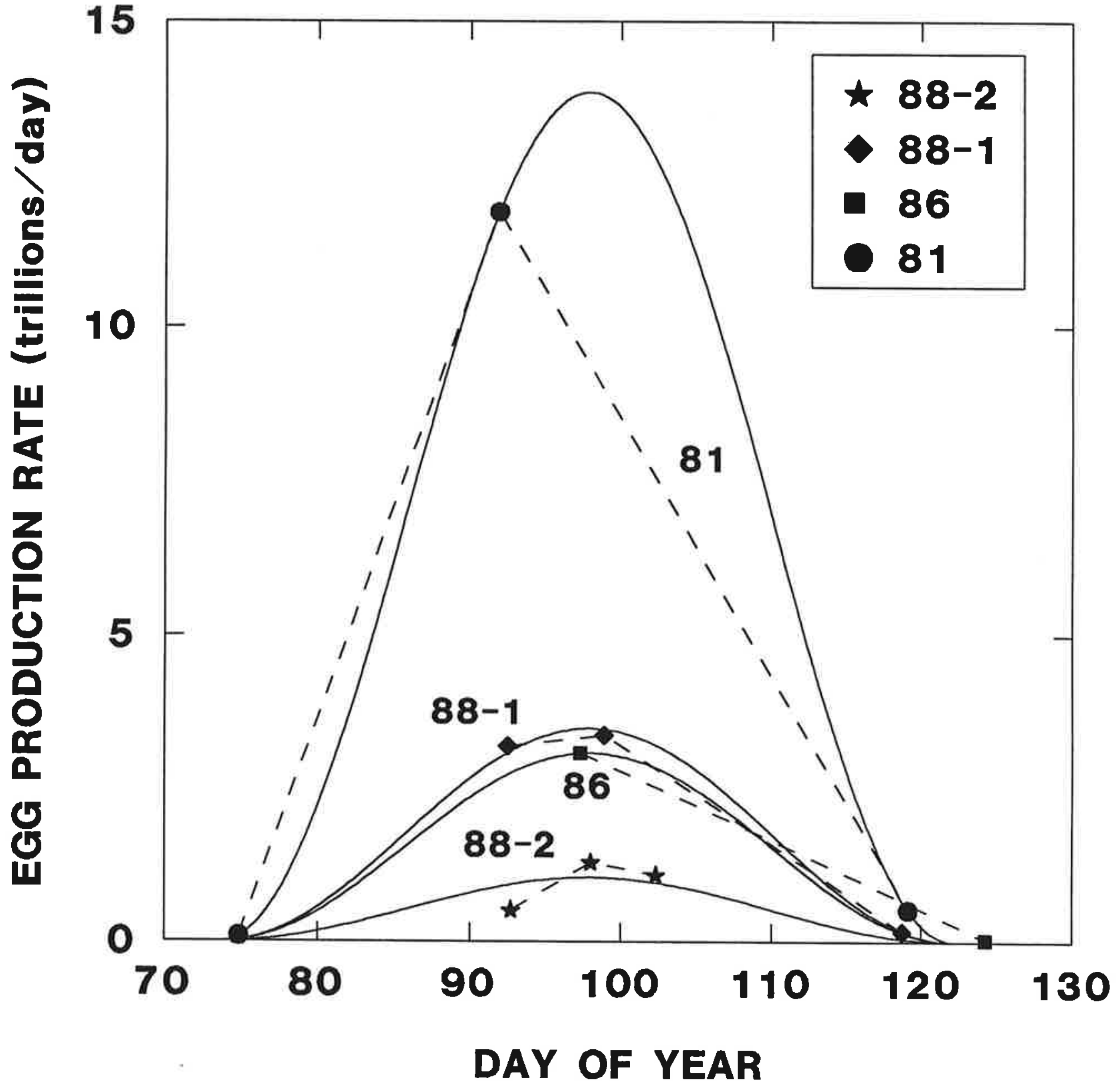

Figure 7. Annual egg production curves. Dotted lines connect production rates of stage-group 2 eggs from surveys conducted during the same year (Eqn. 12). Solid lines show the predicted egg production rate per day for each year (Eqn. 16).

$$N_{sh} = \int_{t_{s-1}}^{t_s} P_{0_y}(D_h - t) * e^{-Z_y t} dt + \varepsilon_{sh} \qquad \text{[Eqn. 17]}$$

where N_{sh} = observed abundance of stage-group s eggs in survey h, as estimated by Equation 12,

t_{s-1} = age of stage-group s at the beginning of the age interval at the mean temperature for the survey, as estimated by Equation 7,

t_s = age of stage-group s at the end of the age interval at the mean temperature for the survey, also as estimated by Equation 7,

t = instantaneous age of an egg,

D_h = mean day-of-the-year of survey h, as estimated by Equation 15 except that the weights are $\left(\sum_{s=2}^{7} N_{s,h(j)}\right) * A_{h(j)}$ instead of $N_{2,h(j)} * A_{h(j)}$,

$D_h - t$ = day-of-the-year that egg of age t in survey h was spawned,

$$P_{0_y}(D_h - t) = \rho_{0_y} * \frac{b}{2\pi} * \left[1 + \cos(b * (D_h - t - \mu))\right] + \gamma \qquad \text{[Eqn. 14]}$$

= estimated egg production per day at day-of-the-year $D_h - t$ in year y as predicted by the annual egg production curve,

b, μ, γ = estimated values of the parameters in the annual egg production curve from Equation 16,

ρ_{0_y} = total egg production over the year y spawning season, excluding the

background level of production at a daily rate γ,

Z_y = instantaneous daily egg mortality rate in year y, and

ε_{sh} = additive error term.

The egg production rate ($P_{0_y}(D_h-t)$) is the annual egg production curve where b, μ, and γ were estimated from Equation 16 in the previous step and are treated as constants in this model. Equation 17 was fit to the data from each year separately, thus the parameter ρ_{0_y} replaced the scaling parameters ρ_{2_y}s in Equation 16. The mortality rate is the usual exponential mortality model where Z_y was assumed to be constant for eggs of all ages within a given year.

The quantity inside the integral of Equation 17 is the predicted abundance of age t eggs on date D_h. To fit the model to the data, Equation 17 was integrated over the age interval defining the stage group (t_{s-1}, t_s) to predict the total abundances of the egg stage groups. It is given by

$$
\begin{aligned}
N_{sh} = \rho_{0_y} * \frac{b}{2\pi} \Bigg\{ & e^{-Z_y * t_{s-1}} * \Bigg[\frac{\rho_{0_y} * b + 2\pi * \gamma}{\rho_{0_y} * b * Z_y} \\
& \quad + \frac{1}{b^2 + Z_y^2} * \big(b * \sin(b * (D_h - t_{s-1} - \mu)) + Z_y * \cos(b * (D_h - t_{s-1} - \mu)) \big) \Bigg] \\
& - e^{-Z_y * t_s} * \Bigg[\frac{\rho_{0_y} * b + 2\pi * \gamma}{\rho_{0_y} * b * Z_y} \\
& \quad + \frac{1}{b^2 + Z_y^2} * \big(b * \sin(b * (D_h - t_s - \mu)) + Z_y * \cos(b * (D_h - t_s - \mu)) \big) \Bigg] \Bigg\} + \varepsilon_{sh}
\end{aligned}
$$

[Eqn. 18].

Total egg production excluding the background level (ρ_{0y}) and mortality (Z_y) were estimated separately for each year by fitting Equation 18 to the estimated abundances of stage-groups 2 through 7 (N_{sh}) from the individual cruises listed in the Z column in Table 1. Equation 18 was fit using weighted nonlinear least squares where the weights were the inverse of the variance about stage-group abundances given by Equation 13 ($1/Var(N_{sh})$), the dependent variable was the total abundances of the stage groups (N_{sh}, s=2 through 7), and the independent variables were the ages at the beginning and ending of the stage groups (t_s and t_{s-1}).

Hypothesis tests were performed to compare the estimated mortality rates between years. The Games and Howell method (Sokal and Rohlf, 1981; Rohlf, 1987) was used because it does not require that variances about Z_y are homogeneous over years.

The egg production model assumes an additive error, a constant mortality rate within each survey, and constant yearly peak spawning date and length of spawning season. It is very possible that the peak spawning date varied between years, but there is not enough information to estimate a different peak for each year; μ and Z_y are highly correlated (mathematically, not biologically) and the model is over-parameterized if one tries to fit both μ and Z_y simultaneously with individual values for each year given the limited number of cruises per year.

