SPAWNING BIOMASS OF THE NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN THE GULF OF CALIFORNIA DURING 1991

CELIA EVA COTERO-ALTAMIRANO
Instituto Nacional de la Pesca, CRIP Ensenada
Apartado Postal 1306
Ensenada, Baja California
México

YANIRA GREEN-RUIZ
Instituto Nacional de la Pesca, CRIP Mazatlán
Apartado Postal 1177
Mazatlán, Sinaloa
México

ABSTRACT

The spawning biomass of northern anchovy (*Engraulis mordax*) in the Gulf of California during 1991 was estimated to be 105,079 metric tons (CV = 0.44), as determined by the daily egg production method.

The principal spawning regions were around the large islands in the north and in two smaller regions close to Guaymas in the south.

INTRODUCTION

The populations of small pelagic fishes are characterized by biomass fluctuations (Murphy 1966; Blaxter and Hunter 1982; Pedrín-Osuna et al. 1992). This variability has been attributed both to climatic change and to fishing pressure (Lasker 1981).

Northern anchovy were first detected in the Gulf of California during 1985 by Green-Ruiz and Aguirre-Medina (1989). The discovery of anchovy in the gulf coincided with declines in the availability of sardine and the decline of the sardine fishery in the Gulf of California (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

The identification of anchovy larvae in ichthyoplankton samples and the presence of adults in the fishery catches extended the known geographical range of the anchovy to the Gulf of California (Hammann and Cisneros 1989). Since then, approximately 40,000 metric tons of anchovy have been incidentally taken in the sardine commercial fishery (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993). Later paleoecologic studies by Holmgren-Urba and Baumgartner (1993) demonstrated the presence of the anchovy over 250 years, during alternating periods of high anchovy abundance and high sardine abundance in the Gulf of California.

The increased abundance of *Engraulis mordax* made the stock an alternative resource for the fishing industry and a matter of scientific concern in the Gulf of California. Mexican authorities and scientists decided to estimate its spawning biomass in the Gulf of California. This work was undertaken by the Small Pelagic National Research Program of the National Fishery Institute of Mexico.

Spawning biomass of northern anchovy in the gulf was first estimated with the larval census method (LCM) by Green-Ruiz and Aguirre-Medina (1990). Larval census has been the traditional method for estimating spawning biomass of small pelagic fish (Smith and Richardson 1977) on both the west coast of Baja California (Escudero-Diaz 1976; Olvera-Limas et al. 1983) and in the Gulf of California (Green-Ruiz and Aguirre-Medina 1990). In addition, hydroacoustic estimates of anchovy abundance have been made (Melcer et al. 1976). Data have been collected from fishery catches since the beginning of the incidental fishery (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

The daily egg production method (DEPM) for estimating spawning biomass of pelagic fish was developed in 1980 (Parker 1980; Stauffer and Picquelle 1980; Lasker 1985). The DEPM has been used to estimate the size of clupeoid populations in California (Picquelle and Hewitt 1983, 1984; Hewitt 1985a; Bindman 1986; Scannell et al. 1996; Lo et al. 1996); in Peru (Alheit et al. 1984; Santander et al. 1984); in Portugal (Cunha et al. 1992); in Spain (Uriarte and Motos 1991; Garcia et al. 1992; Santiago and Sanz 1992); in Africa (Armstrong et al. 1988); and in Mexico (Torres 1986).

The National Fishery Institute of Mexico decided to use the DEPM for anchovy in the gulf because the method is relatively precise and because of technical difficulties in converting hydroacoustic data to estimates of anchovy biomass. The DEPM was preferred over the larval census approach because it accommodates variability in the reproductive output of adults.

The DEPM offers additional advantages: (1) Ship time and the associated costs of ichthyoplankton samples are reduced because samples are taken once a year in the peak reproductive season, whereas LCM surveys must be conducted throughout the entire year. (2) Biomass estimates are based on biological parameters and are independent of stock assessment models that require indices of relative abundance. (3) The precision of parameters and biomass estimates can be determined (Hewitt 1985b).

The purpose of this study is to estimate the spawning biomass of anchovy (*Engraulis mordax*) in the Gulf of California during the spawning season of 1991 with the daily egg production method.

METHODS

Survey Design

Data used in previous studies for larval census estimates and commercial catch data were used to estimate

[Manuscript received January 30, 1997.]

the distribution of eggs, larvae, and adult northern anchovy in the Gulf of California, where the peak spawning season is January–February (Green-Ruiz and Aguirre-Medina 1990). Northern anchovy in the gulf spawn until April, and spawning adults have been observed near shore (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

Most pelagic fish eggs in the California Current and on the west coast of Baja California are found between the surface and 70-m depth (Hewitt 1983; Smith et al. 1985). The maximum depth of anchovy eggs is related to depth of the thermocline (Ahlstrom 1959).

There have been no studies of vertical distribution of anchovy eggs in the Gulf of California, but the thermocline is at about 100 m in winter (Robinson 1973). All the above-mentioned factors were considered in designing the sampling program for anchovy in the gulf.

Study Area

In 1991, two simultaneous surveys were conducted in the Gulf of California to estimate the spawning biomass of northern anchovy with the DEPM. Two ships (the RV *BIP*[1] *XI* and RV *BIP XII*) were used from January 24 through February 14, 1991.

