# AGE DEPENDENT FECUNDITY, NUMBER OF SPAWNINGS PER YEAR, SEX RATIO, AND MATURATION STAGES IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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## ABSTRACT

Maturity stage data from fishery sampling programs and ovarian histological data from research cruises were used to develop a method for determining the age-specific number of spawnings per year and annual fecundity of the central stock of northern anchovy, *Engraulis mordax*.

The sex ratio was found to be size and age dependent in both the fishery and trawl surveys with females increasingly dominant in the larger and older size and age classes. The overall sex ratio in trawl surveys was nearly 1:1; the fishery data favored females 1.48:1. The magnitude and duration of maturity stages were size and age dependent with peak spawning occurring earlier in the season in younger fish. Maturity stages and histological classes with hydrated eggs showed essentially the same diurnal pattern for nightly spawning activity indicating that the presence of hydrated eggs could be used as an index of daily spawning. The daily spawning incidence and total annual fecundity were found to be heavily age dependent. Females in their first spawning season had an average of 5.3 spawnings, while those in their fourth had an average of 23.5 spawnings. When combined with the higher batch fecundity of larger fish this results in 4+ year-old females producing nearly 5 times as many eggs per unit of weight as 1-year-olds. When the age-specific fecundity and sex ratio in the fishery are combined it is apparent that the catch of a ton of 4+ year-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-year-olds.

It was concluded that age-specific fecundity in multiple spawning fishes is of greater significance for management than previously thought. It is also significant that much of the observed variance in stock-recruitment relationships for multiple-spawning fishes may be due to the fact that spawning biomass is a poor index of the egg production and reproductive potential of the stock.


Age-specific variation in life history rates is a major factor in population and management models of exploited fishes, and variation in reproductive effort is of great significance in such models. Size and age-specific batch fecundity estimates have been available for many species for decades, and for species which spawn only once per spawning season these are readily incorporated into models. However it has been impossible to determine the age-specific reproductive effort of species which spawn many times during a spawning season because there has been no way to determine the number of spawnings per year.

Recent research on the histology of the ovaries of northern anchovy, *Engraulis mordax*, and anchoveta, *Engraulis ringens*, suggest that they spawn approximately once a week during peak spawning months (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Alheit et al. 1983; Alheit et al. 1984). Hunter and Leong (1981), in their study of the spawning energetics of the northern anchovy, found that northern anchovy spawn about 20 times per year. Hunter and Leong (1981) and Alheit et al. (1983) suggested that annual fecundity per unit of parental biomass may be highly variable and dependent upon the nutritional state and size structure of the stock.

Potentially the recently developed histological techniques could be utilized to determine age-specific annual fecundity; however, this would be very expensive as it would require a very large data set which would necessarily be stratified by age and time of year. The objectives of this report are 1) to demonstrate a method for combining the high resolution reproductive information from the histology of the ovaries with inexpensive, lower resolution reproductive information derived from resource surveys and fishery sampling programs to determine the age-specific reproductive potential of a multiple spawning species, and 2) to evaluate the gross anatomical maturity stages which have been

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utilized in field sampling programs for northern anchovy and to use the historical data from these programs in conjunction with ovarian histological data to describe age-dependent annual fecundity in the central stock of northern anchovy.

## DATA SOURCES

There are three major sources of biological data for adult northern anchovy in California: samples taken from the commercial fishery (Collins and Spratt 1969), samples taken from midwater trawl hauls carried out by the Sea Survey Program (Mais 1974), and samples taken primarily by midwater trawl during egg production cruises (Picquelle and Hewitt 1983). The first two sources are the result of long-term research and monitoring programs carried out by the California Department of Fish and Game, and the third is the result of research cruises carried out by the National Marine Fisheries Service. The fishery data used in this analysis consist of biological information for 60,661 northern anchovy sampled from the San Pedro purse seine fleet during the period of 1966-80 and 4,904 northern anchovy sampled from the Monterey fleet during 1966-78. All northern anchovy in the fishery samples were aged and nearly all were assigned maturity stages. We used a geographically restricted subset of the 1966-83 sea survey data (lat. 29.5°-34.5°N; 54,457 northern anchovy). Maturity stages were not recorded for males in the sea survey data and age determinations were made on only a portion (19,031) of the fish sampled. In both data sets age determinations were made from otoliths with methods described by Collins and Spratt (1969). The third source of data, provided to us by B. Macewicz[3], consists of histological information for the gonads of 8,672 females sampled during the months of February to April from 1977 to 1984. Age determinations were not made and maturity stages were not taken on these fish.

The gross anatomical maturity stage description used for northern anchovy is a slightly modified version of the system developed by Bowers and Holliday (1961) for herring. The system has seven maturity stages which are primarily based on the portion of the body cavity occupied by the gonads and, in the later stages, by the appearance of translucent eggs or milt (Table 1). Herring are considerably larger than anchovy, and they are generally not considered to be multiple spawners; therefore, there are some difficulties in applying the maturity stages to anchovy. The most obvious problem is that a considerable proportion of the anchovy sampled had gonads so small that sex determinations were not made as they would have required magnification. There was also a small proportion of fish in which physical deterioration made sex determination impossible. The California anchovy fishery is primarily for reduction to fish meal, and the quality of the fish was occasionally very poor when the fish were sampled. Another major difficulty is that it is not possible to distinguish between anchovy gonads that are resting (i.e., stage 2) between multiple spawnings in the same season and those resting between spawning seasons. A comparable problem exists with spent fish (stage 7).

TABLE 1.—The international (Hjort) scale of maturity stages of the gonad. From Bowers and Holliday (1961).

| | |
|---|---|
| Stage 1: | Virgin individuals: very small sexual organs close under vertebral column; ovaries wine-colored, torpedo-shaped, about 2-3 cm long and 2-3 cm thick, eggs invisible to naked eye; testes whitish or greyish-brown, knife-shaped, 2-3 cm long and 2-3 cm broad. |
| Stage 2: | Maturing virgins or recovering spents: ovaries somewhat longer than half the length of ventral cavity, about 1 cm diameter, eggs small but visible to naked eye; milt whitish, somewhat bloodshot, of same size as ovaries, but still thin and knife-shaped. |
| Stage 3: | Sexual organs more swollen, occupying about half of ventral cavity. |
| Stage 4: | Ovaries and testes occupying almost two thirds of ventral cavity; eggs not transparent, milt whitish, swollen. |
| Stage 5: | Sexual organs filling ventral cavity; ovaries with some large transparent eggs; milt white, not yet running. |
| Stage 6: | Roe and milt running (spawning). |
| Stage 7: | Spents: ovaries slack with residual eggs; testes baggy, bloodshot. |

## SEX RATIO

Description of the sex ratio in northern anchovy was confounded by the presence of fish for which the sex could not be determined. The relationship between size and the percentage of these unsexed fish is similar for both the commercial purse seine and midwater trawl data. In both data sets, a large percentage of the fish smaller than 100 mm standard length (SL) are of unknown sex, about 10% of the 101-110 mm fish are of unknown sex, and only a small percentage of the fish larger than 110 mm are of unknown sex (Table 2). The percentages of fish with unknown sex at sizes larger than 110 mm in the purse seine data are somewhat higher than those in the midwater trawl data. This is probably due to the occasional occurrences of fish in which

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the condition was too poor to allow sex identification. The relationship between age and the percentage of unsexed fish is similar to that described for size (Table 2). It should be noted that both data sets are biased towards larger and older fish. The age composition of anchovy in the midwater trawl data is biased because of the fact that otoliths were often not taken when trawl hauls were dominated by young-of-the-year fish (Parrish et al. 1985). The purse seine data contain a much smaller percentage of small or young fish than the midwater trawl data. This is primarily caused by the fact that a 5-in (about 108 mm SL) minimum size limit was in effect for most of the 1966-80 period.

