

Comparison of the Mortality Rates of Pacific Sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, Eggs off Peru¹

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ABSTRACT: Egg production and mortality rates were estimated for populations of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, off north and central Peru for August to September 1981. Peruvian anchovy spawned in the entire inshore region, principally within 56 km (30 nmi) of the coast. The Pacific sardine spawned extensively in the northern and southern inshore regions but not in the central region. While spawning of the two species coincided at the regional scale, at the sample scale, the occurrence of eggs of the two species was statistically independent. The egg production rate of Peruvian anchovy was about double that of sardine. The mortality rate of Pacific sardine eggs was much higher than that of Peruvian anchovy. The egg mortality rates of Peruvian anchovy and Pacific sardine were unchanged at stations where Pacific sardine and Peruvian anchovy eggs occurred together, relative to where the two species' eggs occurred separately. Results of this study are used to evaluate cannibalism as a population limiting mechanism. Cannibalism accounts for about 30% of egg mortality in anchovy. Because of the schooling habit of sardines and anchovies, cannibalism, though large-scale, may not vary enough with population size to explain variations in recruitment.

In their review of clupeoid biology, Blaxter and Hunter (1982) emphasized the need to estimate instantaneous rates as the "only way to establish a satisfactory linkage between the fish

and their environment." These instantaneous rates include production of spawn (Lasker 1985) and mortality rate of the eggs and larvae. Predation is thought to be an important cause of mortality, and one form of predation, cannibalism, has been proposed as a mechanism for establishing an upper limit to population density (Ricker 1954; Hunter and Kimbrell 1980; MacCall 1980; Alheit 1987; Pauly and Soriano 1987) of filter-feeding, pelagic spawning, schooling coastal pelagic fishes.

MacCall (1983) has described abundance as a composite of population density and geographic extent: northern anchovy, *Engraulis mordax*, appears to have a central area where density-dependent processes have their greatest effect on local density and a peripheral area where density-dependent processes are less important. Reductions of density in the central area result in contractions of the population to the central area for Pacific sardines, *Sardinops sagax*, (Murphy 1966) and northern anchovy (MacCall 1980). Off California both sardines and anchovy contract to the same area (Ahlstrom 1967).

Microstructure in the sea plays an important role in interaction of predator and prey (Lasker and Smith 1977) at the embryonic and larval stages (Smith 1973; Vlymen 1977; Theilacker 1987). There may also be rapid changes in the microstructure due to dispersal (Smith 1973; Smith and Hewitt 1985b). McGurk (1987) has proposed that small-scale pattern may make mortality rates proportional to patchiness rather than inversely proportional as originally suggested by Brock and Riffenburgh (1960).

Subsequent variations in recruitment may be caused by environmental influences on first-feeding larvae (Hjort 1926; Lasker 1975, 1978, 1981; Peterman and Bradford 1987), and recruitment is regulated by the interaction of growth and mortality rates of juveniles (Shepherd and Cushing 1979; Smith 1985; Butler 1987). Peterman et al. (1988) demonstrated that in a selected subset of years there was no relationship be-

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tween the abundance of northern anchovy larvae off California at 20 days of age and the recruitment at age 1. It had previously been shown that, for a shorter time series in the same habitat, Pacific sardine recruitment at two years old varied 15-fold, while the egg abundance in the year of origin for the same years varied only 3-fold (Smith 1978).

A major barrier to estimating egg mortality in pelagic schooling fish is the tendency of these fish to aggregate closely for external fertilization of spawn (Leong in press), presumably to conserve sperm and ensure high fertilization rates. The eggs are subsequently dispersed by turbulent diffusion (Smith 1973; Smith and Hewitt 1985a). Schooled spawning, with its spatially intense pattern, imposes a high sample variance on the younger eggs, and dispersal reduces the sample variance with time (Smith and Hewitt 1985a).

Precise estimation of survival and egg production rates requires large numbers of samples. The intensity of patchiness is indicated by the maximum values for egg counts. Smith (1973) observed that the concentration of Pacific sardine eggs off California was a maximum of 3,100 eggs/m², and Hunter (1980) observed that a concentration of 1 d old northern anchovy eggs was 4,600 per m². Walsh et al. (1980) reported the results of sample analyses of Peruvian anchovy eggs along the Peruvian coast. From five samples at lat. 10°S and seven samples at 15°S, they found a maximum value of 11,500 Peruvian anchovy eggs/m², and they also found Peruvian anchovy larvae at 100 and 200 per m². Santander et al. (1982) reported on Peruvian anchovy and Pacific sardine off Peru. For Peruvian anchovy, they found a maximum egg concentration of 107,376 eggs/m² (all ages). This count was from the largest of 911 ichthyoplankton tows with Peruvian anchovy eggs out of 4,028 Hensen net samples between 1966 and 1979. For Pacific sardine off Peru, the maximum egg concentration was 58,500 eggs/m² (H. Santander²). This count was from the same set of 4,028 tows.

