

REPRODUCTION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, OFF OREGON AND WASHINGTON

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ABSTRACT

Mean relative fecundity of 21 anchovies from the northern subpopulation off Oregon and Washington was 826 ± 49 oocytes per g ovary-free body weight, or 720 ± 40 oocytes per g total body weight. These estimates are higher than those for the central subpopulation and may represent a racial difference between the two subpopulations. Sexual maturity is not reached in most anchovies off Oregon and Washington until the third summer (age II). The smallest anchovies found in spawning condition were 104 mm (male) and 107 mm (female) standard length. Overall male and female ratio of anchovies before and after spawning was about 1:1, but males outnumbered females 2.6:1 in regions of active spawning. Degeneration and apparent reduced growth among yolked oocytes prior to and after release of one batch of oocytes may limit the number of anchovy spawnings per season off Oregon and Washington.

Ovarian maturation is described from direct observations of whole oocytes including both normally developing and degenerating oocytes and from oocyte size-frequency distributions.

Sexually mature and immature anchovies off Oregon and Washington are segregated during the summer spawning season with mature fish occurring offshore beyond the continental shelf and immature fish occurring in nearshore coastal waters, bays, and estuaries. In winter and spring anchovies of all sizes occur together in nearshore coastal waters.

The northern anchovy, *Engraulis mordax* Girard, occurs along the west coast of North America from Cape San Lucas, Baja California, to the Queen Charlotte Islands, British Columbia (Miller and Lea 1972; Hart 1973). Within this range three subpopulations (northern, central, and southern) have been defined based on meristic characters (McHugh 1951) and blood serum proteins (Vrooman and Paloma²). The central subpopulation, inhabiting the general region between San Francisco, Calif., and Punta Baja, Calif., currently supports major fisheries and has been extensively studied (see most recent review, Huppert et al.³). The northern subpopulation, inhabiting the region north of San Francisco to British Columbia, supports only minor seasonal bait fisheries (Huppert et al. footnote 3) and has been little studied (Richardson in press).

In 1975 we initiated a study to assess the size of the stock of *E. mordax* occurring off Oregon and Washington by egg and larva survey. Knowledge of

individual fecundity (the number of eggs matured as a group and spawned at one time) is essential for this method of stock assessment. Three previous estimates of northern anchovy fecundity, one for the northern subpopulation off British Columbia (Pike 1951) and two for the central subpopulation (MacGregor 1968; Hunter and Goldberg 1980) differed widely in methods and results. Pike's estimate of fecundity based on counts of all oocytes >0.20 mm was 1,369 oocytes/g total body weight. MacGregor's estimate based on counts of only the most advanced, nonhydrated, yolked oocytes (≥ 0.50 mm) was 574 oocytes/total body weight, and Hunter and Goldberg's estimate based on counts of ripe, hydrated oocytes was 389/g ovary-free body weight.

This study was prompted by the discrepancy between estimates of northern anchovy fecundity in the northern and central subpopulations and the general lack of information on other aspects of northern anchovy reproduction off the Oregon-Washington coast. Our primary objective was to determine anchovy fecundity in the northern subpopulation. Additional objectives were to examine length and age at sexual maturity, sex ratio, spawning frequency, ovarian maturation, seasonal gonadal condition, and patterns in geographic distribution related to the reproductive cycle.

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²Vrooman, A. M., and P. A. Paloma. 1975. Subpopulations of northern anchovy, *Engraulis mordax mordax*. Southwest Fish. Cent., NMFS, NOAA, Adm. Rep. LJ-75-62, 10 p.

³Huppert, D., H. Frey, A. MacCall, G. Stauffer, and O. Mathisen. 1977. First draft—Anchovy fishery management plan. 119 p. + append. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

METHODS

All collections of juvenile and adult northern anchovies used in this study were made off the Oregon-Washington coast, 1975-77 (Table 1, Figure 1). Because no commercial anchovy fishery exists in this region our sampling for northern anchovies was exploratory in nature and restricted by available vessel and gear facilities, most of which were not specifically designed for efficient capture of pelagic schooling fishes. In the field, fish were either frozen in plastic bags or preserved in 10% Formalin.⁴ In the laboratory, frozen fish ($\approx 1,400$) were thawed, blotted on paper towels to remove excess moisture, measured (to nearest millimeter standard length, SL), and weighed (to nearest 0.1 g). Fish were slit open and sex and stage of gonadal development were recorded. Both otoliths were removed and placed in a

scale envelope for later age determination. Preserved fish (≈ 700) were soaked in freshwater, blotted on paper towels, measured, and weighed. The paired gonads were then removed and stored in 5% Formalin. These were later weighed (wet weight) to the nearest 0.1 mg on a Mettler electronic balance.

General gonadal condition was determined using the criteria of Lagler (1956). Northern anchovies taken in March, May, and October before and after the spawning season were classified as immature or mature, depending on whether eggs or milt were grossly apparent. Fish taken in July during the spawning season were classified as either immature (no eggs or milt grossly visible), ripe (gonads firm, eggs and milt distinctly visible), or spent (gonads flaccid, often dark in color). Spent female anchovies were further characterized by the absence of oocytes in the posteriormost region of each ovary. No attempt was made to distinguish the spent condition in males or stages of recovery after spawning in either sex. A gonadal index (GI)

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Collection data for juvenile and adult northern anchovies, *Engraulis mordax*, off Oregon and Washington, 1975-77. (Gear abbreviations: ST—shrimp trawl, MST—modified shrimp trawl, IKMT—Isaacs-Kidd midwater trawl, OT—otter trawl, MOT—modified otter trawl, MCPT—modified Cobb pelagic trawl.)

Date	Gear	Sampling effort		Sampling location	Results
		No. tows	Tow duration (min)		
28 April 1975	10 m MOT	2	14	Columbia River mouth just inside north jetty and near buoy 1	0 anchovies
13 May	5 & 8 m ST	8	5	Off Columbia River mouth, buoys 1 and 2	≈ 500 anchovies, 95% juveniles, <100 mm SL
25-29 May	1.8 m IKMT 7 m OT	32	5-40	Off Columbia River mouth, lightship to North Head, between lat. 46°22' and 46°10' N and long. 124°22' and 124°09' W, 20-91 m	Thousands of anchovies, 50-170 mm SL, most captured in OT on or near bottom in daytime at lat. 46° 16.6' N, long. 124°10.9' W, 33-35 m
30 May	5 & 8 m ST	8	5	Off Columbia River mouth, buoys 1 and 2	≈ 200 anchovies, mostly juveniles, 52-123 mm SL
21-25 July	1.8 m IKMT 7 m OT	53	10-20	Off Columbia River mouth, lightship to North Head, inside 91 m contour	≈ 700 anchovies, mostly juveniles, 70-90 mm SL, in small schools near surface at night (few mature fish and none in spawning condition)
15 Aug.	5 m ST Gill net	8 2 sets	5 ≈ 30	Columbia River mouth, just inside south jetty and off Gearhart, Ore. (3.7 km south of mouth)	2 anchovies, <100 mm SL
3-8 Oct.	1.8 m IKMT 7 m OT	72	10-15	Columbia River mouth, inside river along north shore to Tongue Pt. (3.7 km from mouth) and offshore between lightship and North Head inside 91 m contour	Thousands of anchovies, only juveniles (60-90 mm SL) in river near surface, both juveniles and small adults (102-126 mm SL) offshore near bottom and in midwater
7-16 Mar. 1976	12.5 m MST	52	30	Columbia River to Coos Bay, Ore. ≈ 91 -183 m, on commercial shrimp grounds	Thousands of anchovies, ≈ 70 -140 mm SL—most abundant between Astoria Canyon and Tillamook Bay
25-27 May	1.8 m IKMT 7 m OT	53	10-15	Off Columbia River mouth, 20-91 m	Thousands of anchovies, ≈ 50 -170 mm SL, most in midwater, greatest catches in 24-27 m
9-11 July	Dipnet	—	—	≈ 120 -140 km off Newport, Ore.	31 adult anchovies, 104-134 mm SL, most in spawning condition (only caught at night)
19-22 July	1.8 m IKMT	36	10-20	Between Columbia River and Tillamook Bay, 120-157 km offshore	14 adult anchovies, 108-134 mm SL, most in spawning condition, small schools of fish observed near surface around ship
18-26 July 1977	40 m MCPT	11	30	Off Oregon-Washington coast between lat. 47° and 43° N and long. 124°38' and 126° 32.8' W from ≈ 18.5 to 175+ km offshore, trawl depth usually 15-20 m	≈ 640 adult anchovies, 105-147 mm SL, many in spawning condition, taken only at four stations north of lat. 45°41' N between 65 and 120 km offshore

