NWAFC PROCESSED REPORT 90-08

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August 1990

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Estimation of Seasonal Egg Production and Daily Egg Mortality for Walleye Pollock (Theragra chalcogramma) in Shelikof Strait, AK, during the years 1981, 1985, and 1986

by

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August 1990

CONTENTS

CHAPTER 1. Introduction to the analysis of egg survey data.

The main thrust of these analyses was to estimate seasonal egg production and mortality during the incubation period for the years 1981, 1985, 1986 based on egg sampling from the spawning walleye pollock population in Shelikof Strait. This effort was broken down into five veins of analysis.

Chapter 2 describes survey designs and sampling procedures, details preliminary egg catch standardizations, and presents contoured plots of egg distribution and abundance for a few representative developmental stages.

Chapter 3 presents modifications to estimation procedures employed in prior analyses. Preliminary estimates were then obtained for seasonal egg production and daily egg mortality.

Chapter 4 provides a means to evaluate the effectiveness of egg sampling. It is demonstrated that samples provide differing amounts of information as to the numerical abundance of eggs within the survey area. These differences are systematic and the quality of abundance estimates can be improved by changes in survey design.

Chapter 5 examines the variability in egg catches between paired 20 cm bongo nets and attempts to evaluate the representativeness

of a single sample. This information is significant because each egg catch is considered as an estimate of average egg abundance for a large area in the region where the sample was collected. But how variable is an egg catch? And how does this variability change over different regions of the survey area? Further, what are the implications of this station-to-station variability for survey design and the variability of parameter estimates?

Chapter 6 presents a Monte Carlo simulation of sampling from the egg population. The intent here is to demonstrate the effectiveness of the improvements to survey design suggested by prior analyses, and to empirically estimate the variability of parameter estimates via simulation. It is shown that the variability of parameter estimates can be much less than is commonly thought, provided changes in survey design are implemented and the analytical reduction of survey data is of sufficient complexity to take advantage of spatial trends in egg abundance.

Chapter 7 summarizes significant results and conclusions from the foregoing analyses.

Mathematical symbols used throughout the text and their definitions are summarized in Table 1.

Table 1. Definition of mathematical symbols.

ϵ	seasonal egg production (fertilized eggs spawned /survey area /spawning season)
μ	day-of-the-year of peak spawning
σ	one standard deviation in the normal spawning curve (days)
ln	natural logarithm
exp	exponentiation
abs	absolute value
a_i	cumulative time from spawning to the beginning of the developmental stage i (days)
b_i	cumulative time from spawning to the ending of the developmental stage i (days)
i	ith stage of development
j	jth sampling station within the survey area
t	instantaneous age of eggs (days)
A_{ij}	standardized stage abundance, the number of eggs assigned to the ith stage for the jth sample (eggs of stage i /m^2)
B_{ij}	hourly abundance for the ith stage at the jth station (eggs of stage i /hour of stage duration /m^2)
C_i	observed total abundance of the ith stage (eggs of stage i /survey area)
$C_{i'}$	predicted total abundance of the ith stage (eggs of stage i /survey area)
D_i	duration (hours) of the ith stage at the average station temperature
E	total fitting error
G_j	local day-of-the-year of sampling at the jth station
H_i	observed average daily abundance of the ith stage (eggs of stage i /day of stage duration /m^2)
$H_{i'}$	predicted daily abundance of the ith stage
I	number of stages comprising the incubation period
J	number of stations occupied within the survey area during a survey
K_j	number of eggs collected at the jth station
K_{nj}	number of eggs collected by the nth net at the jth station
$\bar{K}_j$	mean egg catch from both nets at the jth station
L_i	estimate of the natural logarithm of the cumulative development time to the end of the ith stage at 0°C
M_i	slope of the log-linear relationship between cumulative development time and temperature for the ith stage

Table 1 (continued). Definition of mathematical symbols.

P_j	polygonal area (m^2) assigned to the jth station based on the method of Sette and Ahlstrom (1948)
Q_{ij}	cumulative development time (hours) to the end of the ith stage at the jth station temperature
S_j	standardized egg catch for the jth station (eggs of all stages /m^2 column of seawater from the surface to the maximum depth attained during the tow)
S_{nj}	standardized egg catch from the nth net of the jth station
$\overline{S}_j$	mean standardized egg catch for the jth station
T	day-of-the-year of the spawning season upon which the survey was centered
U_j	number of eggs staged from the jth sample (eggs /staged subsample j)
V_j	estimated volume filtered by a net during sampling at the jth station (m^3)
W_j	temperature (centigrade) at the jth station
X_{ij}	number of eggs in the ith stage of development from the subsampled catch collected at the jth station (eggs of stage i /staged subsample j)
Y_j	estimated maximum depth attained during the tow at the jth station (m)
Z	coefficient of instantaneous mortality
CV_j	coefficient of variation for a pair of (un)standardized egg catches at the jth station
$[A_{ij} \ P_j]$	polygonal stage abundance (eggs of stage i /polygonal station area j)

CHAPTER 2.   Overview of egg survey data.

INTRODUCTION

This chapter 1) describes the egg survey data available for analysis, 2) summarizes preliminary calculations in the standardization and adjustment of egg catch data, and 3) indicates the nature of egg abundance gradients within the survey area by means of contoured distribution plots.

METHODS

Survey data and definition of the survey area   Data on the spawning of walleye pollock eggs in Shelikof Strait were available from four ichthyoplankton cruises, designated 2MF81, 1PO85, 1MF85, and 1MF86 (Table 2, Figures 1-4). Cruise 1PO85 was conducted by scientists of the U.S.S.R. under a cooperative research program with scientists of the Alaska Fisheries Science Center (AFSC) (Kendall 1981); the remaining cruises were conducted by the AFSC.

Table 2.   Walleye pollock egg cruises in Shelikof Strait, AK.

year	cruise designator	start and end date
1981	2MF81	March 30 - April 8
1985	1PO85	March 29 - April 21
1985	1MF85	April 2 - April 10
1986	1MF86	April 4 - April 12

Figure 1. Station locations for cruise 2MF81, March 30 to April 8, 1981. The survey area employed in analyses is outlined.
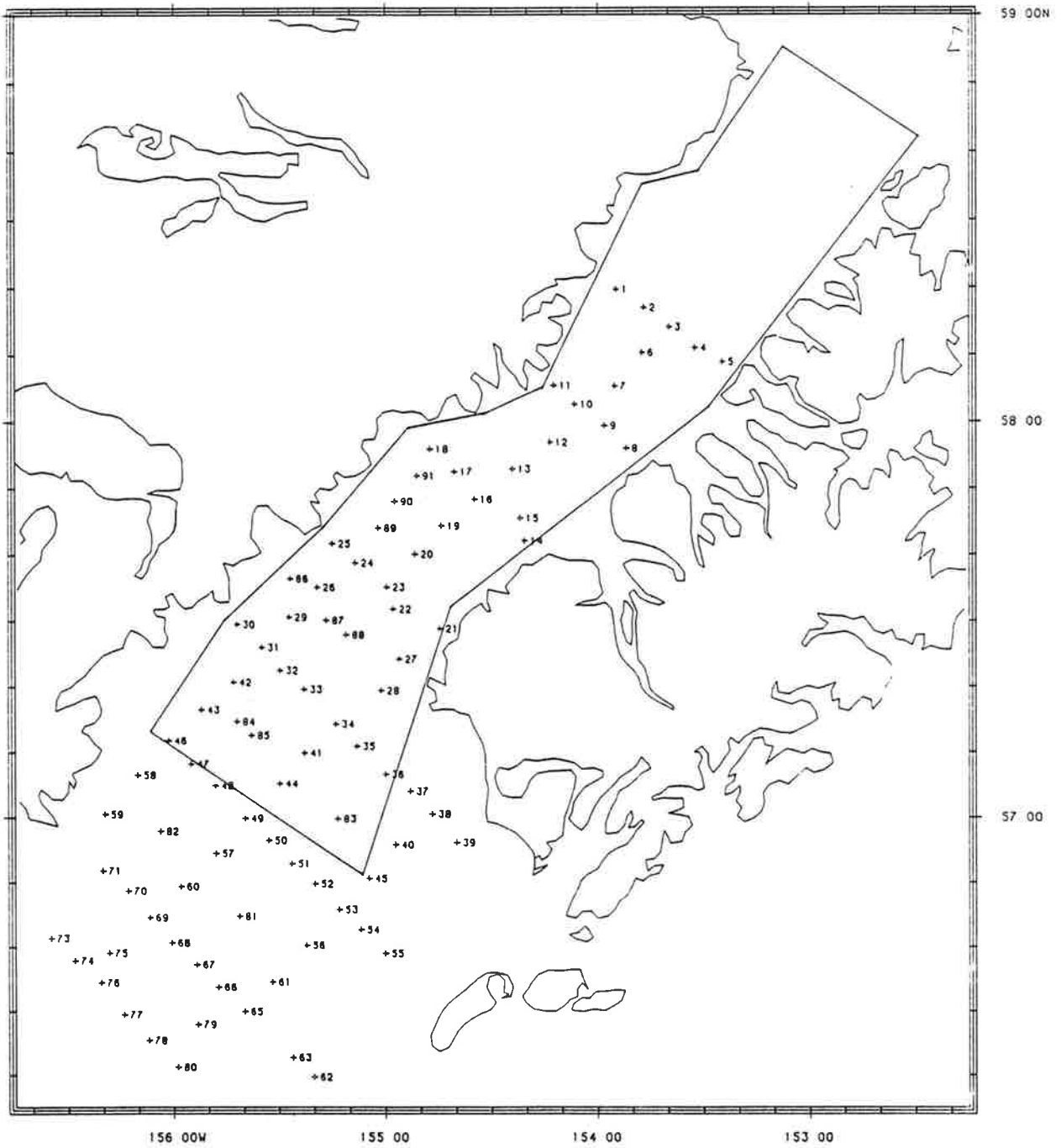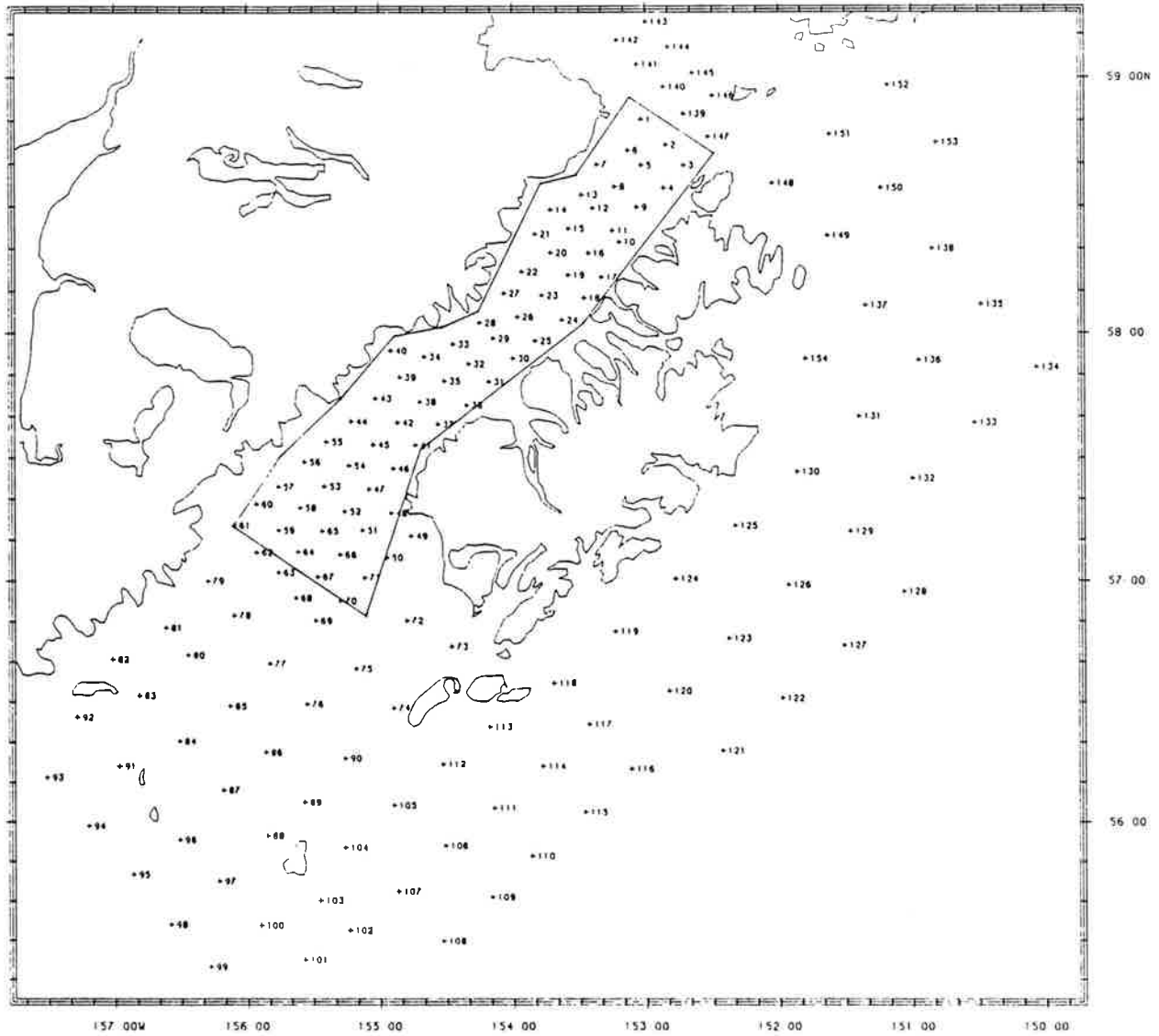
Figure 2. Station locations for cruise 1PO85, March 29 to April 21, 1985. The survey area employed in analyses is outlined.
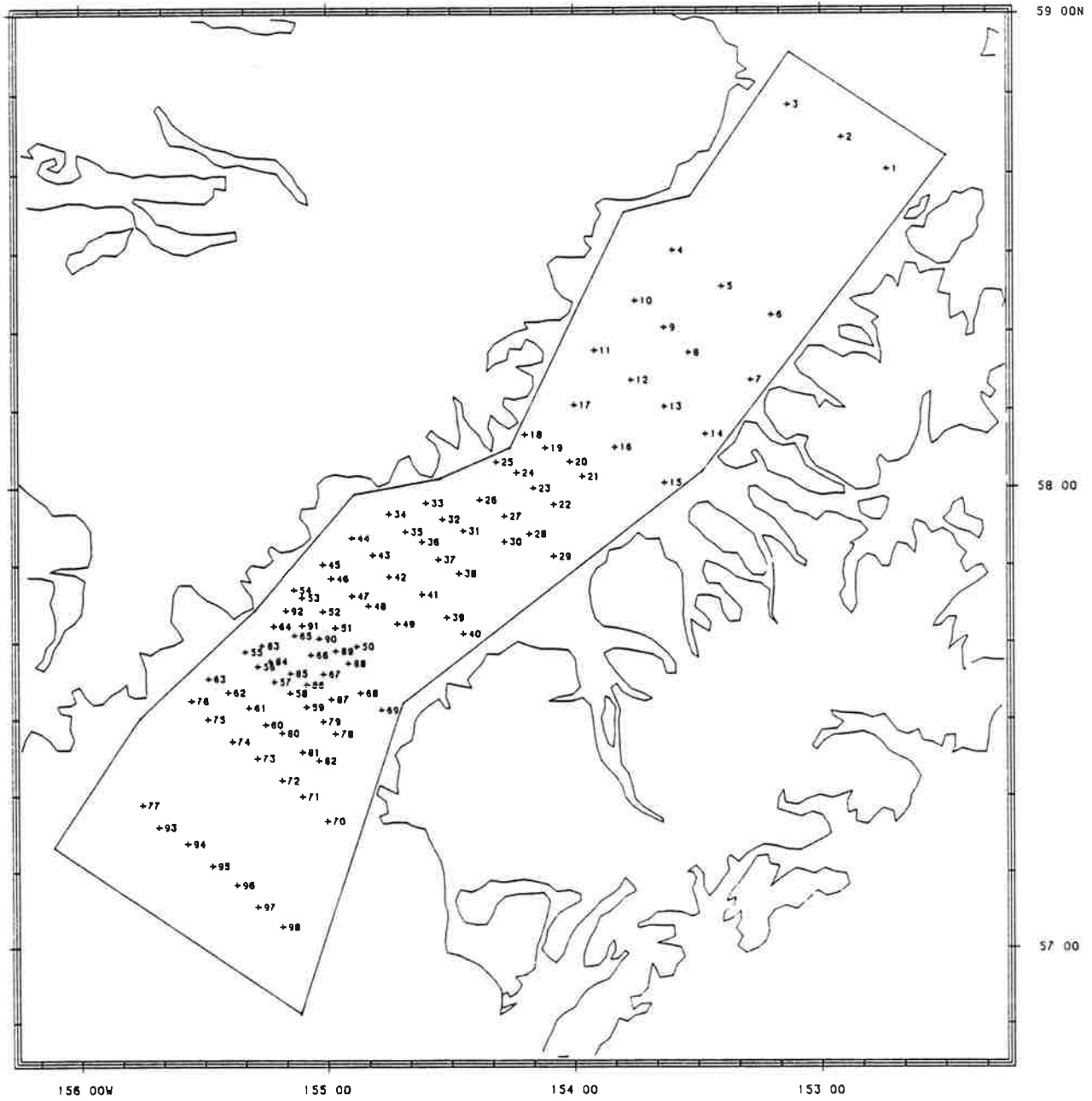
Figure 3. Station locations for cruise 1MF85, April 2 to April 10, 1985. The survey area employed in analyses is outlined.
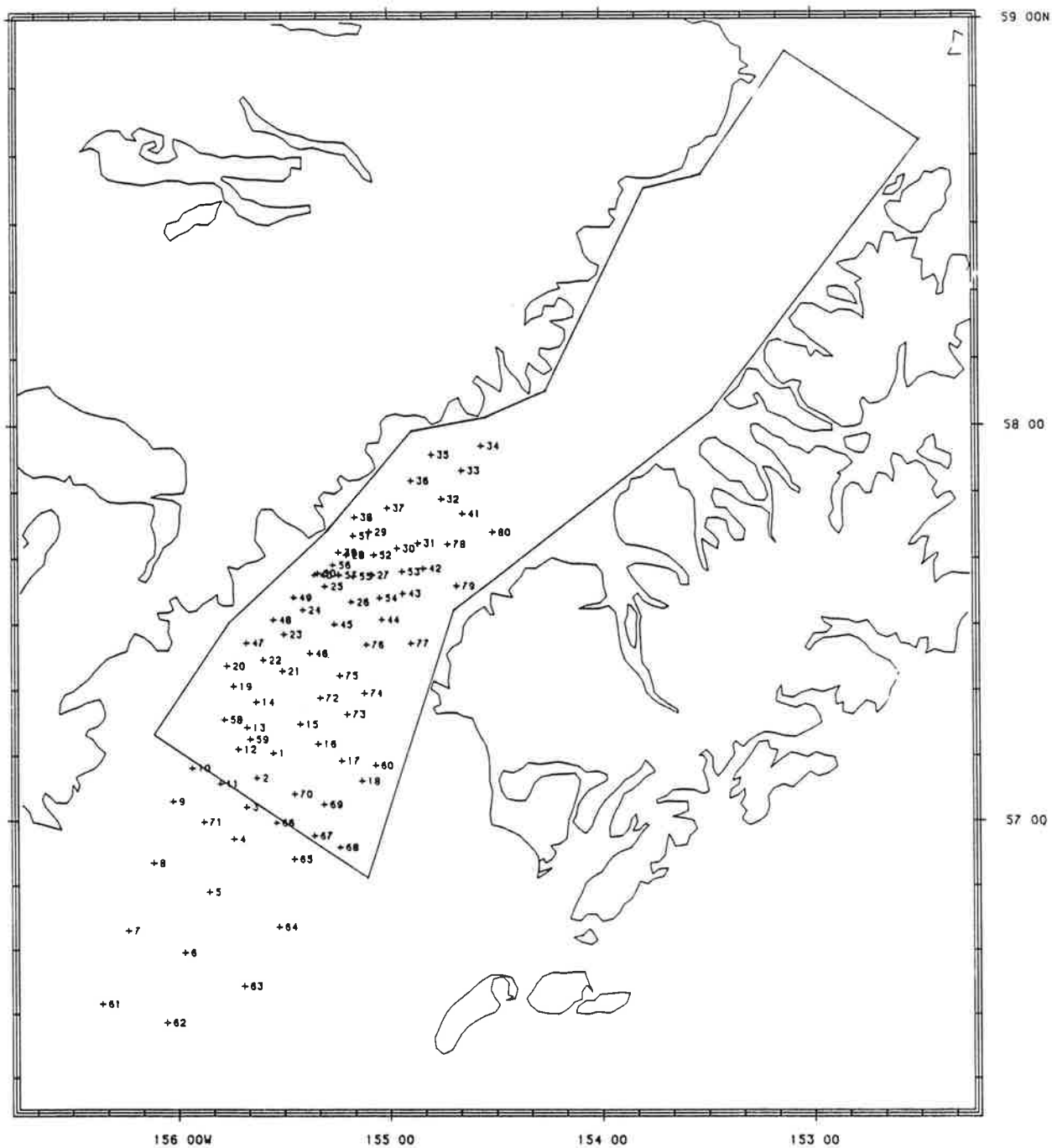
Figure 4. Station locations for cruise 1MF86, April 4 to April 12, 1986. The survey area employed in analyses is outlined.

The cruises covered differing areas in and near Shelikof Strait. For the purposes of this report a standard survey area was defined as that area which included all the sampling stations of survey 1MF85. The size of this area was calculated as 12,200 km^2. Only data obtained from stations falling within this area were employed in subsequent analyses.

The data from cruise 2MF81 required special treatment. 1981 was the first year that eggs from the spawning population of walleye pollock became an important target of study by scientists of the AFSC. Cruise 2MF81 was implemented as two passes through the survey area, the first generally proceeding from the northeast to the southwest and the second proceeding in the opposite direction.

Bates (1987) considered it likely that this design may have inadvertently led to a double sampling of the egg population. During 1981, spawners were aggregated in at least one large, mobile concentration. Sampling operations were conducted in the vicinity of this concentration early in the survey, and operations returned approximately 7 days later to a nearby area to which spawning adults appeared to have migrated. Neither of these egg concentrations could have occurred simultaneously in the abundances that were observed since spawning adults did not occupy both locations simultaneously. The manner by which

sampling was conducted may lead to exaggerated estimates of egg abundance if the data were treated as synoptically collected.

Instead of considering these data as constituting a single survey, Bates partitioned the 2MF81 data into two surveys which were effectively conducted within a week of each other. In implementing this partitioning, stations G001A-G083A were considered as occurring during the first pass through the survey area and these data are herein designated survey 2MF81/lo. Stations G084A-G091A were occupied as the survey area was retraced during subsequent sampling operations. It was assumed that a region of active spawning had shifted by the end of the survey from the vicinity of stations G021A-G024A to the vicinity of stations G084A-G091A and that egg densities had not fundamentally changed in outlying areas over this period of time. Based on these assumptions, the second survey, designated survey 2MF81/hi, was defined as stations G001A-G091A less the stations G021A-G024A.

Field and laboratory procedures Plankton samples were collected with a bongo sampler fitted with 505 μm mesh nets and weighted with a 45 kg lead ball. Two sizes of bongo samplers were employed. 60 cm diameter bongos (Posgay and Marak 1980) were used for surveys 2MF81, 1PO85, and 1MF86, and 20 cm bongos were used for survey 1MF85. It was desired that the towing characteristics of the small bongos should differ as little as

possible from those of a standard bongo tow. This was achieved
by securing the small bongos to the towing cable approximately 3
m above the large bongo array. The towing characteristics of the
small bongos were stabilized by the presence of the large bongos
because the entire array had similar weight and drag as compared
to the large bongo array alone.

The maximum depth of sampling also varied between surveys. Nets
were deployed to a standard target depth of 200 m (Smith and
Richardson 1977) during surveys 2MF81 and 1PO85, and were
subsequently deployed to approximately 5 m above the seabed
during surveys 1MF85 and 1MF86.

Apart from net diameters and sampling target depths, all other
operational characteristics of tows were similar. A flowmeter
was suspended in the center of the mouth of each net to permit an
estimate of the volume of seawater filtered during a tow. A wire
angle indicator and stopwatch were used to monitor the progress
of each tow. Ship's speed was adjusted to maintain a 45° wire
angle. Tow configuration was double oblique, with deployment at
a rate of 50 m of cable paid out per minute of tow and retrieval
at 20 m/min. A time-depth recorder (bathykymogragh or BKG) was
attached to the cable just above the bongo array. Each BKG trace
provided a permanent record of tow profile and permitted an
estimate of maximum tow depth. Plankton samples were preserved
in 5% Formalin and seawater solution buffered with either sodium

borate (cruises 2MF81, 1PO85, and 1MF85) or marble chips (cruise 1MF86).

Not all samples that were collected were preserved and subsequently processed. Only the samples from net 1 were retained during survey 1MF86. Samples from both nets were saved during surveys 2MF81 and 1PO85, with net 2 samples intended for use by Soviet scientists in an ongoing cooperative research program (Kendall 1981) and net 1 samples retained for analysis by American scientists.

The contents of both nets were also saved during survey 1MF85. However, while all samples from net 2 were subsequently processed, only selected samples from net 1 were processed as part of an evaluation of catch variability along a tow path.

Preserved samples were sorted and counted at the Polish Sorting Center, Szczecin, Poland (surveys 2MF81 and 1MF86) or at the AFSC by Debbie Blood (surveys 1PO85 and 1MF85). Egg identifications were performed and counts of walleye pollock eggs verified under the direction of Ann Matarese of the AFSC, Seattle, WA. A subsample of eggs from each catch was visually examined and these eggs were assigned to one of 21 stages of development (Ann Matarese, pers. commun.; Bates (Table 3) 1987). All eggs were staged from those samples which appeared to have collected less than 100 eggs; larger egg catches were subsampled and

approximately 100 eggs from each were staged. Subsampled eggs
that had been crushed or ruptured during collection could be
identified only to a general range of developmental stages and
stages 22-24 were used to accumulate these frequencies.