Pacific sardine spawning off Peru has been essentially stable between 1978 and 1981 (Santander 1981). What are the implications for selection of spawning sites for the two pelagic spawners? Do the two species partition the environment into separate spawning areas or do they concentrate on oceanic sites favorable to

both? What are the relative rates of egg production and mortality where they co-occur?

In this paper we describe regional and inter-specific differences in egg production and mortality off Peru. The Peruvian anchovy data used for this paper have already been used for estimating egg production of the Peruvian anchovy population off north and central Peru (Santander et al. 1984). The Pacific sardine egg data off Peru are adequate for determining egg production per unit area, but contemporaneous adult reproduction rates are lacking; thus, sardine adult biomass has not been estimated.

METHODS

Cruise plan, sampling methods, laboratory methods, and data analysis have been described fully by Santander et al. (1984; an English version can be obtained from the author J. Alheit). Only a brief account of these methods is presented here.

The objective of the investigation was to encompass the Peruvian anchovy and Pacific sardine spawning grounds off northern and central Peru with an intensive grid of ichthyoplankton stations. The survey extended from Pisco (lat. 14°S) in the south to Punta Falsa (6°S) in the north. The background, a computer program for distributing the stations, and other technical details of the cruise plan are described in Smith et al. (1983). The sampling stations were distributed on transects perpendicular to the coastline. The inshore spacing of transects was 10 nmi. Thirty-five transects extended 30 miles offshore and 18 transects extended 90 miles offshore. On all transects the sampling stations were three miles apart. The total number of stations was 925. The area under investigation was subsequently divided into nine regions for some aspects of the analysis (Fig. 1).

Eggs were sampled with the CalVET net (CalCOFI vertical egg tow; Smith et al. 1985). Its mesh size was 333 μm, and its mouth area was 0.05 m². The net was towed vertically from a 70 m depth to the surface within 1 minute. The net filtered 3.5 m³ of water.

Following sorting, the eggs were aged according to their developmental stage, the surface water temperature, and the time of day when the sample was collected. The following is a brief summary of the method for determining Peruvian anchovy egg production; a complete description of these techniques for northern anchovy is found in Picquelle and Stauffer (1985).

²H. Santander, Instituto del Mar del Peru, Apartado 22, Callao, Peru, unpubl. data.

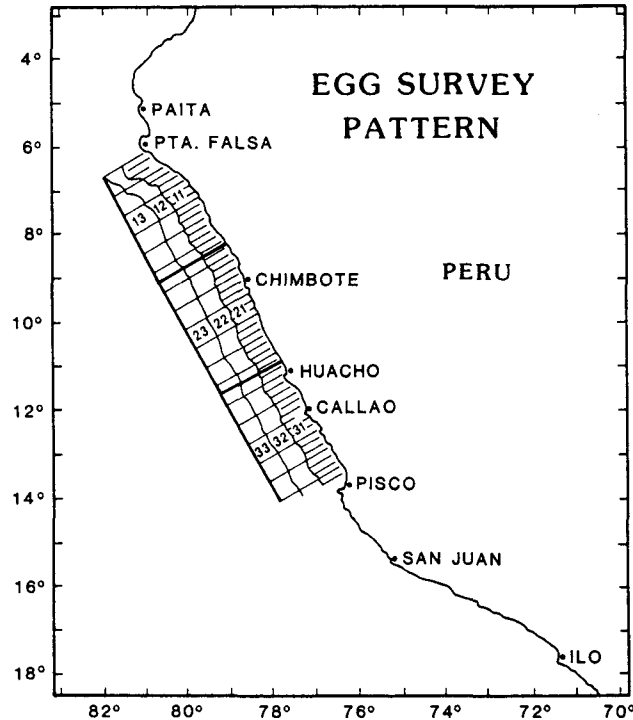


FIGURE 1.—Coastline of Peru and egg survey stations and statistical regions. Egg sampling stations are 3 miles apart in the cross-shelf plane. Regions for statistical summaries are coded. The first digit of each number refers to the north "1", central "2", or south "3" sectors of the coast. The second number refers to the inshore "1", offshore "2", or seaward "3" regions of each sector. In text, codes referred to as IMAR11, IMAR12, etc. to distinguish the codes from numbers. Original station positions and equations for plotting are in Smith et. al. (1983).