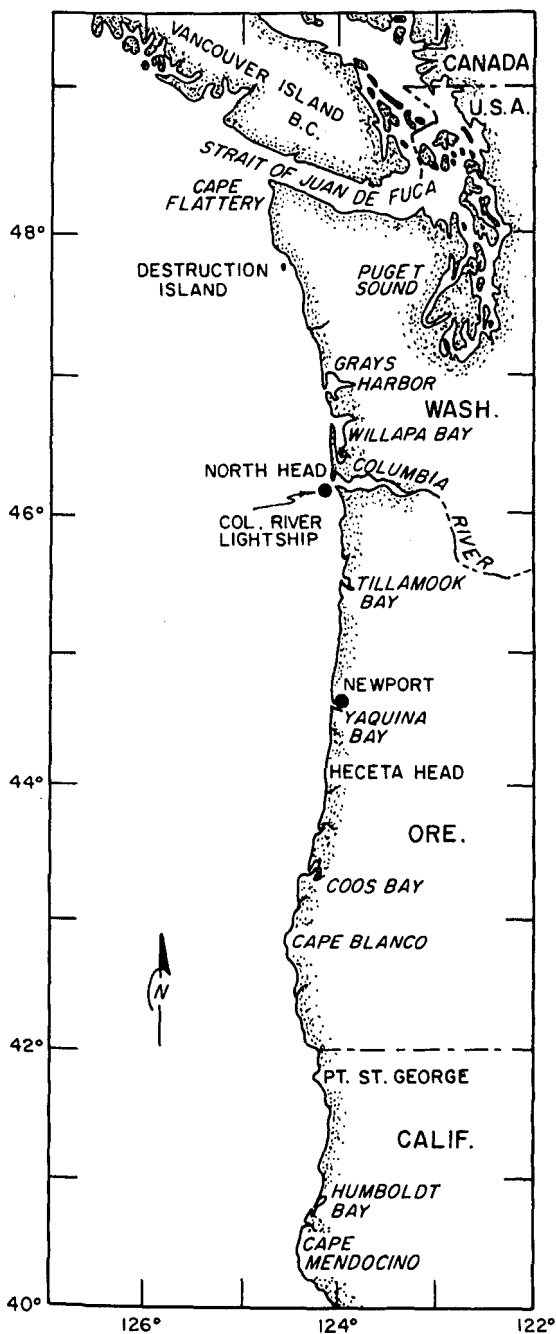


FIGURE 1.—General region of the northeastern Pacific where *Engraulis mordax* from the northern subpopulation have been collected.

was calculated for preserved fish by dividing total gonad weight by body weight (before gonad removal) and multiplying the resultant value by 100.

Oocytes from preserved ovaries were measured to the nearest 0.02 mm at 50 \times magnification with an ocular micrometer in a dissecting microscope. Oocyte diameter was measured until oocytes became elliptical in shape, then length (longest dimension) was measured. Measurements were made of approximately 200 oocytes/maturing fish (with oocytes ≥ 0.14 mm) and 100 oocytes/immature fish (with oocytes ≤ 0.14 mm). Fish were then grouped into 10 stages of ovarian development, depending on the modal length of the largest and most advanced group of oocytes in the ovary (Clark 1934) (Table 2). The size intervals used to define these ovarian stages were arbitrarily chosen and do not necessarily represent actual physiological stages of maturation. Composite oocyte size-frequency distributions based on all anchovies in each stage of ovarian development were derived from the mean number of oocytes in each 0.02 mm size class.

TABLE 2.—Ten stages of ovarian development in *Engraulis mordax* based on modal length of the most advanced oocytes and the length interval containing the mode.

Stage of ovarian development	Location of mode of advanced oocytes (mm)	Stage of ovarian development	Location of mode of advanced oocytes (mm)
1	<0.20	6	0.60-0.68
2	0.20-0.28	7	0.70-0.78
3	0.30-0.38	8	0.80-0.88
4	0.40-0.48	9	0.90-0.98
5	0.50-0.58	10	>1.00

Fecundity estimates were based on counts of only the largest and most advanced oocytes (varying with stage of ovarian development) in three, wet weighed subsamples from the central region of the left, preserved ovary. Chi-square tests of independence indicated no significant difference ($P > 0.05$) in oocyte size-frequency distribution among three different regions, anterior, central, and posterior, within the left ovary or between the central regions of either ovary. Each subsample, consisting of a clump of oocytes, was lifted from the ovary with a forceps and weighed to the nearest 0.1 mg. Subsample weights ranged from 10 to 50 mg. Oocyte counts were made under a dissecting microscope after the subsample had been teased apart in water. Each subsample yielded an estimate of fecundity expressed as total number of advanced oocytes contained in the ovaries, number of advanced oocytes per gram total body weight, and number of advanced oocytes per gram ovary-free body weight. The mean of these subsamples provided the fecundity estimate for each

of 21 northern anchovies. Functional (geometric mean) regressions (Ricker 1973) were used to examine relationships between total fecundity and body weight (grams), standard length (millimeters), and ovary weight (grams). These regression equations can also be used for prediction of fecundity from body weight and standard length. The standard error of each (geometric mean) regression coefficient was obtained by taking the square root of the variance as calculated from Ricker (1973). Ricker also gave procedures to transform functional parameters to predictive if this is desired.

Photomicrographs of oocytes in various stages of development were taken at magnifications of 12.5, 21, or 25 \times through a dissecting microscope using transmitted light.

RESULTS

Length and Age at Sexual Maturity

Estimates of the size when northern anchovies reach sexual maturity were determined from observations of gonads from frozen fish collected in May (991 fish) and July (263 fish) 1975. Estimates of age were based on counts of annuli, the interface between an inner hyaline and outer opaque zone, on otoliths (Collins and Spratt 1969; Spratt 1975) but only data on ages I and II fish are reported here. Otoliths of anchovies collected in May and July with either a hyaline margin but no completed annulus or an annulus at the margin were considered to be age I. Northern anchovies from May and July with one completed annulus on their otoliths and a hyaline margin were considered to be age II.

All fish, <85 mm SL, taken in May (376) were immature. Both mature and immature fish were

found within the size range 85-128 mm SL. Of 79 fish between 85 and 100 mm SL, 69% were immature and 31% were mature. Of 205 fish between 101 and 120 mm SL, only 5% were immature and 95% were mature. Only 3 out of 147 fish between 120 and 128 mm were immature and all fish >128 mm SL were mature.

Of 183 age I fish taken in May and measuring 55-99 mm SL (\bar{x} = 75 mm SL) only 5 males, 84-96 mm SL, appeared to be mature. Yet of 263 age I fish measuring 56-94 mm SL (\bar{x} = 76 mm SL), collected in July during the spawning season, none were mature. Possibly gametes begin to develop in adolescent northern anchovies early in the season but then do not reach the final stages of maturation required for spawning. Hickling (1930, 1935) reported this phenomenon in adolescent hake, *Merluccius merluccius*, from the North Atlantic. Of 14 age II northern anchovies from May (sex was not recorded), 7 were immature and 7 were mature. The smallest northern anchovies observed in spawning condition in July were 104 mm SL (male) and 107 mm SL (female). Ages are not available for these fish. This evidence indicates attainment of sexual maturity in some northern anchovies by age II.

