

COMPARISON OF EGG SAMPLE PROBABILITY DISTRIBUTIONS
OF THE ANCHOVY (*Engraulis ringens*) AND SARDINE
(*Sardinops sagax*) OFF PERU AND THE ANCHOVY (*Engraulis mordax*)
AND THE SARDINE (*Sardinops caerulea*) OFF CALIFORNIA

by

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Resumen

Se dispone de datos de reconocimiento de ictioplancton de más de 20 años del sistema de afloramiento del Perú y de más de 30 años del sistema de afloramiento de California. Se comparan las distribuciones de probabilidad de muestras de huevos de dos especies de clupeidos de estos dos sistemas (*Engraulis ringens* y *Sardinops sagax* del Perú y *E. mordax* y *S. caerulea* de California). El análisis de las distribuciones de las muestras de huevos combinado con datos adicionales permite estudiar actividades biológicas importantes de peces pelágicos, tales como agregación, fertilización, etc. Además se puede determinar la efectividad de canibalismo directo e incidental, de la predación, y de otras causas de mortalidad a través de la distribución inicial de huevos y la dispersión subsiguiente y el transporte hacia afuera de las áreas de desove. La escala e intensidad del patrón cambian con el tiempo y pueden afectar el esfuerzo de muestreo que se requiere para estimar la producción y sobrevivencia de los huevos y pueden complicar el ajuste de las ecuaciones de mortalidad que asumen una varianza constante con términos absolutos o relativos.

INTRODUCTION

The egg sample probability distribution of the Peruvian anchovy (*Engraulis ringens*) has been used to design an egg production survey with precision estimated from existing samples by Santander, Smith, and Alheit (1982). It should be possible, with existing data, to estimate the optimum survey effort for the determination of egg production of the sardine off Peru and California and analogous multiple pelagic-spawners of other species and in other areas, given historical sample data.

It is the purpose of this paper to briefly compare historical data on egg abundance per sample for four stocks from two genera (*Engraulis* and *Sardinops*), from two habitats (Peru and California). While it is not yet possible to infer historical egg production rates from these sets of data it should now be possible to estimate the number of samples needed for a given precision in future surveys. Also the analysis of sample probability distributions may lead to new insights into the origins of patches of eggs and the fate of the spawning products as they disperse (Smith, 1973) and the causes and degree of variation in the survival of the spawning products. This study was part of a cooperative project of the Southwest Fisheries Center, California, the Instituto del Mar del Peru and the "Cooperative Peruvian-German Fisheries Research Project" (PROCOFA) which is financed by the "German Agency of Technical Cooperation" (GTZ).

METHODS

Detailed accounts of sampling and sorting methods are given by Santander and S. de Castillo (1979) for the Peruvian samples and by Kramer et al. (1972) for the Californian samples. Briefly, the IMARPE samples are from a Hensen Egg Net towed vertically from 50 meters depth sampling directly under 0.3 square meters. The CalCOFI samples were towed obliquely from 140 or 210 meters. To report the values in similar units the IMARPE samples are divided by 3 and both are reported here as eggs per square meter sea surface area.

RESULTS

The number of anchovy eggs in the IMARPE samples was greater than the number of anchovy eggs in the CalCOFI samples. The number of sardine eggs in the IMARPE samples was greater than those in the CalCOFI samples. Both species of the genus *Engraulis* yielded number of eggs greater than the cohabitant of the genus *Sardinops* (Figures 1 and 2).

Part of the differences between the numbers of eggs per sample are due to the sampling technique. Some anchovy eggs are lost through the meshes of the CalCOFI net. Also the lower threshold of egg density detected by the IMARPE net is higher (3 eggs per square meter) than that detected by the CalCOFI net (approximately 0.3 eggs per square meter). Since the bulk of the population at the egg stage is in the larger samples, it is not likely that these differences will be important.

