THE SPAWNING ENERGETICS OF FEMALE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The seasonal pattern in incidence of postovulatory follicles in northern anchovy females indicated that they spawn about 20 times per year. The maturation rates of females in the laboratory indicated that they were capable of maturing a spawning batch of eggs at weekly intervals. Examination of the egg size frequency distributions in sea-caught specimens indicated that vitellogenesis and egg maturation continued until the last spawning. We evaluated for northern anchovy the fat-water balance, caloric values of tissues, annual fat cycle, seasonal changes in egg weight, total calories present in a mature ovary, batch fecundity; and determined in the laboratory the gross caloric conversion efficiency (12.8%). These measurements indicated that the caloric equivalent of only two spawning batches are present in a mature ovary at any time and that two-thirds of the annual cost of 20 spawnings could be supplied by fat stores. Estimates of annual reproductive effort (egg calories/ration calories × 100) ranged from 8% for 1 year to 11% for 3-year-old females. A daily ration of copepods equivalent to 4-5% of female wet weight per day is required to support the annual cost of growth and reproduction.

Histological evidence indicated that female northern anchovy, *Engraulis mordax*, spawned about once a week in February 1978 (Hunter and Goldberg 1980) and at 7-10 d intervals from late January through the middle of April 1979 (Hunter and Macewicz 1980). Egg and larva survey data indicate that some spawning occurs throughout the year, although about 50% of the annual production of northern anchovy larvae occurs during the peak months of spawning (February to April) (Lasker and Smith 1977). These findings indicate that northern anchovy females spawn many times per year. Thus, the annual fecundity of northern anchovy is higher than originally suspected by MacGregor (1968) and may be regulated by availability of food. Energy regulation of fecundity has been suggested for other marine fish stocks and could be important as a density-dependent population regulation mechanism (Bagenal 1973).

The objectives of this study were: to validate recent work on northern anchovy spawning by determining if such a high frequency of spawning is developmentally and energetically possible; to estimate the annual energy cost of reproduction; and to discuss the sources of variation. We estimated the average number of spawnings by northern anchovy females in a year and tested the hypothesis that they are capable of maturing eggs at the required rate. We considered the energy cost of reproduction, factors that affected variation in costs, and related reproductive costs to fat stores. Finally we estimated the annual reproductive effort (egg cal/ration cal). In addition to data collected specifically for this study, we used data available at the Southwest Fisheries Center (SWFC), La Jolla, Calif., including many unpublished sources.

METHODS

Field Data

To estimate the annual number of spawnings by northern anchovy, we used the data of Hunter and Goldberg (1980) and Hunter and Macewicz (1980) on the incidence of 24-h-old postovulatory follicles. The proportion of mature females with 24-h-old postovulatory follicles was considered equivalent to the fraction of females spawning per day during a cruise (Hunter and Goldberg 1980). All samples were taken in the Southern California Bight in 1977-79; the number of females analyzed per cruise was 148 from March 1977; 14 from September 1977; 295 from February 1978; 395 from January-February 1979; 557 from March-April 1979; and 33 from June 1979. Data were plotted at the mid-date for the cruises which were 10-22 d long.

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To estimate the rate of egg maturation required for weekly spawning, we used the frequency distributions of egg size in mature northern anchovy ovaries of females taken at sea. We measured distributions in 10 females taken in the Southern California Bight in February 1979, and in 6 taken in Monterey Bay in March 1979 by Hunter and Macewicz (1980). Five of the females from the Southern California Bight had 24-h-old postovulatory follicles indicating spawning had occurred on the day before they were captured, and the other five were mature without evidence of recent spawning. The ovaries of the six females from Monterey were highly atretic and in post-spawning condition, but had yolked eggs (Hunter and Macewicz 1980). This latter group was used to illustrate the condition of ovaries at the cessation of spawning. Our method of measuring the egg size-frequency distributions was similar to that of MacGregor (1968). We counted and measured to the nearest 0.05 mm all eggs >0.05 mm (major axis) in a weighed sample of the ovary.

Seasonal changes in fat content of female northern anchovy were calculated using the original data summarized by Lasker and Smith (1977). Their samples were taken at roughly monthly intervals from February 1965 to June 1967 ($n = 593$). Their data, supplemented by additional data ($n = 338$) taken in the summer and fall of 1979, were used to estimate the relation between wet weight without gonad (W) and fat content (F) and dry weight (without fat) (D). The multiple regression equation for this relation was

$$W = -0.018 + 0.320\,F + 5.469\,D \qquad (1)$$

where all variables are in grams, $r^2 = 0.969$, and $n = 981$. This equation permitted calculation of wet weight of northern anchovy females after fat gain or loss. Wet weight changes only slightly with fat loss because water content increases as fat decreases (Iles and Wood 1965) (Table 1). The same data were used to establish the relation between dry weight (without fat) (D) and standard length (L) where

$$\log_{10} L = 0.313 \log_{10} D + 1.930, \qquad (2)$$

$r^2 = 0.974$. Thus, wet weight can be estimated for northern anchovy of any standard length given the fat content.

Ahlstrom[2] measured the major and minor axes of 50-150 northern anchovy eggs taken in each of 58 standard ichthyoplankton tows (Smith and Richardson 1977) along the coast of California and Baja California in 1955, 1956, 1957, and 1965. These data, combined with an additional 30 tows (100 eggs measured/tow) taken in the same region in 1969, were used to estimate seasonal changes in the size of northern anchovy eggs. We calculated monthly mean egg dimensions for the combined data; number of tows per month varied from 9 to 16 (February-July) and from 1 to 4 in the period of low egg abundance (August-December). We calculated the mean volume of the eggs per month from average egg dimensions using the equation for a prolate spheroid. The volume (V) in cubic millimeters was converted to dry weight (E) in milligrams with the relation established in the laboratory using freshly spawned eggs

$$E = 0.0012 + 0.0930\,V \qquad (3)$$

where $r^2 = 0.646$ and $n = 32$.

Laboratory Data

Three groups of northern anchovy of 1,200-1,300 fish each were matured in the laboratory to measure the rate of ovarian maturation and to estimate gross growth efficiency. The fish were

TABLE 1.—Relationship between fat-free dry weight or length and wet weight for northern anchovy at the average seasonal minimum and maximum fat content. Relationships calculated from regressions; all body weights are without gonads.

Standard length[1] (mm)	Fat-free dry weight (g)	Wet weight and water content at minimum (15%)[2] fat content			Wet weight and water content at maximum (41%)[2] fat content		
		Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)	Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)
106	2.000	0.353	11.03 ± 0.19	79	1.390	11.36 ± 0.11	70
118	2.891	0.510	15.96 ± 0.13	79	2.009	16.44 ± 0.18	70
131	4.000	0.706	22.08 ± 0.12	79	2.780	22.75 ± 0.35	70

[1] From Equation (2) in text.
[2] Percentage of the dry weight including fat.
[3] From Equation (1) in text; 95% confidence intervals calculated using Gauss multipliers (Snedecor and Cochran 1967).
[4] $[W - (D + F)/W] \times 100$, where W = wet weight without ovary, D = fat-free dry weight, and F = weight of fat.

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[2] E. H. Ahlstrom, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, unpubl. data, 1979.

purchased from bait dealers from September to October in 1977 and 1978 and held in circular tanks 4.6 m in diameter × 1 m deep (volume 16.6 m^3) with a fresh seawater inflow of 20 l/min. The fish were exposed to the natural photoperiod but were shielded from direct sunlight. They were fed a ration of Oregon Moist Trout Pellets[3] 6 d/wk. The pellets were dispensed with an automatic feeder over a 4-5 h feeding period beginning at 0800 h (Leong 1971).