Gonadal Condition

General gonadal development was measured in both immature and mature northern anchovies by mean monthly gonadal indices (Table 3). Mean GI's of immature males between 86 and 100 mm SL and females between 96 and 100 mm SL increased between March and May indicating some gonadal growth and differentiation. By July GI's in these size groups were lower than in May indicating no further gonadal development had occurred. Mean GI's of mature fish, >101 mm SL, increased from

TABLE 3.—Mean gonadal indices (\bar{GI}) by month for male (M) and female (F) *Engraulis mordax* in different size (standard length) intervals (N = no. of fish).

Month	Item	81-85 mm		86-90 mm		91-95 mm		96-100 mm		101-110 mm		111-120 mm		121-130 mm		>131 mm	
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
March	N	3	3	10	8	5	12	8	4	14	25	27	28	9	19	1	4
	\bar{GI}	0.22	1.12	0.25	0.99	0.20	1.08	0.36	1.20	0.48	1.18	0.68	1.24	1.22	1.55	0.64	1.70
May	N	9	9	4	7	9	6	5	2	23	9	20	6	10	9	16	36
	\bar{GI}	0.32	0.45	0.77	0.57	1.52	1.07	3.06	3.60	5.10	3.57	5.43	2.68	5.21	4.21	7.21	5.30
June	N	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
	\bar{GI}	—	—	—	—	—	—	—	—	—	—	—	4.77	—	—	—	5.64
July	N	11	4	9	3	4	8	3	2	7	4	26	15	38	23	13	21
	\bar{GI}	0.08	0.32	0.09	0.39	0.11	0.43	0.59	0.55	7.75	10.92	7.53	10.77	8.20	11.66	8.85	10.62
October	N	4	10	4	2	1	3	—	1	4	—	3	—	1	—	—	—
	\bar{GI}	0.07	0.52	0.05	0.50	0.04	0.40	—	0.43	0.11	—	0.18	—	0.14	—	—	—

March through July. October GI's were the lowest values observed in mature fish. Only in May were the GI values of males higher than those of females. The highest mean GI's were observed in July, approximately midway through the spawning season, mid-June to mid-August, (Richardson 1973, footnote 5; Richardson and Pearcy 1977). The highest, 22.90 (female) and 15.39 (male), and lowest, 1.55 (female), individual values of the GI found in July indicated the presence of both running ripe and spent fish, respectively.

Sex Ratio

The male to female ratio of mature and immature northern anchovies before spawning in May; immature, nonspawning, fish in July; and mostly immature fish in October did not deviate significantly from 1:1 ($P > 0.05$; chi-square test for goodness of fit) (Table 4). The sex ratio of 506 northern anchovies taken in March was 1.2:1 which, although close to 1:1, was significantly different ($P < 0.05$). The overall male to female ratio of mature fish caught during active spawning in July at four different locations was 2.6:1. Values for each catch were 2:1 (167 fish), 8.3:1 (278 fish), 1:1 (186 fish), and 5.7:1 (40 fish). The sex ratios in those catches where males outnumbered females all deviated significantly from 1:1 ($P < 0.005$) and may be related to anchovy spawning behavior. In the three catches where males greatly outnumbered females, the percent of ripe females with hydrated oocytes which were either actively spawning or about to spawn ranged from 33 to 46%. In the catch with a 1:1 sex ratio, only 2% of the females were ripe with ovaries full of hydrated oocytes.

Ovarian Maturation

Oocyte Morphology

The smallest oocytes visible at 50× magnification were roughly spherical but by 0.20 mm were becoming elliptical in shape (Figure 2a). Most oocytes < 0.38 mm lacked yolk and were transparent. Vitellogenesis became evident only in oocytes > 0.38 mm. As yolk production continued, oocytes became more opaque and by 0.50 mm the nucleus

TABLE 4.—Male to female ratios of northern anchovies collected in March, May, July, and October off Oregon and Washington.

Month	N	Male: female ratio	Size range (mm SL)
March	506	1.2:1	72-140
May	163	0.9:1	53-162
July:			
Nonspawning	247	1.2:1	56-94
Spawning	646	2.6:1	104-147
October	115	0.7:1	58-126

was obscured. Most oocytes > 0.50 mm were completely opaque, and oocytes between 0.50 and 0.68 appeared dark in transmitted light (Figure 2b). Oocytes between 0.70 and 0.90 mm often appeared less dense and dark than smaller yolked oocytes. A general lightening occurred first at the poles and then throughout the oocyte. These oocytes were grainy in appearance because globules of yolk had replaced the single amorphous yolk mass of smaller oocytes. The yolk of hydrated oocytes, ranging in size from 0.90 to 1.42 mm, was segmented (Figure 2c). Hydration, the accumulation of fluids of lower specific gravity than seawater in oocytes, results in greatly increased volumes and is the final stage of oocyte maturation in many marine fishes ([Fulton 1898] in Leary et al. 1975; Smith 1957). The largest oocytes (1.10-1.42 mm) in Figure 2c had been ovulated, i.e., released from their follicles, and were lying loose in the ovary. The shadowy areas among the opaque oocytes to the left of the transparent ones in this figure are empty follicles. These structures were dispersed throughout the ovary and were visible without the aid of histological techniques. They appeared as thin, flattened mats of tissue about the size and shape of ripe oocytes with a thinner, oval region in the center.

In addition to normally developing oocytes, degenerating or atretic oocytes were found in some anchovy ovaries collected before, during, and after the spawning season. Atresia has been observed in both immature oocytes undergoing vitellogenesis and mature oocytes remaining in the ovary after spawning in many teleosts (Wallace 1903; Matthews 1938; Hoar 1955; Vladykov 1956; Beach 1959; Barr 1968). Degenerating oocytes of all sizes in *E. mordax* most frequently appeared as opaque, irregularly shaped, masses dispersed among the normal yolked and yolkless oocytes (Figure 3a). Another type of abnormal and presumably degenerating oocyte was found primarily in fish with ripe oocytes. These medium-sized, 0.36-0.54 mm, oocytes were in early stages of vitellogenesis and had irregularly shaped nuclei which frequently appeared partially collapsed (Figure 3b). Within

⁵Richardson, S. L. 1977. Abundance, distribution and seasonality of larval fishes collected 2 to 11 km of Yaquina Bay, Oregon from January 1971-August 1972—a data summary. *Oreg. State Univ. Sea Grant Coll. Prog. Publ. ORESU-T-77-003*, 73 p.