The difference in sardine eggs per unit surface area between IMARPE samples and CalCOFI samples is of the same order of magnitude as the difference in anchovy egg sample sizes. In both cases the difference is between 4- and 16-fold. This signals a radical difference between the Peruvian and Californian habitats which directly effects both sardine and anchovy at the time of spawning and during the subsequent dispersal and mortality phase.

DISCUSSION

The most important result of this study is that for a given precision it will be necessary to take more samples in the area of spawning to estimate the egg production of the stocks of *Engraulis* and *Sardinops* off Peru than off California. That this is not inherent in the different methods of sampling or different stock sizes is indicated by the stability of the egg distributions of the Californian sardine when several different samples sizes were used while the spawning biomass changed from 4 million tons to less than 10 thousand tons (Smith and Ricardson, 1977).

FIGURE 1

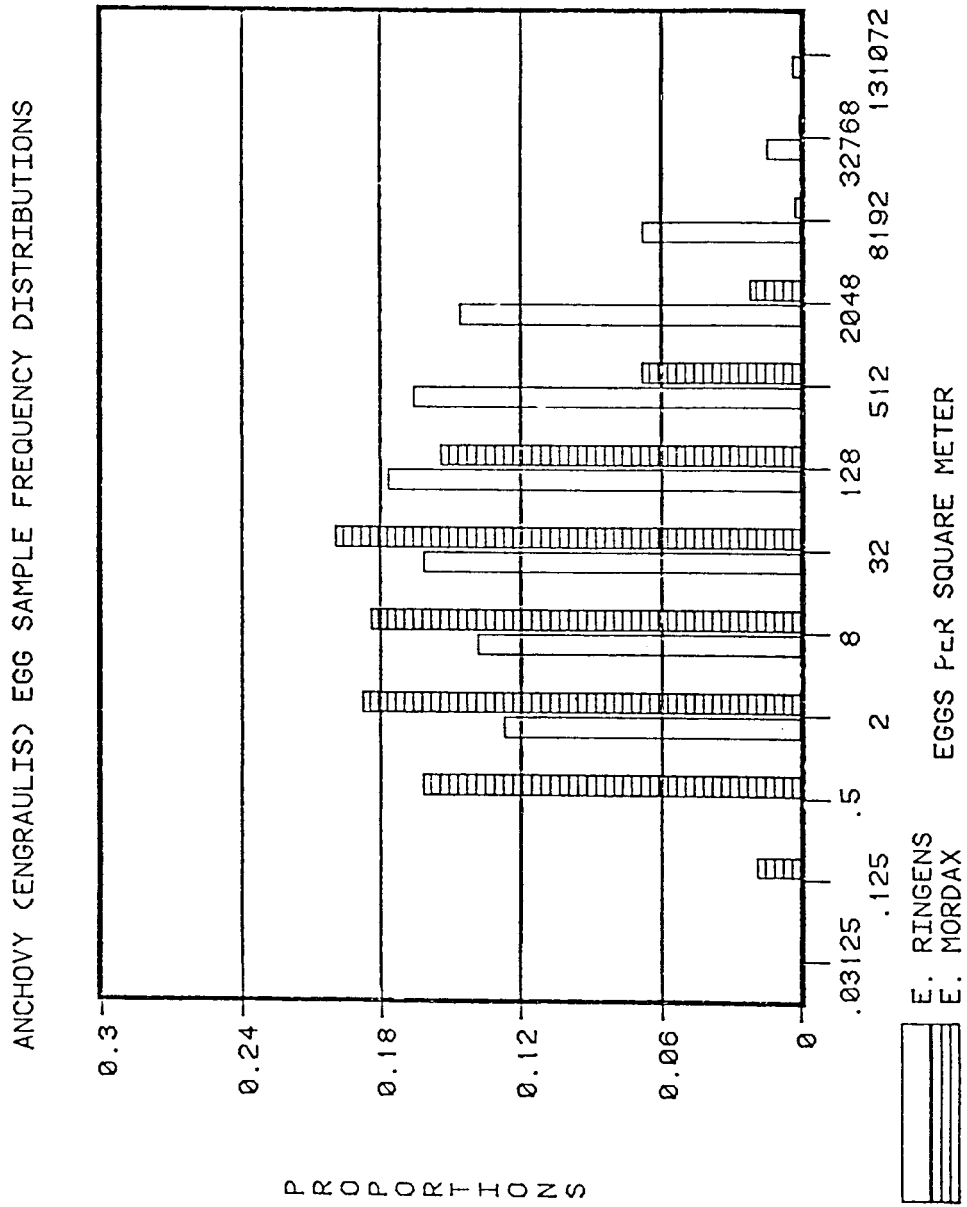
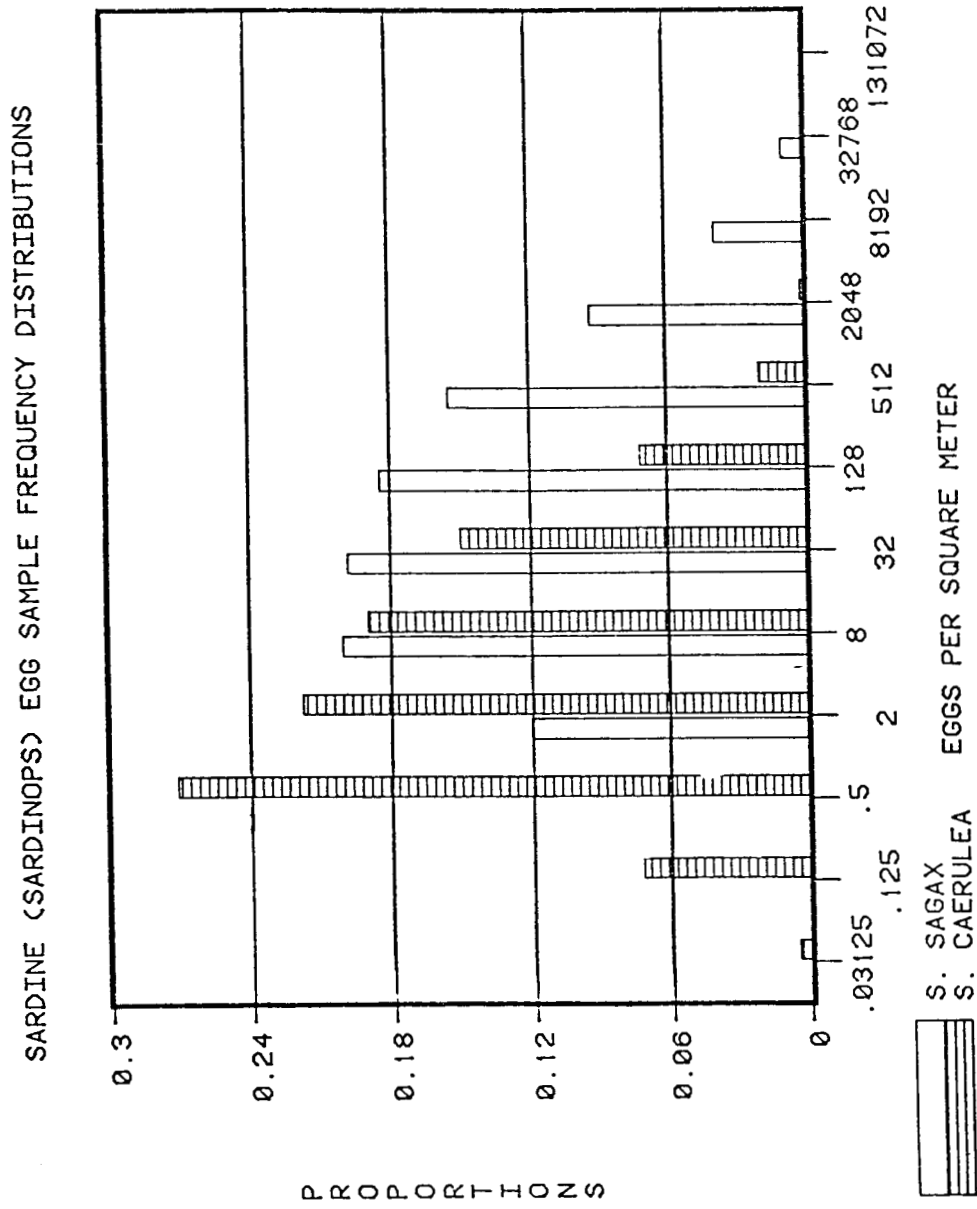


