

Acknowledgments

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EGG CANNIBALISM IN THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

Anchovies feed on their own eggs. Egg cannibalism has been reported for the Argentine anchovy, *Engraulis anchoita* (de Ciechomski 1967); Japanese anchovy, *E. japonicus* (Hayasi 1967); anchoveta, *E. ringens* (Rojas de Mendiola et al.¹); and the northern anchovy, *E. mordax* (Loukashkin 1970). These studies give no indication whether this cannibalism was a significant part of natural mortality and incidence of cannibalism was included only as part of a general description of food habits. We provide evidence that egg cannibalism may account for a considerable proportion of natural egg mortality in the northern anchovy.

Northern anchovy feed by biting larger prey and by filtering smaller ones (Leong and O'Connell 1969). If both large and small prey are offered in the laboratory, northern anchovy in the front of the school bite the larger prey, whereas those at the end of the school feed by filtering the smaller prey (O'Connell 1972). Our laboratory observations indicate that adult northern anchovy feed on their eggs by filtering, whereas even the smallest anchovy larvae (ca. 3-4 mm long) are bitten. Such small larvae are digested beyond identification in 30 min, whereas the identifiable whole chorions and fragments may remain in northern anchovy stomachs up to 8 h although the contents of the egg (embryo and yolk) are digested after about 2 h. Northern anchovy eggs are prolate spheroids and can be easily distinguished from the spherical eggs of other pelagic spawners in the Southern California Bight.

Methods

The incidence of cannibalism in northern anchovy was estimated from an examination of 31 sets of stomach samples, usually of 10 adults each. Samples were taken at the peak of the spawning season, in the Southern California Bight, during March 1976 and 1977 (Table 1). Northern anchovy were collected in a midwater trawl or a commercial lampara net: 28 sets of collections were taken at night between sunset and sunrise and 3 sets during the day. Fish were frozen in liquid nitrogen

¹Rojas de Mendiola, B., N. Ochoa, R. Calienes, and O. Gomez. 1969. Contenido estomacal de anchoveta en cuarto areas de la costa Peruana. *Inst. Mar. Peru Inf. Espec.* (IM-27), 29 p.

TABLE 1.—Incidence of anchovy eggs in stomachs of northern anchovy collected in March 1976 and 1977 in the Los Angeles Bight.

Time of day (h)	Collection number ¹	Number fish per collection	Mean standard length (cm)	Mean weight (g)	Mean percentage full ²	Fish with eggs (%)	Mean number eggs per fish
1300	31	25	10.0	10.2	7	68	1.9
1500	29	23	11.7	17.9	13	96	8.4
1500	30	11	12.4	19.9	14	100	6.4
2000	4	10	13.4	22.7	18	50	2.0
2000	5	10	13.4	23.3	18	10	0.1
2000	7	20	13.4	24.9	12	5	1.0
2000	17	10	10.5	11.7	17	30	.7
2100	1	11	10.7	10.0		82	2.3
2100	8	10	13.5	25.4	15	0	.0
2100	10	10	10.5	12.5		100	3.8
2100	14	10	11.6	16.2	49	40	0.6
2100	20	10	11.4	15.0	32	20	0.2
2100	23	10	12.1	19.1	38	0	.0
2200	6	10				20	0.2
2200	9	10	13.7	28.5	13	40	0.9
2200	15	10	11.4	15.9	56	50	7.1
2200	18	10	11.9	17.9	18	70	4.9
2300	11	10	11.4	16.5	14	10	0.1
2300	21	10	12.1	17.9	39	0	.0
2300	24	10	11.8	18.4	35	20	0.2
2400	2	10	10.6	12.2	4	50	3.0
2400	16	10	11.2	14.2	17	60	11.3
2400	19	10	11.5	15.3	15	90	4.6
0100	12	10	11.8	16.7	13	70	2.1
0100	13	10	11.1	14.7	25	90	22.1
0100	25	10	12.9	23.4	30	0	.0
0200	3	28	9.0	7.9	4	86	39.0
0400	27	10	12.0	17.9	31	90	20.9
0500	22	10	12.3	19.4	18	20	0.4
0500	26	10	12.3	19.3	28	30	0.9
0700	28	10	11.6	16.3	20	50	1.7

