BATCH FECUNDITY AND SPAWNING FREQUENCY OF VARIOUS ANCHOVY (Genus: *Engraulis*) POPULATIONS FROM UPWELLING AREAS AND THEIR USE FOR SPAWNING BIOMASS ESTIMATES*

by

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Resumen

Recientemente se han revelado varias características esenciales de la biología reproductiva de la anchoveta peruana (*Engraulis ringens*) y ahora pueden ser comparadas con aquellas de la anchoveta del norte (*E. mordax*). Así como la anchoveta del norte, la anchoveta de sistema de afloramientos de Perú desova en forma parcial, depositando varias series de huevos a lo largo del año. Ahora se dispone de datos de series de tiempo sobre la fecundidad parcial de varias sub-poblaciones de ambas especies. La variabilidad de la fecundidad parcial es alta dentro de cada año y de un año a otro. En ambas especies, la fecundidad parcial aumenta a medida que aumenta la latitud. Fuera de las épocas principales de desove (Agosto-Septiembre y Enero) la fecundidad parcial de la anchoveta peruana disminuye. Durante El Niño de 1976, la fecundidad parcial de *E. ringes* disminuyó considerablemente. Esto se atribuye a las condiciones desfavorables de alimentación. La fecundidad parcial de *E. capensis* frente al sudoeste de Africa se encuentra dentro del rango de los valores de las otras dos especies. La frecuencia del desove fue determinada por exámenes histólogicos de los ovarios para observar la incidencia de folículos post-ovulatorios. La fracción de hembras maduras que desovan por día fue de 16% en 1961 frente a Perú y 14.5% en 1980 frente a California. Todos los parámetros reproductivos investigados son muy similares en ambas especies, indicando una relación filogénetica estrecha. La importancia de determinar la fecundidad parcial y la frecuencia del desove se basa en su uso para "el método de la producción de huevos" que fue desarrollado recientemente para estimar la biomasa desovante de anchoveta. Este método ha sido aplicado con suceso en los stocks de anchovetas frente a California y Perú. Se discuten los resultados, ventajas y futuras aplicaciones de este método para otras especies de peces pelágicos que forman cardúmenes tales como sardinas.

INTRODUCTION

Recently, a new method, the 'Egg Production Method', was developed by the Southwest Fisheries Center, California, to estimate the spawning biomass of anchovies (Parker, 1980; Stauffer and Picquelle, 1980). This method requires the determination of reproductive parameters like batch fecundity and spawning frequency, i.e. the fraction of mature females spawning per day.

The determination of batch fecundity and spawning frequency for multiple spawning pelagic fish, like the anchovy, posed several problems which were solved by Hunter and Goldberg (1980). In traditional methods, size - frequency diagrams of oocytes were established and it was assumed that fecundity could be determined by counting the number of all oocytes contained in the most advanced mode. Hunter and Goldberg (1980) discussed the problems involved in this method. Instead, they determined the batch fecundity by counting the number of hydrated oocytes in the ovaries. This method takes much less time and yields a higher precision than traditional methods. For the determination of the spawning frequency, Hunter and Goldberg (1980) used the incidence of postovulatory follicles in anchovies. They were able to age postovulatory follicles and to determine the day when a particular female had spawned. All these studies were carried out on the northern anchovy (*Engraulis mordax*). Recently, the same methods were applied successfully, to the Peruvian anchovy (*E. ringens*) (Alheit el al., in prep.; Santander et al., in prep.).

Time series are available now on the batch fecundity of the Peruvian and the northern anchovy. The data were partly gained from previous studies using traditional methods (MacGregor, 1968; Laroche and Richardson, 1980) and from samples collected in Peru during the seventies which were processed recently.

The objectives of this study are (1) to compare the time series on batch fecundity of the two anchovy species, (2) to compare for both species the data on batch fecundity and spawning frequency gained by the new methods, and (3) to discuss their use for estimates of spawning biomass of multiple spawning pelagic fish.

