Quantifying and Disaggregating the Spawner Effect: Incorporating Stock Structure, Spatial
Distribution and Female Influences into Estimates of Annual Population Egg Production

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Abstract

The use of spawning stock biomass as a measure of potential egg production in fish
populations assumes that these two variables are related in a consistent way and that eggs
produced by all females have equal probabilities of surviving. We conducted sensitivity analyses
of egg production estimates to natural variations in population structure and reproductive biology,
including the influence of female traits on egg and larval characteristics. Uncoupling between
population egg production and spawning stock biomass left up to 25% of the variation in
modelled egg production unexplained for cod in the central Baltic Sea (ICES Subdivisions 25-32).
Correlated as well as random variations in model input parameters contributed to this uncoupling.
Resolving egg production spatially (by subdivision) showed that in some years substantial
fractions (up to 75%) of the total annual egg production were lost (in terms of recruit production)
because eggs were exposed to sub-optimal hydrographic (oxygen) concentrations. We conclude
that estimates of reproductive effort can be substantially improved with higher resolution
information and that inconsistencies between egg production and spawning stock biomass likely
confound attempts to isolate the causes of recruitment fluctuations.

Keywords: cod, egg production, spawning stock biomass, stock structure

Introduction

The total annual egg production of a fish population is theoretically one of the most important factors determining recruitment and catch options for an exploited fishery. However, direct in situ estimates of egg production (Alheit 1993, Matsuda et al. 1996) are expensive and not a routine component of many fish stock assessments (e. g., ICES 1997). Instead annual egg production is estimated indirectly with various types of models.

The simplest and probably most frequently used modelling approach is to estimate the biomass of spawning adults from the abundance, weight and maturity of fish in an assessment area. This approach when reliable provides relatively inexpensive and straightforward indices of the reproductive potential of a stock. However this method could potentially produce biased estimates of egg production because inputs such as maturity ogives and sex ratios are often assumed to be constant (e. g., ICES 1996) even though they can vary over time and space and between the sexes (Cooper 1983, Jørgensen 1990, Tomkiewicz et al. 1997). The magnitude or direction of such a bias is not well known, although for heavily exploited populations, it could result in a risk to the stock, particularly if the stock is already at a low level.

Nevertheless, even if the spawning stock biomass could be correctly estimated, recent studies show that the relationship between this variable and egg production is complex and varies between years due to interannual and size-related variations in individual relative fecundity (Marshall et al. in press). Moreover, egg production itself can be a misleading index of reproductive potential of a population because it assumes that all eggs produced by the population have equal probability of surviving to older developmental stages even though some females produce eggs and larvae of different viabilities (Marteinsdottir et al. 1993, Solemdal 1997, Nissling et al. in press) or release their eggs into environments whose hydrographic conditions affect survival probability (Heath and Gallego 1997, 1998). These observations suggest that simple indices of spawning stock biomass may give a misleading perception of the ability of a stock to produce new recruits.

In this study, we estimate the potential annual egg production of a heavily exploited fish stock (cod in the central Baltic Sea: ICES Subdiv. 25-32) and its sensitivity to natural variations in various model inputs (e. g., maturity ogives, sex ratios). We also evaluate the reliability of spawning stock biomass as an index of potential egg production and attempt to include female and batch effects on egg survival probabilities. Our analyses show that potential egg production is more sensitive to observed variations in fecundity-size relationships and sex ratios than to observed variations in maturity ogives, and that disaggregating total egg production by various criteria (e. g., female size, spawning site) could give improved estimates of the reproductive potential of a fish population. Simple estimates of spawning stock biomass may therefore not be reliable estimates of total egg production and reproductive potential in this and some other fish stocks.

Methods

General:

The basic input data necessary to calculate potential egg production in a fish population are numbers, sizes or ages of fish, sex , probability of being mature at different sizes or ages and a fecundity-size relation (e. g., Serebryakov 1990, Picquelle and Megrey 1993). Most of this information is available for Baltic cod, although in many cases, the data quality is questionable because sample sizes, the number of years covered or number of areas sampled is small (Bagge et al. 1994, Schnack et al. 1996). However, in other cases, there are multiple studies of the same topic (e. g., fecundity - size relations: Schopka 1971, Kosior and Strzyzewska 1979, CORE (1998); maturity ogives and sex ratios: ICES 1997, Tomkiewicz et al. 1997). Additional details on data handling, choice of parameter values and implementation are given below. All estimates of egg production refer to the potential number of eggs released, and therefore do not account for atresia or nonfertilization of released eggs for which little information is presently available for the Baltic.

Data sources and preparation:

i) Numbers, sizes, ages, sex ratios, female maturity ogives and spatial distributions.

The numbers, ages and mean weight-at-age of cod for Subdivisions 25-32 are available in ICES (1997). The abundance estimates are derived from VPA runs tuned by research vessel survey estimates. Weights-at-age are not presented on a sex-specific basis, and are assumed in our analyses to represent female weights. The potential bias associated with this assumption is evaluated below. Estimates of the spatial distribution of cod in the Baltic are available from research vessel surveys conducted every spring (prior to the main spawning period) since 1982. The three subdivisions of the central Baltic where cod are most frequently found each have at least one major spawning site (Subdivision 25: Bornholm Basin; Subdivision 26: Gdansk and southern Gotland Basins; Subdivision 28: central and northern Gotland Basin), and therefore disaggregation by subdivision potentially enables estimates of egg production to be resolved at the scale of specific spawning sites.

Tomkiewicz et al. (1997) estimated sex ratios and female maturity ogives for each subdivision by 4-5 year time periods for the years 1980-1996. All data were provided from research vessel surveys. The spatially explicit sex ratios, maturity ogives, and abundances enabled us to produce spatially resolved egg production estimates; in our case the scale of spatial resolution corresponds roughly to one or two spawning areas as defined above.

To produce sex ratios and maturity ogives that could be applied at the stock level, Tomkiewicz et al. (1997) weighted the sex ratios and maturity ogives by the spatial distribution of the stock in each subdivision before averaging. These stock-level ogives were used in most of our calculations.

ii) Fecundity - size relations

Individual fecundity data are available from five studies in different parts of the Baltic in different time periods (Table 1). These relations express total potential fecundity relative to body weight and the range in predicted fecundity based on these relations varies about 2-fold (Table 1).

It is not known which of the observed relationships differ statistically and whether some may be more applicable in some years or areas than others. Until these issues are addressed, it is difficult to determine which fecundity estimate to use in our analyses. In most of our calculations we assumed that the results for 1992 of CORE (1998) were applicable to all years in our time series because these data are approximately in the middle of the range of values available (Table 1). However to evaluate the sensitivity of population egg production to this assumption, we conducted analyses which used the maximum and minimum from the expected range of fecundities. In addition, for some of our analyses, we chose a random value from the entire range of estimates. We assumed that the range of fecundities for females of a given weight represented a normal distribution of possible fecundity estimates. The normal distribution used was derived by assuming the range midpoint equalled the mean, and the range extremes equalled the mean $\pm$ 2 standard deviations (Sokal and Rohlf 1981). A fecundity value was then randomly selected from this range to serve as the best estimate for the given body weight according to:

$$F = mean \pm sd*ran \qquad (eq.\ 1a)$$

where
mean = the range midpoint,
sd = range/4,
ran = standard random normal number

The random effect was held constant for all age-groups within a given year. This configuration assumes therefore that a positive random effect (equivalent to a "good-condition" year) affects all age groups, and that a negative random effect (equivalent to a "bad-condition" year) affects all age groups. Hence if the random effect for a given year was positive, a better than average fecundity estimate is obtained and vice versa for a negative random effect.

iii) Within-female batch effects on egg and larval characteristics. Female cod release their eggs in 10-20 batches during the spawning season (Kjesbu 1989, Kjesbu et al. 1996, Nissling et al. in press) and experimental studies (Nissling et al. 1994, Solemdal 1997, Nissling et al. in press) show that egg characteristics (e. g., sizes, viabilities, buoyancies, etc.) can differ between batches. We accomodated some of these differences when calculating the production of viable eggs and larvae. Details of the methodology are given below under "Model configuration".

Model configuration:

Potential egg production within an age (or size) group can be estimated as:

$$E(age|site) = nos.\ *\ p(mature)\ *\ p(female)\ *\ F \qquad (eq.\ 2)$$

where

E(age|site) = numbers of potential eggs produced by all mature females of a given age in a given

area;

p(female|site) = probability that a fish of age i is female in a given area;

p(mature|site) = probability that a female fish of age i is mature in a given area;

F = potential absolute fecundity for an individual fish (no. of eggs per female)

The population egg production within a site is the sum of egg production over all age groups:

E(site) = sumE(age|site), (eq. 3)

and the total egg production for the entire population is the sum of egg production in each site:

E(total) = sumE(site). (eq. 4)

We modified the simple model above to accomodate three additional processes or factors that affect population egg production. These processes are described below:

i) incidences of missed spawning by mature cod. The maturity ogives used by most assessment working groups (e. g., ICES 1997) represent the probability that fish of given ages or sizes will spawn in the coming year. However, this probability is not necessarily the same as the probability that a fish of a given age is sexually mature, which is another common interpretation of such ogives. These two probabilities can differ if the gonads of a sexually mature fish do not commence or complete gametogenesis in a given year. Studies of the gonadal development of cod show that a portion of the sexually mature population does not spawn every year (Oganesyan 1993, Burton et al. 1997), and that the spawning probability might depend on food conditions during the pre-spawning period (Oganesyan 1993). In practice, the maturity ogives which are available for Baltic cod have been determined by macroscopic visual inspection of the gonads and provide an estimate of the probability of spawning in the coming months. This probability is therefore the product of the probability of being sexually mature and having developing gonads:

P(spawn) = P(mature)*P(developing gonads)

The model shown above (eq. 1) assumes that the probability of all mature females will have developing gonads in a given year is 100%. Variability in the proportion of sexually mature females with developing gonads can be accomodated by multiplying this probability by those in eq. 1.

