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Comparison between Egg Production Method and Larval Census Method for Fish Biomass Assessment

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ABSTRACT

Ichthyoplankton abundance and production are related to the aggregate weight of spawning adults. The problem is first formulated in terms of annual production and fecundity. The abundance of northern anchovy larvae, used to index annual production, is related to the daily production of eggs. Advantages of the egg production method of assessing stock biomass are discussed.

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INTRODUCTION

This final article discusses the general problem of relating ichthyoplankton data to the aggregate weight of spawning adults and reviews various solutions. The first section deals with the problem as traditionally formulated; that is, the annual production of eggs and larvae is related to adult biomass by annual fecundity. The second section reformulates the problem in instantaneous terms; that is, daily production and daily fecundity. The third section relates the two ichthyoplankton methods used to estimate the northern anchovy populations: The larval census method and the egg production method. The fourth section discusses the advantages of the egg production method.

ANNUAL PRODUCTION OF EGGS AND LARVAE

Although ichthyoplankton surveys have been conducted for many purposes—to detect unexploited fish stocks, to study development, biogeography and systematics of fishes, and to forecast future population growth—Hensen and Apstein (1897) initially proposed that the surveys be used to index the spawning population of adults. The idea was appealing because of the ease of sampling eggs and larvae relative to sampling adults. Ichthyoplankters are found in a restricted vertical range of the sea, they have no or very limited ability to avoid capture, and simple sampling gear can be employed which allows for increase in the density of observations.

The basic model relating the weight of the spawning population to production of eggs is (Saville 1964)

$$B = \frac{P}{F \times R}$$

where B is the weight of the spawning population, P is the annual production of eggs, F is the annual female fecundity on a weight basis (annual specific fecundity), and R is the female fraction of the population. Application of the method requires the ability to identify reproductive products of the target species and knowledge of their development rates, the geographic and seasonal extent of spawning, and the determination of batch size and number of batches spawned by a female each year.

The production of eggs can be estimated from egg abundance adjusted for their development time and the mortality suffered during this period (Sette 1943). Annual abundance is estimated by integrating individual observations over both the survey area and the spawning season. Several spatial integration procedures have been employed: Contouring the observations and measuring the topographic volume (Buchanan-Wollaston 1926; Van Cleve and Seymore 1953; Simpson 1959); summing of strata averages raised by strata areas (Sette 1943; Smith 1972; Berrien et al. 1981); and summing individual observations raised by the area that each observation represents (Sette and Ahlstrom 1948). The three methods yielded similar results when applied to surveys of Pacific sardine spawning by Sette and Ahlstrom (1948). Temporal integration has been accomplished by summing successive surveys weighted by the portion of the year that they represent (Sette and Ahlstrom 1948; Berrien et al. 1981) by measuring the area under the curve that describes the survey abundance by time of year (Simpson 1959; Bannister et al. 1974), integrating a normal curve scaled to describe the seasonal variation in spawning activity (Saville 1956), and summing quarterly estimates of average abundance (Smith

(1964) advocated procedures which averaged over space and time because of the large (and unpredictable) variance between observations; he argued that estimates from integrating procedures did not have reliable estimates of variability and were not amenable to comparisons between years. Adjustments for development time and mortality can be made either before integration (e.g., Berrien et al. 1981), after integration (Sette 1943), or in a stepwise mixture of integration and adjustment (e.g., Bannister et al. 1974). Unless there is a strong correlation between abundance and rate of development or mortality within the survey area, the order of calculation should make little difference in the final estimate of annual egg production. If these factors are independent, then the various procedures discussed above are algebraically equivalent.

The most recent statistical advance in the description of ichthyoplankton surveys is the use of a weighted negative binomial distribution to describe the sample distribution (Zweifel and Smith 1981). Individual observations can be weighted for sampling bias and error (e.g., extrusion, avoidance, variations in the sample volume, and development rate), and the mean of the fitted distribution is an unbiased estimate of the production rate with a well-described error structure. Production is estimated by raising this mean over the space-and-time stratum encompassed by the observations. By fitting a weighted negative binomial to successive stage-specific sample distributions, an age-specific production curve may be derived (Hewitt 1982). Application of this procedure to the 30-yr time series of northern anchovy larvae surveys revealed a change in the microdistribution pattern (patch dispersal) of larvae as they grew and a change in the mortality rate with the level of egg production (Hewitt 1982).