Total egg production (P_{a_y}) was estimated using a function of parameters from both the annual egg production curve and the egg production model. It is the sum of egg production during the spawning season ρ_{0_y} and the background rate of spawning (γ) multiplied by the length of the spawning season.

$$P_{a_y} = \rho_{0_y} + \gamma * \frac{2\pi}{b} \qquad \text{[Eqn. 19]}$$

The variance of the total egg production is simply the sum of the variances of these two quantities because they are independent random variables.

$$\begin{aligned} Var(P_{a_y}) &= Var(\rho_{0_y}) + (2\pi)^2 * Var(\frac{\gamma}{b}) \\ &= Var(\rho_{0_y}) + (2\pi)^2 * \left[\frac{1}{b^2} * Var(\gamma) + \frac{\gamma^2}{b^4} * Var(b) - 2 * \frac{\gamma}{b^3} * Cov(b,\gamma)\right] \end{aligned}$$

[Eqn. 20]

where $Var(\rho_{0_y})$ was estimated using the nonlinear regression fit for the egg production model (Equation 18), $Var(\frac{\gamma}{b})$ was approximated in Equation 20 using the delta method (Seber, 1982), and $Var(\gamma)$, $Var(b)$, and $Cov(\gamma,b)$ were all estimated using the nonlinear regression fit for the annual egg production curve (Equation 16).

If the estimate of background level (γ) is not significantly different from 0, then P_{a_y} may be estimated by the fitted values of ρ_{0_y} from the egg production model.

$$P_{a_y} = \rho_{0_y}$$ [Eqn. 21]

$$Var(P_{a_y}) = Var(\rho_{0_y})$$ [Eqn. 22]

FECUNDITY

Another parameter needed to estimate spawning biomass is the inverse of annual relative (weight-specific) fecundity, E^{-1}, where annual relative fecundity is defined as the total number of eggs spawned by a mature female during the spawning season per unit weight. E^{-1} is used in the biomass estimate to convert the number of eggs produced (P_a) into the amount of mature female biomass required to have produced those eggs (B_f in Equation 1).

Annual relative fecundity is a function of potential annual fecundity and body weight. These parameters were estimated from samples of pre-spawning females which were subsampled from trawl catches conducted during February or March; this assured that the total standing stock of oocytes in the ovaries contained all the eggs to be spawned in the upcoming spawning season. Potential annual fecundity (F) was estimated by the total number of advanced yolked oocytes in the female pollock ovaries (Hunter et al., 1985; Hunter et al., 1992). This total was estimated for each female in the fecundity sample from several (n = 3 to 7) subsamples of each ovary (Miller et al., 1986; Hinckley, 1987). Sources of imprecision include the measurement error due to misidentification of oocytes and the variability between subsamples from each ovary. The incidence of misidentification was assumed to be negligible and was ignored. Variability between subsamples within an ovary was small, with a coefficient of variation generally less than 10% and was also ignored (Megrey, 1989; Hinckley, 1987). Egg counts measured potential annual fecundity because they were uncorrected for loss due to atresia (resorption of yolked eggs). Potential annual fecundity overestimates annual fecundity and the magnitude of this bias depends on the proportion of eggs that are resorbed; it was assumed that the number of oocytes resorbed is negligible. Further research on the fecundity of walleye pollock is currently being conducted by the Alaska Fisheries Science Center to address this assumption.

Female body weight (W) is also required to estimate annual relative fecundity. Whole body weight and ovary-free weight were collected for all the females sampled for fecundity, except for 1982 when only ovary-free body weight was recorded. Whole body weight was estimated for the females in the 1982 fecundity sample using a linear relationship between whole body weight and ovary-free body weight derived from the 1986 to 1989 data.

The inverse of annual relative fecundity (E^{-1}) is the number of grams of female weight required to produce one egg, and has a constant value only if annual fecundity (F) and body weight (W) are directly proportional. This assumption was tested by fitting a pair of models to annual fecundity and weight:

$$W = b_1 * (F * 10^{-3})^{b_2} \qquad \text{[Eqn. 23]}$$

$$W = b_1 * (F * 10^{-3}) \qquad \text{[Eqn. 24]}$$

where F = annual fecundity,

b_1 = slope parameter,

b_2 = exponent parameter, and

W = whole body weight in grams.

The constant 10^{-3} was included in the models to rescale fecundity so that both fecundity and weight are the same order of magnitude, thus reducing rounding errors. Equations 23 and 24 are a rearrangement of the standard fecundity-weight model:

$$F = a_1 * W^{a_2} \qquad \text{[Eqn. 25]}$$

$$F = a_1 * W \qquad \text{[Eqn. 26]}$$

Equation 23 allows the relationship between fecundity and weight to be curvilinear. If the parameter b_2 is not significantly different from 1.0, then we may assume a value of 1.0 for b_2 and Equation 23 simplifies to Equation 24, and one can conclude that relative fecundity is directly proportional to weight. Then the parameter E^{-1} and its variance can be simply estimated by b_1, the slope in Equation 24, and its associated variance from the regression.

Before fitting Equations 23 and 24 to the fecundity data, the hypothesis of no annual differences in the weight-fecundity relationship was tested. This was accomplished by linearizing Equation 23 by log-transforming the data, then performing an analysis of covariance where the categorical variable was year and the covariate was the natural logarithm of fecundity. The interaction term between year and fecundity was included in the model to allow each year to have different values for both the parameters b_1 and b_2 in

Equation 23. The increasing spread in W with increasing F observed in Figure 8 suggests a multiplicative error was appropriate, thus log-transforming the data also equalized the variance about weight over the range of fecundity values.

Equations 23 and 24 were fit by regressing whole-body weight (W) on annual fecundity (F) for data from each year separately. Rather than log-transform the model as was done for the analysis of covariance above, the error term was modeled using a log-transformed objective function instead of least squares:

$$\text{minimize} \sum_{k=1}^{K} (\ln(W_k) - \ln(\hat{W}_k))^2$$

where W_k = whole body weight for the kth female in the fecundity sample (estimated from ovary-free body weight for 1982),

$\hat{W}_k$ = predicted whole body weight for the kth female, and

K = number of females in the fecundity sample.

Fecundity samples have been collected for years 1982 and 1986 through 1989. Unfortunately, these years do not completely coincide with the years for which egg production estimates were computed. No fecundity data were collected in 1981 and 1985, so fecundity was estimated for these years by the mean of the estimated E^{-1}'s from the years with fecundity data. Standard errors for these two years were estimated by the average yearly standard error.