FIGURE 2



To explore the meaning of the egg sample distributions presented here, it is necessary to postulate a conceptual framework for the four stocks of fish which incorporates spatial distribution of mature adult fish at the time of spawning and the time distribution of the spawning process.

Spatial scale and intensity of distribution: Unfortunately the features of spatial scale and intensity are not equally well known for the four stocks examined here. The geographic distribution of all four species is well known. Also, the stock boundaries are well known in the offshore-onshore plane, but are less well known along the coast and these stock divisions may fluctuate with season and with interannual climatic conditions of changes in stock biomass (see MacCall, in prep.).

For scales of distribution below the species, and stock or subpopulation, only the beginning of perception has been reached for *Engraulis mordax*. Schools are unevenly distributed in the habitat and the aggregations of schools are called "school groups" or "shoal groups" (Fiedler, 1978). These can be characterized as 3000 schools in a 6 nautical mile (10 km) disc with 100 schools per square nautical mile. While most of the schools are small (15 m radius) most of the fish are in large schools (50 m radius). The school groups probably include all ages and sizes of fish but the schools probably consist of either "0" group or adult but not both.

Hewitt, Smith and Brown (1976) estimated that the schools contained 15 kilograms of mature fish per square meter of which some fraction are ready to spawn each night. It is not known what fraction of males participate in spawning each night. The females spawn in the height of the spawning season each 6 to 8 nights (Hunter and Macewicz, 1980; Alheit et al., this volume). That the spawners for a given night segregate within the school before spawning is suggested by the odd sex ratios (3 or 4 males per female) and above average proportions of spawning females.

It is also not known how the various spawners are arrayed at the time of spawning. The quantity of sperm available probably limits the volume through which the eggs are distributed. For the purpose of this discussion we shall use the concentration of ten thousand to one hundred thousand eggs per cubic meter.

In summary, the species involved in this paper extend for one or two thousand miles of coastline in the temperate zone of the Pacific coast of North and South America and into the tropics of South America. The species are apparently subdivided into stocks or subpopulations extending a few hundred miles along the coast within tens of miles of the coastline in South America and within a few hundred miles of the coast in North America. We assume that these stocks form school groups of a few nautical miles extent and these are comprised of schools of tens of meters radius concentrated at 100 schools per nautical square mile. Within the schools in daytime, there are about 15 kilograms of fish per square meter of surface area. The night-time concentration is assumed to be less dense. Also, in the spawning season, the spawning females and their male attendants segregate early in the evening to spawn and fertilize the spawn and reaggregate with the schools before dawn.

Temporal scales of egg production: The early work on spawning frequency (Hunter and Goldberg, 1979; Alheit et al., this volume) indicates that a female of the genus *Engraulis* may spawn a hundred or so batches of eggs in her lifetime. The female may spawn a limited number of times in the first year of life and in later years may spawn 30 times per year. The spawning appears to be intensified seasonally, beginning in the winter months and persisting for some months, depending on the age, size, and condition of the female and the feeding conditions. Hunter (pers. comm.) believes that spawning rate in *Engraulis mordax* is controlled by the amount of fat stored in previous summer and the feeding conditions at the time of spawning. Hunter and Leong (1981) state that 10 to 15 batches could be spawned using the energy in stored fat and that subsequent spawnings would be derived from feeding during the spawning season. Smith and Eppley (1982) found a correlation suggestive of a link between the zooplankton abundance in the preceeding summer and the larva abundance in the spawning season. Hunter (pers. comm.) believes the pattern of atresia or resorption of oocytes prior to spawning matches this viewpoint since atresia is most common in young fish with little stored fat and with older fish late in the season of heaviest spawning.