Annual specific fecundity is estimated from knowledge of the number of eggs released per unit weight per spawning and the number of spawnings per year. Both factors can be affected by environmental conditions such as the amount, quality, and availability of food. For boreal species, for which spawning seasons tend to be distinct, short, and predictable, estimating annual specific fecundity may be less of a problem than for temperate and tropical populations, with protracted or even continuous spawning seasons. The problem of estimating annual specific fecundity may be sidestepped by assuming that production or abundance of eggs and larvae is proportional to the weight of the adult population; the proportionality constant is estimated by regressing the abundance of larvae on an independent estimate of population size (Smith 1972; Saville and Schnack 1981). Thus

$$B = k \times C \qquad \text{(Smith 1972)}$$

where C is the annual census of larvae and k is the proportionality constant. This procedure has come to be known as the Larval Census Method (Smith and Richardson 1977). Application of the method assumes that annual specific fecundity does not vary between years nor does the larval mortality rate (hence the use of larval abundance rather than production). To the extent that specific fecundity and larval mortality rate are independent of population size, violation of the assumptions introduces error but not bias in the estimate of the constant of proportionality.

The theory and conduct of ichthyoplankton surveys are discussed thoroughly in Smith and Richardson (1977); their bibliography (Smith and Richardson 1979) contains over 1,000 citations and is complete through 1973, including proceedings of the first Symposium on the Early Life History of Fish held at Oban, Scotland in 1973 (Blaxter 1974). The estimation of adult spawning stock size from egg and larval surveys is also discussed by Saville (1964, 1977), Hempel (1973), and Ulltang (1977). The proceedings of both symposia on the Early Life History of Fish (Blaxter 1974; Lasker and Sherman 1981) include several reports of estimates of stock size from ichthyoplankton surveys and provide a good introduction to a much larger body of literature.

DAILY PRODUCTION OF EGGS AND LARVAE

Development of the ability to determine the near-term reproductive status of a female allowed the stock-estimation problem to be reformulated in terms of parameters that were easier to measure. Hunter and Goldberg (1980) and Hunter and Macewicz (1980) developed criteria to describe the anchovy spawning cycle apparent in gonad tissue with a resolution of one day; i.e., it is possible to classify fish that were spawning on the day of capture, those that spawned the day previous to capture, those that spawned 2 days previous to capture, etc. Thus a direct measure of daily specific fecundity is possible as the product of the fraction of females spawning per day times the weight-specific batch fecundity. It is not necessary to integrate egg production over the spawning season because both fecundity and production can be expressed on a daily basis. The model relating the weight of the population to the daily production of eggs is (Parker 1980)

$$B = \frac{P_O}{F_s \times R}$$

where B is the weight of the spawning population, P_O is the daily production of eggs, F_s is the specific daily fecundity, and R is the female portion of the population. These parameters can be estimated from a representative sample obtained over the spawning habitat. For a fish that spawns continuously over a protracted spawning season (e.g., anchovy), the observations need not be made synoptically; rather, data collected over a 30-day cruise can be pooled without introducing large errors. This method has been used since 1980 to estimate the spawning stock of northern anchovy (Picquelle and Hewitt 1983a, b).

The production of eggs was estimated from the age-specific production curve (Fig. 1). The production rate of eggs at time zero (spawning) was raised over the survey area to estimate daily production by the population. The variance of this estimate was reduced using postsurvey stratification of the survey area.

Specific daily fecundity was estimated as the product of three parameters:

$$F_s = \frac{F \times S}{W}$$

where F is the average batch fecundity, S is the average fraction of adult females spawning per day, and W is the average weight of an adult female. These parameters were estimated from a sample of adult fish obtained concurrently with a sample of their eggs. The adult sample consists of ∿100 trawl stations, and the egg sample ∿1,000 plankton stations. Results of the four surveys conducted through 1983 are summarized in Table 1.