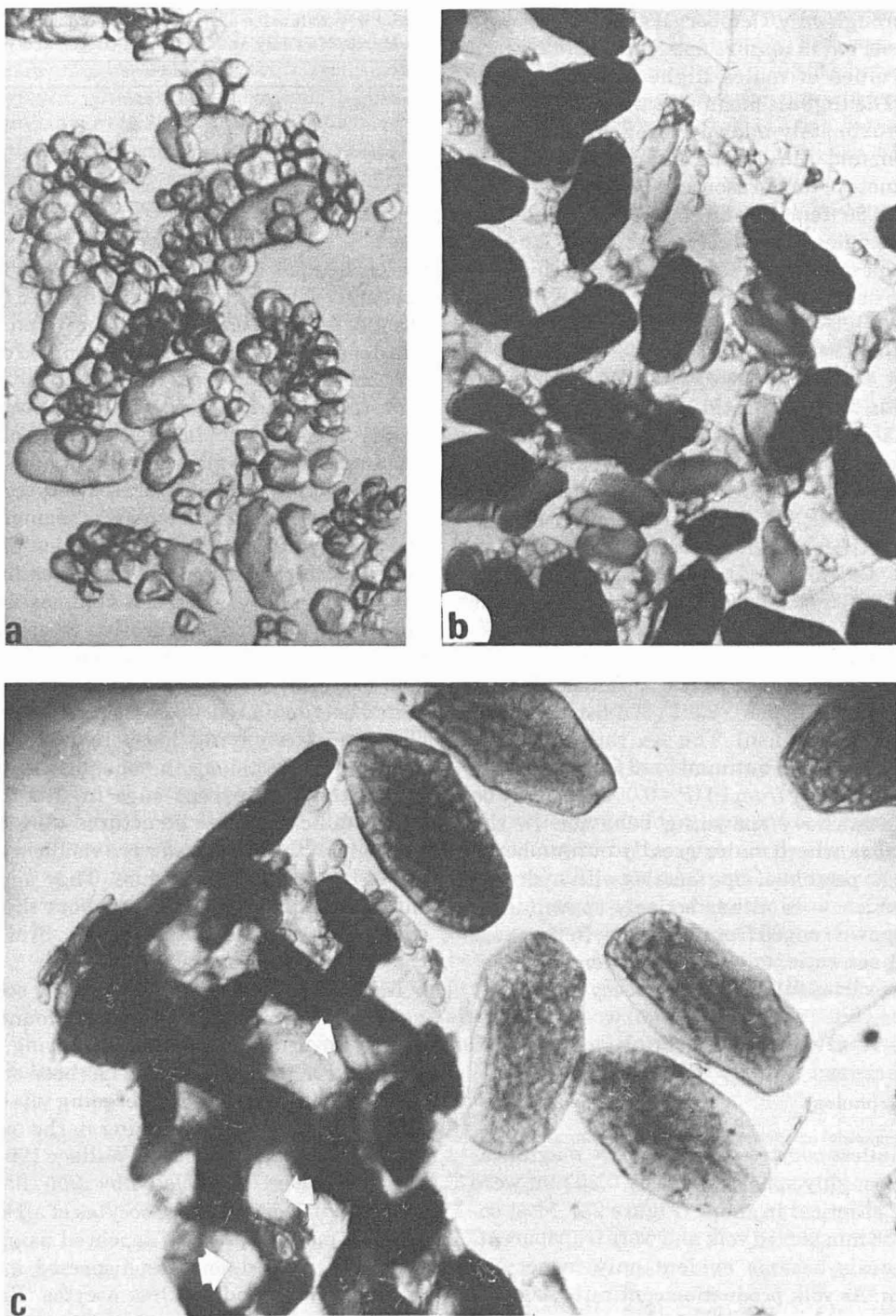


FIGURE 2.—Photomicrographs of normally developing, ovarian oocytes from *Engraulis mordax*. a. Yolkless oocytes, ranging from 0.14 to 0.28 mm length, from a northern anchovy captured in March ($\times 25$). b. Yolked (opaque) and yolkless (transparent) oocytes from a northern anchovy captured in June ($\times 12.5$). c. Ovulated oocytes (right) and empty follicles (arrows left) from a northern anchovy captured in July ($\times 12.5$).

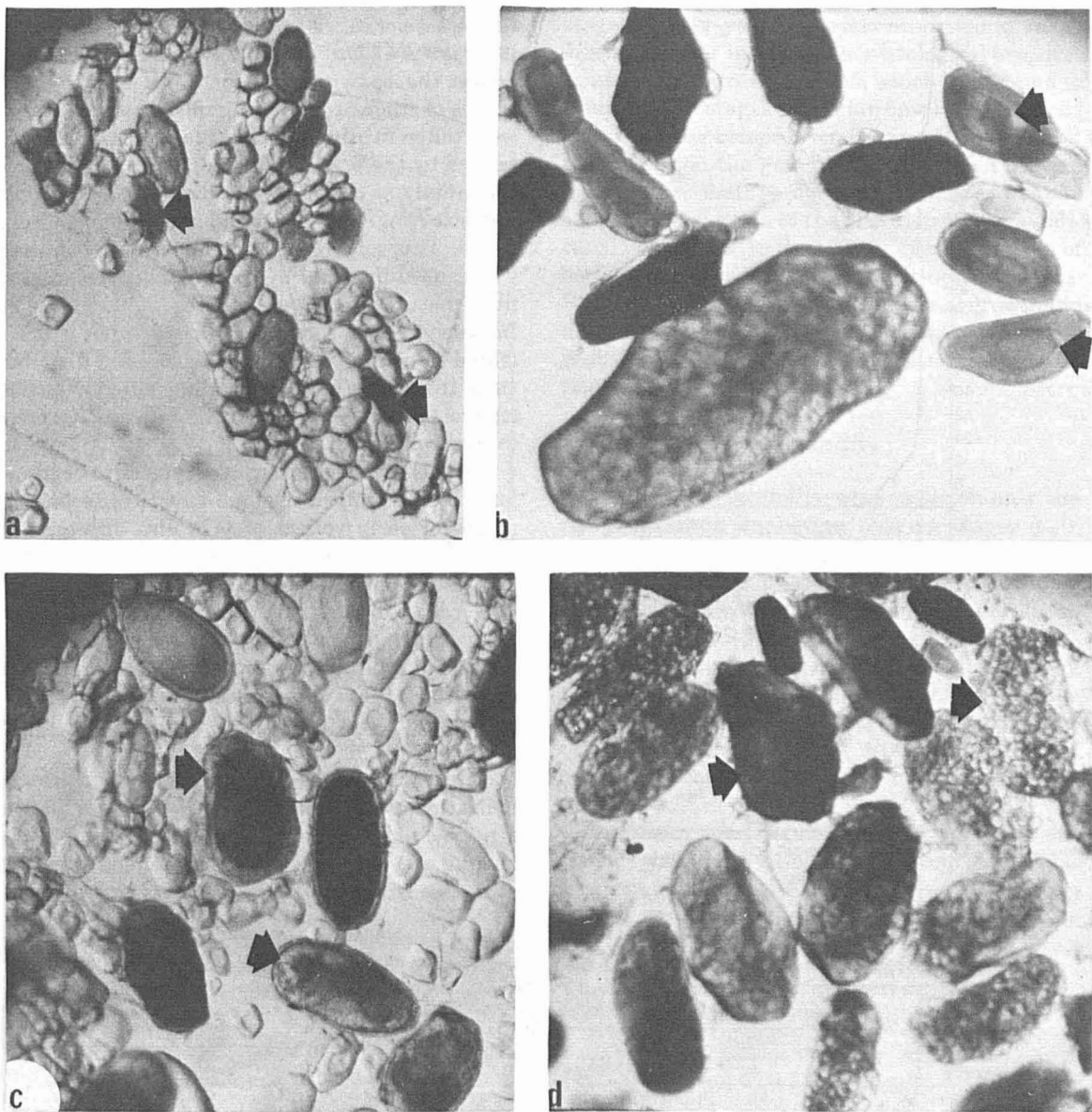


FIGURE 3.—Photomicrographs of degenerating ovarian oocytes from *Engraulis mordax*. a. Degenerating oocytes (arrows) from a northern anchovy captured in July ($\times 25$). b. Degenerating oocytes with abnormal nuclei (arrows) from a ripe northern anchovy captured in July ($\times 25$). c. Degenerating oocytes (arrows) from a northern anchovy captured in May ($\times 25$). d. Degenerating ripe oocytes (arrows) from a northern anchovy captured in July ($\times 12.5$).

more mature, degenerating oocytes the yolk appeared mottled and often the outline of the oocyte was irregular (Figure 3c). Ripe, ovulated oocytes that were degenerating differed from normal ones primarily in the appearance of the yolk. Instead of the honeycomblike, segmented yolk of normal oocytes, yolk in degenerating, ripe oocytes was either a solid opaque mass, or was dispersed into

individual globules that looked like oil droplets (Figure 3d).