Catch standardizations Egg abundance at a sampling station is
usually expressed in terms of a standardized catch (Sette and
Ahlstrom 1948, Smith and Richardson 1977) which, in its simplest
form, represents the product of the egg catch at the jth sampling
station, K_j, and the ratio of depth sampled to volume filtered,
Y_j/V_j:

(eq. 1) $$S_j = K_j \ \frac{Y_j}{V_j}$$

where
K_j number of eggs collected at the jth station
Y_j estimated maximum depth attained during the tow at
         the jth station (m)
V_j estimated volume filtered by a net during sampling
         at the jth station (m^3)
S_j standardized egg catch for the jth station
         (eggs of all stages /m^2 column of seawater from the
         surface to the maximum depth attained during the tow).

A standardized abundance for each developmental stage of each
sample was also required for subsequent calculations. A
frequency distribution of the number of eggs in each stage of
development was obtained for each sample by staging a subsample
of up to approximately 100 eggs from each catch, as described
above. Standardized stage abundances, A_{ij}, were then obtained by
partitioning a catch according to the fraction of eggs, X_{ij}/U_j,

that each developmental stage represented in the staged
subsample:

(eq. 2) $\quad A_{ij} = \dfrac{X_{ij}}{U_j} \; S_j$

where

X_{ij} number of eggs in the ith stage of development from
the subsampled catch collected at the jth station
(eggs of stage i /staged subsample j)

U_j number of eggs staged from the jth sample
(eggs /staged subsample j)

A_{ij} standardized stage abundance, the number of eggs
assigned to the ith stage for the jth sample
(eggs of stage i /m^2).

Adjustment of catches   Walleye pollock eggs are spawned at depth
(Kim 1987) and the sampling gear must pass through the entire
water column to capture all the eggs to be found at a sampling
location. The 200 m maximum target depth used during earlier
surveys sometimes left unsampled a substantial portion of the
water column. In addition, in order that the bongo array not be
lost by collision of the gear with the sea bottom, the maximum
depth targeted for shallow stations was sometimes made well above
the actual station depth. Since a substantial portion of the egg
population may have been missed by these procedures, egg catches
could underestimate the number of eggs to be found at a number of
sampling locations. In order to compensate for this, catches
were extrapolated upwards (Kendall and Picquelle 1990) based on
sample depth, station depth, and a presumed distribution of eggs
by depth.

Egg ages and stage durations The approximate age of a group of
eggs was determined on the basis of a log-linear relationship
between incubation temperature and cumulative development time
(Bates 1987). Twenty-one equations were developed, one for each
developmental stage, and these equations were of the form:

(eq. 3) $\ln(Q_{ij}) = L_i + M_i W_j$

where
$\ln(Q_{ij})$ estimate of the natural logarithm of the cumulative
               development time (hours) to the end of the ith stage at
               the jth station temperature
L_i Y intercept, the natural logarithm of the cumulative
               development time to the end of the ith stage at 0°C
M_i slope of the log-linear relationship for the ith stage
W_j temperature (centigrade) at the jth station.

Calculation of hourly stage abundance Since developmental stages
ranged from a few hours to a few days in length, stage abundance
data could only be compared by value after standardization for
stage duration:

(eq. 4) $B_{ij} = \dfrac{A_{ij}}{D_i}$

where
D_i duration (hours) of the ith stage at the average
               station temperature
B_{ij} hourly abundance for the ith stage at the jth station
               (eggs of stage i /hour of stage duration /m^2).

Stage durations, D_i, were calculated as the difference in the
estimated cumulative development times, Q_{ij}, between the ith and
ith-1 developmental stages.

Contouring of hourly stage abundance data Smoothed contour plots
were prepared using the computer program Surfer from Golden

Software, CA. A certain amount of extrapolation of the trends in data is necessary in preparing contour plots. Since contours of egg densities cannot sensibly extend over land, a series of dummy stations were added near shore to each data set in order to prevent the program from generating such a pattern. Egg catches for dummy stations and for stations where no eggs were found were assigned arbitrarily small positive values, and all catch data were then transformed using common logarithms prior to contouring. Contours represent common log cycles of hourly stage abundance $[\log_{10}(\text{eggs of a stage /hour of spawning /m}^2)]$. That is, each contour level represents egg densities approximately 10 times as great as the next lower contour level.

RESULTS

Walleye pollock eggs were ubiquitous at the times surveyed; at least one egg was collected at most sampling station. Excluding collections where no eggs were captured, 0.1 eggs of all stages /m^2 was the lowest abundance found and this value approximately defines the minimal level of resolution attainable by the sampling gear and procedures employed. The largest standardized egg catches (eggs of all stages /m^2) were 350,010 (adjusted for depth) for 2MF81, 176,678 (adjusted for depth) for survey 1PO85, 23,171 for survey 1MF85, and 25,287 for survey 1MF86.

The distributions and relative abundances of developmental stages 6, 12, and 18 are shown for surveys 2MF81/lo, 1PO85, 1MF85, and 1MF86 in Figures 5-16. Excluding collections where no eggs of a stage were collected, standardized stage abundances ranged from slightly less than -1 to just over 5 common log cycles. The highest log cycle was seldom observed, and where found, occurred for only a limited geographic extent (for example, stage 6 of surveys 2MF81/lo and 1PO85). Eggs were commonly found in nearly all stages of development at stations with moderate to high catches.

DISCUSSION

Egg abundance gradients throughout the survey area varied in character over the three years surveyed. The data for 1981 showed steep gradients, that is, small regions of relatively high abundances which rapidly tapered off to relatively low abundances for the bulk of the survey area. In contrast, the data for the years 1985 and 1986 presented a much more homogeneous pattern of egg catches, with most of the survey area having moderate abundances.

The character of abundance gradients is of significance when the data are used in population estimation. The abundance found at a sampling location may be extrapolated to a surrounding area with

Figure 5. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 6 for the survey 2MF81/1o. Contours are common log cycles of standardized egg catch.

Figure 6. Distribution and abundance of walleye pollock eggs, *Theragra chalcogramma*, in developmental stage 6 for the survey 1PO85. Contours are common log cycles of standardized egg catch.

Figure 7. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 6 for the survey 1MF85. Contours are common log cycles of standardized egg catch.

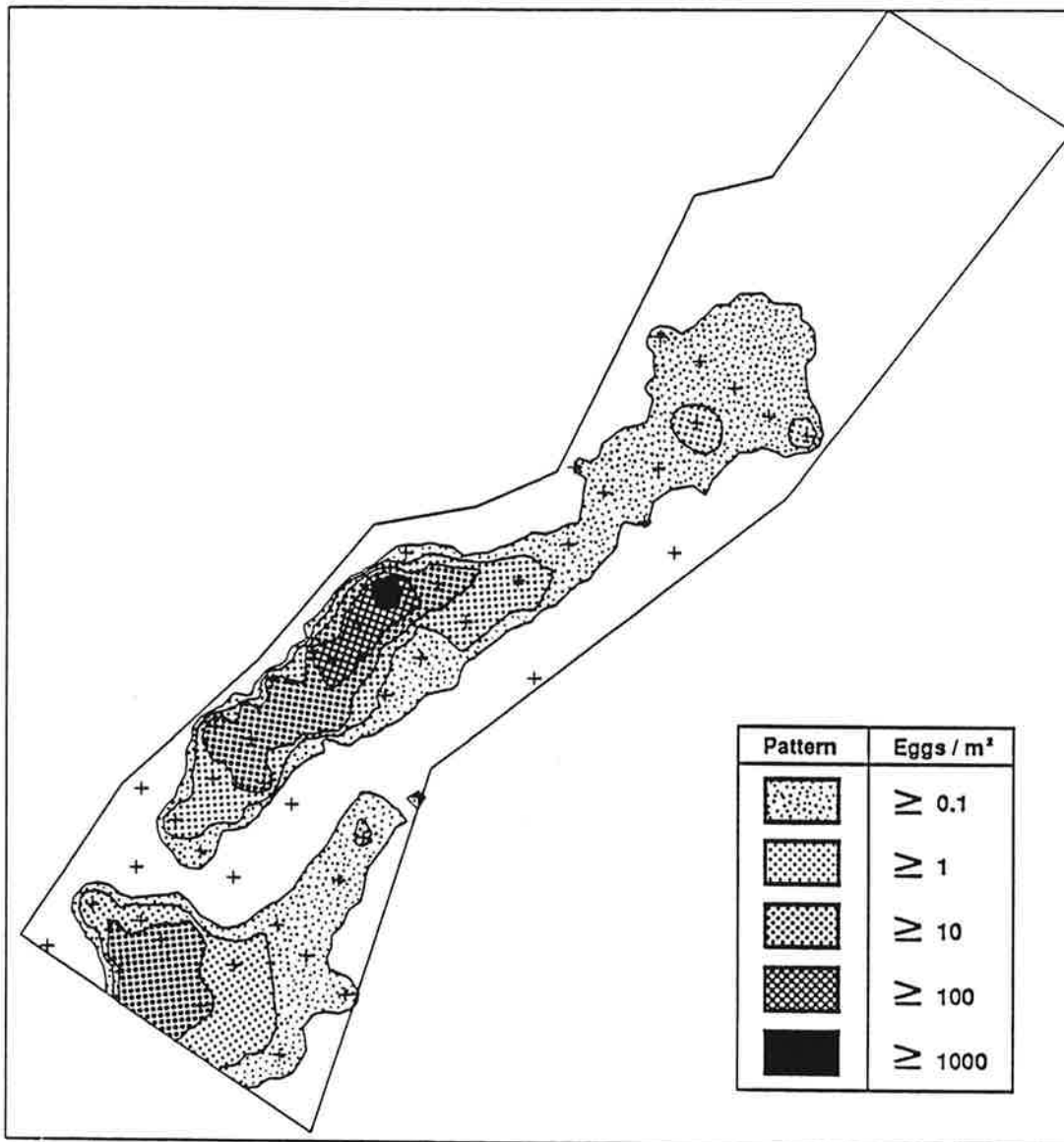| Pattern	Eggs / m²
	≥ 0.1
	≥ 1
	≥ 10
	≥ 100
	≥ 1000

Figure 8. Distribution and abundance of walleye pollock eggs, Theragra chalcogramma, in developmental stage 6 for the survey 1MF86. Contours are common log cycles of standardized egg catch.

Figure 9. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 12 for the survey 2MF81/lo. Contours are common log cycles of standardized egg catch.
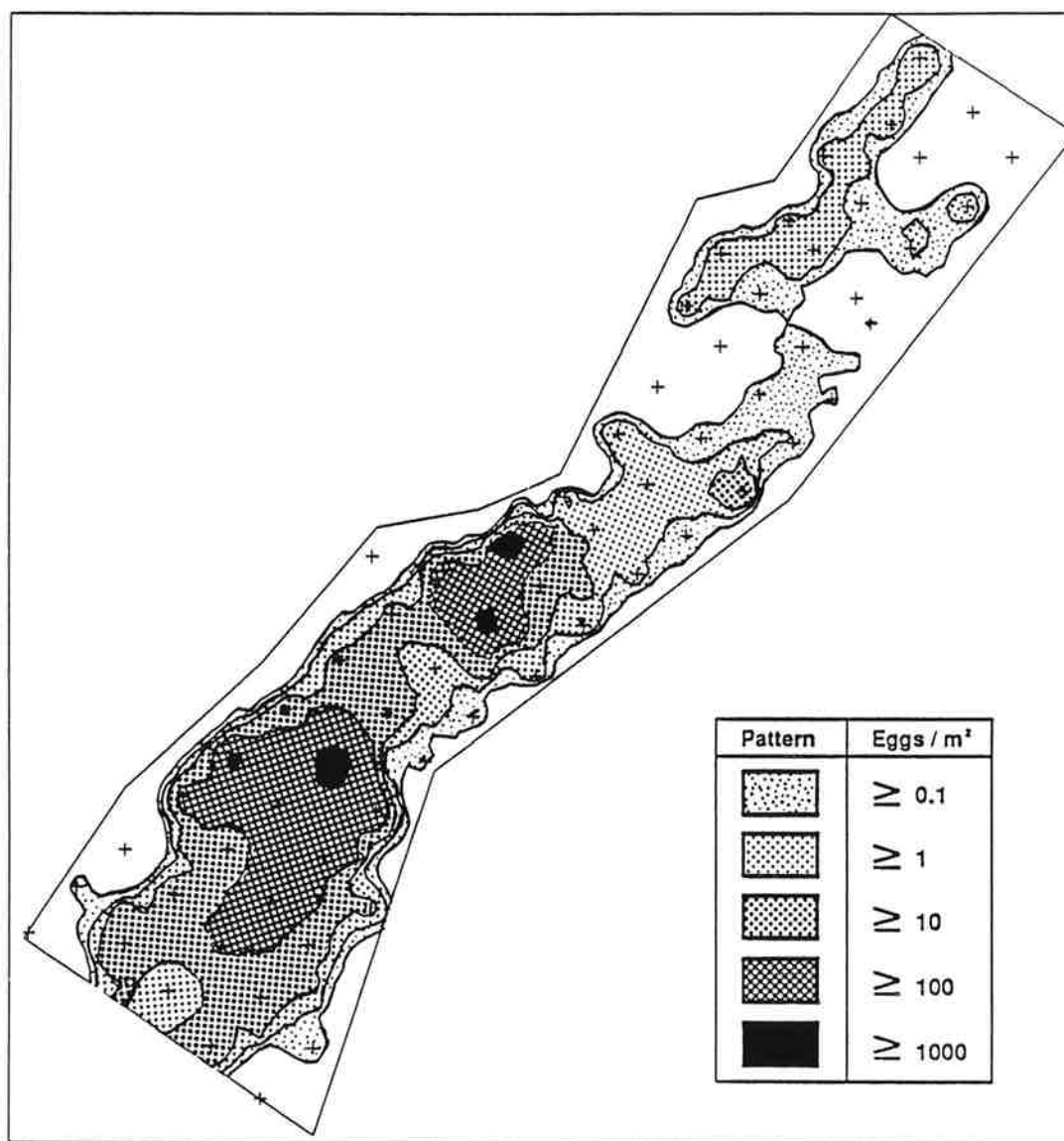
Figure 10. Distribution and abundance of walleye pollock eggs, _Theragra_ _chalcogramma_, in developmental stage 12 for the survey 1PO85. Contours are common log cycles of standardized egg catch.
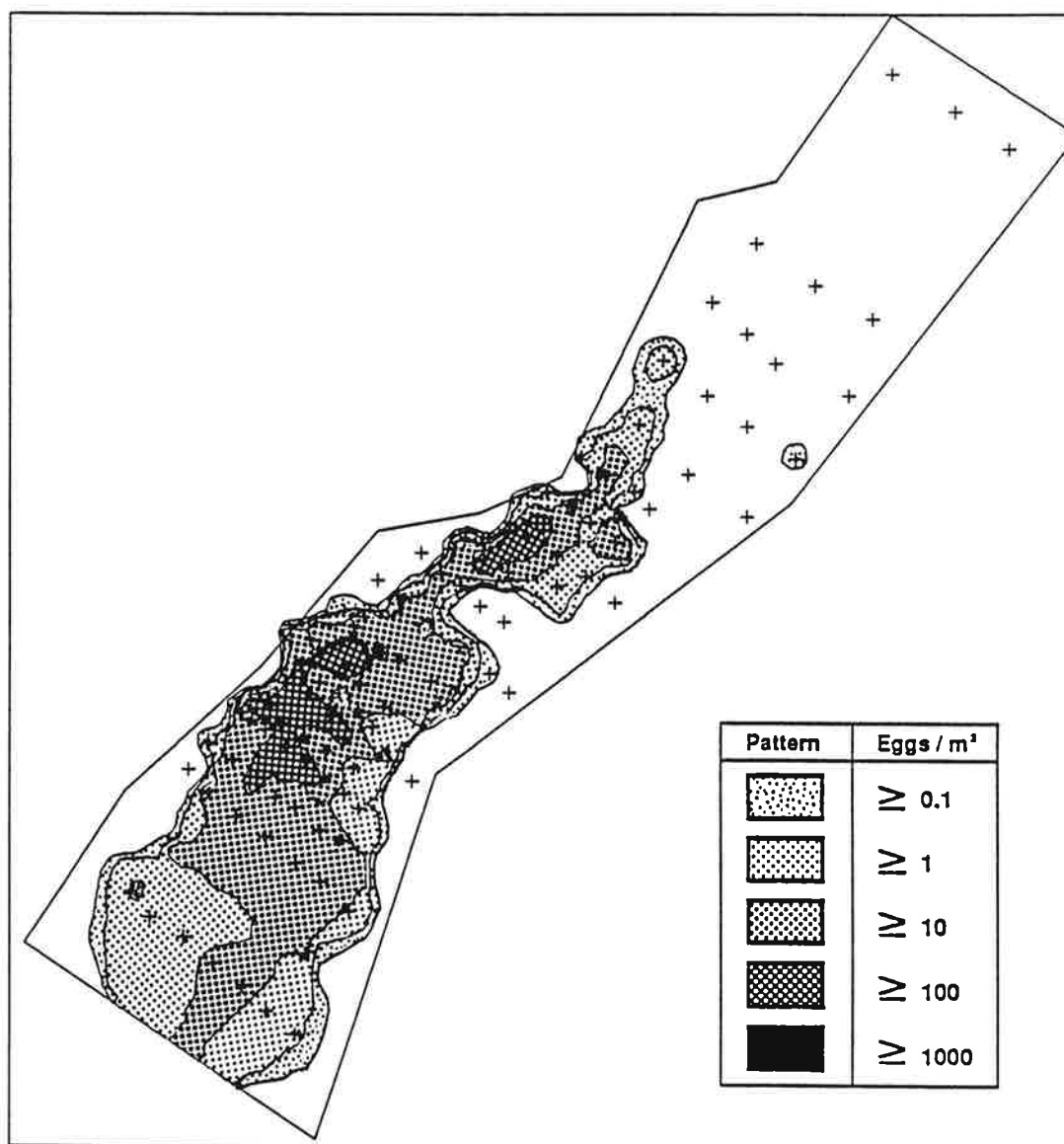
Figure 11. Distribution and abundance of walleye pollock eggs, Theragra chalcogramma, in developmental stage 12 for the survey 1MF85. Contours are common log cycles of standardized egg catch.

Pattern	Eggs / m²
	≥ 0.1
	≥ 1
	≥ 10
	≥ 100
	≥ 1000

Figure 12. Distribution and abundance of walleye pollock eggs, _Theragra_ _chalcogramma_, in developmental stage 12 for the survey 1MF86. Contours are common log cycles of standardized egg catch.

Figure 13. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 18 for the survey 2MF81/lo. Contours are common log cycles of standardized egg catch.

Figure 14. Distribution and abundance of walleye pollock eggs, *Theragra chalcogramma*, in developmental stage 18 for the survey 1PO85. Contours are common log cycles of standardized egg catch.
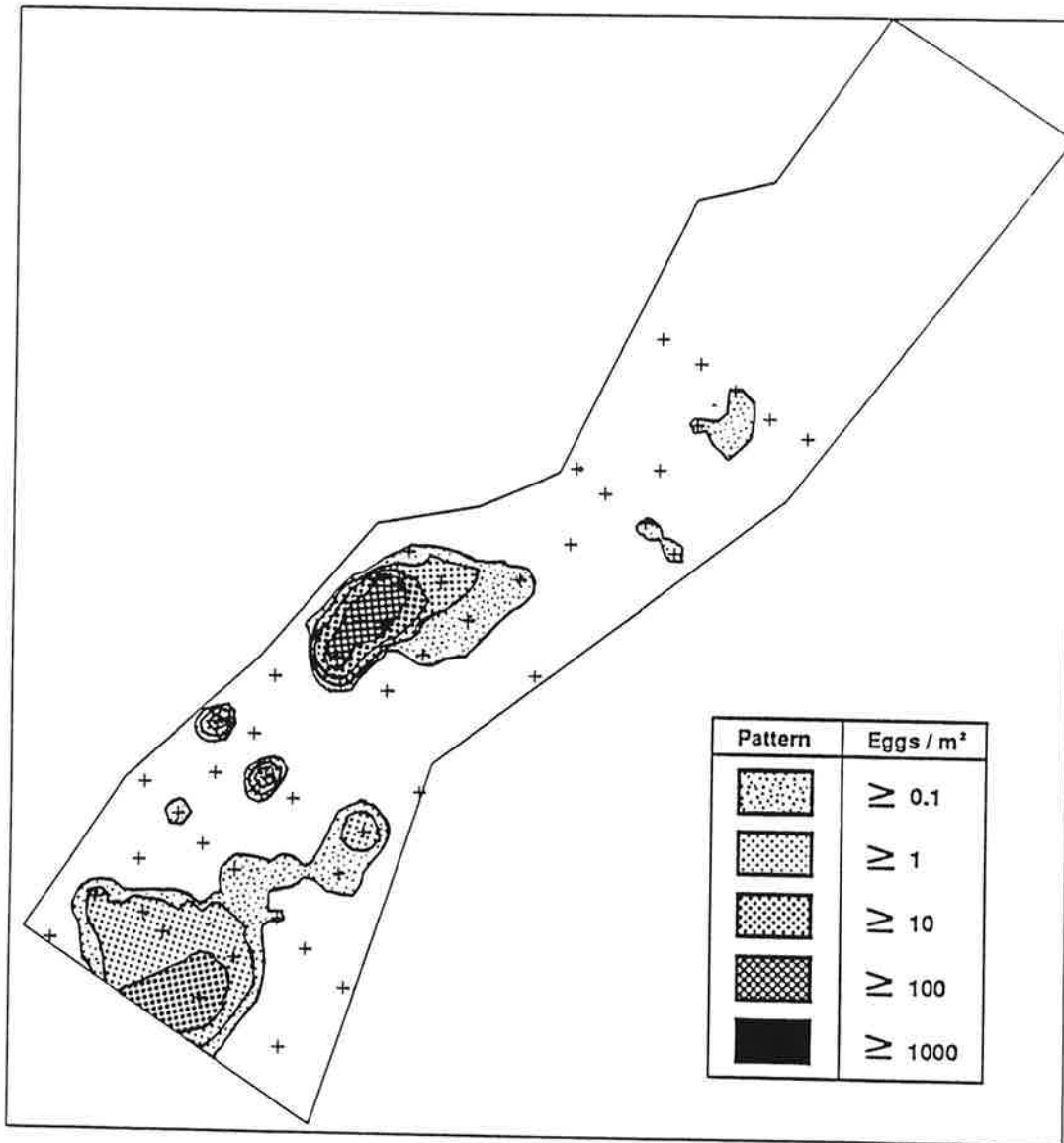
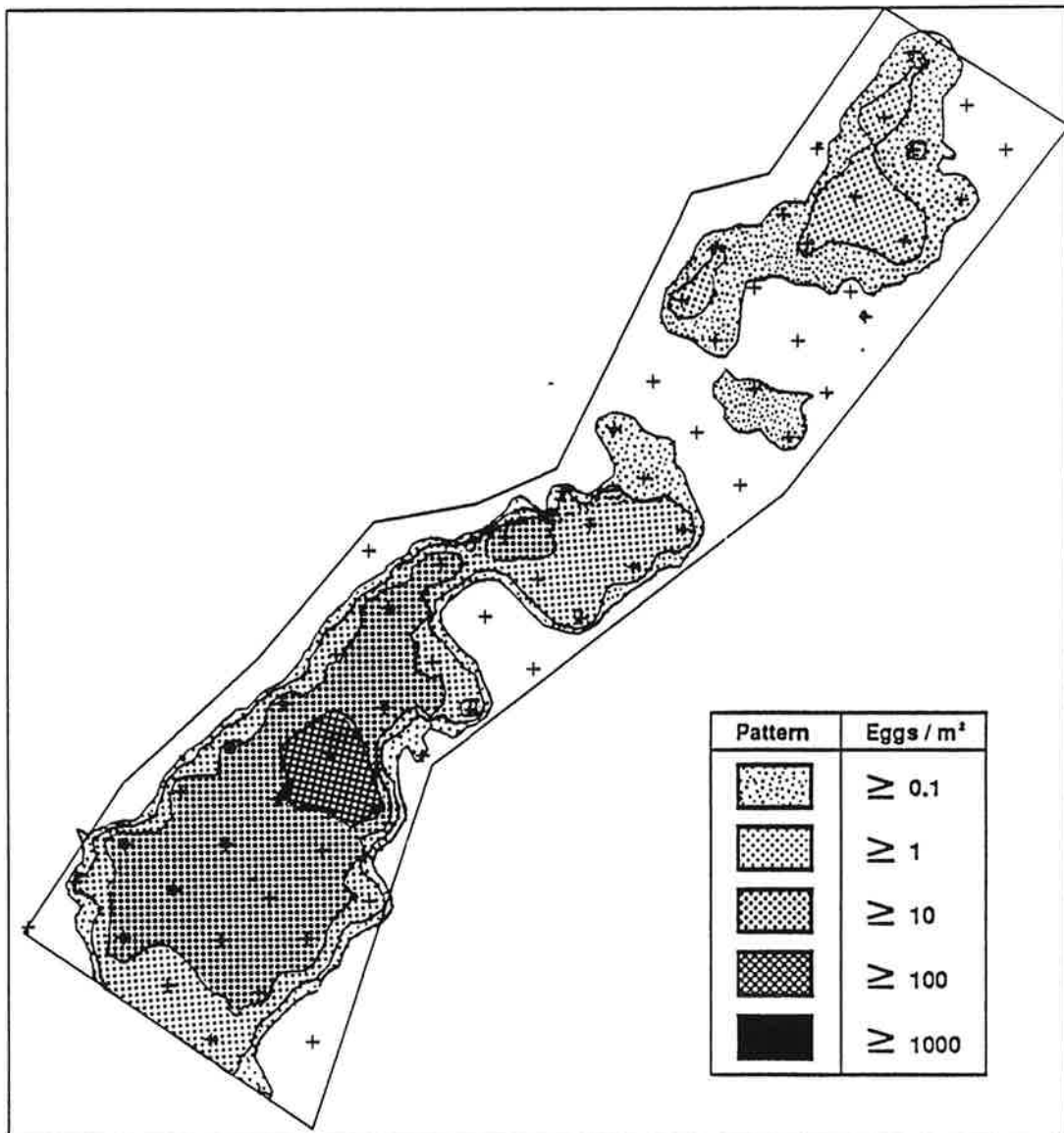| Pattern	Eggs / m²
	≥ 0.1
	≥ 1
	≥ 10
	≥ 100
	≥ 1000