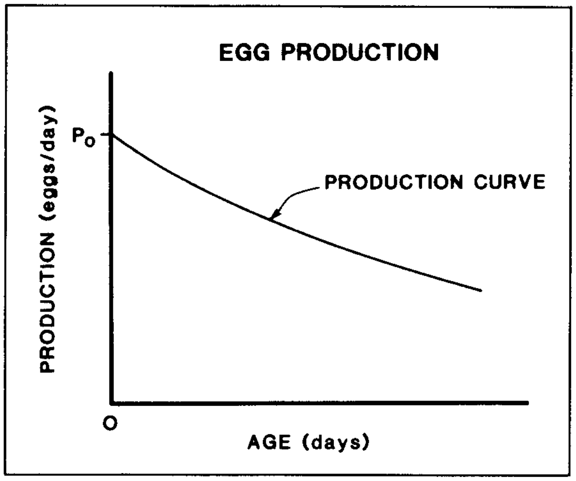

Figure 1.—Age-specific production curve of fish eggs. The curve is estimated from abundance-at-age data and the intercept is defined as the production rate (per unit area) of eggs at time zero (spawning).

RELATIONSHIP BETWEEN EGG PRODUCTION AND LARVAL CENSUS

The standing stock of larvae results from the production of eggs modified by mortality. Eggs are spawned continually by the adult population; some of them hatch, some of the larvae survive to metamorphosis, and many more perish as eggs or larvae. The average abundance of eggs and larvae is the sum of this process over all ages; i.e., the area under the production curve (Fig. 2). Thus, egg production is proportional to the zero intercept of the production curve, and the larval census is proportional to the area below the production curve. Both are raised above the survey area for population estimates and have a constant relationship to the extent that mortality is constant. The annual northern anchovy larval census was the latter value summed over four quarters (Smith 1972).

The expected abundance of northern anchovy larvae is the integral of the larval production curve from the time of hatch to 30 days (the oldest age at which anchovy larvae are effectively caught). The larval production curve is an extension of the egg production curve, and this is the basis for an analytical connection between the two methods. The larval production curve may be parameterized as (Lo 1985; Hewitt and Brewer 1983)

$$P_t = P_h \left(\frac{t_h}{t}\right)^{\beta} \quad \text{for } t < t_h$$

where P_t is the production of t-day old larvae, t_h is the age at hatch, and β is the larval mortality coefficient which describes how rapidly survival improves with age. The egg production curve may be parameterized as (Picquelle and Hewitt 1983a)

$$P_t = P_O e^{-Zt}$$

Table 1.—Egg production estimates of northern anchovy spawning biomass (1980-83). C.V. = coefficient of variation (standard deviation/mean).

		1980[1,4]		1981 (Feb)[1,4]		1981 (Apr)[1,4]		1982[2,4]		1983[3,5]	
		Est.	C.V.	Est.	C.V.	Est.	C.V.	Est.	C.V.	Est.	C.V.
Daily egg production ($\times 10^{12}$ eggs/d)	P_O	26.34	0.111	20.96	0.101	12.59	0.087	13.51	0.237	17.25	
Fraction of mature females spawning/d	S	0.142	0.125	0.106	0.122	0.125	0.092	0.120	0.038	0.094	
Sex ratio of weight (females/total)	R	0.478	0.120	0.501	0.063	0.495	0.051	0.472	0.081	0.549	
Batch fecundity (no. eggs/batch)	F	7,751	0.075	8,329	0.052	8,846	0.045	10,845	0.047	5,297	
Average female weight ($\times 10^{-6}$ t)	W	17.44	0.055	13.37	0.039	16.20	0.029	18.83	0.019	11.20	
Daily population fecundity ($\times 10^{-6}$ eggs/day-ton)	$q = SRF/W$	30.28		33.03		33.84		32.53		24.35	
Spawning biomass	$B = P_O/q$	870	0.225	635	0.183	372	0.147	415	0.257	652	0.211

[1]Documented in Stauffer, G.D., and S. J. Picquelle (Unpubl. manuscr.) Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. SWFC, La Jolla, CA.

[2]Documented in Picquelle and Hewitt (1983a).

[3]Documented in Picquelle and Hewitt (1983b).

[4]These surveys were conducted with a 333-μm mesh net estimated to retain 91% of the eggs. Original estimates were elevated by a factor of 1/0.91.

[5]Biomass estimate was actually calculated as the sum of three regional biomass estimates. Parameter estimates reported here are averaged over the entire survey area for comparison purposes. See Picquelle and Hewitt (1983b) for regional parameter estimates.