To evaluate the seasonal cycle of the occurrence of northern anchovy for which the sex could not be identified, the monthly percentages of females, males, and anchovy with unknown sex were determined by age group for the San Pedro fishery (Fig. 1). In all age groups the minimum percentages of fish which could not be sexed occurred from about January to May in association with the spawning season. Higher percentages occurred both before and after the spawning season, particularly in the first potential spawning season. This implies that a significant percentage of anchovy mature, or at least partially mature, and then reabsorb their gonadal tissue to the point that their gonads are so small that they cannot be sexed without magnification. It also implies that a bias due to the unsexed fish exists. This bias is at a minimum from January to May and it primarily affects the analyses of fish in their first potential spawning season.

Klingbeil (1978) found the female:male ratios of northern anchovy sampled in the Sea Survey Program and in the commercial fishery to be 1.03:1 and 1.60:1 respectively. The additional years of information from these two sources, in our data sets, pro-

TABLE 2.—Proportion of northern anchovies with unknown sex and sex ratio by size (A) and by age (B).

| | San Pedro anchovy fishery | | | | Sea survey (lat 29.5°-34.5°N) | | | |
|---|---|---|---|---|---|---|---|---|
| Length (mm) | Unknown sex | Females/male | Mean SL | Number | Unknown sex | Females/male | Mean SL | Number |
| | | | | A | | | | |
| 61- 70 | 1.000 | — | — | 1 | 0.996 | 0.00 | — | 273 |
| 71- 80 | 0.676 | 0.71 | — | 37 | 0.941 | 0.94 | — | 597 |
| 81- 90 | 0.437 | 0.67 | — | 252 | 0.810 | 0.78 | — | 1,396 |
| 91-100 | 0.283 | 0.77 | — | 2,261 | 0.500 | 0.84 | — | 2,208 |
| 101-110 | 0.114 | 1.06 | — | 8,684 | 0.100 | 0.82 | — | 2,882 |
| 111-120 | 0.057 | 1.30 | — | 17,186 | 0.016 | 0.78 | — | 4,141 |
| 121-130 | 0.029 | 1.53 | — | 19,396 | 0.007 | 1.07 | — | 4,016 |
| 131-140 | 0.014 | 2.10 | — | 10,010 | 0.003 | 1.43 | — | 2,439 |
| 141-150 | 0.007 | 2.90 | — | 2,354 | 0.003 | 2.56 | — | 772 |
| 151-160 | 0.009 | 4.43 | — | 438 | 0.005 | 3.09 | — | 185 |
| 161 + | 0.024 | 7.20 | — | 42 | 0.000 | 9.67 | — | 32 |
| Total | 0.057 | 1.48 | — | 60,661 | 0.187 | 1.02 | — | 19,031 |
| | | | | B | | | | |
| Age | | | | Annual | | | | |
| 0 | 0.202 | 0.83 | 104.2 | 1,862 | 0.779 | 0.81 | 88.7 | 3,616 |
| 1 | 0.090 | 1.15 | 112.8 | 16,167 | 0.122 | 0.88 | 107.2 | 4,812 |
| 2 | 0.046 | 1.49 | 121.1 | 20,885 | 0.022 | 0.86 | 119.4 | 4,733 |
| 3 | 0.036 | 1.76 | 126.3 | 14,174 | 0.010 | 1.15 | 126.4 | 3,543 |
| 4+ | 0.022 | 2.01 | 134.0 | 7,573 | 0.003 | 1.66 | 135.0 | 2,327 |
| Total | 0.057 | 1.48 | 121.2 | 60,661 | 0.187 | 1.02 | 113.7 | 19,031 |
| Age | | | | February-April | | | | |
| 0 | — | — | — | 0 | — | — | — | 0 |
| 1 | 0.093 | 0.95 | 106.5 | 4,646 | 0.153 | 0.79 | 101.0 | 2,271 |
| 2 | 0.027 | 1.33 | 116.2 | 4,279 | 0.004 | 0.78 | 117.3 | 2,035 |
| 3 | 0.018 | 1.45 | 123.3 | 3,410 | 0.002 | 1.04 | 125.3 | 1,928 |
| 4+ | 0.014 | 1.69 | 134.4 | 3,620 | 0.001 | 1.55 | 134.6 | 1,382 |
| Total | 0.041 | 1.30 | 119.0 | 15,955 | 0.048 | 0.96 | 117.6 | 7,616 |
| Age | | | | August-December | | | | |
| 0 | 0.259 | 0.77 | 104.2 | 1,204 | 0.831 | 0.78 | 88.6 | 3,216 |
| 1 | 0.083 | 1.19 | 117.6 | 6,411 | 0.104 | 0.97 | 112.2 | 2,198 |
| 2 | 0.060 | 1.59 | 123.1 | 12,082 | 0.035 | 0.91 | 120.5 | 2,311 |
| 3 | 0.051 | 1.92 | 127.7 | 7,648 | 0.021 | 1.28 | 128.1 | 1,255 |
| 4+ | 0.039 | 2.33 | 132.9 | 2,532 | 0.007 | 1.57 | 135.4 | 560 |
| Total | 0.069 | 1.58 | 123.2 | 29,877 | 0.316 | 1.02 | 109.7 | 9,540 |

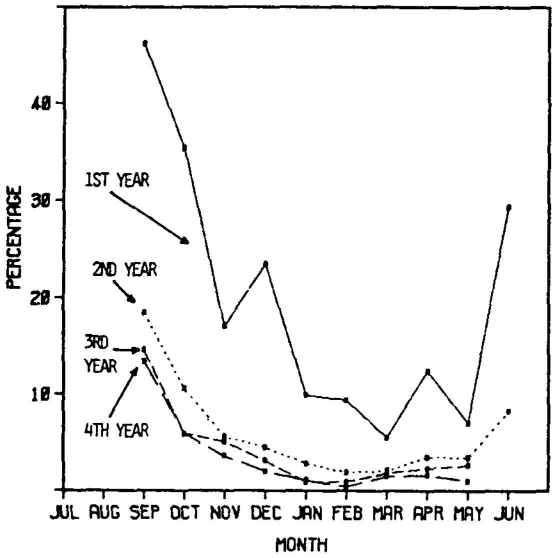



FIGURE 1.—The monthly percentages of northern anchovies with unknown sex, by age group, in samples from the San Pedro fishery.

duced essentially no change in the sex ratio in the sea survey data (1.02:1). However, there was a reduction in the proportion of females in the fishery data (1.48:1) which was associated with a reduction in the average age of anchovy in the catch after 1977 (Mais 1981). Sunada and Silva (1980) also found a female:male sex ratio greater than unity in the northern Baja California purse seine fishery, 2.15:1 in 1976 and 1.44:1 in 1977. Alheit et al. (1984) reported a sex ratio of 1.30:1 in purse seine caught Peruvian anchoveta sampled during their spawning season. Klingbeil (1978) and Alheit et al. (1984) reported that during the spawning season there were unexpectedly large numbers of samples in which sex ratios were heavily dominated by either males or females. Alheit et al. (1984) suggested that "hydrated females segregate, either by depth or area, from the 'normal' school, taking a high percentage of males with them forming 'spawning schools' dominated by males."