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METHODS

The batch fecundity of the Peruvian anchovy samples collected in the seventies was determined by macerating the connective tissue of the ovaries in Gilson's fluid (Simpson, 1951), a process which releases the oocytes. The size of the oocytes was measured and the number of oocytes in the most advanced mode was determined by means of probability paper (Cassie, 1954). The recent batch fecundity data for the Peruvian and northern anchovy were gained by using hydrated oocytes (Hunter and Goldberg, 1980). The methods used for determining the batch fecundity of other anchovy populations presented here are described in MacGregor (1968) for the northern anchovy in 1951-60, in Laroche and Richardson (1980) for the northern population of the northern anchovy and in LeClus (1979) for the anchovy off South West Africa (*E. capensis*). The spawning frequency was determined according to the methods described by Hunter and Goldberg (1980), Stauffer and Picquelle (1980) and Alheit et al. (in prep.).

Table 1: Mean number of oocytes per gram ovary, mean number of oocytes per gram female and geometric mean regression (Ricker, 1973) of eggs per spawn (= batch fecundity) on gonad-free female wet weight.

No.	Species	Sub-population	Year	Month	Sample Size	Size Range of fish (gonad-free weight in g)	Mean Nr Oocytes per g female	S.D.	Mean Nr. Oocytes per g Ovary	S.D.	r	Slope	Y-intercept
1	E. ringens	central	1970	Jan	19	15.2 - 40.0	7 123	± 2719	375	± 147	.685	1 048	-16 627
2	" "	"	1973	Sep	26	15.1 - 38.7	5 998	± 2728	410	± 172	.564	746	- 8 527
3	" "	"	1974	Jan	8	22.8 - 43.2	9 231	± 1938	489	± 133	.554	847	-13 125
4	" "	"	"	Feb	8	32.2 - 44.2	6 011	± 999	326	± 91	.126	667	-13 506
5	" "	"	"	Aug	12	17.7 - 41.3	7 067	± 2049	484	± 157	.717	1 517	-31 194
6	" "	"	"	Sep	9	21.0 - 48.4	8 233	± 1577	410	± 142	.692	705	- 8 814
7	" "	"	"	Oct	18	16.3 - 54.5	6 607	± 2295	268	± 110	.799	558	- 8 804
8	" "	"	1976	Aug	32	6.8 - 34.5	11 606	± 5447	415	± 143	.813	424	- 227
9	" "	"	"	"	11	15.0 - 34.5	7 686	± 1800	414	± 149	.509	360	1 257
10	" "	southern	1973	Sep	19	14.1 - 21.7	7 205	± 3125	395	± 122	.614	1 352	-17 490
11	" "	"	1974	Aug	23	9.0 - 41.3	6 432	± 2351	446	± 175	.831	1 087	-13 545
12	" "	northern + central	1981	Aug/Sep	437	15.0 - 38.0	*)		580	± 139	.806	981	-10 279
13	E. ringens	central	1981	Aug/Sep	254	15.0 - 38.0	*)		637	± 134	.769	1 213	-14 745
14	" "	northern	"	Aug/Sep	183	15.0 - 38.0	*)		502	± 103	.883	824	- 7 655
15	E. mordax[1]	central	1951-1960		19	9.3 - 32.1	12 253	± 2737	606	± 151	.795	670	- 1 247
16	" "	"	1978		23	9.3 - 31.9	*)		389	± 141	.511	528	- 2 790
17	" "	"	1979		44	9.3 - 28.1	*)		438	± 150	.784	881	- 7 917
18	" "	"	1980		33	17.11+)	*)		444	± 80	.903	624	- 2 933
19	" "	"	1981		127	14.75+)	*)		601	± 180	.873	872	- 3 711
20	" "	"	1982		109	16.54+)	*)		606	± 151	.724	852	- 4 061
21	" "	northern[2]	1977		17	14.4 - 31.3	7 137	± 3997	869	± 213	.860	1 494	-12 015
22	E. capensis[3]		1977		14	17.5 - 24.3	4 491	± 851	644	± 153	.451	1 542	-18 657

1) From MacGregor (1968) 2) From LaRoche and Richardson (1980) 3) From LeClus (1979)
*) Parameter not calculated as hydrated oocytes were used +) Average weight