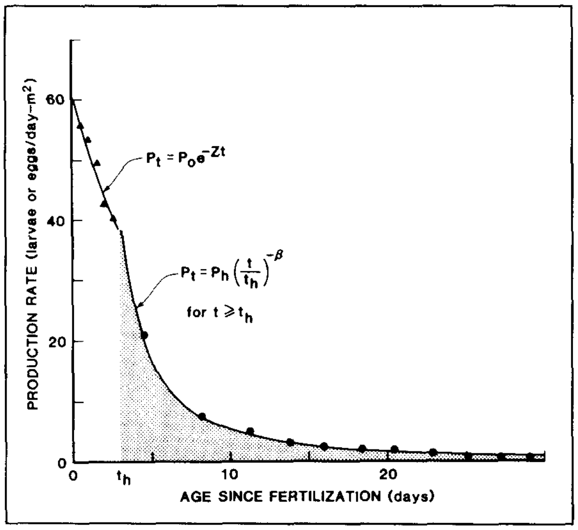

Figure 2.—Age-specific production curve of anchovy eggs and larvae. The average abundance of larvae is the shaded area under the larval production curve.

where Z is the instantaneous mortality coefficient, assumed to be constant over the incubation period. The production of eggs at the end of the incubation period may be substituted for the production of larvae at t_h.

The annual census of larvae averaged 2.12 times the standing stock during the spawning season (Stauffer and Picquelle 1980). The annual larval census also underestimated the true abundance of larvae because of losses due to extrusion and avoidance (Smith 1972; Lenarz 1972, 1973; Lo 1983). Thus, the annual census of larvae may be related to the daily production of eggs:

$$\hat{C} = 2.12(r)\, P_O e^{-Zt} \left(\frac{t_h}{\beta-1}\right)(1 - (t_h/30)^{\beta-1})$$

where r is the fraction of the larval population represented in an ichthyoplankton sample; r is a variable which is dependent on the size distribution of the larvae caught and the time of their capture. These relationships are developed in more detail by Stauffer (1983), Picquelle and Hewitt (1983a, b), and Lo (1985).

As was noted above, spawning biomass may be estimated using the larval census method by multiplying C times the constant of proportionality; this assumes no variability in reproductive output or early mortality. Spawning biomass may be estimated using the egg production method by dividing P_O by the daily specific fecundity; this procedure specifically accounts for variability in reproductive output and early mortality.

Results from the time series of egg production are listed below, together with projected larval census estimates. During the first two years larval surveys were conducted concurrently, and the measured larval census agreed well with the projected larval census.

YEAR	P_O ($\times 10^{12}$ eggs/d)	C ($\times 10^9$ larvae)	C ($\times 10^9$ larvae)
1980	26.34	17.22	18.10
1981 (Feb.)	20.96	35.12	28.58
(Apr.)	12.59	30.85	
1982	13.51	20.97	
1983	17.25	15.80	

The egg production surveys were conducted with the CalVET sampler described in Smith et al. (1985). The CalVET sampler has a 25-cm diameter mouth and is retrieved vertically to the surface from 70 m depth; it was designed to sample a small volume of water in a short period of time relative to the standard CalCOFI bongo sampler used to conduct larval surveys. The bongo sampler is a paired net with 60-cm diameter mouths and is retrieved obliquely to the surface from 210 m depth. Although the sampling gears are quite different, they yield consistent and compatible estimates of ichthyoplankton production.

These relationships may also be used to estimate historical egg production from the production curve of larvae and the abundance of eggs (Lo 1985). MacCall and Methot (1983) assembled the various measures of anchovy spawning biomass (egg production, back-projected egg production, acoustic surveys, and aerial spotter logs); they used acoustic and aerial data to fill in missing ichthyoplankton survey years and scaled the measures to the recent (1980-82) egg production estimates of biomass. The resulting 30-yr time series is the basis for a population model used to manage the harvest of anchovy (Pacific Fishery Management Council 1983).

ADVANTAGES OF THE EGG PRODUCTION METHOD

The egg production method is based on a model which uses instantaneous rates (daily egg production and daily specific fecundity). As such, a great economy is realized relative to annual estimates, because the necessary field data can be obtained on a single cruise. In the case of anchovy, at least four surveys were required to define the annual spawning activity (Smith 1972). Thus a major advantage to the egg production method is the relatively low cost of collecting field data.