Analysis of the sex ratio by size and age groups shows that there are increasingly larger proportions of females in the larger and older groups (Table 2). This trend is evident in both the fishery and sea survey data. In the fishery data there are more males than females identified in the fish smaller than 100 mm SL and in age group 0. The proportion of females increases until there are more than twice as many females as males among fish larger than 130 mm and in age group 4+. There is a similar trend in the sea survey data; however, females do not outnumber males until the fish are larger than 120 mm and 3 yr of age. The sex ratio in age group 4+ is 1.66:1. The apparent dominance of females in the larger size classes may be partially caused by sex related differences in growth rates; however, their dominance in the older age classes of both the purse seine and midwater trawl samples cannot be explained by differences in growth. We grouped our data sets into the spawning months (February-April) and nonspawning months (August-December) in order to evaluate features which might be caused by behavioral differences that may occur during the spawning season. This analysis shows that the overall sex ratio in northern anchovy taken by midwater trawl is close to 1:1 in both nonspawning and spawning seasons (Table 2B). It also shows that the sex ratios in younger fish are dominated by males and those in older fish are dominated by females. The overall sex ratio in northern anchovy sampled in the purse seine fishery is heavily dominated by females; however, the sex ratio is higher in the nonspawning season (1.58:1) than in the spawning season (1.30:1). The crossover from male to female dominance of the sex ratio occurs between age group 2 and 3 in the sea survey data and at age 1 in the fishery data.

## MATURITY STAGES IN NORTHERN ANCHOVY

### Seasonal Variation in Maturity Stages

To determine which of the various data sets available for northern anchovy were best suited for evaluating maturity stages in the central stock, we examined the seasonality of three grouped maturity stages of four data subsets. The grouped stages included immature or resting females (stages 1 and 2); females just beginning to mature (stage 3); and the highly mature, spawning, and spent females (stages 4-7). The data consisted of two sets of samples from the commercial fishery (Monterey and San Pedro) and the sea survey samples from southern California (lat. 32.5°-34.5°N) and northern Baja California (29.5°-32.5°N).

The seasonal patterns of the grouped maturity stages of females sampled in the San Pedro fishery (Fig. 2A), the sea survey in southern California (Fig. 2B), and the sea survey in northern Baja California (Fig. 2C) are quite similar. The pattern in the Monterey fishery differs from that in the other data sets in that spawning is at the highest levels in April and September (Fig. 2D). It cannot presently be determined if there are one or two peaks of spawning in

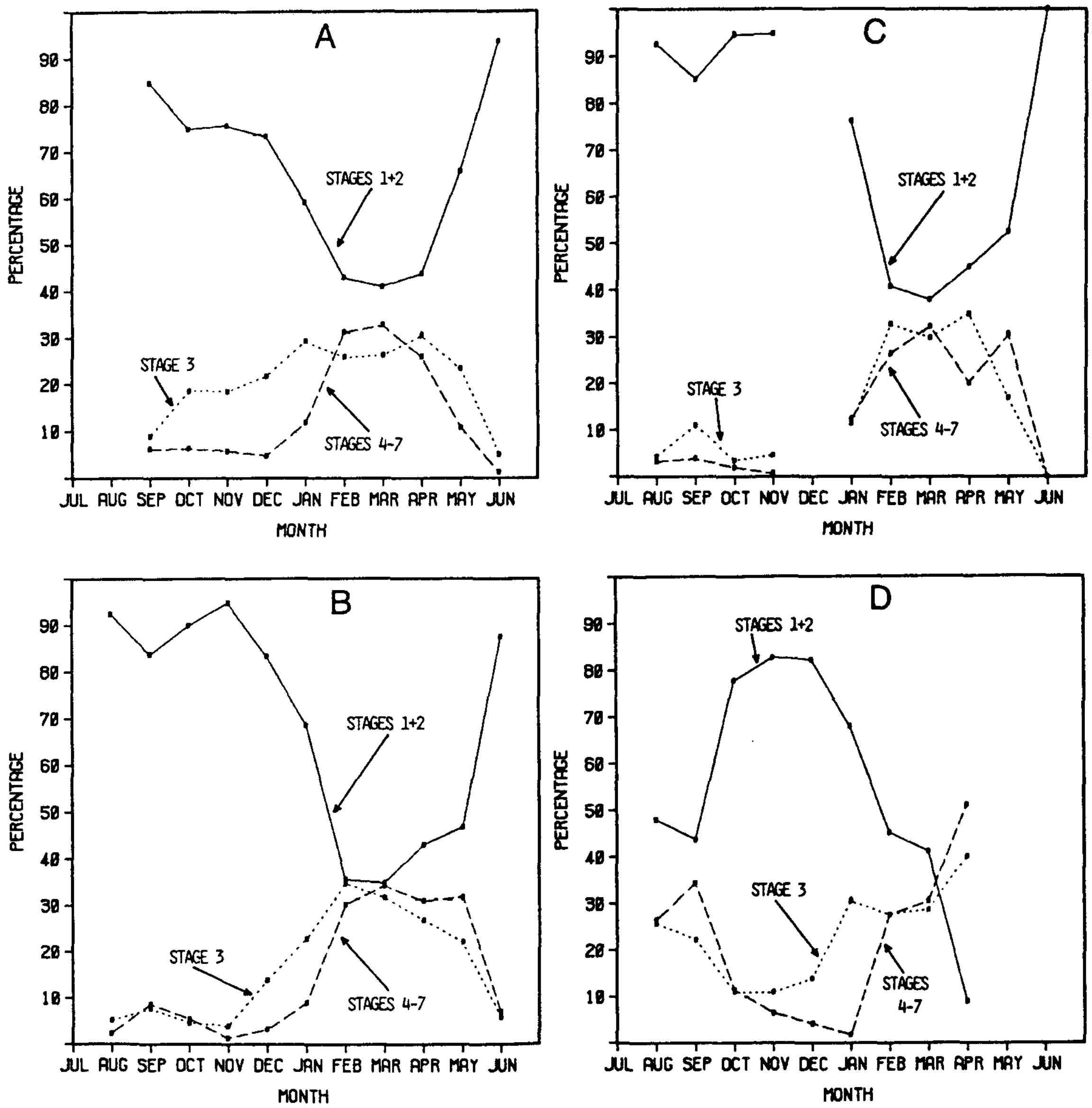



FIGURE 2.—The monthly percentages of grouped maturity stages for female northern anchovies sampled in A, San Pedro fishery; B, Sea survey (lat. 32.5°-34.5°N); C, Sea survey (29.5°-32.5°N); D, Monterey fishery.

the Monterey area due to the lack of data from May to July. Because of the different seasonal pattern of the grouped maturity stages in the Monterey fishery data and because there is more than one stock in this region (Vrooman et al. 1981), it was decided to exclude this area from further analysis. The analyses that follow are based on the combined San Pedro fishery and southern California-northern Baja California sea survey data sets (52,352 females of which 41,930 were aged).

To obtain a first approximation of the magnitude and duration of maturity stages in the central stock of northern anchovy, the monthly percentages of fish with each maturity stage were calculated for females and for males. The seasonal patterns were found to be essentially the same for males and females; however, the males tended to have somewhat larger percentages of fish in the higher maturity stages. Our presentation is limited to information on females.

The proportion of females classified as stage 1, virgin individuals, is at a minimum during the spawning season, comprising <10% of the females sampled during February, March, and April. However, during the summer more than half of the females were classified as stage 1 (Fig. 3A). Stage 2 females, maturing virgins and recovering spents, are at a minimum in August (when most females are classified as stage 1). From September until January between 40 and 60% of the females are classified as stage 2. During the spawning season, and just after, the percentage of stage 2 females dropped between 30 and 40%. The August to September decline in the percentage of stage 1 females is primarily caused by the sharp increase in the proportion of stage 2 females. Thus, the combined percentage of stages 1 and 2 females is probably a reasonable inverse indicator of the seasonality of spawning. However, during the spawning season an unknown proportion of those classified as stages 1 and 2 are females that have recently spawned and are between multiple spawnings.