Incidences of missed spawning seasons in cod are generally poorly known but range from 7-100% for some size-groups of cod in some areas of the Barents Sea (Oganesyan 1993); unfortunately the number of fish sampled for these estimates is not known and the reliability of the proportions is uncertain. In an attempt to investigate how variations in the seasonal development of gonads (hereafter referred to as P{devgon}) might influence potential egg production we

assumed that an average proportion of all mature females would spawn in a given year. The mean and standard deviation of these proportions were arbitrarily set to 90% and 18% respectively. Hence for a given year, P(devgon) was defined for all age groups as

$$P(devgon) = .9 + .18*ran \qquad (eq. 5)$$

where ran = a standard normal random number, and P(devgon) $\leq$ 1.

These estimates of P(devgon) were used below when calculating individual fecundity.

ii) coupling between individual fecundity and cod spawning probability.

It is possible that in nature both relative fecundity and developing gonad probability will be above average in years when female condition is good and below average in years when female condition is poor because both variables seem to be related to condition and food supply (Oganesyan 1993, Burton et al. 1997). We allowed for the possibility that P(devgon) and fecundity were positively correlated in one series of our model calculations by directly coupling spawning probability to individual fecundity estimates. The coupling was done in two ways: 1) the same random number was used in calculating fecundity and developing gonad probabilities in equations 1a and 5; and 2) the individual fecundity estimates from eq. 1a were adjusted from their expected randomly chosen values by multiplying by p(devgon), i. e.:

$$F = P(devgon)*(mean \pm sd*ran) \qquad (eq. 1b)$$

In this way, developing gonad probability and individual fecundity are directly coupled within a given year. This coupling was incorporated in a separate series of our calculations (details below).

iii) female and batch effects on the production of viable eggs and larvae.

As indicated under "Data sources", egg and larval characteristics can differ within a female due to "batch effects". We investigated how differences in egg and larval viability between batches, and how the dependance of this relationship on female characteristics (e. g., size), might influence the level of viable egg and larval production. In Baltic cod, egg viability (i. e., hatch success *per se*) in the laboratory under suitable oxygen, salinity and temperature conditions varies independently of batch number during the spawning season, female spawning history (i. e., first-time vs. repeat spawners), female age and female size (Nissling et al. in press), and is on average 84.7 $\pm$ 11.1% (Nissling et al. in press). As a result, we did not consider variations in egg viability in further calculations.

However, based on relations between female size, egg size and larval survival, Nissling et al. (in press) have suggested that larval viability (i. e., survival to day 10 in the laboratory in the absence of food or predators) is related both to female size and batch number within a female. Survival to day 10 increases with female size and for batches produced early in a female's spawning season (Nissling et al. in press).

We evaluated the sensitivity of annual larval production to these female and batch effects using simulated larval survival probabilities which depended on female size and batch number

within the spawning season. Females were assumed to produce 15 batches of eggs and females were divided into two size classes (< or > 70 cm) representing younger spawners (including first and second time spawners) and well-established repeat spawners. Larval survival for eggs produced by the large females was assumed to be 90% for the first 3 batches and then to decrease linearly with batch number to 60% (Table 2). Larval survival for the small females was assumed to be 70% for the first 3 batches and then decrease linearly to 40% for the remaining 12 batches.

It is necessary to know the number of eggs that an individual female releases per batch during her spawning season ("batch fecundity"; Kjsebu 1989, Kjesbu et al. 1996) when estimating distributions of egg or larval characteristics produced by individual females. Batch fecundity estimaes are not available for Baltic cod. We assumed that the pattern of seasonal variation in batch fecundity observed by Kjesbu and colleagues (1989, 1996) for Arcto-Norwegian cod applies to Baltic cod. They showed that the temporal variation in batch fecundity differed between females and also within a female between years. In some cases, there was no apparent trend in batch fecundity, while in other cases batch fecundity tended to increase during the first several batches, after which it remained constant before declining during the last few batches. The ratio between the highest and lowest batch fecundities was about 5-7:1 in most cases. Based on these results, we constructed a schematic batch fecundity schedule for the proportions of a female's seasonal egg production represented by each batch (Table 2). These proportions were used to assign larval survival probabilities to the eggs that an individual female would release during each batch during a year.

The number of larvae surviving to day 10 from each size group of females was then summed within a year to estimate the total number of surviving larvae. Since ICES (1997) provides weight-at-age data, we converted the threshold body size of 70 cm to a weight of 3500 g using the length-weight regressions for female cod captured during the first quarter of the years 1968-1972 in the Bornholm and Gdansk Basins (Kosior 1976). The conversion to weight was preferred over conversion to age because length-at-age of Baltic cod has increased significantly during the last 10-15 years (Bagge et al. 1992) whereas there is presently no evidence to indicate that the length-weight relation has varied significantly between years.

Types of Analyses

1) Sensitivity to variations in single input variables.

Calculations were conducted to assess levels of variation in potential egg production for three important variables related to cod reproductive biology (sex ratio, maturity ogive, and potential fecundity). These variables were of particular interest: ICES (1997) has recently changed its maturity ogive and sex ratio for this stock because data for several more years and areas have become available (Tomkiewicz et al. 1997), and several authors (e. g., Rijnsdorp et al. 1991, CORE 1998, Marshall et al. in press) have shown that interannual fecundity variations can be significant in cod populations.

The combinations of data sets used in these calculations are shown in Table 3. When sex ratios and female maturity ogives were being varied ("key" variables), a mean fecundity estimate was used based on 1992 sampling. We used the mean and mean ± 2 standard deviations for both

sex ratio and female maturity from the database of Tomkiewicz et al. (1997) in sensitivity analyses of these variables. In addition, mean values for these variables from other data sources were also used in other analyses. When individual fecundity was the key variable, we used a random estimate of sex ratio and female maturity drawn from the time-period specific means and standard deviations given by Tomkiewicz et al. (1997).

We also conducted a simulation in which we used the Weber (1989) maturity ogive and an even sex ratio for all age-groups. This calculation uses the same ogive and sex ratio as previous Baltic assessment working groups (ICES 1996) and allows us to compare directly the magnitude of change in estimated egg production using the new and old data sets and methodologies.

2) Spawning stock biomass as a consistent index of egg production.

We hypothesized that if spawner biomass (as commonly estimated by assessment working groups) and egg production (calculated using input values having observed levels of random variation) were closely correlated there would be a consistently high correlation between these variables. Regressions of egg production vs. spawning stock biomass were produced and correlation coefficients, slopes and intercepts from the regression models were then compared.

In these comparisons, spawning stock biomass (ssb) was estimated according to ICES (1996):

ssb = (number-at-age) * (probability of maturity) * (weight-at-age).

This index employs a maturity ogive reported by Weber (1989) which has been applied to both sexes and for all years and subdivisions within the assessment. This ogive had been used by the Baltic Fisheries Assessment Working Group until 1997.

Two types of egg production estimates were developed for these calculations:

i) coupled random variation in fecundity and developing gonad probability values. 20 different time series of random numbers were obtained from SAS (1985) and used in eq. 1b and 5 to estimate fecundity and developing gonad probability. Each series of random numbers for these variables consists of 31 random numbers corresponding to each year in our time series; each random number within a series signifies a simulated "good" or "bad" condition year for all age-classes. For a given year within a time series, the same random number was used in both equations 1b and 5 for all age-groups.

Input parameter values for the female maturity ogive and sex ratio were also chosen randomly. Random numbers were selected from the mean and standard deviation of the stock-level ogives and sex ratios calculated for different time periods by Tomkiewicz et al. (1997). For these variables, each of the 20 time series consisted of 217 (= 31 years x 7 age-classes) randomly chosen numbers. Hence each age-group in each year was assigned two random numbers based on the time-period and age-specific means and standard deviations compiled by Tomkiewicz et al. (1997); one of these random numbers was used to calculate the probability that the fish was a female.(sex ratio) and the second (independent) random number was used to calculate the

probability that the female was sexually mature.

ii) the same calculation as in i) but assuming that fecundity and gonad development probability were not coupled (i.e., P(devgon) = 1). The regression analyses and comparisons done in i) were then repeated and compared with results in i) above.

3) Within-female "batch effects" on viability of eggs and larvae

Batch effects on larval viability were assessed for two scenarios of larval survival dependance on batch number within a female. Details of the batch survival schedules and analyses conducted are given under Model Configuration.

In these calculations, the mean time-period specific female maturity ogives and sex ratios (Tomkiewicz et al. 1997) were used. The 1992 fecundity-weight relation of CORE (1998) was applied for all years in the time series.

4) Spatial variability in total potential egg production.