Means \pm 2 SE of mean:

Night ($N = 28$)	11.8 \pm .04	17.5 \pm 1.8	23 \pm 4	42 \pm 12	4.6 \pm 3.3
Day ($N = 3$)	11.4 \pm 1.4	16.0 \pm 5.9	12 \pm 5	88 \pm 20	5.6 \pm 3.5

¹ Collections 1-9, night trawls, March 1976; collections 10-25, night trawls, March 1977; collections 26-28 night lampara sets, March 1977; and collections 29-31 day lampara sets, March 1976.² Volume stomach contents/volume maximum contents \times 100. Maximum stomach volume was size specific and derived from the relationship developed in the text.

at the time of capture, except for the day collections where formaldehyde preservation was used.

A standard oblique plankton tow (Smith and Richardson 1977) from 70 m (depth of water permitting) to the surface, was taken before and after each night trawl sample using a 1 m ring net (505 μ m mesh) or Bongo net (333 μ m mesh) and was preserved in 10% Formalin.² The 505 μ m mesh net was corrected for extrusion of eggs using the coefficient of Lenarz (1972). These collections were used to estimate the abundance of northern anchovy eggs in the regions where anchovy were sampled by night trawls. For one of the day samples, two plankton tows were taken in front and two taken behind the school. The plankton samples were taken with a 0.5 m ring net with 102 μ m mesh, towed for 2 min at 15 m (the depth of the school as determined acoustically). These two sets of plankton samples enabled us to measure directly the effect of feeding by a school on the egg density. No plankton tows were associated with the commercial lampara net samples.

² Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

For each fish we determined standard length (SL) and weight, numbers of eggs and larvae in the stomach, and compacted stomach volume. The stomach volume was compacted by centrifuging the contents for 6 min at 3,700 r/min and then was measured to the nearest 0.1 ml. Volumes were expressed as a percentage of the maximum stomach volume. Maximum volume (V) was determined using the same volumetric technique for northern anchovy fed to satiation with adult *Artemia salina* in the laboratory; it was expressed as a function of standard length (L) in centimeters, where $\ln V = 2.051 \ln L - 3.954$ and $r^2 = 0.759$. The length range was 4.6-13.5 cm.

To estimate the ration from observed incidence of eggs in the stomach, the rate of gastric evacuation of eggs must be known. To estimate this rate, we fed only northern anchovy eggs to 155 northern anchovy for 1 h at a density of 38 eggs/l at 15.2° C, which approximates typical spawning temperatures. After feeding, fish were transferred to a tank without food and 10-15 fish sampled at 2-h intervals until 10 h after feeding. The rate of gastric evacuation was expressed as the slope of the regression of natural logarithm of the mean

eggs in the stomach as a function of elapsed time (Figure 1).

Incidence of Cannibalism

No relationship existed between the volume of the stomach contents and the time of collection, indicating that anchovy fed throughout the night and day (Table 1). In the night samples, the mean stomach volume was 23% of that of a full stomach and was 12% in the 3 day samples. Nearly all stomachs contained greenish to brownish material, presumably phytoplankton remains, and somewhat less frequently copepods and euphausiids were mixed with this material.

Larval fishes occurred in only 7 of the 368 stomachs (2%) and only 1 stomach contained larvae that could be identified as northern anchovy. This stomach contained 21 relatively large northern anchovy larvae; the only measurable specimen was 17 mm SL. Northern anchovy eggs occurred more frequently than larvae. Forty-two

percent of the northern anchovy stomachs sampled at night contained northern anchovy eggs and 88% of those sampled in the day contained eggs. Other fish eggs were rare, occurring in 4.2 ± 2.7 (± 2 SE) of the stomachs. The mean number of anchovy eggs per stomach, including zeros, was 4.6 ± 3.3 (± 2 SE) for night samples, 5.6 ± 3.5 for day samples, and the mean for night and day was 5.1 eggs/stomach.