The survey followed a station plan established by the National Program of Small Pelagics for the Gulf of California. The ichthyoplankton survey started in the north (line 140) and continued south (to line 440) in 30 perpendicular lines separated by 10 nautical miles (n mi). Sampling stations were 5 n mi apart along each line (figure 1).

A total of 352 plankton samples were taken with a CalVET net of 25-cm diameter, 333-micron mesh, and 1.5-m length, retrieved vertically from a depth of 100 m (Smith et al. 1985). Ichthyoplankton samples were taken during both day and night. Samples were fixed with 3% neutral buffered formalin (Moser and Ahlstrom 1985). A Nansen bottle and deep-sea reversing thermometers were used to record temperatures at the surface and at 10-m depth.

Adult Survey

Midwater trawls intended to sample spawning adults were made at 70 stations along both coasts of the Gulf of California (figure 2), with a 4-panel, 47-m-long midwater trawl of 2.5-cm mesh and a vertical and horizontal opening of 27 m. Trawls lasted 30 minutes, mostly at night. Trawls were made when anchovy schools were detected by video echo sounder, following the sampling criteria described by Picquelle (1985) and Smith and Hewitt (1985). The sea-surface temperature was recorded for each trawl.

[1]Barco de Investigación Pesquera.

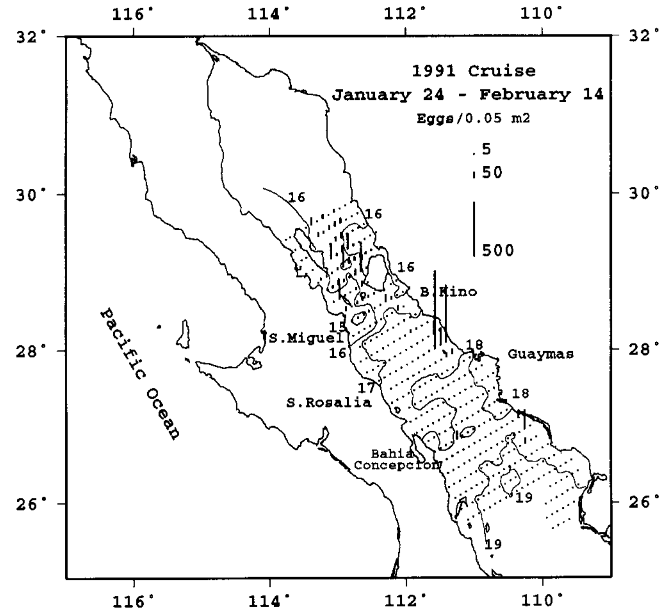

Figure 1. Station plan of the 1991 ichthyoplankton survey and geographic distribution of northern anchovy (*Engraulis mordax*) from CalVET samples, and 10-m isotherms.

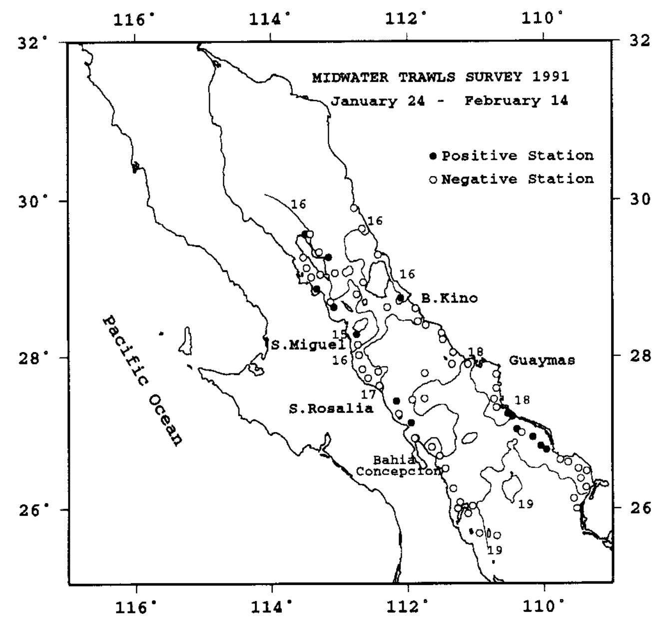

Figure 2. Geographic distribution of trawl stations, positive stations, and 10-m isotherms.

Anchovy were randomly sampled from the trawl catches. The first 50 fish were sexed and measured (standard length). The total weight, gonad-free body weight, and maturity were determined by macroscopic examination. In most cases, gonad-free body weight and maturity were determined from the first 25 mature females (Picquelle and Hewitt 1983). Sometimes additional hydrated females were selected to increase the number of females for fecundity estimates, but these additional samples were not included in the estimate of spawning fraction.

BIOMASS ESTIMATE MODEL

Spawning biomass was estimated with the model developed by Parker (1980) and modified by Stauffer and Picquelle (1980). The spawning biomass is defined as the quotient of the daily production of eggs in the sea and the daily fecundity (per ton of spawners) of the population:

$$B = \frac{kP_0AW}{RSF} \qquad (1)$$

Where B = spawning biomass estimate in metric tons;
P_0 = daily egg production rate in number of eggs per day per 0.05 m^2 of sea surface;
A = area of survey in m^2;
W = average weight of mature females in grams;
R = female fraction of the population by weight;
F = batch fecundity in number of eggs;
S = fraction of mature females spawning per day;
k = conversion factor from grams to metric tons (10^{-6} t/g).