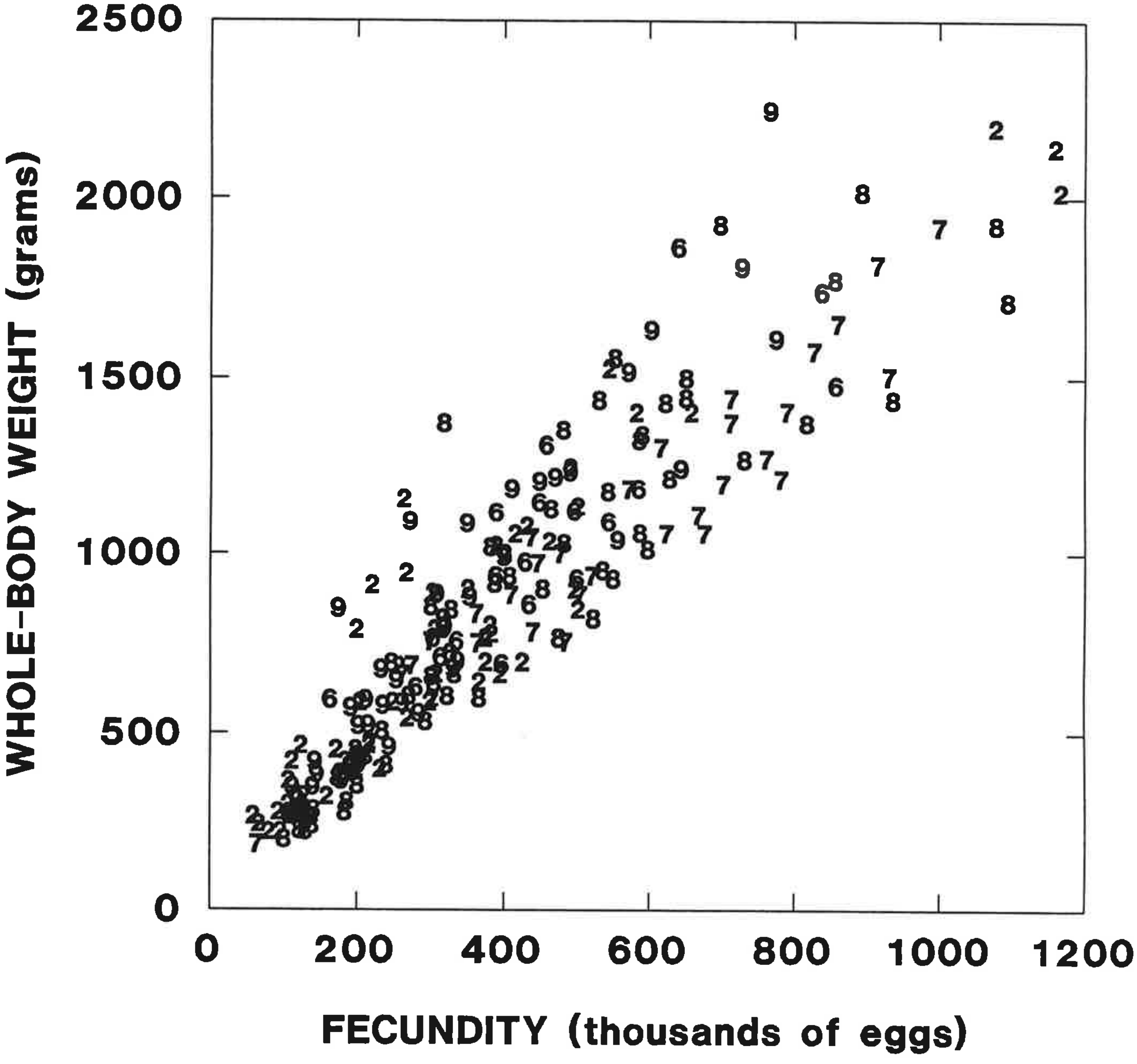

Figure 8. Relationship between potential annual fecundity and whole-body weight for 1982 and 1986 through 1989. Plotted numbers indicate year sample was collected.

SEX RATIO

Sex ratio was estimated from trawl data collected on the acoustic surveys in 1985 through 1991; 1988 data was omitted because only two trawls sampled mature pollock. Sex ratio is difficult to estimate during the spawning period because spawning aggregations during this period are very fluid and dynamic with respect to the segregation of the sexes (E. Nunnallee, AFSC, pers. comm., 1990). Rather than rely on data prone to high variance from few trawls, a constant sex ratio of 1:1 was assumed. This value is probably reasonable in units of numbers of fish, but the parameter R^{-1} is in units of weight. Adult walleye pollock exhibit sexual dimorphism, females weigh more than males of the same age, so R^{-1} was adjusted to account for this:

$$R^{-1} = \frac{N_F*\bar{W}_F + N_M*\bar{W}_M}{N_F*\bar{W}_F}$$

$$= \frac{\bar{W}_F + \bar{W}_M}{\bar{W}_F} \quad \text{assuming } N_F=N_M$$

$$= 1 + \frac{\bar{W}_M}{\bar{W}_F} \qquad \text{[Eqn. 27]}$$

where N_F = number of mature females,

$\bar{W}_F$ = average weight of a mature female,

N_M = number of mature males, and

$\bar{W}_M$ = average weight of a mature male.

Estimation of $\bar{W}_M/\bar{W}_F$, the ratio of the average mature male weight to average mature female weight, was complicated by the fact that the average fish weight in a sample depends on the depth at which the sample was taken. Smaller fish tend to occur higher in the water column (Fig. 9a). This problem can be resolved by stratifying the trawl samples by depth, but the existing trawl samples were not collected with that design. Another solution is to estimate the ratio of average weights from each trawl and then compute the mean of these ratios. The ratio of average male weight to average female weight is constant over trawl depth (Fig. 9b), thus avoiding the bias of uneven sampling over depth. The parameter R^{-1} and its variance was estimated by

$$R^{-1} = 1 + \frac{\sum_{l=1}^{n} C_l * \frac{\bar{W}_{M_l}}{\bar{W}_{F_l}}}{\sum_{l=1}^{n} C_l} \qquad \text{[Eqn. 28]}$$

$$Var(R^{-1}) = \frac{n}{\left(\sum_{l=1}^{n} C_l\right)^2} \frac{\sum_{l=1}^{n}\left[C_l * \left(\frac{\bar{W}_{M_l}}{\bar{W}_{F_l}} - (R^{-1}-1)\right)\right]^2}{n-1} \qquad \text{[Eqn. 29]}$$

where C_l = catch of mature fish in trawl l,

$\bar{W}_{M_l}$ = average weight of mature males in trawl l,

$$= \frac{\sum_{k=1}^{m_{M_l}} W_{M_{lk}}}{m_{M_l}},$$

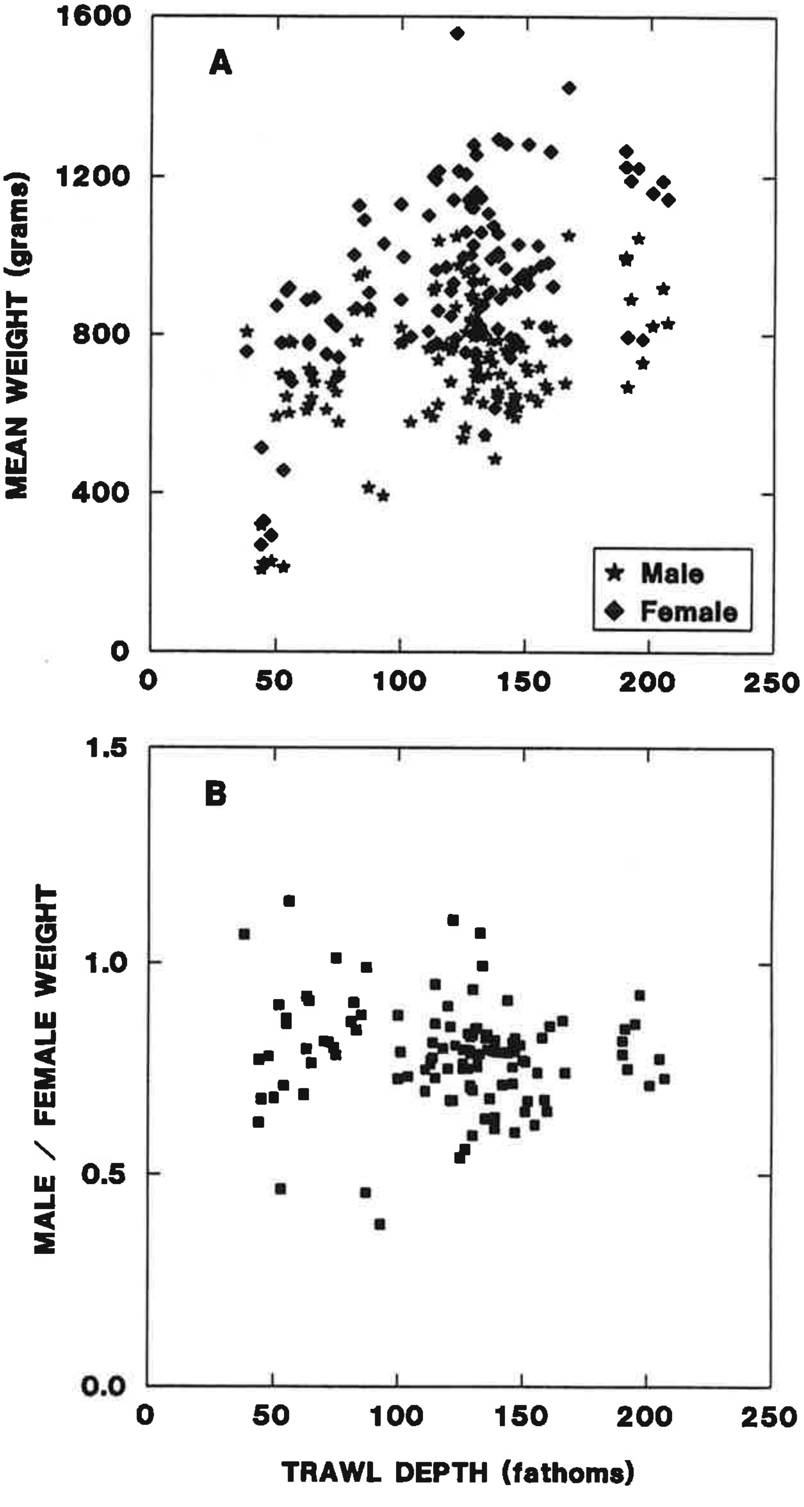

Figure 9. Relationship between mature pollock weight and trawl depth. 9a: Average female and male weight from each trawl plotted against depth of trawl. 9b: Ratio of average male weight to average female weight from each trawl plotted against trawl depth.