The distribution of the number of eggs consumed per fish was highly skewed; about 90% of the eggs occurred in only 38% of the stomach samples containing eggs (19% of all stomachs). The maximum number of eggs in a single stomach was 730, which was about 32% of all the eggs found in stomachs. The patchiness of northern anchovy eggs in the sea may be responsible for this skewed distribution. The distribution was not greatly different from that of northern anchovy eggs taken in plankton samples. For example, Smith³ found that about 90% of northern anchovy eggs occurred in only 20% of the positive plankton net hauls ($N = 453$).

The mean number of eggs per fish in a sample (night trawl samples) increased with egg density in the sea (Figure 2). Although variability was high ($r^2 = 0.47$), the 99% confidence interval about the regression coefficient was 1.107-2.095 and did not include a coefficient value of 1. This indicates that the relation was exponential and that the mean number of eggs in the stomach was not increasing in direct proportion to the mean egg abundance. Patchiness of eggs combined with selectivity in filtering could explain the exponential nature of the relationship. Certainly, oblique net tows provided only a relative measure of egg density encountered by filtering northern anchovy. Tows were begun at 70 m (below the maximum depth of northern anchovy larvae (Hunter and Sanchez 1977), or in shallow water near the bottom to insure that all eggs in the water column were sampled. Stomach contents, on the other hand, would be expected to be more closely related to the size of patches and density of eggs within egg patches and not to the integrated egg density for the water column.

Measurements of the density of eggs behind and in front of a single northern anchovy school were probably a more realistic measurement of the

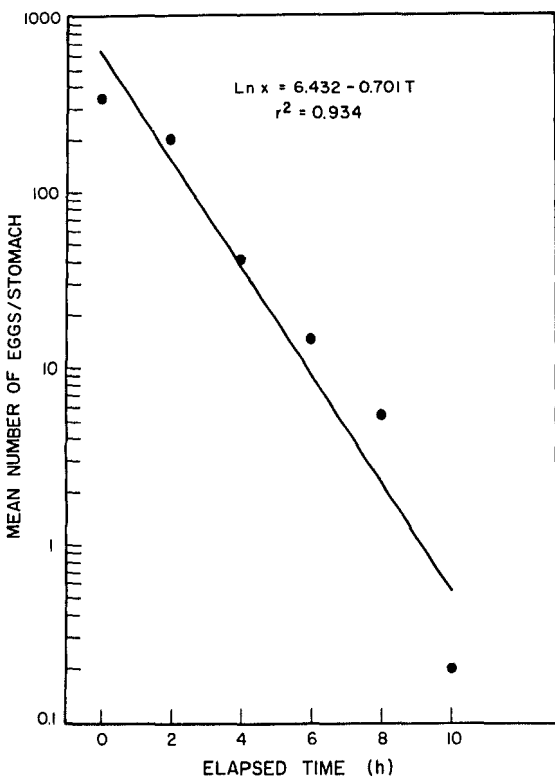


FIGURE 1.—Rate of gastric evacuation of northern anchovy fed northern anchovy eggs. Points are \log_e mean number of eggs per stomach for 10-15 fish sampled at 2-h intervals after feeding.

³ P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1979.

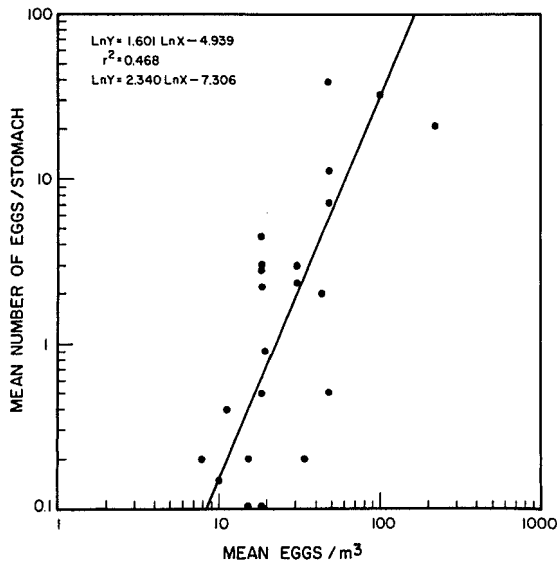


FIGURE 2.—Mean density of northern anchovy eggs in the sea and mean number of eggs in northern anchovy stomachs taken in the Los Angeles Bight in March 1976 and 1977. Points are means for 10 or more fish and means of 2-4 plankton tows. Upper equation and the line is the geometric mean regression (Ricker 1973); lower equation is the predictive equation.