An estimate of variance for the biomass assessment was derived with the delta method (Picquelle and Hewitt 1983; Parker 1985; Bindman 1986):

$$\hat{\mathrm{Var}}(B) \cong B^2 \left\{ \frac{\mathrm{Var}(P_0)}{P_0^2} + \frac{\mathrm{Var}(W)}{W^2} + \frac{\mathrm{Var}(R)}{R^2} + \frac{\mathrm{Var}(F)}{F^2} + \frac{\mathrm{Var}(S)}{S^2} + 2\left[\frac{\mathrm{Cov}(P_0W)}{P_0W} - \frac{\mathrm{Cov}(P_0R)}{P_0R} - \frac{\mathrm{Cov}(P_0F)}{P_0F} - \frac{\mathrm{Cov}(P_0S)}{P_0S} - \frac{\mathrm{Cov}(P_0WR)}{WR} - \frac{\mathrm{Cov}(WF)}{WF} - \frac{\mathrm{Cov}(WS)}{WS} + \frac{\mathrm{Cov}(RF)}{RF} + \frac{\mathrm{Cov}(RS)}{RS} + \frac{\mathrm{Cov}(FS)}{FS} \right] \right\} \qquad (2)$$

where Cov(RS), for example, is the covariance between female fraction and the fraction mature.

DATA PROCESSING

Temperature-Dependent Anchovy Egg Development

Daily egg production was determined from ichthyoplankton samples and the embryonic developmental stage of each egg. Developmental stages were determined by microscopic inspection (Moser and Ahlstrom 1985), and ages were assigned on the basis of sea temperature at 10-m depth at the sampling station where the eggs were collected, according to a model for temperature-dependent northern anchovy egg development (Lo 1985).

The standard length of preserved larvae (SLP) was measured to the nearest 0.5 mm with a micrometrical ocular. Only larvae smaller than 7.0 mm were included in egg production estimates. Because representative samples of larger larvae cannot be taken with a CalVET net (Lo 1983), age of yolk-sac larvae was estimated from a temperature-dependent growth curve (Zweifel and Lasker 1976).

Egg Production (P_0) and Egg Mortality (Z)

In order to estimate daily egg production and mortality rate, a single equation model (SEM) was fit to the age and the daily production of eggs and larvae (Lo 1986). The SEM integrates the information about eggs and larvae, assuming that eggs and yolk-sac larvae (larvae <5 mm SLP; Zweifel and Lasker 1976) have the same mortality rate. Before the SEM was applied, numbers of eggs and larvae were corrected for duration, retention, extrusion, and avoidance (Lo 1983).

The single equation model is

$$E(\bar{y}i) = P_0 e^{\alpha x_{1i}} \left(\frac{x_{2i}}{u_i} \right)^{-\beta} \qquad (3)$$

Where P_0 = daily egg production;
α = daily embryonic mortality rate;
x_{1i} = independent variable

$$x_{1i} = \frac{t_i \text{ for } t_i \le u_1}{u_1 \;\; u_1 \le t_i \le 20};$$

x_{2i} = independent variable

$$x_{2i} = \frac{u_1 \text{ for } t_i \le u_1}{t_i \;\; u_1 \le t_i \le 20};$$

t = age of eggs and yolk-sac larvae;
u_1 = maximum age of mortality stanza, when larvae absorbed the yolk sac;
β/t = daily larval mortality rate between 5.5 and 10 mm (fixed length).

For egg samples, the survey area was poststratified into stratum 1 (the area containing positive tows) and stratum 0 (devoid of eggs). Stratum 1 covered 74% and stratum 0 covered 26% of the total area (figure 1).

Adult Parameters

In the laboratory, preserved gonads from both sexes were weighed to the nearest milligram. A sample was taken from the central part of each for histological examination. The samples were dehydrated in alcohol in gradual steps at concentrations from 70% to 100%. Next, they were soaked in xilene and acetone, and embedded in Amerafin. They were then cut into 5–7-micron sections. The tissue samples were stained with the traditional hematoxylin and eosin histotechnique (Humason 1979).

Each gonad was analyzed and classified histologically in order to estimate the fraction of females and males that were mature, and to measure spawning rate for histological classification (Hunter and Goldberg 1980; Hunter and Macewicz 1985; Macewicz et al. 1996; Cotero-Altamirano 1987).

Batch Fecundity

The number of eggs spawned by spawning batch—the batch fecundity—was estimated from the number of hydrated oocytes in the ovary (Hunter et al. 1985). All hydrated females from the adult survey were used to estimate batch fecundity. Both ovaries from each female were examined histologically to identify females that had begun to ovulate and spawn (ovaries with hydrated oocytes and new postovulatory follicles). We eliminated these females to avoid underestimating batch fecundity. We tested for how location of tissue sample affected batch fecundity estimates, but found that fecundity estimates were not affected by sampling location. We estimated mean batch fecundity from data for 63 hydrated females and then determined the relation between batch fecundity and gonad-free weight by linear regression.