We derived spatially explicit estimates of annual egg production for the stock because some spawning areas within the assessment area in some years have little chance of supporting egg development due to low oxygen levels at the depths where cod eggs are neutrally buoyant (Plikshs et al. 1993, Wieland et al. 1994, Nissling et al. 1994, MacKenzie et al. submitted). In addition, the level of predation on cod eggs likely varies between spawning areas due to hydrographically-induced differences in the vertical overlap of predators and prey (Köster and Schnack 1994).

Egg production in each of the three main subdivisions of the Baltic Proper were calculated using spatial distributions of adult cod (ICES 1997) and subdivision-specific female maturity ogives and sex ratios (Tomkiewicz et al. 1997). The fecundity relation used for these calculations was a random estimate based on the 5-model range described above. The proportion of the total egg production contributed by each area was calculated for each year.

Results:

1) Sensitivity to variations in single input variables.

Differences in sex ratio between studies resulted in differences in egg production up to ~35% (i. e., 100*(upper estimate B lower estimate)/lower estimate) when all other model inputs were held constant (Fig. 1a). In particular, assuming a 1:1 sex ratio for all age groups results in considerably lower rates of egg production than if sex ratios are permitted to vary with age. When sex ratios are age-specific, variability in egg production rates is much lower (< 10% range based on the mean ± 2 st. dev. from Tomkiewciz et al. 1997). Egg production estimated using the Berner and Vaske (1981) and mean Tomkiewicz et al. (1997) sex ratios were nearly identical, but both were higher than those estimated using the Kosior and Skolski (1992) sex ratios.

The sensitivity of egg production to female maturity ogives was similar to that seen for

different sex ratios (Fig. 2). The variability in the range of egg production estimated using the mean and 2 st. dev. of the Tomkiewicz et al. (1997) maturity ogive was about 7% (Fig. 2). However, if the Weber (1989) or Kosior and Skolskii (1992) ogives were used, egg production was 15-20% higher than the estimate based on the mean ogive from Tomkiewicz et al. (1997).

The results for both the sex ratio and maturity ogive analyses show that the egg production estimated using an even sex ratio and the Weber ogive lie respectively below and above the ranges encompassed by those obtained using the mean ± 2 st. dev of the Tomkiewicz et al. inputs (Fig. 1, 2). As a result, egg production rates calculated using the Weber (1989) ogive and an even sex ratio is nearly identical to that calculated using the mean sex ratio and maturity ogive of Tomkiewicz et al. (1997; Fig. 2).

Egg production rates appeared to be more sensitive to variations in fecundity than sex ratio or maturity ogive (Fig. 3). The upper limit of the range spanned by the 5 fecundity-weight models was 70-80% higher than the lower limit.

2) coupled variations in fecundity-size relations and spawning probability, and comparison with spawning stock biomass.

These analyses used random estimates of maturity and sex ratio based on the means and standard deviations given by Tomkiewicz et al. (1997). When egg production time series were estimated from 20 realizations using 20 different randomly-selected fecundity and spawning probability estimates, regression analysis showed that egg production was in all cases significantly correlated to spawning stock biomass. However, the correlation coefficient (R^2) was only ~75%, indicating that 25% of the variation in egg production became uncoupled from the spawning stock biomass estimate (Fig. 4). A regression analysis of the 620 egg production estimates (i. e. 31 years x 20 random estimates per year) vs. spawning stock biomass showed that 72% of the variation in these egg production series could be explained by spawning stock biomass (Fig. 5), and that the regression model predictions were outside 2-standard error ranges for nearly half of the 31 estimates of mean egg production (Fig. 5).

When the same analysis was repeated for the case where spawning probability was assumed to be 100%, the correlation between spawning stock biomass and egg production increased to 85% (Fig. 4).

3) Female and batch effects on the production of viable eggs and larvae.

The production of 10-day old larvae is assumed to represent one measure of egg and larval viability in Baltic cod (Nissling et al. in press). The time series of age 10 larval production follows closely and is highly correlated with the time series of egg production, and on average represents ca. 58% of the total number of eggs produced (Fig. 6). It should be noted that the data after 1983 are more reliable than those before because in the earlier years ICES (1997) used constant weight-at-age data for the years 1966-1982. For the two extreme years in the period 1983-1996, we compared the number of age 10 larvae produced by the two size-groups of females. This comparison showed that the smaller size group produced 23.9 and 46.7 trillion 10-day old larvae, or 73 and 96 % of the total number of age 10 larvae, in 1991 and 1996 respectively (Fig. 7a).

Since these results are likely sensitive to the particular batch fecundity proportions and

batch survival schedules that we used, we repeated the calculations assuming a more extreme female effect on larval survival to investigate how the contribution of the older females to total age 10 larval production would change. For this series of analyses we assumed that batch survival probability of *all* eggs produced by females < and > 3500 g was respectively 25% and 100%. In this case, and as expected, the contribution of the larger females to total age 10 larval production increased to 52 and 10 % for 1991 and 1996 (Fig. 7b). However, age 10 larval production estimated assuming the extreme-case larval viability schedule was highly correlated to both total egg production (R^2 = 96%) and age 10 larval production estimated assuming the larval viability schedule from the first series of analyses in which viability depended also on batch number (R^2 = 97%).

4) Spatial variability in total potential egg production.

The time series of potential egg production in three subdivisions of the Baltic Proper showed that there are large spatial differences in the contribution of the different areas to the total production, and that these contributions have changed in relative terms over time (Fig. 8a, b). In the beginning of the series (from 1982) egg production was dominated by Subdivision 28 (60-70%), but this contribution has fallen to about 5% during the last 15 years (Fig. 8a, b). In contrast, egg production in Subdivision 25 has remained comparatively stable (20-60 trillion eggs/year), although its contribution as a proportion of the total has increased from about 15% to 40-50%. Egg production in Subdivision 26 decreased slowly during the 1980's and dropped further in the early 1990's; the total change was from about 30 to 8 trillion eggs/year. However, egg production in this area has increased in 1995 and 1996 to the highest levels in the period, and the relative contribution to total egg production has now increased to about 30% from 8-15% during the 1980's.

Discussion

Annual population egg production estimates for central Baltic cod have undergone major fluctuations during the last 31 years. The temporal pattern of these fluctuations appears similar regardless of which input time series is used and therefore seems robust to the choice of most input parameters considered. However, the range in egg production for a given spawning stock biomass can be seen to vary by >50%, particularly due to interannual differences in individual fecundity. These results support recent findings for Barents Sea cod by Marshall et al. (in press) who found that large differences in egg production for a given spawning stock biomass occur depending on the demographics and condition of the population. Improved estimates of population egg production can therefore probably be achieved by estimating individual fecundity and atresia more regularly than has been done in the past (see also Marshall et al. in press).

We emphasize that our estimates of egg production variability for a given level of spawning stock biomass should probably be considered as conservative. Most of our calculations used mean values for model inputs whereas in nature, these inputs are variable; inclusion of this variability in our analyses would have resulted in a higher degree of uncoupling between egg production and spawning stock biomass. For example, in one series of simulations using random

fluctuations in model inputs, a typical estimate of spawning stock biomass left ~25% of the variation in modelled egg production unexplained. Improved estimates of egg production may therefore increase the reliability of stock-based recruitment predictions (Marshall et al. in press), and could potentially allow identification of environmental processes affecting recruitment and the way these processes interact with stock structure.

Most of our calculations involved variations in only one parameter at a time; this practice enabled us to interpret variations in the given input relatively easily. However in nature, two or more parameters can vary simultaneously. Variations in these parameters could be correlated, or independent of each other. In cases where the variations are correlated, true interannual fluctuations in egg production could be dampened or enhanced depending on the nature (e. g., positive vs. negative, strength, magnitude, linearity) of the relationship between variables.

We attempted to represent one example of a possible coupled variation in input parameters (i. e., spawning probability and individual fecundity). This example used literature sources to infer a link between individual fecundity, spawning probability by sexually mature females, and indirectly the overall condition of the female. Although this link is presently poorly documented, our analyses showed that coupled variations between spawning probability and fecundity can contribute to residual variation in the relation between spawning stock biomass and estimated population egg production. The amount of residual variation depends both on the choice of parameter values (e. g., mean and standard deviation of spawning probability) and the way variables are related to each other; alternative choices which might better represent true values in nature could result in higher levels of residual variation.

Other such couplings between variables that affect population egg production rates exist in nature (e. g., relations between atresia and fecundity; growth rates and maturity ogives) but in most cases empirical relationships between the variables are too poorly documented, or theoretical models (e. g. fish bioenergetics: Ney 1993) of how such variables might fluctuate are too parameter-rich (in comparison to data compilations available in stock assessment working group reports), to be included in models of egg production. Nevertheless simple indices of egg production such as spawning stock biomass (as estimated by ICES 1996 and many other assessment working groups) that neither accomodate correlated variations in input parameters, nor interannual variations in fecundity (Marshall et al in press), will likely yield biased estimates of the reproductive potential of a population

Our preliminary analyses involving batch and female effects on larval viability showed that the number of viable 10-day old larvae produced by the population was strongly correlated to the total number of eggs produced by the population. The strength of this result was partly unexpected because we had hypothesized that different population structures would have produced larger differences in the production of viable 10-day old larvae.