Stage 3 females (ovary enlarged, occupying about half of the length of the ventral cavity) have a considerably different pattern. There is a gradual increase from about 5% in August to about 30% in January. This percentage is maintained until April, i.e., through the spawning season; it then drops to about 5% in June. The monthly percentages of the higher maturity stages (4, 5, and 6) clearly delineate the spawning season as primarily a January-May event (Fig. 3B). The relatively constant low level of stage 7 females is unexpected as the maximum proportion of spent fish would be expected to occur just after the peak of spawning.

## Maturity Stage Relationships with Size and Age

To examine potential relationships between the size and age of northern anchovy and the duration and magnitude of maturity stages we calculated the monthly percentages of grouped maturity stages for four size classes (81-100, 101-120, 121-140, and 141-160 mm SL) and four age groups (1, 2, 3, and 4+). Age group 1 includes fish prior to and after their first potential spawning season (i.e., young-of-the-year fish in July through the following June). Age group 4+ includes fish in their fourth and subsequent spawning seasons. The grouped maturity stages (1, 2, 3, and 4-7) are the same as those presented earlier.

Size has a large effect on both the duration and magnitude of maturity stages in northern anchovy. With the exception of those sampled from February to April nearly all of the 81-100 mm SL females were classified as immature or resting (Fig. 4A). In addition, the majority of this size anchovy have gonads too small to determine their sex without magnification (Table 2). As the size class increases the percentage of stages 1 and 2 decreases; this occurs in all months; however, the minimum percentage of

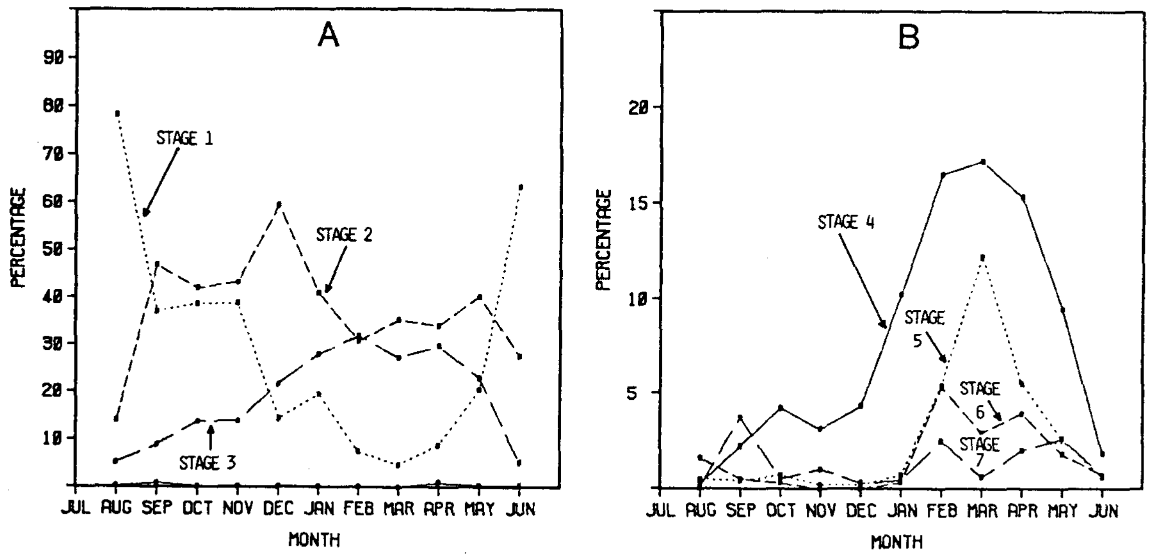
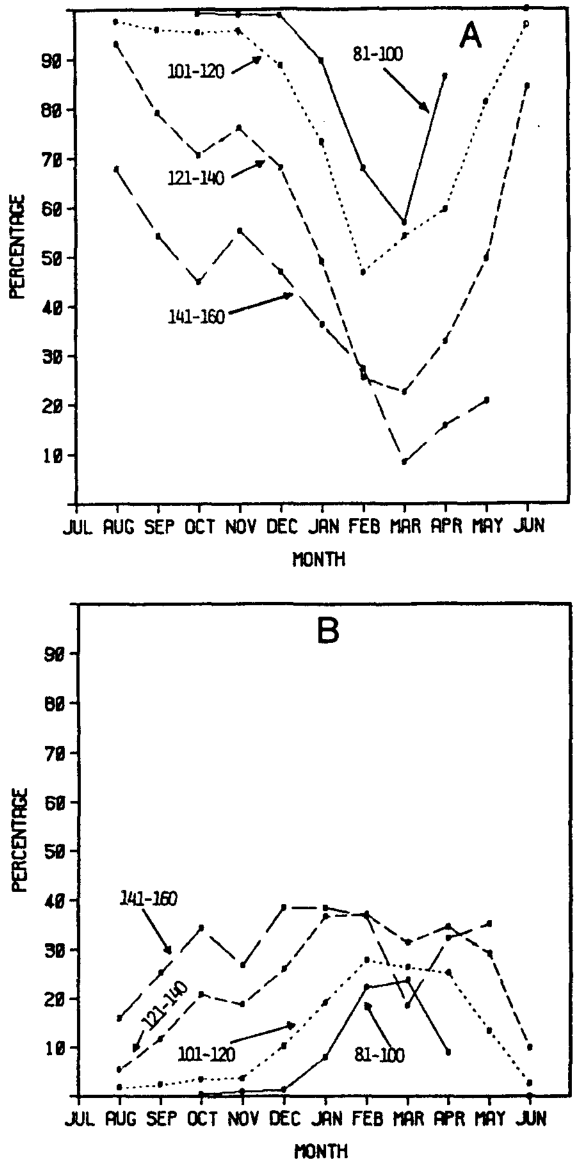



FIGURE 3.—The monthly percentages of individual maturity stages for female northern anchovies. A. Stages 1-3. B. Stages 4-7.



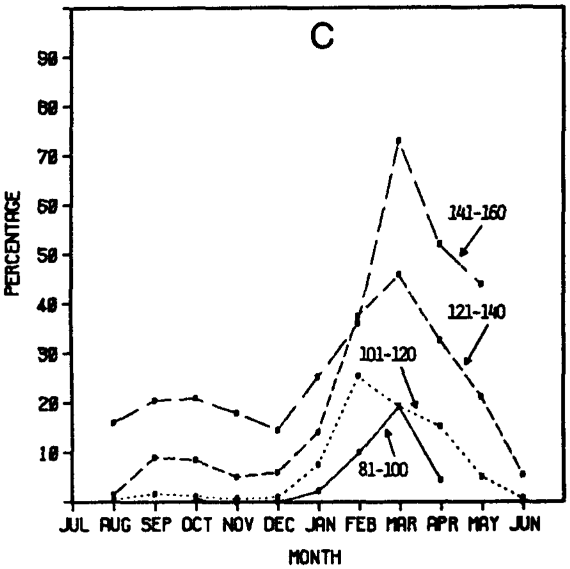




FIGURE 4.—The monthly percentages of grouped maturity stages for female northern anchovies, by size group. A. Stages 1+2 B. Stage 3. C. Stages 4-7.

stages 1 + 2 occurs in February to April. The percentage of females just beginning to mature (i.e., stage 3) has an abrupt peak in February-March in the smallest size class (Fig. 4B). This peak becomes increasingly spread out in the larger size classes. The higher maturity stages (4-7) are most abundant from February to April in all size classes (Fig. 4C). The larger size classes have much larger percentages of females in the higher maturity stages than the smaller size classes, and there is a minor peak in the percentage of the higher maturity stages during the fall in the two largest size classes. Analysis of the data by age group showed, as would be expected, that increased age has essentially the same effect as increased size on the magnitude and duration of maturation stages.