RESULTS

Time series on fecundity of Peruvian anchovy. 14 different data sets on fecundity of the Peruvian anchovy are available (Table 1). They originate from different years, months and areas. There are no trends recognizable for the mean number of oocytes per gram female, however, some interesting features can be pointed out. Only one data set, January 1970, was collected before the crash of the Peruvian anchovy in 1972. This value is relatively, but not particularly low. The data set from August 1976 was collected during an 'El Niño' year. The collection includes many very small mature females between 7 and 15 g. To make this data more comparable, another data set comprising only the larger specimens (11 fish) is presented separately. The values from August 1976 lie just within the range of the other data sets. There are two data sets from the south, but they are not outliers. The only remarkable feature is the difference between the relatively low values from the seventies and the high values from 1981. This difference is probably not caused by the use of different methods. In 1981, two data sets were taken, one from the central region and one from the northern region. The one from the central region is with 637 eggs per gram female; much higher than the 499 eggs per gram female from the northern region. This might not necessarily be a regional difference, as the northern samples were, on average, collected two weeks later than the central samples. It could be that the value for the number of eggs per gram female is very flexible and can change very fast towards the end of the spawning season. In general, one can observe a decrease of the mean number of eggs per gram female after the main spawning periods in August/September and January, e.g. in 1974 and 1981. The number of oocytes per gram ovary, does not show any trend. Only the value for the large data set from August 1976 lies outside of the range of the other values. However, this high value is caused, solely, by the high number of very small mature females. The mean number of oocytes per gram ovary is not given for 1981, as this value changes during the process of hydration.

The relationship between batch fecundity and female weight (ovary-free) was investigated further by using the geometric mean regression (Ricker, 1973). Whereas all other data from the Peruvian anchovy have a relatively high Y - intercept, only the data from August 1976 have a positive and a relatively low negative value (Table 1). Differences between the 14 data sets become more obvious from the regression lines in Figures 1-3. They are presented in three different groups whereby the whole data set from August 1981 serves as a reference line. Group 1 includes all the data collected during the yearly peak spawning periods in August/September and January (Figure 1). These regression lines are not too different from each other. The second group comprises the 'El Niño' data from August 1976 and data sets collected at February 1974 and October 1974, outside of the yearly main spawning periods (Figure 2). These data sets have in common a relatively low batch fecundity for females larger than 30 g. The third group demonstrates regional differences. Obviously the fecundity values from the southern Peruvian anchovy stock are higher than in the central and northern stock. Although the data sets were taken in

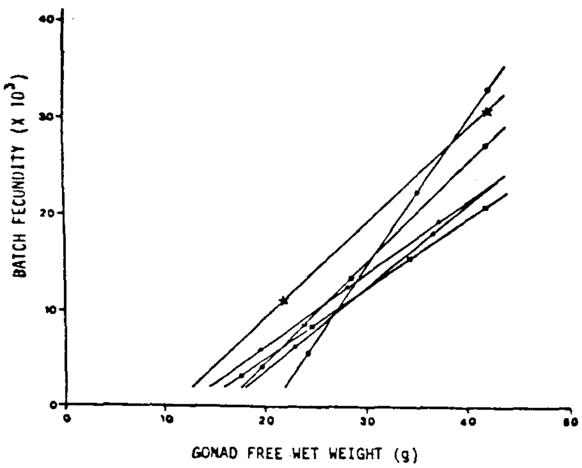


Fig. 1. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14 ○ = Lot 1
● = Lot 11 ▲ = Lot 2
△ = Lot 3 ■ = Lot 6

different years, they indicate, that the batch fecundity increases with increasing latitude (Figure 3).

Comparison of fecundity of different anchovy species. Batch fecundity data are available for the Peruvian anchovy, the northern anchovy and the anchovy from South West Africa. The values for the mean number of oocytes per gram female from the northern anchovy and the anchovy off South West Africa lie within the range of the Peruvian data (Table 1). The only exception is the high value for the northern population of the northern anchovy. From 1978 to 1982 the values of the central population of the northern anchovy increased steadily from 389 to 606 eggs per gram female weight.

The regression lines of the central population of the northern anchovy are relatively uniform (Figure 4). However, the regression line of the northern population is very distinct and demonstrates that females with more than 15 g weight have a much higher batch fecundity than in the central population. Again, as in Peru, the batch fecundity of anchovy populations increases with increasing latitude.