The high correlation between egg and viable larval production in this specific case is probably a consequence of two inter-related factors. First, our representation of the relationships between female size, batch fecundity and batch viability is based on a modest number of laboratory experiments with both Baltic and Arcto-Norwegian cod. Although this representation was intended to reflect the main experimental results, it does not fully reflect the variation or pattern of these relationships. In addition, many of the experimental results have been obtained with a limited number of females and female characteristics (e. g., sizes, ages, reproductive

histories). This results in low statistical power to detect differences between experimental groups (Peterman 1989). Patterns which may exist in nature may therefore be difficult to resolve in laboratory situations with limited sample sizes. In this case, methods to extend or link the laboratory results that have been derived from modest numbers of females and characteristics to entire field populations could be particularly useful.

Second our configuration of the relationship between larval viability and female size assumes a threshold effect on larval viability at a female size of 70 cm. If further investigations with a wider range of female sizes show that the relationship between female size and larval viability is, for example, linear, the influence of population size structure on viable larval production could become more apparent. Hence our intepretations of the influence of population size structure on viable larval production must be considered as preliminary until more experimental results become available.

When comparing the effects of different sex ratios and female maturity ogives on population egg production, we found that the change in sex ratio and maturity ogive from the Weber (1989) compilation (which was used by Baltic assessment working groups from 1989-1996; ICES 1996) to the Tomkiewicz et al. (1997) compilation resulted in an apparent decrease in annual egg production by 15-20%. Reasons for the differences in sex ratios and ogives between time periods are unclear and require further investigation. However, the largest difference in these comparisons of modelled egg production was found among those involving the sex ratio and maturity ogive from Kosior and Skolskii (1992). This difference is probably due to sampling methods for the sex ratio and maturity data. The data collected by Kosior and Skolskii (1992) were obtained from commercial fishing vessels in Subdivision 26, whereas the other data were obtained from research vessel surveys. Cod in the Baltic (Chrzan 1950, Tomkiewicz et al. 1998) and elsewhere (Morgan and Trippel 1996) form sex-specific aggregations at and near spawning areas. These aggregations are the main target of the directed cod fishery in the Baltic (Bagge et al. 1994). Also, in the Baltic males arrive at and remain in spawning areas longer than females and are vulnerable to commercial fishing gear for longer periods than females (Chrzan 1950). As a result the sex ratio and maturity ogives obtained by Kosior and Skolskii (1992) probably represent reproductive characteristics of the catch more accurately than those for the stock as a whole. While these data can be applied in other contexts (e. g., effects of fishing activity on egg production), they could introduce a bias to *stock* egg production estimates if applied to the stock.

As described in the Introduction, there is growing evidence to suggest there may be systematic differences in the contributions to survival and recruitment that females within a given population can make. These differences can arise from a variety of factors, including the location and timing of spawning relative to the locations of favorable hydrographic conditions for egg development (Heath and Gallego 1997). Our spatially-resolved time series of egg production estimates show that egg production among the Subdivisions and spawning areas has varied greatly over the last 15 years. This variation is likely important for the successful reproduction of the stock; oxygen conditions vary spatially and temporally in the Baltic (Plikshs et al. 1993) and the range of these variations includes that which threatens the survival of cod eggs (Wieland et al. 1994).

Comparison of the available suitable egg habitat in different spawning areas (Plikshs et al. 1993, MacKenzie et al. submitted) with the distribution of egg production shows that in some

years large proportions of the annual egg production can have little or no chance of survival. For example during 1981 and 1982, conditions in the Gdansk Basin, and the southern and central Gotland Basin are not expected to have permitted cod eggs to hatch (Plikshs et al. 1993, MacKenzie et al. submitted). During these years, ~75% of the population egg production occurred in these areas. This mismatch of egg production with suitable conditions for egg development is believed to be a major reason for the decline in recruitment during the early 1980's despite high levels of egg production (Sparholt 1996, Jarre-Teichmann et al. in press, MacKenzie et al. submitted).

In this context, we note that interactions between the size/age composition of the stock and hydrographic conditions will also likely affect egg production and survival. Nissling et al. (1994) and Vallin and Nissling (submitted) have shown that egg buoyancy in Baltic cod depends on female size and batch number within the female. Egg buoyancy is critical to the survival probability of cod eggs in the Baltic because buoyant eggs have a higher probability of exposure to oxygenated water in the upper layers of the water column than less-buoyant eggs (Nissling et al. 1994). In years when oxygen concentrations in deep water are low, denser eggs will likely have a higher anoxia-related mortality rate than eggs of higher buoyancy (Nissling et al. 1994; Vallin and Nissling submitted); however, in years when oxygen conditions are sufficient for egg development or if adults migrate to areas where oxygen conditions are sufficient, the difference in survival between eggs of different buoyancy will probably be less. These relationships indicate that stock structure, stock spatial distribution and environmental conditions interact in ways that can have a major impact on the fate of eggs produced by the stock, and the ability of the stock to produce new recruits.

Although we have evaluated the sensitivity of egg production estimates to natural levels of variation in some key model inputs, and have investigated ways of incorporating higher resolution information (e. g., spatial distribution of adults, batch effects on larval viability) into these estimates, there are several other variables and relationships which we have not considered. For example, weight-at-age differs between the sexes in the Baltic for the years 1989-1998, particularly among ages 7+ (ICES 1998a). Our analyses used combined-sex weights-at-age as compiled in the standard assessment (ICES 1997) and are probably closely correlated to what would be expected had we used female weights-at-age, especially since the numbers of females older than age 7 is small in the Baltic (ICES 1997).

Lastly there may be important effects of male reproductive biology on the production of viable fertilized eggs. For example, male sperm quality can vary with salinity in the Baltic (Westin and Nissling 1991) and male spawning probability is variable (Oganesyan 1993). Moreover if cod spawning behaviour (Brawn 1962) includes size-assortive mating, then the skewed sex ratios at older ages (and bigger sizes) may result in production of a large portion of unfertilized eggs by large females if large females mate with small males (see also Morgan and Trippel 1996). These aspects of cod spawning behaviour are however unknown and merit further study.

Consequences for stock management:

Stocks which are below or near minimal biologically acceptable limits (sensu FAO 1995) may require a more cautious exploitation and assessment approach than has been used in the past.

Aside from a reduction in overall fishing effort (assuming that this can be implemented), this approach might include application of more scientific knowledge (Ulltang 1996) to minimize the risk of inadvertent overfishing. In the case of egg production, this knowledge might include additional information (e. g., improved sampling for model inputs, better understanding of reproductive biology) related to the coupling between spawning stock biomass and egg production.

In the case of cod in the central Baltic, one such approach might be to adopt a strategy which ensures that the vast majority of fish have a chance to reproduce at least once during their lifetimes. According to the most recent maturity ogive (Tomkiewicz et al. 1997), by the time female cod reach age 6, 95% have probably spawned at least once (Fig. 9). However, age-specific fishing mortalities (ICES 1997) during much of the 1980's and early 1990's have been so high on younger age groups that many fish are captured before having spawned or reached age 6+ (Fig. 9).

Exploitation of immature cod in the Baltic has occurred since at least the 1940's (Chrzan 1950). Estimated fishing mortality rates and effort levels are believed to be lower at that time than in recent decades (Bagge et al. 1994) and the stock could probably sustain itself despite the exploitation of juveniles. However management strategies that include both high fishing mortality rates and exploitation of immature fish are not likely sustainable on a long-term basis (Cook et al. 1997; ICES 1998b). If minimum legal size was increased, more fish would have the opportunity to reproduce at least once; this would increase the total egg production and probably improve the chances of long-term sustainability. We note also that cod at older ages approach sizes which increase larval viability and buoyancy of the eggs. An increase in minimum legal size would therefore appear to have several positive benefits for the long-term reproductive success of this population. Conversely, removing fish before they reach sexual maturity imposes several risks (lower egg production, larval viability and egg buoyancy) to long-term population sustainability.

Conclusions:

We have shown that modelled egg production per unit spawning stock biomass can vary both with population structure and reproductive biology in central Baltic cod. These variations occur for other fish populations and contribute to the difficulty in predicting recruitment using stock parameters and environmental variables. Development and implementation of egg production models which account for within and between female differences in reproductive biology (e. g., fecundity, spawning time and location) and egg characteristics may reduce the risk of inadvertent overfishing.

Acknowledgements:

Table 1. Relationships between individual fecundity (numbers of eggs) and body weight (g) for Baltic cod.

Reference	Relationship	Sampling Years	Subdiv.
Schopka 1971	$F = 859*W^{0.9936}$	1968	24, 25
Kosior & Strzyzewska 1979	$F = 526*W + 173.8$	1959-1962	26
Bleil & Oberst 1996	$F = 558.07*W + 186279$	1994	25
CORE 1998	$F = 697.93*W - 75182$	1992	25
CORE 1998	$F = 841.73*W + 12666$	1996	25

Table 2. Assumed relative batch fecundities (proportion of an individual cod's total egg production produced in each batch during a spawning season) and larval survival probabilities to age 10 for female cod < and > 3500 g.

Batch Number	Relative Batch Fecundity	Batch Larval Survival Probability (female wt. < 3500 g)	Batch Larval Survival Probability (female wt. > 3500 g)
1	.015	.7	.9
2	.04	.7	.9
3	.055	.7	.9
4	.07	.675	.875
5	.08	.65	.85
6	.08	.625	.825
7	.08	.6	.8
8	.08	.575	.775
9	.08	.55	.75
10	.08	.525	.725
11	.08	.5	.7
12	.08	.475	.675
13	.0725	.45	.65
14	.06	.425	.625
15	.0475	.4	.6

Table 3. Summary of combinations of data sets used in egg production modelling analyses. Maturity ogives are for females unless noted otherwise.