We estimated adult parameters: female weight (W), batch fecundity (F), spawning fraction (S), and sex ratio (R) from anchovy caught by midwater trawl. We used weighted sample mean variance estimators (Picquelle and Stauffer 1985):

$$\bar{\bar{y}} = \frac{\sum_{i=1}^{n} m_i \bar{y}_i}{\sum_{i=1}^{n} m_i} \quad (4)$$

$$\hat{\text{Var}}\ \bar{\bar{y}} = \frac{\sum_{i=1}^{n} m_i^2 (\bar{y}_i - \bar{\bar{y}})^2}{\left(\sum_{i=1}^{n} \frac{m_i}{n}\right)^2 n(n-1)} \quad (5)$$

Where m_i = number of fish subsampled from the ith trawl;

n = number of positive trawls;

$\bar{y}_i$ = average for the ith trawl = $\sum_{j=1}^{mi} \frac{y_{ij}}{mi}$;

y_{ij} = observed value for the jth fish in the ith trawl.

RESULTS

Oceanography and Distribution of Anchovy Eggs

During the survey, temperature at 10 m ranged from 14.5° to 19°C. We observed two cold-water masses, one in the north from Angel de la Guarda Island to Cape San Miguel and the other near the Sonora coast in front of Punta Kino (figure 1).

The ichthyoplankton survey took 382 samples; 92 were positive for anchovy eggs. The principal spawning region was in the north around the large islands. Anchovy eggs were also found in two smaller regions close to Guaymas in the south (figure 1).

Daily Egg Production

The estimated daily egg production (P_0) was 7.8 eggs/0.05/m^2/day (CV = 0.33), and the estimated daily embryonic mortality rate (Z) was 0.35/day (CV = 0.17; figure 3, table 1).

Adult Distribution

The adult survey consisted of 70 midwater trawls; 14 were positive for anchovy. Adults were found where surface temperatures ranged from 15.4° to 17.8°C. The greatest abundance of adults was in the north around large islands, and southward near Guaymas (figure 2). The distribution of schools of spawning anchovy coincided with the distribution of eggs (figures 1, 2).

Length and Maturity

The length of female adults in the samples ranged from 90 to 125 mm, mean 105 mm (CV = 0.25). Length of male adults ranged from 93 to 124 mm, mean 103

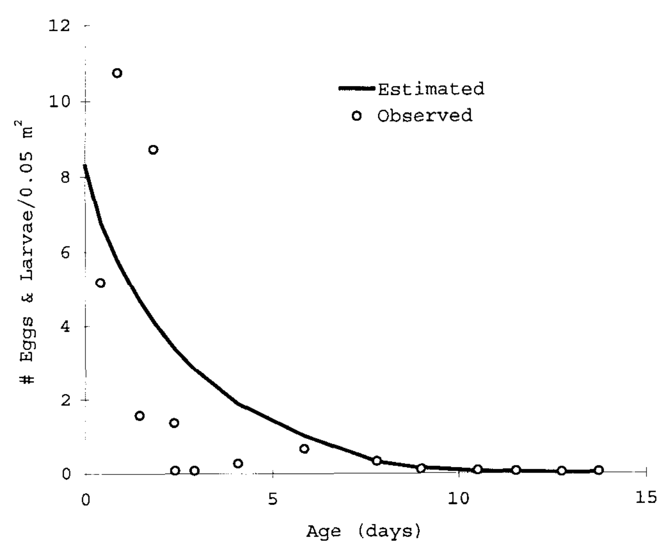

Figure 3. Embryonic mortality curve for northern anchovy (*Engraulis mordax*) eggs and yolk-sac larvae from the 1991 daily egg production method survey.

TABLE 1
Abundance by Size and Age of 1991 Field-Caught Anchovy Eggs (E) and Larvae, Used to Estimate Daily Egg Production (P_0) and Instantaneous Mortality Rate (z)

Size[a] (mm)	Age (days)	No. of eggs or larvae/0.05 m^2
E	0.409	5.1900
E	0.853	10.7500
E	1.448	1.5790
E	1.834	8.7300
E	2.369	1.3610
2.67	2.380	0.0765
3.12	2.900	0.0701
3.69	4.070	0.2745
4.24	5.860	0.6643
4.79	7.800	0.3294
5.32	8.990	0.1148
5.85	10.510	0.0842
6.37	11.530	0.0517
6.89	12.750	0.0348
7.4	13.740	0.0310

[a]Fixed length (corrected)

mm (CV = 0.19; figure 4). We defined "first maturation" as "when 50% of the famales are mature." We used logistic regression to determine the length at 50% mature. Females taken in the survey were 50% sexually mature at a standard length of 104.7 mm; males at 102 mm (figure 5). The length at 50% maturity for the anchovy in the Gulf of California was less than that estimated for the Pacific coast (table 2).

Female Weight

Before estimating average female weights, we corrected the weight of hydrated females in the sample for bias due to the presence of females with hydrated ovaries (Picquelle and Stauffer 1985). We adjusted weights with a regression of whole-body weight on ovary-free weight estimated for females without hydrated ovaries,

$$W = -0.7369 + 1.155\omega \quad (6)$$

where ω is the ovary-free weight (R^2 = 94.2%). The estimated average female weight was 13.4, with a variance of 0.0643.