$W_{M_{kl}}$ = weight of kth mature male in trawl l,

m_{M_l} = number of mature males in weight subsample from trawl l,

$\bar{W}_{F_l}$ = average weight of mature females in trawl l,

$$= \frac{\sum_{k=1}^{m_{F_l}} W_{F_{kl}}}{m_{F_l}},$$

$W_{F_{kl}}$ = weight of kth mature female in trawl l,

m_{F_l} = number of mature females in weight subsample from trawl l, and

n = number of trawls containing both mature males and mature females.

Sex ratio and its standard error were estimated for 1981 and 1988 by the mean of yearly estimates of sex ratio and standard error from 1985 to 1991.

BIOMASS ESTIMATE

Walleye pollock spawning biomass and variance were estimated for each year using the annual egg production method (Eqns. 3 and 4). Biomass estimates were compared between years with the Games and Howell multiple comparison test.

Comparisons were also performed between spawning biomasses estimated here and those estimated from acoustic surveys and the stock synthesis method. Nonparametric methods were employed because variances are presently unavailable for the acoustic and stock synthesis estimates. Biomass estimates were modelled with a two-way randomized block ANOVA where the fixed factor was the estimation method and the random factor was year. Two nonparametric test statistics were computed from the ANOVA using the Friedman test and the Quade test (Conover, 1980). Unfortunately, there were only four years when all three estimates are available: 1981, 1985, 1986 and 1988.

The acoustic biomass estimates from Nunnallee and Williamson (1989) include some immature fish. For purposes of this comparison, acoustic biomass estimates were converted to spawning biomass by using the product of age-specific acoustic biomass estimates (Nunnallee and Williamson, 1989) and an average maturity ogive (Hollowed and Megrey, 1991). The maturity ogive was fit to annual maturity-at-age data for 1981 to 1989 (Nunnallee and Williamson, 1989). Acoustic biomass estimates are accompanied by variances estimated using cluster sampling theory (Williamson, 1982). However, the data manipulation described above precluded calculation of variances for acoustic spawning biomass estimates because the effect of correcting for maturity on the variance is undetermined.

The stock synthesis spawning biomass estimate uses age composition and catch data from the commercial fishery from the western and central Gulf of Alaska management regions, and is calibrated to both the acoustic biomass estimates and the biomass estimates from the triennial bottom trawl survey (Megrey et al., 1990; Hollowed and Megrey, 1990, 1991). Stock synthesis spawning biomass estimates are sensitive to the relative weight that is given to the acoustic or bottom trawl biomass estimates. Variances of stock synthesis estimates are not available. Stock synthesis biomass estimates reported in Hollowed and

Megrey (1990, 1991) incorporate data from the entire Gulf of Alaska population, whereas the spawning biomass estimates from both the annual egg production method and the acoustic surveys include only the portion of the population that spawns in Shelikof Strait. To make the stock synthesis estimates directly comparable to the egg production estimates, they have been adjusted to include only the portion of the pollock population that spawn in Shelikof Strait in the spring (A. Hollowed, AFSC, pers. comm., 1991). There is insufficient data to estimate the proportion of the population that spawn in Shelikof Strait independently for each year; the stock synthesis model estimated a single value of 68% that best explained the difference between the estimated total Gulf of Alaska pollock spawning biomass and the estimated biomass that spawn in Shelikof Strait.

RESULTS

SURVEYS

The egg densities used to estimate the annual egg production curve and egg production model are illustrated in Figures 4 and 5, respectively. In general, egg density appears to follow the bathymetry of Shelikof Strait (Fig. 1b), with the highest densities occurring in the deep water on the peninsula side of the Strait. This pattern is consistent with the distribution of adults as observed by acoustic surveys conducted just prior to the egg surveys (Nunnallee, 1988). The spawning area, indicated by high egg densities in Figure 5, is centered off Cape Kekurnoi in the southwestern end of Shelikof Strait and is quite consistent over years. The years with highest egg abundance (1981 and 1985) do not appear to have an expanded spawning area, instead they contain higher egg densities.

EGG STAGES AND STAGE DEVELOPMENT TIMES

Figure 10 illustrates the results of fitting Equation 7 to stage development time data for stage-groups 1 through 7. Development time decreases with increasing temperature. Parameters for the 7 fitted models and associated R^2s (coefficients of determination) are presented in Table 2. The R^2s are inflated because the model uses two parameters to fit only three data points.

The temperature-dependent stage development models were used to estimate the age intervals of the six stage groups from each cruise used to estimate egg production (listed in

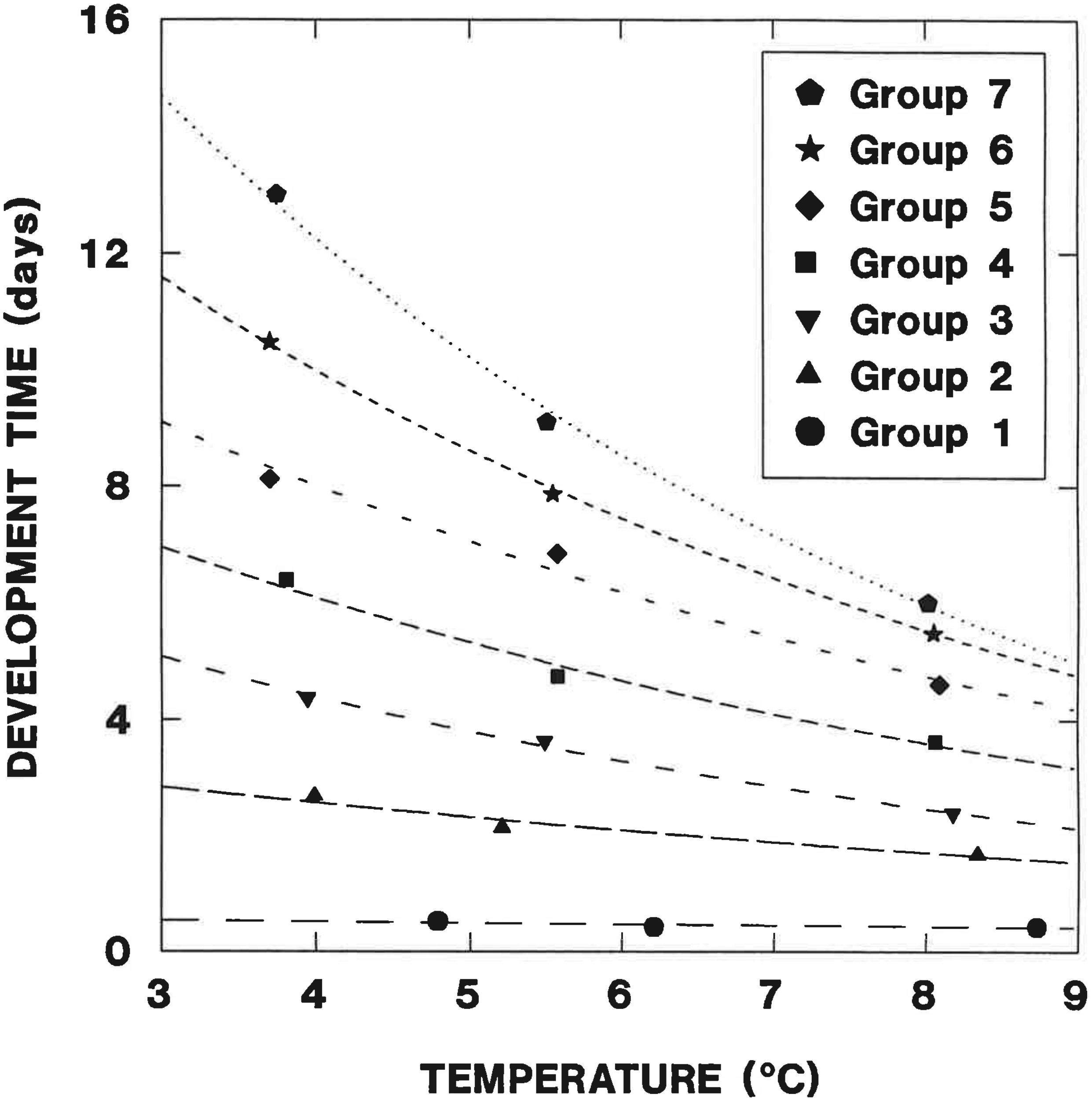

Figure 10. Egg development schedules for stage-groups 1 through 7. Points are observed age at end of stage group at temperature. Smooth lines are modelled development times to end of stage group (Eqn. 7).