On the daily time scale, the collective spawning interval extends from about sundown to a couple of hours after midnight with a propensity to spawn within 3 hours of midnight. It appears that individual females spawn in a very short time because the increasing incidence of samples with newly spawned eggs (fraction of samples with newly spawned eggs) and the increasing abundance of newly spawned eggs (newly spawned eggs per sample) with time are nearly parallel. If individual females spawned over an 8 hours period one would expect the incidence of newly spawned eggs to rise rapidly with the change in abundance following many hours later.

These general features appear to be similar for *Engraulis mordax* and *E. ringens*. The life span of the *Sardinops* is much longer but the number of spawnings or the maximum rate of spawning is not known for this genus. However the daily cycle of spawning is similar in *Sardinops caerulea* (Smith, 1973).

Changes of spatial scale with time: At the moment of spawning, the *Engraulis* schools are at the scale of tens of meters and the scale of the egg patches of *Sardinops* and *Engraulis* are on the scale of hundreds of meters (Smith, 1973; Smith and Hewitt MS) and the yolk sac larvae patches are on the scale of a few thousand meters (Hewitt, 1982). In a period of five days after spawning turbulent diffusion has spread the newly spawned eggs, covering at most a few tenths of one percent of the sea surface in the spawning area to covering nearly 70% of the sea surface at hatching time.

There may be different explanations for the greater intensity of *Sardinops* and *Engraulis* egg distribution off Peru as compared to California and the differences between the *Engraulis* in both hemispheres and the *Sardinops* in both hemispheres. To consider these, we must establish some useful categories of causes for differences in the scale and intensity of patches of eggs. One category of difference can be termed "demographic". That is if the age distribution of the females is older the stock will be made up of larger fishes and for the two genera the size distribution of *Sardinops* females will be larger than *Engraulis* females. Another category of difference can be labeled "behavioral". That is if the individual females behave in such a way as to distribute their spawn in smaller, more compact patches this would retard subsequent dispersal rates relative to females which disperse their spawn in larger, more diffuse patches. Another category of difference causing changes in distribution of sample sizes of eggs could be labeled "environmental". That is the subsequent mixing of the spawning products or the pattern of mortality could in time impose a different sample frequency distribution. We shall discuss these categories in more detail.

Demographic factors affecting the number of eggs per sample: The relationships between fish weight and eggs per gram of fish weight are not completely known for *Engraulis mordax*, *Engraulis ringens*, *Sardinops caerulea*, and *Sardinops sagax*. For *Engraulis mordax*, the relationship is apparently linear (Picquelle and Hewitt, 1982; Alheit et al., in prep.) for the period 1980 through 1982 for the central subpopulation. Neither *E. mordax* nor *E. ringens* have been examined with regard to age-specific fecundity as distinguished from size-specific fecundity. Even though age and weight are related, the differences between weight at age and the ranges of weights and ages could explain the differences apparent in the linearity of the fecundity with weight. It is not known how this would affect the distribution of eggs in the sea. If the older or larger females were capable of spawning more eggs into a column of water there could be persistent changes in the egg sample distribution. However, it appears that the *Sardinops* places fewer eggs in a column of water even though the female of the genus *Sardinops* is larger than the female of the genus *Engraulis*.

Another demographic feature is age and size at first maturity. Females of genus *Engraulis* appear to begin maturation in the first year of life while the females of the genus *Sardinops* mature somewhat later and at a larger size. Within *Engraulis mordax* females it is characteristic for the "0" group females to begin spawning later in the season and stop sooner than females of the older cohorts. If there were similar maturational features in the genus *Sardinops*, this could lead to both inter-specific and inter-generic differences by some influence on the number of eggs spawned in a column of water according to size. In this case, smaller movements of smaller females would tend to increase the number of eggs per unit surface area. While this would explain the inter-generic differences it is contrary to the interspecific differences in *E. mordax* with an average female weight of 16 grams while *E. ringens* with higher numbers of eggs per unit surface area had female weights in the range of 25 grams.