Anchovy and sardine eggs were grouped in 12 h intervals. Newly spawned eggs collected during the spawning interval and older eggs collected during hatching were eliminated from the calculations. The remaining egg counts were regressed on age to fit a mortality function of the egg data. The daily egg production was then estimated by zero intercept of the exponential mortality function. The following exponential model can be fit to the egg data by the nonlinear, least squares regression (Stauffer and Picquelle 1980³):

$$P_0 = P_i e^{-zt}$$

³Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. U.S. Dep. Commer., NOAA, NMFS SWFC Adm. Rep. LJ-80-09, 41 p.

where P_0 = daily egg production;

P_i = number of eggs of age t_i sampled during the time interval t_i, t_{i+1} ;

t = time elapsed between spawning and the i th time interval; and,

Z = instantaneous daily rate of egg mortality.

The P_0 is the intercept of the exponential curve. The model assumes that all eggs are spawned and fertilized at an instant, that the eggs have a constant rate of mortality, and that the sampling was representative and includes all areas where eggs may be found.

RESULTS

Peruvian anchovy and Pacific sardine co-occur along the north and central coast of Peru

(Santander 1981). In 1981, the Peruvian anchovy egg distribution was essentially continuous near the coast, with some extension offshore to 30 miles offshore of Chimbote (Fig. 2). In contrast, the Pacific sardine eggs occurred in two groups separated by about 120 nmi between Huacho and Chimbote. The Pacific sardine eggs extended farther offshore than Peruvian anchovy eggs and were not as abundant in the nearshore stations.

Of the 925 samples that were taken (Santander et al. 1984), 575 came from the inshore regions IMAR11, IMAR21, and IMAR31 (Fig. 1). Twenty-one percent of the samples in the inshore regions had both Peruvian anchovy and Pacific sardine eggs, 32% had only Peruvian anchovy eggs, 18% only Pacific sardine eggs, and 28% had neither Peruvian anchovy nor Pacific sardine eggs (Table 1).

There were fourfold fewer $\frac{1}{2}$ d old Pacific sardine eggs per station in the samples with Pacific sardine eggs in the absence of Peruvian anchovy eggs as compared with Pacific sardine eggs per station when Peruvian anchovy eggs were also present (Table 2). By way of contrast, the Peruvian anchovy eggs appeared to be equally abundant, with or without Pacific sardine eggs in the sample. There appeared to be a trend of Pacific

TABLE 1.—Number (% in parentheses) of plankton hauls in which Peruvian anchovy, *Engraulis ringens*, and/or Peruvian sardine, *Sardinops sagax*, eggs occurred in the three inshore regions.

| Region | Both anchovy and sardine | Anchovy only | Sardine only | Neither anchovy nor sardine | Total |
|--------|--------------------------|--------------|--------------|-----------------------------|-------|
| IMAR11 | 51 (27) | 26 (14) | 65 (35) | 45 (24) | 187 |
| IMAR21 | 34 (17) | 91 (46) | 18 (9) | 54 (27) | 197 |
| IMAR31 | 36 (19) | 69 (36) | 22 (12) | 64 (34) | 191 |
| Total | 121 (21) | 186 (32) | 105 (18) | 163 (28) | 575 |

sardine egg abundance in absence of Peruvian anchovy eggs becoming proportionally less abundant with age, but the trend was mostly concealed by the high standard errors of the two categories. Of course these rates cannot be known precisely from exploratory data analysis; the absolute rates would have to result from specifically designed studies with higher precision.

On a regional basis, sardine egg production was highest in the northern region (IMAR11), negligible in the central region (IMAR21), and higher in the southern region (IMAR31, Table

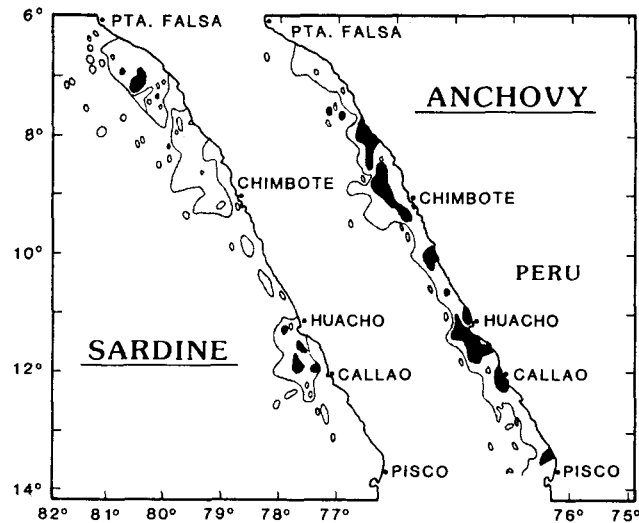


FIGURE 2.—Pacific sardine (left) and Peruvian anchovy (right) egg abundance in August to September 1981. For each species, shaded areas indicate where their eggs were taken at densities of 1–100 eggs/0.05 m², and black areas indicated 101 or more eggs/0.05 m². Peruvian anchovy data has also been mapped in units of eggs per square meter in Santander (1987, Map No. 78, p. 204).