Figure 15. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 18 for the survey 1MF85. Contours are common log cycles of standardized egg catch.
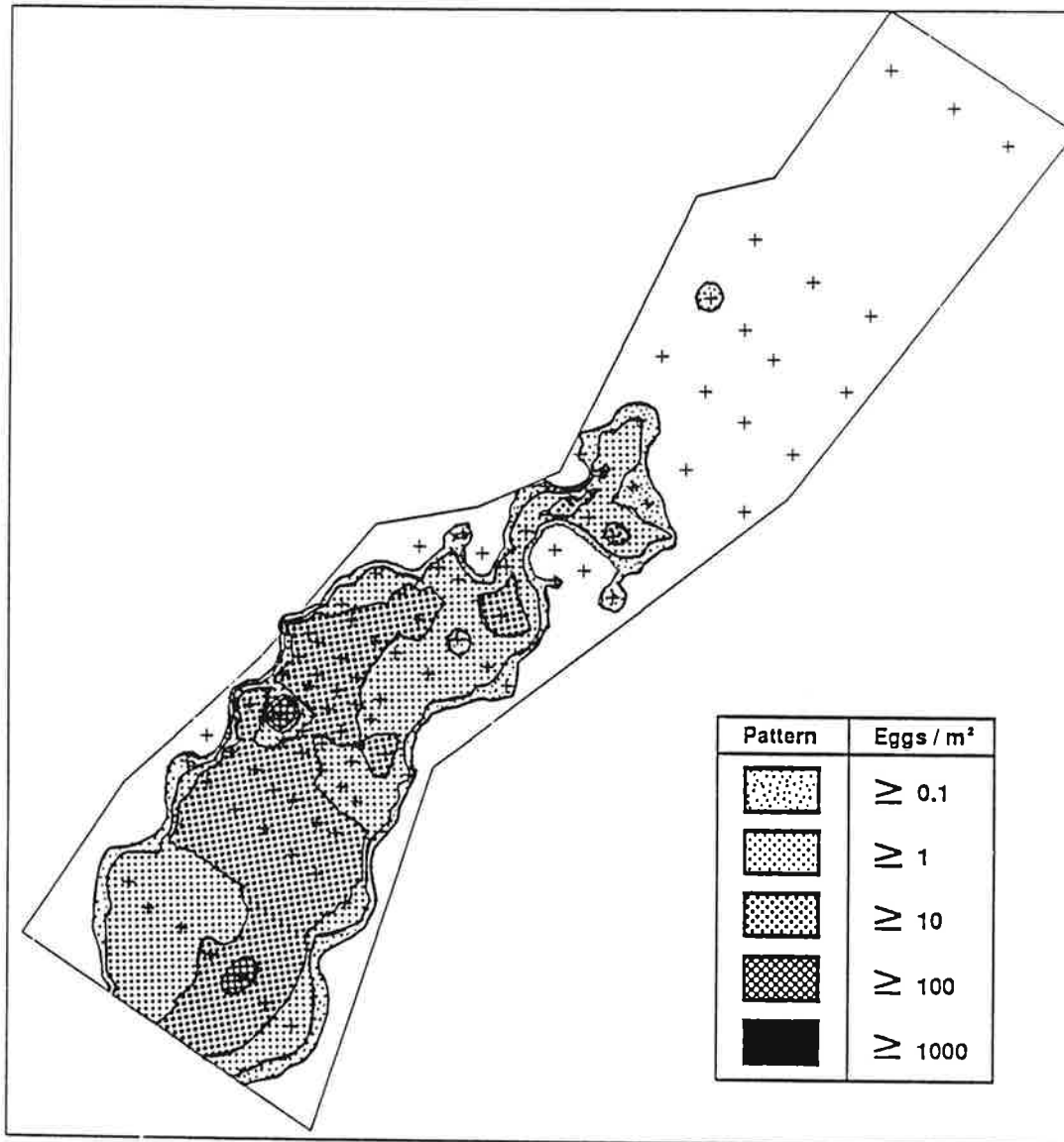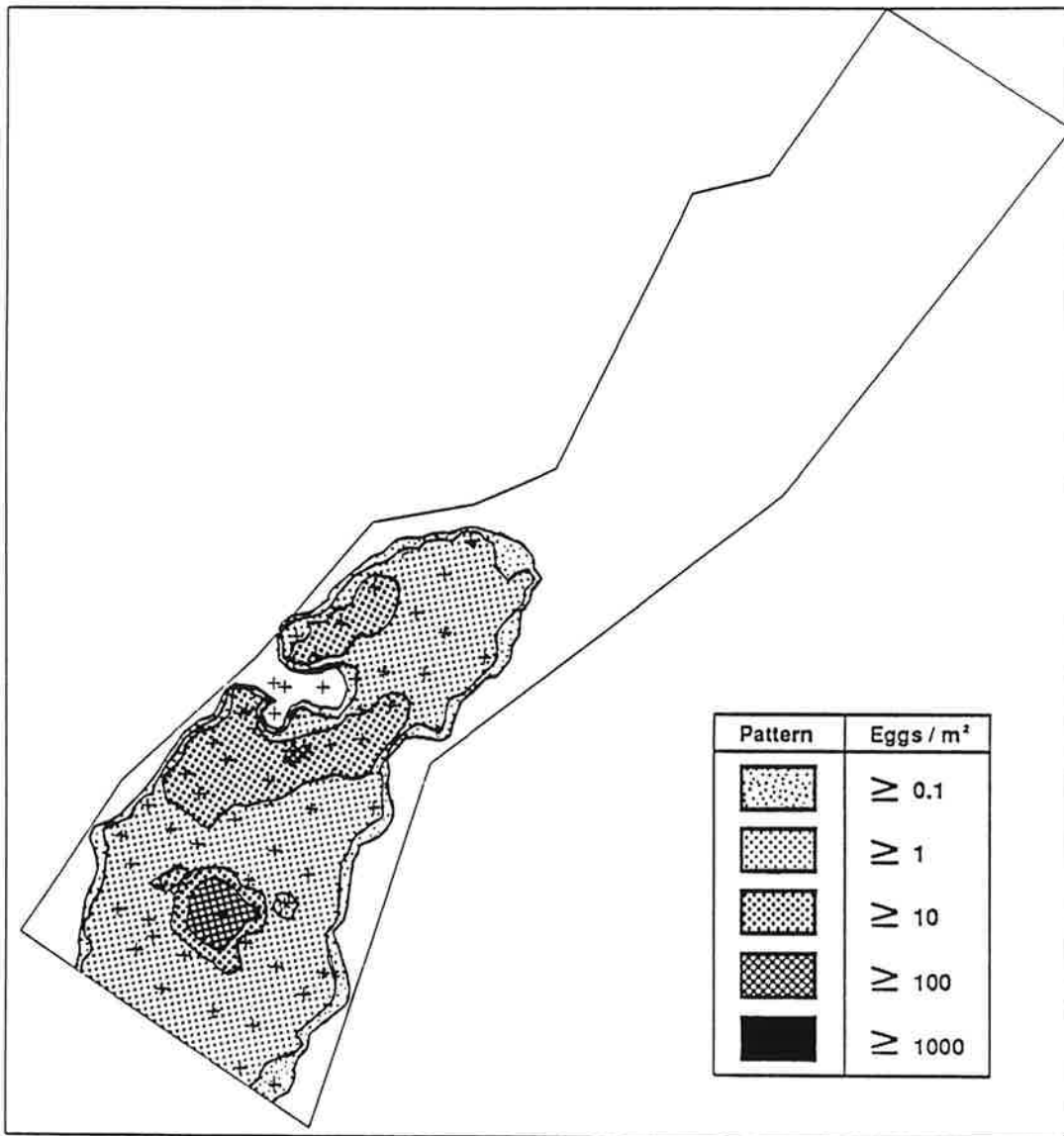
Figure 16. Distribution and abundance of walleye pollock eggs, _Theragra chalcogramma_, in developmental stage 18 for the survey 1MF86. Contours are common log cycles of standardized egg catch.

greater confidence if gradients in the vicinity of this station are moderate. It is much more hazardous to extrapolate a catch to a surrounding area if the gradients are rapidly changing. It will be seen in Chapter 6 that the steepness of abundance gradients had a noticeable impact on the sampling distributions of certain parameters which were obtained from a computer simulation of sampling.

CHAPTER 3. Preliminary estimation of seasonal egg production and the daily rate of egg mortality for the years 1981, 1985, and 1986.

INTRODUCTION

The purposes of this chapter are 1) to adapt and improve the procedures of Bates (1987) for the estimation of seasonal egg production and daily egg mortality, and 2) to obtain preliminary estimates of these parameters for the years 1981, 1985, and 1986.

METHODS

<u>Polygonal station areas</u> Egg sampling was sometimes concentrated in certain regions of the survey area and, in order that this preferential sampling should not bias subsequent analyses, it was necessary to weigh egg catch data by area. Area weighting factors were determined by the polygonal station method of Sette and Ahlstrom (1948). Polygonal station areas were constructed from perpendicular bisectors between adjacent stations. Bisectors were extended to the perimeter of the survey area for those stations occurring nearest to the outer reaches of the survey area. Polygonal station areas are shown in Figures 17-21.

<u>Calculation of observed catch abundances</u> The total abundance of a developmental stage within the survey area was calculated as:

Figure 17. Survey area, station locations, and polygonal station areas for survey 2MF81/lo.
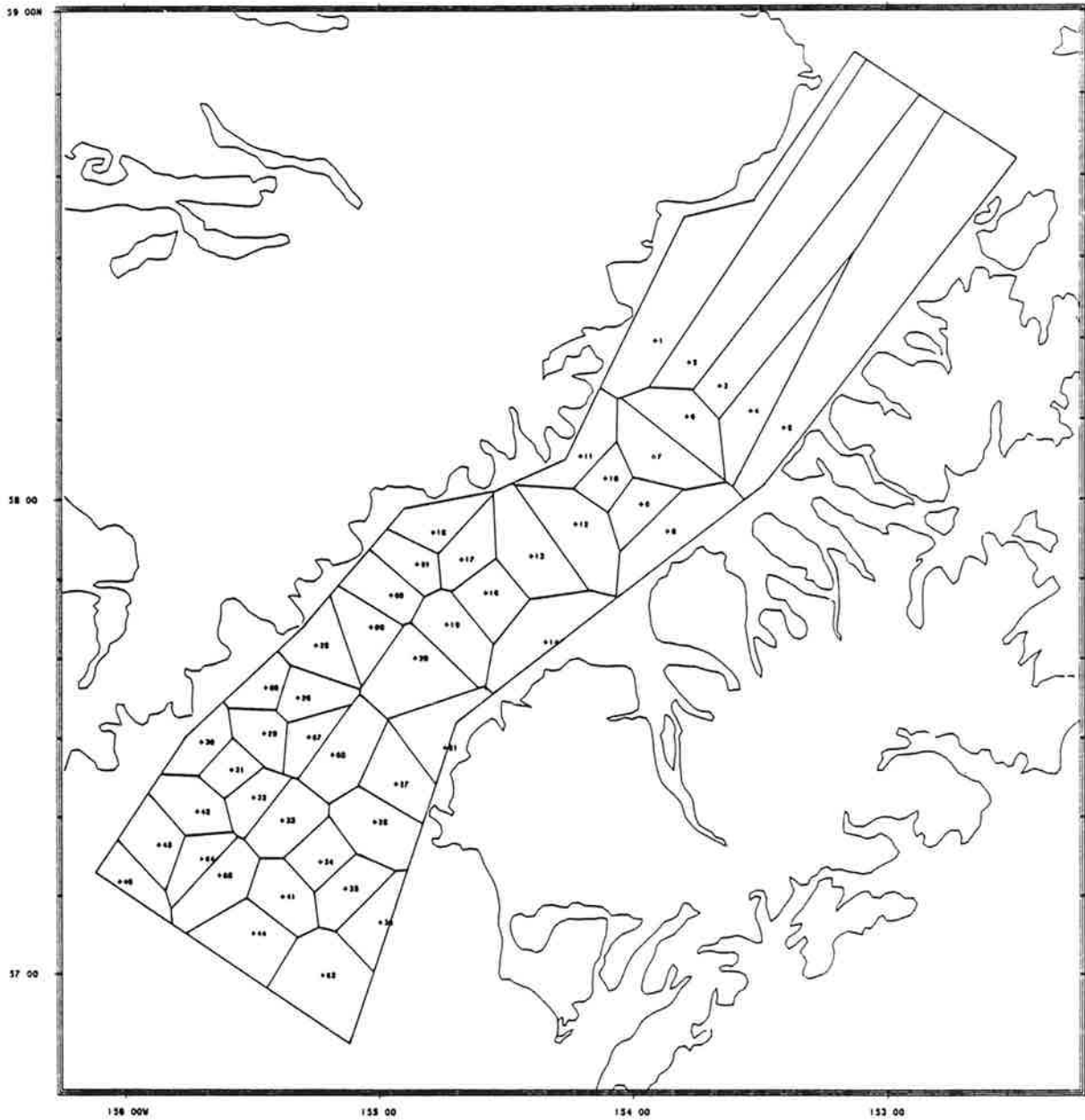
Figure 18. Survey area, station locations, and polygonal station areas for survey 2MF81/hi.
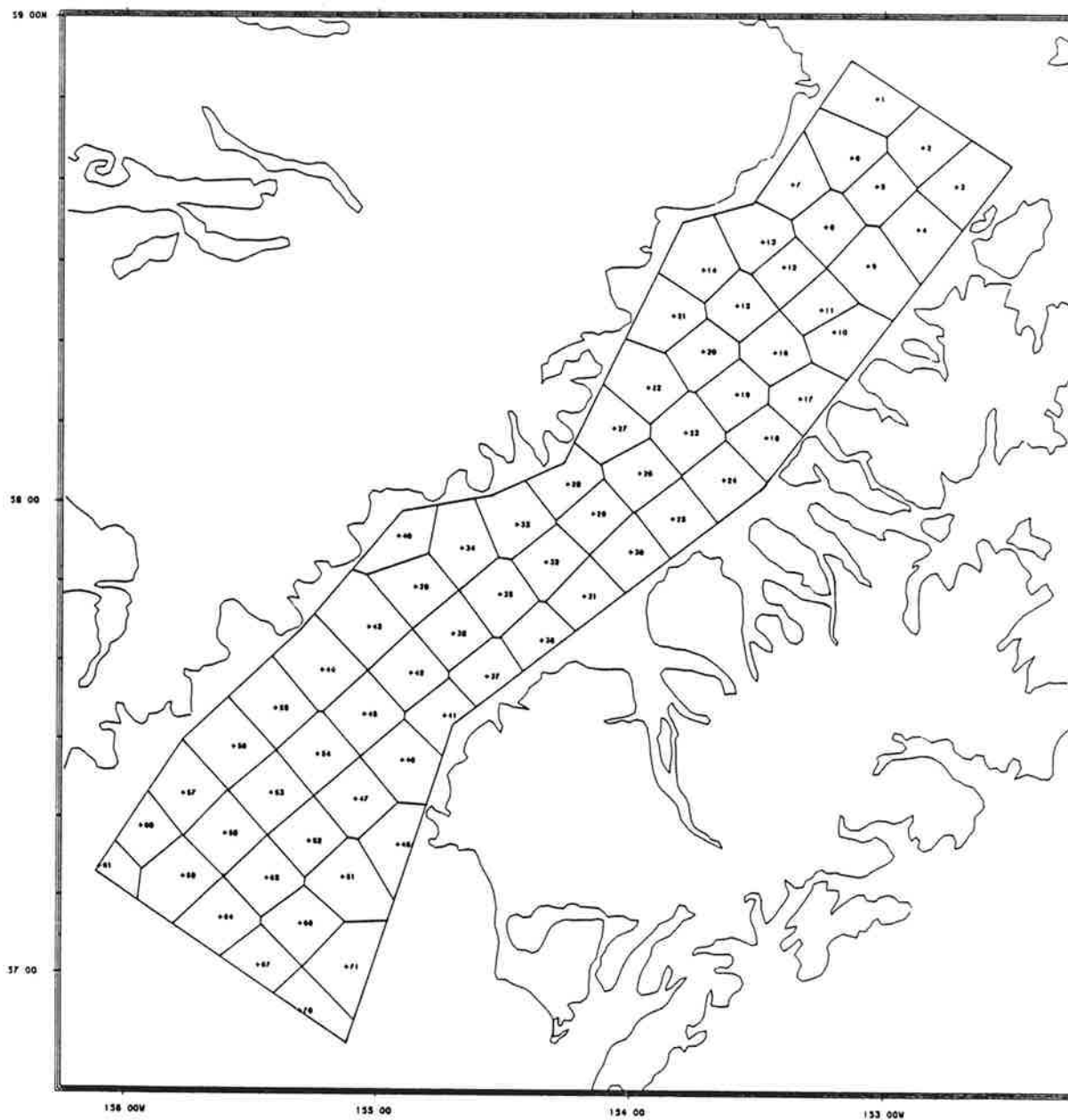
Figure 19. Survey area, station locations, and polygonal station
areas for survey 1PO85.
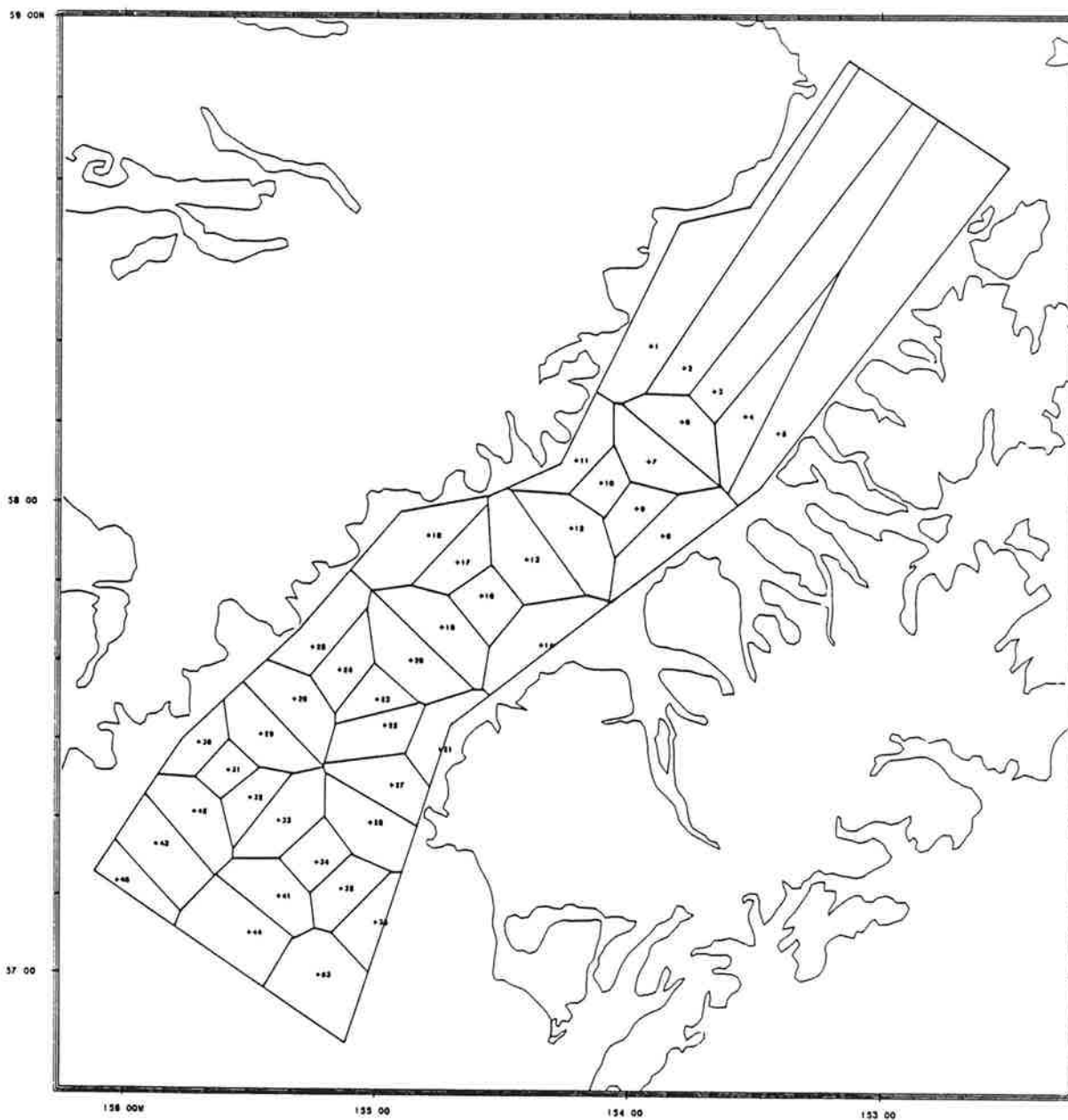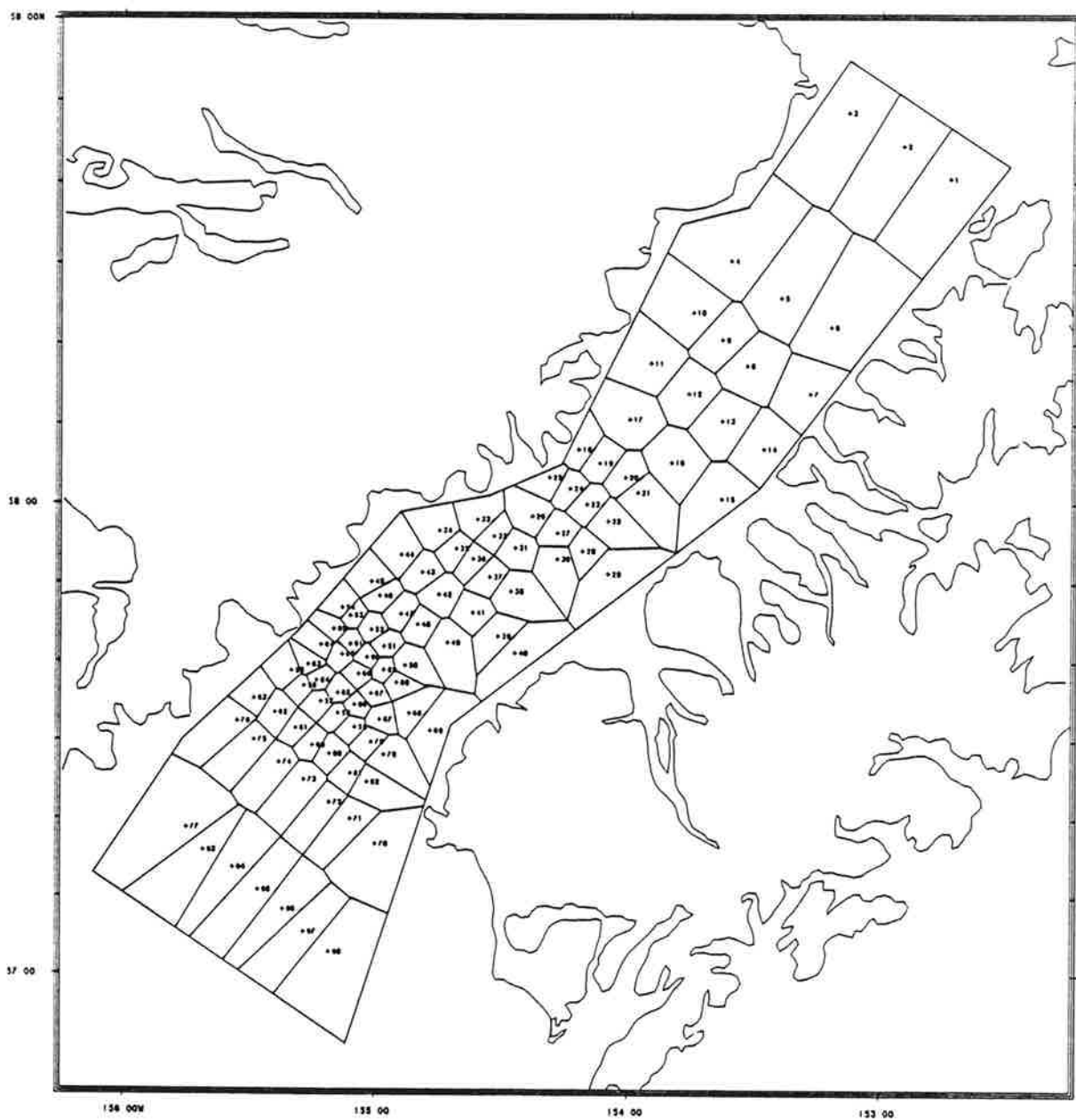
Figure 20. Survey area, station locations, and polygonal station areas for survey 1MF85.
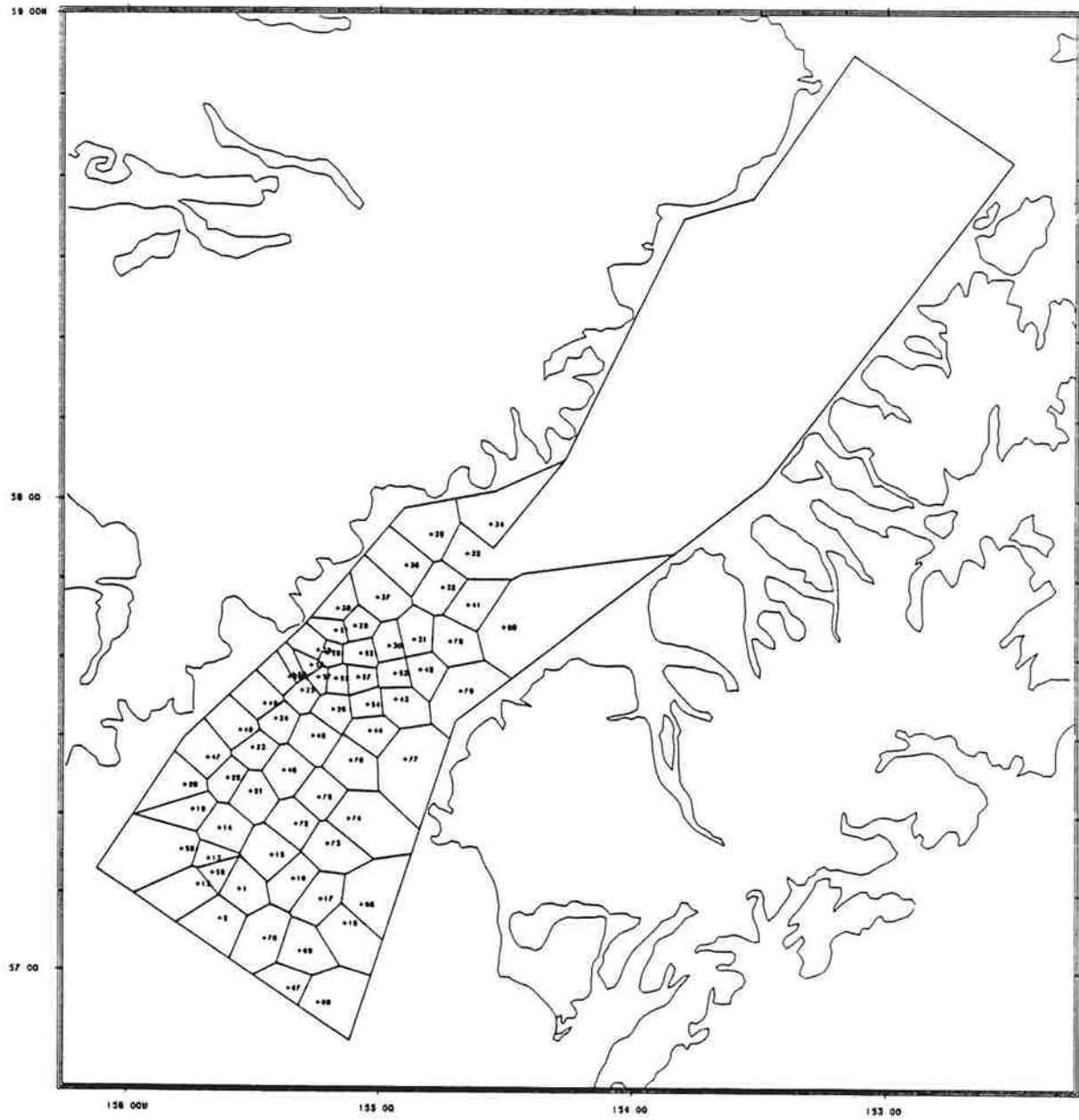
Figure 21. Survey area, station locations, and polygonal station areas for survey 1MF86.