Oocyte Size-Frequency Distributions

Oocyte growth was traced through the composite size-frequency curves of 51 northern anchovies, representing nine stages of ovarian development,

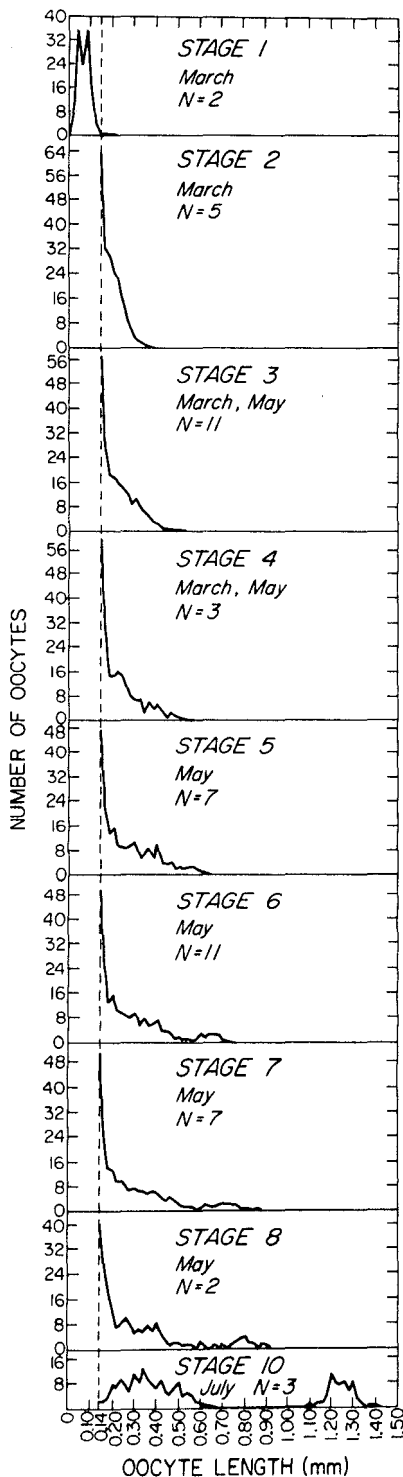


FIGURE 4.—Composite oocyte size-frequency curves representing nine stages of ovarian development in *Engraulis mordax*. (N = no. of fish.)

that were arranged in increasing order of maturity (Figure 4). Only fish taken in March and May before the spawning season were used for the curves of stages 1-8, although fish in these stages were taken in other months. Stage 10 fish, characterized by the presence of hydrated oocytes, were taken only in July. Few oocytes in the 0.90-0.98 mm size range were seen and no stage 9 fish were found. This apparent break in size distribution was caused by rapid hydration of oocytes during final maturation to ripe oocytes >0.90 mm. The increase in oocyte size during hydration is illustrated by the comparison of oocyte size distributions in stage 10 fish before and after ovulation (the release of oocytes from their follicles just prior to spawning) (Figure 5).

The most mature group of oocytes first began to form a distinct mode in stage 4 ovaries. Secondary modes of early yolked oocytes also appeared in stage 4 and were present in stages 5 through 10 but one of these groups never separated from the yolkless oocytes to form a distinct intermediate mode. These same groups of early yolked oocytes, especially the mode between 0.45 and 0.50 mm, were in essentially the same position in the oocyte size distributions of spent and ovulated stage 10 fish (Figure 5).

At least two stages of oocyte maturation prior to hydration were indicated by two modes in the size-frequency distributions of all completely opaque oocytes in weighed subsamples from two

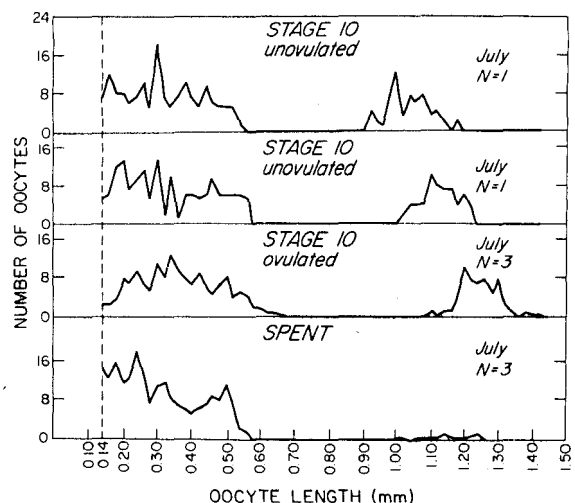


FIGURE 5.—Composite oocyte size-frequency curves from northern anchovies in ovarian stage 10, before and after ovulation, and in spent condition. (N = no. of fish.)

mature northern anchovies (130 and 141 mm SL) captured in July (Figure 6). Four maturation

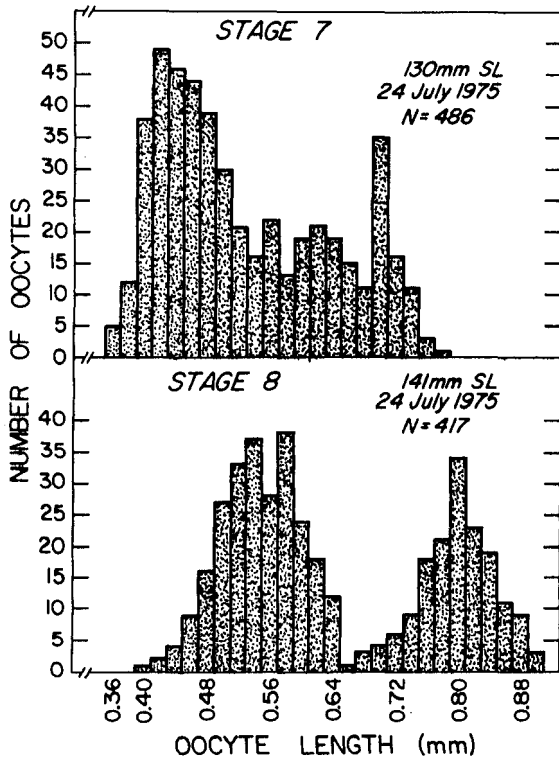


FIGURE 6.—Size-frequency histograms of all completely opaque oocytes in weighed subsamples from two northern anchovies, one in ovarian stage 7 and one in ovarian stage 8. (N = total number of oocytes measured.)

stages among yolked oocytes were found in *E. japonicus* after inspection of histological preparations, a more precise method, which were found to coincide with stages of ovarian development based on oocyte size composition (Usami 1963). At 50 \times magnification the general appearance of oocytes from the two mature, northern anchovies was the same but inspection of the size distributions indicated two groups. In the 130 mm fish, two modes of oocytes were apparent but not distinctly separate. But in the 141 mm fish, after additional growth the mode of larger oocytes became distinct and were probably ready to undergo hydration and ovulation subsequent to spawning.

Fecundity

Estimates of fecundity were made on only the ripest northern anchovies, ovarian stages 6-10, captured in July during the spawning season when recruitment of yolked oocytes to the most advanced mode was nearly complete (Table 5). Fish in stages 6-8 used for fecundity determinations had not spawned recently as evidenced by the absence of empty follicles or degenerating ripe oocytes in their ovaries. Oocytes in stage 10 fish had not been ovulated yet; therefore, none had been lost because of spawning or handling during capture.

The mean total fecundity of 21 northern anchovies was $16,826 \pm 1,563$ oocytes, and mean relative fecundity was 720 ± 40 oocytes/g total body weight or 826 ± 49 oocytes/g ovary-free body

TABLE 5.—Data for 21 female northern anchovies, *Engraulis mordax*, collected off the Oregon-Washington coast in July 1975-77 used to estimate fecundity. Gonadal index (1) and relative fecundity (1) were calculated using body weight + ovary weight. Gonadal index (2) and relative fecundity (2) were calculated using ovary-free body weight.