TABLE 2.—Mean number of Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, eggs per station by age group. The age group code A1 refers to eggs aged in the first half of the first day after spawning; A2 refers to eggs aged in the second half of the first day; B1 refers to eggs aged in the first half of the second day; and B2 refers to eggs aged in the second half of the second day. "All" refers to all stations where that species' eggs were present. Only the inshore regions (IMAR11, IMAR21, IMAR31) combined were considered for estimation of these parameters. "Both" refers to those stations where eggs of both species were present. "Only" refers to stations where that species' eggs were present.

| Age group | Variable | Anchovy | | | Sardine | | |
|-----------|----------|---------|-------|-------|---------|-------|------|
| | | All | Both | Only | All | Both | Only |
| A1 | Mean | 62.92 | 67.49 | 59.11 | 19.53 | 26.58 | 6.66 |
| | SE | 8.70 | 12.70 | 11.99 | 7.01 | 10.70 | 2.33 |
| A2 | Mean | 22.90 | 36.07 | 16.32 | 6.73 | 12.35 | 2.16 |
| | SE | 3.73 | 9.34 | 2.93 | 1.84 | 3.91 | 0.66 |
| B1 | Mean | 31.05 | 37.59 | 26.60 | 2.14 | 2.88 | 0.77 |
| | SE | 5.35 | 7.92 | 7.25 | 0.48 | 0.71 | 0.33 |
| B2 | Mean | 9.36 | 11.15 | 8.46 | 1.32 | 2.62 | 0.23 |
| | SE | 1.31 | 2.37 | 1.58 | 0.57 | 1.24 | 0.12 |

3). Peruvian anchovy egg production was relatively even in all sectors of the inshore region. The mortality rates of both Pacific sardine and Peruvian anchovy were highest in the northern region. Pacific sardine mortality rates were higher than Peruvian anchovy mortality rates in each region.

Mortality rates of Peruvian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same samples (Table 4). Pacific sardine egg production, in areas where Pacific sardine eggs were not accompanied by Peruvian anchovy eggs in a sample, was only a third of that where the two species' eggs were found together. As in the case of abundance, Peruvian anchovy egg production and mortality rates do not appear to be related to the presence of Pacific sardine eggs in the sample.

The spatial overlap of the Pacific sardine spawning areas and Peruvian anchovy spawning areas cannot be distinguished from randomness. The probability that a 0.05 m² sampler will miss a Peruvian anchovy egg patch was 0.47 and for a Pacific sardine egg was 0.61 in August–September of 1981 off northern and central Peru. The joint probability of a sampler of this size missing both species' eggs as estimated from the product of the individual species' probabilities was 0.29. The measured probability of missing both species was 0.28 (Table 1). Therefore based on occurrence in a 0.05 m² mouth area sampler,

the small-scale spatial distribution of Pacific sardine and Peruvian anchovy eggs was indistinguishable from total independence of each other.

In summary, the results of this study show that Pacific sardines and Peruvian anchovies spawned along the coast over the latitudinal extent of northern and central Peru with the preponderance of spawning within 30 nmi of the coast. The production rate of Peruvian anchovy eggs per unit area (104 eggs/0.05 m² d⁻¹) was about double that for Pacific sardine (56 eggs/0.05 m² d⁻¹) and the mortality rate of Peruvian anchovy eggs ($z = -1.12$ or 67% d⁻¹) was substantially lower than that of Pacific sardine ($z = -2.12$ or 88% d⁻¹). The highest mortality rate for both species occurred in the northern region (IMAR11). For the Pacific sardine in the northern region, the instantaneous rate was -3.88 (98% d⁻¹). For the Peruvian anchovy in the north, the instantaneous rate was -2.14 or 88% d⁻¹. Mortality rates of Peru-

TABLE 3.—Regional egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy as estimated by a nonlinear least squares procedure assuming an exponential model.