## SPAWNING INCIDENCE AND FECUNDITY

Studies by Hunter and Goldberg (1980) in California and Alheit et al. (1983) in Peru examined postovulatory follicles to determine the spawning frequency of female anchovies (i.e., the time interval between spawnings). A second method would be to determine the percentage of females with hydrated eggs. Hunter and Macewicz (1980) showed that northern anchovy begin hydrating eggs at about 0600 in the morning and by sunset about 14% of the females have hydrated eggs. They felt that the best indicator of the time of spawning was the occurrence of both hydrated eggs and new postovulatory follicles. This occurred in a low percentage of their samples indicating that spawning was completed rapidly; the time of maximum spawning occurred between 2100 and 0200 with a peak between 2200 and 2300. Hunter and Macewicz (1980) divided the nightly pattern of spawning in anchovy into three periods: "early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated stage; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new postovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration." A considerable amount of new histological data is now available as a result of a series of egg production biomass surveys for northern anchovy. B. Macewicz (fn. 3) has analyzed the histology of the ovaries of 8,672 anchovy sampled in these surveys, and our analysis of this new information verifies the temporal patterns which Hunter and Macewicz (1980) described from a much smaller sample (Fig. 5).

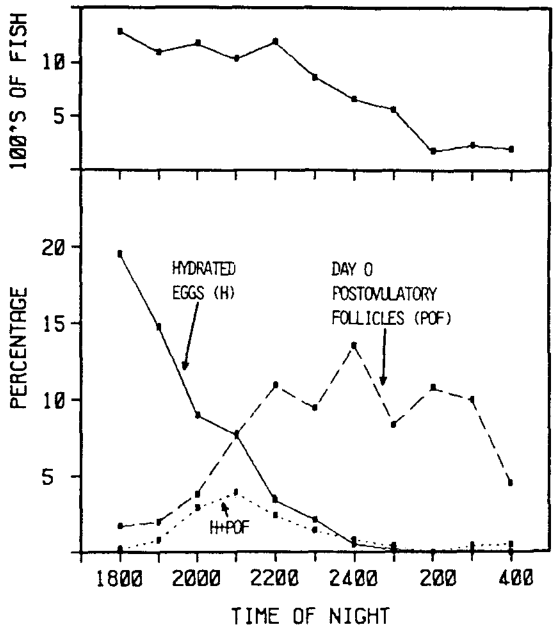



FIGURE 5.—The percentages of female northern anchovies with ovaries in three histological classes, by time of night.

## Comparison of Maturity Stages and Histology Classes

The histological data show that during the early evening the percentage of females with hydrated eggs could be an indicator of the percentage of females spawning per day (i.e., the spawning incidence). To use the extensive maturity stage data available for northern anchovy it is necessary to determine the relationships between the histology of the gonads and the maturity stages used in the California Department of Fish and Game's sampling programs. To date histological and field maturity stage data have not been taken on the same individuals; therefore, analysis is limited to comparisons of the two data sets. In the following comparisons the sea survey and histology data sets were limited to samples taken during the period 1977-84 and during the principal spawning season (i.e., February-April). Since nearly all of the trawls were taken at night, the data were limited to those taken from 1800 to 0500 h. The midwater trawl hauls were normally 15 min in duration, and about 30% of the fish in the histological data set and 30% in the maturity stage data sets were taken in the same trawl hauls during cooperative cruises.

The histological data are divided into six classes (B. Macewicz fn. 3):

1. Ovaries with hydrated eggs and no day-0 postovulatory follicles.
2. Ovaries with hydrated eggs and day-0 postovulatory follicles.
3. Ovaries with day-0 postovulatory follicles and no hydrated eggs.
4. Ovaries with day-1 postovulatory follicles.
5. Mature ovaries with no hydrated eggs, no day-0 nor day-1 postovulatory follicles.
6. Immature ovaries, few or no yolked oocytes, no atresia present in the ovary other than late-stage corpora atretica.

Northern anchovy, spawning on the night they were sampled (day 0), include the first three classes; those that spawned on the night before they were sampled (day 1) are class four.

A comparison of the percentages of hydrated females in the sea survey data (i.e., stages 5 + 6) with that in the histological data (i.e., classes 1 + 2) shows that they have essentially the same pattern from the onset of spawning in the early evening until spawning is completed in the early morning (Fig. 6). This implies that in the early evening maturity stages 5 + 6 can be used to estimate the spawning incidence; however, within a few hours after sunset the percentage of females with hydrated eggs (i.e., stages 5 + 6) rapidly becomes an underestimate of the incidence of spawning due to the completion of spawning. If only the females ($n$ = 2,161) sampled between the hours of 1800 and 2000 are considered, then the percentage in maturity stages 5 + 6 (15.3%) is quite close to the percentage of day-0 females calculated for the total histology data set (15.9%).

The variation throughout the night of the percentages of the other maturity stages is also of interest as it offers some insight into the meaning of maturity stages in anchovy. Hunter and Macewicz (1980) showed that spawning primarily occurs between the hours of 1800 and 0200. In the sea survey data the percentage of stages 5 + 6 falls from 15.3 to 1.6% over this time period (Fig. 7). The expected maturity stage that should increase over this time period is stage 7 (i.e., spents: ovaries slack with residual eggs). This, however, is not the case. The percentage of stage-7 females has very little variation over the 1900-0200 period; going from 2% at 1900 to 3.6% at 0200. This suggests that residual eggs occur in only a small percentage of anchovy and that stage 7 cannot be used to determine if an anchovy has spawned within 24 h. This is consistent with Stauffer and Picquelle's (1980) observation that field-spawned northern anchovy were found to release nearly 100% of their hydrated eggs. The percentages of the other maturity stages show considerable variation from 1900 to 0200 h. Stages in which the ovary is small (i.e., 1+2) occur in about 37% of the females in the early evening. This increases rapidly after 2300 and by 0200 these stages comprise about 46% of the females. Stages 3 + 4, in which the ovaries occupy from one half to two thirds of the ventral cavity, occur in about 46% of females in the early evening. This rises to a peak of about 54% at 2300-2400 and then declines to about 49% at 0200.

Our interpretation of the patterns exhibited by the sea survey data is that the percentage of females at stages 5 + 6 in the early evening (i.e., 15.3%) is a valid estimate of the percentage of sampled females with hydrated eggs. However, as the night progresses the percentage of stages 5 + 6 declines. At the peak of spawning, just before midnight, many females appear to be misidentified as stages 3 + 4. This could occur if they had spawned part of their eggs before they were captured and if the person making the maturity stage determinations used the size of the ovary, rather than the presence of hydrated eggs, to determine the maturity stage. After midnight an increasing percentage of spawning females have

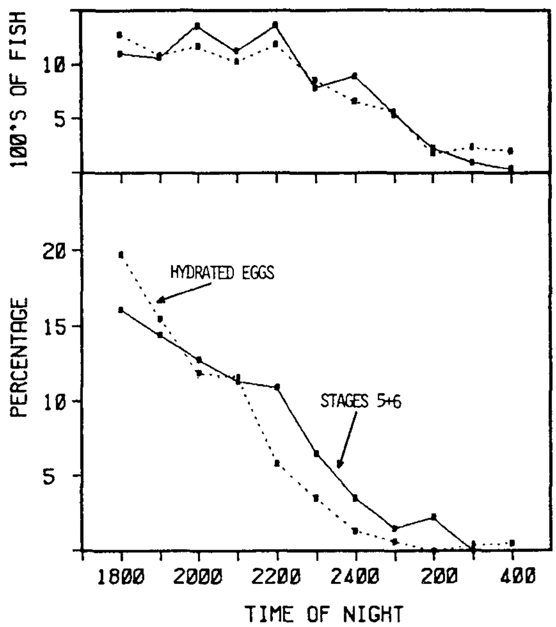



FIGURE 6.—The percentages of female northern anchovies with hydrated eggs and with maturity stages 5+6, by time of night.