TABLE 2

Parameters for the model predicting development time for the egg stage groups.

$$t_{s,T}=\alpha_s * e^{-\beta_s * T} \qquad \text{[Eqn. 7]}$$

STAGE GROUP	α	β	R^2
1	0.6114	0.04450	0.601
2	3.839	0.1021	0.949
3	7.887	0.1458	0.996
4	10.27	0.1312	0.985
5	13.48	0.1298	0.982
6	18.08	0.1484	0.999
7	25.18	0.1802	0.997

column Z in Table 1). The mean temperatures from each year that were used to predict development time are shown in Figure 11. Error bars in Figure 11 are the standard deviations (square root of Eqn. 10) and show the variability of temperature over the survey region. Sample sizes are listed in the figure to indicate the extent of geographic coverage. Only two years (1981 and 1985) had good geographical coverage. The remaining years had few CTD stations which were distributed over a small area. These features are reflected in the size of the standard deviations. In 1986, 1987, and 1988 temperatures were taken over a small area and hence are less variable. Temperatures were very homogenous for all years, with a maximum range of 2°C in 1985. The narrow range reduces the amount of error in using mean temperatures instead of actual station temperatures to estimate the ages at each station.

EGG ABUNDANCE ESTIMATION BY STAGE GROUP

The abundances of the 6 stage groups from the cruises used to estimate egg production are shown in Figure 12. The area of the bars is the estimated total abundance of the stage group (Eqn. 12), the height of the bars is the estimated stage-group abundance per day, and the width of the bar is the estimated age interval for the stage group as described above. Standard error bars are for the area of the bar (square root of Eqn. 13).

ANNUAL EGG PRODUCTION CURVE

The shape of the fitted annual egg production curve is specified by very few points (Fig. 7). The years 1981 and 1986 give no information on the shape of the curve, only the end points. The beginning of the spawning season is not well established, the first cruise in

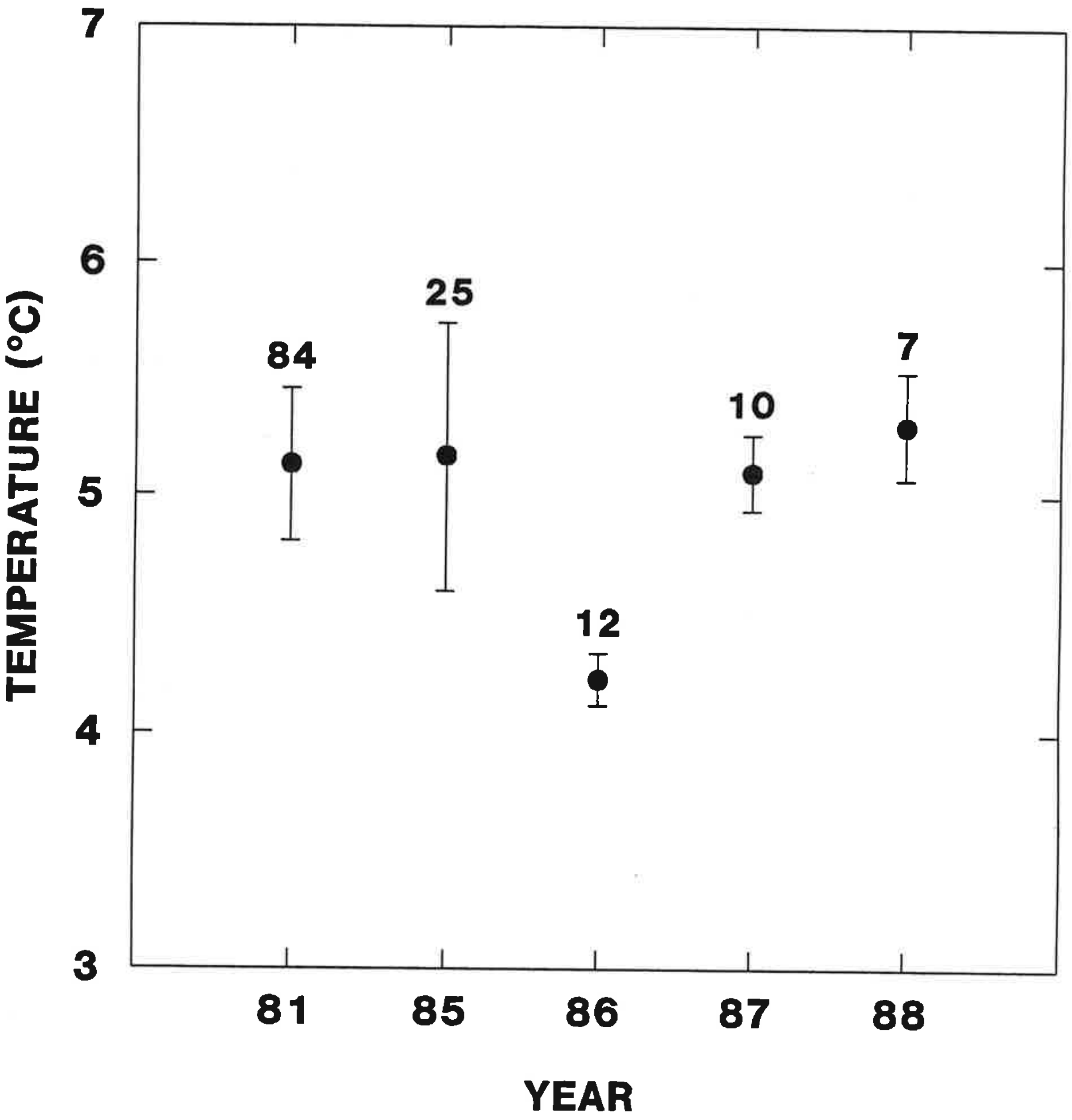

Figure 11. Mean temperature during peak spawning time in survey region (Eqn. 9). Error bars are standard deviations (Eqn. 10) with sample sizes shown.

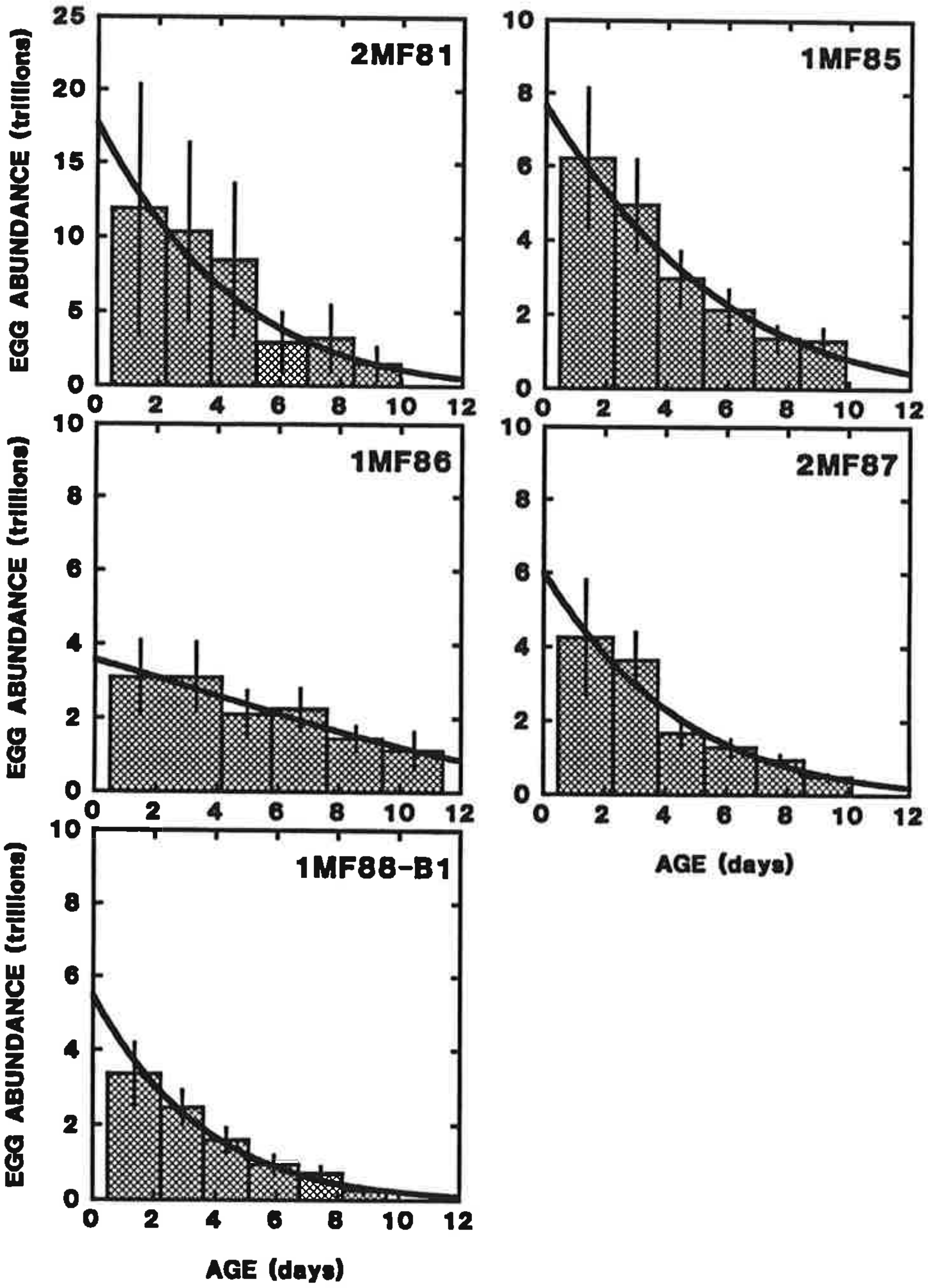

Figure 12. Estimated and predicted age-specific abundances from each survey. The Y-axis is egg abundance per day, the X-axis is development time at the mean cruise temperature. The area of each bar is the estimated abundance of the stage group (N_s from Eqn. 12), the width of the bar is the age interval for the stage group ($t_{s,T}$ - $t_{s-1,T}$ from Eqn. 7), and the height of the bar is the stage-group abundance per day ($N_s/(t_{s,T} - t_{s-1,T})$). Standard error bars are for the area of the bar (total abundance) (square root of Eqn. 13). The smooth line is the fitted egg production model (Eqn. 18). The predicted stage-group abundance is the area under the smooth line over the stage group's age interval.