| Species | Category | Production (SE) eggs/0.05 m ² /d | Mortality (SE) daily instantaneous |
|---------|----------|--|--|
| Sardine | IMAR11 | 16.6 (2.6) | 3.88 (0.39) |
| | IMAR21 | 0.4 (0.1) | 1.28 (0.35) |
| | IMAR31 | 8.7 (1.5) | 1.47 (0.28) |
| Anchovy | IMAR11 | 22.0 (9.2) | 2.14 (0.83) |
| | IMAR21 | 23.7 (6.7) | 0.93 (0.36) |
| | IMAR31 | 17.0 (4.9) | 0.90 (0.35) |

TABLE 4.—Egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy for all inshore regions where samples are positive for either species. "All" refers to all stations where eggs of that species were present. "Only" refers to stations which were positive for one species but the eggs of the other species were absent. "Both" refers to stations where eggs of both species were present.

| Species | Category | Production (SE) eggs/0.05 m ² /d | Mortality (SE) daily instantaneous |
|---------|----------|--|--|
| Sardine | All | 56.3 (3.2) | 2.12 (0.10) |
| | Only | 20.2 (0.4) | 2.22 (0.03) |
| | Both | 64.1 (9.2) | 1.75 (0.22) |
| Anchovy | All | 104.7 (37.2) | 1.12 (0.44) |
| | Only | 109.9 (47.0) | 1.35 (0.58) |
| | Both | 104.0 (25.5) | 0.90 (0.28) |

vian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same sample.

DISCUSSION

In this section we will discuss Pacific sardine and Peruvian anchovy egg production and mortality off Peru, fundamental statistical problems to be overcome in future studies, some other mechanisms of population control, and egg cannibalism and population control in pelagic spawning, schooling coastal pelagic fishes.

Pacific Sardine and Peruvian Anchovy Egg Production and Mortality

It appears that Pacific sardines and Peruvian anchovies off Peru select the same large-scale sites for egg deposition but select independently of each other at the small scale. While the eggs of both species were concentrated in the inner 30 miles of the survey pattern (Fig. 2), the probability of occurrence on a sample-by-sample basis was not demonstrably different from independent distributions for the two species (Table 1).

Where Pacific sardine and Peruvian anchovy eggs occurred together, Peruvian anchovy egg production rates were equal to those sites where Peruvian anchovy eggs occurred alone, but Pacific sardine egg production rates were higher at co-occurring sites than those sites where only Pacific sardine eggs were taken. Mortality rates where both occurred were marginally lower than where each occurred separately: this implies that the proximity of the adults of the other species does not affect the egg mortality rates. The northern region had the maximum rate of mortality for both Peruvian anchovy and Pacific sardine. The northern region had also the maximum regional rate of production for Pacific sardine, virtually equal to the Peruvian anchovy egg production rates of the other two regions (Table 3).

In all regions, the Pacific sardine mortality rate was higher than the anchovy mortality rate. Of an estimated 2,094 eggs produced/m² d⁻¹ by Peruvian anchovy, 1,410 (67%) died on the first day. Of an estimated 1,126 eggs produced/m² d⁻¹ by Pacific sardine, 990 (88%) died on the first day. We suggest two explanations for the cause of higher mortality rate of Pacific sardine eggs relative to Peruvian anchovy eggs in the same region: Moser⁴ pointed out that the

ovoid shape of the anchovy egg (0.7 × 1.4 mm) as compared with the spherical sardine egg (1.4 mm) may reduce the chance of being eaten by filter-feeders. Author H. Santander has observed that sardine eggs are more delicate to handle in the laboratory. This may mean that the integument of the sardine egg is more susceptible than the anchovy egg to physical damage by predators in the sea. Their susceptibility to damage might also explain their apparent low incidence in juvenile and adult sardine and anchovy stomachs, because broken eggs might not be detected (Santander et al. 1983).

Fundamental Statistical Problems

Errors in the estimation of the slope parameter induce errors of the same sign in the intercept parameter: for this reason there are major problems in comparing adult spawning biomass concentration derived from the intercept parameter and egg mortality rate derived from the slope parameter. Thus, for the purpose of this paper, the comparison of spawning biomass concentration and egg mortality is not reported as a result of this research. Instead, Figure 3 and Table 6 are points of discussion. The data come from a plan for stock assessment and as such are not definitive on the question of biomass concentration and egg mortality rate. The relationship is suggestive, however, and may be used to design a study of cannibalism that is not statistically confounded.

The statistical problem of patchiness (Taft 1960), encountered when estimating the abundance of fish eggs, becomes more severe when estimating production and mortality of eggs because the intensity of patchiness changes with age (Smith 1973, 1981; Smith and Hewitt 1985a, 1985b; McGurk 1987). Since the mortality estimate requires the arithmetic means (Southwood 1978), log transformation to stabilize variance is not used.