(eq. 5) $\quad C_i = \sum_{j=1}^{J} [A_{ij}\, P_j]$

where

J	number of stations occupied during a survey
P_j	polygonal area (m^2) assigned to the jth station based on the method of Sette and Ahlstrom (1948)
C_i	total abundance of the ith stage within the survey area (eggs of stage i /survey area).

The expression in brackets in eq. 5 shall hereafter be referred to as a polygonal stage abundance (eggs of stage i /polygonal station area j). [See addendum 1]

The date of sampling (T) for a survey

The effective date of the spawning season around which a survey was centered was calculated as a weighted average of the dates and times that each station was occupied. Polygonal stage abundances were employed as weights. This weighting scheme resulted in a central date of sampling for a survey that approximated the date that most eggs were collected:

(eq.6) $\quad T = \dfrac{\displaystyle\sum_{j=1}^{J}\sum_{i=1}^{I} G_j\, [A_{ij}P_j]}{\displaystyle\sum_{j=1}^{J}\sum_{i=1}^{I} [A_{ij}P_j]}$

where

I	the 21 developmental stages comprising the incubation period
G_j	local day-of-the-year of sampling at the jth station
T	day-of-the-year of the spawning season upon which the survey was centered.

Calculation of predicted values for total stage abundances Bates (1987) argued that egg mortality could not be estimated in the usual way when the rate of spawning was rapidly changing. To do so would require solution for I+1 unknowns (I unknown values for egg production and the unknown mortality coefficient) when only I data points were available (I stage abundance values). He developed an approach to predict the abundance of an egg cohort by assuming that the seasonal spawning curve can be expressed as a nonconstant but deterministic function of time. Mathematically, his approach combined the normal probability density function with the exponential function. The normal curve describes the changing rates of spawning over the spawning season as a function of spawning date. The exponential curve implies that a constant fraction of the surviving eggs are removed from the population per unit interval of age.

A predicted value for total stage abundance under the foregoing assumptions of a normal spawning curve and constant exponential mortality was obtained by numerically integrating the following equation between appropriate ages:

$$\text{eq. 7} \quad C_{i'} = \int_{a_i}^{b_i} \frac{\epsilon}{\sqrt{2\pi\sigma^2}} \exp\left[\frac{(T-t-\mu)^2}{-2\sigma^2}\right] \exp[-Zt] \; dt$$

where

ϵ seasonal egg production (fertilized eggs spawned /survey area /spawning season)

μ day-of-the-year of peak spawning

σ one standard deviation in the normal spawning curve (days)

Z coefficient of instantaneous mortality

t	instantaneous age of eggs (days)
a_i	cumulative time from spawning to the beginning of the developmental stage i (days)
b_i	cumulative time from spawning to the ending of the developmental stage i (days)
c_i.	predicted total stage abundance for the ith stage (eggs of the ith stage /survey area).

The constants a_i and b_i were obtained for stage i using eq. 3 and an average temperature for a survey. Average temperatures were 5.2°C for cruise 2MF81, 5.6°C for cruises 1PO85 and 1MF85, and 4.2°C for cruise 1MF86 (Kim, pers. commun.). Parameters to be estimated are Z, μ, σ, and ϵ.

The solution of eq. 7 requires 1) a procedure to calculate the predicted abundance of each age group, 2) an error function to define an optimal fit, and 3) a numerical fitting procedure to provide best fitting parameter estimates. The approaches taken to satisfy each of these requirements will now be addressed.

The exact determination of a predicted stage abundance would require an integration of eq. 7. However, this equation cannot be evaluated exactly since the normal curve cannot be integrated into elementary functions. Instead, each trial value for a predicted stage abundance was numerically determined by a series of trapezoidal integrations. In performing these integrations, instantaneous abundances were calculated at hourly intervals of age throughout the range of ages a_i to b_i comprising the stage. Each instantaneous abundance was determined by evaluating the integrand of eq. 7 using an age (t, $a_i < t < b_i$), the date of

sampling for the survey (T), and current trial values for the
parameters ϵ, μ, σ, and Z. The instantaneous abundances were
then summed over the age interval to produce the predicted stage
abundance for that trial.

The nonconstant stage durations again played a role in
calculations. Stage durations varied from a few hours to a few
days in duration. Stage abundance data can be expected to
deviate somewhat from the best fitting trend and this lack of fit
will, in general, be greatest for stages having the longest
durations as the error from the lack of fit accumulates over the
longer durations. In order to remedy the effect of stage
duration on fitting errors, both observed and predicted egg
abundances were first standardized to equal intervals of spawning
before evaluation under the error criterion. Average daily stage
abundances, H_i and $H_{i'}$, were obtained by dividing the total
abundances C_i and $C_{i'}$ (eqs. 5 and 7) by stage duration, D_i, in
days and the size of the survey area in m^2.

A logarithmic error term was employed in the fitting criterion.
The effect of a logarithmic fit was to encourage predicted
abundances to approximate the same log cycle as observed
abundances. This is an improvement to the absolute error
criterion used by Bates (1987) since predicted values are now
more likely to approximate the magnitude of observed stage
abundances for all developmental stages employed in the analysis.

The objective function to be minimized was defined as the sum of the log-transformed absolute differences between observed and predicted daily stage abundances:

$$\text{(eq. 8)} \qquad E = \sum_{i=1}^{I} \ln(\text{abs} (H_{i\prime} - H_i))$$

where

H_i	observed average daily abundance of stage i (eggs of stage i /day of stage duration /m^2)
H_i	$= \dfrac{C_i * 24}{D_i}$
$H_{i\prime}$	predicted daily abundance of stage i
$H_{i\prime}$	$= \dfrac{C_{i\prime} * 24}{D_i}$
E	total fitting error.

Best fitting estimates for parameters of eq. 7 were obtained by brute computational force using a self-directing search procedure called the simplex method (Spendley, et al. 1962, Kowalik and Osborne 1968). Beginning with user-supplied initial values for all parameters, the simplex procedure repeatedly modifies these values until either a local minimum in the error function is attained up to a specifiable level of precision or until the procedure is no longer able to create trial values that would result in a decrease in the total fitting error.

A series of calculations were performed within each iteration of the simplex procedure. First, using the currently assumed values for model parameters, a tentative value was calculated for each predicted stage abundance. Differences between these tentative abundances and their corresponding observed stage abundances were then determined and accumulated. The results of each set of such

trial fittings were then used to generate improved trial values
for model parameters before the next iteration was begun.

Restrictions placed on data and parameter values Abundance data
for stages 1-6 and 21-24 were discarded prior to fitting the
model to the survey data. The developmental stages immediately
following fertilization are often underrepresented in planktonic
egg samples (Sette and Ahlstrom 1948, Bates 1987). The observed
abundance of the stage just prior to hatching, stage 21, may also
be unrepresentative and was ignored. Stages 22-24 represent
broad ranges of age which overlap a number of developmental
stages; these were used only to accumulate frequencies for staged
eggs that could not be assigned to a particular stage within the
developmental stages 1-21. Only data for the remaining 14
stages, stages 7-20, were employed in the estimation of model
parameters.

Only two of the four model parameters were estimated from survey
data because of data limitations. Only one survey was conducted
during the spawning season for the years 1985 and 1986; with only
one survey per season available, the best fitting estimates for
the parameters of the seasonal spawning curve, μ and σ, were
heavily dependent on the precision of observed stage abundance
values. For the purposes of this analysis, μ was set to day-of-
the-year 91 and σ was set to 7 days in duration, and the values
for ϵ and Z were determined from the egg data.

RESULTS

Figures 22-26 show for each survey the observed values for stage
abundances and the fitted trend based on the best fitting
estimates for the parameters ϵ and Z and the assumed values for μ
and σ. Observed values are indicated by a "+" symbol. The upper
plot indicates the magnitude and direction of fitting errors.
The observed and predicted values were log transformed in the
upper plot; the lower plot shows the untransformed values. Both
plots illustrate the corresponding shape of the normal-
exponential function that was fit to the data. Note that the
variability among observed stage abundances in the lower plot is
greatest for the younger stages than for the older stages.

Table 3. Parameter estimates for the spawning of walleye pollock
during the years 1981, 1985, and 1986. Model parameters are
seasonal egg production, ϵ; date of peak spawning, μ; one
standard deviation in the normal curve representing seasonal egg
production, σ; and the coefficient of instantaneous egg
mortality, Z. Biological information outside of egg survey data
was available to define μ and σ. μ was equated to day-of-the-
year 91 and σ was equated to 7 days in duration. With μ and σ
set, the remaining parameters ϵ and Z were determined from the
observed stage abundance data for developmental stages 7-20.

survey designator	ϵ (10^{12} eggs)	μ (day-of-the-year)	σ (days)	Z
2MF81/lo	172.2	91	7	0.68
2MF81/hi	189.9	91	7	0.26
1PO85	114.9	91	7	0.20
1MF85	154.0	91	7	0.25
1MF86	181.9	91	7	0.23

Figure 22. Results for survey 2MF81/lo when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 23. Results for survey 2MF81/hi when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.
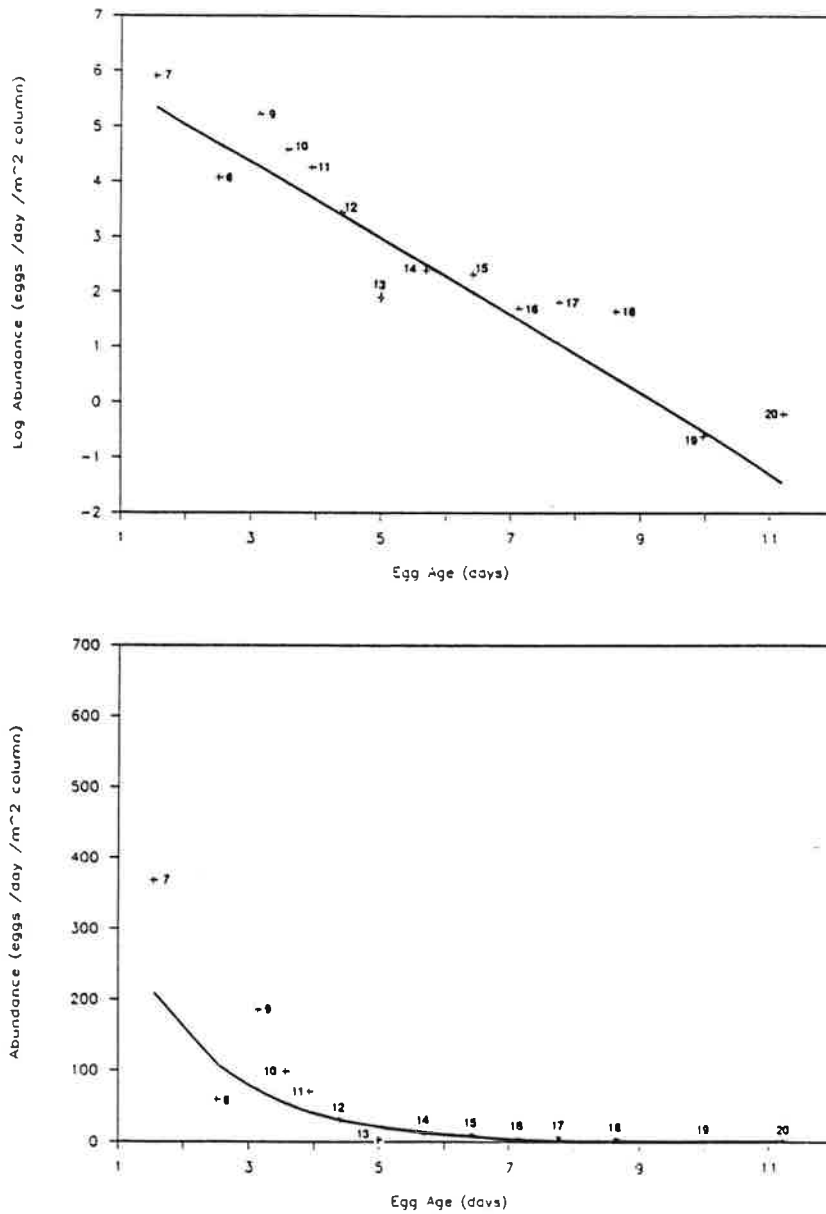
Figure 24. Results for survey 1PO85 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 25. Results for survey 1MF85 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.
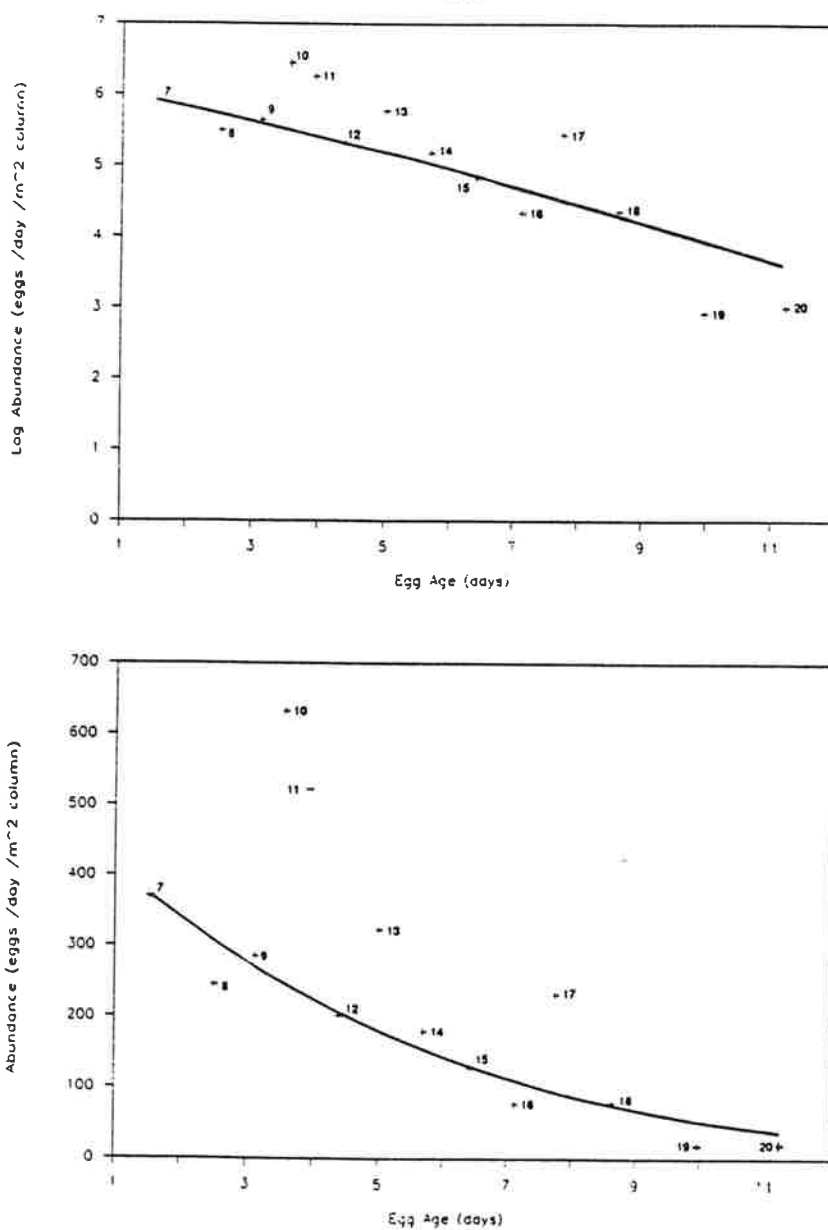
Figure 26. Results for survey 1MF86 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.
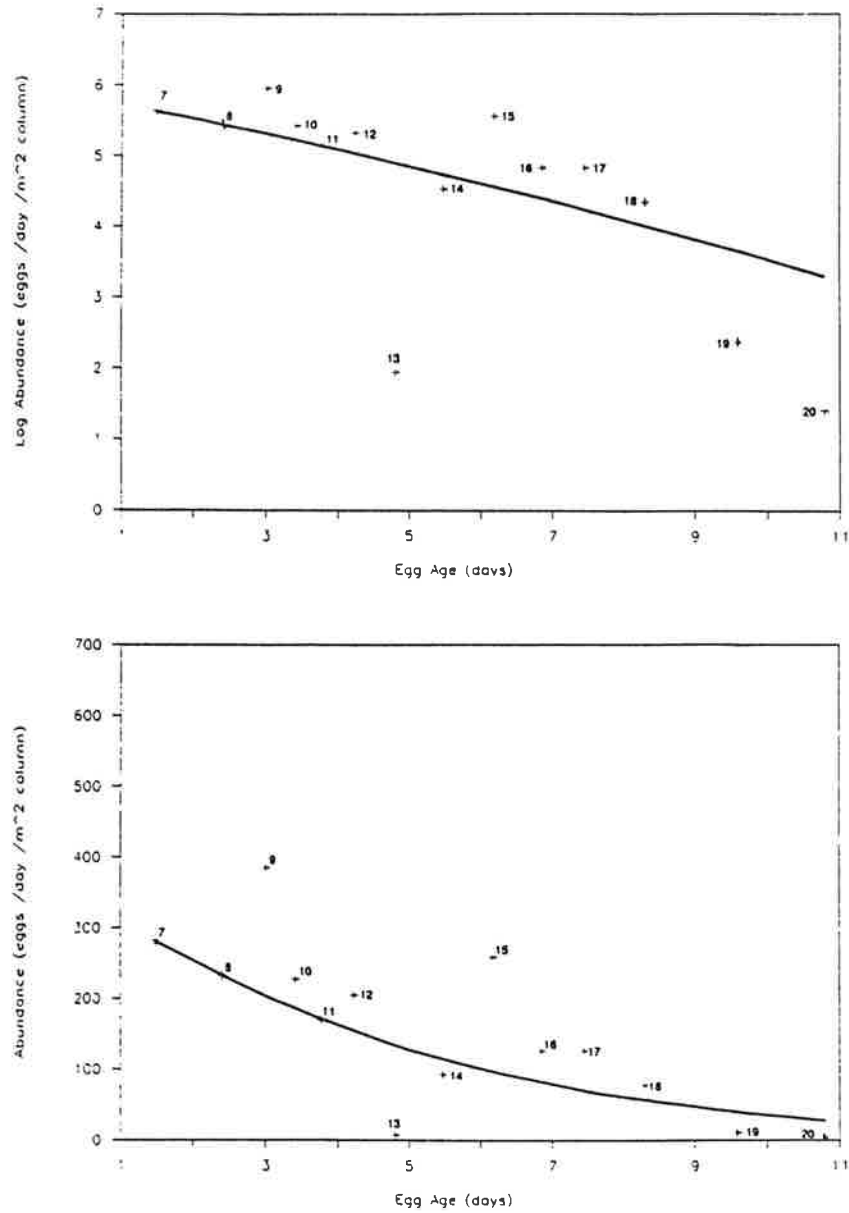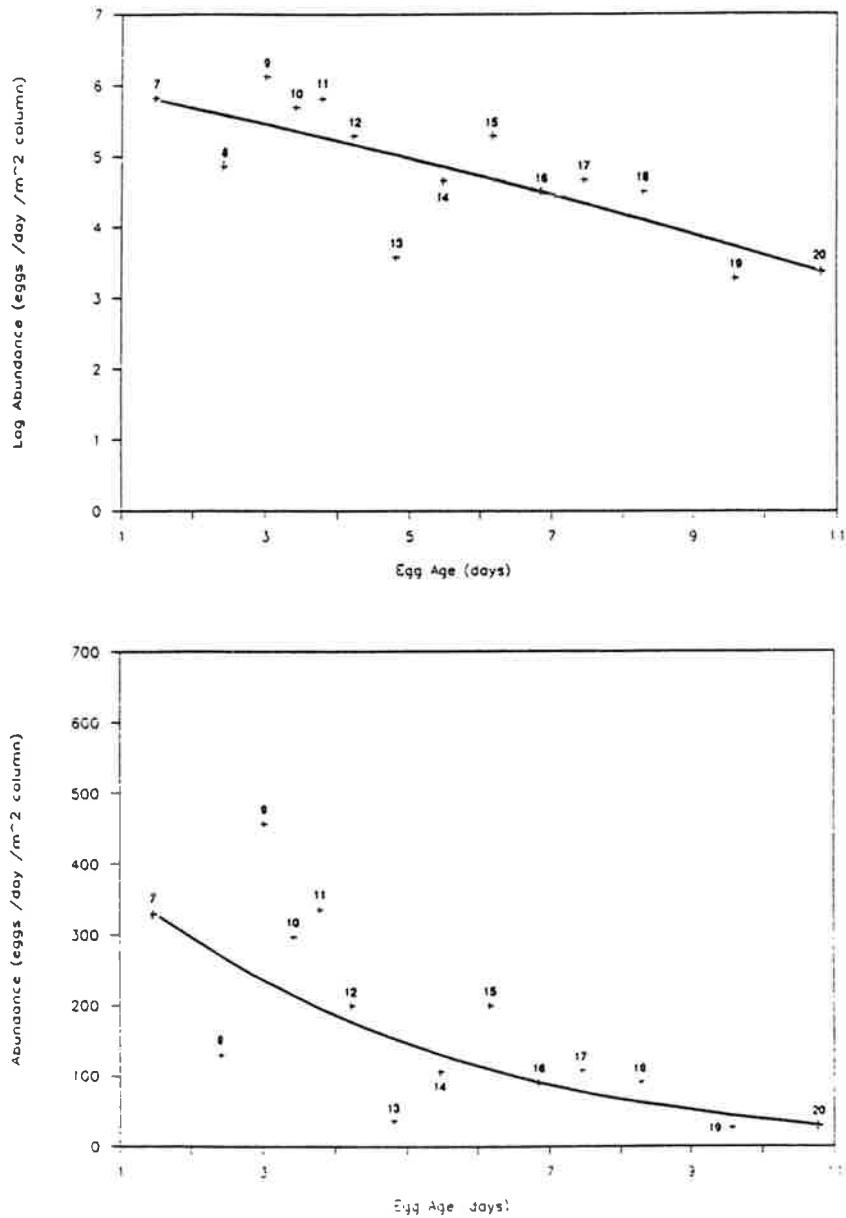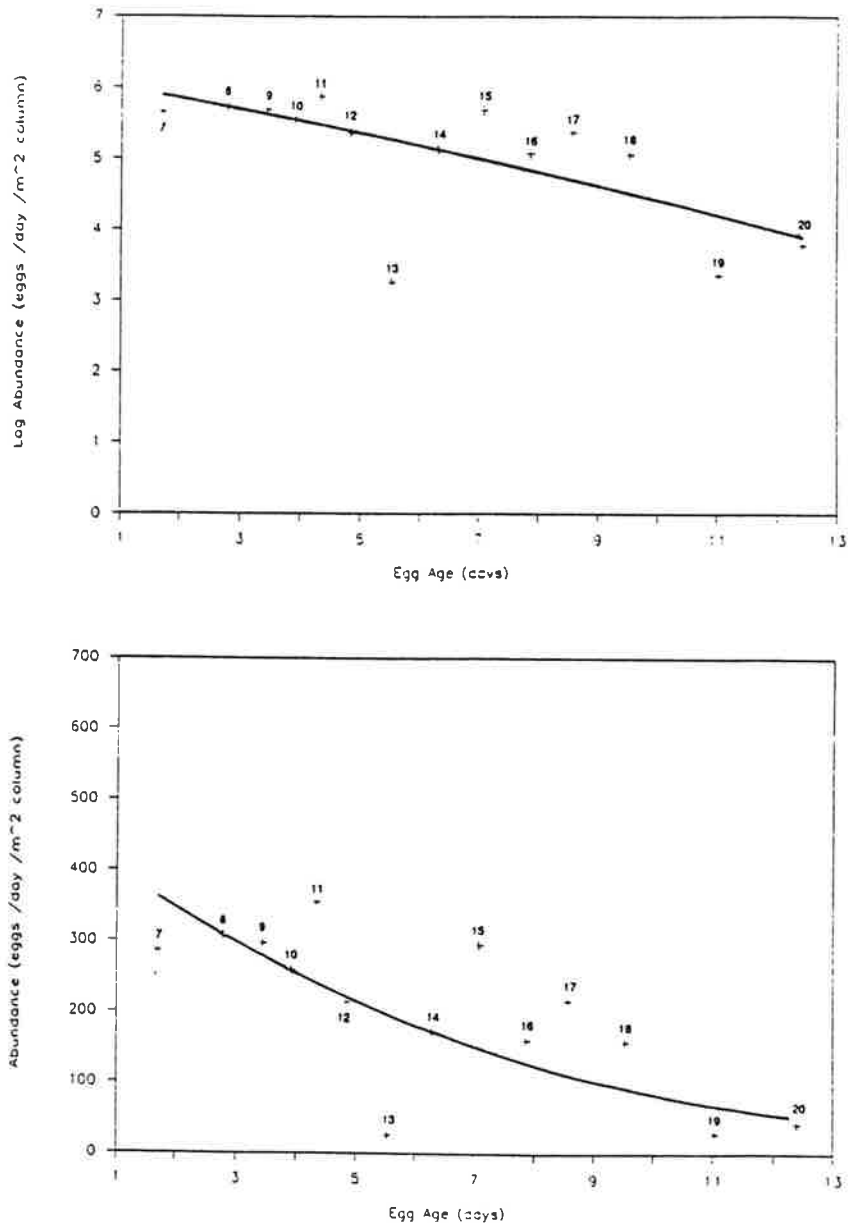
Best fitting estimates of the parameters ϵ and Z in eq. 7 are given in Table 3 for the years 1981, 1985, and 1986. Based on the egg data available and the analytical extrapolations employed, seasonal egg production within the survey area was approximately the same for the years 1981 and 1986, but egg production during 1985 was only two-thirds of this level. Estimates of the daily mortality coefficient generally ranged between 0.20 and 0.26, although a value of 0.68 was obtained for survey 2MF81/lo. A reassessment of these preliminary parameter values and a gauge of their probable significance are developed in Chapter 6.