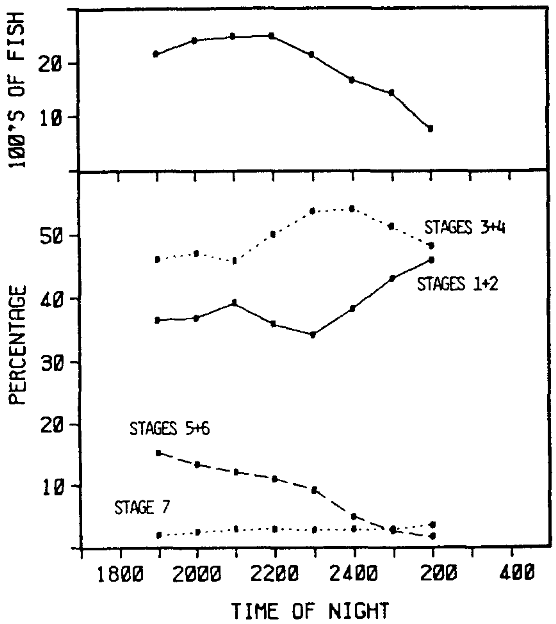



FIGURE 7.—The percentages of grouped maturity stages for female northern anchovies by time of night. (Two hour moving average.)

apparently spawned all of their hydrated eggs and they are then classified as stage 1 or 2. The meaning of stage 7 in female anchovy remains a mystery.

The seasonal and diurnal patterns described above indicate that, with the exception of stages defined by the presence of hydrated eggs, gross anatomical maturity stages have little utility other than describing the seasonality of spawning. However, field identifications of the presence of hydrated eggs, if they are calibrated with histological data and if the diurnal pattern of hydration is known, can potentially be used to determine spawning incidence.

Several authors have pointed out that females with hydrated eggs and actively spawning females were more numerous than females with day-1 postovulatory follicles, and have suggested that hydrated and actively spawning females may be more susceptible to capture due to behavioral or physiological factors (Hunter and Goldberg 1980; Stauffer and Picquelle 1980; Alheit et al. 1984). Previous workers have therefore used the percentage of day-1 females as the index of the daily spawning incidence. The overall percentages of day-0 and day-1 females in the histology data set (8,672 females) used in our analyses are 15.9 and 11.5%. Alheit et al. (1983) found the overall percentages of day-1 and day-2 Peruvian anchoveta females to be 17.26 and 14.81%. Hunter and Goldberg (1980), and subsequent workers on the northern anchovy, took their samples at night whereas Alheit et al. (1983) took their Peruvian anchoveta samples primarily during the day. Therefore the definition of day-1 is somewhat different in studies of the two species. In our analysis both day-0 and day-1 females appear to be more susceptible to capture by midwater trawl in the early evening than later at night. The percentages of both decline as the night progresses; however, the decline is more extreme in the day-0 females (Fig. 8).

The use of maturity stages 5 + 6 could result in several sources of bias that would tend to produce overestimates of the spawning incidence of northern anchovy. If females with hydrated eggs are more susceptible to capture, there will be a tendency to produce biased estimates. However, this bias would not be expected to be size or age dependent, nor would it be expected to vary during the spawning season. The same bias would be expected to occur in 1- and 4-yr-old hydrated females and the same bias would be expected in February and April. Therefore the use of the percentages of hydrated females or maturity stages 5 + 6 females may result in overestimates of the total spawning incidence or annual fecundity, but the relative spawning incidence or relative annual fecundity of the different age groups would not be biased. A second source of bias is that an unknown number of females have ovaries so small that visual determination of sex is impossible without magnification. Therefore, the incidence of spawning is overestimated because it is calculated by dividing the number of stages 5 + 6 females by less than the total number of females. This bias is size and age dependent, being much more common in smaller and younger anchovy, but not month dependent. Note that the various studies of the spawning incidence in northern anchovy and Peruvian anchoveta have defined the spawning incidence to be the number of females spawning per day divided by the number of *mature* females, i.e., these studies exclude immature females, which are primarily the smaller and younger fish, from the calculation.

There are also several sources of bias that would tend to produce underestimates of the spawning incidence. The anchovy fishery in southern California primarily occurs at night during the fall months and during the daylight hours in the spring. A period of low availability to the commercial fishery is associated with the spawning season. Mais (1974) associated this phenomenon with variation in schooling behavior and showed that acoustic surveys detect relatively few "commercial-sized" anchovy schools during the spawning season. If low availability to the commercial fishery is associated with spawning ac-

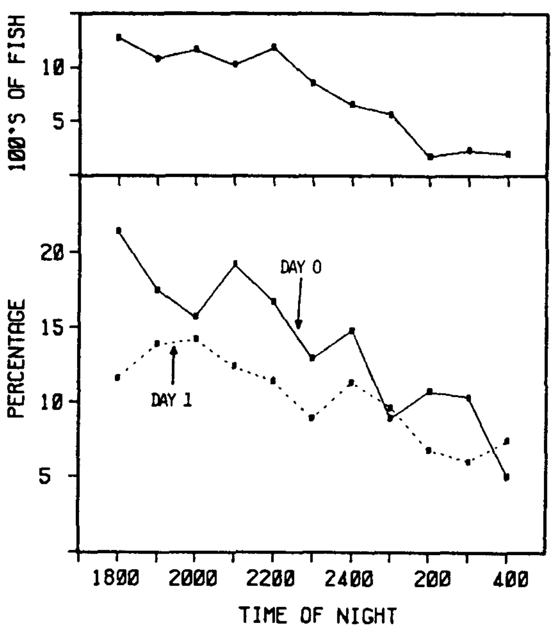



FIGURE 8.—The percentages of day-0 and day-1 female northern anchovies by time of night.

tivity, it is probable that the fishery undersamples the active spawners. In addition, a proportion of the commercial catches occur during the time of day when the females do not have hydrated eggs. The fishery data will therefore tend to underestimate the spawning incidence. The total sea survey data will also produce an underestimate as it includes samples taken throughout the night.

The combined fishery-sea survey data used in our analyses will therefore provide only an index of the daily spawning incidence. To evaluate the potential net bias of this index we calculated the percentage of females with maturity stages 5 + 6, in the combined fishery-sea survey data, and the percentage of females with day-1 postovulatory follicles, in the histological data. To make the data comparable we used the period 1977-84 and the months February-April. The percentage of females with maturity stages 5 + 6 and the percentage of females with day-1 postovulatory follicles was 10.9 and 11.5%. Use of the maturity stage data will therefore slightly underestimate the daily spawning incidence (i.e., 10.9/11.5 = 0.948).

## Size Dependent Batch Fecundity

Annual fecundity in the northern anchovy is dependent upon the batch fecundity and the number of spawnings per year. Batch fecundity is size dependent and the best average estimate over six seasons (Hunter et al. 1985) is given below. Note that Hunter et al. found significant variation (ANOVA) among years.

$$\text{batch fecundity} = -1{,}104 + 614\ (\text{WT})$$

where WT = female wet weight, minus ovaries, in grams. During the spawning season ovary free weight of northern anchovy is equal to 95% of the total wet weight (Hunter and Leong 1981). Batch fecundity, with the above relationships, for a typical 1-yr-old (12 g) and a typical 4-yr-old (24 g) are 5,896 eggs and 12,895 eggs. On a per unit weight basis the 24 g fish would produce only 9.4% more eggs than the 12 g fish. Age-dependent variations in batch fecundity are therefore of only minor significance in the relationship between spawning biomass and annual fecundity. There is the possibility that batch fecundity could vary over the spawning season, and since we have shown an age-dependent seasonality in the spawning incidence of northern anchovy, this could potentially contribute to age-dependent differences in annual fecundity. Hunter and Leong (1981), however, found average batch fecundity to be essentially the same in samples taken in January-February and in March-April.