The egg production method is also more precise than other ichthyoplankton methods. Early mortality and adult reproductive output are both measured rather than assumed or extrapolated from other observations. The extrapolated estimates may be accurate but they have a finite error associated with the estimation process that is eliminated when these parameters are measured directly. In the case of anchovy, the egg production method is also probably more accurate than the larval census method (Picquelle and Hewitt 1983a). This is because of inaccuracies in estimating the proportionality constant between the annual census of larvae and the weight of the adult stocks.

The egg production estimate of spawning biomass can be broken down into several factors each of which can be estimated, with an associated variance, from a sample of the population. These variances, together with the covariance between the parameters, may be used to estimate the variance of the estimate of spawning biomass. This is not so easily done with estimates based on annual rates because certain factors must be estimated without an idea of their variance (e.g., the number of batches spawned per year). It is also possible to measure the real variance of the egg production estimate of spawning biomass by conducting multiple surveys during the same year as was done in 1981.

LITERATURE CITED

BANNISTER, R. C. A., D. HARDING, and S. J. LOCKWOOD.
1974. Larval mortality and subsequent year class strength in the plaice (*Pleuronectes platessa* L.). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 21-37. Springer-Verlag, N.Y.

BERRIEN, P. L., N. A. NAPLIN, and M. R. PENNINGTON.
1981. Atlantic mackerel, *Scomber scombrus*, egg production and spawning population estimates for 1977 in the Gulf of Maine, Georges Bank and Middle Atlantic Bight. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:279-288.

BLAXTER, J. H. S. (editor).
1974. The early life history of Fish. Springer-Verlag, N.Y., 765 p.

BUCHANAN-WOLLASTON, H. J.
1926. Plaice-egg production in 1920-21, treated as a statistical problem, with comparison between the data from 1911, 1914 and 1921. Fish. Invest. Ser. 2 Mar. Fish., G.B. Minist. Agric. Fish. Food 9 (2).

ENGLISH, T. S.
1964. A theoretical model for estimating the abundance of planktonic fish eggs. Rapp. P.-v. Réun. Cons. int. Explor. Mer 155:174-182.

HEMPEL, G. (editor).
1973. Fish egg and larval surveys. FAO Fish. Tech. Pap. 122, 82 p.

HENSEN, V., and C. APSTEIN.
1897. Die Nordsee-Expedition 1895 des Deutschen see fischerei-vereins. Uber die eimenge de winter laichenden fische. Helgol. Wiss. Meeresunters. 2(2), 101 p.

HEWITT, R. P.
1982. Spatial pattern and survival of anchovy larvae: Implications of adult reproductive strategy. Ph.D. thesis, Univ. Calif. San Diego, 187 p.

HEWITT, R. P., and G. D. BREWER.
1983. Nearshore production of young anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 24:235-244.

HUNTER, J. R., and S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., and B. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.

LASKER, R., and K. SHERMAN (editors).
1981. The early life history of fish: Recent studies. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178, 607 p.

LENARZ, W. H.
1972. Mesh retention of larvae of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. Fish. Bull., U.S. 70:839-848.
1973. Dependence of catch rates on size of fish larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:270-275.

LO, N. C. H.
1983. Re-examination of three parameters associated with anchovy egg and larval abundance: Temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo. TM-NMFS-SWFC-31, 33 p.
1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951-82. Fish. Bull., U.S. 83:137-150.

MacCALL, A. D., and R. D. METHOT.
1983. The historical spawning biomass estimates and population model in the 1983 anchovy fishery management plan. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent. Admin. Rep. LJ-83-17, 53 p.

PACIFIC FISHERY MANAGEMENT COUNCIL.
1983. Northern anchovy fishery management plan. Pac. Fish. Mgmt. Counc., Portland, OR 97201.

PARKER, K.
1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541-544.

PICQUELLE, S. J., and R. P. HEWITT.
1983a. The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif. Coop. Ocean Fish. Invest. Rep. 24:16-28.
1983b. Estimates of the spawning biomass of the northern anchovy for the 1983-84 California fishing season. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent., La Jolla, CA, Admin. Rep. LJ-83-15, 40 p.