DISCUSSION

Values for μ and σ assumed Survey data were not sufficient to define the duration and date of peak spawning under the normal-exponential model. When data are only available from a limited fraction of the spawning season, the best fitting estimates of the parameters μ and σ are heavily dependent on the observed trend in stage abundance data. Until total stage abundances can be determined with substantial precision, survey data that is centered on a narrow time frame cannot be relied on to dependably provide information on the character of spawning over the remaining spawning season.

The fact that stage abundances only weakly conform to the fitted trend (the lower plots of Figures 22-26) indicates that it is hazardous to rely on the stage abundance data from a single survey to suggest plausible estimates for the date parameters μ and σ. In effect, one is trying to extract date information from the data that primarily reflects the variability of abundance information. If this were attempted, the estimate for μ suggested by the fitting procedure could well be quite different from a date in early spring generally considered as the approximate date of peak spawning. Similarly, the best fitting estimate for σ might be an equally improbable value, such as one year or 2 days in length. Dubious values of these magnitudes were indeed obtained in preliminary fitting experiments using a series of hypothetical data sets. This indicates that the model containing μ and σ as unknown parameters is specified too generally relative to the data.

Since the fitting procedure cannot be allowed unlimited latitude to suggest values for model parameters, the procedure must be constrained in some way to insure that best fitting values do not violate credulity. One way to mathematically accomplish this is to add penalty terms to the error function (Daniels 1978). Fortunately, additional mathematical complications were not necessary since the determination of the date of peak spawning and seasonal spawning duration are not totally dependent on egg survey data alone.

Additional information was available outside of egg survey data
to define reasonable values for the date parameters μ and σ. For
example, since the spawning season is thought to be at least one
month in duration (Bates 1987, Kim 1987), the best fitting value
for σ would be expected to fall somewhere within a range of, say,
5-10 days. Similarly, the best fitting value for μ would be
expected to fall within a week of, say, April 1. Estimates for
the date parameters μ and σ must occur within a narrow absolute
range to conform with biological reality. However, values for
the abundance parameters ϵ and Z are truly unknown, and
estimation of these parameters is entirely dependent on egg
survey data.

<u>Selecting an error criterion</u> In fitting a model to data by
minimizing an objective function, the choice of an error
criterion resolves the questions 1) whether to evaluate
differences between observed and predicted values in absolute or
in relative terms and 2) whether to respond strongly to, or
minimize the importance of, large differences between observed
and predicted values. For reasons that will now be developed,
the choices made here were to use relative errors and to reduce
the impact of large errors on the magnitudes of best fitting
estimates. [See addendum 2]

<u>Absolute versus relative differences</u> An absolute differences
criterion allowed certain age groups to powerfully influence the

magnitudes of parameter estimates. In preliminary fitting experiments on the 2MF81 survey data, the estimation procedure attempted to generate predicted stage abundances which would as closely as possible approximate the observed values of the more abundant, younger stages. Yet, to do this, the predicted abundances for the less abundant, older stages were often forced toward zero. [See addendum 3]

These results from an absolute error criterion were the consequence of an implicit down-weighting of all but early stage abundance data. To see this, consider the differences between an observed low abundance and a predicted value of zero. This difference is small in absolute terms, particularly when compared to the absolute fitting errors associated with stages that are several orders of magnitude more abundant. For example, the difference between 0 and 100 eggs/ day/ m^2 is small compared to the difference between 2×10^4 and 3×10^4. The latter contributes greatly to the total lack of fit while the former contributes little. All differences would need to be of similar magnitude, for example 10^4, for an absolute differences criterion to be useful for fitting purposes. [See addendum 4]

In addition to numerical considerations, a relative error criterion was also preferred because of the statistical information contained in abundance data. It is implicitly assumed when using an absolute error criterion that the

measurement error for all data points are approximately equal;
this is a separate consideration from the lack of fit discussed
previously. However, the precision associated with estimates of
observed stage abundances (eq. 2) are known to vary
systematically with the magnitude of the observed values (Bates
1987). The precision of observed stage abundance estimates is
often poorest for the more recently spawned age groups. For this
reason, their importance must be down weighted.

Scaling the importance of differences Many numerical approaches
are available for weighting the impact on total fitting error of
individual differences between observed and predicted stage
abundances. Possible examples include taking the absolute value
of differences, squaring differences, cubing differences, or
using a higher power function (Daniels 1978). An error criterion
commonly employed in fitting procedures is the "sum of squared
differences", which has the desirable property of producing
maximum likelihood parameter estimates if the errors are additive
and distributed normally (Draper and Smith 1981). This criterion
is an outgrowth of the theory of moments of a random variable,
specifically the second moment about the mean of the distribution
of a random variable (Mood and Graybill 1963).

In the present analytical problem, the unweighted squared error
criterion was not optimal in providing best fitting estimates
that were numerically robust; broader sampling distributions were

obtained for model parameters in preliminary fitting experiments under the squared error criterion than under the absolute value criterion. This degradation in fitting utility was due to the importance accorded to outliers by the squared error criterion. The term "outliers" is used here in the sense of observations which deviate the most from a trend fitted to a set of data. The influence of these outliers on the shape and location of a fitted trend, and thereby on the magnitudes of parameter estimates, becomes increasingly powerful when a function of squared or higher power is used in the error criterion. [See addendum 5]

Moreover, in addition to empirical considerations, the squared differences criterion was not required since total stage abundances were not estimated in a formal statistical sense. Instead, one of the chief aims of this chapter was to seek a robust fitting procedure for eq. 7, a procedure that could be expected to lead to similar values for individual parameters when using any plausible set of data drawn from the egg population.

CHAPTER 4. The influence of certain data on estimates of total stage abundance.

INTRODUCTION

Provisional values for the parameters ϵ and Z, representing seasonal egg production and the coefficient of daily mortality, were estimated in Chapter 3 but no variance estimates were calculated. This chapter and the next two chapters will provide perspectives by which the robustness of the estimation procedures can be assessed. The task can loosely be divided into evaluations of 1) the adequacy of the survey design in sampling the biological population and 2) the adequacy of the analytical methods in representing both biological and sampling events.

The adequacy of sampling can be assessed, in part, by examining the relative influence that each data point had on the estimates of total stage abundance, an important intermediate value in the stream of calculations performed in Chapter 3. Relative influences were gauged by the fraction of total stage abundance contributed by the abundance of each developmental stage for the region around each sampling station.

Again, variance estimates will not be generated; the intent here is not to provide some measure of the possible variability of estimates, but to look beyond this toward the robust estimation of total stage abundances.

METHODS

Each estimate of total stage abundance, C_i, was determined by summing polygonal stage abundances, $[A_{ij} \ P_j]$, over all stations within the survey area (eq. 5). Percentage contribution plots were constructed to visually indicate the contribution of each polygonal stage abundance relative to total stage abundance (Figures 27-31).

Each percentage contribution plot is composed of 14 columns which correspond to the developmental stages 7-20. A column represents 100% of the estimated total abundance for a stage, irrespective of the actual magnitude of this estimate. A polygonal stage abundance contributes some definable fraction to the estimate of total stage abundance, and this fractional contribution was plotted as a rectangular area within a column. Fractional contributions were ranked within a column from the largest (bottom) to the smallest (top).

RESULTS

Survey design and fractional contributions The fractional contributions varied in size and the range of sizes varied between surveys. The widest ranges were associated with the data from cruise 2MF81. Three stations from survey 2MF81/lo and three different stations from survey 2MF81/hi formed roughly 75% of the

Figure 27. Percentage contribution plot for survey 2MF81/lo, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.
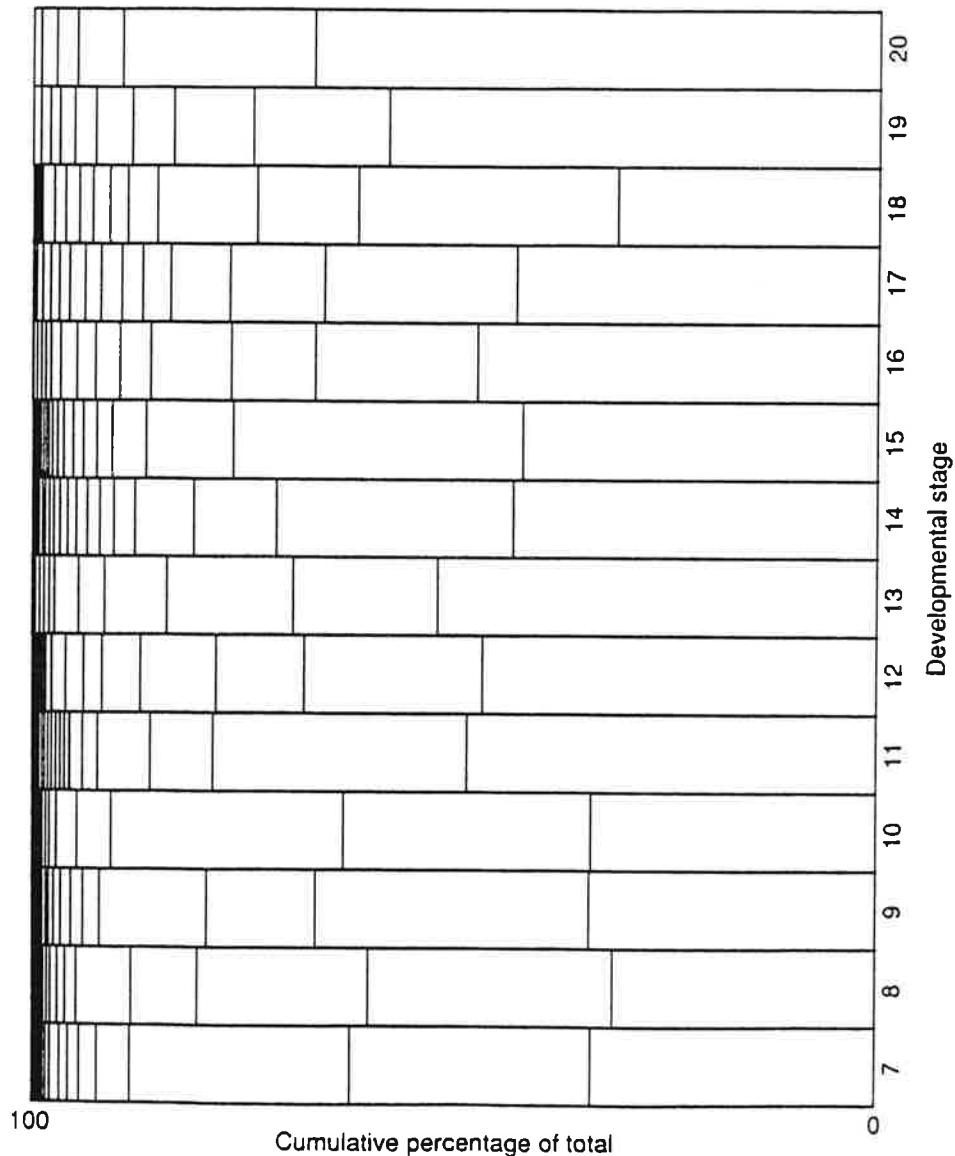
Figure 28. Percentage contribution plot for survey 2MF81/hi, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.
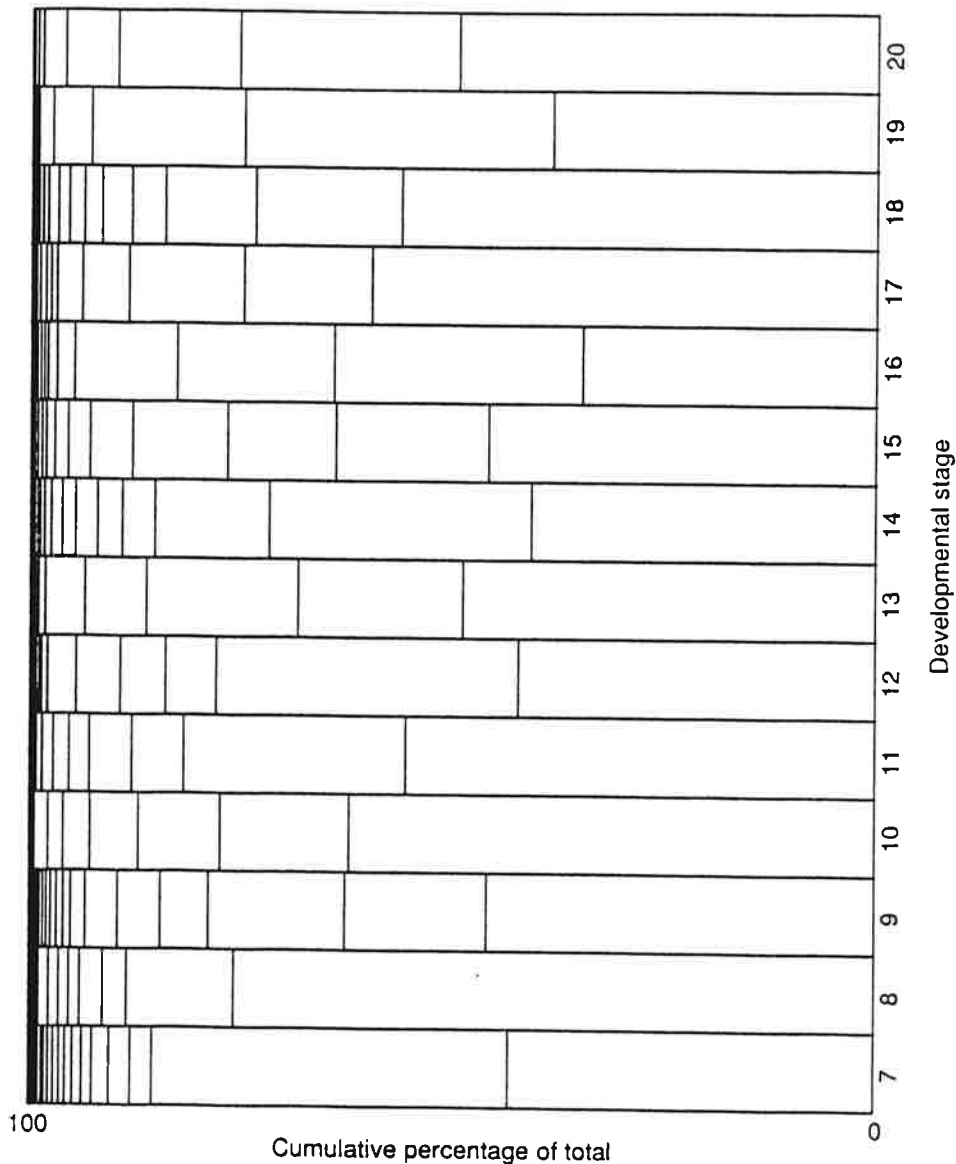
Figure 29. Percentage contribution plot for survey 1PO85, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.

Figure 30. Percentage contribution plot for survey 1MF85,
showing the fraction contributed by each polygonal stage
abundance to each estimate of total stage abundance. The columns
represent 100% of the estimated abundance within the survey area
of walleye pollock eggs in each of the developmental stages 7-20.
The survey area was completely divided into polygonal areas. A
polygonal stage abundance represents the abundance of a
developmental stage within the polygonal area surrounding a
sampling station. Polygonal stage abundances are depicted as
fractions of the total abundance of a stage and are ranked from
the largest contribution, at the bottom of each column, to the
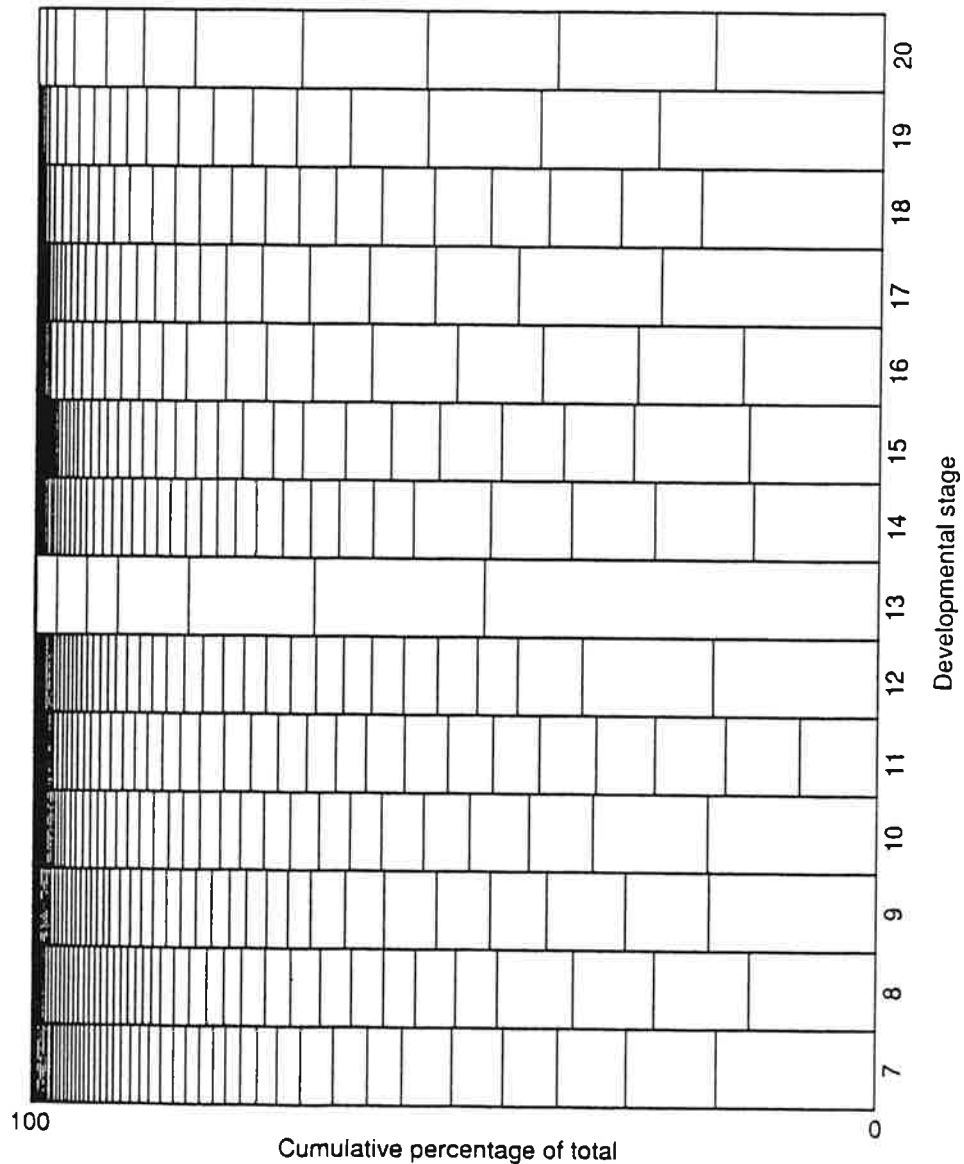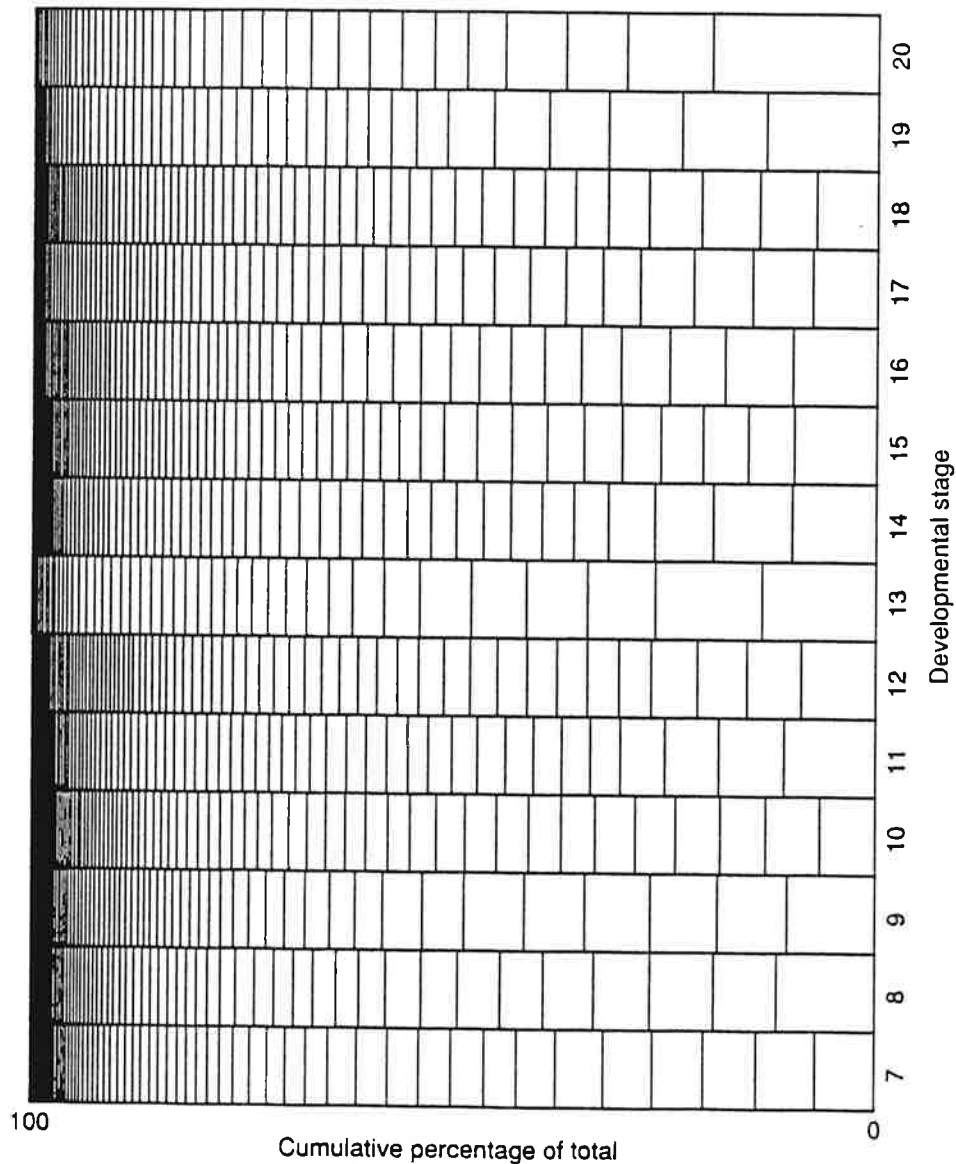smallest contribution, at the top.