Batch Fecundity

The batch fecundity for each mature female was estimated by regression of batch fecundity on ovary-free

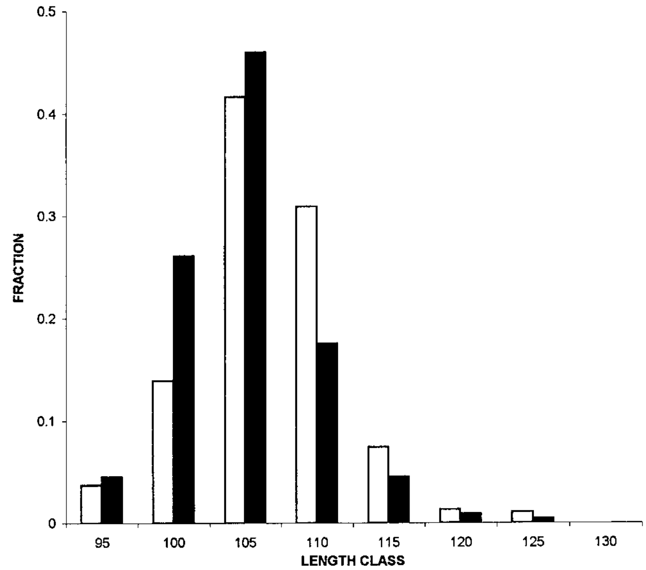

Figure 4. Standard length distribution for northern anchovy (*Engraulis mordax*) taken in all trawls. Females (*open bars*); males (*filled bars*).

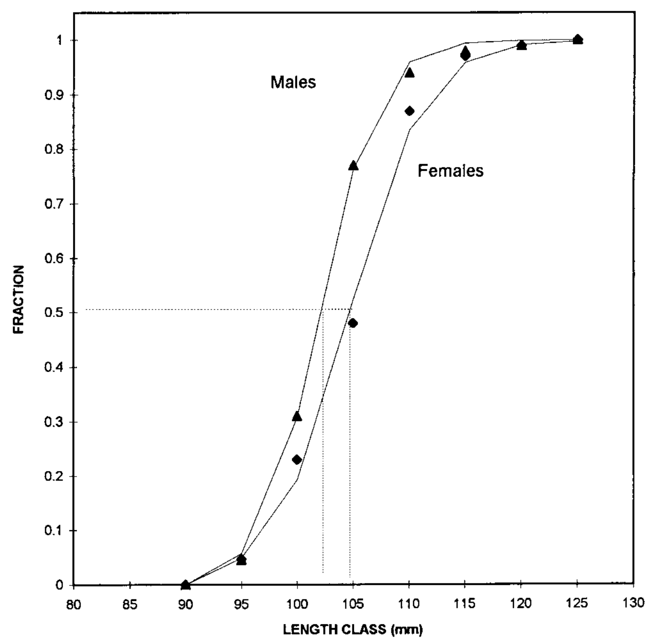

Figure 5. Fraction of northern anchovy (*Engraulis mordax*) females and males that were sexually mature as a function of standard length. *Dotted lines* are estimated length at which females (104.7 mm) and males (102 mm) were mature.

TABLE 2
Length at Maturity of *Engraulis mordax* off the California and Baja California Coasts and in the Gulf of California

	Length at maturity (mm)			
	Female	Male	Both	Authority
Baja California west coast			130	Clark and Phillips 1952
Oregon, Washington	107	104		Laroche and Richardson 1980
Central California			96	Hunter and Macewicz 1980
Ensenada, B.C.	111	98		Cotero-Altamirano 1987
Gulf of California	104.7	102		Authors' survey

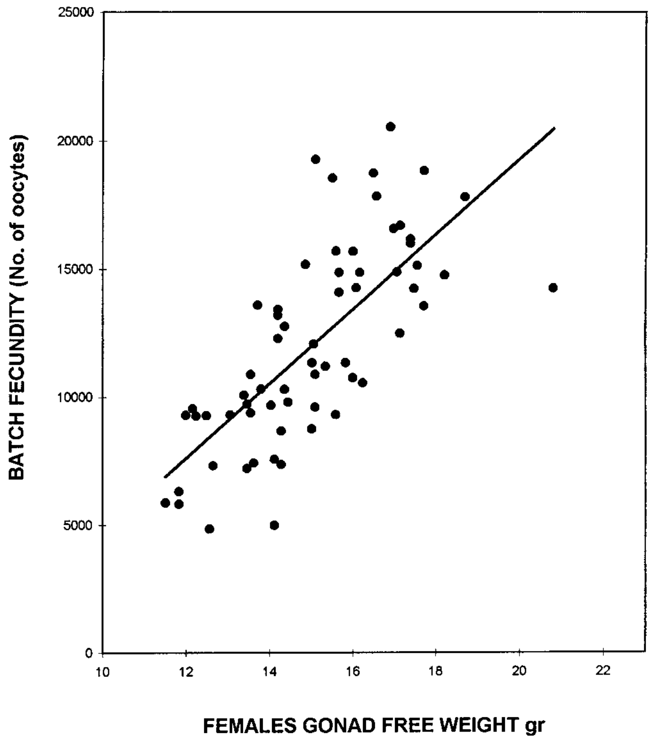

Figure 6. Linear regression of batch fecundity on ovary-free weight fitted to females with hydrated eggs.

weight as estimated for a sample of 63 hydrated females (without new postovulatory follicles) taken during the survey.

The relation between female ovary-free weight (W) and batch fecundity (F) was:

$$F = -9897 + 1458W \qquad (7)$$

where R^2 = 53%, and the female ovary-free weight ranged from 11.5 to 20.8 g (figure 6).