SAVILLE, A.
1956. Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. Mar. Res. Dep. Agric. Fish. Scotl. 4.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. Rapp. P.-v. Réun Cons. int. Explor. Mer 155:164-173.

SAVILLE, A. (editor).
1977. Survey methods of appraising fishery resources. FAO Fish. Tech. Pap. 171, 76 p.

SAVILLE, A., and D. SCHNACK.
1981. Some thoughts on the current status of studies of fish egg and larval distribution and abundance. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:153-157.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1: Early life history, including the growth, drift and mortality of the egg and larval populations. U.S. Fish. Wildl. Serv., Fish. Bull. 50:149-237.

SETTE, O. E., and E. H. AHLSTROM.
1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7:511-542.

SIMPSON, A. C.
1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. Fish. Invest. Ser. 2 Mar. Fish., G.B. Minist. Agric. Fish. Food 22(7), 111 p.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SMITH, P. E., and S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Pap. 175, 100 p.
1979. Selected bibliography on pelagic fish egg and larval surveys. FAO Fish. Circ. 706, 97 p.

SMITH, P. E., W. FLERX, and R. HEWITT.
1985. The CalCOFI vertical egg tow (CalVET) net. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 27-32. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

STAUFFER, G. D.
1983. Calibration of northern anchovy spawning biomass estimates derived by egg production and larval census methods. Calif. Coop. Oceanic Fish. Invest. Rep. 24:11-15.

STAUFFER, G. D., and S. J. PICQUELLE.
1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Natl. Mar. Fish. Serv., NOAA, Southw. Fish. Cent. Admin. Rep. LJ-80-09, 41 p.

ULLTANG, O.
1977. Methods of measuring stock abundance other than by the use of commercial catch and effort data. FAO Fish. Tech. Pap. 176, 23 p.

VAN CLEVE, R., and A. H. SEYMORE.
1953. The production of halibut eggs on the Cape St. James spawning bank off the coast of British Columbia 1935-46. Rep. Int. Pac. Halibut Comm. 19, 44 p.

ZWEIFEL, J. R., and P. E. SMITH.
1981. Estimates of abundance and mortality of larval anchovies (1951-75): Application of a new method. Rapp. P.-v. Réun Cons. int. Explor. Mer 178: 248-259.

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE

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April 16, 1987

MEMORANDUM FOR: USERS OF THE EGG PRODUCTION METHOD FOR ESTIMATING SPAWNING BIOMASS OF PELAGIC FISH.

FROM: REUBEN LASKER

SUBJECT: ERRATA FOR NOAA TECHNICAL REPORT NMFS 36; "AN EGG PRODUCTION METHOD FOR ESTIMATING SPAWNING BIOMASS OF PELAGIC FISH: APPLICATION TO THE NORTHERN ANCHOVY".

A number of printing errors have been discovered by Dr. Sachiko Tsuji in the published account of the egg production method. These are important and warrant this memo. Please make these corrections in your copy.

p. 5, Abstract, 4th line should read:
"be estimable and spawning rate constant over the field sampling interval."

p. 12, in equation 8, $\hat{\beta}$ should be β.

p. 17, Table 1. on the January line +3.5 should be -3.5.

p. 20, two lines under the formula in the second column, "sample size" should be "sample scale" and σ_i should read σ_i^2. Five lines under the formula "larger observations" should be "bigger scales."

p. 22, 1st para., No. 3 last line should be simulation, not stimulation.

p. 23. 1st para., line 7. "Table 9" should read "Table 6."

p. 44. Temperature table in second column on the page.
The temperatures read 13.9
13.5
16.2

The correct temperatures are 13.9
15.2
16.2.

p.45. Second column, $y_{i,t,k}$ should read $y_{i,t}$.

p.46 1st Para., line 7, change the word "spawning" to "tows, $\hat{T}$".

p.49. Table 5d. Strike out the words "within or" in the second line of the heading.

p.55. 9th line from the bottom, x_1 should be x_i.

p.56. First. para. second column, sixth line, 26 should read *25.*

p.63. Under "Preservation" $Na_2H_2PO_4$ should be Na_2HPO_4.

p.93. In table 1, atretic state e, change > to <.

p.97. In the! formula after the second para. change < to >.

p.98. In the formula in the first column change -Zt to $-Zt_h$.