## Size-Dependent Histology Classes

Hunter and Macewicz (1980) found no relationship between size and the percentage of mature female northern anchovy with day-1 postovulatory follicles. Later work by Picquelle and Hewitt (1984) showed that weight and spawning incidence were highly correlated in the northern portion of the central stocks range. They stated that this implied that the larger females spawned more frequently or that the smaller females had a much shorter spawning season. We analyzed the larger histology data set now available and found that the percentages of females with hydrated oocytes or with day-1 postovulatory follicles, as well as the percentage of females with maturity stages 5 + 6, were dependent upon the size of the females (Fig. 9).

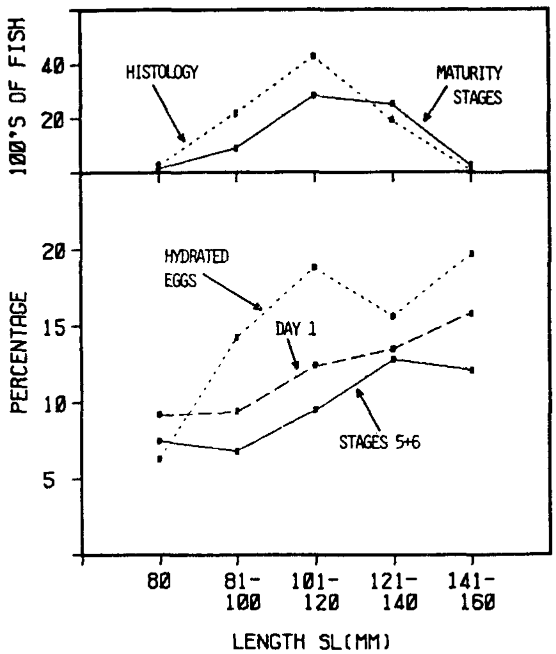



FIGURE 9.—The percentages of female northern anchovies with hydrated eggs, with maturity stages 5+6, and day-1 histological classes by size group.

## Age-Dependent Spawning Incidence and Annual Fecundity

To assess age-dependent, annual fecundity in the central stock of northern anchovy we calculated the number of spawnings and the fecundity on a monthly basis for age groups 1, 2, 3, and 4+. Average monthly wet weight by age was taken from Mallicoate and Parrish (1981). The number of spawnings per month was calculated from the number of days per month and the index of daily spawning (i.e., the proportion of stages 5 + 6). Note that the bias due to the unknown sex problem discussed earlier would tend to cause an overestimation of the daily spawning incidence: particularly in females in their first spawning season. Also note that the index of daily spawning underestimates the spawning incidence by about 5%.

Our analysis shows that there are large, age-dependent variations in the proportions of female northern anchovy spawning as the spawning season progresses (Fig. 10). From July until January all age groups have a very low daily spawning index. Intensive spawning commences in February and all age groups have roughly the same spawning index (9-12%). In March the spawning index of age group 1 declines to about 2%; it increases slightly in April and declines to about 1% in May. In age group 2 the spawning index increases to 13% in March and then declines to about 2% by May. Age groups 3 and 4+ have peak spawning indices in March (25 and 27%), considerable spawning in April (10 and 17%) and lesser amounts in May (3 and 6%) and June (3 and 6%).

Older females have a much larger number of spawnings per spawning season than younger

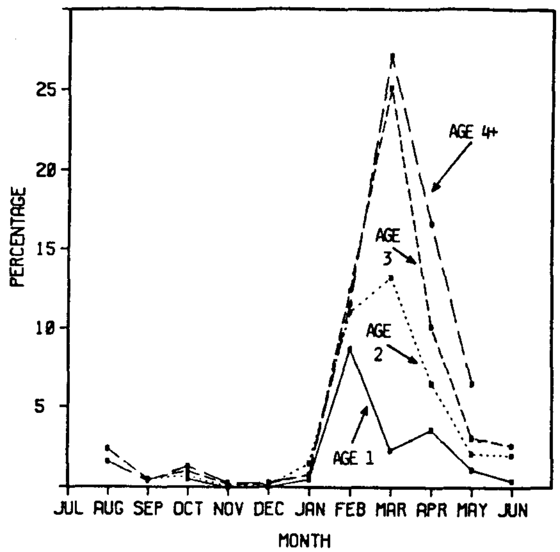



FIGURE 10.—The monthly percentages of female northern anchovies with maturity stages 5+6, by age group.

females (Table 3). In their first spawning season females have an average of 5.3 spawnings. In their second spawning season this rises to 11.9 and in their third and fourth plus seasons the number of spawnings rises to 19.2 and 23.5. The increase in the number of spawnings associated with increasing age appears to be primarily due to the increase in the length of the spawning season that occurs in older fish. The average number of spawnings per season for all females sampled was 15.1. This is less than the estimate that Hunter and Leong (1981) developed from the energetics of female northern anchovy (i.e., 20 spawnings per year). Their calculations indicated that mature female northern anchovy spawned on the average 15 times between February and September; their calculation of the number of spawnings from October to January (5) was estimated indirectly from the relative monthly larval abundance in 1953-60. Our estimate of the number of spawnings from February to September (14.3) is very close to the Hunter and Leong (1981) estimate which was based on a smaller histology data set. However, our estimate of the number of spawnings from October to January is only 0.8 and is much less than their indirect estimate based on the relative seasonal larval abundance for the 1953-60 period. The central stock of northern anchovy was at a much smaller population size in 1953-60 than it was in 1966-84 (MacCall 1980) and northern fish, with a seasonal spawning pattern similar to that occurring in the Monterey data, may have comprised a larger proportion of the anchovy population off California during the 1953-60 period than at present thus inflating Hunter and Leong's estimate for the October-January period.

Our analysis indicates that annual fecundity in the central stock of northern anchovy is heavily age dependent; the average 4+ yr-old female produces nearly 10 times as many eggs as a 1-yr-old female (Table 3). Our calculations show that central stock, female anchovy produce 2,803, 6,550, 11,434, and 13,861 eggs/g of body weight per spawning season in their 1st, 2d, 3d, and 4th plus spawning seasons. Females 4 yr of age and older produce nearly 5 times as many eggs per unit of weight as 1-yr-olds.

## DISCUSSION

Over the last decade it has become apparent that recruitment failure is the major threat to many of the world's largest fisheries. In addition, variation in recruitment is a significant causal factor in the interyear variation of the annual catches of many fisheries. Stocks of small pelagic fishes appear to

TABLE 3.—Proportion of maturity stages 5 + 6, number of spawnings and fecundity of female northern anchovies sampled in the Sea Survey Program (lat. 29.5°-34.5°N) and San Pedro fishery.