To estimate the rate of egg maturation (group 1), 8-12 females were sampled twice weekly for 6 wk. The ovaries of nearly all females were immature (no yolked oocytes) when sampling began; the mean standard length (SL) of females was 112.4 mm increasing to 116.4 mm in 6 wk. The fish were held at ambient temperatures which ranged from 17.9° to 22.0° C and averaged 19.7° C; daily temperatures closely followed those taken at the Scripps Institution of Oceanography pier. We measured standard length, wet weight, and determined the frequency distribution of egg sizes within the ovary for each female sampled. We used as a measure of the state of sexual maturity, the mean size of eggs (major axis) within the most advanced spawning batch. The number of eggs within a batch was calculated from the wet weight of the female using the batch fecundity equation of Hunter and Macewicz (1980)

$$\log_e T = 4.248 + 1.620 \log_e W. \qquad (4)$$

(Equation corrected for bias in taking the antilog; Beauchamp and Olson 1973), where T = total number of eggs in a spawning batch and W = female wet weight (without ovary) in grams.

To measure growth efficiency, two groups (groups 2 and 3) were held under similar tank conditions, but were sampled at 2-wk intervals beginning at the end of November and ending in mid-February. Group 2 was in captivity for about 1 mo and group 3 for 2 wk prior to sampling. Group 2 was held at 15.6° C while group 3 was held at ambient temperatures which ranged from 15.2° to 17.0° C and averaged 16.0° C. Mean standard length of fish in groups 2 and 3 was 107.2 mm at the beginning and 121.4 mm at the end of the experiment.

The stomach contents of each fish sampled from groups 2 and 3 were weighed and used to determine the mean ration for the experiment. The ration was calculated from the equation

$$R = r \cdot s \cdot t + S_e \qquad (5)$$

where R = ration, expressed as wet weight food consumed/wet weight fish (in grams); r = rate of gastric evacuation (dashed line, Figure 1); s = average weight of food in stomach/fish weight during the period of gut filling (solid line, Figure 1); t = duration of feeding (4 h, group 2; 5 h, group 3); and S_e = weight of food in stomach/fish weight

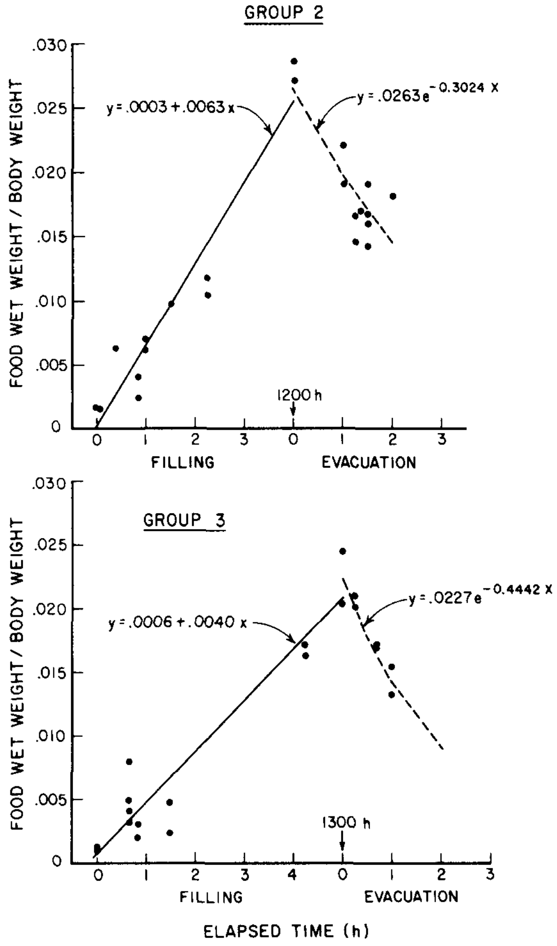

FIGURE 1.—Rate of stomach filling and gastric evacuation in two groups of northern anchovy fed Oregon Moist Trout Pellets. Weight of stomach contents expressed as a proportion of fish weight; each point is mean for 8-12 fish; feeding began at 0 h (*filling*) and ended at 0 h (*evacuation*) (*arrow*); *time of day when feeding ended is above arrow.* Daily ration calculated from these data was 4.4% body weight/d, group 2; and 4.6% body weight/d, group 3.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

at end of feeding period. Similar functions have been used by Tyler (1970), discussed and used by Eggers (1977), and discussed by Elliot and Persson (1978). The daily pattern of feeding and evacuation and the data used to calculate the parameters for the ration equation are given in Figure 1. We use an exponential equation to estimate rate of gastric evacuation (r) because it is required by theory and the above model and use a linear regression equation for gut filling because the equation is used only to provide an empirical estimate of the mean stomach contents (s) during feeding.

The mean ration for a feeding day was 0.0437 g/g body wet weight (group 2) and 0.0462 g/g body wet weight (group 3); these values were multiplied by the mean wet weight of fish sampled (18.6 g, group 2; 17.6 g, group 3) to express the ration in terms of the average fish weight in each experiment. This value was adjusted by the ratio, total number of feeding periods/duration of the experiment (days) (ratio = 59/69, group 2; 67/78, group 3), to adjust the ration for days when no feeding occurred. This daily ration for the experiment was converted to calories by multiplying by 0.656 (average ratio of dry to wet weight for stomach contents of northern anchovy fed Oregon Moist Trout Pellets) and by 4,912, the caloric value per gram for this food (Table 2). The daily ration for fish in group 2 was 2,238 cal/d and was 2,245 cal/d for fish in group 3.

TABLE 2.—Mean calories per gram dry weight of various northern anchovy tissues and food.

Tissues or food	*n*	Mean calories	SD
Anchovy fat	4	9,227	40
Anchovy eggs (including fat)	4	5,450	90
Whole female anchovy, less ovary (fat free)	11	4,129	176
Anchovy ovary (fat free)	29	4,960	79
Anchovy ovary with 18%[1] fat	—	5,710	—
Oregon Moist Trout Pellets	4	4,912	214

[1] 18% is the mean fat content of northern anchovy ovaries; caloric value was calculated from the values for fat and fat-free ovary.

Dry weight and fat content of northern anchovy were determined for the first and last samples of groups 2 and 3. Fish were dried in an oven at 60° C until constant weight and fat extracted using Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950).

Caloric values of northern anchovy oil, newly spawned eggs, ovaries and whole females (without ovaries), and Oregon Moist Trout Pellets were estimated using a Parr bomb calorimeter and standard techniques (Table 2). Laboratory fish were used for all measurements except for the caloric value of northern anchovy oil where sea-caught specimens were used.

SPAWNING FREQUENCY AND RATE OF EGG MATURATION

Number of Spawnings per Year

We plotted the fraction of females spawning per day (females with 24-h-old postovulatory follicles) as a function of sampling date to estimate the number of spawnings produced by female northern anchovy in 1 yr. The seasonal change in the fraction of females spawning followed the seasonal change in the average relative larval abundance for 1953-60 (Lasker and Smith 1977) (Figure 2). The fraction of females spawning was the highest during peak spawning months and declined to zero by September. In peak spawning months the percentage of mature females spawning per day was 16-14%, indicating that individual females spawned every 6-7 d. The seasonal decline in the fraction of females spawning per day could be caused by an increase in the interval between spawnings in individual females, or by a complete cessation of spawning by an increasingly larger proportion of the population, or by a combination of these events.

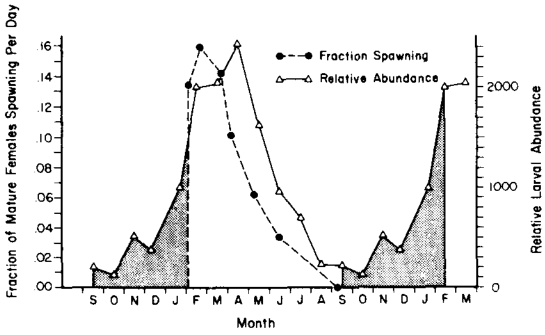

FIGURE 2.—Fraction of mature northern anchovy females from the Southern California Bight spawning per day during various months (dots). Fraction calculated from incidence of females with 24-h-old postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980). Triangles indicate relative larval abundance per month from 1953 to 1960 (Lasker and Smith 1977). Shaded areas indicate months where spawning fraction was not estimated; total spawnings per year by northern anchovy females was estimated from areas under the two curves (see text).