Input varied	Fecundity relation	Maturity ogive	Sex ratio
Age specific sex ratio	1992 data (CORE 1998)	Tomkiewicz et al. (1997; mean)	(Tomkiewicz et al. 1997; mean $\pm$ 2 SD)
			Kosior & Skolskii (1992)
			Berner & Vaske (1981)
			Even (1:1)
Maturity ogive	1992 data (CORE 1998)	Tomkiewicz et al. (1997; mean $\pm$ 2 SD)	Tomkiewicz et al. (1997 mean)
		Kosior & Skolskii (1992; mean)	
		Weber (1989; combined-sexes)	
		Weber (1989; combined-sexes)	Even (1:1)
Fecundity-size	random estimate from 5-model range (Table 1)	Tomkiewicz et al. (1997; mean)	Tomkiewicz et al. (1997; mean)
	upper limit of 5-model range (Table 1)		
	lower limit of 5-model range (Table 1)		

Figure Captions:

Figure 1a, b. Annual potential egg production for cod in ICES Subdivisions 25-32 assuming different age-specific sex ratios (probability of a cod being female) and CORE (1998) fecundity-weight relationship for 1992. Population numbers and size at age data from ICES (1997); maturity ogive data from Tomkiewicz et al. (1997).

Figure 2a, b. Annual potential egg production for cod in ICES Subdivisions 25-32 assuming different female maturity ogives and CORE (1998) fecundity-weight relationship for 1992. Population numbers and size at age data from ICES (1997); sex ratio data from Tomkiewicz et al. (1997) unless noted otherwise.

Figure 3. Annual potential egg production for cod in ICES Subdivisions 25-32 different fecundity – weight relationships. The upper and lower ranges show egg production assuming the highest and lowest values from a range based on five fecundity - weight relations (Table 1). The random egg production estimate used a random fecundity value within the range defined by the 5 models in Table 1. Female maturity ogive and sex ratio from Tomkiewicz et al. (1997); population numbers and size at age data from ICES (1997).

Figure 4. Correlation coefficients and regression model slopes for the relationship between population egg production and spawning stock biomass for 20 randomly derived estimates of egg production. Spawning stock is estimated from weight-at-age and a constant combined-sex maturity ogive (Weber 1989). Egg production is estimated assuming temporally-varying maturity ogives and age-specific sex ratios (Tomkiewicz et al. 1997) which allowed for random variation; fecundity is a random estimate based on the five models listed in Table 1. A. Egg production assumes that spawning probability by mature females is 100%. B. Egg production assumes that spawning probability by mature females = 90% (st. dev. = 18%) and that fecundity is coupled to spawning probability. See text for additional details.

Figure 5. Decoupling between population egg production and spawning stock biomass for cod in ICES Subdivisions 25-32. Spawning stock is estimated from weight-at-age and a constant combined-sex maturity ogive (Weber 1989). Egg production estimates were derived assuming a random fecundity estimate (see text for details) coupled to a hypothetical randomly chosen spawning probability; maturity ogives and sex ratios were randomly chosen from Tomkiewicz et al. (1997). Each egg production estimate for a given level of spawning stock biomass is a mean of 20 randomizations (see Fig. 4b). The regression model shown uses all 620 pairs of observations (31 years x 20 runs); in the panel means and standard errors are shown for clarity.

Figure 6. A. Time series of population egg production and age 10 larval production for cod in

ICES Subdivisions 25-32. B. Age 10 larval production expressed as proportion of total egg production. Larval production estimates assumed viabilities that depended on female size and batch number. See text and Table 2 for details.

Figure 7. Number and percent of viable 10-day old larvae produced by cod < and > 3500 g in 1991 and 1996 in the ICES Subdivisions 25-32. Calculations used female maturity and sex ratio data from Tomkiewicz et al. (1997), fecundity – size relation for 1992 from CORE (1998), and numbers and weight-at-age data from ICES (1997). A. Calculations assumed batch fecundities and larval survival probabilities to age 10 followed schedules given in Table 2. B. Calculations assumed that larval survival to age 10 was 25% and 100% for the smaller and larger females respectively.

Figure 8. A. Annual potential cod egg production in three ICES Subdivisions (25, 26, and 28) of the central Baltic Sea during the years 1982-1996. Calculations used maturity ogives and sex ratios from Tomkiewicz et al. (1997) and a random fecundity estimate based on 5 Baltic cod fecundity - weight relations (Table 1). B. Proportion of potential cod egg production in the three ICES Subdivisions (25, 26, and 28) of the central Baltic Sea during the years 1982-1996. Calculations used same inputs as panel (A).

Figure 9. Fishing mortality rates for ages 4-7 (ICES 1997) and probabilities that female cod in the eastern Baltic (ICES Subdiv. 25-32) have spawned at least once in their lifetimes. P(repeat spawner) at age t is assumed equal to P(mature) at age t – 1. A spatially-averaged female maturity ogive for the years 1995-1997 was used (Tomkiewicz et al. 1997).
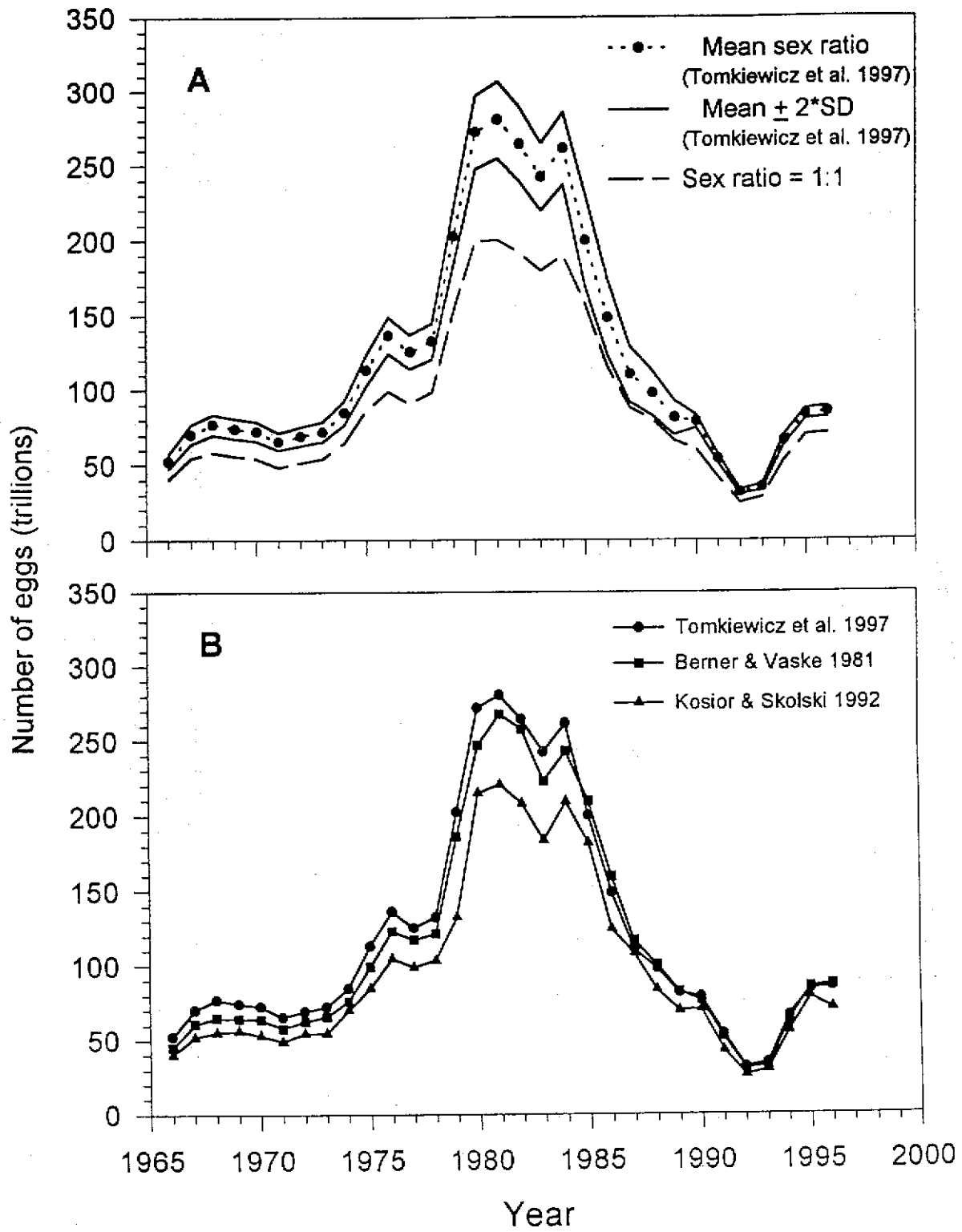
Effects of Age-Specific Sex Ratio Variability
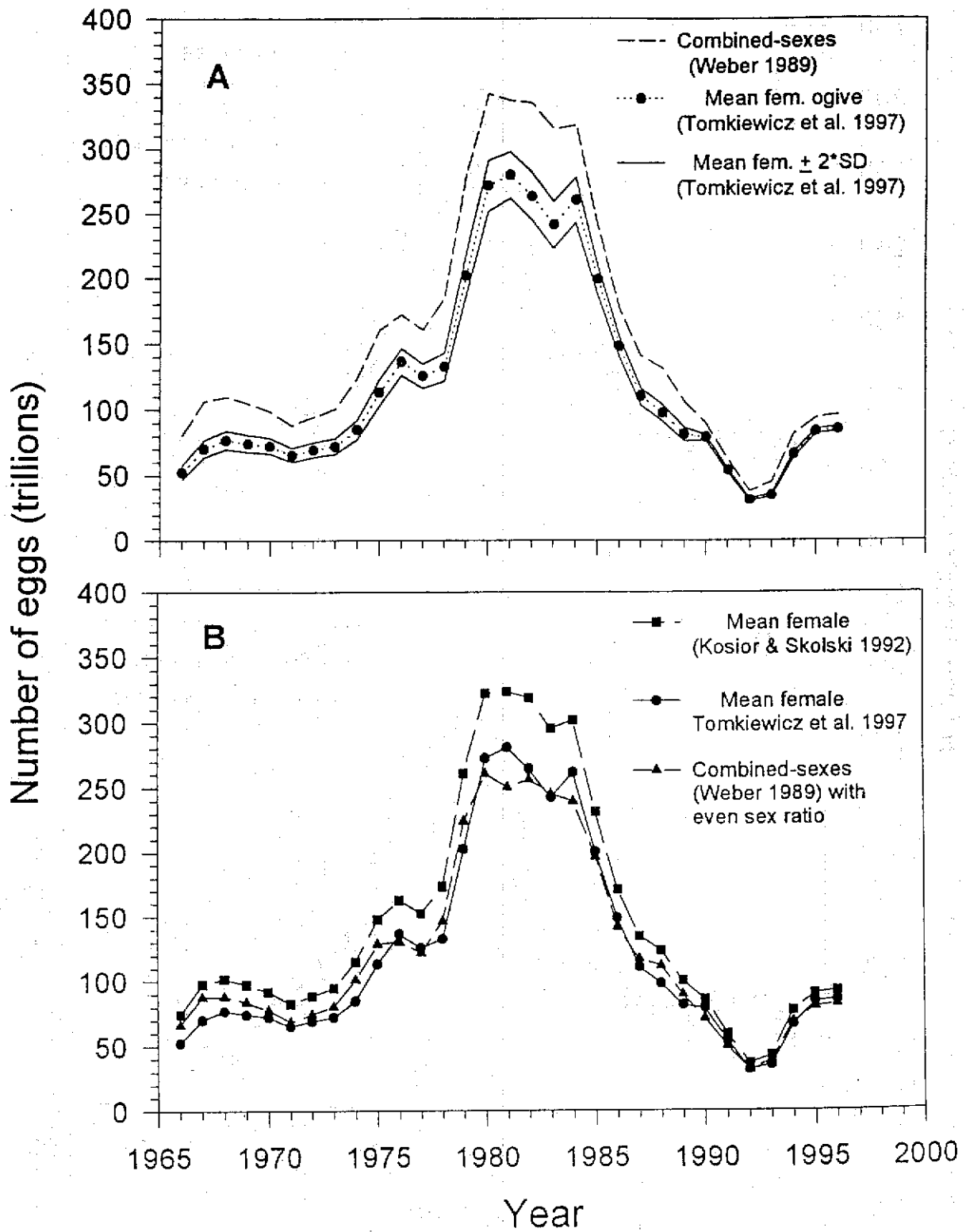