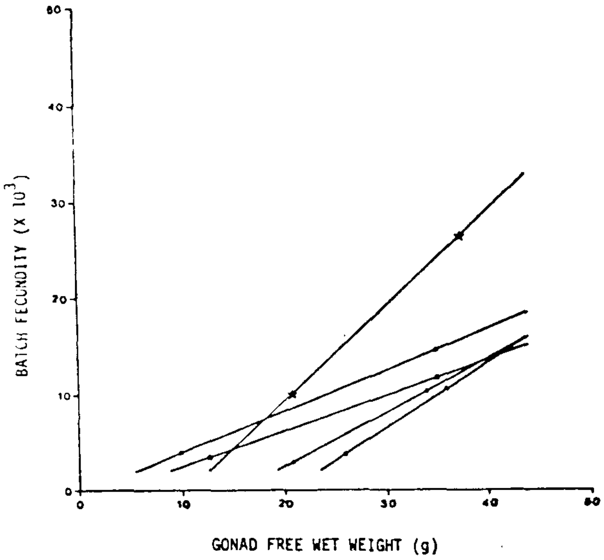
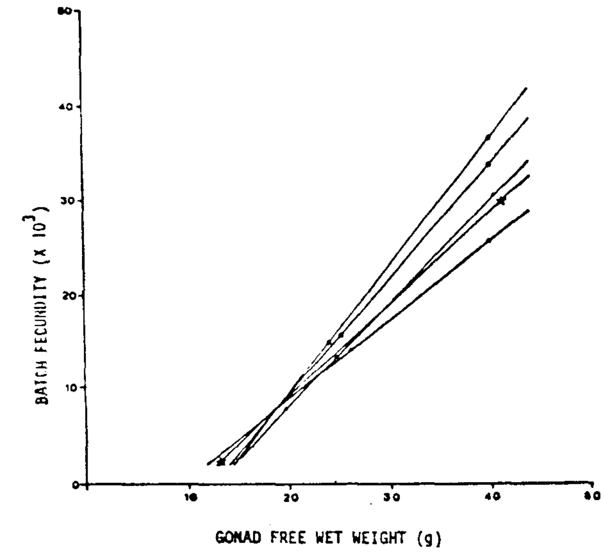


Fig. 2. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 8
▲ = Lot 7
o = Lot 8 (only females >12 g).
Δ = Lot 4

Fig. 3. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 10
▲ = Lot 11
o = Lot 13
Δ = Lot 4



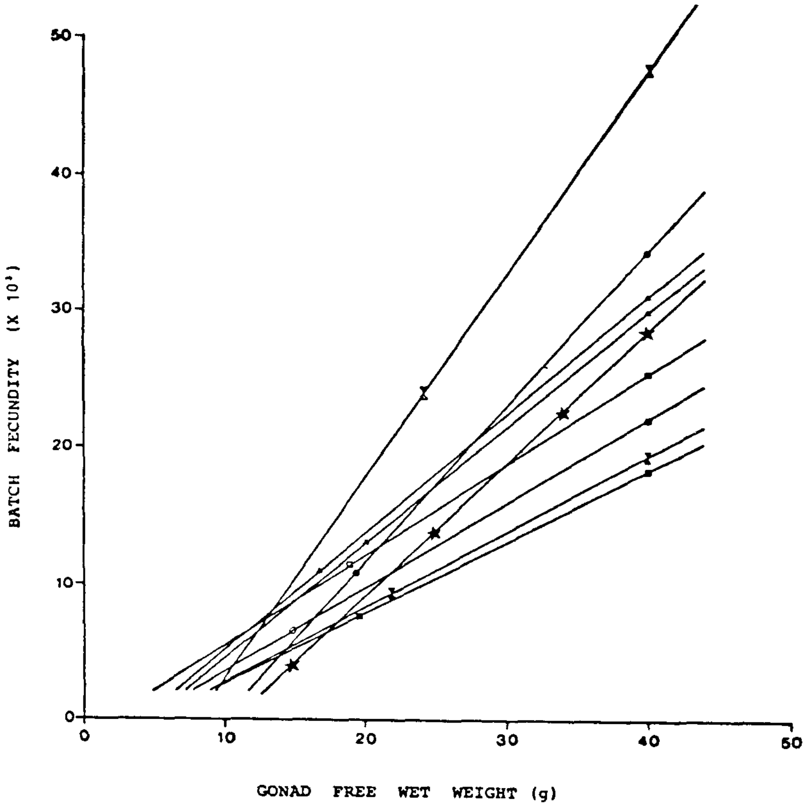


Fig. 4. Comparison of Different Species. Batch fecundity of anchovy populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★	= Lots 12 - 14	*E. ringens*	⧗	= Lot 21	*E. mordax*
●	= Lot 17	*E. mordax*	△	= Lot 19	*E. mordax*
▲	= Lot 20	*E. mordax*	□	= Lot 15	*E. mordax*
○	= Lot 18	*E. mordax*	■	= Lot 16	*E. mordax*, 1978, central population
⧗	= Lot 22	*E. capensis*			

Spawning frequency. The fraction of mature females spawning per day was determined for the Peruvian anchovy in August/September 1981. As a purse seiner was used to collect the adult anchovies, fish samples could be obtained at any time of the day and two data sets were established, one giving the fraction of females which spawned one day before being collected and the other one giving the fraction of females which had spawned two days before being sampled. These two spawning fractions were 17.26% and 14.81%, respectively (Alheit el al., in prep.).