Collection year	Standard length (mm)	Body weight (g)	Ovary weight (g)	Gonadal index (1)	Gonadal index (2)	Ovarian stage	Total fecundity	Relative fecundity (1)	Relative fecundity (2)	Size range of advanced oocytes (mm)
1975	130	23.83	1.1733	4.92	5.18	7	10,409	437	459	~0.56-0.78
	141	28.60	2.1407	7.48	8.09	8	14,561	510	550	0.68-0.90
1976	110	16.07	0.9072	5.65	5.98	6	9,514	592	628	0.58-0.70
	129	24.24	1.8615	7.68	8.32	7	20,766	857	928	0.60-0.76
1977	115	17.86	3.2030	17.93	21.85	10	12,426	696	848	1.13-1.40
	117	16.33	1.5167	9.29	10.24	7-8	17,039	1,044	1,151	0.63-0.83
	117	21.11	4.8348	22.90	29.70	10	17,712	839	1,088	1.08-1.33
	118	15.47	0.8538	5.52	5.84	7	8,694	562	595	0.63-0.78
	120	20.29	1.0179	5.02	5.28	7-8	12,294	606	638	0.65-0.83
	120	18.57	2.8745	15.48	18.30	10	10,922	588	696	1.18-1.38
	120	20.22	2.5489	12.61	14.43	10	8,673	429	491	1.13-1.38
	120	17.77	3.3445	18.82	23.18	10	13,813	777	957	0.95-1.25
	124	22.68	3.6194	15.96	18.99	10	15,089	665	792	1.03-1.23
	124	21.60	3.3617	15.56	18.43	10	13,369	630	733	1.02-1.22
	127	23.63	1.7524	7.42	8.01	7-8	19,451	823	889	0.68-0.85
	127	23.44	4.7776	20.38	25.60	10	19,623	837	1,052	1.03-1.28
	128	23.57	1.0465	4.44	4.65	6-7	14,157	601	629	0.60-0.78
133	29.90	5.9563	20.84	24.88	10	22,012	736	919	1.05-1.31	
139	30.37	2.2317	7.35	7.93	7	28,235	929	1,003	0.63-0.75	
140	31.37	6.2765	20.01	25.02	10	29,035	926	1,157	0.92-1.18	
147	34.53	3.2000	9.27	10.21	7-8	35,561	1,030	1,135	0.68-0.85	

weight (Table 6). These two expressions of relative fecundity were calculated to allow comparisons with results of previous studies and to illustrate how each method might bias fecundity estimates. Mean relative fecundity based on total body weight of fish in ovarian stages 6-8 and 10 was similar. But mean relative fecundity based on ovary-free body weight in these two groups differed by nearly 100 oocytes. Because oocyte hydration substantially increases ovary weight in ripe fish, the best (least biased) estimate of mean relative fecundity, when individual estimates are based on fish captured both prior to and after oocyte hydration, is oocytes per unit ovary-free body weight. Yet either expression of relative fecundity can be biased if there are changes in somatic weight associated with the reproductive cycle or changes in condition, i.e., the length-weight relationship from year-to-year or among geographical regions (Bagenal 1967).

Linear and exponential (based on \log_{10} transformed variates) expressions yielded similar fits to the relationship between fecundity (TF) and total body weight (W) and between TF and standard length (SL) with r values ranging from 0.73 to 0.82 (Table 7). The linear equations describing the relationship between TF and ovary weight (OVW) also yielded high r values, 0.92 for stages 6-8 fish

TABLE 6.—Mean fecundity (\pm SE) of *Engraulis mordax* collected off the Oregon-Washington coast. Total fecundity = number of advanced oocytes in ovaries; relative fecundity = (1) number advanced oocytes per gram total body weight (ovary weight included) and (2) number advanced oocytes per gram ovary-free body weight.

Classification	Ovarian stages 6-8 (11 fish)	Ovarian stage 10 (10 fish)	Ovarian stages 6-10 (21 fish)
Total fecundity	17,335 \pm 2,525	16,267 \pm 1,881	16,826 \pm 1,563
Relative fecundity (1)	726 \pm 65	712 \pm 43	720 \pm 40
Relative fecundity (2)	782 \pm 75	873 \pm 63	826 \pm 49

TABLE 7.—Functional (geometric mean) regression equations, sample size (N), standard error of the regression coefficient (SE), and correlation coefficient (r) for the relationship between total fecundity (TF) and total body weight (W), standard length (SL), and ovary weight (OVW) in *Engraulis mordax* collected off the Oregon-Washington coast.

Equations	N	SE	r
Ovarian stages 6-10:			
$TF = -13,889.91 + 1,339.57W$	21	176.54	0.82
$\log_{10} TF = 1.91 + 1.69 \log_{10} W$	21	0.24	0.77
$TF = -76,286.31 + 738.99 SL$	21	108.56	0.77
$\log_{10} TF = -6.80 + 5.23 \log_{10} SL$	21	0.82	0.73
Ovarian stages 6-8:			
$TF = -1,181.63 + 11,506.73 OVW$	11	1,534.23	0.92
Ovarian stage 10:			
$TF = -2,654.20 + 4,637.89 OVW$	10	433.83	0.96

and 0.96 for stage 10 fish. The apparent difference between the slopes of these two equations, 11,506.73 for stages 6-8 and 4,637.89 for stage 10, can be explained by the substantial increase in ovary weight in stage 10 fish caused by oocyte hydration, and not by an actual decrease in number of oocytes in these fish. Fecundity would be underestimated if an equation relating TF to OVW in fish with hydrated oocytes was used to predict fecundity. The relationship between TF and OVW , if based on fish captured both prior to and after oocyte hydration, would yield a low correlation coefficient (r).

Spawning Frequency

The number of times a female anchovy in the northern subpopulation spawns during the year could not be determined directly with available data. Oocyte observations, however, provided some information pertinent to the question of spawning frequency in these fish.

Degenerating, immature, yolked oocytes (those with abnormal-looking nuclei) were found in ripe northern anchovies during the spawning season. Although relative numbers of these oocytes were not determined, their presence suggests that oocytes in early stages of vitellogenesis in July may eventually degenerate and be absorbed. Higham and Nicholson (1964) also found disintegrating intermediate and maturing oocytes in the ovaries of recently spent Atlantic menhaden, *Brevoortia tyrannus*, indicating perhaps that this species may also absorb immature, yolked oocytes after spawning.

The presence of a distinct, intermediate mode of oocytes, indicating simultaneous maturation of a new batch of oocytes while a group of advanced oocytes is still in the ovary, is considered to be strong evidence of multiple spawning (Clark 1929; MacGregor 1976). In the oocyte size distributions of mature northern anchovies an intermediate mode of yolked oocytes never became distinctly separate from the smaller, yolkless oocytes (Figure 5). There was some indication of continued growth among intermediate-sized, yolked oocytes (0.56-0.66 mm) in five stage 10 fish (both unovulated and ovulated) before spawning. Yet oocytes in this size range were absent in three spent fish (Figure 5). The mode of intermediate-sized, yolked oocytes at 0.50 mm in these spent fish was in essentially the same position as in stage 10 (ovulated) fish, indicating little additional oocyte growth for some un-

determined period of time after spawning (Figure 5). Similarly shaped oocyte size distributions were used as indirect evidence of a single seasonal spawning in the Hawaiian anchovy, *Stolephorus purpurus* (Leary et al. 1975), the anchoveta, *Cetengraulis mysticetus* (Howard and Landa 1958), and the Pacific and jack mackerels, *Scomber japonicus* and *Trachurus symmetricus* (MacGregor 1976).

A secondary batch of oocytes, numerically equal to the group of hydrated oocytes about to be spawned was not found in stage 10 fish. The number of intermediate-sized, 0.46-0.62 mm, yolked oocytes, the next most advanced oocytes in ovaries of all stage 10 fish, was 427 oocytes/g. ovary-free body weight (mean of three subsamples) in a 154 mm SL, stage 10 anchovy. This value, expressed as an estimate of relative fecundity, was about one-half the value of mean relative fecundity of ten stage 10 fish (Table 6) and lay outside the range of all 21 individual fecundity estimates (Table 5).

DISCUSSION

Length and Age at First Maturity

Published reports of size and age at first maturity of anchovies in the central subpopulation are somewhat conflicting. Clark and Phillips (1952) found that only 30% of the fish in the size range 100-120 mm SL (ages I and II) were mature and only 50% in the size range 120-139 mm SL (ages II and III) were mature. Yet Huppert et al. (footnote 3) reported a recent study that found all northern anchovies older than 24 mo, \approx 120 mm SL, to be mature.