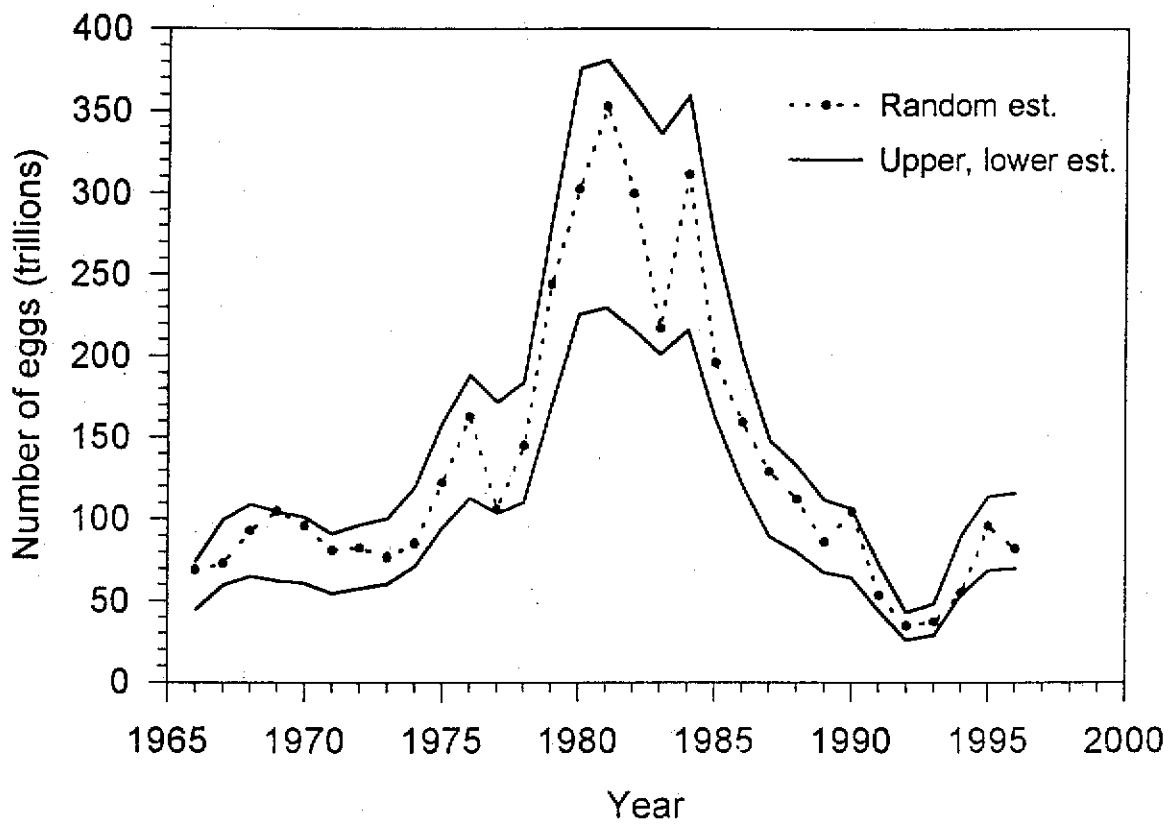Fig. 1
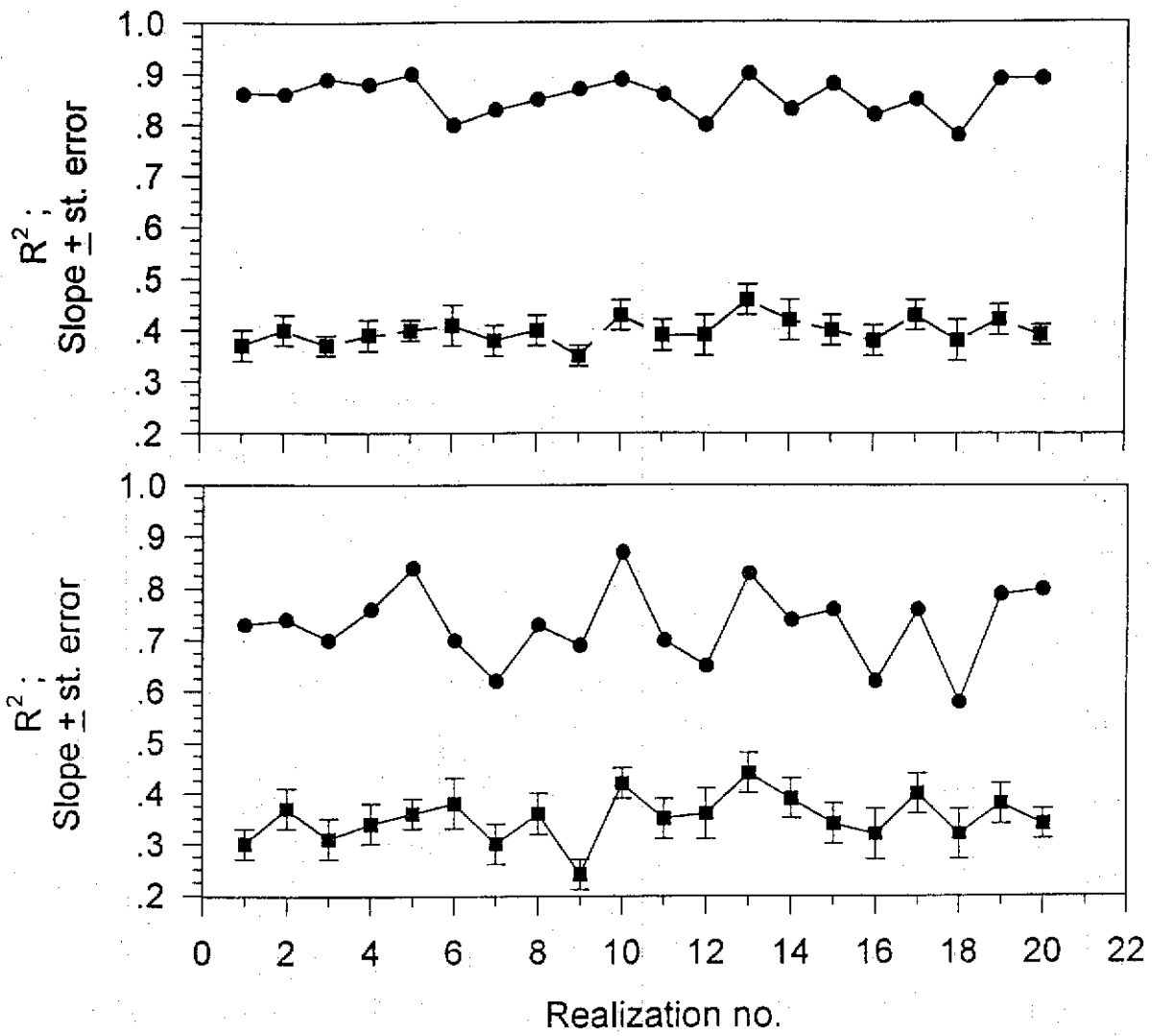
Effects of Variability of Maturity Ogives