The area under the curve for fraction of females spawning per day is an estimate of the number of spawnings produced per female from February to September. This calculation indicated that each mature female northern anchovy spawned on the average 15 times between February and September. The number of spawnings that occurred in October-January (shaded area, Figure 2) had to be estimated indirectly because no ovary samples existed. We assumed that the number of spawnings was proportional to the relative larval abundance in October-January, adjusted by the ratio of the areas under the spawning fraction and larval abundance curves for Feburary to September. This calculation indicated that about five spawnings would have had to occur in October-January to account for the abundance of larvae in that period; this brings the total number of spawnings for female to 20 for the year.

Form of Frequency Distribution of Egg Size

The form of the egg size distribution in mature northern anchovy ovaries is illustrated for a female taken 24 h after spawning and a mature female without evidence of recent spawning (nonspawning) (Figure 3). Ovarian egg size distributions typically resemble these except for females with hydrated eggs, where the hydrated eggs stand out as a discontinuous group of large eggs. In mature females (without hydrated eggs) the egg size distributions are continuous and typically have one or two modes as illustrated. In the nonspawning female a major mode of large yolked eggs existed between 0.6 and 0.8 mm (major egg axis) and in the spawned female the first modal group occurred at about 0.5 mm. Eggs <0.2 mm are the most abundant size class in both ovaries. These small eggs, also abundant in immature ovaries, form part of the reservoir of immature unyolked eggs which are matured during each spawning season.

Yolk appears in the egg when the major axis of the egg reaches about 0.4 mm. The ovary of the spawned female (20.2 g) in Figure 3 contained 9,384 yolked eggs, whereas that of the nonspawning female (25.3 g) contained 26,761 yolked eggs. The batch fecundity equation (Equation (4)) predicts a batch size of 9,110 eggs for the spawned female and 13,120 eggs for the nonspawning female. Hence, about one spawning batch of yolked eggs existed in the spawned female and about two in the nonspawning female. If a female were to spawn more than a few times in one season, it would have to mature and yolk many of the small unyolked eggs in the ovary. If spawning were to occur at weekly intervals for months, this would be a continuous process.

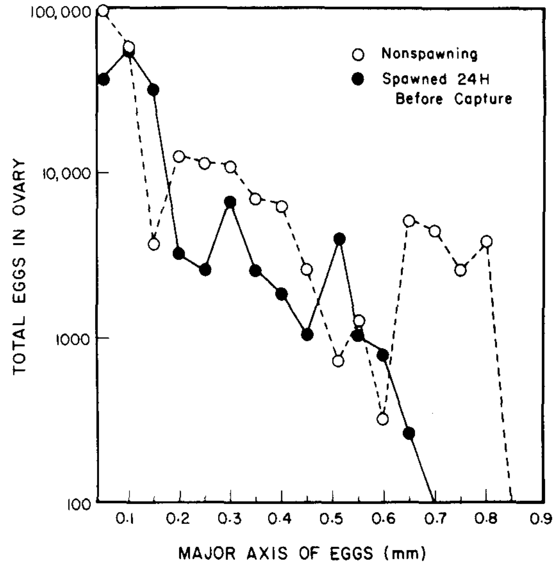

FIGURE 3.—Total eggs in ovary ($\log_{10}$ scale) as a function of the major egg axis for a 20.2 g female northern anchovy (ovary-free weight) captured 24 h after spawning and for a 25.3 g female, showing no evidence of recent spawning (nonspawning). Smallest eggs measured were 0.05 mm; measurements were made in increments of 0.05 mm. Females were captured in January to February 1979 in the Southern California Bight.

Rate of Egg Maturation Required for Continuous Production of Eggs Compared With Laboratory Maturation Rate

For northern anchovy to continually mature and add yolk to a series of egg batches, the abundance of egg sizes in the ovary must vary inversely with the rate of egg maturation. Thus, a hypothetical curve for the rate of maturation of anchovy eggs can be constructed from the average size of eggs in each potential spawning batch within an ovary, if the time between batches or spawning frequency is known. This hypothetical rate can then be compared with the rate of egg maturation in the laboratory to determine if the predicted rate is possible.

To conduct this test for northern anchovy, we partitioned the total number of eggs in the ovary of 10 sea-caught fish into successive spawning batches (starting with the largest eggs) and calculated the mean major axis of eggs in each successive batch. The number of eggs per batch was estimated from the wet weight of the females using the batch fecundity Equation (4).

As might be expected, the mean major axis of eggs in each of the potential spawning batches for the five females taken 24 h after spawning was about one spawning batch out of phase from the five nonspawning fish (Figure 4, upper). When the most advanced spawning batch of the recently spawned group was lagged by one spawning interval, the function was the same for both groups (Figure 4, lower) and similar to data on "nonspawning females" in Hunter and Goldberg (1980). The lower curves indicate that about four spawning batches of eggs >0.15 mm exist in the ovary of females near spawning condition. Hunter and Goldberg (1980) determined for 38 mature nonspawning females that the mean size of eggs in the most mature batch was 0.59 mm; and in the 5 females in the present analysis, the mean size was 0.71 mm. Thus a batch of eggs of 0.15 mm mean size major axis would have to reach about 0.6-0.7 mm in about 4 wk (28 d) if females were to spawn five or more times at weekly intervals.

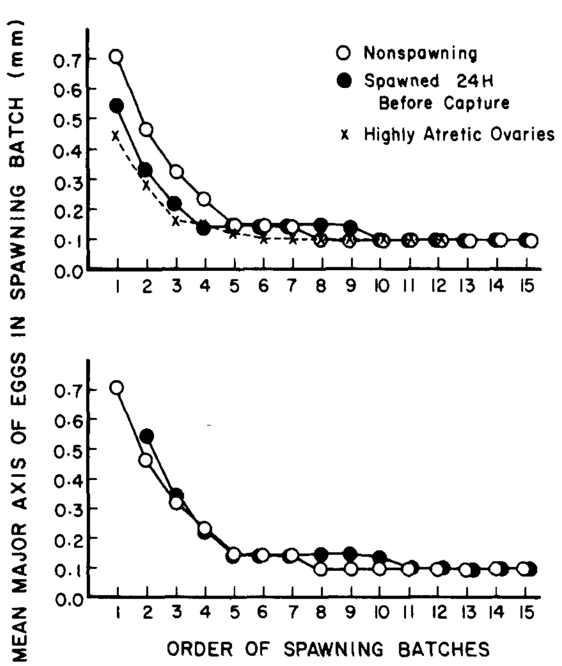

FIGURE 4.—Mean major axis of eggs in successive spawning batches within the ovary of northern anchovy. Number of eggs per batch estimated for each female from Equation (4). Numbers on abscissa indicate order of spawning batch with 1 = the most advanced batch. Circles are means of five nonspawning females (no evidence of recent spawning), and dots are means for five females having spawned within 24 h (females taken in the Southern California Bight); the X's are means for six females with highly atretic ovaries taken in Monterey Bay in 1979. The lower panel illustrates the correspondence between average egg size in successive batches in nonatretic ovaries when recently spawned females are lagged by one spawning batch interval. Only the 15 batches containing the largest eggs are shown.

