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ICHTHYOPLANKTON METHODS FOR ESTIMATING FISH BIOMASS INTRODUCTION AND TERMINOLOGY

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The biomass of a fish stock can be estimated from the abundance of its spawn. This idea, first proposed by Hensen and Apstein (1897), has led to the development of ichthyoplankton methods currently used around the world to estimate biomass, and monitor trends in fish abundance. In recent years, ichthyoplankton based approaches have become more important because of increased demands for fishery-independent information. Five ichthyoplankton based methods for biomass estimation were described in this symposium: annual egg production method (AEPM), annual larval production method (ALPM), daily egg production method (DEPM), daily fecundity reduction method (DFRM), and egg deposition method (EDM). A variety of inexpensive ichthyoplankton indices of fish abundance was also described.

The AEPM (Saville, 1964) was the only ichthyoplankton method for estimating biomass until the 1980's. In the AEPM, biomass is computed from annual estimates of egg production and the potential annual fecundity of females. Eggs collected in plankton tows over the entire spawning season are used to calculate annual egg production. Annual fecundity per unit weight is calculated from the number of advanced yolked oocytes in ovaries of females taken just prior to spawning season.

$$B = P_a A/ER \quad (1)$$

where B is the biomass for area A, P_a is the annual egg production per unit sea surface area, A is area size, E is the total (annual) fecundity per unit weight of female, and R is the female fraction of the biomass (sex ratio). An important assumption of the AEPM is that potential annual fecundity is determinate, that is, fecundity becomes fixed prior to the beginning of the spawning season. The paper by Picquelle and Megrey on Alaskan pollock, is an example of the AEPM from this symposium.

Determinate fecundity seems to be common in boreal species such as herring and pollock but a common error is to assume that potential annual fecundity is fixed in all fishes. It became apparent in the 1970's and 1980's that the AEPM could not be used for the temperate species such as northern anchovy, queen fish, and tropical tunas because the standing stock of advanced oocytes in the ovary was not equivalent to annual fecundity. For example, female anchovy spawn 10 to 20 times per year, but the number of yolked oocytes in the ovary never exceeded those needed for 1 to 3 spawnings (Hunter and Leong, 1981). Thus, annual fecundity in anchovy is indeterminate and cannot be estimated by counting the standing stock of advanced oocytes in the ovary.

An alternative method, the DEPM, was developed for fishes like northern anchovy that have indeterminate annual fecundity (Lasker, 1985). In the DEPM, biomass estimates are based on daily, rather than annual, fecundity. Daily egg production was calculated from numbers of staged eggs taken in plankton samples. The relationship between daily spawning of eggs and spawning biomass was determined from the fraction of females spawning per day and batch fecundity:

$$B_s = P_0 A/(R/W_f)SF \quad (2)$$

where B_s is the spawning biomass for area A, P_0 is the daily egg production at

age 0 day per unit sea surface area, W_f is average female weight, S is the fraction of females spawning per day, F is the batch fecundity, and A and R are defined as in equation 1.

Since the publication of the DEPM for northern anchovy (Lasker, 1985), the method has been applied to a variety of fish stocks. These applications provide new perspectives and augment the basic method. In this symposium, Alheit reviews application of the DEPM to clupeoid fishes including Peruvian anchoveta and the Spanish sardine. He surveys the literature, much of which is not generally available, and examines the extent to which the basic parameters in equation 2 vary among stocks of anchovy and sardines. Somerton demonstrates that the DEPM can be used to measure weekly changes in biomass of nehu, a small tropical anchovy, that spawns every other day, and lives less than a year. Shelton, Armstrong, and Roel review the use of the DEPM in South Africa where it has been used to make annual estimates anchovy biomass since 1984. In South Africa, the DEPM has been integrated with an annual acoustic trawl survey for anchovy in a way that yields more precise biomass estimates at a modest increase in cost.