In summary, it is not clear how demographic features could by themselves explain the differences in eggs per unit surface area. It seems more likely that demographic features would be coupled with behavioral and environmental factors to change the distribution of spawn.

Behavioural factors affecting the number of eggs per sample: On the geographic scale, if the adults of the species aggregate on a specific spawning site this would tend to increase the number of eggs per unit area within the spawning area. It is known that *Sardinops caerulea* migrated to a spawning site hundreds of miles from the feeding zone. To what degree the *Engraulis* species do this is not known but the *Engraulis ringens* spawning zone appears to be much more restricted in distance from shore than that for *Engraulis mordax*. Thus one source to be considered for the differences in the number of eggs per sample is the degree to which the spawners aggregate for spawning. This increases the chance that areas with new spawn would overlap other spawning sites from previous days and thus the number of eggs per unit surface area would be higher. If this were the main cause the order of concentration at spawning time would be *Engraulis ringens*, *Engraulis mordax*, *Sardinops sagax* and *Sardinops caerulea*. This behavioural factor could interact with population demography if the older and larger females were more capable of assembling denser spawning aggregations.

Another behavioral factor could apply at the individual spawning fish scale. For example, if one species, say an *Engraulis* in this case, were to continually turn and circle while spawning and *Sardinops* were to undertake long spawning runs in a straight line, this could affect the initial concentration of eggs and the subsequent dispersal rate. If linear spawning runs were the usual, this would also interact with the demographic factors by faster swimming rates.

Environmental factors affecting the number of eggs per sample: Temperature, turbulence, predation and production are environmental factors affecting the number of eggs per sample. Temperature influences the developmental rate of the eggs (Table 1) and thus influences the probability that the eggs from two different spawning concentrations would be found in a single sample. For example the largest sample of 1300 samples of *Sardinops caerulea* eggs taken between 1951 and 1959 contained two ages of eggs two days apart in age (Smith, 1973). The probability of this kind of event would increase in colder water. The duration of the egg stage at 13 degrees Celsius is about four days for *Sardinops* and *Engraulis* and two days at 18 degrees. This does not appear to be the case for the stocks under investigation. The IMARPE samples are from warmer temperature than the CalCOFI samples.

Table 1
TEMPERATURE AND INCUBATION TIME FOR
ENGRAULIS MORDAX AND *SARDINOPS CAERULEA*
(ZWEIFEL AND LASKER, 1976)

INCUBATION TEMPERATURE	<i>ENGRAULIS MORDAX</i>	<i>SARDINOPS CAERULEA</i>
11		5.8 days
11.1	4.7 days	
12		4.8
12.5	4.1	
13		3.9
13.8	3.3	
14		3.3
15		2.8
15.2	2.6	
16		2.5
16.6	2.3	
17		2.2
18	2.0	2.0
19		1.8
19.4	1.7	
20		1.6
20.8	1.5	
21		1.4

Turbulent diffusion could have a major effect on the number of eggs per sample. It appears that both *Engraulis* species and *Sardinops* select areas and seasons which minimize turbulent diffusion and offshore transport (Bakun and Parrish, 1982; Husby and Nelson, 1982) off the Pacific coastline of both North and South America. It seems likely that the differences in egg sample numbers could be controlled by the rate of the turbulent diffusion or by a combination of higher initial concentrations of eggs interacting with the lower rate of turbulent diffusion which this would imply.