The ovaries of all laboratory females were immature when the maturation experiment began (elapsed time = 0, Figure 5) although the mean size of eggs in the most advanced spawning batch was quite variable among females (mean egg size ranged from 0.13 to 0.48 mm). To illustrate the rate of ovarian maturation we used the average of the mean egg size in the spawning batch of individual females (Figure 5). The rate of maturation of ovaries in the laboratory group was similar to that predicted from egg size frequency distributions of wild fish, if one assumes spawning in the sea occurs weekly (line, Figure 5). The average of the mean size of eggs in the most advanced spawning batch was 0.15 mm after the first week of the experiment and was 0.62 mm 4 wk later. Thus maturation of eggs from 0.15 to 0.62 mm occurred in four wk and is about the same as the theoretical estimate based on egg size distributions in sea-caught specimens. This demonstrates that the rate of egg maturation required for continuous production of egg batches

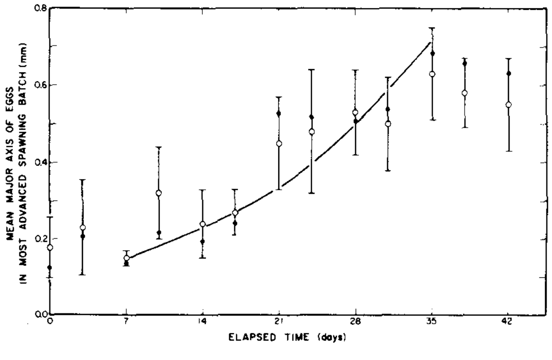

FIGURE 5.—Maturation of eggs in the most advanced spawning batch of laboratory-held northern anchovy as a function of elapsed time. Maturity is achieved when average egg size in batch attains 0.6-0.7 mm. Circles are averages of the mean size of eggs in the most advanced spawning batch of females sampled on a particular day, dots the median, and bars are ±2 SE. Number of eggs used to calculate the mean for each female was determined using Equation (4). The solid line is hypothetical maturation rate of egg batches from 0.15 mm (major egg axis), assuming females spawn at weekly intervals; the line is derived from data in Figure 4.

at 7-10 d intervals occurs in the laboratory and could occur in the sea. In addition, the forms of the theoretical and the laboratory maturation curves were similar, with maturation of small unyolked eggs being much slower than that of larger yolked eggs.

Cessation of Spawning

An assumption of some fecundity studies of multiple spawning fishes is that all eggs to be spawned in a season are yolked at the beginning of the season and spawning ends when these yolked eggs are depleted. The preceding analysis indicated that yolking of eggs from the reservoir of small unyolked eggs is a continuous process in northern anchovy. In this section we determined whether spawning ceases because of a lack of eggs of an appropriate size for maturation. We compared egg size-frequency distributions from six females with highly atretic ovaries with those of reproductively active females. Although the ovaries of the six females contained yolked eggs, they were highly atretic and judged to be in postspawning condition, using histological criteria presented by Hunter and Macewicz (1980).

The form of the line relating the mean major axis of eggs to successive spawning batches (dashed line, Figure 4, upper) was similar in form to those of the other groups. The eggs in the most advanced spawning batch were smaller (0.45 mm) in atretic ovaries than in those of females that had spawned 24 h before capture (0.55 mm). Hunter and Goldberg (1980) showed that the mean major axis of the most advanced eggs (excluding hydrated eggs) was 0.46 mm in females captured on the night of spawning. This value is very close to the mean for highly atretic ovaries. Thus, oocyte maturation, at least in these six females, probably continued up to the time of the last spawning, whereupon maturation ceased and the remaining oocytes became atretic. Spawning did not cease because of lack of yolked eggs; the atretic ovaries of these six females had the same distribution of egg sizes as any female ovary immediately after spawning.

ENERGY COST OF SPAWNING

We consider here three variables affecting the cost of reproduction: Number of eggs in a spawning batch, size of eggs, and the energy existing in a mature ovary. Factors not considered include the metabolic costs of egg maturation and reproductive behavior and variation in the caloric content of eggs.

Number of Eggs

The spawning batch fecundity (number of hydrated eggs) of northern anchovy varies exponentially with female weight (Equation (4)). Similar to many other fishes (Bagenal 1973), fecundity among females of the same size or weight is highly variable. Variability may be caused by variations in egg size, food availability, and number of previous spawnings within the season.

Feeding conditions may not greatly affect batch fecundity in northern anchovy. Females matured in the laboratory (groups 2 and 3) were fed a high ration and grew about four times faster than those in the sea, yet the batch fecundity was about the same as field-caught specimens, which consume a lower ration (Table 3). Although the laboratory females had not begun spawning, their batch fecundity was similar to that of fish taken in the sea between January and April. This indicates that the average batch fecundity may not change over the first months of spawning. The fact that fecundity of females captured in March-April 1979 was about the same as that for January-February 1979 (Hunter and Macewicz 1980) also supports

TABLE 3.—Comparison of the batch fecundity of northern anchovy females matured in laboratory and in the sea within two weight classes.

Weight class (g)	Locality	n	Mean weight (without ovary) (g)	Batch fecundity (total eggs) Mean ± 2 SE	Batch fecundity (total eggs) Estimated for mean weight from fecundity equation for sea-caught female[1]
15-19.9	Laboratory[2]	38	17.9	8,910 ± 1,210	7,420
	Sea[3]	17	16.7	6,800 ± 1,150	6,690
20-24.9	Laboratory[2]	12	22.8	11,900 ± 950	11,100
	Sea[3]	21	22.6	10,400 ± 1,540	10,900

[1] From Equation (4) (Hunter and Macewicz 1980); intercept increased by 0.0647 ($\frac{1}{2}s^2$) to adjust for bias in taking antilog (Beauchamp and Olson 1973).

[2] Batch fecundity = number eggs in most advanced mode in ovary where mean egg size ≥0.65 mm (major axis; eggs not hydrated).

[3] Batch fecundity = number of hydrated eggs in females without *new postovulatory follicles* (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

this view. We conclude that, at least over the first few months of spawning, the mean number of eggs per spawning batch may be independent of past spawning history.

Size of Eggs

The size of spawned northern anchovy eggs varies seasonally as do those of other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Smith and Richardson (1977) demonstrated that the major axes of northern anchovy eggs spawned in February 1972 were larger than those of eggs spawned in August 1972 ($P = 0.05$). The seasonal trend in dimensions of northern anchovy eggs is illustrated in Figure 6 (upper). The dry weight of eggs (calculated from their volume (Equation (3)) varies by about 20% over the spawning season; thus, females could produce about five more spawnings/yr at the minimum egg size than at the maximum with no increase in energy demand. The seasonal trend in egg dry weight is similar to the relative larval abundance (shaded area of Figure 6), with the largest eggs produced in February to April when most of the spawning occurs and the smallest eggs late in the summer when the least spawning occurs. Several possible explanations exist for the seasonal trend in egg size. Females may produce smaller eggs as the spawning season progresses or, alternatively, large females which begin spawning earlier may produce larger eggs than small females. Regardless of the mechanism, it probably is adaptive to produce larger eggs early in the spawning season when water temperatures are cooler since the advantage falls to larger eggs as water temperature declines, because incubation periods are longer (Ware 1975).

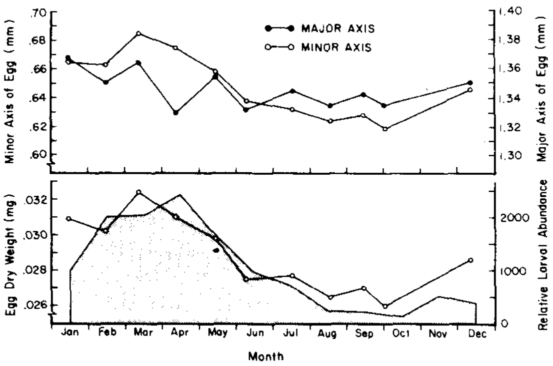

FIGURE 6.—Mean size of northern anchovy eggs taken in routine plankton tows by month. Upper, mean major and minor axes of eggs; lower, mean weight of eggs calculated from average dimensions of eggs given in upper figure using Equation (3); shaded area is the relative larval abundance for years 1953-60, from Lasker and Smith (1977).