Fig. 2

Fig. 3

Fig. 4 a, b

R² = 72%; P < 0.0001

E = 0.35*SSB - 9.5

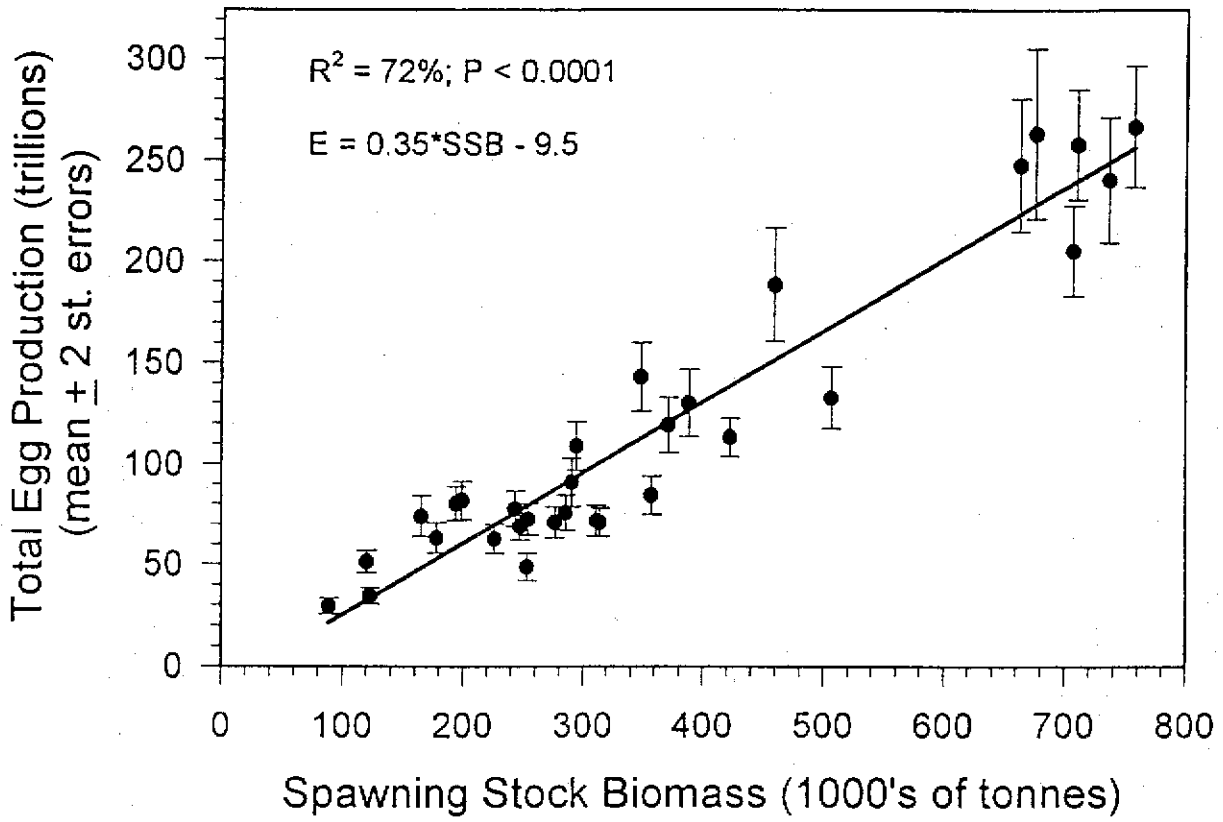Total Egg Production (trillions) (mean ± 2 st. errors)
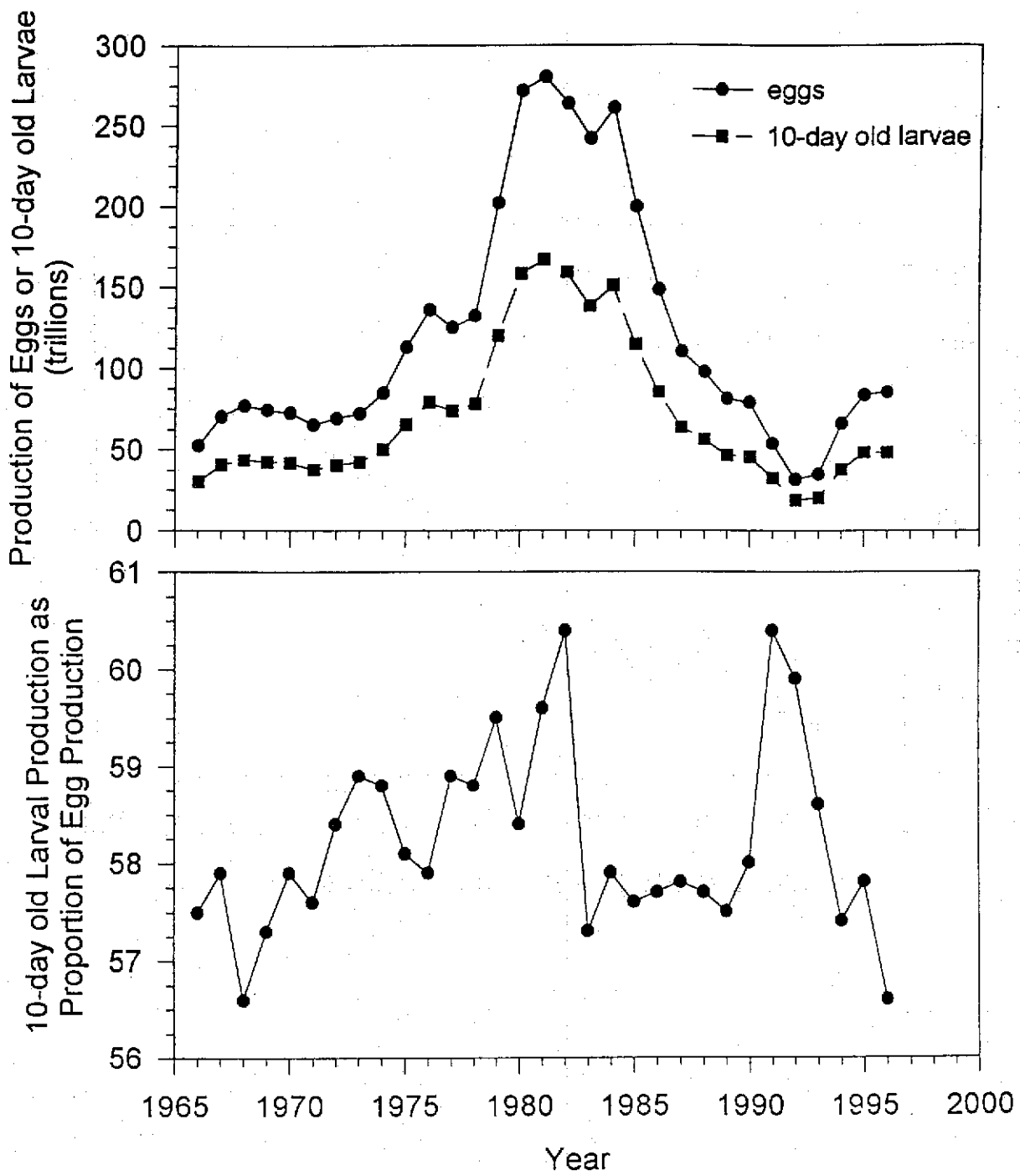