Figure 31. Percentage contribution plot for survey 1MF86, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution (bottom) to the smallest contribution (top).

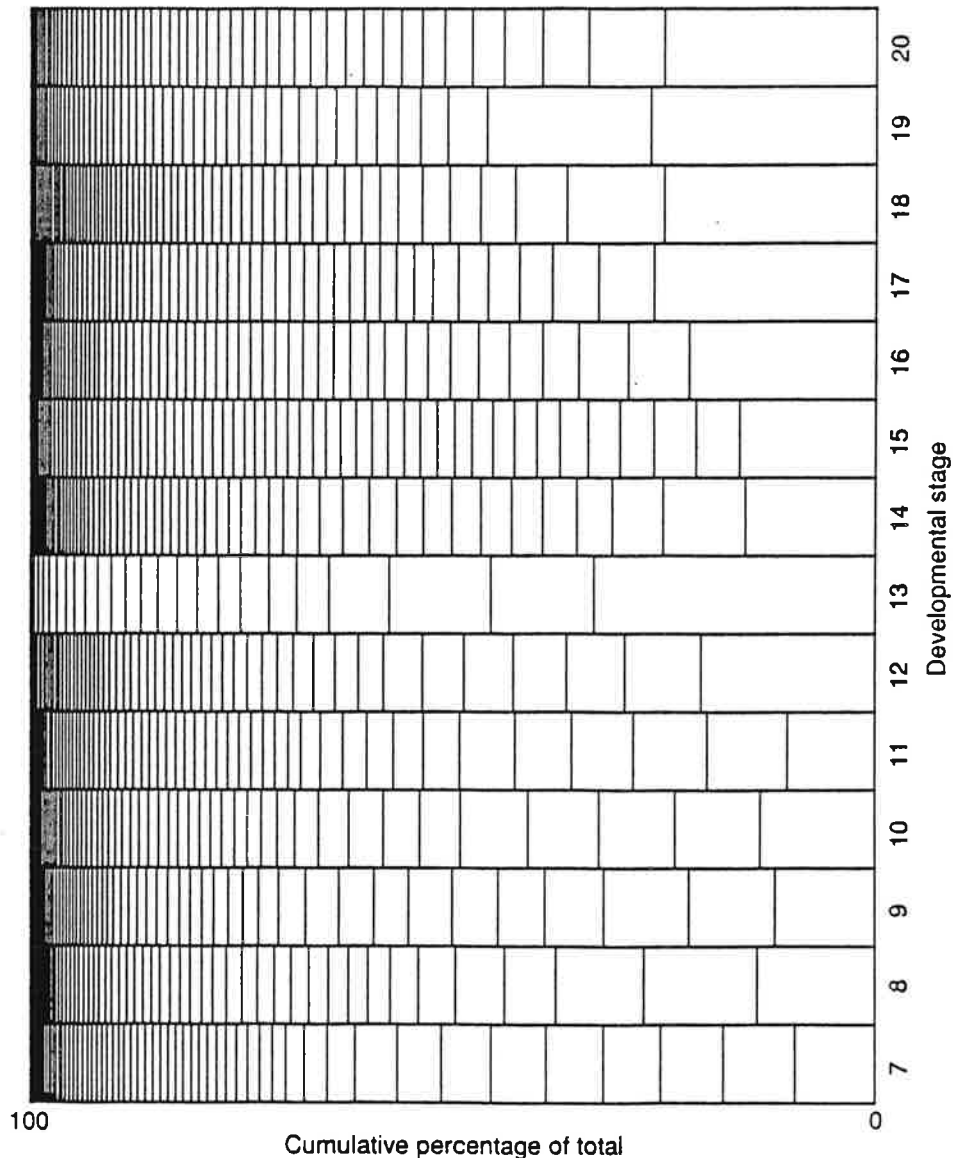observed total abundance for each developmental stage (generally the lower three rectangles of each column of Figures 27-28). By contrast, all fractional contributions for surveys 1PO85, 1MF85, and 1MF86 were more nearly the same size and, therefore, estimates of total stage abundance were seldom dominated by data from a few samples.

The range of sizes for fractional contributions was a function of survey design and of the heterogeneity of egg abundances. A grid of regularly spaced stations was employed during cruise 2MF81; since egg abundances for this year were the most heterogeneous found, the percentage contribution plot for this survey was dominated by the data from a few samples. A grid design was also employed for survey 1PO85, but fractional contributions were more nearly the same size because egg abundances throughout the survey area appeared to be more homogeneous than those of 1981 (e.g., Figure 11 versus Figure 10).

Instead of employing a grid design, surveys 1MF85 and 1MF86 were designed to have a greater station density in regions that were either expected to have high egg densities, or were found to have high densities as the survey was being conducted. The concentration of stations in regions of the survey area where eggs were observed resulted in a corresponding reduction in the sizes of polygonal station areas. As a consequence of this

strategy, the dominance of a few, large egg catches over all other sample data was moderated. [See addendum 6]

Pivotal samples and adjacent developmental stages When the estimated totals were dominated by data from only a few stations, as was the case for the 1981 surveys, these same few stations generally comprised a large fraction of the estimated totals for a series of adjacent developmental stages. For survey 2MF81/hi (Figure 1), stations G086A-G091A dominated all stages to various degrees. For survey 2MF81/lo, stations G022A-G024A dominated stages 7-12, stations G041A, G043A, and G044A dominated stages 9-15, station G029A dominated stages 14-19, and station G083A dominated stages 18-20.

For the surveys 1PO85 and 1MF85 (Figures 2-3), certain stations were also relatively dominant over a range of stages, but their impact was considerably less and no samples were of overwhelming influence in defining the eventual magnitude of total stage abundances estimates. For survey 1MF86, station G033A dominated. However, this was not the result of a large egg catch obtained in a region of substantial abundance, but rather the result of the large polygonal area defined for this station (Figure 21) in order that station areas completely encompass the survey area.

The rarity of stage 13 Some surveys yielded relatively few samples containing eggs in developmental stage 13. Fractional

contribution plots show a few large rectangles for stage 13 for survey 1PO85 (Figure 29) and perhaps also for survey 1MF86 (Figure 31), indicating that the egg catches at these few stations dominated the eventual estimate of total abundance for this stage. Survey 1MF85, on the other hand, provided fractional contributions that were similar in size to those of adjacent columns.

The dissimilarity of stage 13 data from that for other stages was not related to the laboratory where egg staging was performed. The Szczecin laboratory found relatively few occurrences of stage 13 eggs for survey 1MF86 and relatively many for survey 1MF85. And the AFSC laboratory found relatively few occurrences for survey 1PO85. It is difficult to assess the pattern for survey 2MF81, which was staged at the AFSC laboratory, since catches from a few stations dominate all stages and not just stage 13.

DISCUSSION

<u>Implications of pivotal data on population estimates</u> If the magnitude of an estimated total was largely determined by only a few polygonal stage abundances, then one is required to assume, generally without adequate supporting evidence, that these few catches and their corresponding polygonal areas were reliable representations of the surveyed population, both as to mean abundance and spatial extent.

In addition to questions of representativeness, the estimates of total stage abundance can be subject to unanticipated complications when the estimated total is allowed to be a function of the data from a few samples. Bates (1987) noted that the magnitude of mortality coefficients can be an artifact of localized patterns of spawning and dependent on a very few, critical data points. The confounding of mortality estimation with trends in stage abundances at a few pivotal stations was reduced in the 1985 and 1986 surveys by the concentration of stations in regions of relatively high egg abundance.

<u>A proposed test for the adequacy of sampling</u> A useful, visual test for the adequacy of sampling is to examine the relative sizes of fractional contributions in a percent composition plot. All rectangles within a column and between columns should be approximately the same size. This would indicate that polygonal stage abundances contribute equally to the estimate of total stage abundance and that a subset of the data was not critical in defining this total.

This simple test has implications regarding the design and implementation of a survey. Few stations should be allocated to areas thought to contain very few eggs, and many stations should be located in areas of high egg abundance. This allocation may be done prior to sampling, or as sampling is occurring and a concentration of eggs is discovered. Since the locations of egg

concentrations are usually not known ahead of time, it is perhaps best to disperse stations somewhat. This would allow the survey area to be searched for other concentrations of eggs while still denying a few stations a pivotal importance in the estimation of population parameters. [See addendum 7]

CHAPTER 5. The variability of egg catches between paired nets.

INTRODUCTION

An egg catch is usually assumed to be representative of egg densities for some definable area around a sampling station. However, the density of eggs is not constant throughout this region, but is instead a statistical quantity whose sampling distribution can be characterized. How confident can one be in extrapolating an egg catch to some encompassing region? An examination of the nature of catch variability over small scales of distance can provide some insight on the precision of an estimated mean based on one observation.

The purposes of this chapter are 1) to report on data collected during survey 1MF85, where both cod ends from each tow were saved, and to evaluate the magnitude of net-to-net variability in egg catches between paired nets, 2) to estimate station-to-station variability in standardized egg catches for use in the next chapter, and 3) to anticipate certain improvements in sampling design.

METHODS

Both cod ends from 20 cm bongo tows were preserved during survey 1MF85. A flowmeter was suspended in the mouth of each net to

provide separate volume estimates. Egg catch and volume data were analyzed for 28 paired tows conducted throughout the survey area. Sampling procedures and catch standardizations were discussed in Chapter 2.

A coefficient of variation for each paired catch was calculated for raw catches, K_j, and standardized catches, S_j, using the formula:

$$(eq.9) \quad CV_j = \frac{\sqrt{\sum_{n=1}^{2} (K_{nj} - \bar{K}_j)^2}}{\bar{K}_j}$$

or

$$CV_j = \frac{\sqrt{\sum_{n=1}^{2} (S_{nj} - \bar{S}_j)^2}}{\bar{S}_j}$$

where

$\bar{K}_j$	mean egg catch from both nets at the jth station (eq. 1)
K_{nj}	egg catch from the nth net at the jth station
$\bar{S}_j$	mean standardized egg catch (eq. 1) for the jth station
S_{nj}	standardized egg catch from the nth net of the jth station
CV_j	coefficient of variation for a pair of (un)standardized egg catches at the jth station.

An average coefficient of variation and a standard deviation of this coefficient were calculated for both unstandardized and standardized data sets (Cochran 1977 [eq. 2.47]).

RESULTS

Patterns observed in calculated volumes filtered and raw catches

Consistent differences were found in the calculated volumes filtered, V_{nj}, between paired nets. In absolute terms, the calculated volume filtered by net 2 was always greater than the calculated volume filtered by net 1, with an average difference of 6 m^3 (standard deviation 1.4 m^3). In relative terms, the calculated volumes indicated that net 1 filtered 15.7% less volume (ratio standard deviation 3.5%) than net 2.

Consistent differences were also found for the number of eggs collected, K_{nj}, in paired nets. The egg catch in net 1, K_{1j}, exceeded the catch in net 2, K_{2j}, in 20 out of 28 paired samples. However, coefficients of variation based on paired samples were within 5% for 18 samples and exceeded 5% for 10 samples, of which 8 samples had higher numbers caught in net 1.

Magnitude of net-to-net variability during a tow Table 4

summarizes the magnitude and variability of egg catches from paired nets for both unstandardized and standardized catches. The standardization process resulted in each standardized value being roughly 10 times larger than a corresponding unstandardized value.

Table 4. Variability in catches of walleye pollock eggs between paired 20 cm bongo nets.

station	egg catch K_{nj}			standardized egg catch S_{nj}		
	net 1	net 2	CV(%)	net 1	net 2	CV(%)
G026A	2616	2580	1	18656	15892	11
G035A	333	336	1	2094	1853	9
G042A	822	782	4	4799	3880	15
G046A	1138	895	17	8387	5492	29
G048A	277	271	2	1999	1632	14
G049A	741	655	9	5400	3949	22
G051A	578	512	9	4551	3356	21
G052A	2611	2253	10	24276	16514	27
G053A	3839	3843	0	27552	23171	12
G054A	649	641	1	3837	3343	10
G055A	1169	1595	22	7414	8826	12
G056A	1660	1446	10	12368	8843	24
G057A	2398	2320	2	16315	13305	14
G058A	1620	1613	0	12261	9911	15
G059A	1131	1107	2	7928	6374	15
G060A	1260	1236	1	9683	8159	12
G062A	2804	2120	20	21323	13278	33
G064A	2217	2862	18	16889	17929	4
G065A	1237	1288	3	10182	8521	13
G066A	1428	1493	3	10976	9431	11
G067A	2429	2493	2	18246	16145	9
G068A	877	895	1	6349	5441	11
G070A	575	478	13	3983	2862	23
G071A	516	483	5	3702	2971	15
G072A	773	766	1	5922	4567	18
G073A	667	680	1	4589	4103	8
G077A	464	462	0	2748	2566	5
G080A	768	513	28	5373	3004	40

The coefficients of variation between egg catches from paired 20 cm bongo nets were plotted against mean catch size in Figure 32 for unstandardized catches (top) and standaruized catches (bottom). Based on a fit by eye, these coefficients were independent of catch size. Being independent, an average coefficient of variation can be calculated without respect to the
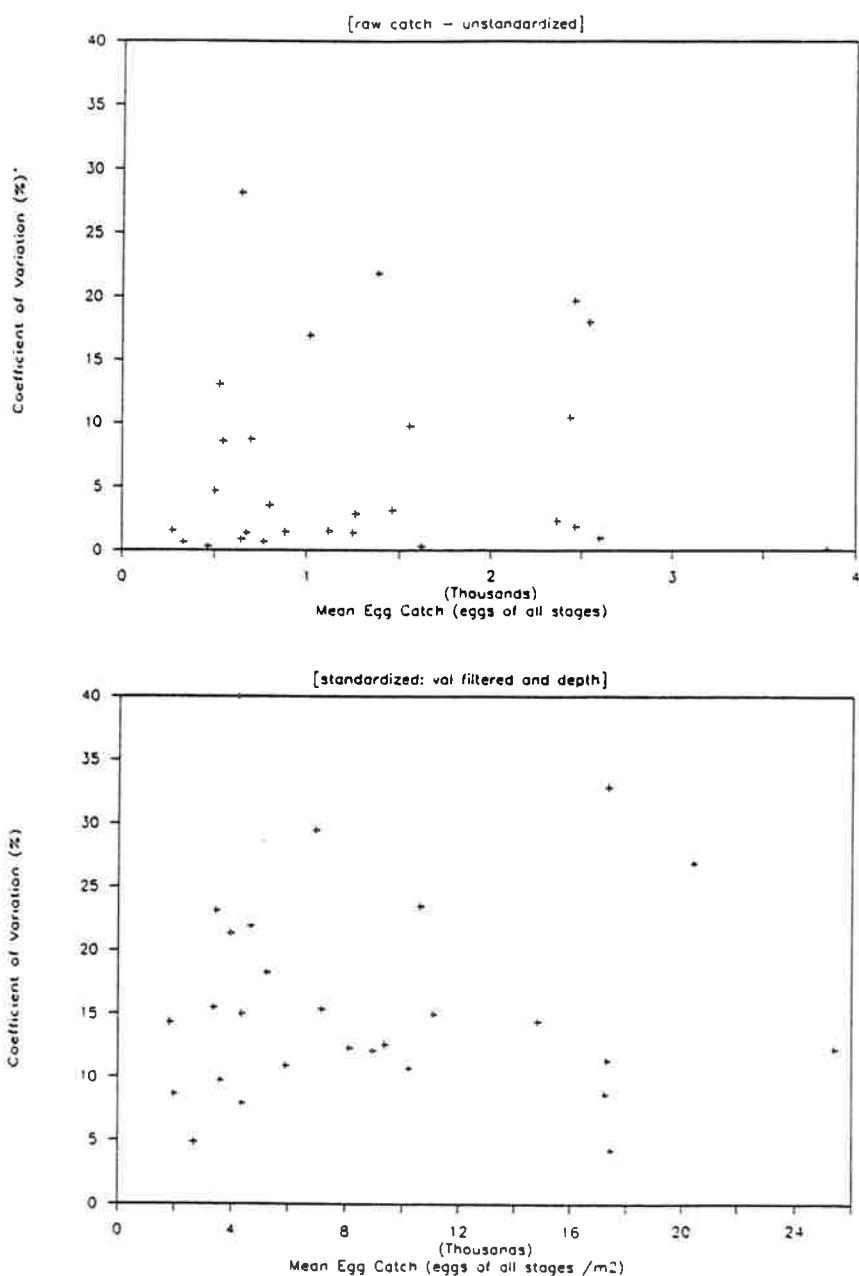
Figure 32. Coefficients of variation for eggs of walleye pollock in paired 20 cm bongo nets as a function of average (un)standardized catch from both nets. Each coefficient was calculated as the standard deviation of (un)standardized catches from paired nets divided by the mean for the nets. The coefficients are independent of the size of the catch and averaged CV=7% (ratio standard deviation 9%) for unstandardized catches (top) and averaged CV=16% (ratio standard deviation 10%) for standardized catches (bottom).

magnitudes of net-to-net egg catches. This average coefficient was 6.8% (ratio standard deviation 9.2%) before standardization and 16.1% (ratio standard deviation 10.4%) following standardization. Modal values for coefficients of variation were approximately 1% and 15% respectively.

DISCUSSION

<u>Catch differences before and after standardization</u> A coefficient of variation will not change if the data are rescaled by constant values. The increases observed in most coefficients following the standardization process, which is a simple rescaling of data, thus indicate the presence of systematic differences in the estimated volumes filtered by paired 20 cm bongo nets. Volume differences do not appear to have resulted from a partial blockage of unrestricted flow into the nets. The most likely causes for the observed differences were due to imprecision in the calibration of flowmeters and to a deviation of flowmeters with use from their calibrated condition.

<u>Catch variability over various scales of distance</u> Whatever the cause of dissimilarities in the volumes filtered and the number of eggs collected by paired nets, only a portion of the variability in standardized egg catches can be accounted for by tow characteristics. The remaining variability must be attributed to an inherent level of variability in egg densities

along a tow path. Only a fraction of a meter separated paired
nets on a 20 cm bongo. Thus, in regard to the representativeness
of samples from these nets, the variability in egg densities over
a few centimeters of distance approximates 16% standard deviation
on average after catch standardization. Although raw catches
were less variable, standardized catches, not raw catches, are
required in virtually all analyses of abundance data.

The variability in egg densities within a survey area can be
conceptually partitioned into a number of arbitrary components as
a function of the distance between sampling stations. These
components are arbitrary since egg densities vary over space as a
continuum rather than in discrete increments as a function of
distance. For analytical convenience, the continuum of catch
variability may be partitioned into four components. Proceeding
along a continuous scale of distance from the local to the
global, these categories are 1) variability between paired nets
during a tow along adjacent tow paths, 2) variability between
multiple tows at a sampling station, 3) variability between
stations within a local region defined by an area of arbitrary
size, and 4) variability between regions within the survey area.

Egg catch variability attributed to the first component, i.e.
between paired catches from the same tow, was found to
approximate 16% following the standardization process. This

coefficient was obtained for 20 cm bongos; net-to-net variability might be smaller for nets having a larger mouth diameter, such as the 60 cm bongo, since the larger cross-sectional area would integrate variations in egg densities over a somewhat larger distance orthogonal to the tow path.

Sample-to-sample variability (components 1 and 2) may be crudely estimated by rounding the instantaneous variability upwards to 20%. No data are available from the current set of surveys to usefully evaluate this or higher categories of variability. Bates (1987) found that the last component (variability over the survey area) approximated 40% near the time of peak spawning during the 1981 spawning season. However, he argued that this value understates the precision with which an estimated total can be known because the common statistical models he examined ignore spatial trends, trends which are known to occur in the distribution of eggs throughout a survey area. These models are less than appropriate for the additional reason that samples are often obtained under some form of a systematic grid rather than at random as required under the theoretical formulation of these models.

CONCLUSION

Improvements to survey design The analysis in this chapter suggests that relative variability between replicate tows at a

station may approximate 20%. It was demonstrated in chapter 4 that a few egg catches can be instrumental in defining the magnitude of an estimated total stage abundance. Taking these two observations together, this implies that the reproducibility of an estimated total can be extremely limited if the total is based on very few egg catches of very dubious reproducibility themselves.

But these analyses also indicate ways that both sampling design and estimation procedures can be improved. Before these improvements are suggested, however, a number of constraints on the sampling of walleye pollock eggs must be recognized.

The location and intensity of spawning by adults is constantly shifting within Shelikof Strait and can radically change within the course of a week. For this reason egg surveys should be completed within approximately one week so that data may be considered as a synoptic representation of egg distributions and densities.

Moreover, severe weather frequently forces the discarding of sampling schedules and the positions of projected sampling stations. This will probably always remain an unavoidable constraint on the quality of survey data.

Finally, the total number of bongo tows are not likely to change, given the current level of resources and the time required to obtain these samples. Sample size ranges from 50 to 100 per survey. This limitation, however, is not a serious constraint to the improvement of population estimates.

Given these sampling constraints, the next chapter demonstrates by simulation that improvements in the robustness of estimation procedures can be achieved simply by varying station density throughout the survey area in proportion to anticipated or known levels of egg abundance. The next chapter also provides perspective on the magnitude and precision of parameter estimates developed in Chapter 3.

CHAPTER 6. A Monte Carlo assessment of variability in the estimates of seasonal egg production and daily egg mortality.

INTRODUCTION

This chapter will extend the results of Bates (1987) concerning the results of sampling by mathematical simulations of the walleye pollock egg population in Shelikof Strait. Further information is now available to refine simulations. In addition to the 1981 data, the distribution and abundance of eggs throughout the survey area can be described for the years 1985 and 1986. And the analysis of Chapter 5 indicated that the coefficient of variation for egg catches at a sampling location is at least 20%.

This chapter will address the questions: 1) Would a focused sampling design provide more robust estimates than a grid sampling design? and 2) What empirical range of variability could be associated with the estimated parameters ϵ and Z of eq. 7?

METHODS

The generation of grid and focused samples The basic approach employed in Monte Carlo simulations was described in Chapter 4 of Bates (1987). In the present analysis, the method was extended

to simulate the distribution and abundance of each of the 21 developmental stages of walleye pollock eggs, rather than simply the total number of eggs collected. Chapter 5 of Bates (1987) described the methods used for the estimation of seasonal egg production and daily egg mortality. An improved error criterion was developed in Chapter 3 of this paper.

The procedure for the sampling of stations was also reworked. Simulated sampling stations were positioned both parallel and transverse to a line oriented along the main axis of Shelikof Strait. The position of this line was determined by a pivot point and orientation point. The pivot point for each simulated survey was at 57°37'N 155°08'W, which approximated the center of egg concentrations for all surveys other than 2MF81/lo. The orientation point was selected such that a line through it and the pivot point would pass down the main axis of Shelikof Strait.

Grid sampling and focused sampling were the sampling designs employed in simulations. In grid sampling, stations were spaced 9.5 km along and 5.0 km transverse to the main axis of Shelikof Strait. The initial position of the first station of the grid template was randomly located within the survey area for each simulation. Station spacing was sufficient to yield an average of 76 stations (standard deviation 1.7 stations) per simulation.

In focused sampling, stations were concentrated in an area of high egg abundance and station spacing increased with increasing distance away from this point (Figure 33). The center of focused station template was randomly positioned within 1 km of the pivot point for each simulation run. Station spacing was sufficient to yield an average of 76 stations (standard deviation 1.2 stations) per simulation. [See addendum 8]

Data employed in simulations Information on the distribution and abundance of walleye pollock eggs for the years 1981, 1985 and 1986 were provided by the surveys 2MF81/lo, 2MF81/hi, 1PO85, 1MF85, and 1MF86. A spatial abundance model was constructed from each of the five survey data sets for each of the 21 developmental stages of walleye pollock eggs. One hundred simulated surveys were generated for each combination of survey abundance model and sampling design. Approximately 76 simulated stations were generated for each simulated survey. Simulated egg abundances were calculated from the local trend at a simulated station for each of the 21 developmental stages. Thus, a total of approximately 1,596,000 simulated stage abundances were generated (2 sampling designs X 5 survey models of abundance X 100 simulated surveys X 76 simulated stations X 21 developmental stages).