Maturation of Eggs

Northern anchovy eggs < 0.1 mm are spherical; they become oblate spheroids between 0.1 and 0.25 mm (major axis) and thereafter retain the same proportionality between axes through hydration and spawning (Figure 7, upper). Hydration of the spawning batch of eggs (rapid uptake of fluid) begins about 12 h before spawning (Hunter and

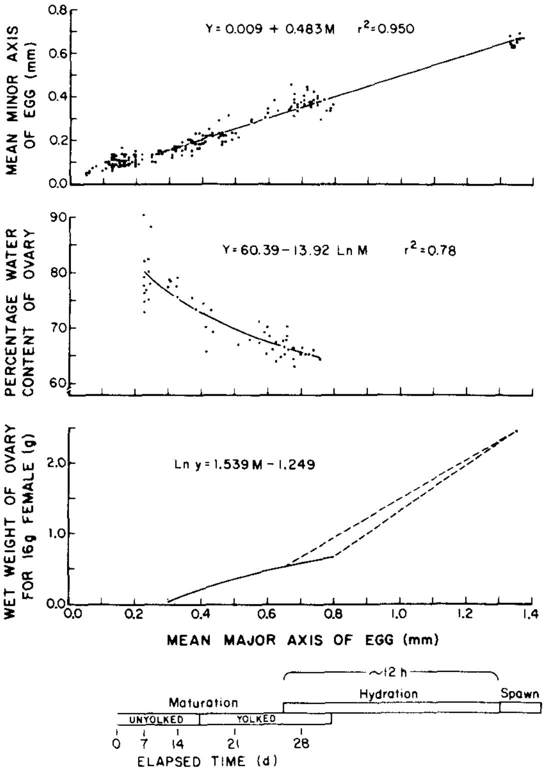

FIGURE 7.—The mean length of the minor egg axis (upper), water content of the ovary (middle), and ovary wet weight of a 16 g northern anchovy female calculated from Equation (6) (bottom), as functions of the mean major egg axis of eggs in the most advanced spawning batch (natural logarithms were used). Original data for Equation (6) (solid line, bottom) given in Hunter and Goldberg (1980); dashed lines indicate the range of egg sizes that may hydrate; and they converge at the average weight of a hydrated ovary in a 16 g female. Time scale on abscissa is based on hypothetical rate of egg maturation required for weekly spawning (see Figure 4).

Macewicz 1980), resulting in a rapid increase in ovary wet weight (Figure 7, lower) but no change in dry weight (Le Clus 1979). The mean size of eggs in a spawning batch, just before hydration, ranges from 0.6 to 0.8 mm; eggs >0.8 mm nearly always show histological signs of hydration. The average size of eggs that are hydrated would be expected to vary since the size of spawned eggs is variable.

The wet weight of the ovary (G) increases during maturation and is a function of the mean major axis of the eggs in the most mature spawning batch (M) and female wet weight without ovary (W); in northern anchovy this function is expressed as

$$\log_e G = -4.213 + 1.069 \log_e W + 0.555\, M \log_e W \qquad (6)$$

(Hunter and Goldberg 1980) (Figure 7, lower). The water content of the ovary of laboratory females (group 1) declined during maturation from 80 to 65% just before hydration (Figure 7, center). The fat content did not change significantly over the maturation period; mean ovarian fat content of laboratory-matured northern anchovy was 18.6±1.2% (±2 SE of mean, n = 41) of ovary dry weight. As the fat content did not change, the caloric value of ovarian tissue can be considered to be constant at 5,710 cal/g dry weight (Table 2).

Using Equation (6), caloric values (Table 2), and water content of ovary (Figure 7), we estimate the ovary of a 16.4 g female contains 933 cal just after spawning when the mean major axis of most advanced eggs = 0.46 mm (Hunter and Goldberg 1980). The spawning batch of a 16.4 g female contains 6,500 eggs or 1,066 cal (from Equation (4)). Thus, just before spawning the ovary contains about 2,059 cal and the most advanced spawning batch constitutes about 52% of the calories in the ovary (documentation given in Table 4). Similar calculations can be made using the volume of eggs in the ovary and egg dimensions given in Figure 7 (upper) or by calculating the wet weight of the ovary at 0.46 mm egg major axis (after spawning) and at 0.81 mm egg major axis (at onset of hydration) using Equation (6). All calculations yield similar results when converted to dry weight or calories, i.e., about one-half of the calories in the ovary are lost in one spawning. We conclude that the calories invested in a mature ovary are small relative to the total reproductive cost of 20 spawnings.

ANNUAL FAT CYCLE AND SPAWNING

As the caloric equivalent of only two spawnings exists in the ovary at one time, northern anchovy must use energy stored in other tissues and food income to support reproduction. Lasker and Smith (1977) showed that the fat content of northern anchovy, like many other clupeoids (Blaxter and Holliday 1963; Shul'man 1974) varies seasonally. The fat accumulates in the body rapidly between April and July, matching the annual spring bloom of zooplankton (Lasker and Smith 1977). It usually remains high through December and then declines to a minimum between February and May (Figure 8). The decline in fat occurs during the months of maximum spawning. Thus, fat stored

TABLE 4.—Reproductive characteristics for the average female northern anchovy.

Item	Value	Explanation and data source
Weight and fecundity:		
Mean female wet weight, less ovary	16.4 g	For 1978 and 1979 (Hunter and Macewicz 1980)
Ovary wet weight after spawning[1]	.601 g	Equation (6) where M = 0.46 mm
Ovary dry weight after spawning[1]	.174 g	Percentage water in ovary from Figure 7 (center)
Number of eggs in one spawning batch	6,500 eggs	Equation (4)
Number of eggs spawned/yr	130,000 eggs	Assume 20 spawnings (Figure 2)
Dry weight one spawned egg	.0301 mg	Mean of monthly dry weight: (Figure 6) weighted by relative monthly larval abundance (Lasker and Smith 1977)
Caloric content of ovaries and spawn:		
Calories in one spawning batch	1,066 cal	Caloric value of eggs = 5,450 cal/g (Table 2)
Calories in ovary after spawning	993 cal	Caloric value of ovary = 5,710 cal/g (Table 2)
Calories in ovary just before spawning	2,059 cal	
Percentage of calories in ovary lost in one spawning batch	52%	
Daily spawning cost during peak spawning months	152 cal/d	Assume spawning interval = 7 d
Spawning related to fat stores:		
Maximum fat in body	2.009 g	Equation (1) where 41% of dry weight = fat
Minimum fat in body	.510 g	Equation (1) where 15% of dry weight = fat
Total fat stores	13,831 cal	Caloric value of fat = 9,227 cal/g (Table 2)
Fat stores in spawning batch equivalents	13 batches	

[1] Females with postovulatory follicles <24 h old.

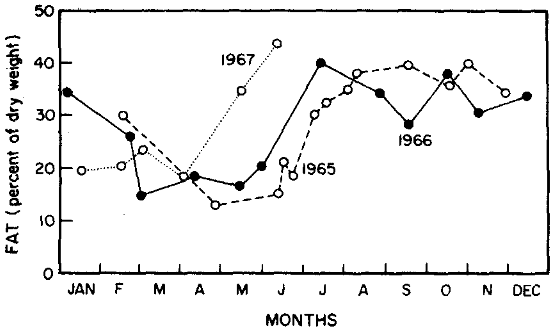

FIGURE 8.—Annual fat cycle of northern anchovy. Fat content expressed as a percentage of dry weight for various months in 1965, 1966, and 1967. Data from Lasker and Smith (1977).

from the previous spring and summer may be used the following year to support reproduction. Fat stores may not be used directly to promote egg production, which are largely protein, but rather to provide energy needed for metabolism, permitting energy from food to be used for egg maturation.

We calculated the number of spawnings that could be financed by the annual decline in fat stores, assuming that this energy or its equivalent is used for reproduction. We used the average minimum and maximum fat level for the 3 yr (Table 5) to estimate the grams of fat annually available for reproduction. Using the dry weight, fat, and wet weight relation (Equation (1)), we calculate that a 16.4 g female would store annually 13,831 cal of fat (Table 4) which is equivalent to 13 spawning batches. Thus, about two-thirds of the annual cost of egg production can be accounted for by the annual decline in fat stores.