The agreement of these two data sets demonstrates the validity of the method introduced by Hunter and Goldberg (1980). The spawning frequency determined for the Peruvian anchovy by combining these two data sets was 16.04%. That means every day during August/September 1981, on average, 16.04% of the mature females were spawning, or in other words, a female of the central and northern Peruvian stock spawned, on average, every 6.2 days a new batch of eggs. The spawning frequency recorded for the northern anchovy in 1981 was 14.5% (Stauffer and Picquelle, 1980) a value very similar to that one of the Peruvian anchovy.

Use of data on reproductive biology for estimates of spawning biomass. Batch fecundity and spawning frequency are two of the five parameters used for determining the spawning biomass of anchovies by means of the 'Egg Production Method' (Parker, 1980; Stauffer and Picquelle, 1980). So far, this method has been applied in California and Peru. The results of the Californian survey from 1980 (Stauffer and Picquelle, 1980) and from the Peruvian survey from 1981 (Santander et al., in prep.) are listed in Table 2.

Table 2: Results of spawning biomass estimates gained by application of 'Egg Production Method' in Peru 1981 and California 1980. Parameter estimates ($\hat{X}$) and estimates of spawning biomass with associated coefficient of variation ($CV_{\hat{X}}$). The data for Peru comes from Santander et al. (in prep.) and for California from Stauffer and Picquelle (1980).

	Peru 1981		California 1980	
	$\hat{x}$	$CV_{\hat{x}}$	$\hat{x}$	$CV_{\hat{x}}$
Daily egg production in survey area	$6.985.10^3$	0.2586	(10.50)*	0.103
Average female weight (g)	25.84	0.0259	17.50	0.0547
Fraction of females	0.564	0.0459	0.476	0.120
Batch fecundity (eggs/female)	15 401	0.0427	7 788	0.0749
Spawning frequency	0.160	0.0588	0.145	0.125
Spawning biomass (million tons)	1.295	0.2739	0.859	0.225

* This value is the number of eggs per ton.

DISCUSSION

The comparison of the batch fecundity data of different anchovy populations demonstrates clearly the high plasticity in batch fecundity of anchovies. There is a high variability in batch fecundity within years and between years as the Peruvian and Californian data show. One can only speculate about what causes this variability. Sufficient quantities of the right food are probably a very important condition for a fish to build up a high batch fecundity as argued by Bagenal (1978) and Wootton (1979). This might be indicated by the low fecundity values during the 'El Niño' year 1976 when feeding conditions were unfavourable for the Peruvian anchovy.

Tsukayama and Alvarez (1980) reported that during the 'El Niño' 1976 growth of the Peruvian anchovy was retarded and that the mean size of mature females was considerably less than in normal years. They suggested that the high proportion of small females would reduce the fecundity of the whole population. This hypothesis is confirmed by the data presented here. Population fecundity in 1976 was further reduced by the much lowered fecundity values of the larger females in comparison to other years (Figure 2). This lowered population fecundity is caused by the combined effect of a high proportion of small females and of large females having a lower batch fecundity than in normal years and certainly exerted a negative influence on subsequent recruitment.

The importance of the determination of batch fecundity and spawning frequency is based on their applications in the 'Egg Production Method' to estimate the spawning biomass of anchovies. The main advantages of the 'Egg Production Method' are its high precision and that it needs relatively little ship time. It consists of 5 biological parameters and error estimates can be determined for each of them (Table 2). To date, it has been applied four times in the Californian upwelling system (1980-1983) and once in Peru (1981).

Up to now, it was applied only to anchovies. However, it is suitable for other multiple spawning pelagic fish species, too. Recently, postovulatory follicles have been identified and aged for the Peruvian sardine (*Sardinops sagax sagax*) (Alarcon et al., in prep.), a vital step towards the application of the 'Egg Production Method' for sardines.

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