In addition to the DEPM and AEPM, three other biomass estimation procedures are presented in this symposium: the annual larval production method (ALPM); egg deposition method (EDM); and the daily fecundity reduction method (DFRM). All three are based on the assumption of determinate annual fecundity. Heath describes an application of the ALPM to herring and summarizes a large, and not generally available literature. Heath describes how the ALPM was used to monitor the remarkable recovery of European herring stocks. The EDM for Pacific herring described by Schweigert is interesting because plankton samples were not used, instead, divers measured the density and area of spawn on the bottom. Pacific herring spawn in intertidal and subtidal zones where their sticky eggs adhere to algae or the substrate. The spawning grounds are easily found because of the clouds of milt produced during spawning.

The last method of biomass estimation considered in the symposium is the DFRM (Lo et al., 1992). This is a new daily method, that has yet to be formally tested as a management tool. The DFRM is designed to estimate the biomass of fish that spawn more than once per season but have determinate annual fecundity. It does not require measurement of batch fecundity and spawning frequency as do other daily methods. Instead, DFRM uses the daily decline in total fecundities to measure daily population fecundity.

$$B = P_0A/(R/W_f)D = P_0A/K \qquad (3)$$

where B is the biomass for area A, P_0 is the daily production of eggs per 10 m^2 sea surface, K is daily population fecundity = $(R/W_f)D$, in eggs/body weight/day, $D = d(E \cdot G)/dt$, the daily fecundity per female, E is the total number of advanced oocytes present in the ovary at time t (before spawning, E in equations 1 and 3 are equal), G is the fraction of females that have active ovaries at time t, and R and W are defined as before. If the spawning season is long, the fecundity reduction method requires less ship time than annual method since data from only a portion of the spawning season are needed.

Selection of the optimal ichthyoplankton-based method for biomass estimation is dependent upon a variety of factors including the spawning habits of the parents, whether annual fecundity is determinate or indeterminate, the level of precision desired, costs, and availability of other information. Two symposium papers consider biological issues related to the selection of methods. Zeldis reviews the reproductive biology of three New Zealand fishes: snapper, orange roughy, and hoki, and identifies what he believes to be the optimal ichthyoplankton method

for each. Priede and Watson compare estimates of biomass of Atlantic mackerel using the AEPM and DEPM. The calculations for each method use the same ichthyoplankton data but different fecundity data. The results are surprising, because the two methods yielded biomass estimates that differed by only 16%. The estimates may have been similar because oocytes as small as 0.13 mm in diameter were included in the potential annual fecundity of mackerel. If only advanced yolked oocytes were included, the annual fecundity would have been much lower, and, consequently, the biomass based on the AEPM would have been much higher than the one based on the DEPM.

Ichthyoplankton data can be used to monitor trends in relative abundance of marine fishes as well as to estimate their actual biomass. Indices of relative abundance based on ichthyoplankton data are not corrected for variation in population fecundity, and consequently, are less costly and less precise than biomass estimates we have discussed thus far. Although no correction for population fecundity is made, indices may be adjusted for growth and mortality of larvae, or in the simplest case, may be simply the standing stock of larvae or eggs. Regardless of computational details, larva indices are surprisingly sensitive to major changes in stock abundance. For example, Scott et al. show that a larva index based on only 100 plankton samples distributed over 100,000 square miles of ocean can be used to follow major trends in the abundance of bluefin tuna. The possibility that a widespread stock such as bluefin tuna can be monitored with as few as 100 samples is certainly remarkable.

Why do simple ichthyoplankton indices of relative abundance work? Smith, explains that stock size and the area occupied by spawn are correlated, and that the presence and absence of larvae in plankton samples is an efficient measure of spawning area. Larva density, a more costly parameter to estimate precisely, has little importance in determining the size of the spawning area. Smith suggests larva density is of less consequence because most of the determinants of larva density, such rates as predation and starvation, are not related to the size of the spawning stock. In addition, in schooling fish, egg and larva density is probably related to school density which may not vary with biomass.

Many of the methods discussed in the symposium contain assumptions that could bias biomass estimates. Typical assumptions are that current year fecundity, egg mortality, larva mortality, and larva growth do not differ over time or among stocks. Estimates of egg or larva production were imprecise in some cases because the number of samples required for a precise estimate was too expensive to collect. The most precise estimates, in which all parameters are estimated in the same spawning season, have a coefficient of variation of 20 to 30%.