The rate of increase in fat in the spring was similar in the 3 yr (1965-67) although the timing of the onset varied by 2-3 mo. The maximum rate occurred in the late spring or summer over a period of about 63 d (Table 5). Nearly all fat stores were accumulated over this period; on the average fat increased from 16.5 to 40.5% of the dry weight over the 63 d. Thus, calories would accumulate in a 16.4 g fish at a rate of about 200 cal/d or the caloric equivalent of one spawning batch would be stored about every 5 d.

TABLE 5.—Maximum and minimum fat content of female northern anchovy from Southern California Bight in 1965-67.[1]

	Fat content (% dry weight)				Period of maximum rate of increase in fat stores	
	Minimum		Maximum			
Year	Mo.	%	Mo.	%	Mo.	Total days
1965	Apr.	13.0	Nov.	39.8	June-Aug.	59
1966	Mar.	15.0	July	40.0	May-June	60
1967	Apr.	18.2	June	43.5	Mar.-May	69
Mean		15.4		41.1		63

[1] Data illustrated in Figure 8; from Lasker and Smith (1977).

This analysis indicates that the annual spring bloom might regulate the reproductive potential of the northern anchovy population. This effect may have a 1-yr lag because fat accumulated in the late spring and summer would presumably be used to support reproduction the following year because most spawning occurs in February through April. On the other hand, if 20 spawnings occur, about one-third of them would have to be supported from energy gained during the current year. Thus, production of plankton might have an effect on egg production late in the spawning season, but the major effect of the spring bloom on reproduction may occur the following year.

ENERGY BUDGET FOR FEMALE GROWTH AND REPRODUCTION

In this section we calculate an annual energy budget for reproduction and growth in female northern anchovy based on relationships established in past sections and in the laboratory ration study outlined below. Food ration (R) may be partitioned into energy losses of metabolism (Q), excretion (X), digestive losses (I), reproductive costs (S), gains in growth (N) and fat stores (F) where

$$R = Q + X + I + S + N + F. \tag{7}$$

We do not estimate Q, X, or I, but rather calculate for laboratory females the gross conversion efficiency (C) where

$$C = \frac{S + N + F}{R}. \tag{8}$$

Variables N and F were calculated by subtracting weight and fat content of females determined at the beginning of the experiment from that determined at the end (Table 6); reproductive cost S was simply the increase in weight of the ovary since the fish did not spawn during the experiment; and R was calculated using Equation (5).

The coefficient C was used to estimate ration for natural populations using

$$R = \frac{S + N}{C}. \tag{9}$$

TABLE 6.—Calories gained per day and daily ration of two groups of northern anchovy fed Oregon Moist Trout Pellets.

Item	Standard length (mm)		Fat-free dry weight (without ovary) (g)		Fat in body (without ovary) (g)		Ovary dry weight (including fat) (g)	
	Beginning	End	Beginning	End	Beginning	End	Beginning	End
Group 2								
Mean	108	120	2.38	3.27	1.17	2.66	0.14	0.38
SE of mean	.86	1.04	.09	.12	.30	.18	.02	.02
Number of fish	21	19	21	19	21	19	21	21
Group 3								
Mean	106	122	2.16	3.30	.70	2.54	.04	.38
SE of mean	1.51	1.31	.10	.08	.03	.11	.02	.03
Number of fish	24	18	24	18	24	18	24	18

Group	Duration of experiment (d)	Daily ration[2] (cal)	Calories gained per day[1]			
			Body (less ovary) (fat free)	Fat	Ovary (including fat)	Total
2	69	2,238	53	199	19.8	271
3	78	2,245	60	218	24.9	303
Mean	73.5	2,241	56	208	22.4	287
Percentage of ration			2.5	9.2	1.0	12.8

[1] Caloric values in Table 2.

[2] Method of calculation of ration outlined in methods.

Fat stores (F) are included in calculation of C in the laboratory work (Equation (8)) but not in the ration for natural populations (Equation (9)) because on an annual basis it is assumed to be subsumed in the annual cost of reproduction. The caloric value used for growth was set at the minimum fat content of the year (15.4% of the dry weight) using values in Table 2 and Equation (1).

Laboratory Growth Efficiency

Northern anchovy (groups 2 and 3) maintained in the laboratory grew much faster than those in the sea. The growth in length was about four times that estimated for wild northern anchovy by Spratt (1975) but was seven times faster when Spratt's data were converted to wet weight using the length-weight conversion for females of Collins (1969) (solid line, Figure 9). Thus, the average ration consumed by northern anchovy in the laboratory, 2,241 cal/d (about 124 cal/g fish wet weight per d) is probably much larger than the one consumed in the sea. On a wet weight basis, the laboratory ration (4.5% of fish wet weight/d) is deceptively low because the pelleted food had a much lower water content (35%) than natural foods (85%). A caloric equivalent ration of natural foods (copepods) would be about 16% of the wet weight/d.

Spawning did not begin during the experiment, hence the proportion of the daily ration incorporated into the ovaries (0.8%) was a function of only maturation of the ovary (Table 6). The median of the mean major axis of the eggs in the most advanced batch in the ovary increased from 0.55 to 0.63 mm in group 2 and from <0.25 to 0.63 mm for group 3. Most of the caloric gain was in fat; the percentage of the dry weight that contained fat increased from 32.6 to 44.2% in group 2 and from 24.5 to 43.2% in group 3 and accounted for about 9.2% of the daily ration. The caloric conversion efficiency for the total gain of calories in the body (including ovary and fat) was 12.8%. We calculated from data of Takahashi and Hatanaka (1960)

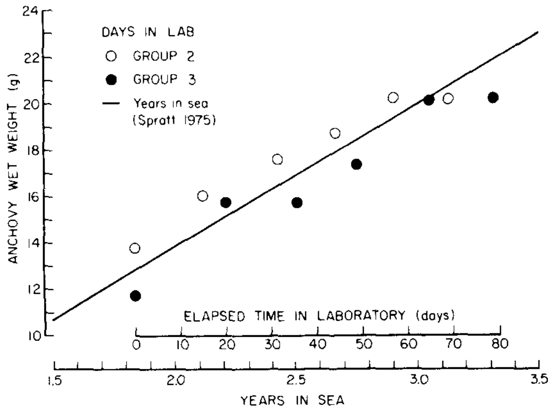

FIGURE 9.—Growth in days of two groups of northern anchovy in the laboratory (dots and circles) compared with the growth over years of northern anchovy in the sea (solid line). Growth in the laboratory is plotted using upper scale (elapsed time days), and growth in sea (solid line, from Spratt 1975; Collins 1969) is plotted on lower scale (years); and ratio between scales is about 1:7. Each point is mean weight for 8-12 fish. Laboratory fish were fed a pelleted trout ration which was the caloric equivalent in natural foods of about 16% of the fish wet weight per day.

that the Japanese anchovy, *Engraulis japonicus*, fed *Euphausia pacifica* in the laboratory, had a gross growth efficiency (in calories) of 11.9%, which is similar to our estimate of 12.8% for *E. mordax*.

Energy Budget

Growth of northern anchovy in the sea from age 1 to 2 yr is equivalent to a gain of 6.2 × 10^3 cal, and the energy cost of 20 spawnings for a 1-yr-old female is about 10 × 10^3 cal (documentation given in Table 7). Assuming that the caloric conversion efficiency for northern anchovy in the sea is the same as in the laboratory (12.8%), 1-yr-old females (mean weight 10.3 g) consume annually about 127 × 10^3 cal of which 8% would be used for reproduction and 5% for growth. This implies a daily rate of consumption in the sea of 348 cal/d, or, on a wet weight basis, about 4% body wet weight/d in copepods (copepods = 5,252 cal/g dry weight, Laurence (1976); water content of *Calanus* = 84.7%, Lovegrove (1966)). Sirotenko and Danilevskiy (1977) estimated from stomach content analysis that the Black Sea anchovy, *E. encrasicholus*, consumed 1.5-3.7% of their body weight/d; Mikhman and Tomanovich (1977) estimated from field captured specimens that *E. encrasicholus* consumed 1.4-3.0% of their body weight/d when they fed upon phytoplankton, 3.4% when they ate zooplankton, and 9.3% when they ate benthic animals. Our estimate of 4-5% body weight/d for females 1-3 yr old is within the range of these values.