Egg production (P_0) and mortality rate (Z) are determined using the exponential mortality model (Picquelle and Stauffer 1985). It has been determined that the midpoint of spawning is at 2200 hours but samples from the spawning interval are biased (Smith and Hewitt 1985a). The intercept and mortality rate could be systematically underestimated if the actual mortality rate

⁴H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, Natl. Mar. Fish. Serv., La Jolla, CA 92038, pers. commun. May 1983.

in the initial period was higher owing to an interaction between local density and mortality rate on eggs at the highest distributional densities (McGurk 1987).

The Central Limit Theorem requires independence among sample values. With the spawning of Pacific sardine and Peruvian anchovy off Peru compressed against the coast in a 30 mile band in 1981, abundance estimates from stations separated in the cross-shelf dimension at 3 mile intervals are not likely to be independent. The effect will be an underestimate of sample standard error of the mean (Table 2). The degree of the same type of error in the along-shelf plane was probably smaller because the transects are 10 nmi apart. Also the collection of sites used for the estimates of abundance of 1 and 2 d old eggs in the first half of each day (A1 and B1 in Table 2) are from different stations from those used for estimates of abundance of 1 and 2 d old eggs in the second half of each day (A2 and B2 in Table 2).

Other Mechanisms

Egg cannibalism is probably only one of several possible population controlling mechanisms in anchovies. For example, cannibalism could occur at life stages other than the egg stage. There have been recent observations, in the laboratory, of older anchovy larvae consuming younger larvae (Brownell 1985). In these observations, the larvae became more vulnerable as pigmentation formed in their eyes and integument.

Energy demands for egg production and spawning could lead to aggregations of adults where food production and, coincidentally, egg mortality are both high. That, in both Pacific sardine and Peruvian anchovy, higher rates of egg mortality and egg production occurred in the same region (IMAR11) seems to support this view. Lastly, from laboratory observations, northern anchovy larvae, only a day old, may seek and maintain position in patches of *Gymnodinium*, making these larvae vulnerable to enhanced feeding activity by many other organisms in the same patch or layer (Hunter and Thomas 1974).

Egg Cannibalism and Population Control

For the northern anchovy, *Engraulis mordax*, Peterman et al. (1988) concluded that the

size of the recruited stock is not determined in the first 20 days following spawning. On the other hand, Pauly⁵ concluded that egg mortality due to cannibalism by the adult stock is a primary density dependent control on recruitment in the Peruvian anchovy, *Engraulis ringens*. Smith (1985) lists three situations in which cannibalism by schooling pelagic spawners would be an effective population controlling activity: 1) directed filtering behavior on dense aggregations of eggs; 2) encounter with other schools' patches of eggs; and, 3) anchovy population switching from biting to filtering behavior.

Directed Filtering

In the first few hours after spawning, before much dispersal has taken place, directed filtering could be an important source of mortality (Smith and Hewitt 1985b; McGurk 1987). Hunter and Dorr (1982) found that adult northern anchovy filtering was induced by 5 northern anchovy eggs/L and sustained by 1 or 2 eggs/L in laboratory tanks. Given that the level of artificial feeding is higher for laboratory animals and that probably the quality of water for sensing prey is lower, these thresholds may be higher in the laboratory than in the sea. One disadvantage of this mechanism for population size control is that, because of proximity, the most likely school to encounter the newly spawned patch is the school from which the spawn was produced. Santander et al. (1983) found that Peruvian anchovy eggs < 2 hours old were overrepresented by a factor of three in the stomachs of Peruvian anchovy relative to their incidence in the sea. In a typical spawning school (Santander et al. 1984; Alheit 1985), there would be 10 times as many Peruvian anchovies feeding on eggs than females spawning eggs. While the mortality rate might be sufficient, it is difficult to see how a change, in population size or in density over thousands of square kilometers, could materially affect a species grazing for a few hours on its own eggs over a range of a few hundred meters. This source of mortality, although large, may not be sufficiently variable with population density to control recruitment.

⁵The estimate of instantaneous mortality "z" derived by Pauly (1987) is strongly biased downward at low mortality rates but should still be valid at high levels of parent stock. Daniel Pauly, International Center for Living Aquatic Resources Management, Manila, Philippines, pers. commun. March 1989.

Encounter

Incidental filtering of eggs by encounter of other schools' patches of eggs would appear to be a direct mechanism for parental control of recruitment rate and population density. If one combines the information on egg cannibalism rate by Alheit (1987) and the demographic influence on population annual fecundity reported by Pauly and Soriano (1987) (Table 5), one can see that the effective fecundity (eggs hatched after cannibalism) would be low when the stock was composed primarily of juveniles and first-year spawners.