We used equation 7 to estimate batch fecundity for all mature females from each trawl. The mean batch fecundity for mature females in trawl samples was estimated to be 8,220 oocytes (CV = 0.079).

Spawning Fraction

The average fraction of females spawning per day was 0.174/day (CV = 0.20), estimated from females that spawned the night before capture.

Sex Ratio

Sex ratio is the fraction of females in the anchovy stock based on fish weight. For northern anchovy in the gulf during our survey, the estimated sex ratio was 0.68 (CV = 0.027).

Biomass Estimate

The spawning biomass estimate was 105,079 metric tons (CV = 0.44). Estimates of the rate of egg mortality and adult reproductive parameters are summarized in table 3.

DISCUSSION

Peak spawning time was estimated to be 2200 hours, based on 1991 data similar to that for the anchovy off California (Picquelle and Hewitt 1983). To estimate the peak spawning time, we followed the procedures used by Lo et al. (1996) for Pacific sardine, in which the 50th percentile of the cumulative proportions of stage 2 eggs since sunset (1800) was assumed to be the peak capture time for stage 2 eggs (figure 7). The peak spawning time was computed as: 50th percentile of capture time from sunset − the age of stage 2 eggs + the sunset time = 11 − 7 + 18 = 2200 hrs.

In 1991, the temperature of the sea at 10-m depth ranged from 14.5° to 19.0°C (average 17.6°). Green-Ruiz and Hinojosa-Corona (in press) found that *Engraulis mordax* spawns at higher temperatures in the Gulf of California than off the California coast, and found the highest abundance of eggs at 17°.

We compared spawning biomass estimates from our survey with values obtained in 1987 by means of the larval census method (Green-Ruiz and Aguirre-Medina

TABLE 3
Estimates of Daily Egg Production and Adult Reproductive Parameters for Spawning Biomass of *E. mordax* in the Gulf of California for 1991, from Daily Egg Production Method

Parameters		Mean	Variance	Coefficient of variation
Daily egg production (10^{12}) eggs/day)	P_0A	7.49	4.9×10^6	0.44
Average female weight (g)	W	13.64	0.06425	0.019
Batch fecundity (eggs/batch/mature female)	F	8220	4.2×10^5	0.079
Spawning fraction (spawning females/total females)	S	0.174	1.28×10^{-3}	0.206
Sex ratio (females/total)	R	0.68	3.31×10^{-4}	0.027
Daily specific fecundity (eggs/g biomass/day)		72		
Spawning biomass (metric tons)	B	105,079	2.18×10^9	0.445
Egg mortality rate	z	0.35	3.54×10^{-3}	0.17
Average temperature (°C)		17.6		
Average temperature of positive stations (°C)		16.4		
Positive stations (%)		21.0		

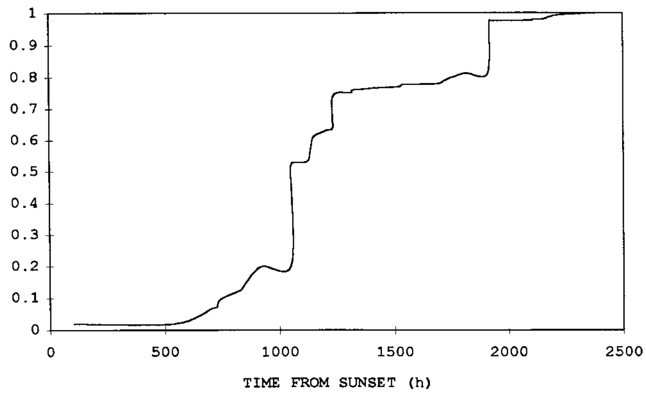

Figure 7. Cumulative proportion of time from sunset (1800) for stage 2 northern anchovy (*Engraulis mordax*) eggs during survey.

1990). The difference (106,000 t vs 421,000 t) indicates that the two methods yield comparable results, but detailed comparison is not possible because the estimates were for different years.

The coefficient of variation (0.44) for our biomass estimate was high, mainly because our estimate of egg mortality (z) was relatively imprecise (CV = 0.17), partly because it came from a single-equation model where both egg and larval data were used. Otherwise, the estimate of the mortality rate may have a higher variance because the distribution of eggs in the sea is patchy, and too few eggs in early stages were caught (Smith 1981).

Comparisons between Gulf and West Coast Stocks

Anchovy in the Gulf of California are less abundant than off California. Biomass in the gulf ranged from 12% to 34% lower than estimates for the Pacific coast. The egg mortality rate for anchovy in the Gulf of California was higher than that estimated for anchovy along the Pacific coast of California during 1981–85. Only in 1980 was the California estimate higher. Adult parameters for anchovy in the gulf were generally similar to estimates for anchovy off California (table 4).

The small pelagic fishes in the Gulf of California vary in abundance. It is therefore necessary to continue assessing the anchovy population in order to understand the dynamic behavior of this important species in the Gulf of California.

ACKNOWLEDGMENTS

We thank the scientific and ships'crews of RV *BIP XI* and RV *BIP XII* for their work during the 1991 egg production survey. We are grateful to Nancy Lo for her help with methods and programs, and for her comments on this work. We also thank Beverly Macewicz for her assistance with computer programs. This paper greatly benefited from suggestions by George Hemingway, Larry Jacobson, and two anonymous reviewers. Support for this work was provided by Instituto Nacional de la Pesca. We also thank Cámara de la Industria Pesquera, Sec. Guaymas, Son., for support for laboratory technician.