actual density of eggs encountered by a school. These measurements were derived from horizontal tows made at the acoustically determined depth of the school (15 m). Estimates from the two tows taken in front of the school were 150 and 122 eggs/m³, whereas those from the two tows taken behind the school were 75 and 54 eggs/m³. The ratio of the means for these two sets (65:136) indicated that 48% of the eggs in the water may have been consumed by the school. Thus, a school encountering a density of about 140 eggs/m³ may

have consumed a large proportion of the eggs. The density of eggs usually encountered by schools during the peak spawning months may be in excess of 140 eggs/m³ because the mean number of eggs per stomach for fish in this school, 1.9 ± 0.6 eggs (Collection 31, Table 1) was less than the mean for all collections, 5.1. The typical density of northern anchovy eggs within patches is not known, but a value as high as 31,000 eggs/m³ has been recorded (Hunter in press).

The daily ration of eggs consumed by northern anchovy was estimated from the equation, $D = A \times B \times C$ where D = ration (number of eggs), B = rate of gastric evacuation (0.701), A = mean stomach contents, and C = duration of feeding (24 h). This function has been used by Tyler (1970), discussed and used by Eggers (1977), and criticized and discussed by Elliott and Persson (1978). We used for mean stomach contents (C), the mean of the averages for day and night. Using the above equation, the daily ration was 85.8 eggs/fish or 5.1 eggs/g of fish (Table 2).

The simplest method for evaluating potential effects of egg consumption is to calculate the proportion of the nightly production of eggs consumed by northern anchovy schools. Northern anchovy produce 371 eggs/g of female per spawning and during peak breeding periods, about 16% of the females spawn each night (Hunter and Goldberg 1980). Thus each night, 0.16×371 , or 59.4 eggs are spawned per gram of female in a school. Assuming a sex ratio of 1:1, half this amount, or 29.7 eggs, are produced per gram school weight. The percentage of daily egg production consumed by a school per day (eggs consumed/eggs spawned) was 17.2% (Table 2). Smith (foot-note 3) estimated the natural mortality of anchovy

TABLE 2.—Number of anchovy eggs eaten, per day, proportion of egg production consumed, and the proportion of natural egg mortality attributable to egg cannibalism in northern anchovy.

	Variable	Value	SE of mean	Data source
A	Mean eggs/stomach	5.1	¹ ± 1.6	Mean of night and day averages (Table 1)
B	Rate of gastric evacuation	.701	± 0.092	See text
C	Duration of feeding (h)	24		
D	Ration, eggs/fish per day	85.80		$A \times B \times C$
E	Mean fish weight (g)	16.8	¹ ± 0.9	Mean of night and day averages (Table 1)
F	Ration, eggs/grams wet weight	5.1		D/E
G	Eggs spawned/grams ovary-free female weight	389	± 30	Hunter and Goldberg 1980
H	Ratio of ovary-free weight to total female weight	.954		Hunter and Macewicz ²
I	Eggs spawned/grams total female weight	371	± 28	$G \times H$
J	Ratio of females spawning/night	.16	± 0.02	Hunter and Goldberg 1980
K	Ration of females/school	.50		Assumed 1:1 sex ratio
L	Eggs/gram school weight	29.7		$I \times J \times K$
M	Percent of egg production consumed/day	17.2		F/L
N	Natural egg mortality percentage/day	53		Smith and Lasker 1978
O	Percentage natural mortality from cannibalism	32.4		M/N

¹ From the night samples, Table 1.

² Hunter, J. R., and B. J. Macewicz. 1979. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Manuscript submitted for publication.

eggs to be about 53%/d. Thus, egg cannibalism may be the cause of 32% of the natural egg mortality in northern anchovy.