| | July[1] | Aug.[1] | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June | Total[2] | Eggs/g[3] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| First spawning season | | | | | | | | | | | | | | |
| Prop. 5 + 6 | 0.000 | 0.000 | 0.000 | 0.005 | 0.000 | 0.000 | 0.005 | 0.087 | 0.023 | 0.036 | 0.011 | 0.004 | | |
| Spawnings | 0.000 | 0.000 | 0.000 | 0.155 | 0.000 | 0.000 | 0.155 | 2.436 | 0.713 | 1.080 | 0.341 | 0.120 | 5.3 | |
| Wt. (g) | — | — | 11.2 | 11.1 | 12.0 | 11.0 | 11.4 | 11.6 | 12.8 | 13.7 | 15.4 | 13.6 | | |
| No. eggs | 0 | 0 | 0 | 832 | 0 | 0 | 860 | 13,793 | 4,536 | 7,438 | 2,687 | 819 | 32,514 | 2,803 |
| Second spawning season | | | | | | | | | | | | | | |
| Prop 5 + 6 | 0.002 | 0.000 | 0.005 | 0.007 | 0.001 | 0.001 | 0.015 | 0.110 | 0.132 | 0.065 | 0.021 | 0.020 | | |
| Spawnings | 0.062 | 0.000 | 0.150 | 0.217 | 0.030 | 0.031 | 0.465 | 3.080 | 4.092 | 1.950 | 0.651 | 0.600 | 11.9 | |
| Wt. (g) | 15.5 | 15.5 | 17.4 | 16.8 | 17.2 | 16.3 | 16.2 | 15.6 | 16.5 | 17.7 | 18.3 | 17.5 | | |
| No. eggs | 492 | 0 | 1,357 | 1,887 | 268 | 261 | 8,881 | 24,626 | 34,866 | 17,980 | 6,230 | 5,462 | 102,174 | 6,550 |
| Third spawning season | | | | | | | | | | | | | | |
| Prop. 5 + 6 | 0.022 | 0.024 | 0.005 | 0.010 | 0.002 | 0.002 | 0.008 | 0.124 | 0.251 | 0.101 | 0.031 | 0.026 | | |
| Spawnings | 0.682 | 0.744 | 0.150 | 0.310 | 0.060 | 0.062 | 0.248 | 3.472 | 7.781 | 3.030 | 0.961 | 0.780 | 19.2 | |
| Wt. (g) | 18.3 | 18.3 | 19.1 | 19.3 | 19.2 | 19.3 | 19.1 | 18.0 | 20.7 | 22.2 | 20.9 | 22.7 | | |
| No. eggs | 6,527 | 7,120 | 1,506 | 3,148 | 606 | 630 | 2,489 | 33,836 | 85,360 | 35,891 | 10,655 | 9,467 | 205,819 | 11,434 |
| Fourth-plus spawning seasons | | | | | | | | | | | | | | |
| Prop. 5 + 6 | 0.021 | 0.016 | 0.004 | 0.013 | 0.003 | 0.003 | 0.008 | 0.115 | 0.271 | 0.166 | 0.065 | 0.056 | | |
| Spawnings | 0.651 | 0.496 | 0.120 | 0.403 | 0.090 | 0.093 | 0.248 | 3.220 | 8.401 | 4.980 | 2.015 | 1.680 | 23.5 | |
| Wt. (g) | 20.1 | 20.1 | 20.9 | 21.8 | 22.3 | 22.2 | 23.6 | 23.3 | 26.6 | 26.5 | 25.7 | 25.7 | | |
| No. eggs | 6,914 | 5,268 | 1,330 | 4,680 | 1,071 | 1,102 | 2,952 | 37,390 | 110,293 | 67,123 | 26,454 | 18,136 | 322,957 | 13,861 |
| All spawning seasons combined | | | | | | | | | | | | | | |
| Prop. 5 + 6 | 0.017 | 0.021 | 0.008 | 0.011 | 0.002 | 0.002 | 0.010 | 0.107 | 0.151 | 0.094 | 0.044 | 0.012 | | |
| Spawnings | 0.527 | 0.651 | 0.240 | 0.341 | 0.060 | 0.062 | 0.310 | 2.996 | 4.681 | 2.820 | 1.364 | 0.360 | 15.1 | |

[1]Missing data estimated from adjacent months.
[2]Includes 5% correction for spawning incidence bias.
[3]Total eggs/February weight.

be particularly susceptible to collapse; however, perturbations of recruitment is a potential threat to any fishery in which one or two year classes comprise the bulk of the landings. The stock-recruitment approach to understanding or predicting recruitment has fallen into disfavor, at least in the small pelagic fishes, because stock size has not proven to be a good predictor of recruitment. In its pure form (Beverton and Holt 1957; Cushing 1971; Ricker 1975) the stock-recruitment concept is based on two factors: 1) Parent stock size is a measure of the reproductive potential of the stock, and 2) there are compensatory mechanisms which reduce the number of recruits per spawner as the size of the parent stock increases. This compensation occurs through some mix of reduced fecundity of the parent stock, reduced growth of the recruiting cohort and increased mortality of the recruiting cohort. Recruitment variations are usually attributed to changes in environmental conditions, usually unknown, and the causal mechanisms, also usually unknown, are thought to occur during the early life history stages. The present emphasis of recruitment research is on the growth and mortality of the early life history stages. Potential variations of stock fecundity as a factor in recruitment variations has largely been ignored.

There are now 6 years of egg production estimates available for the central stock of northern anchovy (Bindman 1985). The mean spawning incidence for these years is 0.124 and the spawning incidence varied from 0.094 in the El Niño year of 1983 to 0.160 in 1984. This implies that the central stock produced 70% more eggs, per unit of spawning biomass, in 1984 than in 1983. Santander (1980) showed that the Peruvian anchoveta had both reduced spawning and an alteration of the seasonality of spawning during the 1972 El Niño. The results presented here, which show that fecundity is strongly age dependent, suggest that the reduction in age composition caused by heavy exploitation will greatly reduce the average fecundity per unit of biomass and also result in a reduction in the length of the spawning season. It appears that interyear variations in the age composition of a stock or in environmental factors associated with energy reserves or egg production are likely to alter greatly a stock's reproductive potential. If this is the case in other species which have multiple spawning, much of the variance in the stock-recruitment relationships of these fishes may be due to the fact that spawning biomass is a poor index of the reproductive potential of the stock.

To date information concerning age-specific reproductive potential has not been available for multiple spawning fishes because of the difficulty of determining the number of spawnings per year. The pioneering work by Hunter and Goldberg (1980) and later studies based on this work clearly demonstrate that, at least for many clupeids, the spawning incidence or spawning frequency can be determined with properly designed histological studies. Unfortunately a research program designed to determine age-specific reproductive potential would be very expensive as it would require a field sampling progam extending over the whole spawning season, in many cases the entire year; and it would require histological analysis and aging of a large number of females, both quite labor intensive.

It appears that the only way it may be possible to determine age-specific reproductive potential for many fishes is to use the approach developed here which combines two methodologies: histological assessment of ovaries because it unambiguously and accurately measure spawning rate and a traditional fishery sampling program which utilizes an inexpensive rapid index of reproductive condition, such as the maturity stage system or a gonado-somatic index, in which thousands of specimens can be processed. Whichever anatomical grading system is used, its principal purpose would be to determine the percentage of hydrated females. Most of the maturity stages (i.e., 1-4, 7) in the system used for northern anchovy are only of value in describing the seasonality of spawning. The only stages (i.e., 5 and 6) which can be used to determine the number of spawnings are those in which the eggs are hydrated, and they can be directly used as an index in northern anchovy because it is known that the duration of hydrated eggs in the ovary is <24 h. The traditional fishery sampling program may, as in the case for northern anchovy, already be available. If this is the case the principal work will be to calibrate properly the maturity stage or gonado-somatic index with the histological analysis. For this approach to work the fishery must, of course, take hydrated females.

## CONCLUSIONS

It is important for those managing fisheries which are susceptible to recruitment overfishing to realize that the alteration in the age structure of a stock that occurs under heavy exploitation may have greater effects on the total fecundity and seasonality of spawning than previously recognized. Management strategies which decrease the exploitation of older, more fecund females could increase yields and also provide increased protection against recruitment overfishing. In northern anchovy there is the additional factor that the sex ratio in the fishery is age dependent (i.e., the female:male ratio for 1-yr-old anchovy in the San Pedro fishery is 0.83:1, whereas that for 4+ yr-olds is 2.01:1). When this factor is multiplied by the difference in the fecundity of the two age groups, it is apparent that the catch of a ton of 4+ yr-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-yr-old fish.

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