The effect of predation on the numbers of eggs in each sample would be to change the probability of more than one day's spawning being taken at the same time. It would also be important to know if predation interacted with behavioral features of the predators including cannibals. For example if the predation were merely incidental to feeding on other food particles there would be a proportional drop in all ages of eggs in numbers per unit area. If there were directed predation on the densest concentrations of eggs there would disproportionately higher losses in the earlier ages at the highest concentrations. This could also have an effect on the differences between *Engraulis* and *Sardinops* eggs as the latter are much larger and may be filtered by more predators. The difference in effects would rest on the relative concentrations per unit volume even though the effect would eventually be expressed in numbers of eggs per unit sea surface. The relative visibility of the *Engraulis* and *Sardinops* eggs would be important for visual predators. The differences between the stocks in different hemispheres would also depend on the abundance and effectiveness of the predators found in those waters in the spawning season. Production may influence the numbers of eggs per sample. One way in which food production could control the numbers of eggs per sample is by increasing the frequency of spawning. So far the applications of the SWFC Egg Production Method have found the frequency of spawning off California to be 14.5% in April of 1980, 10.6% in February of 1981, 12.5% in April of 1981, and 12.0% in February of 1982. Off Peru in August-September of 1981, the percent spawning was 16%. This translates to a group average of mature females spawning each 6 days respectively. Spawning at high frequency would influence the chance of two spawning patches overlapping which would increase the range of egg numbers and increase the chances of sampling the origin of an egg patch which would increase the frequency of sampling large numbers of eggs less than the maximum.

Another mechanism for production to influence the number of eggs in a sample is by controlling the feeding behavior of the reproducing stock. For example if the stock were distributed so as not to depress the number of herbivores, the feeding behavior of *Engraulis* and *Sardinops* would be by biting-diminishing the incidence of cannibalism by inadvertant filtering. If production were lower and the growth of the herbivore populations were depressed by the fish, then the incidence of filter feeding and incidental cannibalism would increase, diminishing the numbers of eggs per sample.

Another factor controlled by production would be if the mean motion of that portion of a school which is spawning were reduced in favorable feeding areas and increased in less favorable feeding areas. For example a daytime school may contain 15,000 grams of adult fish per square meter of sea surface area over the school. With no net motion nor spreading of the school at night, there would be 7,500 grams of females and about 1000 grams of spawning females per square meter of sea surface area. With a batch fecundity of 500 eggs per gram, there would be 500,000 eggs per square meter, a number higher than yet observed for any of the four stocks considered here. If the feeding activities carried the school 250 meters during the half-hour spawning period there would be 2000 eggs per square meter. This number is exceeded in about 20% of the samples of *E. ringens*, 3% of the samples of *E. mordax*, 15% of the *S. sagax*, and less than 1% of the samples of *S. caerulea*.

SUMMARY

- 1) The numbers of eggs of *Engraulis ringens* off Peru per square meter exceed those of *Engraulis mordax* off California.
 - 2) The numbers of eggs of *Sardinops sagax* off Peru per square meter exceed those of *Sardinops caerulea* off California.
 - 3) Both off Peru and California the numbers of eggs from the genus *Engraulis* exceed those of the genus *Sardinops*.
 - 4) A wide variety of demographic, behavioural and environmental factors has been discussed singly and jointly and there needs to be special research conducted to identify the most important influences. It seems plausible that the differences in numbers of eggs per square meter between the genera *Engraulis* and *Sardinops* are caused primarily by demographic differences in the populations and that the differences between the Peruvian stocks and Californian stocks are caused primarily by environmental factors in concert with behaviour.
 - 5) Regardless of the causes of the difference in egg distribution among the four stocks off Peru and California, caution is warranted in establishing the optimum number of samples for calculating the egg mortality using the Southwest Fisheries Center Egg Production Method. It appears that more samples will be needed for a fixed precision in the Peruvian anchoveta compared with the other three stocks.
 - 6) Some of the features distinguishing the four stocks studied here may effect the efficacy of the mortality regression method and its precision. Particularly those features implying selective predation and cannibalism (Santander *et al.*, MS) could strongly affect the assumption of equal variance in real or proportional terms for the regression of egg abundance on time. Also environmental changes in the rate of dispersal of the eggs could also complicate regression methods which require stability of variance among the elements of the regression.
 - 7) The degree of difference among the eggs per unit surface area, when all have likely had an origin in a compact volume for external fertilization, is likely to portend great differences in the biology of the embryonic stages and the ultimate contribution of fluctuations of position and survival during this stage to population control mechanisms.
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