From these simulated stage abundance data, 21,000 estimates of total stage abundance (eq. 5) were calculated. However, some
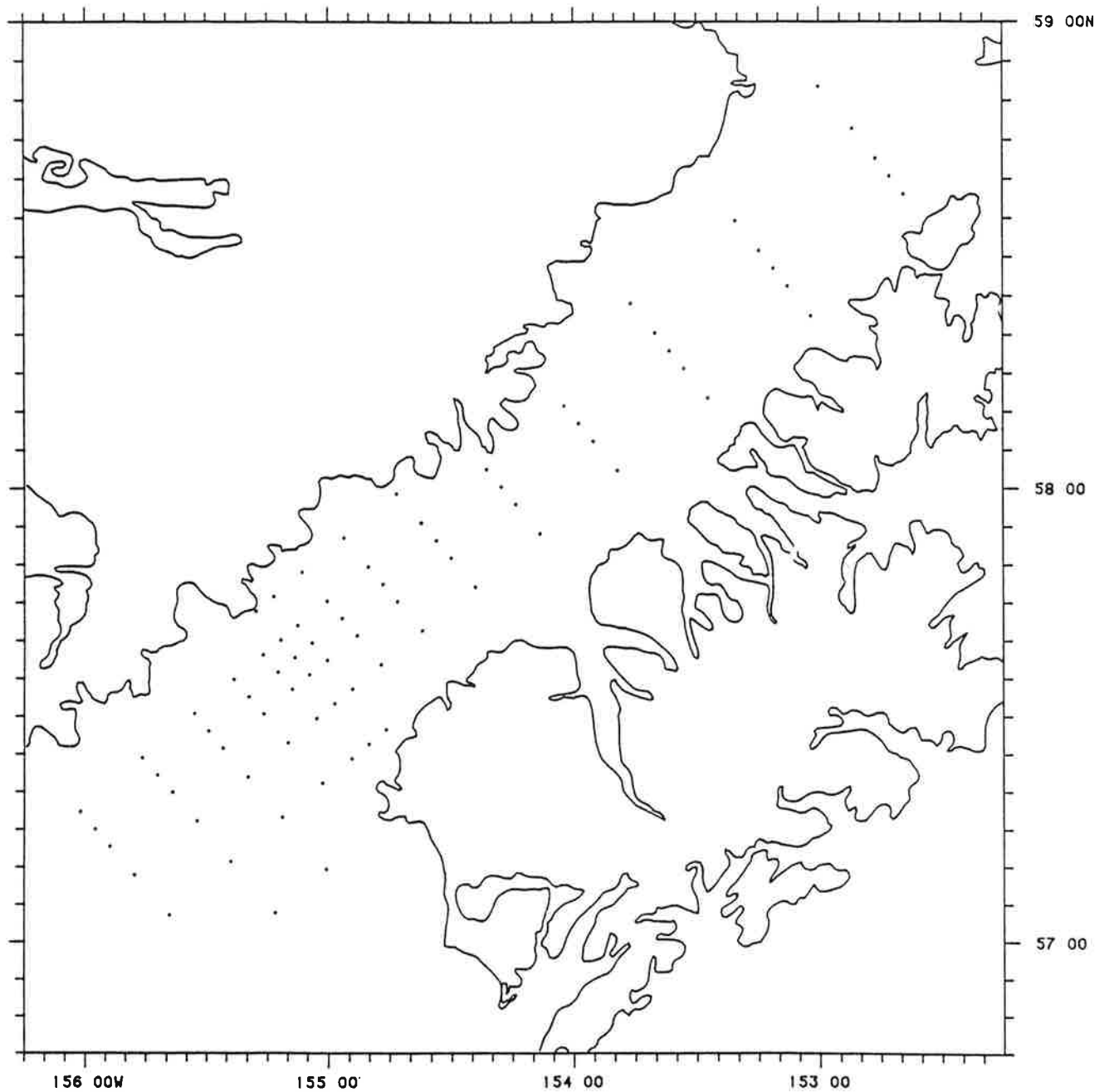
Figure 33. An example of a focused sampling grid generated during a Monte Carlo simulation of walleye pollock egg sampling.

estimates were used only in preliminary comparisons; only those estimates from stages 7-12 and 14-20 were subsequently fitted to eq. 7. The reasons for eliminating stage 1-6 and 21-24 were discussed in Chapter 3. Also, in Chapter 4 it was argued that the abundance of stage 13 was underrepresented in stage frequency data, and this stage was eliminated from model fitting in an attempt to improve the fit to the remaining data. There currently appears to be no justifiable reason to further discard or combine data in order to improve the fit to eq. 7.

RESULTS

Sampling distributions of simulated catches Figures 34-38 show the results of simulated abundances obtained using either a focused sampling design (above) or a grid sampling design (below). Estimates of average hourly stage abundance are shown for stages 1-20 from each of the 100 simulated surveys, with each estimate represented by a "+" symbol. Data for stage 21 were not included in the plots in order that the last three days of the incubation period could be eliminated and the remaining data shown over an expanded scale. The diversity of values that were obtained indicate the variety of stage estimates that could potentially be produced from an ichthyoplankton survey for the time of the spawning season and the region in which the surveys were conducted.
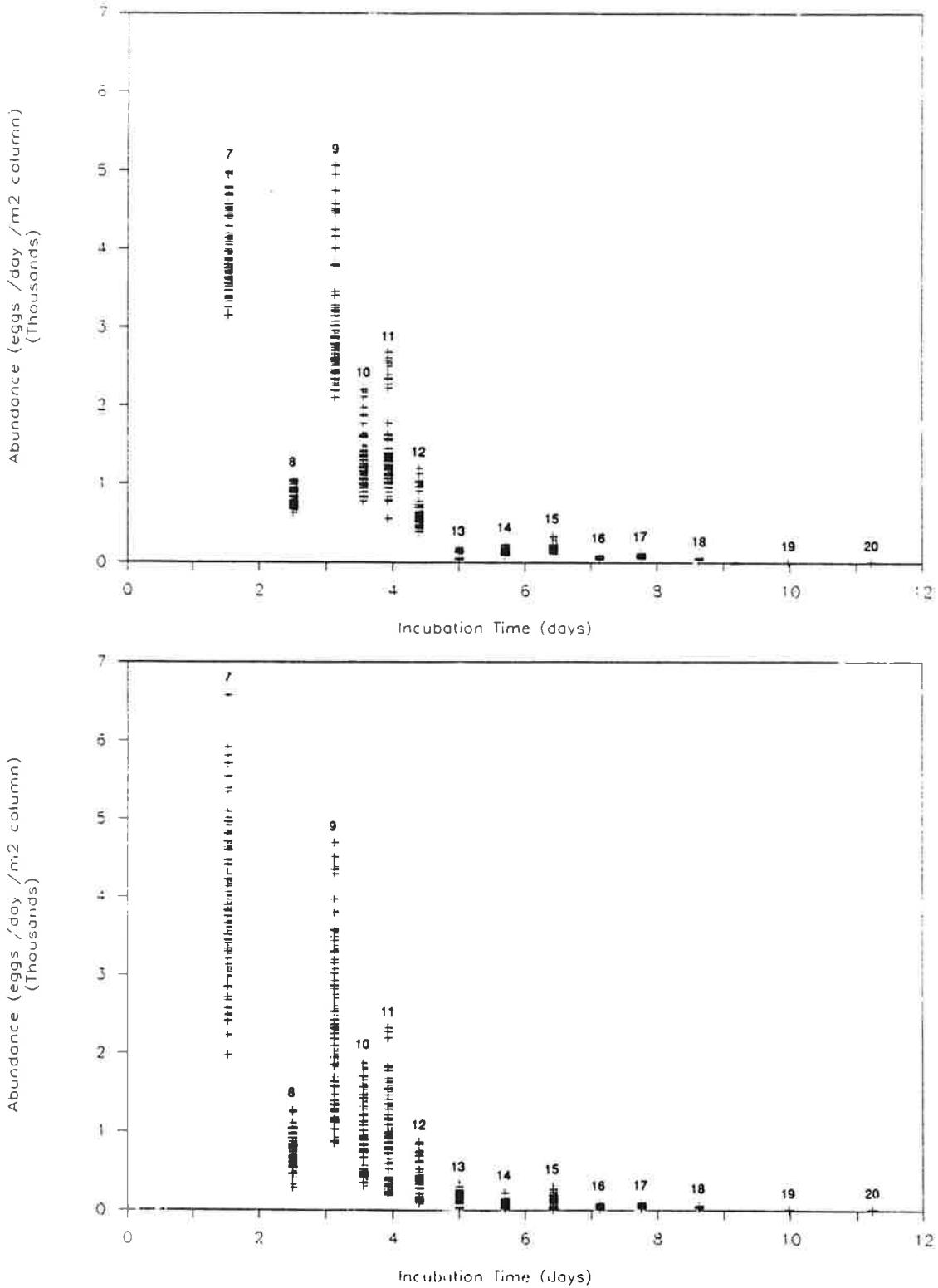
Figure 34. Average stage abundances obtained for survey 2MF81/lo
by Monte Carlo simulations of sampling under focused (upper plot)
and grid (lower plot) sampling designs. 100 values were obtained
for each developmental stage and the results are shown for
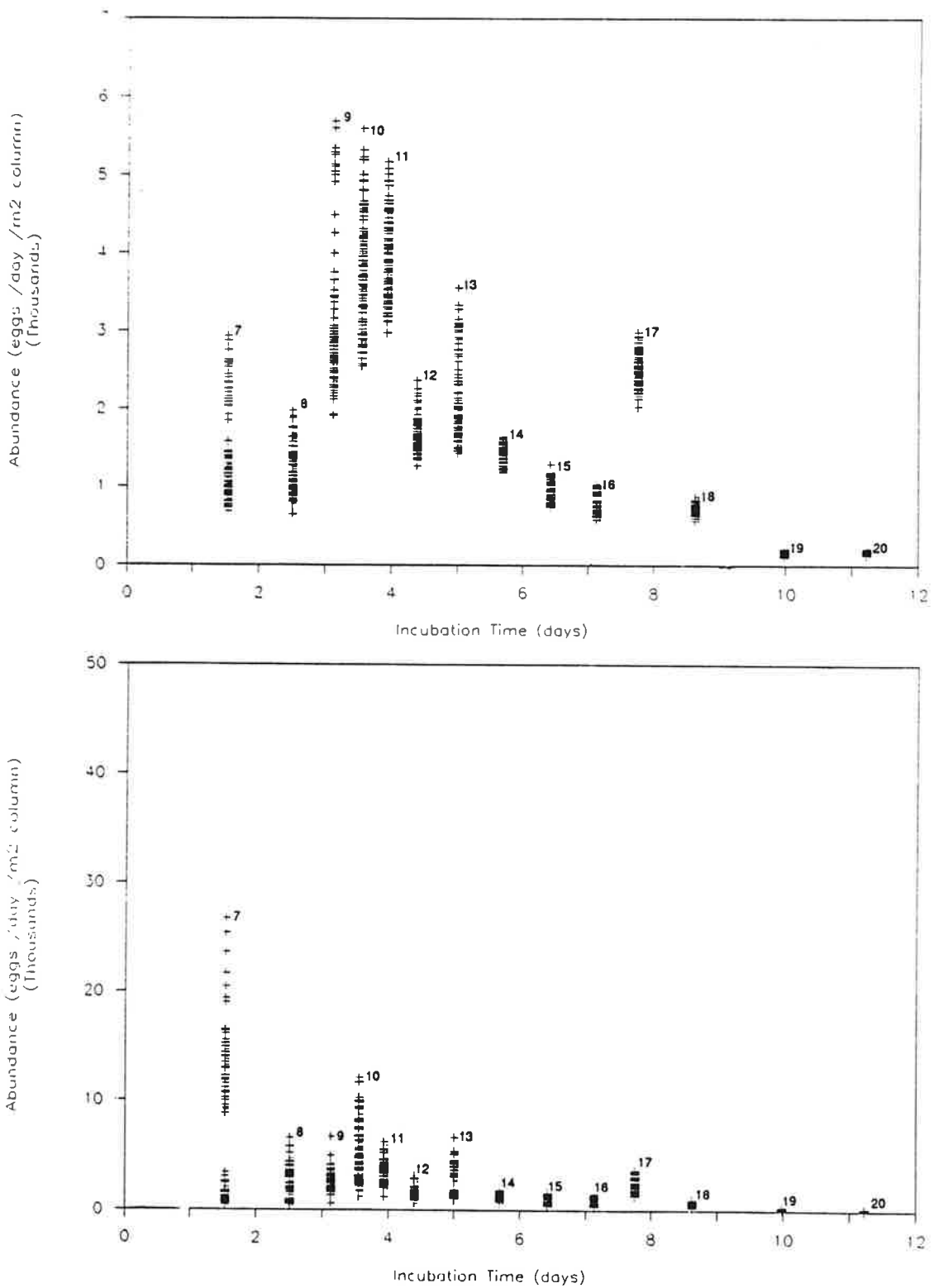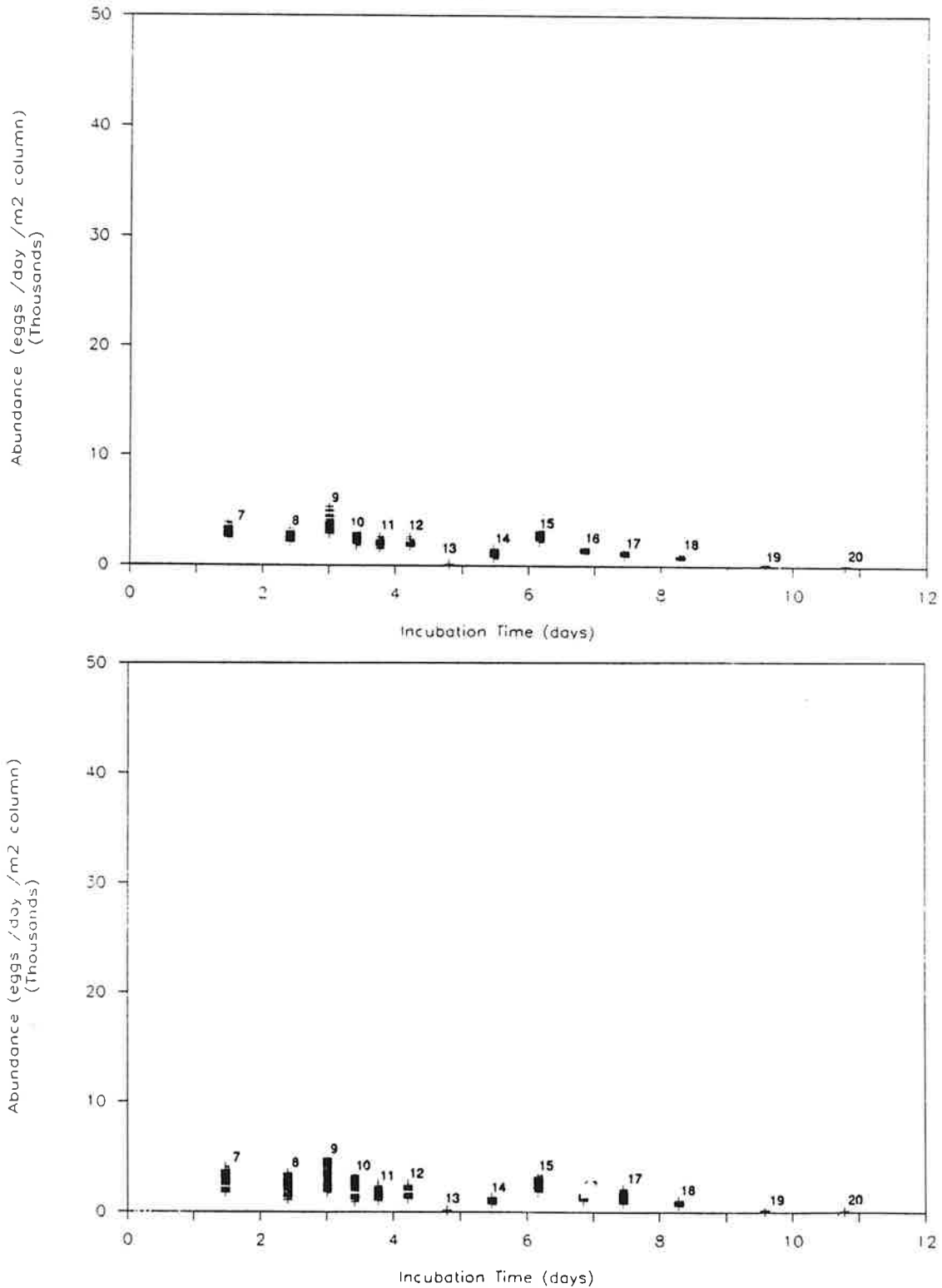developmental stages 1-20.

Figure 35. Average stage abundances obtained for survey 2MF81/hi
by Monte Carlo simulations of sampling under focused (upper plot)
and grid (lower plot) sampling designs. 100 values were obtained
for each developmental stage and the results are shown for
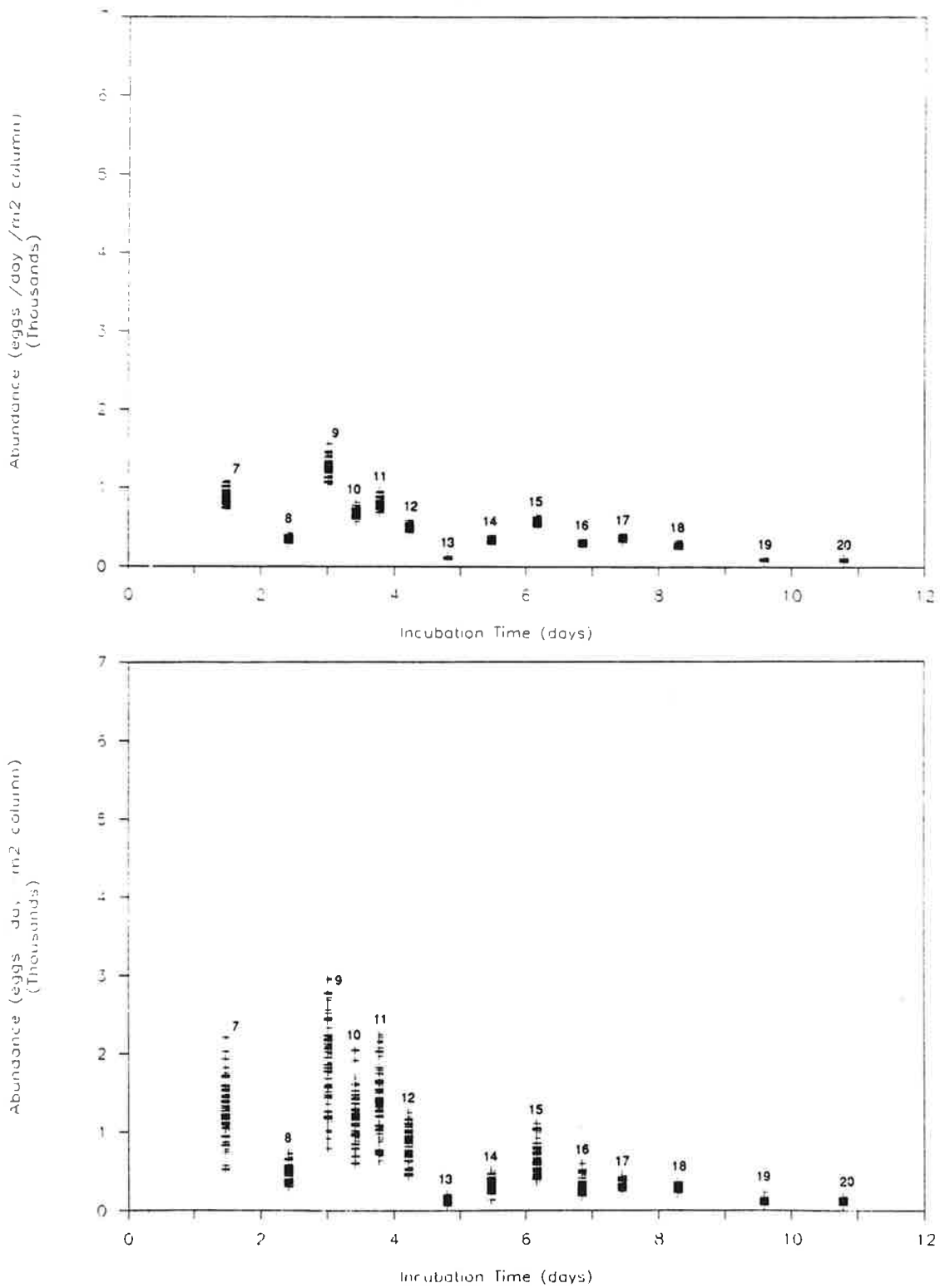developmental stages 1-20.

Figure 36. Average stage abundances obtained for survey 1P085 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.
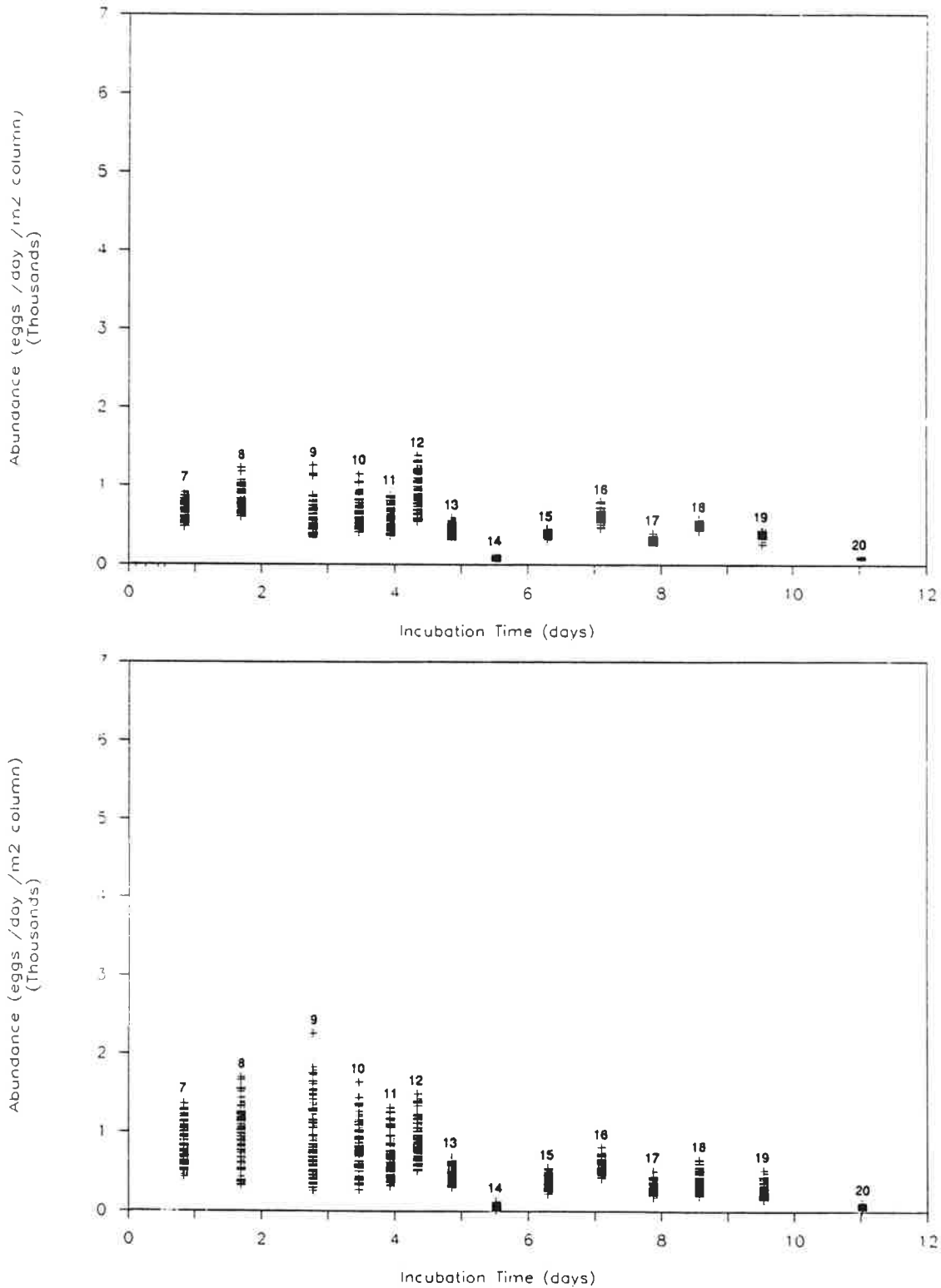
Figure 37. Average stage abundances obtained for survey 1MF85 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 38. Average stage abundances obtained for survey 1MF86 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Different scales along the Y-axis were necessary to show the relatively high abundances of early stage eggs for some surveys. For comparative purposes, the data were plotted over either a small scale, with an upper limit of 7 $X10^{15}$ eggs, or a large scale, with an upper limit of 50 $X10^{15}$ eggs. The large scale was employed for the results of both grid and focused sampling from survey 1PO85. Both scales were used for survey 2MF81/hi, with the small scale for focused sampling results and the large scale for grid sampling results. The small scale was used on both upper and lower plots for surveys 2MF81/lo, 1MF85 and 1MF86.

Variability of stage abundances as a function of sampling design
Focused sampling (upper plots) resulted in substantially less variability in the estimates of average hourly stage abundance than did grid sampling (lower plots), except for 2MF81/hi. This is indicated in the Figures by the fact that abundance estimates are distributed over smaller ranges in each upper plot than in the corresponding lower plot. The reduction in variability is directly proportional to magnitude of the average hourly stage abundance. [See addendum 9]

Approximate conformity of the trend in stage abundances to analytical models The trends in average hourly stage abundances conformed only approximately to the normal-exponential model (eq. 7). Contrary to the trend expected, average hourly stage abundances early in incubation period (stages 1-6) were often

substantially smaller than the average hourly abundances for stages of intermediate age (stages 7-12). The one exception was survey 1PO85.

The apparent trend in average hourly stage abundances conformed to the predicted trend more closely for some surveys than for others. Ignoring data from those stages not included in subsequent procedures for parameter estimation (stage 1-6, 13, 21), the trend in average hourly stage abundances was highly variable for surveys 2MF81/lo, 2MF81/hi and 1PO85, whereas the trend was much smoother for surveys 1MF85 and 1MF86. The trend was slightly more sharply defined by the data from survey 1MF85 than by the data for survey 1MF86.

<u>Sampling distributions for estimates of ϵ and Z</u> Average hourly stage abundance data from the simulated surveys was fit to eq. 7 and the resulting estimates of seasonal egg production and daily egg mortality are shown in Figures 39-40. Again, as is indicated by the reduction in the range of parameter estimates for each survey, a focused sampling design provided estimates which have a more consistent magnitude.