DISCUSSION

Spawning Frequency

Northern anchovy females matured eggs in the laboratory at the rate required for weekly spawning, thus supporting the conclusions of Hunter and Goldberg (1980) and Hunter and Macewicz (1980). Our estimates of reproductive effort (egg calories/ration calories) of 8-11% (Table 7) seem reasonable, thereby supporting our estimate of 20 spawnings/female per year. Our calculations indicate that this effort could be sustained by a daily ration of natural foods of 4-5% of the fish wet weight/d which is similar to the natural ration of *E. encrasicholus* (Sirotenko and Danilevskiy 1977; Mikhman and Tomanovich 1977). Few estimates of reproductive effort exist for fishes. Lasker (1970) estimated that the cost of reproduction in Pacific sardine, *Sardinops sagax*, was about 1% of the total annual caloric requirement. He assumed the caloric equivalent of the ovary is spawned per year, which now seems an underestimate. Constantz (1976) estimated that reproductive effort ranged from 4 to 15% in two populations of *Poeciliopsis occidentalis*. Hirshfield (1977) found in laboratory studies that reproductive effort was related in a complex fashion to temperature and ration in medaka, *Oryzias latipes*; he estimated reproductive effort ranged from 10 to 18% in two natural Japanese populations. We conclude that 20 spawnings/yr is a reasonable estimate of the number of spawnings produced by females in the northern anchovy central subpopulation. The fact that two-thirds of the cost could be supported by the average annual decline in fat stores supports this conclusion.

An implication of this study is that egg maturation and vitellogenesis are continuous during peak spawning months. Evidence for this includes: the large fraction of the females in the population spawning per day during peak spawning months (10-16%); the presence of the caloric equivalent of only one or two spawning batches in the ovary at any time; the inverse relation between the abundance of egg sizes in the ovary and oocyte maturation rate; and the continuation of egg maturation until the last batch of eggs is spawned. Although maturation and vitellogenesis probably continue for extended periods, the rates probably vary. The seasonal decline in the fraction of females in the

TABLE 7.—Annual energy budget for female northern anchovy.

Age (yr) Beginning-end	SL[1] (mm) Beginning-end	Wet weight[2] (g) Beginning-end	Annual energy budget (thousands of calories)			Percentage of ration	
			Growth[3]	Reproduction[4]	Ration[5]	Growth	Reproduction
1-2	93-112	7.33-13.25	6.24	10.00	127	5	8
2-3	112-126	13.25-19.33	6.38	21.0	214	3	10
3-4	126-136	19.33-24.69	5.60	34.3	312	2	11

[1] From Spratt (1975).
[2] From Equations (1) and (2) where 15.4% of dry weight = fat.
[3] Gain in calories assuming 15.4% of dry weight = fat; caloric values in Table 2.
[4] Caloric content of 20 spawning batches; batch size calculated for mean female wet weight over the year (method illustrated in Table 4).
[5] Reproduction calories + growth calories/0.128, where 0.128 is growth conversion efficiency determined in laboratory (Table 6).

population spawning per day indicates that either the interval between spawnings in individual females increases in the latter part of the spawning season, or that an increasing number of females cease spawning as the season progresses, or a combination of both events. Rates of egg maturation and vitellogenesis probably also vary within a single maturation-spawning cycle. The caloric content of a northern anchovy ovary about doubles over the interval between spawnings (7-10 d in peak spawning months), indicating a rapid rate of vitellogenesis after spawning. In *Brachydanio rerio*, which spawns at 5-d intervals, a marked increase in gonadotropic activity occurs in the pituitary immediately after spawning (Lambert and van Oordt 1974), followed 1-2 d later by histological signs of an increase in lipoprotein production in the liver correlated with an increase in vitellogenesis (Peute et al. 1978). Similar processes may occur in northern anchovy, causing cyclic changes in the rates of vitellogenesis and egg maturation within the interval between spawnings.

Our estimate of 20 spawnings/yr is much higher than the number of spawnings estimated for many other pelagic spawning clupeoid fishes or for pelagic spawners in general. Multiple spawning fishes such as pilchards, sardines, anchovies, jack mackerels, and mackerels are often believed to produce one to three and possibly more spawning batches per year. These conclusions are based on the fact that frequently two modes of yolked eggs and sometimes three (in females with hydrated eggs) are observed in frequency distributions of ovarian egg sizes. Eggs are distributed in the same way in the northern anchovy (MacGregor 1968; Hunter and Goldberg 1980), but as present studies indicate, estimates of one to three spawnings would be in error by a factor of about 10. Thus, comparisons of annual fecundity among pelagic spawning clupeoids are meaningless at present, and spawning biomass estimated from egg and larval surveys may be in error because the total fecundity is inaccurate. Because of this it is essential that spawning frequency be estimated for additional species.

The best approach, at present, is the histological technique of Hunter and Goldberg (1980), but counts of the number of females with hydrated eggs could be used if histological techniques are impractical. Females with hydrated eggs are often rare in collections of clupeoid females taken during the spawning season (Higham and Nicholson 1964; Leary et al. 1975). Females with hydrated eggs may be available for sampling for only a short period of each day because hydration is rapid and spawning soon follows hydration. In northern anchovy, hydration is completed in about 12 h, but the earliest stage may not be evident without histological examination. In tropical species the time available for sampling females with hydrated eggs may be even less because of elevated temperature. The daily pattern of hydration and spawning must be known to use hydrated eggs as a measure of spawning frequency. It may also require sampling of fish in the day, because many pelagic spawners such as the northern anchovy begin spawning at sunset (Blaxter and Holliday 1963; Leary et al. 1975; Hunter and Macewicz 1980).

Variation in Egg Production and Reproductive Effort

Annual egg production and/or reproductive effort in northern anchovy populations can be modulated by changes in batch fecundity, annual number of spawnings, female size at first maturity, egg size, and egg cannibalism. Some evidence exists for each of these mechanisms in northern anchovy populations; we consider the evidence below.

Batch fecundity was relatively constant over 1978-79 (Hunter and Macewicz 1980) and was similar to that of laboratory specimens fed a large food ration. On the other hand, MacGregor (1968) estimated a somewhat higher fecundity for the central stock in the 1950's than Hunter and Macewicz (1980) did for the 1970's, and Laroche and Richardson (1981) found that batch fecundity of the northern subpopulation (Oregon coast) was much higher than all estimates for the central stock. Batch fecundity certainly differs between central and northern subpopulations, and it seems possible that it may have varied within the central stock over the last decades. Nevertheless, batch fecundity within a subpopulation may be a relatively more stable reproductive characteristic than other reproductive traits.

Weight at first maturity and age structure of the spawning population have a major effect on egg production, since batch size in northern anchovy increases exponentially with weight. Clark and Phillips (1952) concluded for females taken in 1946-52 from the central subpopulation that 50% of northern anchovy reach maturity at 130 mm SL whereas Hunter and Macewicz (1980) estimated for 1979 that 50% of females of 96 mm SL were mature. Laroche and Richardson (1981) reported that only 31% of females 85-100 mm SL from the northern stock were mature. Thus, size at sexual maturity varies between subpopulations and may have varied within the central subpopulation over the last decade.