TABLE 5.—Age-specific rates of cannibalism and egg production for anchovy.

| Age (yr) | Anchovy egg production ¹ (eggs/g/d) | Anchovy egg consumption ² (eggs/g/d) | Effective fecundity (eggs/g/d) |
|------------------------|--|---|--------------------------------|
| Juveniles ³ | 0. | 9.3 | -9.3 |
| 1 | 3.9 | 9.3 | -5.4 |
| 2 | 9.0 | 9.3 | -0.3 |
| 3 | 15.7 | 9.3 | 6.4 |
| 4 | 18.4 | 9.3 | 9.0 |

¹Pauly and Soriano 1987

²Alheit 1987

³Ciechowski 1967

Switching

It is also possible for cannibalism to interact indirectly with population density. An indirect method for population control is evident if one considers a system where the anchovy prefer to feed by biting relatively large zooplankton and where filtering occurs only when large zooplankton are low in abundance (O'Connell 1972). Under these circumstances predation by anchovy on the major herbivores could result in a larger standing crop of phytoplankton and in increased rates of anchovy filtering (MacCall 1980). In the course of switching to a preponderance of feeding by filtering, the anchovy would inadvertently filter anchovy eggs at a higher rate.

Egg production rate was sixfold higher in Peruvian anchovy compared with northern anchovy off California (Smith and Hewitt 1985a). Of the 2,094 Peruvian anchovy eggs produced per square meter, 67% died on the first day while off California; of the 300 northern anchovy eggs produced per m², 22% died on the first day. While anchovy are omnivorous in both areas,

phytophagy is considered more pronounced off Peru (MacCall 1980).

Pauly (1987) found that knowledge of the rate of cannibalism appears crucial for managing the Peruvian anchovy. The rate of cannibalism on eggs is admittedly high, but it may be that the variation in the rate of cannibalism is insufficient to explain the variation in the rates of recruitment. It remains to be seen if interannual differences in the relative proportion of feeding by filtration on the one hand and biting on the other hand are sufficient to explain differences in recruitment.

The difference in conclusions regarding northern anchovy egg cannibalism between Peterman et al. (1988) for California anchovy and Pauly (1987) for the Peruvian anchovy, may be due to a simple difference in population density between the two regions, California having a much lower population density than Peru. Pauly (1987) showed the relationship between population size and egg mortality: a better relationship would be between local population density and egg mortality (Csirke 1980; MacCall 1980; Ware and Tsukayama 1981).

Egg mortality rate and adult biomass density are closely related in interregional and interannual egg production assessments (Fig. 3). The relationship is surprisingly close when one considers biomass of juvenile anchovy, the biomass of other filtering fishes, particularly sardines, and the biomass of invertebrate predators have been neglected. In Table 6, one can see that northern anchovy assessment studies off California (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986) and South Africa (Armstrong et al. 1988) differ a great deal from the assessment study reported in this paper for Peru. The median biomass density of adult anchovy was 6 g/m² off California between 1980 and 1985, while the median percent eggs dying each day was 16%/d. In the south Benguela Current, the mean biomass density of adult anchovy was 12 g/m², and the mean percentage of eggs dying per day was 22% (Armstrong et al. 1988). The median regional estimate for 1981 of biomass density of adult anchovy was 33 g/m² off Peru, and the egg mortality was 61% egg mortality per day. While these observations suggest cannibalism as a cause, the mortality rate of eggs may only be a consequence of generally higher populations of a wide range of other vertebrate and invertebrate predators in prime schooling fish-feeding areas.

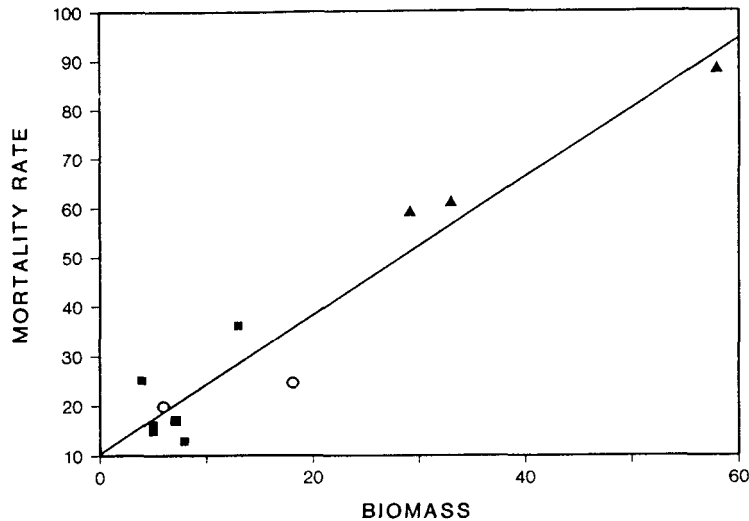


FIGURE 3.—Mortality rates in percent per day of anchovy eggs as a function of anchovy spawning biomass concentration in grams per square meter: closed triangles, Peru in nearshore regions IMAR11, IMAR21, IMAR31 (this paper); closed squares, values for the entire spawning region off California from 1980 to 1985 (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986); and, open circles, for the entire spawning region off South Africa in 1985 and 1986 (Armstrong et al. 1988).