Sexual maturity is also attained in northern anchovies of the northern subpopulation at the end of the second year. Pike (1951) found that 96% of the northern anchovies in the size range 105-109 mm SL (age II fish), from commercial catches, were mature while only 14% of the fish ranging from 100 to 104 mm SL (<2 yr old) were mature. Northern anchovies off Oregon similarly do not attain sexual maturity until after the second year (i.e., in the third summer). The smallest northern anchovies taken in this study in spawning condition were 104 mm SL (male) and 107 mm SL (female). Size at maturity seems to be somewhat smaller in the northern subpopulation, possibly reflecting differences in growth rates between the two subpopulations.

Sex Ratio

It appears that the overall sex ratio in both the central and northern subpopulations is \approx 1:1. Klingbeil (1978) reported that the overall male to female ratio of northern anchovies from sea survey samples off California combined for the years 1966-75 was 0.97:1. Monthly sex ratios in commercial catches from February to August off British Columbia were approximately 1:1 with females slightly outnumbering males (0.77:1 the lowest ratio) (Pike 1951). The male to female ratio of both mature and immature anchovies off Oregon before the spawning season (May) and immature fish during and after the spawning (July and October) was also about 1:1.

Yet samples from both central and northern subpopulations were found with unexpectedly higher numbers of either males or females. Klingbeil (1978) suggested that adult northern anchovies may often be segregated by sex, although no seasonal trends could be discerned in their data. Hunter and Goldberg (1980) found that in trawl collections of northern anchovies off California dominated by males, 40% of the females had spawned on the night of capture. But in female dominated collections only about 10% of the females had spawned the night of capture. They suggested that changing sex ratios in northern anchovy schools may be associated with reproductive behavior. The overall male to female ratio of mature fish caught in July in areas of active spawning off Oregon and Washington was 2.6:1, with sex ratios in individual catches ranging from 1:1 to 8:1. The highest male to female ratios were also associated with catches containing high numbers of ripe females which were or soon would be spawning. The percent of these ripe females in male dominated schools off Oregon and Washington ranged from 33 to 40% and was similar to the percent of most recently spawned females in male dominated schools off California (Hunter and Goldberg 1980). Pike (1951) found that the relative number of male anchovies increased as the spawning season approached and in July males slightly outnumbered females. But by August, at the end of the spawning season, the male to female ratio was 0.71:1.

Fecundity

The only previous estimate of northern anchovy fecundity in the northern subpopulation,

Spawning Frequency

1,369±148 oocytes/g total body weight ($n = 4$) (Pike 1951), differs from our estimate of 720±40 oocytes/g total body weight ($n = 21$). Our estimate is more accurate than Pike's because it is based on counts of only the most advanced oocytes in ripe or nearly ripe fish. Pike's fecundity estimate was based on the assumption that northern anchovies spawn three equal batches of oocytes per year and was calculated by dividing the total number of oocytes >0.20 mm by three. His assumption of spawning frequency, based on the number of modal peaks in oocyte size-frequency distributions, is still unproven and could lead to erroneous fecundity estimates depending on the actual number of spawnings per fish.

Northern anchovies in the northern subpopulation off Oregon and Washington apparently have a greater fecundity (based on ovary-free body weight), 826 ($n = 21$), than those in the central subpopulation off California, based on estimates by MacGregor (1968) and Hunter and Goldberg (1980), 606 ($n = 19$) and 389 ($n = 23$), respectively. An analysis of variance (single classification) indicated the presence of a highly significant ($P < 0.01$) added variance component between individual relative fecundity estimates (based on ovary-free body weight) of our fish and those examined by MacGregor (1968). Hunter and Goldberg's mean value, which is more directly comparable than MacGregor's with our estimate because it was similarly based on ripe fish with hydrated oocytes, was even lower than MacGregor's, although statistical comparisons were not possible (individual fecundity values were not listed). The difference between the two California estimates may have been due primarily to differences in the stage of ovarian maturation of the fish used for fecundity determinations. Difficulty in distinguishing the most mature oocytes from less mature ones before hydration could have caused the higher estimate obtained by MacGregor who used only fish with unhydrated oocytes.

The higher fecundity of northern anchovies off Oregon and Washington may represent a true racial difference between fish in the northern and central subpopulations. Racial differences in fecundity have been demonstrated in many species of fish with probable causes being either environmental or genetic factors (Bagenal 1957, 1967). Bagenal (1966) speculated that geographic differences in plaice fecundity were caused by differences in food availability and population density.

Fish, such as the northern anchovy, with asynchronous oocyte development have the potential to spawn more than once during the season (de Vlaming 1974). Yet the actual number of times a female northern anchovy spawns during a year has not been conclusively documented in any of the subpopulations. Pike (1951) estimated that northern anchovies in the northern subpopulation off British Columbia spawn three times during the 3-mo spawning season. MacGregor (1968) suggested that at least some fish in the central subpopulation spawn more than once during the spawning season, which may include all 12 mo of the year. Hunter and Goldberg (1980) estimated the spawning frequency of northern anchovies in the central subpopulation to be once every 6-7 d during months of peak spawning.

Pike's (1951) conclusion was based solely on the presence of multiple modes in oocyte size distributions and ambiguous data on changes in the ratio of immature to advanced oocytes during the spawning season. These data alone cannot be used to determine spawning frequency in fishes. MacGregor (1968) concluded that spawning later in the year represented repeat spawning by some northern anchovies because early in the spawning season all mature females had well-developed eggs or were recently spent. Christiansen and Cousseau (1971), using histological techniques, found that some female *M. merluccius* had the physiological ability to recover more rapidly after spawning than the rest of the population and that these fish spawned a second time later in the season off Argentina. It seems likely, therefore, that anchovies in the central subpopulation spawn more than once during the protracted spawning season. But the number of spawnings per year may be variable because environmental conditions such as temperature and food supply, which are known to influence reproductive cycling in fishes, can vary from year to year (Bagenal 1966, 1969; de Vlaming 1971, 1974; Hodder 1972; Tyler and Dunn 1976). Recently, Brewer (1978) suggested that food availability may limit both the number of eggs spawned and the number of spawnings per year by northern anchovies in San Pedro Bay, Calif.

Hunter and Goldberg's (1980) estimate of spawning frequency was based on the mean percent incidence of northern anchovies with 1-d-old ovarian follicles in trawl samples taken during a 2-wk period in February. Their determination of

spawning frequency depended on the, as yet, unproven assumption that all mature females in the central subpopulation spawn during 1 mo of the peak spawning period. Even if this assumption is correct the dependence of this method on obtaining samples which accurately reflect the proportion of spawning and nonspawning females in the population poses another problem. Spawning frequency will be overestimated if nonspawning females are not as susceptible as spawning fish to capture by sampling gear because of differences in spatial distribution or behavior of the two groups.

Our oocyte observations alone, without data on rates of oocyte maturation and degeneration, did not yield an estimate of northern anchovy spawning frequency in the northern subpopulation. But our findings indicated that oocyte degeneration and apparent reduced growth among intermediate-sized, yolked oocytes prior to and after release of one batch of oocytes may limit the number of subsequent spawnings. In addition, the actual length of the spawning season off Oregon and Washington is only 2 mo, although water temperatures favorable for northern anchovy spawning (13°-17.5° C at 10 m depth, Baxter 1967) are present in this region for 5-6 mo. This discrepancy supports our interpretation of the oocyte observations by indicating that environmental factors may not be suitable for complete maturation of all yolked oocytes present in northern anchovy ovaries in the northern subpopulation. Only data from laboratory experiments designed to determine rates of oocyte maturation (and degeneration) under varying environmental conditions, such as photoperiod, temperature, and food supply, will provide a definitive answer to the question of how many times northern anchovies spawn per year.

Seasonal Distribution Associated with Reproduction

A distinct geographic segregation of mature and immature northern anchovies and hence an inferred spawning migration during the summer-time spawning season occurs in the northern subpopulation off Washington, Oregon, and northern California but apparently not around British Columbia. Evidence for this resulted from a summary of data from a number of sources including data and cruise reports (Table 8), Tillman,⁶ and personal observations from our own sampling efforts (Table 1, Figure 1). These seasonal patterns in

the northern subpopulation, described here for the first time, were evident even though the data were obtained with various types of sampling gear and unequal sampling effort.