The relatively short 2-mo spawning season of the northern subpopulation of northern anchovy (perhaps 4 to 8 spawnings, Hunter and Macewicz 1980) compared with the central subpopulation (20 spawnings) is evidence of the great plasticity in the annual number of spawnings. Plasticity in the number of spawnings of the central stock is also indicated by the dynamics of the central population over the last decades. Smith (1972) pointed out that the decline of the Pacific sardine population was accompanied by an increase in the duration of the northern anchovy spawning period. Before the Pacific sardine decline, most northern anchovy spawning occurred in the winter quarter, whereas now larval production in both quarters is about equal. This increase in the duration of the peak period of spawning indicates that the annual number of spawning batches produced by northern anchovy has changed significantly since the demise of the Pacific sardine population. Food made available by the collapse of the Pacific sardine population may have been used by the northern anchovy population to increase the number of spawning batches produced annually. The fact that these additional spawnings occurred during the period Pacific sardine normally spawned may have had an important effect on the Pacific sardine population.

The annual seasonal decline in egg size in northern anchovy population (central stock) resembles that reported for other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Production of smaller eggs late in the season may be an energy-sparing mechanism whereby fecundity is maintained constant but at a lower reproductive effort. This could represent a 20% savings in reproductive costs in northern anchovy. Bagenal (1973) concluded in his review of the literature that it seems likely a negative correlation exists between fecundity and egg size. Several other mechanisms are possible; egg size may increase with female age (Hirshfield 1977), and the seasonal change could be caused by seasonal changes in the age structure of the spawners. In this case smaller eggs may compensate for the energy cost of faster growth in young fish. Alternatively, egg size may decline in females as ration increases during the spring and summer. Bagenal (1969) found that higher ration in brown trout resulted in more and smaller eggs. On the other hand, Hislop et al. (1978) found that the dry weight of eggs produced by haddock in the laboratory declined with successive spawnings and that the dry weight of eggs tended to be lower in females fed a lower ration. In northern anchovy, there may be a change in the partitioning of energy between growth and reproduction during late spring and summer when the potential for growth is higher, and this could result in the production of smaller eggs. As egg size alters the survival potential of the larva (Blaxter and Hempel 1963), any of these mechanisms could have important consequences because it could alter the relative contribution to recruitment of spawn produced in the latter part of the spawning season.

Egg cannibalism may also be an important factor regulating the effective egg production, as intensity of cannibalism could change with population size. Hunter and Kimbrell (1981) concluded that ingestion of eggs by northern anchovy could account for 17% of the daily egg production during peak spawning months.

This discussion indicates that egg production and reproductive effort of northern anchovy populations probably changes in a complex manner in relation to food, growth, temperature, population size, and age structure. All the reproductive parameters we have discussed may vary to some degree over years, between subpopulations, or within a season.

Studies of the reproductive energetics of northern anchovy populations will eventually require consideration of males as well as females. We know little about males at present. Our laboratory data indicated that males consume slightly less food than females, but no difference existed when consumption was expressed on a unit weight basis. Growth curves for male and female northern anchovy (Collins 1969) indicate that females are slightly longer than males of the same age, but the difference is small (about a 2% difference in length) and probably not statistically significant. Other than this small difference in size, no obvious sexual dimorphic characters exist. Schools have highly biased sex ratios (Klingbeil 1978), and males predominate in actively spawning schools (Hunter and Goldberg 1980). This suggests that males may remain reproductively active for longer periods within the spawning season and may not have as well defined spawning cycles as do females. These differences are small relative to the overall great similarity between the sexes.

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LITERATURE CITED

BAGENAL, T. B.
1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish Biol. 1:167-182.
1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:186-198.
BEAUCHAMP, J. J., AND J. S. OLSON.
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.
BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 177-252. Acad. Press, N.Y.
BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. 28:211-240.
BLAXTER, J. H. S., AND F. G. T. HOLLIDAY.
1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1:261-393.
CIECHOMSKI, J. D. DE.
1973. The size of the eggs of the Argentine anchovy, *Engraulis anchoita* (Hubbs & Marini) in relation to the season of the year and to the area of spawning. J. Fish Biol. 5:393-398.
CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. Calif. Fish Game 38:189-207.
COLLINS, R. A.
1969. Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67, and 1967-68 seasons. *In* J. D. Messersmith and staff (editors), The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 56-74. Calif. Dep. Fish Game, Fish Bull. 147.
CONSTANTZ, G. D.
1976. Life history strategy of the gila topminnow, *Poeciliopsis occidentalis*: a field evaluation of theory on the evolution of life histories. Ph.D. Thesis, Arizona State Univ., Tempe, 103 p.
EGGERS, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290-294.
ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.
HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.
HIRSHFIELD, M. F.
1977. The reproductive ecology and energetics of the Japanese medaka, *Oryzias latipes*. Ph.D. Thesis, Univ. Michigan, Ann Arbor, 177 p.
HISLOP, J. R. G., A. P. ROBB, AND J. A. GAULD.
1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish Biol. 13:85-98.
HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.
HUNTER, J. R., AND C. A. KIMBRELL.
1981. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811-816.
HUNTER, J. R., AND B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.
ILES, T. D., AND R. J. WOOD.
1965. The fat/water relationship in North Sea herring (*Clupea harengus*), and its possible significance. J. Mar. Biol. Assoc. U.K. 45:353-366.
KLINGBEIL, R. A.
1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off southern California. Calif. Fish Game 64: 200-209.
KRVARIĆ, M., AND R. MUZINIC.
1950. Investigation into the fat content in the sardine tissues (*Clupea pilchardus* Walb.). Acta Adriat. 4: 289-314.
LAMBERT, J. G. D., AND P. G. W. J. VAN OORDT.
1974. Ovarium hormones in teleosts. Fortschr. Zool. 22: 340-349.
LAROCHE, J. L., AND S. L. RICHARDSON.
1981. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington. Fish. Bull., U.S. 78: 603-618.
LASKER, R.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. *In* J. H. Steele (editor), Marine food chains, p. 265-284. Oliver and Boyd, Edinb.
LASKER, R., AND P. E. SMITH.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.
LAURENCE, G. C.
1976. Caloric values of some North Atlantic calanoid copepods. Fish. Bull., U.S. 74:218-220.

LEARY, D. F., G. I. MURPHY, AND M. MILLER.
1975. Fecundity and length at first spawning of the Hawaiian anchovy, or nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. Pac. Sci. 29:171-180.

LECLUS, F.
1979. Dry mass of yolked oocytes of the southwest African pilchard, *Sardinops ocellata*, in relation to maturity stages and spawning cycles, 1972-1974. Invest. Rep. 119, Ondersoekverslag, p. 1-29.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LOVEGROVE, T.
1966. The determination of the dry weight of plankton and the effect of various factors on the values obtained. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 429-467. Hafner Publ. Co., N.Y.

MACGREGOR, J. S.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.

MIKHMAN, A. S., AND L. V. TOMANOVICH.
1977. The feeding of the Azov anchovy, *Engraulis encrasicholus maeoticus*. J. Ichthyol. 17:240-244.

PEUTE, J., M. A. VAN DER GAAG, AND J. G. D. LAMBERT.
1978. Ultrastructure and lipid content of the liver of the zebrafish, *Brachydanio rerio*, related to vitellogenin synthesis. Cell Tissue Res. 186:297-308.

SHUL'MAN, G. E.
1974. Life cycles of fish. Physiology and biochemistry. Wiley, N.Y., 258 p.

SIROTENKO, M. D., AND N. N. DANILEVSKIY.
1977. Quantitative indices of the feeding of the Black Sea anchovy, *Engraulis encrasicholus ponticus*. J. Ichthyol. 17:610-617.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

SPRATT, J. D.
1975. Growth rate of the northern anchovy, *Engraulis mordax*, in southern California waters, calculated from otoliths. Calif. Fish Game 61:116-126.

TAKAHASHI, M., AND M. A. HATANAKA.
1960. Experimental study on utilization of food by young anchovy, *Engraulis japonicus* Temminck et Schlegel. Tohoku J. Agric. Res. 11:161-170.

TYLER, A. V.
1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27:1177-1189.

WARE, D. M.
1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32: 2503-2512.