TABLE 6.—Anchovy egg mortality rate and adult spawning biomass concentration in the Humboldt (*Engraulis ringens*), California (*E. mordax*), and southern Benguela (*E. capensis*) currents.

| Year/region | Spawning area (km ² × 10 ⁻³) | Spawning biomass (tons × 10 ⁻³) | Biomass concentration (g m ⁻²) | Egg mortality (% d ⁻¹) |
|---------------------------|---|---|--|------------------------------------|
| Peru 8108 | | | | |
| IMAR11 | 7.9 | 460 | 58 | 88 |
| IMAR21 | 12.9 | 420 | 33 | 61 |
| IMAR31 | 11.2 | 320 | 29 | 59 |
| CalCOFI 8003 ¹ | 66.1 | 870 | 13 | 36 |
| CalCOFI 8102 ² | 77.5 | 635 | 8 | 13 |
| CalCOFI 8202 ³ | 83.0 | 415 | 5 | 15 |
| CalCOFI 8302 ⁴ | 94.7 | 652 | 7 | 17 |
| CalCOFI 8402 ⁵ | 61.6 | 309 | 5 | 16 |
| CalCOFI 8502 ⁶ | 132.2 | 522 | 4 | 25 |
| Benguela | | | | |
| 1985 ⁷ | 107.1 | 614 | 6 | 20 |
| 1986 ⁷ | 109.8 | 2006 | 18 | 24 |

¹Stauffer and Picquelle 1981.

²Stauffer and Charter 1982.

³Picquelle and Hewitt 1983.

⁴Picquelle and Hewitt 1984.

⁵Hewitt 1985.

⁶Bindman 1986.

⁷Armstrong et al. 1988.

CONCLUSION

MacCall (1980) stated that only 10% of the apparent control of northern anchovy recruitment off California may be due to stock size, with the vast majority of control arising from means that are independent of stock size. Lasker and MacCall (1983) concluded that the best measures of the stock recruitment curve are not sufficient to control for cannibalism to be a "major regulatory mechanism". Also, it appears from examination of the life stages of northern anchovy (Smith 1985, table 3) moderate reproductive failures could happen at the fecundity, embryonic, larval, and juvenile prerecruit stages, but a reproductive success of great proportions would most likely arise at the embryonic and larval stages. The size of the recruited year class will accumulate the rates of early stages, and the later the prerecruits are evaluated, the more likely the reproductive success will have been established. Peterman et al. (1988) evaluated only the first 20 days of life.

For 6 successive years (included in Peterman et al. (1988)), the interannual coefficient of variation of the spawning biomass was 35% and the interannual coefficient of variation of recruit-

ment was 104%. Only two life history parameters varied more than the spawning biomass (35%): adult density per unit area (47%) and egg mortality (38%) (Smith and Moser 1988). While cannibalism is sufficiently important as a source of egg mortality to control the size of populations like sardine and anchovy over the long term, it is unlikely that the interannual variation in rates of mortality due to cannibalism are sufficient to cause major recruitment variations. One would suspect that variability in egg mortality rate could arise from the 70% of egg mortality not due to cannibalism. Off California, Theilacker (1988) has estimated that the rate of northern anchovy egg consumption by juvenile and adult euphausiids may account for 28% of the egg mortality. Other influences on recruitment could arise from copepod predation on yolk-sac larvae (Lillelund and Lasker 1971) and predation of Pacific mackerel on juveniles (Methot 1986⁶).

To manage variable stocks like the sardine and anchovy it may be sufficient to monitor the age structure of the catch and the production and survival of the embryonic stage (Methot and Lo 1987⁷). A decrease in the number of older, highly fecund, spawning age classes will decrease effective population fecundity. In filter feeders like sardine and anchovy, cannibalism by younger age classes may lower the survival of eggs. Thus, merely by monitoring age structure and egg survival one can project when large, unusually successful year classes are possible. New techniques for monitoring juvenile abundance and growth will be required when a sardine or anchovy fishery becomes so intensive that an early recruitment prediction is necessary.

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