In winter, January through March, both mature and immature northern anchovies of all sizes (≈50-180 mm) occur in nearshore coastal areas off British Columbia, Washington, and Oregon. Small schools were seen in British Columbia coastal waters. Concentrations were found off Washington between Cape Flattery and Destruction Island (over 31-313 m depths) and between Grays Harbor and the Columbia River (42-101 m depths). Off Oregon, northern anchovies were taken between the Columbia River and Coos Bay (91-183 m depths) with largest numbers occurring between the Columbia River and Tillamook Bay. Fish off Washington and Oregon were observed or captured near the bottom or in midwater in coastal areas, but were not commonly taken in bays and estuaries. Small catches of fish were taken in the Strait of Juan de Fuca but none were taken in Puget Sound, Wash.; Yaquina Bay, Oreg; or Humboldt Bay, Calif. A few rare occurrences (50-70 mm FL) have been reported from Tillamook Bay, Oreg.

In spring, April through mid-June, northern anchovies still occur in nearshore coastal waters. Fish, 80-160 mm SL, were taken in the seine fishery of the 1940's in British Columbia coastal waters. Although no schools were observed off the northern Washington coast, northern anchovies, 50-170 mm SL, were consistently taken near the bottom or in midwater in the vicinity of the Columbia River mouth (20-91 m depth). Northern anchovies, mostly <100 mm, were collected in the spring in Tillamook Bay, Yaquina Bay, and Coos Bay, Oreg. (sizes not given). Northern anchovies of all sizes entered Humboldt Bay in April and remained there into June and July.

In summer, mid-June through September, both mature and immature anchovies (up to 160 mm SL) occur in nearshore coastal waters of British Columbia where they supported a major seine fishery in the 1940's. Although few ripe or spent adults were taken, spawning is reported to occur in bays and inlets around southern British Columbia in summer. Off Washington and Oregon, sexually mature and immature northern anchovies are geographically separated. Adult fish

⁶M. F. Tillman, Northwest and Alaska Fisheries Center Marine Mammal Division, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, pers. commun. April 1975.

TABLE 8.—Summary of additional studies in which juvenile and adult *Engraulis mordax* from the northern subpopulation were collected.

General area	Dates	Principal gear	Sampling effort	Reference
British Columbia, bays and inlets	1940-50; mostly Feb.-Sept. 1947 and June-July 1948	Commercial purse seine	40 random samples	Pike (1951)
British Columbia, Saanich Inlet	23 Apr.-21 July 1968	6 m surface trawl	≈ weekly, 116 tows	Barraclough et al. ¹
British Columbia, Strait of Georgia	4-6 July 1967	6 m surface trawl	24 tows	Robinson ²
Puget Sound, Strait of Juan de Fuca, Washington coast from Mukkaw Bay to Columbia River (15-220 fm)	10-28 Jan. 1966	Standard Cobb pelagic trawl and 2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	19 tows	BCF exploratory cruise no. 75, RV <i>John N. Cobb</i> ³
Washington coast between Cape Flattery and Columbia River (10-140 fm)	6 Apr.-4 May 1966	Standard Cobb pelagic trawl and 2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	6 tows	BCF exploratory cruise no. 77, RV <i>John N. Cobb</i> ³
Washington coast between Cape Flattery and Destruction Island (20-100 fm) and between Grays Harbor and Columbia River (10-50 fm)	8-18 Nov. 1966	2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	2 tows	BCF exploratory cruise no. 82, RV <i>John N. Cobb</i> ³
Washington-Oregon coast between Cape Flattery and Yaquina Bay	18 Nov.-16 Dec. 1966 and 3 Jan.-8 Apr. 1967	Standard Cobb pelagic trawl, 2/3 scale Cobb pelagic trawl, and 2 experimental anchovy trawls (echosounder used to locate fish schools)	71 tows (most tows made in Jan.-Apr.)	BCF gear research cruise no. 8, MV <i>Baron</i> ³
Washington-Oregon coast between Cape Flattery and Heceta Head (15-100 fm)	15 May-2 June 1967	BCF Universal trawl (echosounder used to locate fish schools)	7 tows	BCF exploratory cruise no. 87, RV <i>John N. Cobb</i> ³
Tillamook Bay, Oreg.	May 1974-May 1976	6 m try net; 46 m beach seine	≈biweekly, then monthly	Forsberg et al. ⁴
Yaquina Bay, Oreg.	July 1964-Sept. 1967	61 m otter trawl (plus other gear)	≈monthly	Beardsley (1969)
Coos Bay, Oreg.	June-Sept. 1970	61 m beach seine; 30 m bag seine (plus other gear)	Not specified	Cummings and Schwartz ⁵
Humboldt Bay, Calif.	Apr. 1974-Oct. 1976	Echosounder—to determine distribution of anchovy schools; 200 m lampara bait seine 66.7 × 6.7 m purse seine (plus other gear)	Weekly echosounder surveys plus 45 net hauls	Waldvogel (1977)

¹Barraclough, W. E., D. G. Robinson, and J. D. Fulton. 1968. Data record—Number, size composition, weight, and food of larval and juvenile fish caught with a two-boat surface trawl in Saanich Inlet April 23-July 21, 1968. Fish. Res. Board Can., Manusc. Rep. Ser. 1004, 305 p.

²Robinson, D. G. 1969. Data record—Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4-6, 1967. Fish. Res. Board Can., Manusc. Rep. Ser. 1012, 71 p.

³Information from cruise reports, Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

⁴Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1977. Identification, distribution, and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oreg. Dep. Fish Wildl. Res. Sec., Fed. Aid Prog. Rep. Fish. 1977, 117 p.

⁵Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Dep. Fish Wildl., Coastal rivers invest.—Inf. Rep. 70-11, 22 p.

in spawning condition were found offshore with main concentrations between lat. 43° and 47° N and ≈65-157 km offshore. They occurred in small schools near the surface at night and deeper in the water column during daylight. Immature fish (mostly <100 mm SL) remained in nearshore coastal areas or in bays. They were taken in Grays Harbor, Wash., around the Columbia River mouth, in Tillamook Bay, Yaquina Bay, and Coos Bay, where they were observed feeding at the surface during daylight. In Humboldt Bay, mature fish left in June and July leaving only immature fish in the bay through the summer. Adults presumably moved offshore to spawn, although it is not known whether they moved north off Oregon and Washington or elsewhere. Adults returned to the bay around mid-September in spent condition.

In fall, October through December, northern anchovies are no longer abundant around British Columbia. The fishery of the 1940's was generally not in operation that season. Off Washington and

Oregon, adults eventually return to coastal waters from offshore spawning areas although few adults were collected in the fall. Fall catches occurred mainly off the Columbia River mouth (13-61 m depth) and Grays Harbor (35-37 m depth). Immature fish appeared to leave the bays and estuaries and returned to nearshore coastal waters. Young fish were seen in the Columbia River in October, feeding at the surface. No anchovies were collected in Tillamook Bay, Yaquina Bay, or Coos Bay. Juveniles and adults left Humboldt Bay in late October-November.

A pronounced and well-defined onshore-offshore segregation of mature and immature fish and inferred offshore spawning migration during the spawning period as observed in the northern subpopulation off Washington, Oregon, and northern California has not been documented for northern anchovies in the central or southern subpopulations. Baxter (1967) stated that off California northern anchovies apparently move offshore in

fall and winter, during the peak spawning period, and return inshore in spring. Huppert et al. (footnote 3) indicated similar movements but provided little additional information. Brewer (1978) suggested that mature northern anchovies in the vicinity of San Pedro Bay move to deeper, cooler waters offshore to spawn. The distinct geographic segregation of mature and immature northern anchovies in the northern subpopulation which occurs because of an offshore migration of spawning fish may represent an additional racial difference among the three northern anchovy subpopulations in the northeast Pacific.

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