1981 was conducted before spawning began and we may only conclude that spawning began sometime between days 75 and 95. Information on the shape of the curve is provided only by the two series from 1988 which have multiple observations during the time period of high egg production. These cruises indicate the rate of decline in egg production on either side of peak spawning, so the estimated values of μ and b may be appropriate only for 1988.

Parameters estimated from the annual egg production curve define the shape of the spawning season. These three parameters are: (1) peak spawning date (μ = day-of-the-year 97.88, s.e. = 0.8844), (2) the parameter that determines the length of the season (b = 0.1299/d, s.e. = 0.008571), and (3) the background level of egg production (γ = $0.005382*10^{12}$ eggs/day, s.e. = $0.2079*10^{12}$). The modelled spawning season has a duration of 48 days, running from 15 March to 2 May, with a peak on 8 April. The background spawning rate is not significantly different from 0 (df = 4, t = 0.05383, $p > 0.05$), but it was left in the model to maintain generality of the model and because spawning never completely ceases.

EGG PRODUCTION

The fitted egg production models for the five cruises from the peak spawning time are shown in Figure 12. The smooth line is the egg production model which combines the effects of mortality and varying production rates on the abundances of the different stage groups in the cruise. The model allows each stage group to be spawned on a different date and predicts its abundance based on the production rate on that date and the amount of mortality that has occurred between the spawning date and sampling date. The slope of the line depends both on the mortality rate (Z) and the date of the survey (D) relative to the peak spawning date (μ). The egg production model contributed two parameters: the mortality rate (Z), and the total egg production over the spawning season excluding the background level (ρ_0). The parameter P_a needed for the spawning biomass estimate is the total egg production including the background level (Eqn. 19). However, the estimate of background level (γ) is not significantly different from 0 and is negligible, so P_a is estimated by the fitted values of ρ_0 from the egg production model.

Estimates of P_a and Z and their associated standard errors are listed in Table 3. The Games and Howell multiple comparison test found a significant difference in mortality rates between 1986 and 1988 (df = 6, G&H = 7.631, $p < 0.01$). The rates are in the same range of values estimated from other sources (Kim and Gunderson, 1989; Bates, 1987, 1990); the lowest mortality occurred in 1986 with 38% survival to hatch and 1988 had the highest mortality with only 2% survival.

The model appears to fit the stage-group abundances quite well except for 1981. This year has the highest production and the worst fit. The first year an egg survey that targeted pollock was conducted was 1981 and the data are somewhat tenuous because the station egg densities had to be estimated due to insufficient tow depths as described earlier. The spatial distribution of eggs was also more patchy than in the other years, which decreased the

TABLE 3

Egg production P_a, egg mortality Z, sex ratio parameter R^{-1} (ratio of spawning biomass to mature female biomass), fecundity parameter E^{-1} (grams female weight per egg produced), and spawning biomass B_s (million metric tons) by year. Standard errors of parameter estimates are in parentheses. Sample sizes are in square brackets; n for P_a and Z is the number of bongo tows in the egg survey during peak spawning, n for R^{-1} is the number of trawls in the acoustic survey, and n for E^{-1} is the number of female pollock in the fecundity sample. Sample size of n=0 indicates a year with missing data and parameter estimate in table is mean of all years, n^* shows the total sample size from all years used to estimate the missing value.

YEAR	P_a $*10^{12}$ eggs	Z	R^{-1}	E^{-1} $*10^{-3}$ grams per egg	B_s $*10^6$ metric tons
81	448.6 (108.7) [n=86]	0.1962 (0.04410) [n=86]	1.777 (0.02768) [n=0, n^*=118]	2.230 (0.06235) [n=0, n^*=215]	1.777 (0.4346)
85	188.4 (27.87) [n=88]	0.1598 (0.02548) [n=88]	1.793 (0.01359) [n=27]	2.230 (0.06235) [n=0, n^*=215]	0.7532 (0.1136)
86	86.57 (9.000) [n=80]	0.06149 (0.01580) [n=80]	1.789 (0.004347) [n=12]	2.339 (0.09560) [n=23]	0.3622 (0.04050)
87	145.7 (24.29) [n=121]	0.2123 (0.02495) [n=121]	1.731 (0.02561) [n=16]	1.859 (0.03547) [n=33]	0.4689 (0.07899)
88	132.8 (17.77) [n=105]	0.2893 (0.02533) [n=105]	1.777 (0.02768) [n=0, n^*=118]	2.045 (0.04603) [n=58]	0.4822 (0.06590)

precision of the stage-group abundances. This resulted in larger variances about the estimates of ρ_0 and Z when compared to other years.

An unusual feature of 1986 was the occurrence of many old eggs and relatively few young eggs, which produced a very low mortality rate and egg production. Another explanation of this age distribution is that the actual peak spawning date was earlier than assumed so that the older eggs were produced at a higher rate and younger eggs were produced at a lower rate than the model expects. The annual egg production curve may best describe the 1988 spawning season because this is the only year with enough data to specify the shape of the curve. This gives added credibility to the 1988 estimates of ρ_0 and Z, and creates a potential for suspicion about these parameters for the other years because estimates of P_a and Z are highly dependent on the shape of the annual egg production curve. Mortality estimates from all years are quite similar, except for 1986 which is the only year that is significantly different from 1988, casting further doubt on the validity of the 1986 parameter estimates. This year also had the coldest mean temperature based on only a few CTD stations. If the true temperature was warmer than the estimated mean, then the age intervals were actually shorter and the mortality higher than estimated. Both of these possible problems would produce underestimates of ρ_0 and Z, which in turn would lead to an underestimate of spawning biomass.

FECUNDITY

The fecundity parameter needed to estimate spawning biomass is E^{-1} -- the number of grams of mature female needed to produce one egg. The analysis of covariance showed that the relationship between whole body weight of females and potential annual fecundity varied significantly between years. Both of the parameters in Equation 23 were significantly different over years (b_1: F = 4.477, df = 4, 205, p = 0.002; b_2: F = 4.214, df = 4, 205, $p < 0.0005$). This necessitated that Equations 23 and 24 be fit separately for every year.

The parameter estimates for both Equations 23 and 24 by year are shown in Table 4. The 95% confidence interval about the exponent in Equation 23 (b_2) included 1.0, thus simplifying to Equation 24, for every year except 1982. The fecundity data from 1982 was not used directly but was only needed as a component of the average value of E^{-1} averaged over all years, which estimated the fecundity parameter for 1981 and 1985. Although the curvilinearity in the 1982 data was statistically significant, the data did not show much curvilinearity (Fig. 8), the fit to the linear model was only slightly worse than the fit to the curvilinear model, and the residuals from the linear model did not show any curvilinearity. Thus Equation 24 was used for the 1982 fecundity data to make it consistent with the data from other years and to produce an estimate of E^{-1} that could be averaged with the estimates from the other years.

TABLE 4

Parameter estimates for regression models relating whole body weight and potential annual fecundity by year. Confidence intervals of parameter estimates are in parentheses.