The estimation of the production of eggs (P_0) is straightforward and the lack of precision and potential biases are not usually the results of improper sampling or computational approach, but rather, reflect decisions based on costs. Smith makes some suggestions in regard to the frequency of biomass estimates and the precision of such estimates. He concludes that a precise annual estimate can seldom be justified in terms of fishery management and intervals longer than 1 year are more cost effective.

Fecundity estimates continue to be the Achilles heel of ichthyoplankton-based biomass estimation. Unlike estimates of egg or larva production, where procedures are standardized and well understood (Smith and Richardson, 1977), fecundity work may have a number of untested underlying assumptions which may be unsuspected or unspecified. AEPM and the DRFM require that the potential annual fecundity becomes fixed prior to spawning, but this assumption is not valid for all fishes and is seldom tested prior to application of annual methods.

Other typically untested assumptions underlying the annual method are that potential fecundity is equivalent to annual fecundity; females used to estimate potential annual fecundity have not spawned during the current reproductive season and all the oocytes that constitute the potential annual fecundity can be identified in samples. Procedures used to test these assumptions are described by Hunter et al. (1992). In the DEPM one must assume that batch fecundity, usually estimated from numbers of hydrated oocytes in the ovary, is equivalent to the number of eggs actually spawned and fertilized. To our knowledge, this assumption has never been tested. Usually some hydrated oocytes are retained in the lumen of the ovary and are not spawned, indicating that the correspondence between spawned eggs and hydrated oocytes is not exact.

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Definitions

Annual Egg Production Method (AEPM).—Spawning biomass estimated from the ratio of the annual production of planktonic eggs to the potential annual fecundity of the stock.

Annual Fecundity.—The total number of eggs spawned by a female per year.

Annual Larval Production Method (ALPM).—Biomass estimated from the total annual production of larvae, estimated by back-calculating abundance at hatching from abundance at capture length and date, using estimates of growth and mortality rates, and integrated over the spawning area and period.

Batch Fecundity.—The number of hydrated oocytes released in one spawning; usually determined by counting the number of hydrated oocytes in the ovary.

Daily Egg Production Method (DEPM).—Spawning biomass estimated from the ratio of the daily production of planktonic eggs to the daily fecundity of the spawning population.

Daily Fecundity.—The number of eggs spawned per day per gram of fish in the population. In the DEPM it is calculated from the batch fecundity and daily spawning fraction of the stock, while in the DFRM it is calculated from the daily decline in standing stock of advanced oocytes.

Daily Fecundity Reduction Method (DFRM).—Biomass (vulnerable to trawls) estimated from the ratio of the daily production of planktonic eggs to the daily reduction in the total fecundity of the stock.

Determinate Fecundity.—Annual fecundity is determinate when the potential annual fecundity becomes fixed prior to the onset of spawning. In fishes with determinate fecundity, total fecundity decreases with each spawning because the standing stock of advanced yolked oocytes is not replaced during the spawning season.

Egg Deposition Method (EDM).—Spawning biomass estimated from measurement of the numbers of demersal eggs deposited on the bottom by demersally spawning fishes.

Egg and Larva Indices of Abundance (ELIA).—Use of the standing stock of eggs or larvae, or the area occupied by spawn, as an index of spawning biomass.

Indeterminate Annual Fecundity.—Annual fecundity is indeterminate when the potential annual fecundity of a female is not fixed prior to the onset of spawning and unyolked oocytes continue to be matured and spawned during the spawning season.

Potential Annual Fecundity.—Total number of advanced yolked oocytes matured per year, uncorrected for atretic losses. In species with determinate fecundity, potential annual fecundity is usually assumed to be equivalent to the total fecundity prior to the onset of spawning.

Relative Fecundity.—Fecundity divided by female weight.

Total Fecundity.—The standing stock of advanced yolked oocytes.

Other Suggested Notations

W: fish weight, W_f: female fish weight, W_m: male fish weight, L: fish length, L_f: female fish length, L_m: male fish length, V, σ^2: variance, $\bar{x}$: sample mean, SD: sample standard deviation, SE: sample standard error, COV: covariance, CV: coefficient of variation, r: correlation coefficient, r^2: coefficient of determination, T: temperature, df: degrees of freedom, z: instantaneous mortality rate and t: age.

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