DISCUSSION

A crude statement of variability for parameter estimates can be obtained from the observed ranges of parameter estimates. Assume
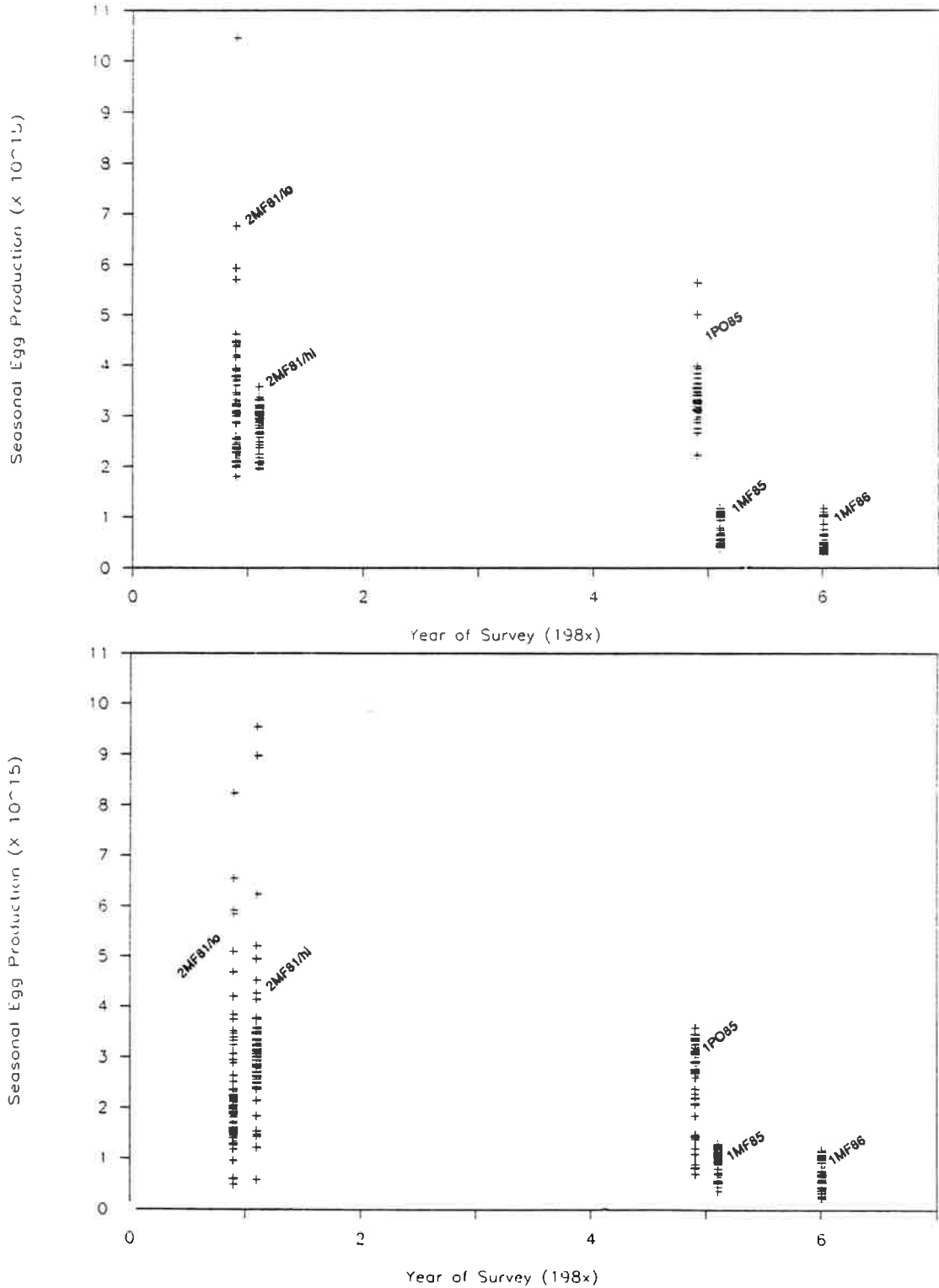
Figure 39. Estimates for seasonal egg production, ϵ, obtained for the surveys 2MF81/lo, 2MF81/hi, 1PO85, 1MF85, and 1MF86 under focused (upper plot) and grid (lower plot) sampling designs. Data were obtained by Monte Carlo simulations of sampling, and the resulting calculated values of total abundances for the stages 7-12 and 14-20 were then used to estimate the normal-exponential relationship between spawning season, abundance, and egg age.
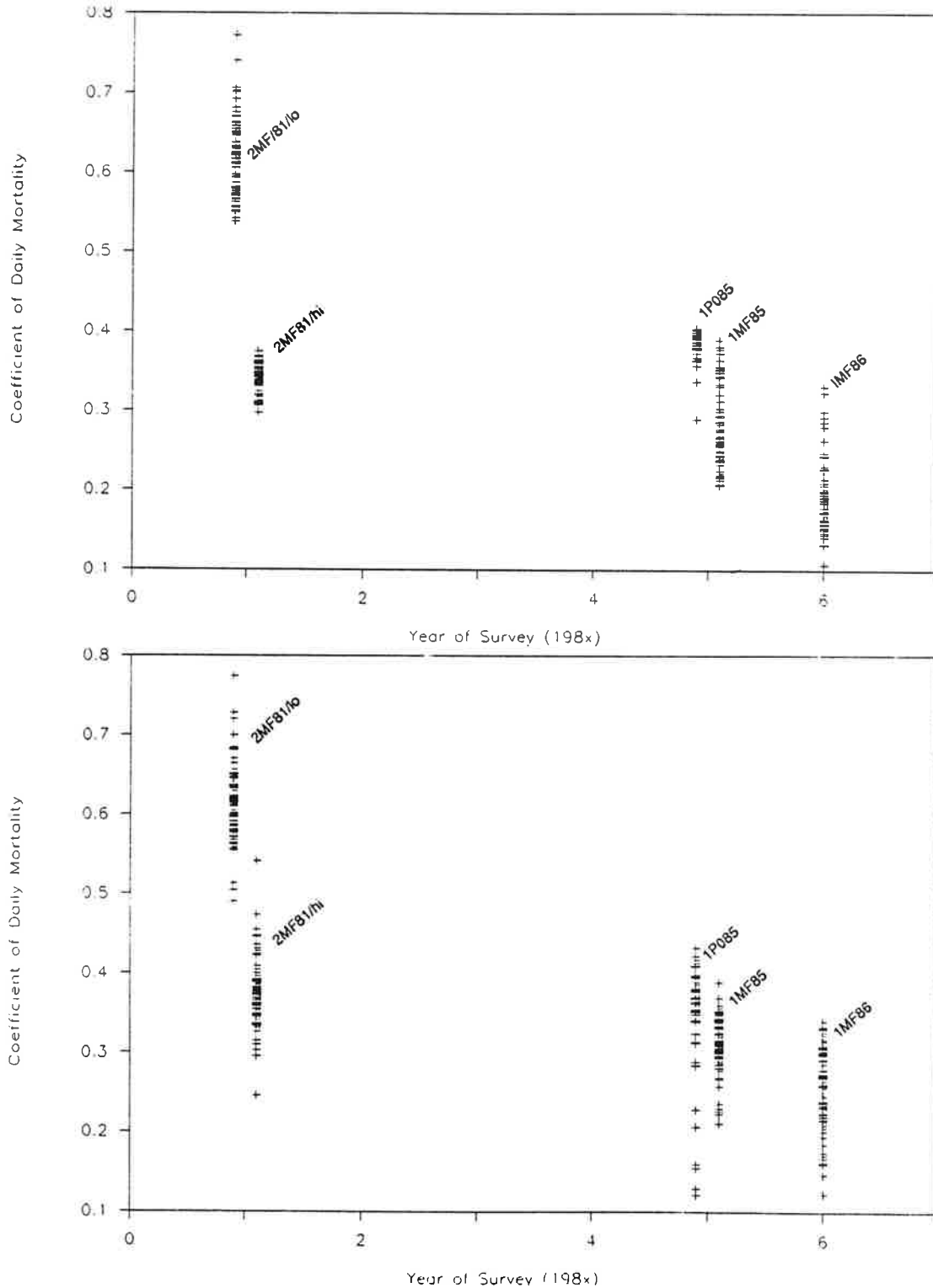
Figure 40. Estimates for mortality during the incubation period, Z, obtained for the surveys 2MF81/lo, 2MF81/hi, 1PO85, 1MF85, and 1MF86 under focused (upper plot) and grid (lower plot) sampling designs. Data were obtained by Monte Carlo simulations of sampling, and the resulting calculated values of total abundances for the stages 7-12 and 14-20 were then used to estimate the normal-exponential relationship between spawning season, abundance, and egg age.

that the range of estimates for a parameter approximates the length of a 95% confidence interval for a statistic, a length which is defined as ±1.96σ. The range of a 95% confidence interval approximates 4 standard deviations in length (two standard deviations to the left of the sample mean and two to the right). If the range is given, then σ can be crudely estimated as σ = range/4. (σ is used here in its usual sense as a measure of dispersion for a sampling distribution of a random variable, and not as the parameter from eq. 7 reflecting the duration of spawning season.) Estimates of ϵ generally ranged over approximately 2 units of the Y-axis (Figure 39) and estimates of Z generally ranged over approximately 0.2 units (Figure 40). Thus the estimate for σ is .5 units for the parameter ϵ and the estimate is 0.05 units for the parameter Z.

The significant figure convention holds that only digits known with certainty plus the first uncertain digit should be included in a reported value of an estimated parameter. The results of the previous paragraph indicated that the first decimal digit is uncertain in ϵ and the second digit is uncertain in Z. Table 5 gives the results of Monte Carlo simulations using this convention.

Table 5. Estimates of seasonal egg production, ϵ, and
instantaneous egg mortality, Z, based on Monte Carlo simulations
of sampling of egg populations from Shelikof Strait, AK for the
years 1981, 1985, and 1986.

year	survey	ϵ	Z
1981	2MF81/lo	$3.0(\pm0.5)$ X10^{15}	$0.65(\pm.05)$
	2MF81/hi	$3.0(\pm0.5)$ X10^{15}	$0.35(\pm.05)$
1985	1PO85	$3.0(\pm0.5)$ X10^{15}	$0.35(\pm.05)$
	1MF85	$0.5(\pm0.5)$ X10^{15}	$0.30(\pm.05)$
1986	1MF86	$0.5(\pm0.5)$ X10^{15}	$0.20(\pm.05)$

Surveys that sampled the same time of the spawning season and
region, and therefore presumably sampled the same egg population,
yielded dissimilar results. The 1981 estimate of the
instantaneous mortality coefficient for survey 2MF81/lo was
double the estimate obtained for survey 2MF81/hi. And the 1985
estimate of seasonal egg production for survey 1PO85 was six
times as great as the estimate obtained for survey 1MF85. [See
addendum 10]

Sources for these inconsistencies can be identified. It was
demonstrated in Chapter 4 that the 1981 data are known to be
dependent on a few pivotal samples. Moreover, the trends in age
data were biased by dissimilar histories of spawning in the
vicinity that these pivotal samples were obtained (Bates, 1987).
As for the 1985 data, the differences between surveys 1PO85 and
1MF85 could be due to the 20% coefficient of variation being an

underestimate of station-to-station variability. Such an underestimate could lead to too little variability in estimates of total stage abundances, and thereby to an underestimation of the range for the ϵ parameter.

Chapter 7.   Summary of results and conclusions.

Chapter 2.   Walleye pollock eggs were ubiquitous throughout the
survey area.   Sampling distributions for standardized stage
abundances per hour of stage duration ranged over 6 log cycles.
Egg distributions showed steep abundance gradients and the
gradients were much steeper for survey 2MF81 than for subsequent
surveys.   Samples obtained at stations that occur in a region of
high and rapidly changing egg abundances can become pivotal in
the results of analytical calculations.

Chapter 3.   The parameter estimation approach of Bates (1987) was
modified to make it a much more robust fitting procedure.
Preliminary population estimates were obtained using this
modified approach.

Data from a single survey can theoretically be used to estimate
the duration of the spawning season and the date of peak
spawning.   However, this proved impossible from a practical
standpoint because the calculated values for total stage
abundances did not conform well to the model proposed.   This was
due in large part to the poor precision in the calculated values,
particularly for the earlier developmental stages.

Chapter 4: A visual test was proposed to evaluate the effectiveness of sampling to estimate total stage abundances. This test was based on the idea that every catch on a stage-by-stage basis and the associated spatial area onto which these abundances will be extrapolated should, taken together, contribute a similar fraction to each estimate of total stage abundance. No individual or set of samples could then prove pivotal in calculations derived from the survey data. In looking at the ichthyoplankton data available, estimates of stage abundance for cruise 2MF81 were indeed dominated by a few samples and, relative to this cruise, the other surveys were considered to be more reliably representative.

Steps can be taken to prevent a few samples from dominating other data in the definition of abundance trends. Grid sampling does not provide as much information on numerical abundance as does a focused sampling design. Sampling effort should be concentrated in areas of relatively high abundance and effort minimized in areas of low abundance. Sampling effort should also be concentrated in regions of the survey area where population gradients change rapidly between relatively high to low abundances. [See addendum 11]

Chapter 5: Net-to-net differences in unstandardized egg catches in paired 20 cm bongo nets were generally < 5%, but were as great as 20-30%. Volume estimates are required for catch

standardization but, being relatively imprecise, they increased net-to-net coefficients of variation to a minimum of approximately 15%. Based on these data, the variability between replicate tows at a station was estimated as 20%.

Chapter 6: Monte Carlo simulations provide a measure of just how different parameter estimates could be if the opportunity existed for synoptic resurveys of an egg population. Monte Carlo simulations served a number of important purposes in the present analyses of survey data. Simulations identified an approximate range of values over which estimates of total stage abundance can be expected to vary given the apparent distribution and abundance of the egg population within Shelikof Strait. Simulations also reaffirmed the conclusion developed earlier that the variability in estimates of population parameters can be reduced by a focused sampling design, particularly under conditions of high variability in egg catches and steep gradients of abundance over small regions of the survey area. Finally, simulations allowed empirical limits to be determined for population parameters.

Estimates of seasonal egg production and coefficients of daily mortality are given in Table 5 for the years 1981, 1985, and 1986. Inconsistencies in results were attributed to the introduction of artifacts due to the presence of pivotal samples and to station-to-station variability probably being greater than 20%.

ACKNOWLEDGEMENTS

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Figure 15.   Distribution and abundance of walleye pollock eggs, Theragra chalcogramma, in developmental stage 18 for the survey 1MF85.   Contours are common log cycles of standardized egg catch.

Figure 16.   Distribution and abundance of walleye pollock eggs, Theragra chalcogramma, in developmental stage 18 for the survey 1MF86.   Contours are common log cycles of standardized egg catch.

Figure 17.   Survey area, station locations, and polygonal station areas for survey 2MF81/lo.

Figure 18.   Survey area, station locations, and polygonal station areas for survey 2MF81/hi.

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Figure 20.   Survey area, station locations, and polygonal station areas for survey 1MF85.

Figure 21.   Survey area, station locations, and polygonal station areas for survey 1MF86.

Figure 22.   Results for survey 2MF81/lo when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age.   The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances.   The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 23.   Results for survey 2MF81/hi when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age.   The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances.   The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 24. Results for survey 1PO85 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 25. Results for survey 1MF85 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 26. Results for survey 1MF86 when calculated values for total stage abundances were used to estimate the normal-exponential relationship between spawning season, abundance, and age. The upper plot shows the trend fitted to the data and the residuals under the error criterion of absolute differences between log transformed observed and predicted abundances. The lower plot illustrates the appearance of the fitted trend and data after back transformation.

Figure 27. Percentage contribution plot for survey 2MF81/lo, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.

Figure 28. Percentage contribution plot for survey 2MF81/hi, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.

Figure 29. Percentage contribution plot for survey 1PO85, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.

Figure 30. Percentage contribution plot for survey 1MF85, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution, at the bottom of each column, to the smallest contribution, at the top.

Figure 31. Percentage contribution plot for survey 1MF86, showing the fraction contributed by each polygonal stage abundance to each estimate of total stage abundance. The columns represent 100% of the estimated abundance within the survey area of walleye pollock eggs in each of the developmental stages 7-20. The survey area was completely divided into polygonal areas. A polygonal stage abundance represents the abundance of a developmental stage within the polygonal area surrounding a sampling station. Polygonal stage abundances are depicted as fractions of the total abundance of a stage and are ranked from the largest contribution (bottom) to the smallest contribution (top).

Figure 32. Coefficients of variation for eggs of walleye pollock in paired 20 cm bongo nets as a function of average (un)standardized catch from both nets. Each coefficient was calculated as the standard deviation of (un)standardized catches from paired nets divided by the mean for the nets. The coefficients are independent of the size of the catch and averaged CV=7% (ratio standard deviation 9%) for unstandardized catches (top) and averaged CV=16% (ratio standard deviation 10%) for standardized catches (bottom).

Figure 33. An example of a focused sampling grid generated during a Monte Carlo simulation of walleye pollock egg sampling.

Figure 34. Average stage abundances obtained for survey 2MF81/lo by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 35. Average stage abundances obtained for survey 2MF81/hi by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 36. Average stage abundances obtained for survey 1PO85 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 37. Average stage abundances obtained for survey 1MF85 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 38. Average stage abundances obtained for survey 1MF86 by Monte Carlo simulations of sampling under focused (upper plot) and grid (lower plot) sampling designs. 100 values were obtained for each developmental stage and the results are shown for developmental stages 1-20.

Figure 39. Estimates for seasonal egg production, ϵ, obtained for the surveys 2MF81/lo, 2MF81/hi, 1PO85, 1MF85, and 1MF86 under focused (upper plot) and grid (lower plot) sampling designs. Data were obtained by Monte Carlo simulations of sampling, and the resulting calculated values of total abundances for the stages 7-12 and 14-20 were then used to estimate the normal-exponential relationship between spawning season, abundance, and egg age.

Figure 40. Estimates for mortality during the incubation period, Z, obtained for the surveys 2MF81/lo, 2MF81/hi, 1PO85, 1MF85, and 1MF86 under focused (upper plot) and grid (lower plot) sampling designs. Data were obtained by Monte Carlo simulations of sampling, and the resulting calculated values of total abundances for the stages 7-12 and 14-20 were then used to estimate the normal-exponential relationship between spawning season, abundance, and egg age.

LIST OF TABLES

ADDENDUM

(written by Susan Picquelle, AFSC)

1. Variances of the C_i's may be estimated using standard statistical methods from probability sampling (Jessen 1978, Kendall and Picquelle (appendix 1) 1990). This method allows the sample units to have different probabilities of being selected for the sample, instead of equal probabilities as in a random sample. In this application, the sample units are the volume of water below 1 m^2 of surface area, and the probability of selection is determined by the size of the polygonal area.

$$(eq. 5a) \quad \hat{Var} \; C_i = \frac{J}{J-1} \sum_{j=1}^{J} \left(A_{ij} P_j - \frac{C_i}{J} \right)^2$$

This estimator is valid only if the P_j's are specified before the survey is conducted.

2. Another desirable feature of an error criterion is that it produces maximum likelihood estimates of the model parameters. To do this, it is necessary to know the statistical distribution of the error term in the total stage abundance model (eq. 7). The error term is not explicitly shown in equation 7, but is equal to the difference between the observed and predicted total stage abundance ($C_i - C_{i'}$) if it is an additive error term. If the

error term is multiplicative it is equal to the ratio of the
observed to the predicted total stage abundance (C_i/C_{i_1}). If
the errors are additive and distributed normally, then the
least squares error criterion leads to maximum likelihood
estimates. If the errors are multiplicative and have a log-
normal distribution, then minimizing the sum of the squared
log errors will give maximum likelihood estimates. If the
errors are additive and follow a double exponential
distribution, then minimizing the sum of absolute errors
produces maximum likelihood estimates (Draper and Smith
1981). However, in this analysis no assumptions were made
about the error distribution, hence, maximum likelihood
estimation was not possible.

3. This systematic underestimation of the older stage
    abundances may indicate that the model of constant mortality
    rate does not fit the data; perhaps the mortality rate
    declines with age of the egg. The total stage abundance
    model could be modified to allow mortality to be time-
    dependent by replacing Z in equation 7 with Z(t), where Z(t)
    is a hypothesized function that declines with t. This
    alternative model would more closely follow the steep
    decline of the early stage abundances without forcing the
    older stage abundances so close to zero. There are
    plausible biological mechanisms that would produce an age-
    dependent egg mortality rate; eggs with genetic defects die

first so that the only the more genetically fit eggs survive to the older ages, or perhaps it is related to the age-dependent depth distribution of the eggs (Kendall and Kim 1989).

4. The error term in the total stage abundance model would also have to be additive for the absolute difference criterion to be appropriate. Instead, the fitting errors appear to be proportional to the magnitude of the observed value, which suggests that the error term is multiplicative. An objective function on a log scale rather than an absolute scale is more appropriate for multiplicative errors.

5. This shortcoming might be overcome by recognizing that the error term in the total stage abundance model is probably multiplicative, not additive as is assumed for the unweighted squared error criterion. This would suggest log-transforming the total stage abundance model to convert the multiplicative error term to an additive term and then use the least squares objective function:

(eq. 8a) $\quad E = \sum_{i=1}^{I} (\ln(H_i) - \ln(H_{i,}))^2$

This would produce maximum likelihood estimates if the error term has a log-normal distribution.

Another approach would be to use weighted least squares,

where the weight applied to each total stage abundance is proportional to the inverse of the estimated variance about each stage abundance (Draper and Smith 1981). This would give more weight to those stages that are measured with greater precision, in this case the older stages, and would give less weight to the younger stages which are measured with less precision and also include most of the above-mentioned outliers.

6. Modifying the sample design during the survey in response to the observed data precludes the use of methodology from sampling theory to estimate variance (i.e. using eq. 5a to estimate the variance about C_i based on probability sampling is no longer valid). The resulting sample is a judgement sample and not a probability sample, which violates the basic assumption in sampling theory that the elements within a population are sampled with probabilities specified a priori (Jessen 1978).

7. In sampling theory, the sample is an accurate representation of the population if the sample is drawn with probabilities specified a priori (random sampling is a special case of this), assuming that the sampling gear is catching 100% of the target population contained in the sample unit, and assuming that the estimators employed are appropriate for the sample design. Here, accurate representation is defined

as unbiasedness, that is, if a sample was drawn many times
and a sample mean was computed for each sample (estimated by
the appropriate method), then the mean of the sample means
would equal the true population mean. Any one sample may
produce a mean that is quite different than the true mean;
the variability of the sample means determines the precision
of the estimate. Any one sample mean is an unbiased
estimate of the true mean, but it may be very imprecise.
If the sample mean is greatly influenced by a few extreme
observations, then the sample mean is imprecise, that is, if
the survey were repeated many times the sample means would
vary greatly depending on how many of the rare extreme
observations were contained in the sample. Hence it is
desirable to improve the precision of the sample mean and it
is important to be able to estimate the precision of the
estimated population mean.

The precision of the sample mean is a function of the survey
design, the sample size, and the inherent noise in the
population. Improvements in the precision of the estimated
stage totals in 1985 and 1986 were attained by improving the
sample design (as in 1MF85 and 1MF86) and because the egg
distribution was less noisy (patchy) than it was in 1981 (as
deduced by comparing the percent composition plots for 2MF81
and 1PO85 (Figures 27-29), both of which were grid surveys).
The improvement in sample design was achieved by increasing

station density in areas of high egg density, instead of
equal station density. The 1MF85 and 1MF86 surveys look
like probability samples, where the probability of a station
being selected for the sample is related to the egg
abundance at that station, however, they are actually
judgement samples because the sampling probabilities were
not specified a priori.

 Great improvements in the precision can be made if the
sample probabilities are highly correlated to the egg
abundance. The precision of the total stage abundances is
maximized when the polygonal stage abundances are all the
same (and the relative sizes of the fractional contributions
in the percent composition plot are all equal). This can be
seen by examining eq. 5a, the estimated variance about the
total stage abundance; when the polygonal stage abundances
$(A_{ij} P_j)$ are all equal then $A_{ij} P_j = C_i/J$ for every j and
$\hat{Var}(C_i) = 0$. Obviously this optimal sample design can never
be attained, but this does illustrate the mechanism for
increasing the precision of the estimate of total stage
abundance -- have small polygonal areas (hence high station
density and high sampling probabilities) in regions with
high egg density. However, in order to use the sample data
to estimate the variance about the estimated total stage
abundance, the sampling probabilities must be specified a
priori, otherwise eq. 5a is not valid. This requires

knowledge of the egg distribution prior to the survey. Some
information is available to predict (guess) what the egg
distribution will be, such as previous years' egg
distributions as indicated by the egg surveys, and the
observed distribution of the adult spawning population from
the immediately preceding hydro-acoustic survey of Shelikof
Strait.

8. In this application, focused sampling is in fact probability
    sampling. The location of the center of the focused survey
    is a random point within 1 km of the predetermined pivot
    point. Thus, the probability of each sampling unit being
    selected for the sample is known a priori, and is not
    modified during the course of the survey as was done during
    the 1MF85 and 1MF86 surveys. Recall that 1MF85 and 1MF86
    were judgement samples, not probability samples.

9. The effectiveness of focused sampling in reducing the
    variability is a function of how close the probabilities of
    selecting each sample unit are to being proportional to the
    egg abundance at each sample unit. That is, if the sample
    density is highly correlated to egg density, then the
    variability will be much less than the variability from the
    grid survey where the sample density is independent of egg
    abundance. Conversely, if sample density is negatively
    correlated to egg density, the variability will be larger

than that from a grid survey (Jessen 1978).

10. Another inconsistency is that the egg production estimates
     from Chapter 3 are an order of magnitude smaller than the
     estimates of egg production in Table 5. The estimates from
     Chapter 3 should vary randomly about the mean of the 100
     simulated egg production estimates, but instead they appear
     to be systematically much smaller.

11. The recommended survey design is a well-documented sampling
     methodology called probability sampling. It has the
     potential of greatly increasing the precision of the
     estimates of total stage abundance. This increase in
     precision is accomplished by reducing the variability in the
     polygonal stage abundances by using small polygonal areas
     where egg abundances are high. If the sampling pattern is
     specified prior to the survey and not modified during the
     course of the survey in response to observed egg abundances,
     then probability sampling theory provides an estimate of the
     variance about total stage abundances. Conversely, if the
     sampling pattern is altered during the survey, then the
     sample is a judgement sample and the methods from sampling
     theory no longer apply.