YEAR	$W = b_1 * (F * 10^{-3})^{b_2}$ (Eqn. 23)		$W = b_1 * (F * 10^{-3})$ (Eqn. 24)
	b_1	b_2	b_1
82	6.32 (3.40,9.23)	0.829 (0.747,0.911)	2.44 (2.28,2.60)
86	4.81 (0.250,9.38)	0.881 (0.725,1.04)	2.34 (2.14,2.54)
87	3.50 (1.23,5.76)	0.905 (0.808,1.00)	1.86 (1.79,1.93)
88	2.00 (1.16,2.83)	1.00 (0.933,1.07)	2.04 (1.95,2.14)
89	3.14 (1.59,4.70)	0.957 (0.870,1.04)	2.47 (2.35,2.58)

Table 3 shows the estimates of E^{-1} for each year, where 1981 and 1985 were estimated by the mean over all years because no fecundity data was collected in those years. Estimates of E^{-1} range from .001859 (=537.9 eggs per gram) in 1987 to .002339 (=374.7 eggs per gram) in 1986.

SEX RATIO

Estimates of sex ratio are quite consistent over years (Table 3). The values for R^{-1} are less than two, indicating that males weigh less than females. R^{-1} could not be estimated directly for 1981 and 1988 because no data was available for 1981 and there was not a sufficient number of trawls conducted in 1988. Sex ratio was estimated for these two years by the grand mean of the yearly sex ratios from 1985 to 1991.

BIOMASS ESTIMATE

The annual egg production method estimates of walleye pollock spawning biomass in Shelikof Strait are displayed in Table 3 and Figure 13. Estimates of B_S range from $0.3622 * 10^6$ metric tons in 1986 to $1.777 * 10^6$ metric tons in 1981. There appears to be a downward trend in biomass over time, although significant differences were not detectable using the Games and Howell method to compare the biomass estimates between years. Both nonparametric ANOVA tests comparing the annual egg production spawning biomass estimates with those from the acoustic and stock synthesis methods found no significant differences (Friedman = 0.2, df = 2,6, $p > 0.05$; Quade = 0.913, df = 2,6, $p > 0.05$).

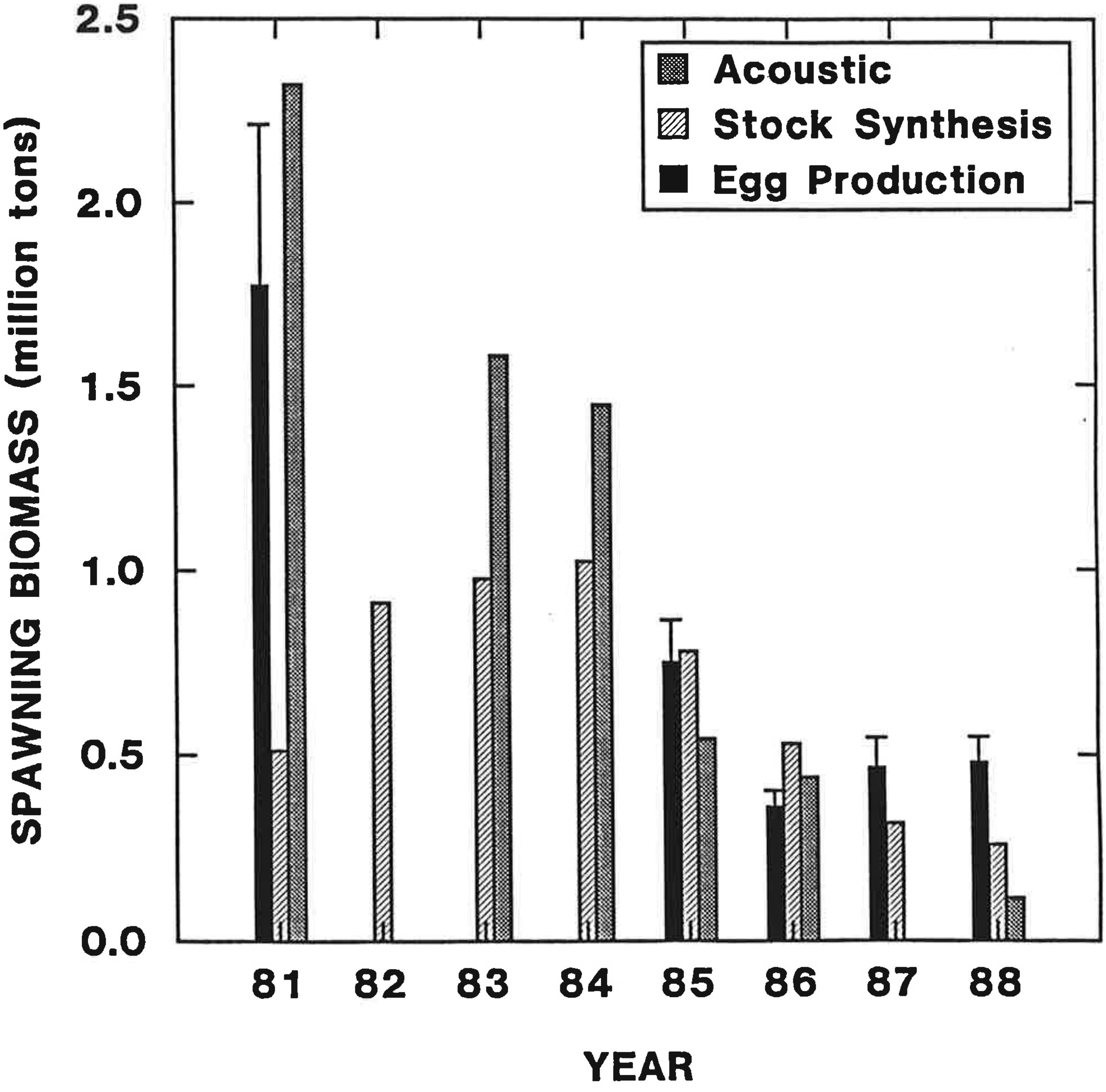

Figure 13. Time series of spawning biomass estimates from three methods: annual egg production method, acoustic survey, and stock synthesis model. There are no egg production estimates for years 1982-1984 and acoustic estimates are unavailable for years 1982 and 1987. The egg production biomass estimates have standard error bars. Acoustic and stock synthesis biomass estimates have been modified to include only mature pollock that spawn in Shelikof Strait.

Although the stock synthesis estimates are much lower than the other estimates for the years 1981-1984, there is no consistent pattern among the rankings of the estimates for the years where all three estimates are available. The egg production spawning biomass estimate produced in this study for 1981 ($1.77*10^6$ metric tons) is between the 1981 egg production spawning biomass estimates produced by two earlier studies: Kim and Gunderson (1989) estimated $3.1*10^6$ metric tons, and Bates (1987) produced three estimates using three different methods to estimate egg production, $0.29*10^6$, $0.31*10^6$, and $1.23*10^6$ metric tons.

DISCUSSION

BIOMASS COMPARISONS

With the implementation of the annual egg production method of estimating walleye pollock spawning biomass in Shelikof Strait, there are three sources of spawning biomass estimates: acoustic, stock assessment using the stock synthesis model, and egg production. Figure 13 compares these estimators.

Although the acoustic surveys of pollock in Shelikof Strait are done just prior to the egg surveys (Nunnallee and Williamson, 1989), the two estimators actually measure different parts of the population. The annual egg production method estimates only the portion of the population that is mature, requiring that the acoustic estimate be modified to remove the immature fish for this comparison. The acoustic method underestimates the portion of the biomass that resides very near the ocean floor. It is also very sensitive to the estimate of the target strength parameter. For most years, the acoustic spawning biomass estimates agree very well with the annual egg production spawning biomass estimates.

Stock synthesis spawning biomass estimates are also very similar to the annual egg production spawning biomass estimates. The peak in biomass estimated for 1983 reflects the series of five strong year classes (1975-1979) moving through the population. Unfortunately, there are no annual egg production biomass estimates for the years 1982 through 1984 so it is unknown if this method would have produced the same trend as the stock synthesis biomass estimates over these years. Again, there are differences in the target population of the stock synthesis biomass and the annual egg production biomass. Stock synthesis estimates reported in Hollowed and Megrey (1991) required modification to include only the portion of population that spawns in Shelikof Strait. There is also a temporal difference between the two populations being estimated by stock synthesis and by egg production. The stock synthesis method estimates the number of fish on 1 January based on surveys conducted in spring and throughout the summer, and converts this to spawning biomass using weight-at-age and maturity-at-age estimates from 1 March. The ichthyoplankton surveys were conducted over a narrower date range in the spring and estimates spawning biomass in Shelikof Strait over the spawning season, 15 March to 2 May.

Comparison of the annual egg production spawning biomass estimates to the other two biomass estimates corroborates the suspicion that the 1986 estimate is too low. The 1986 estimate is questionable because the distribution of egg ages was very different than the other years' distribution of egg ages (Fig. 12). It is possible that egg mortality and production are underestimated in 1986 because of a shift in the annual egg production curve relative to other years. This emphasizes the need to estimate this curve independently every year. This will require a considerable increase in survey effort and expense over the current level and this may be the determining factor for the routine use of the annual egg production method to estimate biomass.