LITERATURE CITED

Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull., U.S. 60:106–146.

Alheit J., V. H. Alarcón, and B. J. Macewicz. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25:43–52.

Armstrong, M., P. Shelton, I. Hampton, G. Jolly, and Y. Melo. 1988. Egg production of anchovy biomass in the southern Benguela System. Calif. Coop. Oceanic Fish. Invest. Rep. 29:137–157.

Bindman, A. G. 1986. The 1985 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep.27:16–24.

Blaxter, J. H. S., and J. R. Hunter. 1982. The biology of clupeoid fishes. Adv. Mar. Biol. vol. 20, Blaxter, Russell, and Yonge, eds. Academic Press.

Cisneros-Mata, M. A., M. O. Nevárez-Martínez, G. Montemayor, J. P. Santos-Molina, and A. R. Morales-Azpeitia. 1991. Pesquería de sardina en el Golfo de California 1988/89–1989/90. Instituto Nacional de la Pesca. Rep. Adm. CRIP Guaymas.

Clark, F. N., and J. B. Phillips. 1952. The northern anchovy (*Engraulis mordax*) in the California fishery. Calif. Fish Game 38(2):189–207.

Cotero-Altamirano, C. E. 1987. Ciclo reproductivo, madurez y fecundidad de la anchoveta *Engraulis mordax*: análisis comparativo en el período 1981–1983. Tesis de maestria. CICESE. Ensenada, B.C. 59 pp.

Cunha, M. E., I. Figueiredo, A. Farinha, and M. Santos. 1992. Estimation of sardine spawning biomass of Portugal by the daily egg production method. Bol. Inst. Esp. Oceanogr. 8(1):139–153.

Escudero-Díaz, M., and R. M. Olvera. 1976. Estimación de la biomasa reproductora de anchoveta *Engraulis mordax* Girard a partir del censo larval en la costa occidental de Baja California, México (nov. 1974 dic. 1975). Mem. Simp. Rec. Pesq. Mas. de México. Ensenada, B.C. Tomo 1:295–313.

TABLE 4
Time Series of Egg Production Parameters for Estimating Spawning Biomass of *E. mordax* in the California Current (1980–85)[a] and in the Gulf of California (1991)

Parameters		1980	1981	1982	1983	1984	1985	1991
Daily egg production (10^{12}) eggs/day)	P_0A	26.34	20.96	13.51	17.25	12.98	16.95	7.49
Egg mortality rate	Z	0.45	0.14	0.16	0.18	0.17	0.29	0.35
Average female weight (g)	W	17.44	13.37	18.83	11.20	12.02	14.50	13.64
Batch fecundity (eggs)	F	7,751	8,329	10,845	5,297	5,485	7,343	8,220
Spawning fraction	S	0.142	0.106	0.120	0.094	0.160	0.120	0.174
Sex ratio	R	0.478	0.501	0.472	0.549	0.582	0.609	0.68
Daily specific fecundity (eggs/g)	F/W	444	623	576	473	456	501	603
Spawning biomass (10^3 t)	B	870	635	415	652	309	522	105

[a]Bindman 1986.

Garcia, A., N. Pérez, N. C. H. Lo, A. Lago de Lanzós, and A. Solá. 1992. The egg production method applied to the spawning biomass estimation of sardine, *Sardina pilchardus* (Walb.), on the North Atlantic Spanish coast. Biol. Inst. Exp. Oceanogr. 8(1):123–138.

Green-Ruiz, Y., and Aguirre-Medina. 1989. Larvas de *Engraulis mordax* en el Golfo de California. IV. Reunión de la Sociedad Mexicana de Planctología. La Paz, B.C.S. Resumen.

———. 1990. Estimación de la biomasa reproductora de la anchoveta (*Engraulis mordax* Girard, 1896) en el Golfo de California (enero-febrero 1987). VII Congreso Nal. Ocean. Mazatlán, Sin. Resumen.

Green-Ruiz., Y., and A. Hinojosa-Corona. (In press). Study of the spawning area of the northern anchovy in the Gulf of California from 1990–1994: using satellite image of sea surface temperature. J. Plankton Res.

Hammann, M. G., and M. A. Cisneros-Mata. 1989. Range extension and commercial capture of the northern anchovy *Engraulis mordax* Girard, in the Gulf of California, Mexico. Calif. Fish Game 75(1):49–52.

Hewitt, R. 1983. Roll heave and vertical ichthyoplankton tows. Ocean. Sci. Eng. 8:41–51.

———. 1985a. 1984 northern anchovy spawning biomass. Calif. Coop. Oceanic Fish. Invest. Rep. 26:17–25.

———. 1985b. Comparison between egg production method and larval census method for fish biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 95–99.

Holmgren-Urba, D., and T. R. Baumgartner. 1993. A 250-year history of pelagic fish abundances from the anaerobic sediments of the central Gulf of California. Calif. Coop. Oceanic Fish. Invest. Rep. 34:60–68.

Humason, L. G. 1979. Animal tissue techniques. W. W. Freeman and Co.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. 77(3):641–652.

Hunter, J. R., and B. J. 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.

———. 1985. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 79–94.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 63–79.

Laroche, J. L., and S. L. Richardson. 1980. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington. Fish. Bull. 78(3): 603–618.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975–1978. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 178:375–388.

———. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer. NOAA Tech Rep. NMFS 36, pp. 7–15.

Lo, N. C. H. 1983. Re-estimation 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. NOAA-TM-NMFS-SWFC, 31. NOAA Tech. Memo. NMFS. U.S. Dep. Commer., NOAA, NMFS, SWFC. 33 pp.

———. 1985. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 43–53.

———. 1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. Fish. Bull., U.S. 84(2):395–407.

Lo, N. C. H., Y. A. Green-Ruiz, M. J. Cervantes, H. G. Moser, and R. Lynn. 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. Calif. Coop. Oceanic Fish. Invest. Rep. 37:160–174.

Macewicz, B. J., J. J. Castro-González, C. E. Cotero-Altamirano, and J. R. Hunter. 1996. Adult reproductive parameters of Pacific sardine (*Sardinops sagax*) during 1994. Calif. Coop. Oceanic Fish. Invest. Rep. 37:140–151.

Melcer, J., W. García, and E. Mondragón. 1976. Estimación de la biomasa y distribución de peces pelágicos frente a la costa occidental de B. C. Mem. Prim. Sim. Nal. Rec. Pesq. Mas. México.

Moser, H. G., and E. H. Ahlstrom. 1985. Staging anchovy eggs. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 37–41.

Murphy, G. I. 1966. Population biology of the Pacific sardine *Sardinops caerulea*. Proc. Calif. Acad. Sci. 34(1):1–34.

Nevárez-Martínez, M. O., R. Morales-Azpeitia, M. A. Martínez-Zavala, J. P. Santos-Molina, and M. A. Cisneros-Mata. 1993. Pesquería de pelágicos menores en el Golfo de California. Temporada 1990/991. Inst. Nal. Pesca. Rep. Adm. CRIP Guaymas.

Olvera-Limas, R. M., M. Escudero, S. de la Campa, and M. A. Padilla. 1983. Estimación de la biomasa reproductora de anchoveta (*Engraulis mordax*) en la costa occidental de Baja California, temporadas 1976 y 1977. Ciencia Pesquera Inst. Nac. de la Pesca. México. (5):1–15.

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

———. 1985. Biomass model for the egg production method. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 5–6.

Pedrín-Osuna, O. A., M. L. Granados Gallegos, and A. Cota-Villavicencio. 1992. Tasas de explotacion y mortalidad por pesca de la anchoveta nortena (*Engraulis mordax*) para el período de 1974 a 1989. Ciencias Marinas 18(4): 97–113.

Picquelle, S. 1985. Sampling requirements for the adult fish survey. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 55–57.

Picquelle, S. J., and R. P. Hewitt. 1983. The northern anchovy spawning biomass for the 1982–83 California fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 24:16–28.

———. 1984. The 1983 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 25:16–27.

Picquelle, S., and G. Stauffer. 1985. Parameter estimation for an egg production method of northern anchovy biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 7–15.

Robinson, M. K. 1973. Atlas of monthly mean sea surface and subsurface temperatures in the Gulf of California, Mexico. San Diego Soc. Nat. Hist. Mem. 5. 97 pp.

Santander, H., J. Alheit, and P. E. Smith. 1984. Estimación de la biomasa de la población desovante de anchoveta peruana *Engraulis ringens*, en 1981 por aplicación del "Método de producción de huevos". Bol. Inst. Mar. Perú ISSN-0378-7699. 8(6):211–250.

Santiago, J., and A. Sanz. 1992. Egg production estimates of the Bay of Biscay anchovy, *Engraulis encrasicolus* (L.), spawning stock in 1987 and 1988. Bol. Inst. Esp. Oceanogr. 8(1):225–230.

Scannell, C. L., T. Dickerson, P. Wolf, and K. Worcester. 1996. Application of an egg production method to estimate the spawning biomass of Pacific sardines off southern California in 1986. SWFSC, NMFS Admin. Rep. LJ-96-01, 37 pp.

Smith, P. E. 1981. Fisheries on coastal pelagic schooling fish. *In* Marine fish larvae: morphology, ecology, and relation to fisheries, R. Lasker, ed. Wash. Sea Grant Prog. Seattle: Univ. Wash. Press, 131 pp.

Smith, P. E., and R. P. Hewitt. 1985. Sea survey design and analysis for an egg production method of northern anchovy biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 17–26.

Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larva survey. FAO Fish. Tech. Pap. 175. 100 pp.

Smith, P. E., W. Flerx, and R. P. Hewitt. 1985. The CalCOFI vertical egg tow (CalVET) net. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U.S. Dep. Commer., NOAA Tech Rep. NMFS36, pp. 27–32.

Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the subpopulation of northern anchovy. NMFS, SWFC Admin. Rep. LJ-80-09. 41 pp.

Torres, V. J. R. 1986. Evaluación de la biomasa reproductora de *Sardinops sagax* por el método de producción de huevos en la Bahía Magdalena, B.C.S., México, CICIMAR-IPN. Tesis maestría en ciencias.

Uriarte, A., and L. Motos. 1991. Informe de la pesquería de la anchoa en el año 1990. Instituto de Investigación y Tecnología para la Oceanografía, Pesca y Alimentación. Depto. de Agricultura y Pesca Gobierno Vasco. 25 pp.

Zweifel, J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes: a general model. Fish. Bull. 74(3):609–621.