Discussion

We have not tried to trace the error terms through the pyramid of calculations required to estimate the proportion of natural egg mortality attributable to cannibalism, although we give in Table 2 the standard error of the mean where estimates are available. The error in our estimate most likely will be equivalent or higher than that of the most variable parameter (i.e., mean eggs per stomach and natural mortality of northern anchovy eggs). We have no estimate of the error for the natural mortality of northern anchovy eggs but mortality rates of pelagic fish eggs are known to be high and variable; estimates range from 2 to 95% for various species (Jones and Hall 1974; Vladimirov 1975). Regardless of the uncertainties, we believe the results indicate that egg cannibalism may be a major source of egg mortality in the northern anchovy and a combination of patchiness of eggs and selectivity in filter feeding may be important in regulating the consumption of eggs.

Cannibalism is a mechanism for density-dependent regulation of fish populations (Cushing 1977), and egg cannibalism may be one of the many mechanisms regulating the size of anchovy populations. A simple model could be developed to test this hypothesis if random filtering and a random egg distribution were assumed. Although the development of such a model is beyond the scope of this paper, we wish to consider the extent our observations differ from predictions based on assumptions of randomness because this would be a critical decision in the development of the model.

The mean density of eggs in trawl associated plankton tows was 32 eggs/m³ and the maximum filtering rate of northern anchovy of mean weight 16.8 g, is 0.158 m³/h (Leong and O'Connell 1969). For a northern anchovy (weight 16.8 g) to obtain the estimated ration of 85.8 eggs/d, it would have to filter continuously for 17 h at a density of 32 eggs/m³. Another approach is to estimate the percentage of the volume of the habitat that could be randomly filtered by a group of northern anchovy schools. The mean weight of northern anchovy schools in 20' grid squares is 2.05×10^7 kg (excluding grid squares without northern anchovy) (Mais⁴); assuming the maximum depth of eggs is 30 m (Hunter and Sanchez 1977), the

volume of the habitat is 2.86×10^{10} m³. These schools would have to filter for 24 h to consume 17% of the nightly egg production. The number of hours of filtering required to obtain the average daily ration of eggs in the first calculation or to consume 17% of the egg production in the second is too high. Thus a random encounter model does not seem to account for the relatively high egg consumption that was observed and patchiness and selectivity in feeding may be the reasons.

Northern anchovy eggs exist in patches (Hewitt in press), probably in patterns similar to those described for sardine eggs (Smith 1973). Our observations of northern anchovy feeding on eggs in the laboratory indicate that filtering may be intensified when egg patches are encountered. When we added a beaker containing anchovy eggs to a 3.3 m diameter tank containing about 200 northern anchovy, they soon interrupted their circuit of the tank, formed a tight mill at the site of introduction, and filtered the region intensively. If northern anchovy display such patterns of behavior in the sea, the ration of eggs would be expected to be higher than one predicted from random filtering. Thus, present evidence indicates that an assumption of randomness would be unacceptable in a model to measure effects of cannibalism as a regulatory mechanism.

Larval cannibalism might also be significant. Northern anchovy larvae are readily eaten by adults in the laboratory. The absence of small northern anchovy larvae in stomachs may have been caused by the rapid rate of digestion (<30 min) and the low incidence of larger larvae (0.3%) caused by their low abundance in the sea. Thus, cannibalism on larvae as well as that on eggs might play a role in the regulation of northern anchovy populations but additional information is needed on feeding behavior, and on the size and density of egg and larval patches, before an evaluation of population effects can be made.

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⁴Mais, K. F. California Department of Fish and Game, Cruise Reports 76-A-3 and 77-A-3. California Department of Fish and Game, Marine Resources Region, Long Beach, Calif.

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DEPTH DISTRIBUTION AND SEASONAL AND DIEL MOVEMENTS OF RATFISH, *HYDROLAGUS COLLIEI*, IN PUGET SOUND, WASHINGTON¹

The ratfish, *Hydrolagus colliei*, inhabits the coastal waters of North America from Alaska to the Gulf of California (Hart 1973). One aspect of the biology of this species which has attracted attention is its vision physiology. It is generally accepted that most deepwater fish, regardless of phylogenetic position, have retinal pigments with maximum absorption at about 490 nm or less (Munz 1971; Lythgoe 1972). For example, *H. affinis*, the species of chimaeroid found in deep water of the western Atlantic, has retinal pigments with maximum absorbance at 477 nm (Denton and Nicol 1964). In contrast, a shallow-water species of chimaeroid (*Callorhynchus callorhynchus*) found off Chile has retinal pigments with

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