BIASES AND ASSUMPTIONS

The most important criteria required to apply the annual egg production method of estimating spawning biomass is that the fecundity of pollock is determinate. Hinckley (1987) showed that walleye pollock are determinate spawners, however if this assumption were false then the total standing stock of oocytes per female would underestimate the potential annual fecundity (Hunter et al., 1985; Hunter et al., 1992). Fecundity would also be underestimated if some of the females in the fecundity sample had already spawned some of their eggs during the current season. It was also assumed that the loss of eggs to atresia is negligible, which, if significant, would lead to an overestimate of fecundity. A source of imprecision is the measurement error in estimating total fecundity for each female due to misidentification of oocytes and the variability between subsamples from each ovary. These measurement errors are assumed to be negligible and were ignored. Further investigations into the fecundity of walleye pollock are currently being conducted by the Alaska Fisheries Science Center to address many of these assumptions.

Other assumptions about the adult population of walleye pollock are as follows. Sex ratio in units of numbers is assumed to be 1:1; this assumption is unavoidable due to sampling problems caused by the segregation of the sexes. Also, if the annual egg production biomass estimate or the acoustic biomass estimate are to be used to estimate the walleye pollock population in the Gulf of Alaska, then it must be assumed that a known and constant fraction of the Gulf of Alaska population of walleye pollock spawn in the Shelikof Strait. Pollock eggs and larvae have been found outside Shelikof Strait (Kendall and Picquelle, 1990), and the contention that the proportion of the population that spawns elsewhere is negligible is a topic of current debate and requires further study.

Sampling problems during the ichthyoplankton surveys are a potential source of many biases. Many of these problems were due to the fact that the surveys were not all designed for the primary purpose of estimating egg production. The annual egg production biomass estimates were produced from available data which were accompanied by a variety of sampling peculiarities. Ideally, the survey area should cover the entire geographic range of eggs from this spawning aggregation; in this study the survey area is fixed and it is assumed that the surveys missed only a small portion of the eggs. It was also assumed that the ichthyoplankton surveys did not systematically under-sample certain ages of eggs because of age-specific differences in the spatial distribution. For example, eggs occur at depths where water currents are slow (Schumacher et al., 1990), so it is unlikely that older eggs drift southwest and out of the survey area. Kendall and Kim (1989) have shown that the vertical distribution of eggs varies with age, thus surveys conducted in 1981 which did not sample deep enough may have produced a biased age distribution. The model used to correct egg densities from shallow stations does not consider the vertical distribution of ages and the variances about the estimated densities from the correction are ignored in subsequent analyses. This problem was avoided in subsequent years by sampling over the entire depth range of the eggs. Another potential sampling bias is that bongo nets may not sample all ages of eggs with 100% efficiency (i.e. extrusion or damage to the eggs). Eggs in stage group 1 are apparently under-sampled and more study is needed to overcome this sampling bias; currently stage-group 1 eggs are not used in the analysis. Similarly, it is assumed that there is no bias in selecting subsamples of eggs for staging.

A source of imprecision is that ichthyoplankton surveys are not synoptic. The egg production model assumes that all eggs were sampled on the same day within each survey -- the mean survey date. The error introduced by this assumption is slight if the survey has a short duration, which is frequently the case because the geographic area is small. However, the small survey area leads to bias in the variance estimates of egg abundance. Because the area is small, stations were close together, and observed densities may be spatially correlated (Smith and Hewitt, 1985). The variance estimator assumes that all observations are independent, but in some instances they were not. This leads to an underestimate of the variance by overstating the degrees of freedom. The implications of this problem have not been investigated, but corrections for this feature are possible with more sophisticated models that incorporate a spatial component. The variance would also be underestimated if stations were selected during the survey in response to observed egg densities, as was sometimes done in earlier surveys. Observations would not be independent making standard estimators inappropriate. The Sette-Ahlstrom abundance estimator controls the bias introduced in the abundance estimates by weighting each station by its polygonal area. The bias in the variance estimates was ignored for this study because its occurrence was undocumented and probably infrequent and later surveys followed a more rigorous statistical survey design.

The primary assumption of the egg production model (Eqn. 17) is that all spawned eggs are fertilized. If a significant portion of the eggs are left unfertilized, then spawning biomass is underestimated. This assumption will be tested by collecting samples specifically targeted on unfertilized walleye pollock eggs during the 1992 Shelikof Strait field season. The model also makes assumptions about the mortality and production rate. Specifically, egg mortality is assumed to be constant over ages and survey area. An alternative assumption is that mortality rate is a function of development time, either increasing with age or more likely decreasing with age. Egg production rate is assumed to follow the specified mathematical model, with the peak at the same day of year and have the same shape for all years. As mentioned earlier, this assumption is probably not valid; age structure of the adult population and the environment may influence the egg production rate, but more egg surveys conducted throughout the spawning season are required to validate this assumption.

Several assumptions are required for the estimation of ages from the stages. Data used to model the development times of stage groups were from just one experiment, thus it is assumed that the fitted models do not vary over time or space. Development time experiments will be repeated to assess the constancy of development rates. Also, the temperatures used to estimate age from the models were mean temperatures from the survey and not the temperatures that the eggs actually developed in. Future egg surveys will measure the temperature profile at each bongo station. The resulting estimated ages were used as the independent variable in the egg production model, but the measurement error about the ages was ignored. This leads to an underestimate of the variances of the egg production model parameters, but this effect is small because the variance of the ages is small compared to the other sources of variability.

The variance of the annual egg production spawning biomass estimate is underestimated due to many problems, several of which have already been mentioned. The main source of bias in the variance is the treatment of peak spawning date and length of spawning season as constants. Ideally, the annual egg production curve and the egg production model would be fit simultaneously so that the variances of all the parameters from both models would reflect the actual degrees of freedom available. This is not presently possible because the mortality rate and peak spawning date are highly correlated and the model fitting both of these is over-parameterized. This problem could be alleviated by conducting more surveys to better describe the egg production rate over the spawning season, which in turn would allow the parameters P_a, Z, b and μ all to be estimated simultaneously from one year's data.

CONCLUSIONS

The annual egg production method has some distinct advantages over other estimation methods. The main advantage of the egg production estimator is that it is based on the sampling of fish eggs which are relatively easy to sample quantitatively compared to adult fish. Fish eggs cannot react to the presence of the net in the water, while all the other life stages are potentially capable of avoiding capture. This does not guarantee that they are sampled without bias, but the sampling problems are greatly reduced when compared to those of the other life stages. One sampling problem that walleye pollock eggs share with schooling adults is that their spatial distribution is very patchy. This requires a large sample size over a short time interval, and a sampling design and abundance estimator that accounts for this spatial distribution. The main disadvantage of the annual egg production method is that it requires multiple ichthyoplankton surveys throughout the spawning season, whereas the acoustic method requires only one survey early in the spawning season.

The spawning biomass estimates and their standard errors produced in this study are reasonable and the method works well for the Shelikof Strait spawning aggregation of walleye pollock in the Gulf of Alaska. All of the parameters required for the annual egg production method are estimable, including variance.

Considering the biases and assumptions of the different biomass estimators described above, the agreement between the annual egg production spawning biomass estimates and the biomass estimated by the other two methods is surprisingly good. The annual egg production method appears to be quite robust in that it tracks the decline in the population as estimated by the other two methods, even though the egg production spawning biomass estimates were reconstructed from historical data collected for a variety of purposes and constrained by a fixed survey area.

FUTURE RESEARCH

Many improvements can be made to the estimation procedure presented here. First, a sensitivity analysis should be performed to identify elements of the procedure that have the greatest influence on final spawning biomass estimates. This should help direct future field and laboratory research. More research needs to be undertaken on fecundity and egg development schedules. Fecundity should be estimated each year because it varies significantly among years. The date of peak spawning may also vary between years, so multiple surveys should be conducted during the spawning season, specifically between late March and late April when egg production rates are high for pollock in Shelikof Strait. Temperature profiles should be measured at each station to get a better estimate of the temperature at which eggs are developing, however, it still must be assumed that there is no change in the temperature over the two week incubation period because it is impossible to track the temperature in which eggs develop throughout their incubation. Egg surveys could be made more precise by placing more stations in areas of high egg densities as predicted by the acoustic survey conducted just prior to the egg survey. Lastly, the question of what proportion of the population spawns in Shelikof Strait each spring must be resolved if this method is to provide a biomass estimate for the entire Gulf of Alaska walleye pollock population. Unfortunately, this is a daunting task that will require extensive synoptic surveys or information on adult migration or routine comparison with other methods that do assess the entire Gulf of Alaska stock.

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