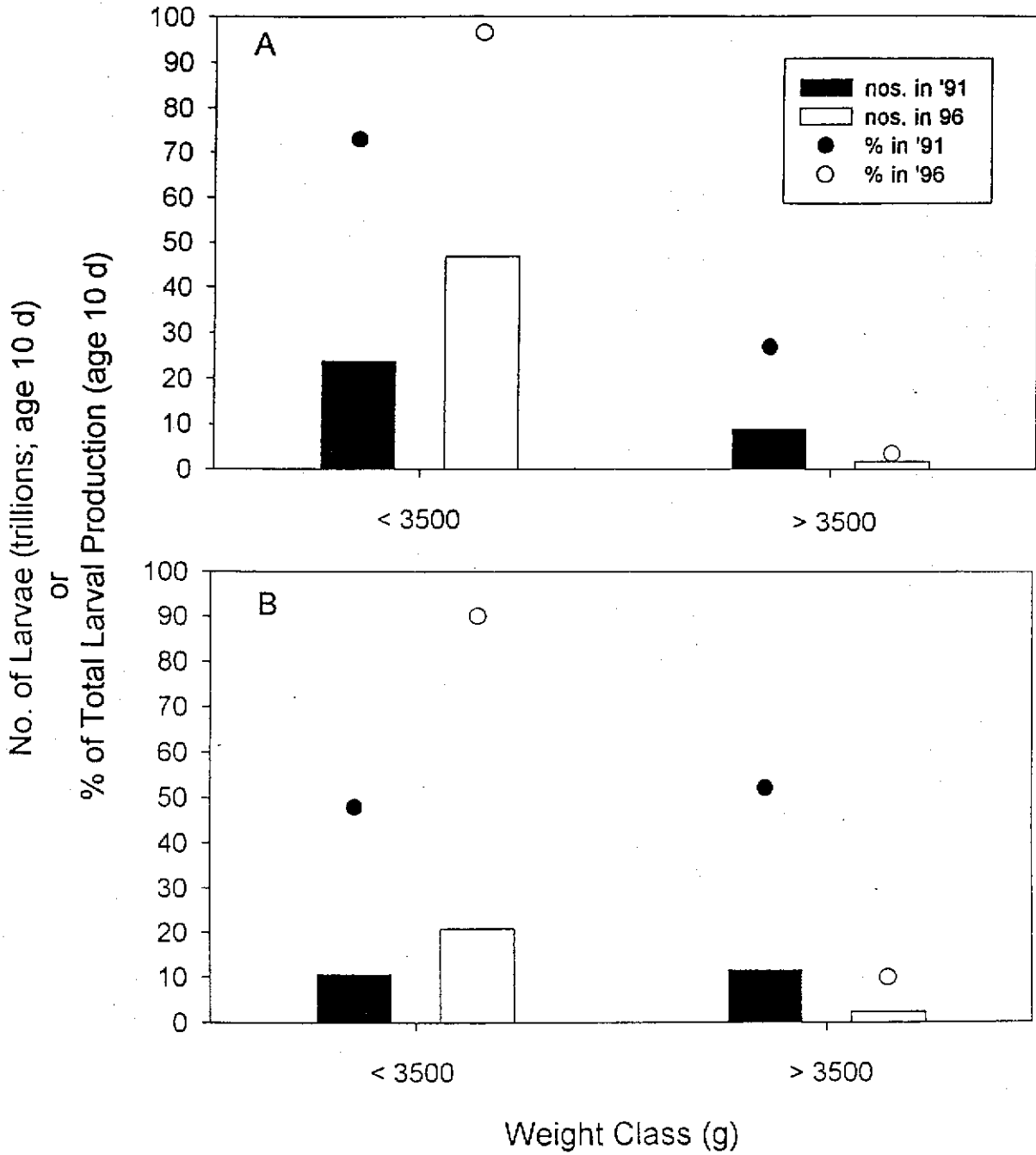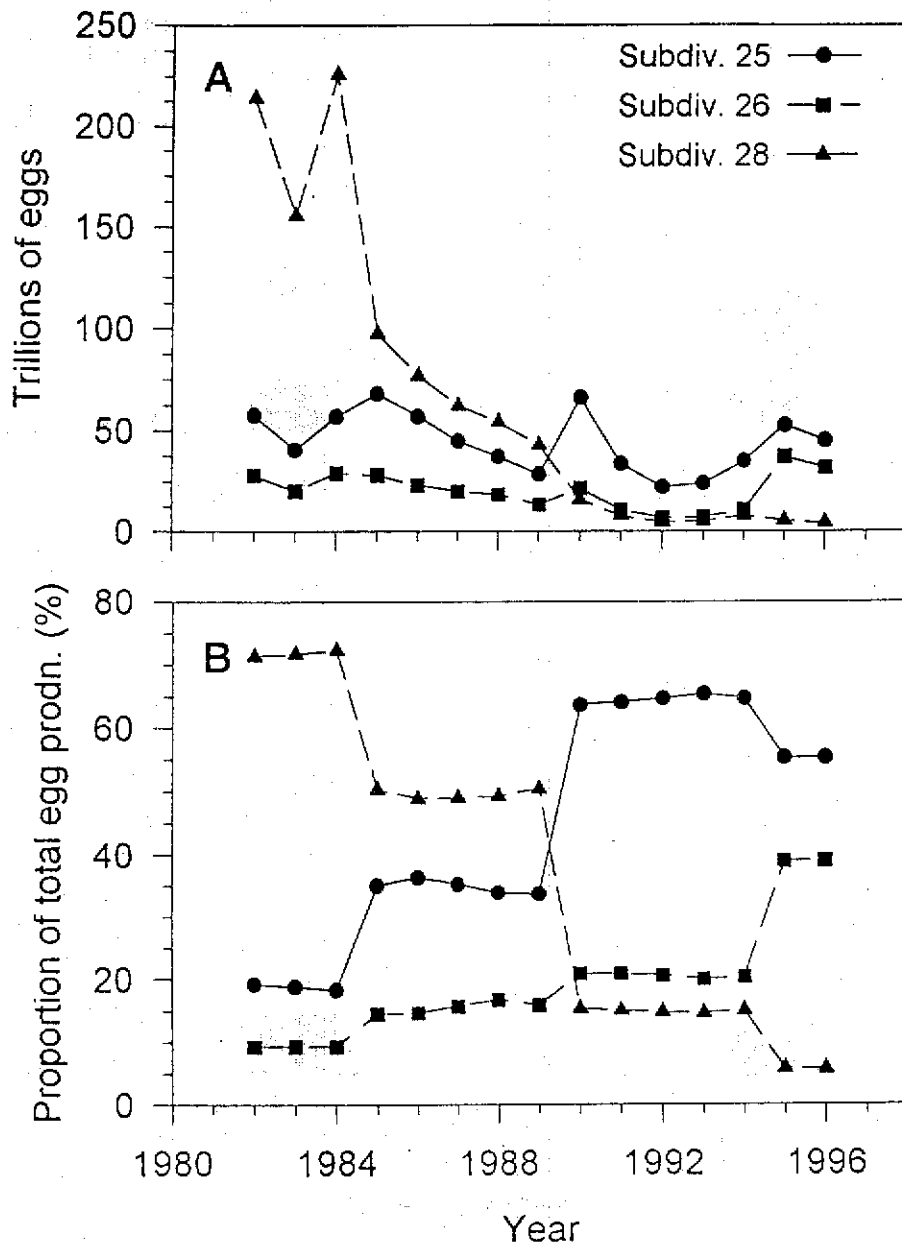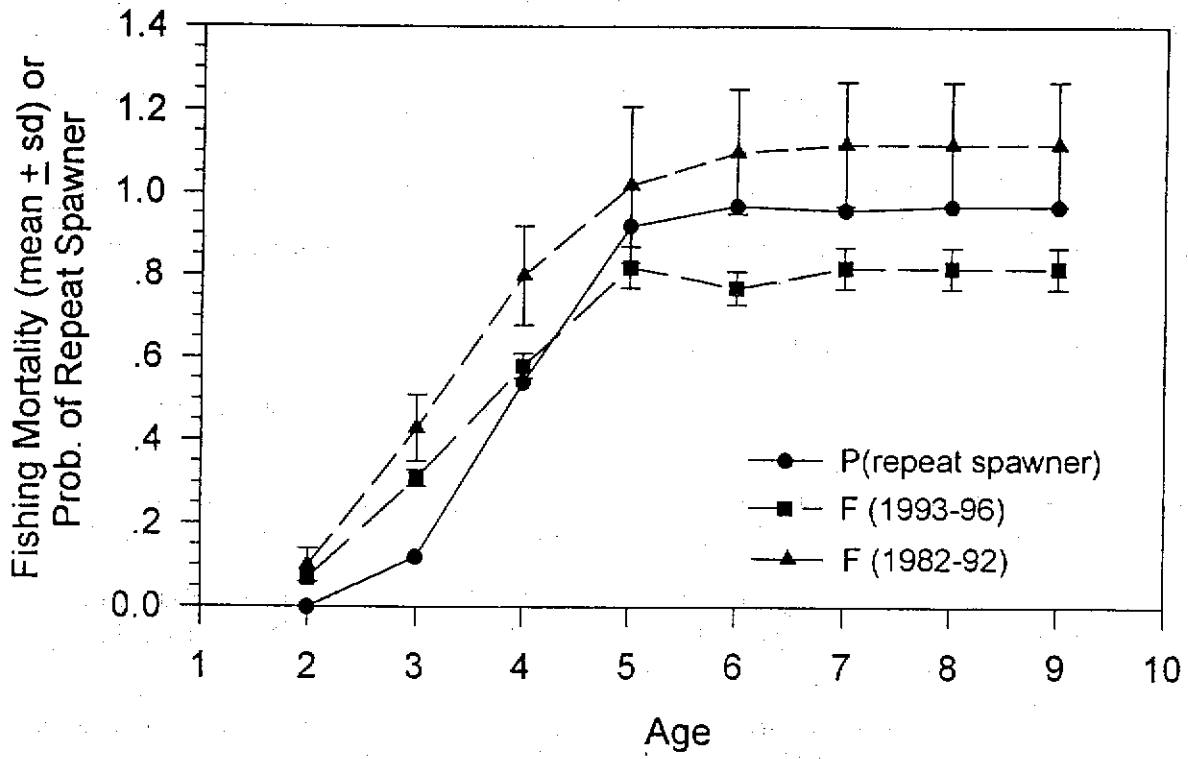Spawning Stock Biomass (1000's of tonnes)

Fig. 5

Fig. 6

Fig. 7

Fig. 8

Fig. 9

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